








## SYSTEMATICS AND PHYLOGENY

## Genetic and morphological data reveal new insights into the taxonomy of *Campanula versicolor* s.l. (Campanulaceae)

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**Abstract** *Campanula versicolor* is a constituent of the *Campanula pyramidalis* complex, distributed in the central and southern Balkan Peninsula with a small disjunct range in SE Italy. The taxonomy of the broadly defined *C. versicolor* was controversial in the past due to high morphological variability of the populations across the range. We used microsatellite DNA data along with morphometric analyses on an extensive population sampling covering the entire range to reconstruct the relationships among populations of the intricate *C. versicolor* s.l. Based on the results three distinct entities can be distinguished, circumscribed here on the subspecies level, with newly established combinations: *C. versicolor* subsp. *versicolor*, *C. versicolor* subsp. *korabensis* and *C. versicolor* subsp. *tenorei*. We propose a new taxonomic treatment of *C. versicolor* s.l. with description, distribution and habitat data for each of the subspecies and a key for their identification.

**Keywords** Apennine Peninsula; Balkan Peninsula; infraspecific variation; microsatellites; morphometrics; taxonomy

**Supporting Information** may be found online in the Supporting Information section at the end of the article.

### ■ INTRODUCTION

The genus *Campanula* L. (Linnaeus, 1753: 163) includes 350–420 (Kovačić, 2004; Lammers, 2007) or even up to 580–600 species when derived genera currently recognized as distinct based on selected morphological characters are also included in it (Mansion & al., 2012). It is one of the most important genera that contribute to the floristic diversity of the Holarctic Kingdom (Jones & al., 2017). The center of species diversity of *Campanula* is considered to be located in the Mediterranean region (Park & al., 2006) where 250 species are recorded (Geslot, 1984). The largest number of endemic taxa is found in the eastern Mediterranean (Phitos, 1964, 1965), circum-Adriatic and west Balkan regions (Kovačić, 2004), and the Caucasus (Gagnidze, 2005).

The *Campanula pyramidalis* complex is a group of morphologically specific “isophylloid” bellflowers (Damboldt, 1965; Kovačić & Nikolić, 2006; Park & al., 2006; Lakušić & al., 2013). Previous studies have shown that the *C. pyramidalis* complex is most closely related to the *C. waldsteiniana* aggregate (Kovačić & Nikolić, 2006; Park & al., 2006; Liber & al., 2008; Mansion & al., 2012; Bogdanović & al., 2014, 2015; Crowl & al., 2016), together representing the “core” of the

isophylloid bellflowers (Park & al., 2006). This complex, along with *C. pyramidalis* L. (Linnaeus, 1753: 164), comprises *C. austroadriatica* Kovačić & D.Lakušić (Lakušić & al., 2013: 519), *C. montenegrina* I.Janković & D.Lakušić (Janković & al., 2016: 77), *C. secundiflora* Vis. & Pančić (Visiani & Pančić, 1862: 20) and *C. versicolor* Andrews (1804: 396). The distribution of the complex stretches from the Gulf of Trieste (Italy) in the northwest to the Peloponnese Peninsula (Greece) in the south and Mt. Konjevska (Bulgaria) in the east, with a small disjunction in southern Italy (Lakušić & al., 2013). Based on phylogenetic analyses of combined plastid and nuclear sequence data (Lakušić & al., 2013), as well as microsatellite markers (Janković & al., 2016), it has been shown that *C. versicolor* s.l. represents a well-identifiable group characterized by the largest distribution range if compared to that of the other species of the *C. pyramidalis* complex. It is distributed in the central and southern parts of the Balkan Peninsula—southern Serbia, southwestern Bulgaria, Republic of North Macedonia, Albania, Greece—and in the southeastern part of the Apennine Peninsula—Apulia and Basilicata administrative regions of Italy (Janković & al., 2017). The southernmost known occurrence of *C. versicolor* is located on the island of Kythira (Strid & Tan, 1996; Yannitsaros, 2004) which lies

between the Peloponnese and Crete in the South Aegean Sea (Strid & Tan, 1996), while the northernmost is at Mt. Konjevaska in the Znepole region in Bulgaria (Ančev, 1984; Asenov, 2009). *Campanula versicolor* mainly grows in limestone rock crevices, rarely in rocky places in meadows, from lowland to 2100 m (Hartvig, 1991). It also occurs in rocky places and walls in cities and villages (Blionis & Vokou, 2005).

Reflecting the morphological variability observed in this group, 15 taxa at the specific and infraspecific levels were described over the years in the broadly defined *C. versicolor* (Lammers, 2007) (Table 1). However, their taxonomic status and morphological and geographical peculiarities were not clear, to the point that the modern floristic and taxonomic literature does not recognize any of these taxa but consider them as synonyms of *C. versicolor* (Pignatti 1982; Hartvig, 1991; Lammers, 2007; Castroviejo & al., 2010; Govaerts & Lammers, 2018).

The results of the phylogenetic study of Lakušić & al. (2013) suggested a geographic structure in north–south direction within *C. versicolor* s.l. populations. The authors observed a differentiation between northern (Bulgaria, southern Serbia, North Macedonia) and southern populations (Greece, southern Italy) based on analyses of chloroplast DNA (cpDNA) data. On the other hand, based on the nuclear ribosomal internal transcribed spacer (nrITS) data, they found a weakly supported west–east subdivision: circum-Ionian and western Greece populations, and the remainder of the populations from eastern Greece, North Macedonia, Serbia, and Bulgaria. However, their population sampling was not extensive (14 populations), calling for further analyses based on a broader sampling (Lakušić & al., 2013). Therefore, for this study we increased

population sampling from 14 to 41 populations, in order to allow for further taxon segregation within *C. versicolor* s.l. Considering all this, the main aim of the present study was to get insight into the genetic diversity and morphological variability of *C. versicolor* s.l. across the entire range of the group based on extensive population sampling.

## ■ MATERIALS AND METHODS

**Plant material.** — Material for molecular and morphometric study was sampled from the entire distribution area of *C. versicolor*. Additionally, recently described taxa from Albania—*C. korabensis* F.K.Mey. (Meyer, 2011: 149), *C. korabensis* subsp. *bicajensis* F.K.Mey. (Meyer, 2011: 150) and *C. longipetiolata* F.K.Mey. (Meyer, 2011: 151)—were included as well, based on the protologues, type materials and personal observations.

For molecular analysis, leaves were collected from 8 to 22 individuals per population yielding a total of 667 individuals from 41 populations (Appendix 1; Fig. 1). For morphometric study, flowering stems, flowers and leaves were collected at full anthesis from 10 to 17 individuals per population yielding a total of 456 individuals from 37 populations (Appendix 1). Sampled material was preserved in glycerol–ethanol (1:1) solution.

Voucher specimens for each investigated population were deposited at the Herbarium of the Institute of Botany and Botanical Garden of the Faculty of Biology, University of Belgrade (BEOU), at the Herbarium of the Natural History Museum Rijeka (NHMR) and at the Herbarium Croaticum of the University of Zagreb (ZA). Details regarding sampled populations are given in Appendix 1. Furthermore, additional material was examined to define the distribution ranges of the investigated taxa (see the Appendix 2).

The Articles of the *International Code of Nomenclature for algae, fungi, and plants (ICN)* cited in the text follow Turland & al. (2018), while the quoted syntaxa follow Mucina & al. (2016). For an easier interpretation of the results and discussion, informal names, without a taxonomic rank, were assigned to the investigated taxa collected from the locus classicus. Those informal names represent the specific or infraspecific epithets of the investigated taxa (Table 1). To all other investigated populations of *C. versicolor* s.l. we assigned the informal name “versicolor”. The population of *C. longipetiolata* was included only in the molecular analysis.

*Campanula planiflora* Willd. (Willdenow, 1809: 210) (= *C. willdenowiana* Schult.) was not included in this study since the locus classicus is not specified in the protologue (Janković & al., 2017).

**Chorological data.** — Chorological data (Appendix 2) were collected during field investigations (personal observations) as well as from relevant herbarium collections. Material at BEO, BEOU, BP, HMMNH, SO, SOA and SOM herbaria has been revised and examined, as well as digital images available via online databases or images of specimens

**Table 1.** Investigated *Campanula* taxa and informal names assigned to the populations from the loci classici.

Taxon	Informal name
1. <i>C. korabensis</i> subsp. <i>bicajensis</i>	bicajensis
2. <i>C. korabensis</i>	korabensis
3. <i>C. longipetiolata</i>	longipetiolata
4. <i>C. versicolor</i> subsp. <i>thessala</i> subvar. <i>lancifolia</i>	lancifolia
5. <i>C. mrkvickana</i> ≡ <i>C. versicolor</i> f. <i>mrkvickana</i>	mrkvickana
6. <i>C. plasonii</i>	plasonii
7. <i>C. corymbosa</i> ≡ <i>C. tenorei</i> ≡ <i>C. rosanoi</i> ≡ <i>C. versicolor</i> var. <i>rosanii</i>	tenorei
8. <i>C. versicolor</i> var. <i>thessala</i>	thessala
9. <i>C. versicolor</i> var. <i>tomentella</i> ≡ <i>C. versicolor</i> var. <i>thessala</i> f. <i>tomentella</i>	tomentella
10. <i>C. versicolor</i> *	versicolor

\*All other investigated populations are marked as versicolor. For details about homotypic synonyms cited in the table see Janković & al. (2017).

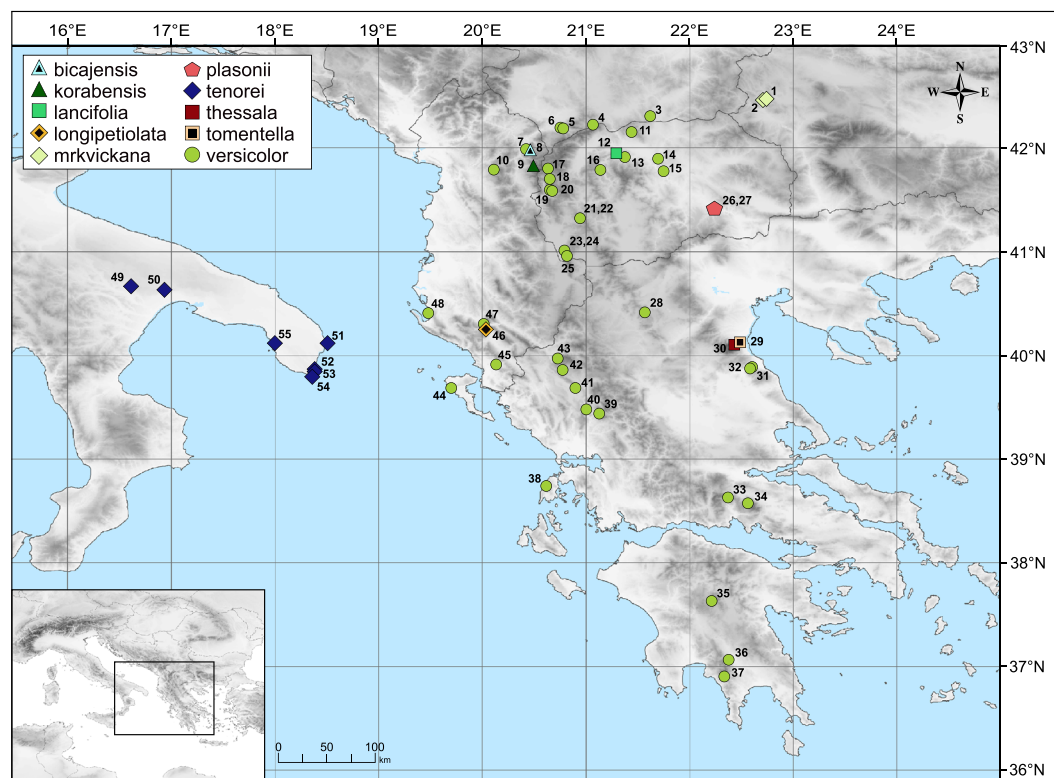
sent by the curators from AMD, B, BM, BP, BRNM, C, CAT, CGE, E, FI, G (G-DC), GE, HAL, HFLA, HMMNH, JE, K, L, LD, LE, MANCH, MNHN, MPU, NAP, NYC, OXF, P, PAD, PAL, PH, PI, PRC, RO, TCD, TO, TOU, U, W and WAG.

**Microsatellite analysis.** — Genomic DNA samples were extracted from silica gel-preserved leaf tissue using the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich, St. Louis, Missouri, U.S.A.) or NucleoSpin Plant II (Macherey-Nagel, Düren, Germany). The molecular analysis was carried out on seven SSR loci (CpUZ001, CpUZ003, CpUZ004, CpUZ005, CpUZ006, CpUZ009, CpUZ010) developed and characterized by Radosavljević & al. (2015), which had shown cross-amplification in *C. versicolor*. A two-step polymerase chain reaction (PCR) protocol with an initial touch-down cycle (Radosavljević & al., 2015) was employed for amplification of the microsatellite loci. The amplified fragments were run on an ABI 3730XL analyser (Applied Biosystems, Foster City, California, U.S.A.) and the results were analyzed with GeneMapper v.4.0 (Applied Biosystems, 2005).

**Genetic diversity and bottlenecks.** — Polymorphism information content (PIC) of each microsatellite marker was calculated as described in Botstein & al. (1980). GENEPOP v.4.0 (Raymond & Rousset, 1995) was used to estimate population genetic parameters (average number of alleles per locus  $N_{av}$ ; observed heterozygosity  $H_O$ ; expected heterozygosity  $H_E$ ; inbreeding coefficient  $F_{IS}$ ) and to test for deviation from Hardy-Weinberg equilibrium (HWE).

Sequential Bonferroni adjustments (Holm, 1979; Rice, 1989) were applied for correction of the effect of multiple tests with SAS release 9.1 (SAS Institute, 2004). MicroChecker v.2.2.3 (Van Oosterhout & al., 2004) was used to check for the presence of null alleles and potential problems related to allele dropout. Frequencies of null alleles were estimated using FreeNA (Chapuis & Estoup, 2007) based on the expectation-maximization algorithm (Dempster & al., 1977). FSTAT v.2.9.3.2 (Goudet, 1995, 2002) was used to estimate allelic richness ( $N_{ar}$ ), while private allelic richness ( $N_{par}$ ) was calculated in HP-Rare v.1.0 (Kalinowski, 2004, 2005). BOTTLENECK v.1.2.02 (Cornuet & Luikart, 1996; Piry & al., 1999) was used to test for evidence of recent bottleneck events on the basis of the theoretical expectation. The observed gene diversity ( $H_O$ ) was compared with the gene diversity expected at mutation–drift equilibrium ( $H_{EQ}$ ) and calculated from the observed number of alleles under different mutation models: infinite allele model (IAM), stepwise mutation model (SMM) and an intermediate two-phase model (TPM). The TPM was applied assuming 30% multistep changes and a variance of 30 (Pascual & al., 2001). Based on the number of loci in our dataset, the Wilcoxon signed-rank test (Luikart & al., 1998) was chosen for the statistical analysis of heterozygote excess or deficiency as recommended by Piry & al. (1999).

**Genetic differentiation and structure.** — Genetic differentiation between all pairs of populations was measured



**Fig. 1.** Location of sampled *Campanula versicolor* s.l. populations. Symbols represent informal names assigned to the investigated taxa. Population numbering and informal names correspond to Appendix 1.



with pairwise fixation indices ( $F_{ST}$ ) estimates. Pairwise  $F_{ST}$  and their respective  $P$ -values for significant differences from zero were calculated in FSTAT. Pairwise Cavalli-Sforza and Edwards's chord distances (Cavalli-Sforza & Edwards, 1967) were calculated, and an unrooted tree was constructed using the Fitch-Margoliash algorithm. To obtain bootstrap support values for branches, cluster analysis was performed with 1000 bootstraps (Felsenstein, 1985) over microsatellite loci as implemented in SEQBOOT, GENDIST, FITCH and CONSENSE programs in the PHYLIP v.3.6b software package (Felsenstein, 1993). Analysis of molecular variance (AMOVA; Excoffier & al., 1992) was performed by means of Arlequin v.3.0 (Excoffier & al., 2005) to partition the total microsatellite diversity among and within populations, among groups identified with STRUCTURE analysis, among populations within groups and within populations within groups. The variance components were tested statistically by non-parametric randomization tests with 10,000 permutations. A model-based clustering method was applied to infer genetic structure and to define the number of clusters using STRUCTURE v.2.3.3 (Pritchard & al., 2000). Thirty runs per cluster ( $K$ ; from  $K=1$  to  $K=21$ ) were carried out on the Isabella computer cluster at the University of Zagreb, University Computing Centre (SRCE). Each run consisted of a burn-in period of 200,000 steps, followed by 1 million Monte Carlo Markov chain (MCMC) replicates, assuming an admixture model and correlated allele frequencies. The choice of the most likely number of clusters was carried out by comparing the average estimates of the likelihood of the data,  $\ln(\Pr(X|K))$  for each value of  $K$  (Pritchard & al., 2000) and calculating the statistic  $\Delta K$  based on the rate of change in the log probability of the data between successive  $K$  values, as described by Evanno & al. (2005) using STRUCTURE HARVESTER v.0.6.92 (Earl & Holdt, 2012). Runs were clustered and averaged in CLUMPAK (Kopelman & al., 2015). Isolation by distance (IBD) among populations was tested by the method of Rousset (1997). A Mantel test ( $10^6$  permutations of population locations among all locations) on the matrix of pairwise  $F_{ST}/(1-F_{ST})$  ratios and on the natural logarithm of geographical distances (in km) between pairs of populations was performed using NTSYS-pc v.2.02 (Rohlf, 1997).

**Morphometric data analysis.** — Plant material for morphometric analyses was prepared as described in Janković & al. (2016). In total, 50 quantitative morphological characters (23 floral characters; height of the plant, inflorescence length and stem height; 8 characters each of basal, middle and upper leaves) of 456 individuals from 37 populations were analyzed (Appendix 1, 3). All characters were measured with Digimizer Image Analysis 4.0.0.0 (MedCalc Software, 2005). Statistical analyses were performed using Statistica v.5.1 (StatSoft, 1996).

Descriptive statistics (mean, standard deviation, minimum, maximum and coefficient of variation) were calculated for each quantitative character. The number of characters included in further multivariate analyses was reduced according to the

results of pairwise Spearman correlations, retaining only one out of character pairs with absolute values of correlation coefficients exceeding 0.9.

To get insight into the relationships between the analyzed populations, we performed an UPGMA (unweighted pair group method with arithmetic mean) clustering analysis based on Mahalanobis distances calculated with discriminant analysis defining 37 populations as *a priori* groups. Thereafter, canonical discriminant analysis (CDA) was used to test the hypothesis of morphological segregation of the populations *a priori* classified into three groups according to the results from the STRUCTURE analysis for  $K = 3$ . Canonical scores for each case (individual) were calculated with the aim to measure the distances between the individuals, and a scatterplot of canonical scores was made to visualize the relationships between the *a priori* defined groups. The percentage of correctly classified cases in each group was calculated with the classification function. Finally, a discriminant function analysis (DFA) was performed to estimate the contribution of individual characters to the overall discrimination.

## RESULTS

**Intrapopulation genetic diversity.** — For this study, seven microsatellite markers were selected (Table 2). One hundred and twenty-one alleles were detected, a mean of 17 alleles per locus. The number of alleles per locus ranged from 9 at CpUZ001 to 33 at CpUZ003. Six of seven microsatellites showed a high PIC  $>0.7$  (Table 2).

Generally, the observed heterozygosities ( $H_O$ ) showed slightly lower values than the expected heterozygosities ( $H_E$ ), while the expected heterozygosities were high for most populations, except for the mrkvickana population 1 BG-Zemen ( $H_E = 0.091$ ). This population had the lowest values among all populations for all the genetic variability estimates (Table 3). Multilocus estimates of Wright's inbreeding coefficient within populations ( $F_{IS}$ ) showed no significant deviation from zero ( $P > 0.05$ ) in 32 of 41 populations, suggesting that HWE was met for each population. A significant deficit

**Table 2.** Allelic diversity of seven microsatellite loci scored in 41 populations of *Campanula versicolor* s.l.

No.	Locus	Repeat motif	Size range (bp)	$N_a$	PIC
1	CpUZ001	ACT	148–172	9	0.761
2	CpUZ003	GA	184–296	33	0.937
3	CpUZ004	AGA	133–232	20	0.752
4	CpUZ005	GT	127–163	13	0.385
5	CpUZ006	GT	212–246	15	0.778
6	CpUZ009	GA	175–217	16	0.814
7	CpUZ010	ATC	154–196	15	0.796
Average				17	

$N_a$  = total number of alleles per locus; PIC = polymorphism information content.

**Table 3.** Genetic diversity and sample size of 41 populations of *Campanula versicolor* s.l.

No.	Pop. code	<i>n</i>	<i>N</i> <sub>av</sub>	<i>N</i> <sub>ar</sub>	<i>N</i> <sub>pr</sub>	<i>N</i> <sub>par</sub>	<i>H</i> <sub>O</sub>	<i>H</i> <sub>E</sub>	<i>F</i> <sub>IS</sub>
1	BG-Zemen <b>a</b>	10	1.429	1.254	0	0.000	0.086	0.091	0.061 ns
3	RS-Preševo	20	3.000	2.125	1	0.154	0.279	0.387	<b>0.278***</b>
4	RS-Gotovuša	10	3.714	2.898	0	0.044	0.456	0.564	0.192 ns
5	RS-Dušanov grad	11	3.286	2.362	0	0.002	0.293	0.409	<b>0.283*</b>
7	AL-Mt. Gjallica	8	3.429	2.891	0	0.071	0.527	0.540	0.024 ns
8	AL-Shija Gorge <b>b</b>	20	4.429	2.694	0	0.064	0.346	0.439	<b>0.212**</b>
9	AL-Mt. Korab <b>c</b>	21	3.714	2.700	0	0.079	0.462	0.508	0.09 ns
10	AL-Kurbnesh	23	3.714	2.492	1	0.159	0.478	0.475	−0.008 ns
11	MK-Ostruga	13	2.429	2.000	0	0.000	0.418	0.382	−0.092 ns
12	MK-Matka Canyon <b>d</b>	20	6.429	3.631	2	0.146	0.614	0.675	<b>0.09*</b>
14	MK-Katlanovo	21	3.429	2.498	0	0.002	0.442	0.481	0.081 ns
15	MK-Veles	13	3.714	2.726	0	0.109	0.539	0.496	−0.085 ns
16	MK-Kozjak Lake	9	4.429	3.461	0	0.168	0.619	0.642	0.036 ns
18	MK-Radika Gorge	17	4.143	2.840	0	0.005	0.475	0.536	0.115 ns
19	MK-Mt. Bistra	9	3.000	2.443	0	0.000	0.404	0.450	0.104 ns
21	MK-Mt. Ilinska pl.	12	2.000	1.754	0	0.001	0.262	0.316	0.171 ns
23	MK-Ohrid Lake	14	2.571	2.154	0	0.000	0.429	0.387	−0.108 ns
25	MK-Mt. Galičica	19	4.714	2.890	1	0.132	0.368	0.510	<b>0.278***</b>
26	MK-Demir Kapija <b>e</b>	12	2.857	2.153	0	0.000	0.298	0.345	0.137 ns
28	GR-Oros Askion	10	3.286	2.575	1	0.165	0.357	0.484	0.262 ns
29	GR-Mt. Olympus <b>f</b>	9	4.000	3.319	0	0.095	0.603	0.692	0.128 ns
30	GR-Prionia <b>g</b>	20	4.143	2.838	0	0.004	0.561	0.548	−0.023 ns
31	GR-Tempi Gorge	14	4.143	3.183	1	0.157	0.642	0.637	−0.008 ns
33	GR-Mt. Giona	12	5.571	3.808	2	0.202	0.695	0.711	0.022 ns
34	GR-Mt. Parnassus	17	5.429	3.589	0	0.092	0.542	0.660	<b>0.178**</b>
35	GR-Alonistaina	20	5.571	3.606	0	0.090	0.555	0.675	<b>0.179***</b>
37	GR-Mt. Mavrovouni	18	6.429	3.976	2	0.259	0.594	0.719	<b>0.174***</b>
38	GR-Lefkada	15	5.714	3.831	0	0.040	0.673	0.730	0.078 ns
39	GR-Mt. Tzoumerka	22	6.286	3.386	0	0.079	0.571	0.611	0.065 ns
42	GR-Vikos Gorge	20	5.286	3.186	1	0.126	0.573	0.609	0.059 ns
43	GR-Mt. Tymfi	20	4.429	2.812	1	0.116	0.515	0.526	0.022 ns
44	GR-Corfu	16	6.143	3.951	2	0.298	0.607	0.734	<b>0.173*</b>
45	AL-Bistrica	17	5.000	3.205	1	0.193	0.597	0.634	0.059 ns
46	AL-Luzat <b>h</b>	20	6.143	3.642	0	0.040	0.586	0.660	0.112 ns
47	AL-Tepelenë	20	5.429	3.442	0	0.078	0.586	0.631	0.072 ns
48	AL-Vlorë	20	5.857	3.532	1	0.115	0.604	0.648	0.067 ns
49	IT-Matera <b>i</b>	19	2.429	1.999	0	0.001	0.252	0.306	0.175 ns
50	IT-Castellaneta <b>i</b>	20	2.857	2.335	0	0.047	0.403	0.403	−0.001 ns
51	IT-Punta Palascia <b>i</b>	19	3.429	2.544	0	0.096	0.450	0.528	0.147 ns
52	IT-Alessano <b>i</b>	17	3.000	2.420	0	0.007	0.461	0.455	−0.014 ns
55	IT-Gallipoli <b>i</b>	20	2.571	2.068	0	0.000	0.293	0.338	0.133 ns

No. = population numbering; Pop. code = population code based on the two-letter code defined by ISO 3166-1 and population locality; *n* = sample size; *N*<sub>av</sub> = average number of alleles; *N*<sub>ar</sub> = allelic richness; *N*<sub>pr</sub> = number of private alleles; *N*<sub>par</sub> = private allelic richness; *H*<sub>O</sub> = observed heterozygosity; *H*<sub>E</sub> = expected heterozygosity; *F*<sub>IS</sub> = inbreeding coefficient. Significant values are printed in bold (ns = non-significant value; \* = significant at *P* < 0.05; \*\* = significant at *P* < 0.01; \*\*\* = significant at *P* < 0.001). Bold-face letters after the population code indicate a population from the locus classicus: **a**, mrkvickana; **b**, bicajensis; **c**, korabensis; **d**, lancifolia; **e**, plasonii; **f**, tomentella; **g**, thessala; **h**, longipetiolata; **i**, tenorei. Population numbering, codes and details correspond to Appendix 1.

of heterozygotes was found in 9 populations, ranging from  $F_{IS} = 0.09$  (12 MK-Matka Canyon) to  $F_{IS} = 0.283$  (5 RS-Dušanov grad).

A statistically significant departure ( $P < 0.05$ ) from mutation–drift equilibrium was detected in 15 populations (9, 11, 14, 29, 31, 33, 35, 38, 39, 44, 47, 48, 50, 51, 52) when the IAM was applied to the analyses. In contrast, there was no significant departure when the SMM was applied. Finally, according to the TPM, considered as the most appropriate model given the empirical evidence (Di Renzo & al., 1994), significant departures from mutation–drift equilibrium ( $P < 0.05$ ) were detected in four populations (29, 31, 50, 52). One-tailed probability values of the Wilcoxon signed-rank test for heterozygosity excess based on the three mutation models (IAM, TPM, SMM) are presented in Table 4.

**Interpopulation genetic diversity.** — Genetic differentiation between pairs of populations was low, with  $F_{ST}$  values ranging from 0.042 to 0.736 (Appendix 4). The highest  $F_{ST}$  values were observed between the Apennine populations (49–52, 55) and all the other populations, especially central Balkan ones (1, 3–5, 7–12, 14–16, 18, 19, 21, 23, 25, 26). High  $F_{ST}$  values were also found between the mrkvickana population (1 BG-Zemen) and all the other populations.

The unrooted Fitch-Margoliash tree (Fig. 2) revealed two main branches which illustrate a clear genetic differentiation between the populations from the northern part of the range of *C. versicolor* s.l. (Bulgaria 1; Serbia 3–5; northeastern Albania 7–10; North Macedonia 11, 12, 16, 18, 19, 21, 23, 25) and those from the southern part (Greece 28–31, 33–35, 37–39, 42–44; southern Albania 45–48; Italy 49–52, 55). The populations from the northern part of the range of *C. versicolor* s.l. are distributed in the central part of the Balkan Peninsula, while the populations from the southern part of the range are distributed in the southern part of the Balkan Peninsula and the southeastern part of the Apennine Peninsula. The branch of the Fitch-Margoliash tree, where the central Balkan populations were positioned, was marked as “versicolor 1”. Within this branch were also nested the populations informally named bicajensis, korabensis, lancifolia and mrkvickana. The other branch was marked as “versicolor 2” and included the southern Balkan populations and the longipetiolata, thessala and tomentella populations along with the Apennine tenorei populations (Fig. 2). The exception were three central Balkan populations from central (14 MK-Katlanovo, 15 MK-Veles) and southeastern North Macedonia (plasonii, 26 MK-Demir Kapija), which were positioned within the southern Balkan populations (“versicolor 2”), but close to “versicolor 1” (Fig. 2).

The results of the STRUCTURE analysis showed that the highest  $\Delta K$  was obtained at  $K = 2$  ( $\Delta K = 1509.42$ ) followed by that at  $K = 3$  ( $\Delta K = 124.67$ ). Being aware that the maximal  $\Delta K$  at  $K = 2$  might appear to be an artefact resulting from markedly low likelihoods for  $K = 1$ , as suggested by Vigouroux & al. (2008) and Janes & al. (2017), we also provide the results for  $K = 3$ . At  $K$ s larger than 3, the variances increased substantially and  $\Delta K$ s were lower than 5.

**Table 4.** Probability results of the Wilcoxon signed-rank test to assess population bottlenecks in 41 populations of *Campanula versicolor* s.l.

No.	Pop. code	Mutation model		
		IAM	TPM	SMM
1	BG-Zemen	0.875*	0.875	0.875
3	RS-Preševo	0.344	0.422	0.922
4	RS-Gotovuša	0.406	0.469	0.531
5	RS-Dušanov grad	0.719	0.961	0.984
7	AL-Mt. Gjallica	0.289	0.469	0.531
8	AL-Shija Gorge	0.813	0.961	0.988
9	AL-Mt. Korab	<b>0.039</b>	0.078	0.500
10	AL-Kurbnesh	0.289	0.813	0.992
11	MK-Ostruga	<b>0.016</b>	0.078	0.406
12	MK-Matka Canyon	0.188	0.344	0.813
14	MK-Katlanovo	<b>0.023</b>	0.078	0.344
15	MK-Veles	0.219	0.422	0.578
16	MK-Kozjak Lake	0.055	0.344	0.656
18	MK-Radika Gorge	0.188	0.594	0.961
19	MK-Mt. Bistra	0.531	0.711	0.945
21	MK-Mt. Ilinska pl.	0.078	0.078	0.578
23	MK-Ohrid Lake	0.055	0.344	0.578
25	MK-Mt. Galičica	0.281	0.945	0.977
26	MK-Demir Kapija	0.500	0.891	0.953
28	GR-Oros Askion	0.406	0.711	0.766
29	GR-Mt. Olympus	<b>0.012</b>	<b>0.027</b>	0.234
30	GR-Prionia	0.148	0.531	0.813
31	GR-Tempi Gorge	<b>0.008</b>	<b>0.012</b>	0.148
33	GR--Mt. Giona	<b>0.039</b>	0.406	0.766
34	GR-Mt. Parnassus	0.148	0.234	0.656
35	GR-Alonistaina	<b>0.008</b>	0.289	0.766
37	GR-Mt Mavrovouni	0.148	0.234	0.766
38	GR-Lefkada	<b>0.020</b>	0.344	0.469
39	GR-Mt Tzoumerka	<b>0.023</b>	0.656	1.000
42	GR-Vikos Gorge	0.188	0.766	0.973
43	GR-Mt Tymfi	0.531	0.852	0.988
44	GR-Corfu	<b>0.012</b>	0.188	0.852
45	AL-Bistricea	0.188	0.406	0.813
46	AL-Luzat	0.289	0.469	0.766
47	AL-Tepelenë	<b>0.020</b>	0.406	0.945
48	AL-Vlorë	<b>0.020</b>	0.406	0.945
49	IT-Matera	0.063	0.156	0.844
50	IT-Castellaneta	<b>0.016</b>	<b>0.016</b>	0.078
51	IT-Punta Palascia	<b>0.008</b>	0.148	0.188
52	IT-Alessano	<b>0.016</b>	<b>0.023</b>	0.078
55	IT-Gallipoli	0.219	0.578	0.578

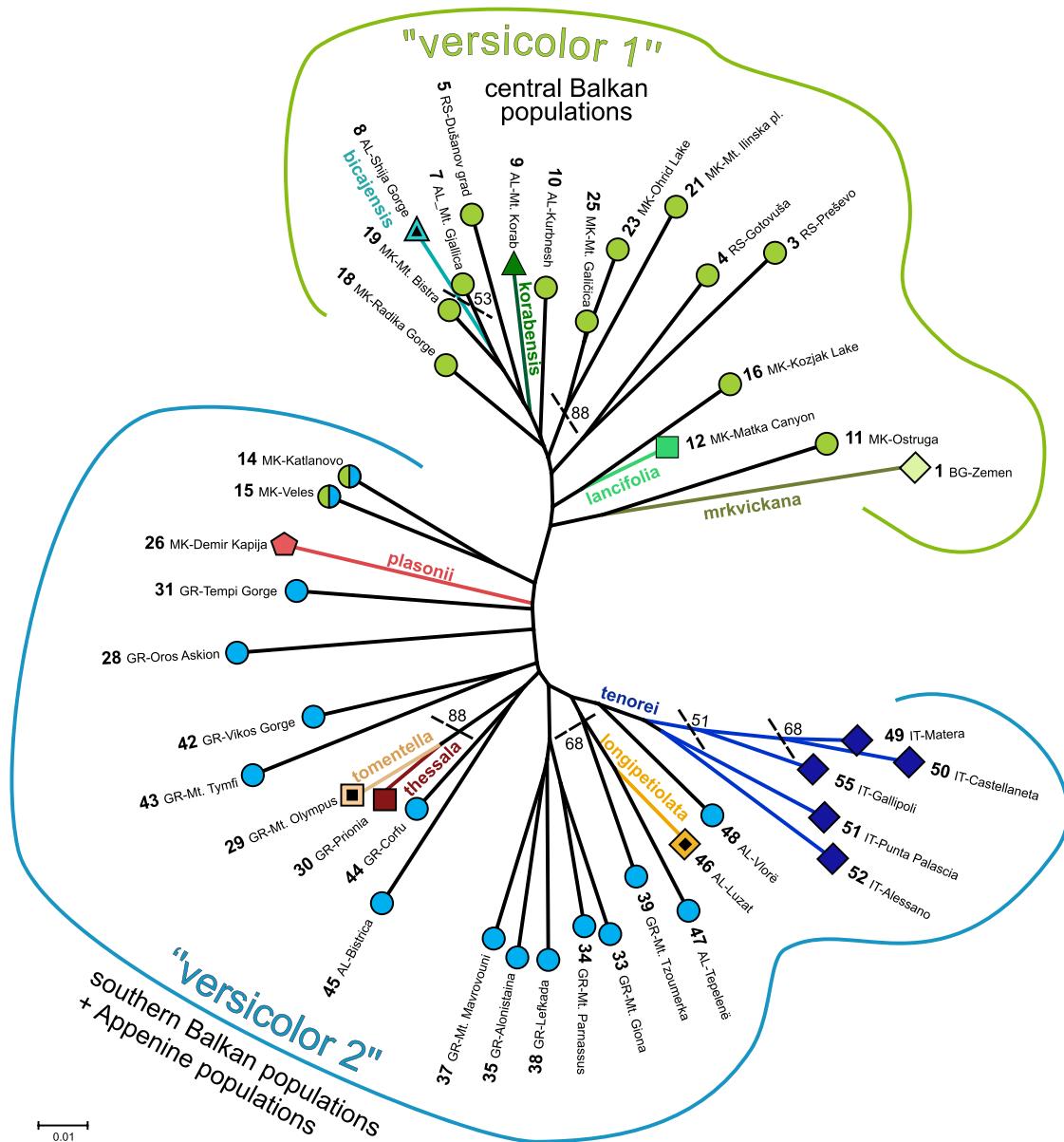
Wilcoxon test  $P$ -values represent one-tailed probabilities for heterozygosity excess based on three mutation models. Values of  $P < 0.05$  are indicated in bold. No. = population numbering; Pop. code = population code based on the two-letter code defined by ISO 3166-1 and population locality; IAM = infinite allele model; TPM = two-phase model; SMM = stepwise mutation model. Population numbering, codes and details correspond to Appendix 1.

At  $K = 2$ , the central Balkan populations were grouped in a single cluster A – “versicolor 1”, where *bicajensis*, *korabensis*, *lancifolia* and *mrkvickana* were also grouped. The southern Balkan populations were grouped in cluster B – “versicolor 2” along with *longipetiolata*, *thessala* and *tomentella*, and the Apennine *tenorei* populations. These two clusters are geographically well defined (Fig. 3A). The results of the STRUCTURE analysis as a model-based clustering method are congruent with the results of the distance-based model (unrooted Fitch-Margoliash tree based on Cavalli-Sforza and Edwards’s chord distance; Fig. 2).

Populations from central (14 MK-Katlanovo, 15 MK-Veles) and southeastern (26 MK-Demir Kapija) North

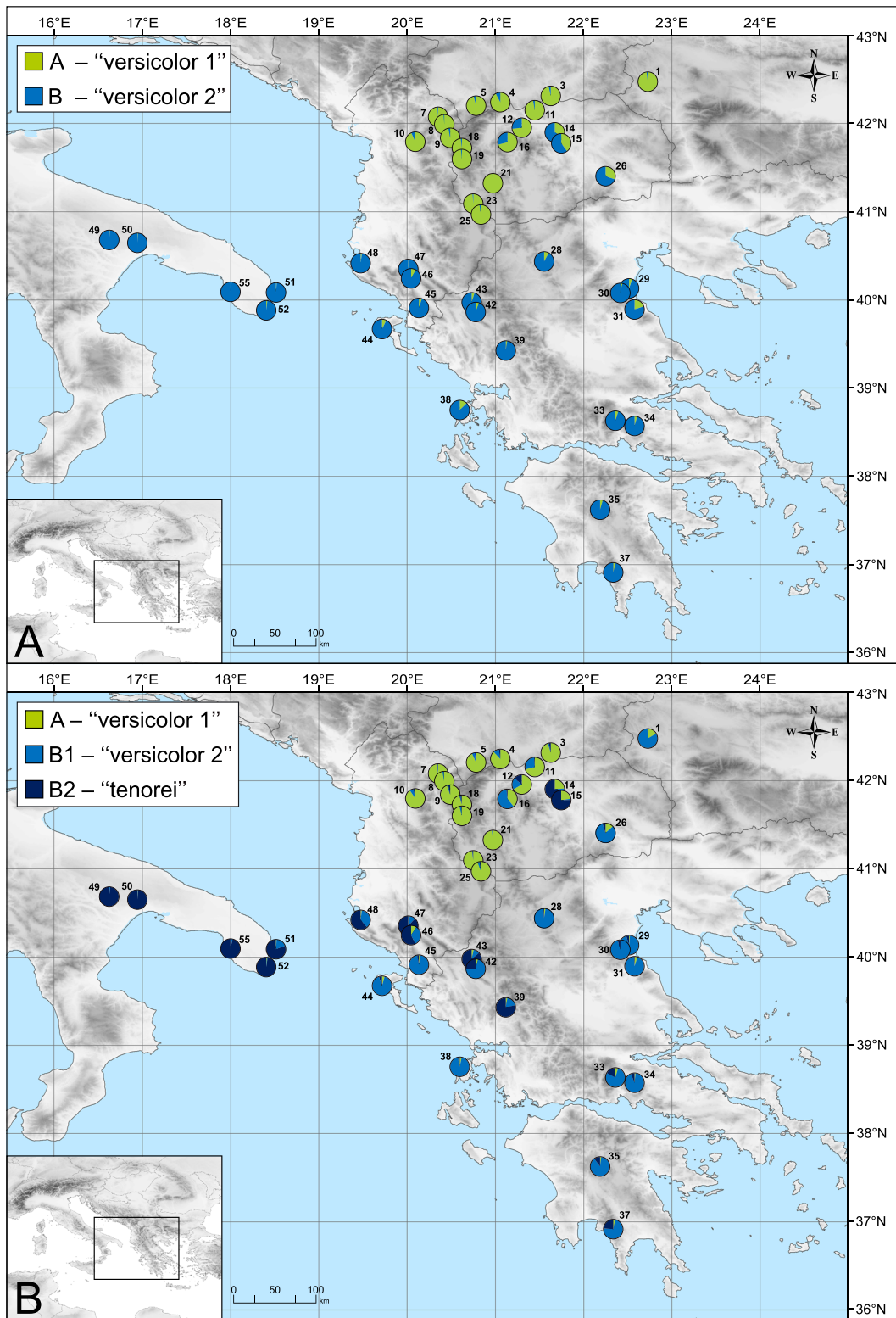
Macedonia were the most admixed. The proportions of ancestry of each population in each of the two clusters ranged from 60.1% (14 MK-Katlanovo) to 99.1% (21 MK-Mt. Ilinska pl. for cluster A and 50 IT-Castellaneta for cluster B).

At  $K = 3$ , cluster B defined for  $K = 2$  split up into clusters B1 – “versicolor 2” and B2 – “tenorei”, the latter representing the Apennine *tenorei* populations (Italy 49–52, 55) and some southern Balkan versicolor populations (southern Albania 46–48; northwestern Greece 39, 43), as well as two versicolor populations from central North Macedonia (14, 15) (Figs. 2, 3B). These three clusters were also geographically well differentiated (Fig. 3B).



**Fig. 2.** Unrooted Fitch-Margoliash tree based on Cavalli-Sforza and Edwards’s chord distances between 41 populations of *Campanula versicolor* s.l. Bootstrap support values >50% based on 1000 replicates are shown. Population numbering, localities and informal names correspond to Appendix 1, while color coding and symbols correspond to Fig. 1.





**Fig. 3.** Geographically presented proportions of assignment of each *Campanula versicolor* s.l. population (pie chart) to each of the (A) two clusters and (B) three clusters as defined by the model-based clustering methods of Pritchard & al. (2000). Population numbering corresponds to Appendix 1.



AMOVA showed that 31.43% of the total microsatellite diversity was attributable to among-population differences (Table 5A). A two-way nested AMOVA (Table 5B) revealed that the differences between the two clusters identified by STRUCTURE analysis amounted to 11.79% while the 23.93% of the total variation was attributable to among-population differences.

The  $F_{ST} / (1 - F_{ST})$  ratio for pairs of populations increased linearly with the natural logarithm of the geographical distance ( $r = 0.229$ ;  $P_{Mantel} < 0.01$ ;  $R^2 = 0.053$ ) (suppl. Fig. S1).

**Morphological variability.** — The analysis of morphological variation revealed that the largest number of the characters showed a moderate degree of variability (CV = 20%–50%). Highly variable characters with a coefficient of

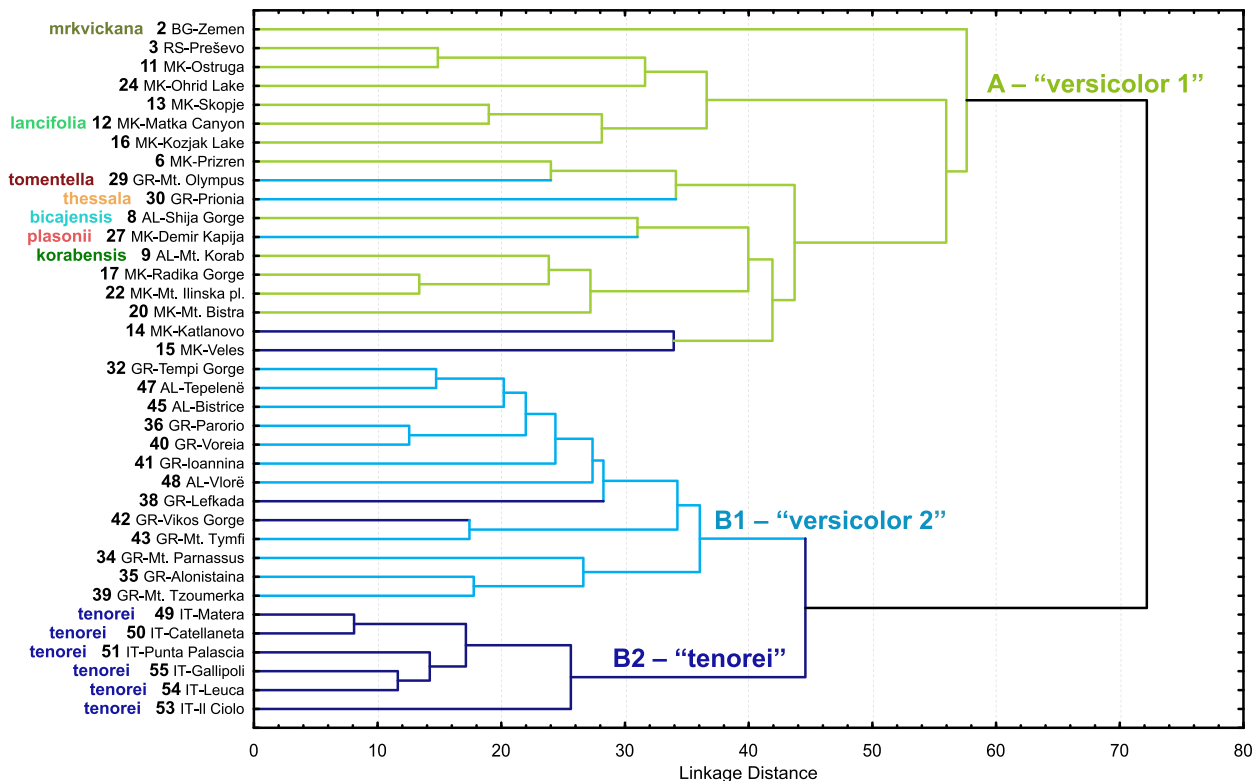
variation higher than 50% were flower pedicel length (CaPe-L), inflorescence length (Inf-L), petiole length (FbPe-L, FmPe-L, FuPe-L) and leaf lamina area (Fb-Ar, Fm-Ar, Fu-Ar). Contrary to them, stable characters with low variability were width of the corolla lobe base (CoL-W), distance from maximal width of the lobe to the corolla base (CoL-h) and stamen base perimeter (StB-Per) (Appendix 3).

UPGMA clustering identified two clusters of populations: one with central Balkan populations from Bulgaria, Serbia, North Macedonia and northeastern Albania and a second one with southern Balkan populations from Greece and southern Albania and Apennine populations from southeastern Italy (Fig. 4). Within the second cluster, *tenorei* populations were grouped in subcluster B2 – “*tenorei*” (Fig. 4), while southern Balkan populations formed subcluster B1 – “*versicolor 2*”

**Table 5.** Analysis of molecular variance (AMOVA) for the partitioning of microsatellite diversity (A) among and within 41 populations of *Campanula versicolor* s.l. and (B) between clusters A and B obtained by STRUCTURE analysis, among populations within clusters and within populations.

Source of variation	d.f.	Variance components	% Total variation	$\phi_{ST}$	$P(\phi_{ST})$
<b>A</b> Among populations	40	0.831	31.43	0.314	<0.0001
Within populations	1293	1.814	68.57		
<b>B</b> Between clusters	1	0.333	11.79	0.118	<0.0001
Among populations within clusters	39	0.675	23.93	0.271	<0.0001
Within populations	1239	1.814	64.29	0.357	<0.0001

$P(\phi_{ST})$ ,  $\phi$  statistics probability level after 10,000 permutations.



**Fig. 4.** UPGMA dendrogram for populations of *C. versicolor* s.l. Population numbering and locality acronyms correspond to Appendix 1. Population markers and lines color were assigned to populations based on the genetic clusters obtained by STRUCTURE analysis for  $K = 3$ .

(Fig. 4). The populations informally named mrkvickana, lancifolia, bicajensis and korabensis as well as plasonii, thessala and tomentella were positioned within the central Balkan cluster (A – “versicolor 1”, Fig. 4).

With CDA we tested the morphological segregation of populations which were *a priori* classified into three groups according to the STRUCTURE analysis of the molecular data (for  $K = 3$ ). The classification function showed that, when using this criterion, quite some individuals were not correctly classified, resulting in a total percentage of correctly classified individuals of 80%. In case of the “versicolor 2” and “tenorei” groups the percentage of correctly classified individuals was low (74.7% and 71.4%, respectively). Namely, according to the STRUCTURE analysis for  $K = 3$ , the Apennine tenorei populations were related with a few southern Balkan populations (“versicolor 2”) from southern Albania and northwestern Greece as well as two populations from central North Macedonia (Figs. 2, 3). However, according to the results of the UPGMA clustering analysis (Fig. 4), the Apennine tenorei populations differ morphologically from the Balkan populations. Therefore, we performed an additional CDA, with the exception of *a priori* classification of tenorei populations according to the STRUCTURE analysis for  $K = 3$ . Namely, tenorei populations were kept alone in the third separate group. With this classification, the total percentage of correctly classified individuals was 97.4%, while in case of the “versicolor 2” and “tenorei” groups it was 96.5% and 94.4%, respectively.

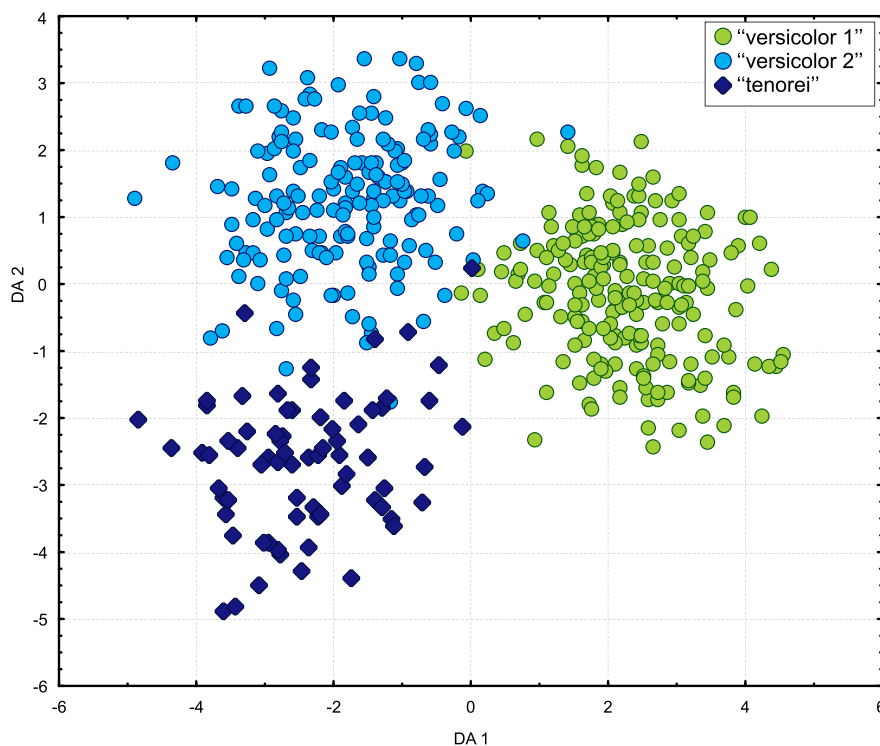
The result of the CDA showed that all three groups were well differentiated and positioned in distinct parts of the DA1–DA2 space (Fig. 5). Finally, DFA showed that morphological characters that contributed most to discrimination were

petiole width and length of middle leaf (FmPe-W, FmPe-L), stamen anther length (StA-L), inflorescence length (Inf-L) and calyx height (Ca-H). The results of descriptive statistics for all measured morphometric characters included in DFA are shown in Table 6.

## DISCUSSION

The results of our study showed that the investigated populations have abundant allelic variation over seven investigated loci and high overall genetic diversity. Substantially lower values of genetic parameters of the mrkvickana population in relation to all the other investigated populations (Table 3) are probably a consequence of restricted gene flow due to geographic isolation of this population. Between the mrkvickana population in southwestern Bulgaria (1 BG-Zemen) and the closest populations in southern Serbia and the northern part of North Macedonia, there is an area about 80 km wide, 100 km long and with altitudes up to about 1000 m where no other populations of *C. versicolor* occur. In addition, the  $F_{ST}$  values between the mrkvickana population (1 BG-Zemen) and all the other populations are high and mostly statistically significant.

The deviation from HWE detected in nine populations (Table 3) can be related to geographic barriers which reduce gene flow, since those populations are narrowly distributed in canyons (3, 5, 8, 12, 35), on islands (44) or high mountains (25, 34, 37). Most of those populations are small and restricted so the inbreeding rate is higher than in the more numerous populations. The deviation from HWE can also be related to the infections of ovaries with larvae of the weevil



**Fig. 5.** Canonical discriminant analysis (CDA) for populations of *C. versicolor* s.l. *a priori* classified into three groups: versicolor 1, versicolor 2, and tenorei.

*Miarus abnormis* Solari (1947: 75) after which the number of flowers and the production of pollen are lower (25). The cause of recent bottleneck signs detected in four populations (29, 31, 50, 52) may be anthropogenic since these populations grow on rocks along roads or on walls in cities.

The results of the AMOVA showed a clear differentiation between clusters of populations and populations within clusters. This might be a result of the populations' isolation and/or restricted gene flow. However, relatively high levels of intrapopulation variability are maintained by the presence of allogamy (Table 5).

The statistically significant IBD pattern indicates that only 5.3% of the genetic differentiation between populations can be explained by geographical distance, although  $F_{ST}$  values are generally the highest (and statistically significant) between populations that are geographically the most distant from each other, i.e., between the Apennine populations (49–52, 55) and all other populations, as well as between the population from Bulgaria (1) and all other populations (Fig. 1; Appendix 4).

The results of the unrooted Fitch-Margoliash tree (Fig. 2) and Bayesian model-based clustering analysis using STRUCTURE at  $K = 2$  (Fig. 3A) revealed two groups/clusters of populations having a geographic structure in north–south direction. This differentiation between central Balkan (southwestern Bulgaria, southern Serbia, northeastern Albania, North Macedonia) and southern Balkan and Apennine populations (Greece, southern Albania, Italy) of *C. versicolor* was also suggested by the cpDNA tree obtained in the molecular phylogenetic study of Lakušić & al. (2013). Lakušić & al. (2013) revealed that all analyzed individuals here treated as members of the “versicolor 2” group formed one strongly supported clade (Bayesian posterior probability 1 and parsimony bootstrap value 86), while the main core of individuals here treated as members of the “versicolor 1” group formed the second strongly supported clade (Bayesian posterior probability 1 and parsimony bootstrap value 84) (fig. 2 in Lakušić & al., 2013). Interestingly, individuals from Demir Kapija, which in our analysis showed admixed characteristics, formed an independent, well-supported clade on the cpDNA tree (Bayesian posterior probability 0.99 and parsimony bootstrap value 64). At the same time, a clear genetic connection between Apennine “tenorei” (IT-Alessano, IT-Tricase) and one western Balkan “versicolor 2” population (GR-Mt. Tymfi) was revealed on the majority-rule consensus tree of combined plastid and nuclear non-coding sequence data (fig. 4 in Lakušić & al., 2013).

The results of STRUCTURE for  $K = 3$  (Fig. 3B) indicate that the Apennine tenorei populations are genetically distinct, which is also supported by higher  $F_{ST}$  values between the tenorei and Balkan populations, as well as with the position of the tenorei populations at the tip of the second main branch of the Fitch-Margoliash tree (Fig. 2). However, the tenorei populations were grouped into the same genetic cluster with a few populations from the western part of the Balkan Peninsula (southern Albania 46–48

and northwestern Greece 39, 43). This relatedness may provide evidence that some time ago the Balkan and Apennine Peninsulas were geographically closer. As a result, nowadays there are plant species distributed on both peninsulas. The phylogeographical connection between these two peninsulas could have happened in the period of the Messinian salinity crisis during the late Miocene when the level of the Adriatic Sea was lower than today (Hsü & al., 1973; De Giuli & al., 1987; Krijgsman & al., 1999; Surina & al., 2014). This assumption is supported by similar disjunct distributions of several other plant species, e.g., *Bromus parvispiculatus* (Karl & Scholz, 2009), *Erica manipuliflora* (Valdés, 2009–), *Euphorbia apios*, *Helictotrichon convolutum* and *Satureja cuneifolia* (Di Pietro & Misano, 2010), *Edraianthus graminifolius* (Surina & al., 2014) and *Linum elegans* (Wagensommer & al., 2017).

According to the UPGMA clustering, bicajensis, korabensis, lancifolia and mrkvickana are similar to the central Balkan populations (Fig. 4), which is in accordance with the obtained relationships in genetic cluster A – “versicolor 1” (Fig. 3). The main differences between genetic clusters and grouping on the morphological level are in the positions of the plasonii, thessala and tomentella populations. The plasonii population is more closely related to the populations from genetic cluster B – “versicolor 2”; (Figs. 2, 3), while on the morphological level according to the UPGMA clustering it is more similar to the populations (Fig. 4) from genetic cluster A – “versicolor 1”. This might be explained by the geographic position of the plasonii population close to the valley and gorge of the Vardar River through which gene flow among central and southern Balkan populations can be hypothesized. This is further supported by the fact that the other two populations that are geographically close to the Vardar River (14 MK-Katlanovo, 15 MK-Veles) share significant portions of genetic clusters A and B. The presence of several *C. versicolor* populations has also been recorded in the gorge of the Vardar River and in the gorges of its tributaries Babuna and Topolka. Although these populations were not included in this study, they are for sure contributing to the gene flow and genetic diversity of the surrounding populations in this region. The thessala and tomentella populations are more related to the populations from genetic cluster B – “versicolor 2” (Figs. 2, 3), but on the morphological level according to the UPGMA clustering they are more similar to “versicolor 1” (Fig. 4). These populations are influenced by the arid Aegean variety of the Mediterranean climate which comes from the East and which is probably the main reason for the occurrence of small individuals in the western central part of the Balkan Peninsula (northern part of the *C. versicolor* range).

The CDA of the morphometric data for three groups (Fig. 5) strongly suggested that the “versicolor 1” (central Balkan) group is most distinct, as well as that the “tenorei” (Apennine) group is more similar to the “versicolor 2” (southern Balkan) group. This pattern of morphological relationships between the investigated groups coincides with their

**Table 6.** Summary of discriminant function analysis and results of descriptive statistics of morphometric characters used for the discriminant function analysis of *Campanula versicolor* s.l. populations *a priori* classified into three groups: “versicolor 1”, “versicolor 2” and “tenorei”

Character code	Character	Discriminant function analysis		Descriptive statistics (mm)			
		Wilk's Lambda	F-remove (2.417)	p	“versicolor 1” – <i>C. versicolor</i> subsp. <i>korabensis</i>	“versicolor 2” – <i>C. versicolor</i> subsp. <i>versicolor</i>	“tenorei” – <i>C. versicolor</i> subsp. <i>tenorei</i>
<b>Corolla</b>							
Co-H	Length	0.066	1.070	0.344	(9.4–)11.1–14.8(–18.3)	(12–)14.5–19.2(–26.2)	(14.2–)16.2–20.1(–22)
Co-De	Depth	0.066	0.006	0.994	(5.5–)7–9.9(–12.7)	(8.4–)10.1–13.4(–17.8)	(8.3–)9.6–12.3(–14.3)
CoL-H	Corolla lobe height	0.069	8.618	<b>0.000</b>	(3.5–)4.3–5.9(–7.4)	(3.4–)5–7.3(–11)	(5.3–)7.2–9.5(–10.4)
CoL-h	Distance from maximal width of the lobe base to the corolla base	0.067	4.690	<b>0.010</b>	(4.6–)5.5–7.1(–8.5)	(5.7–)6.9–9(–11.7)	(6.6–)7.5–9.4(–11.4)
CoL-Wm	Maximal width of the corolla lobe	0.068	8.516	<b>0.000</b>	(4.6–)7.5–10.3(–12.6)	(6.1–)9.8–13.2(–16.2)	(8.7–)10.3–13.2(–16.7)
Co-Per	Base perimeter	0.066	0.550	0.577	(3.5–)4.4–6.1(–7.6)	(3.5–)5–7.2(–9.8)	(5.6–)7–9.3(–10.1)
<b>Calyx</b>							
CaD-W	Width of the teeth base	0.068	8.212	<b>0.000</b>	(1.1–)1.4–1.9(–2.2)	(1.3–)1.7–2.3(–2.9)	(1.7–)2–2.6(–3)
CaD-L	Teeth length	0.067	5.398	<b>0.005</b>	(2.6–)3.7–7.3(–12.1)	(4.4–)6.3–9.5(–13.3)	(3.8–)5–7.6(–9.8)
Ca-H	Height	0.069	11.621	<b>0.000</b>	(1.5–)2–2.9(–4.3)	(1.7–)2.2–2.9(–3.4)	(2.1–)2.3–3.1(–4.2)
CaPe-L	Pedicel length	0.066	1.925	0.147	(0.6–)1.2–4.8(–13.6)	(0.4–)1.2–4.2(–9.4)	(0.2–)1.1–4.6(–11.6)
<b>Pistil</b>							
Pi-L	Length	0.068	5.733	<b>0.003</b>	(8.7–)10.8–14.9(–17.7)	(13.1–)15.6–19.1(–21.9)	(14.8–)16.6–20.6(–22.8)
Pi-Sy	Style length	0.066	0.064	0.938	(3.6–)4.9–7.5(–9.9)	(5.7–)6.8–8.9(–10.8)	(5.9–)7.2–9.2(–10.8)
<b>Stamen</b>							
StB-H	Base height	0.068	7.000	<b>0.001</b>	(1.8–)2.4–3.1(–4)	(2.3–)2.8–3.9(–4.9)	(3.1–)3.6–4.5(–5)
StF-L	Filament length	0.067	2.673	0.070	(0.7–)1.2–2.1(–2.9)	(0.9–)1.5–2.3(–3.5)	(0.9–)1.2–2(–2.9)
StA-L	Anther length	0.074	25.465	<b>0.000</b>	(3.1–)4.3–5.6(–6.3)	(5–)6.4–8.2(–9.8)	(6–)6.9–8.7(–10.5)
StB-Wm	Maximal width of the base	0.067	4.749	<b>0.009</b>	(1.6–)1.9–2.4(–2.8)	(1.9–)2.4–3.1(–3.7)	(2.4–)2.6–3.2(–3.8)
<b>Habitus</b>							
Pl-H	Height of the plant	0.066	2.006	0.136	(78–)257.3–667.4(–1182.5)	(155–)347.3–779.1(–1220)	(130–)230.1–489.8(–720)
Inf-L	Inflorescence length	0.070	11.835	<b>0.000</b>	(30–)63.4–340.1(–760.9)	(50–)122.7–351.7(–655)	(30–)33–159(–310)
Stem-H	Stem height	0.067	2.863	0.058	(23–)120.6–400.4(–680)	(65–)148.6–515.1(–1070)	(100–)173.8–354.1(–510)



Table 6. Continued.

Character code	Character	Discriminant function analysis		Descriptive statistics (mm)			
		Wilk's Lambda	F-remove (2.417)	<i>P</i>	“versicolor 1” – <i>C. versicolor</i> subsp. <i>korabensis</i>	“versicolor 2” – <i>C. versicolor</i> subsp. <i>versicolor</i>	“tenorei” – <i>C. versicolor</i> subsp. <i>tenorei</i>
Basal leaf (Fb)							
Fb-Lm	Lamina length	0.069	8.640	<b>0.000</b>	(24.4–)36.4–71.4(–114.1)	(25.3–)47.8–91.7(–133.3)	(20.4–)34.6–57.9(–74.2)
Fb-Wm	Width of left side	0.066	0.597	0.551	(3.8–)7.8–15(–20.4)	(8.3–)11–21.3(–36)	(6.4–)10.3–17.7(–24.1)
Fb-L	Distance from maximal width to the base of the lamina	0.067	2.418	0.090	(5.3–)10.4–24.8(–42.1)	(6.6–)11–27.8(–44)	(7.9–)10.4–18.9(–26.1)
FbPe-L	Petiole length	0.068	5.494	<b>0.004</b>	(7.3–)23.1–82.1(–149.1)	(7–)27.2–84.1(–149.7)	(5.6–)15.9–62(–133.3)
FbPe-Wb	Petiole base width	0.066	0.554	0.575	(0.5–)2.7–4.8(–7.5)	(1.5–)3.4–5.6(–7.9)	(2.3–)3.6–5.3(–6.5)
FbPe-W	Petiole width	0.066	1.346	0.261	(0.5–)1.5–2.8(–4.1)	(1–)1.3–2.6(–4.6)	(1.5–)1.8–2.4(–2.9)
Middle leaf (Fm)							
Fm-Lm	Lamina length	0.068	8.494	<b>0.000</b>	(13.1–)26.9–56.8(–113.9)	(24.3–)36.9–65(–91.3)	(21.6–)25.6–45.4(–63.3)
Fm-Wm	Width of left side	0.069	9.636	<b>0.000</b>	(2.7–)5.3–12.5(–26)	(4.9–)8.9–16.1(–22.6)	(5.1–)7.9–14.3(–19.1)
Fm-L	Distance from maximal width to the base of the lamina	0.067	4.195	<b>0.016</b>	(4.2–)8.7–21.2(–45.1)	(7.3–)11.4–21.8(–30)	(6.6–)9.2–16.2(–25.8)
FmPe-L	Petiole length	0.071	15.275	<b>0.000</b>	(0.8–)5.2–33.9(–100.6)	(2.5–)6.8–26.3(–61.1)	(1.5–)5.4–23.4(–39.8)
FmPe-Wb	Petiole base width	0.069	9.502	<b>0.000</b>	(0.7–)2.3–3.9(–5.5)	(0.4–)2.9–4.6(–5.9)	(2.3–)3.1–4.7(–6.3)
FmPe-W	Petiole width	0.076	33.500	<b>0.000</b>	(0.8–)1.8–3(–4.5)	(0.9–)1.4–2.9(–4.6)	(1.3–)1.7–2.6(–3.4)
Upper leaf (Fu)							
Fu-Lm	Lamina length	0.066	1.060	0.347	(7.7–)17.3–39.2(–70.7)	(17.6–)23.7–43.8(–73.3)	(10.7–)15.9–29(–48.5)
Fu-Wm	Width of left side	0.066	2.189	0.113	(1.6–)3–8.1(–13.1)	(3.2–)5.1–10.4(–16.5)	(2.9–)4.3–7.9(–13)
Fu-L	Distance from maximal width to the base of the lamina	0.066	0.006	0.994	(2–)6.2–15.8(–32.9)	(4.3–)7.9–17.1(–36.7)	(4.4–)6.2–12(–22)
FuPe-L	Petiole length	0.068	5.669	<b>0.004</b>	(0–)0.2–10.3(–40)	(0–)1.5–8.4(–17.4)	(0–)1.2–8.1(–19.2)
FuPe-Wb	Petiole base width	0.067	4.125	<b>0.017</b>	(0–)1.4–3.5(–4.8)	(0–)1.6–4.1(–5.7)	(0–)2–4(–5)
FuPe-W	Petiole width	0.067	3.358	<b>0.036</b>	(0–)1.2–3.2(–4.6)	(0–)1.1–3(–4.4)	(0–)1.4–2.6(–3.1)

Significant *P*-values are in bold (*P* < 0.05). For descriptive statistics, value ranges correspond to the mean ± standard deviation, with the minimal and maximal values in parentheses.

distribution (Figs. 1, 5). Furthermore, the position of “versicolor 1” on the positive part of the first DA axis and the positions of the “versicolor 2” and “tenorei” on the negative part of the first DA axis correspond with the obtained genetic clusters A, B1 and B2 (Fig. 3B).

According to the results presented in this study, it can be seen that both genetic and morphological groups obtained are mostly geographically well defined. Thus, it is surprising that two populations from the central Balkan (14 MK-Katlanovo, 15 MK-Veles) are related to the Apennine populations from the genetic cluster B2 – “tenorei” based on the results from the STRUCTURE analysis for  $K = 3$  (Fig. 3B). By inspecting allele frequencies by locus for each population, it was found that these two populations have in high frequency the allele C008<sub>178</sub> that became predominant (or even fixed) in the Apennine tenorei populations. However, on the Fitch-Margoliash tree, these two populations are not positioned close to the tenorei populations, but close to the “versicolor 1” group (Fig. 2). Their position on the tree coincides with their intermediate geographical position between the central and southern Balkan populations. Furthermore, the population from Veles (15) and the Apennine populations were also included in the molecular phylogenetic study of Lakušić & al. (2013). According to the phylogenetic trees based on ITS and on combined plastid and nuclear non-coding sequence data, the population from Veles is more related to the central Balkan populations than to the Apennine populations.

## ■ TAXONOMIC TREATMENT

Given that the population sampling of *Campanula versicolor* s.l. analyzed by Lakušić & al. (2013) was poor (14 populations), the present study was focused on a more comprehensive population sampling (41 populations), spanning the whole distribution area of *C. versicolor*. In our study, we employed faster-evolving markers (microsatellites – SSR), capable of differentiating among closely related and recently diverged taxa. Additionally, we performed a morphometric analysis on an extensive population sampling – 456 individuals from 37 populations.

However, our proposed taxonomic treatment is based on both the previous analyses of cpDNA, microsatellite, morphometric and chorological data for all members of the *Campanula pyramidalis* complex (Lakušić & al., 2013; Janković & al., 2016), as well as the results of the current study. According to the cpDNA tree of Lakušić & al. (2013: fig. 2), populations of *C. versicolor* s.l. were grouped into two strongly supported clades, which correspond to the two main branches/groups revealed on the Fitch-Margoliash tree (Fig. 2) based on the microsatellite data. Apennine tenorei populations are positioned at the tip of the second main branch of the Fitch-Margoliash tree (Fig. 2) and according to the results of STRUCTURE for  $K = 3$  (Fig. 3B), those populations are genetically distinct. Along with the tenorei populations in genetic cluster B2 –

“tenorei” are also grouped some populations from the western part of the Balkan Peninsula (southern Albania and northwestern Greece). This genetic connection between Apennine and Balkan populations coincides with the results of the majority-rule consensus tree of combined plastid and nuclear non-coding sequence data of Lakušić & al. (2013: fig. 4).

Taking into account all the results, we propose a new taxonomic treatment of *C. versicolor* s.l. Three distinct entities can be distinguished, circumscribed here on the subspecies level.

A detailed morphological description of *C. versicolor* s.l. is provided, while morphological descriptions of the three subspecies cover only diagnostic morphological characters. In the morphological descriptions, value ranges correspond to mean  $\pm$  standard deviation, with minimal and maximal values in parentheses. Distribution and habitat data are also provided for all three subspecies.

- Campanula versicolor*** Andrews, Bot. Repos.: t. 396. 1804 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 265. 2017): [illustration] “*Campanula versicolor*” in Andrews, Bot. Repos.: t. 396. 1804 [fig. 1A in Janković & al., 2017]. Epitype (designated by Janković & al. in Phytotaxa 323(3): 265. 2017): GREECE. Parnas [Mt. Parnassus], stene, krečnjak [limestone cliffs], 38.56761°N, 22.56891°E, 1564.2 m a.s.l., 21 Aug 2014, D. Lakušić, N. Kuzmanović & I. Janković s.n. (BEOU No. 40045!) [fig. 2 in Janković & al., 2017].
- = *Campanula versicolor* Sibth. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 138. 1806, nom. illeg., non Andrews 1804 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 267. 2017): [illustration] “*Campanula versicolor*” in Sibthorp & Smith, Fl. Graec. 3: t. 207. 1819) [fig. 1B in Janković & al., 2017].
- = *Campanula planiflora* Willd., Enum. Pl.: 210. 1809, nom. illeg., non Lam. 1785  $\equiv$  *C. willdenowiana* Schult. in Roemer & Schultes, Syst. Veg. 5: 107. 1819 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 267. 2017): “Hort. bot. Berol W.” [Horto Botanico Berlinensis/Berlin Botanical Garden Willdenow] (B barcode B -W 03805-01 0 [photo!]).

**Description.** – Perennial plant with 1 or few (usually 1 or 3, rarely 10–30) simple herbaceous flowering stems which are generally semipendulous and slightly arched upward or erect or just arched in the lower part; usually 25–70 cm long. Specimens from high-mountain regions can have only 8 cm long erect stems, while some specimens from low-altitude and shady habitats can have thinner, gentle, pendulous or semipendulous stems up to 1 m long. Plants typically glabrous, rarely with short, bright patent hairs on stems, leaves and calyx. Glabrous and hairy plants can often be found in the same population. The rhizome is a brown, brittle, woody stock with scarfs from old rosette leaves on the elongated parts from where stems arise so that stems are up to 10 cm woody in their lower part (caudex). This is especially noticeable in older specimens. Leaves dark green,

symmetric or somewhat asymmetric, usually once-folded along the central nerve and slightly bent down. Leaf margin glandular, crenulate, crenate or serrate. Rosette usually dense, having many leaves or made of few broadly cordate, triangular-deltoid or broadly elliptic leaves. Lower cauline leaves elliptic, lanceolate or ovate; apex obtuse, subobtuse, mucronate or acute; base cuneate, attenuate, rounded, cordate or truncate; (2–)4–8(–13) cm long and 2–7 cm wide. Petioles narrowly winged. Length of petioles gradually decreases towards the top of the plant while petiole “wings” are wider. Uppermost leaves elliptic, lanceolate or cuneate, with short petioles or sessile; (0.7–)2–4(–8) cm long and 1–2(–4) cm wide. Inflorescence panicate, (3–)7–30(–75) cm long, with clusters of 3–5 flowers, rarely with single flowers. Pedicels (0.2–)1.5–4.5(–10) cm long; rarely with bracteole. Calyx green, conical, with few shallow furrows or trilobular with 3 prominent furrows, (2–)3–4(–5) mm in diameter and (1.5–)2–3(–4) mm long. Calyx teeth green, narrowly triangular or subulate with wider base; (2.5–)4.5–9(–13) mm long and (1–)1.5–2.5(–3) mm wide at the base. Corolla widely campanulate, rotate to flat, divided to one-half, two-thirds or three-fifths; (9.5–)12–19(–26) mm long. Corolla color pale violet to violet, rarely white, with or without dark violet eye in the center of the flower around the base of stamens. Corolla lobes deltoid or triangular, (5.5–)8–12(–18) mm long and (4.5–)6–8(–11) mm wide. Style (9–)12–19(–23) mm long, usually curved upwards, upper half encrusted with pollen-collecting hairs; pollen grains pale yellow, rarely pale violet. Ovary trilobular, with numerous ovules. Stamens 5, (6.5–)9–14(–18) mm long; anthers (3–)5–8(–10) mm long; filaments (1–)1.5–2(–3.5) mm long, basal part of filaments triangular to deltoid, (2–)2.5–4(–5) mm long. Capsule obovoid, shallowly sulcate, pale brownish, dehiscent by basal pores or irregularly rupturing laterally and apically. Seeds numerous, reticulate, elliptic-ovate, light brown.

#### Key to the subspecies of *Campanula versicolor*

The following key makes no allowance for extreme or intermediate individuals (potential hybrids).

1. Calyx wide, conical with 3 prominent furrows; calyx teeth (1.3–)1.7–2.4(–3) mm wide; corolla with dark violet eye in the center; anther length (5.4–)6.7–8.4(–10.5) mm.....2
1. Calyx narrow, conical with few shallow furrows; calyx teeth (1–)1.5–2 mm wide; corolla pale violet, without dark violet eye in the center; anther length (3–)4.5–5.5(–6) mm; southwestern Bulgaria, southern Serbia, northeastern Albania and North Macedonia .....(2) *C. versicolor* subsp. *korabensis*
2. Corolla widely campanulate, rotate and flat with clear dark violet eye; petals bent backwards; inflorescence elongated, (5–)12–35(–66) cm long; Greece and southern and western Albania.....(1) *C. versicolor* subsp. *versicolor*
2. Corolla widely campanulate and conical with a slightly less clear dark violet eye; petals mostly upright;

short internodes; inflorescence thickened, 3–16(–31) cm long; entire stems distinctively thick; southeastern Italy .....(3) *C. versicolor* subsp. *tenorei*

There is no clear boundary between the central and southern populations in the Balkan Peninsula, and this is shown by the occurrence of populations that are transitional at both genetic and morphological levels. The contact zone is located between southern Republic of North Macedonia and northern Greece, especially in the western part of this belt in the area of Lake Prespa and the eastern part of the belt in the gorge of the Vardar River and its tributaries (Fig. 6).

#### (1) *Campanula versicolor* subsp. *versicolor*

= *Campanula versicolor* var. *thessala* Boiss., Fl. Orient. 3: 915. 1875 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 269. 2017): GREECE. In rupibus reg. sylvat. [regione sylvatica] m. Olympi [mount Olympus] Thessaliae, 21 Jul 1851, *T. de Heldreich 400* (G barcode G00330725 [second sheet G00330725\_a] [photo!]).

= *Campanula versicolor* var. *tomentella* Halácsy in Österr. Bot. Z. 42: 372. 1892 ≡ *C. versicolor* [var. *thessala*] f. *tomentella* Halácsy, Consp. Fl. Graec. 2: 263. 1902 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 270. 2017): GREECE. Litachori [Lithochori]: Fels an den Schluchten [rock at the canyons] Megarema (am Olymp), 7 Sep 1891, *P.E.E. Sintenis & J.F.N. Bornmüller 1354* (B barcode B 10 0365469 [photo!]).

= *Campanula longipetiolata* F.K.Mey. in Haussknechtia Beih. 15: 151–152, fig. 25. 2011 – Holotype: ALBANIA: Tepelena, Tal von Luzat, ca. 300 m, 9 Sep 1961, *F.K. Meyer 6035* (JE barcode JE00016710 [photo!]; isotype: JE barcode JE00016711 [photo!]).

*Note.* – On the basis of the obtained results, as well as based on the information from relevant protologues (Boissier, 1875; Halácsy, 1892; Meyer, 2011), study of the original herbarium specimens and personal observations, we concluded that *C. versicolor* var. *tomentella*, *C. versicolor* var. *thessala* and *C. longipetiolata* should be synonymised with the typical subspecies. The population of *C. longipetiolata* was not collected for morphometric study. However, according to the morphological features of the holotype, the protologue (Meyer, 2011) and personal observations we made during our field investigation, it emerged that *C. longipetiolata* is not substantially different from *C. versicolor*. One of the characters usually considered as diagnostic was the long leaf petioles (Meyer, 2011), but this character is no longer reliable since based on our extensive morphometric study we observed that it is highly variable. Longer leaf petioles are probably the consequence of wetter and shaded habitats. Furthermore, the acuminate shape of the leaves with a truncate or rounded base has also been found in individuals of other populations (i.e., populations from Vlorë and Tepelenë in southern Albania).

*Description.* – Perennial plants usually with 1 up to 10 (rarely up to 20) simple herbaceous flowering stems which

are generally semipendulous and slightly arched upward, rarely erect. Leaves with a prominent central nerve and pale, conspicuous glands at the tips of the teeth. Leaf margin serrate, rarely crenate or deeply serrate with larger teeth oriented to the apex of the leaf lamina. Lower cauline leaves widely elliptic, with acuminate, cuspidate, mucronate or acute apex and rounded, obtuse, cordate or truncate base; (3–)5–9(–13) cm long and 2–4(–7) cm wide; widest in the lower part, in the first third or quarter. Petioles typically almost of the same length as leaf lamina or 3 or 4(–6) times shorter. Uppermost leaves elliptic to cuneate with short petioles, rarely sessile; 2–5(–7) cm long and (0.7–)1–2(–3) cm wide. Inflorescence elongated; (5–)12–35(–66) cm long. Calyx widely conical with 3 prominent furrows; (2–)3–4(–5) mm in diameter and (1.7–)2–3 mm long. Calyx teeth narrowly triangular or subulate with wider base; (5–)6–9(–13) mm long and 1.5–2.5(–3) mm wide; bent backward or clinging to the corolla; twice as long as the ovary; longer than the connate part of the corolla. Corolla widely campanulate, rotate or flat, (12–)14.5–19.5(–26) mm long; violet to blue; with clear dark violet eye; divided to two-

thirds, rarely to one-half. Corolla lobes (8.5–)10–13.5(–18) mm long and (5.5–)6.5–8.5(–11) mm wide. Pistil (13.5–)16–19(–22) mm, stamens (9–)11–14(–15.5) mm, anthers (5.5–)6.5–8(–10) mm long. Basal parts of the filaments are violet, on the edges brighter violet and with a short pale violet longitudinal line from the apex to the middle of the filament base (Fig. 7).

*Distribution and ecology.* – Populations of this subspecies can be found in the southern part of the Balkan Peninsula, in Greece and southern Albania (Fig. 6; Appendix 2). The geographical distribution ranges from the south area of Lake Prespa in northwestern Greece to the island of Kythira (Strid & Tan, 1996; Yannitsaros, 2004) south of the Peloponnese and from Mt. Pangeon in northeastern Greece to the island of Othonoi (Halácsy, 1902) in northwestern Greece. Populations occur in the vegetation of rocky crevices (*Asplenietea trichomanes*–*Potentilletalia speciosae*, *Onosmetalia frutescentis*) and more rarely within limestone rocky slopes and screes, at altitudes ranging between 20 and 2000 m a.s.l. This subspecies can also be found on the walls of fortresses, old monasteries and old bridges.

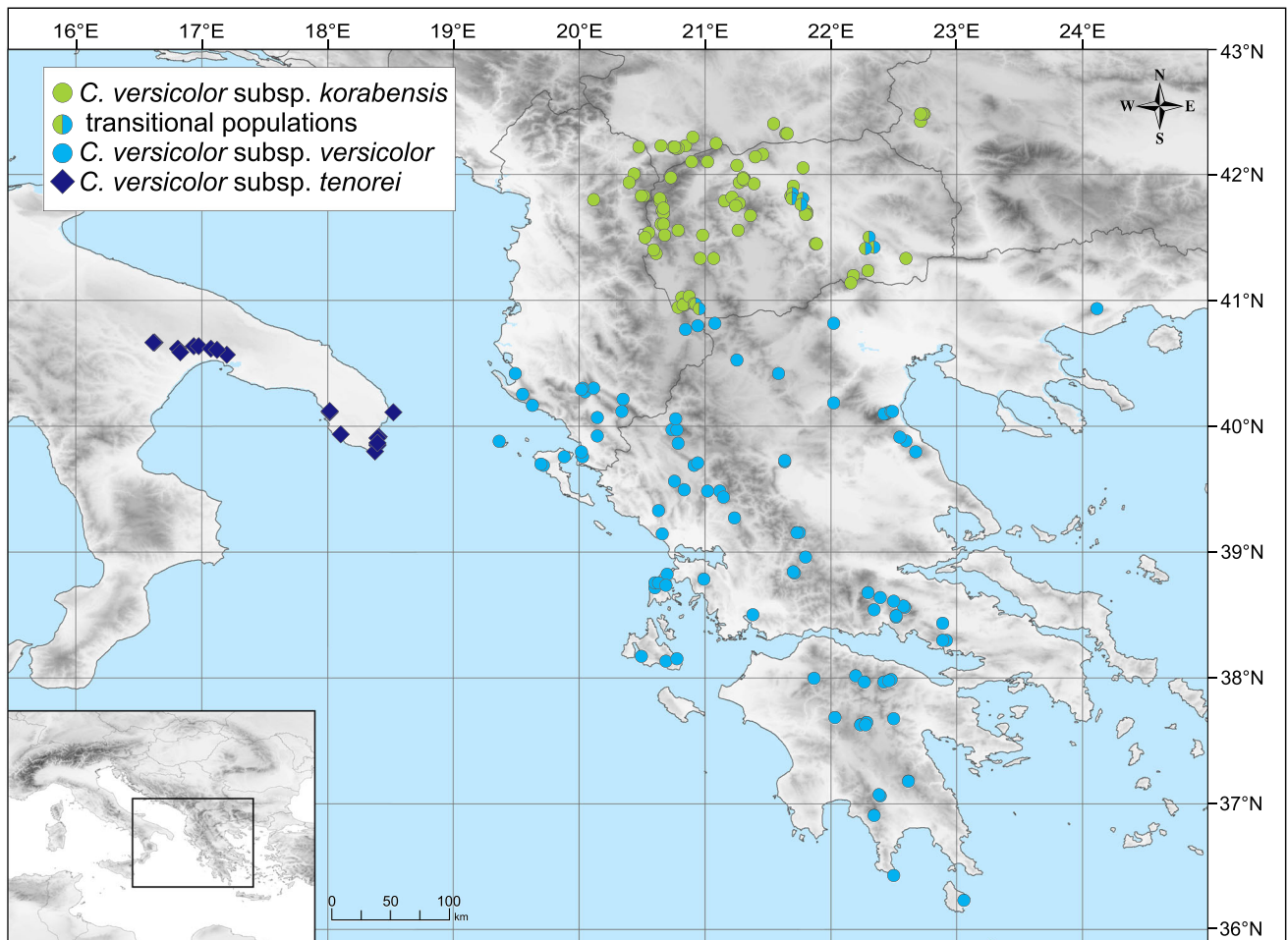
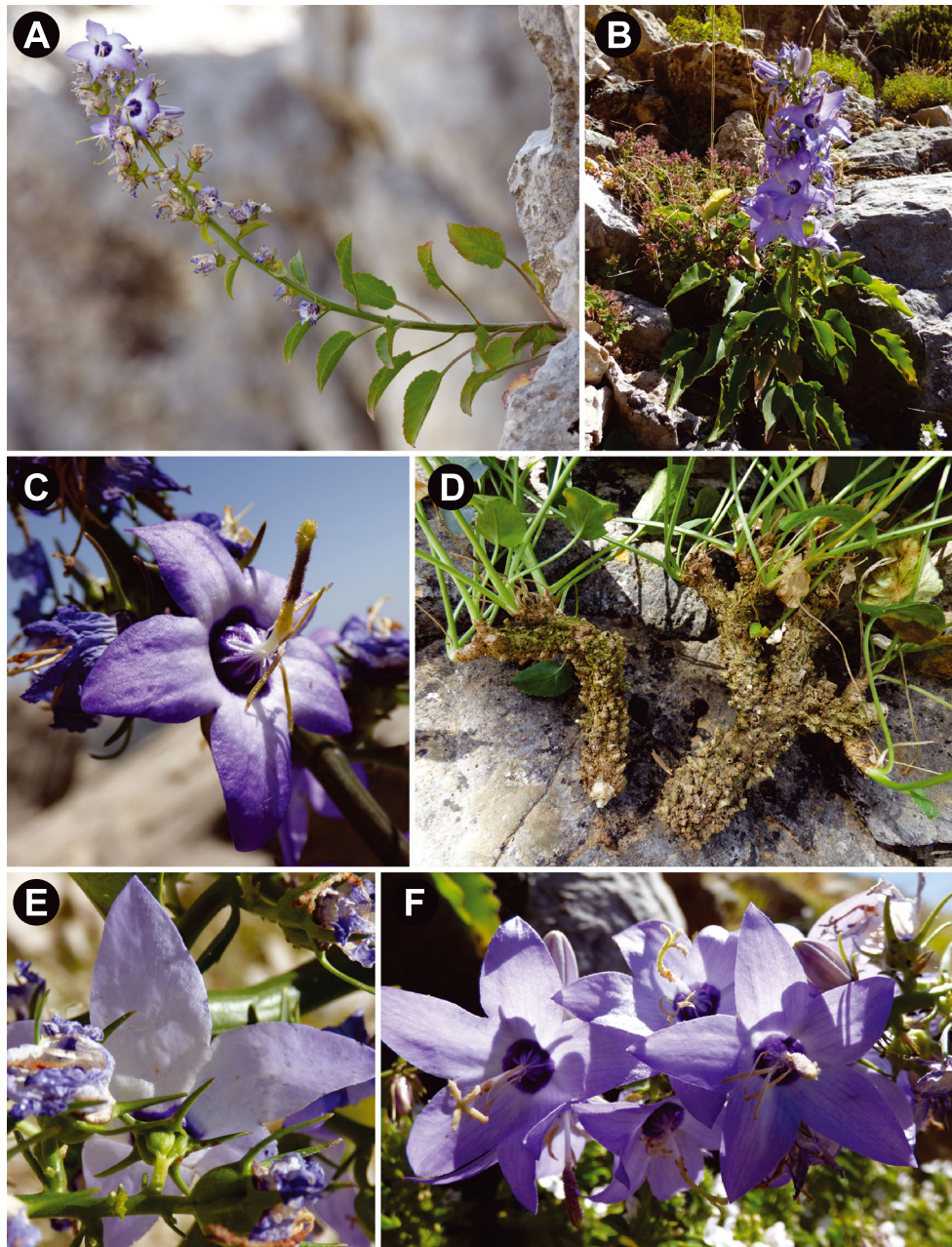


Fig. 6. Distribution map of three subspecies of *C. versicolor* and position of transitional populations.





**Fig. 7.** *Campanula versicolor* subsp. *versicolor*. A & B, Habitus; C, Flower; D, Rhizome; E, Calyx; F, Part of inflorescence. — Photographs: I. Janković.

- (2) *Campanula versicolor* subsp. *korabensis* (F.K.Mey.) I.Janković & D.Lakušić, **comb. & stat. nov.** ≡ *C. korabensis* F.K.Mey. in Haussknechtia Beih. 15: 149–150, fig. 22. 2011 – Holotype: ALBANIA. Korab, Wiesen oberhalb Radomir, ca. 1400 m, an Felsen, 5 Aug 1959, F.K. Meyer 4759 (JE barcode JE00016705 [photo!]; isotype: JE barcode JE00016706 [photo!]).
- = *Campanula plasonii* Formánek in Verh. Naturf. Vereins Brünn 37: 155–156. 1899 – **Lectotype** (first-step designated by Janković & al. in Phytotaxa 323(3): 271. 2017): Republic of NORTH MACEDONIA. Pržigrad Dudica, 1898, *de Ed. Formánek s.n.* (BRNM No. 13259/36

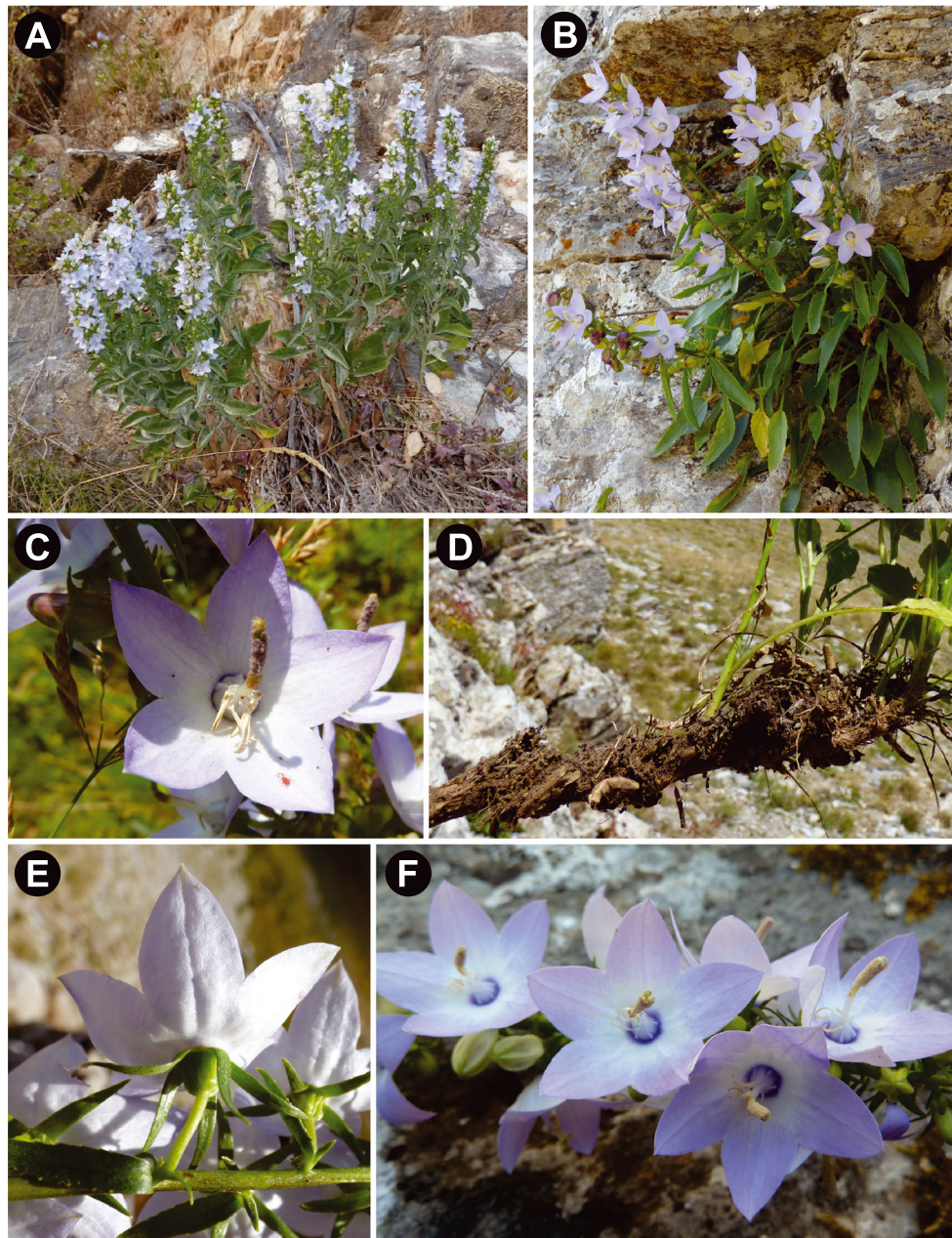
[photo!]), **second-step (designated here):** Republic of NORTH MACEDONIA. (Pržigrad) Dudica, 1895, *de Ed. Formánek s.n.* (BRNM No. 13259/36, the upper right-hand plant turned face down [photo!]).

= *Campanula mrkvickana* Velen. in Allg. Bot. Z. Syst. 11: 44–45. 1905 ≡ *C. versicolor* f. *mrkvickana* (Velen.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(2): 543. 1930 – Lectotype (designated by Ančev in Kožuharov & Ančev, Fl. Reipubl. Bulgaricae 11: 108. 2013): BULGARIA. In siccis calcareis collinis Konjovo Planina ad Kistendil, Aug 1904, *I. Mrkvička s.n.* (PRC barcode PRC 451230!).



- = *Campanula versicolor* [subsp. *thessala*] subvar. *lancifolia* Bornmüller in Bot. Jahrb. Syst. 59: 2–3. 1925 – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 271. 2017): Republic of NORTH MACEDONIA. In valle fl. Treska, ad rupes, 300–500 m, 27 Apr 1918, *J. Bornmüller 4398* (JE barcode JE00007087 [photo!]).
- = *Campanula korabensis* subsp. *bicajensis* F.K.Mey. in Haussknechtia Beih. 15: 150, fig. 23. 2011 – Holotype: ALBANIA. Gjalica e Lumes, Bicaj, Eingang der Schlucht, ca. 400 m, 31 Jul 1959, *F.K. Meyer 4562* (JE barcode JE00016708 [photo!]).

*Note on the second-step lectotypification.* – The first-step lectotypification was published in Janković & al. (2017: 271). The specimen selected as lectotype is part of the original material, and the plants on the sheet fit the description provided in the protologue. Therefore, we do not have arguments to supersede it according to Art. 9.19 of the *ICN*. However, two localities (two gatherings) were cited on the label of this specimen, both mentioned in the protologue (Formánek, 1899: 155) and visited earlier by Formánek in 1895 (Formánek, 1896: 255). The locality Prži Grad is located in the Kavadarci municipality in the Republic of



**Fig. 8.** *Campanula versicolor* subsp. *korabensis* (F.K.Mey.) I.Janković & D.Lakušić, comb. & stat. nov. **A** & **B**, Habitus; **C**, Flower; **D**, Rhizome; **E**, Calyx; **F**, Part of inflorescence. — Photographs: I. Janković.

North Macedonia, at the altitude of 1620 m a.s.l. The locality Dudica (2132 m a.s.l.) is the peak of Mt. Kožuf, which is a border mountain between the Republic of North Macedonia and Greece. The upper right-hand plant, selected here as the second-step lectotype, was most probably collected on Dudica, as this plant is much smaller than the other plants on the herbarium sheet. This pattern of a smaller habitus of plants inhabiting higher altitudes observed during our field investigations was confirmed in this study.

*Note.* – The earliest legitimate name whose epithet could be used for the new combination is *Campanula plasonii* published by Formánek (1899: 155). However, most of the localities Formánek cited in the protologue are situated in a transitional zone between the central and southern Balkan populations. We included in our analyses the population from Demir Kapija, provided in the protologue for *C. plasonii*, and this population is genetically admixed. Bearing in mind the original circumscription of Formánek's *C. plasonii*, as well as the results of our study, we consider that using the epithet *plasonii* would be taxonomically problematic and decided not to use it for making the new combination. The next-earliest legitimate name, *Campanula mrkvickana* of Velenovský (1905: 44), is also taxonomically disruptive: the analyzed population from the locus classicus slightly differs genetically and morphologically from other central Balkan populations because of its isolated position. Therefore, we used the name *Campanula korabensis* of Meyer (2011) as basionym. The designation "*Campanula versicolor* f. *matkae*" was published in a master thesis (Nikolov, 2005: 67), being therefore not validly published according to Art. 29.1 of the *ICN*.

Based on our results, as well as the information from relevant protologues (Formánek, 1899; Bornmüller, 1925; Velenovský, 1905; Meyer, 2011), the original herbarium specimens and personal observations, it is concluded that the following taxa should be synonymised with *C. versicolor* subsp. *korabensis*: *C. versicolor* subsp. *thessala* subvar. *lancifolia*, *C. mrkvickana*, *C. plasonii* and *C. korabensis* subsp. *bicajensis*.

*Description.* – Perennial plants with 1–5 (rarely 10 or more) simple herbaceous flowering stems which are typically erect and arched only in the lower part; rarely whole stems are arched upward. Leaf margin slightly crenulate or obtusely serrate, sometimes slightly undulate like the whole lamina. Glands are rare, small and not present on every leaf tooth. Lower cauline leaves linear elliptic, lanceolate, oblong or elongated cordate; apex subobtusely or acute; base rounded, cuneate, truncate or attenuate, rarely slightly cordate; (2.5–)4–7(–11) cm long and (0.8–)1.5–3(–4) cm wide; widest in the first half or the first third. Petioles are half as long or longer than the leaf lamina. Leaves in the middle part of the stems sessile or with a very short petiole which gradually passes into the attenuate leaf base. Uppermost leaves narrowly elliptic, cuneate or lanceolate, leaf base attenuate to sessile; (0.7)1.5–4(–7) cm long and (0.3–)0.7–1.5(–2.5) cm wide. Inflorescence elongated; (3–)7–33(–74) cm long. Calyx narrower than calyx of flowers of the typical subspecies, conical, with few shallow furrows; (1.7–)2.5–3(–4) mm in

diameter and (1.5–)2–3(–4.5) mm long. Calyx teeth triangular; (2.5–)3.5–7(–12) mm long and (1–)1.5–2 mm wide; slightly bent backward or in line with the upper surface of the ovary (ovary disk); 2–3 times longer than the ovary; shorter than the connate part of the corolla. Corolla widely campanulate and conical, pale violet to almost white, without dark violet eye; divided to one-half, rarely to two-thirds; (10–)11–15(–18) mm long. Corolla lobes triangular to deltoid, upright; (5.5–)7–10(–13) mm long and 5–7(–8) mm wide. Pistil (9–)10.5–15(–18) mm, stamens (6.5–)8–11(–12) mm, anthers (3–)4.5–5.5(–6) mm long. Basal parts of the filaments are pale violet, the same color as the corolla (Fig. 8).

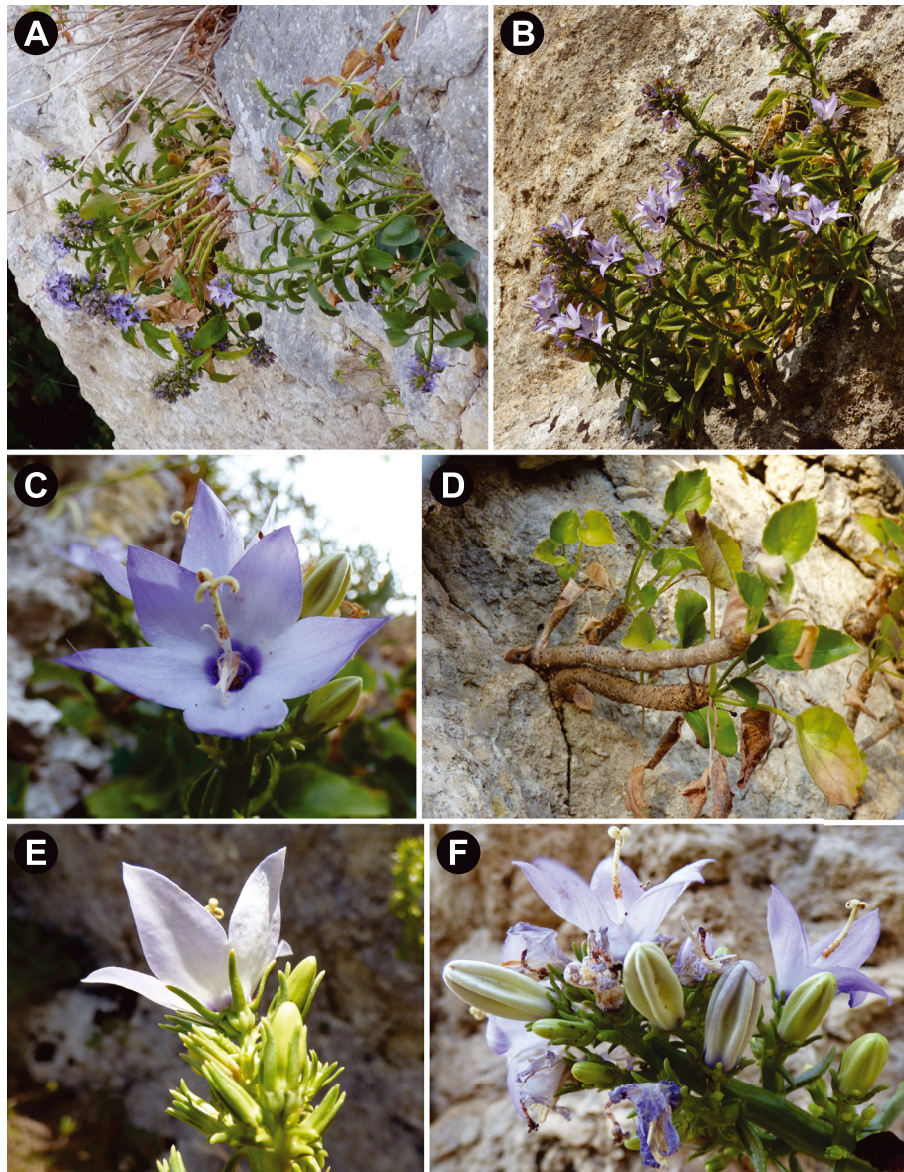
*Distribution and ecology.* – Populations of this subspecies can be found in the central part of the Balkan Peninsula, in southwestern Bulgaria, southern Serbia, Republic of North Macedonia and northeastern Albania (Fig. 6; Appendix 2). Populations mostly occur in the vegetation of rocky crevices (*Asplenieta trichomanes*–*Potentilletalia speciosae*), rarely in the vegetation of screes (*Drypidetalia spinosae*), or on rocky ground; usually on limestone between 200 and 1900 m a.s.l., rarely on serpentine.

- (3) *Campanula versicolor* subsp. *tenorei* (Moretti) I. Janković & D. Lakušić, **comb. & stat. nov.** ≡ *C. tenorei* Moretti in Schouw, Prosp. Descr. Geogr. Piante Ital.: 19 [= in Giorn. Fis. Chim. Storia Nat. Med. Arti, dec. 2, 7: 41]. 1824, nom. nov. pro *C. corymbosa* Ten. ≡ *C. corymbosa* Ten., Fl. Napol. 1: XV. 1811, nom. illeg., non Desf. 1808 ≡ *C. rosanoi* Ten., Fl. Napol. 3: 205–206. 1827, nom. illeg. (Art. 52.1 and 52.2 of the *ICN*) ≡ *C. versicolor* var. *rosanii* (Ten.) Nyman, Consp. Fl. Eur.: 480. 1879, comb. illeg. – Lectotype (designated by Janković & al. in Phytotaxa 323(3): 267. 2017): ITALY. Basilicata, Ginosa, s.d., *M. Tenore s.n.* (NAP!) [fig. 3 in Janković & al., 2017].

*Note.* – This is a new combination based on *C. tenorei* which was published by Moretti (1824) as a replacement name for the illegitimate name *C. corymbosa* Ten. (Tenore, 1811; Art. 53.1 of the *ICN*). Morphological differentiation between subsp. *tenorei* and subsp. *versicolor* is less clear than between subsp. *versicolor* and subsp. *korabensis*. However, *C. versicolor* subsp. *tenorei* is characterized by some qualitative morphological features by which it can be easily recognized, i.e., distinctively thick stems and leaves, short inflorescence, stem with a long woody basal part.

*Description.* – Perennial plants with up to 5 (rarely up to 20) simple herbaceous glabrous flowering stems which are generally semipendulous and whole stems are arched upward, rarely erect. Stems distinctively thick, in the upper part up to 8 mm in diameter. Lower part of stems can be up to 10 cm woody. Leaves also thick, glabrous. Leaf margin irregularly serrate, rarely crenate or deeply serrate with larger teeth oriented to the apex. Glands at the tips of the leaf teeth are pale and small. Lower cauline leaves widely ovate, apex obtuse or subobtusely, base blunt, slightly cordate





**Fig. 9.** *Campanula versicolor* subsp. *tenorei* (Tenore) I.Janković & D.Lakušić, comb. & stat. nov. **A** & **B**, Habitus; **C**, Flower; **D**, Rhizome; **E**, Calyx; **F**, Part of inflorescence. — Photographs: I. Janković.

or truncate; (2–)3.5–6(–7) cm long and (1.5–)2–4(–5) cm wide; widest in the first third or quarter. Petioles typically half as long as the leaf lamina. Uppermost leaves narrowly elliptic, obovate or cuneate with short petioles, rarely sessile; (1–)1.5–3(–5) cm long and (0.5–)1–1.5(–2.5) cm wide. Inflorescence thickened and with short internodes between flower clusters; 3–16(–31) cm long. Calyx green, glabrous, conical with 3 prominent furrows; 3–4(–5) mm in diameter and 2–3(–4) mm long. Calyx teeth green, narrowly triangular; (4–)5–7.5(–10) mm long and (1.7–)2–2.5(–3) mm wide in the base; typically clinging to the corolla; half as long as the ovary. Corolla widely campanulate and conical, divided up to two-thirds, rarely to one-half; (14–)16–20(–22) mm long; violet to pale violet, with or without dark violet eye in the center which is less clearly expressed than in

individuals of the typical subspecies. Corolla lobes triangular to deltoid; upright; (8–)9.5–12(–14) mm long and (6.5–)7–9(–11) mm wide. Pistil (15–)17–21(–23) mm, stamens (11–)12–15(–18) mm, anthers (6–)7–9(–10.5) mm long. Basal parts of stamen filaments of darker color than the corolla if a dark violet eye is present. If the dark violet eye is not present, then the basal part of the filaments are the same color as the corolla (Fig. 9).

*Distribution and ecology.* – Populations of this subspecies can be found in southeastern Italy, in the Apulia and Basilicata administrative regions (Fig. 6; Appendix 2). Populations mostly occur in the vegetation of rocky crevices on limestone as well as on old walls and fortresses; at altitudes ranging from 8 to 400 m a.s.l (Asplenietea trichomanes–Caro multiflori–Aurinion megalocarpaceae).



## ■ AUTHOR CONTRIBUTIONS

DL designed the research. DL, NK, RDP, ZN and IJ collected almost all the analyzed population samples. IR performed the main part of the molecular laboratory work. ZŠ performed the statistical data analysis of microsatellites. ZL and ZŠ contributed to the design of the research and the analysis of the microsatellite data as well as to the interpretation of the results. IJ designed figures, performed the measurements of morphometric characters and with the help of NK conducted the statistical analysis of the morphometric data. NK wrote the part regarding nomenclatural issues. IJ wrote the manuscript with the support of all authors. All authors contributed to the interpretation of the results and to the final version of the manuscript. — IJ, <https://orcid.org/0000-0003-1501-0167>; ZŠ, <https://orcid.org/0000-0002-9848-1601>; ZL, <https://orcid.org/0000-0002-2370-6650>; NK, <https://orcid.org/0000-0003-3463-5541>; RDP, <https://orcid.org/0000-0003-4983-8931>; IR, <https://orcid.org/0000-0001-8900-5112>; DL, <https://orcid.org/0000-0001-6708-6652>

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**Appendix 1.** Information regarding populations of *Campanula versicolor* s.l. used in this study (No. = population numbering; Locality code = country two-letter code defined by ISO 3166-1 plus population locality; G = genetic clusters obtained with STRUCTURE analysis for  $K = 3$ ; S = populations used for molecular analysis; M = populations used for morphometric analysis; Alt. = altitude).

No.	Locality code	Taxon	Informal name	G	S	M	Herbarium and voucher no.	Country and locality	Alt. (m)
<i>C. versicolor</i> subsp. <i>korabensis</i>									
1	BG-Zemen	<i>C. mrkvickana</i>	mrkvickana	A	X		BEOU 30450	Bulgaria, Zemen	750
2	BG-Zemen	<i>C. mrkvickana</i>	mrkvickana			X	BEOU 40039	Bulgaria, Zemen	593
3	RS-Preševo	<i>C. versicolor</i>	versicolor	A	X	X	BEOU 40040	Serbia, Preševo	590
4	RS-Gotovuša	<i>C. versicolor</i>	versicolor	A	X		BEOU 33143	Serbia, Mts. Sharr, Gotovuša	1080
5	RS-Dušanov grad	<i>C. versicolor</i>	versicolor	A	X		BEOU 28087	Serbia, Prizren, Dušanov grad	500
6	RS-Prizren	<i>C. versicolor</i>	versicolor			X	BEOU 40190	Serbia, Prizren, Prizrenska Bistrica Canyon	582
7	AL-Mt. Gjallica	<i>C. versicolor</i>	versicolor	A	X		NHMR 1094	Albania, Mt. Gjallica	500
8	AL-Shija Gorge	<i>C. versicolor</i> subsp. <i>bicajensis</i>	bicajensis	A	X	X	BEOU 46507	Albania, Mt. Gjallica, Shija River Gorge	526
9	AL-Mt. Korab	<i>C. korabensis</i>	korabensis	A	X	X	BEOU 46501	Albania, Mt. Korab, Radmirë	1467

(Continues)



## Appendix 1. Continued.

No.	Locality code	Taxon	Informal name	G	S	M	Herbarium and voucher no.	Country and locality	Alt. (m)
10	AL-Kurbnesh	<i>C. versicolor</i>	versicolor	A	X		BEOU 42620	Albania, Lezhë, Kurbnesh	789
11	MK-Ostruga	<i>C. versicolor</i>	versicolor	A	X	X	BEOU 37599	North Macedonia, Mt. Skopska Crna Gora, Ostruga	1250
12	MK-Matka Canyon	<i>C. versicolor</i> subsp. <i>thessala</i> subvar. <i>lancifolia</i>	lancifolia	A	X	X	BEOU 37606	North Macedonia, Treska river, Matka Canyon	355
13	MK-Skopje	<i>C. versicolor</i>	versicolor			X	BEOU 37609	North Macedonia, Skopje, quarry Govrlevo	435
14	MK-Katlanovo	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 37605	North Macedonia, Katlanovo, Katlanovo spa	945
15	MK-Veles	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 37596	North Macedonia, Veles, Mladost Lake	250
16	MK-Kozjak Lake	<i>C. versicolor</i>	versicolor	A	X	X	BEOU 37601	North Macedonia, Kozjak Lake, Zdunje	530
17	MK-Radika Gorge	<i>C. versicolor</i>	versicolor			X	BEOU 40038	North Macedonia, Radika River Gorge	1309
18	MK-Radika Gorge	<i>C. versicolor</i>	versicolor	A	X		BEOU 33441	North Macedonia, Radika River Gorge	850
19	MK-Mt. Bistra	<i>C. versicolor</i>	versicolor	A	X		BEOU 30785	North Macedonia, Mt. Bistra, Galičnik	1450
20	MK-Mt. Bistra	<i>C. versicolor</i>	versicolor			X	BEOU 37602	North Macedonia, Mt. Bistra, Galičnik	1500
21	MK-Mt. Ilinska pl.	<i>C. versicolor</i>	versicolor	A	X		BEOU 29700	North Macedonia, Mt. Ilinska planina	1869
22	MK-Mt. Ilinska pl.	<i>C. versicolor</i>	versicolor			X	BEOU 40035	North Macedonia, Mt. Ilinska planina	1830
23	MK-Ohrid Lake	<i>C. versicolor</i>	versicolor	A	X		BEOU 27924	North Macedonia, Ohrid Lake, Peštani	700
24	MK-Ohrid Lake	<i>C. versicolor</i>	versicolor			X	BEOU 37575	North Macedonia, Ohrid Lake, Peštani	708
25	MK-Mt. Galičica	<i>C. versicolor</i>	versicolor	A	X		BEOU 37614	North Macedonia, Mt. Galičica	1750
26	MK-Demir Kapija	<i>C. plasonii</i>	plasonii	B1	X		BEOU 37593	North Macedonia, Demir Kapija	190
27	MK-Demir Kapija	<i>C. plasonii</i>	plasonii			X	BEOU 37593	North Macedonia, Demir Kapija	190
<i>C. versicolor</i> subsp. <i>versicolor</i>									
28	GR-Oros Askion	<i>C. versicolor</i>	versicolor	B1	X		BEOU 39009	Greece, Oros Askion	580
29	MK-Mt. Olympus	<i>C. versicolor</i> subsp. <i>tomentella</i>	tomentella	B1	X	X	BEOU 40042	Greece, Mt. Olympus, Prionia	680
30	MK-Prionia	<i>C. versicolor</i> subsp. <i>thessala</i>	thessala	B1	X	X	BEOU 40043	Greece, Mt. Olympus, Prionia	1077
31	GR-Tempi Gorge	<i>C. versicolor</i>	versicolor	B1	X		BEOU 28150	Greece, Pineios river, Tempi Gorge	50
32	GR-Tempi Gorge	<i>C. versicolor</i>	versicolor			X	BEOU 40044	Greece, Pineios river, Tempi Gorge	40
33	GR-Mt. Giona	<i>C. versicolor</i>	versicolor	B1	X		BEOU 28090	Greece, Mt. Giona, Gravia – Amfissa	850
34	GR-Mt. Parnassus	<i>C. versicolor</i>	versicolor	B1	X	X	BEOU 40045	Greece, Mt. Parnassus	1546
35	GR-Alonistaina	<i>C. versicolor</i>	versicolor	B1	X	X	BEOU 40052	Greece, Alonistaina	1160
36	GR-Parorio	<i>C. versicolor</i>	versicolor			X	BEOU 40051	Greece, Mt. Taygetus, Parorio	350
37	GR-Mt. Mavrovouni	<i>C. versicolor</i>	versicolor	B1	X		BEOU 40049	Greece, Mt. Mavrovouni	1700
38	GR-Lefkada	<i>C. versicolor</i>	versicolor	B1	X	X	BEOU 44458	Greece, Lefkada, Exanthia	602
39	GR-Mt. Tzoumerka	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 40055	Greece, Mt. Tzoumerka	1500
40	GR-Voreia	<i>C. versicolor</i>	versicolor			X	BEOU 40056	Greece, Mt. Tzoumerka, Voreia	840
41	GR-Ioannina	<i>C. versicolor</i>	versicolor			X	BEOU 40057	Greece, Ioannina	650
42	GR-Vikos Gorge	<i>C. versicolor</i>	versicolor	B1	X	X	BEOU 40058	Greece, Vikos Gorge, Kokkoros bridge	750
43	GR-Mt. Tymfi	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 40059	Greece, Mt. Tymfi, Mikro Papigo	970
44	GR-Corfu	<i>C. versicolor</i>	versicolor	B1	X		BEOU 44460	Greece, Corfu, Makrades	204
45	AL-Bistirca	<i>C. versicolor</i>	versicolor	B1	X	X	BEOU 40060	Albania, Bistirca	90
46	AL-Luzat	<i>C. longipetiolata</i>	longipetiolata	B2	X		BEOU 40061	Albania, Tepelenë, Luzat	220
47	AL-Tepelenë	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 40063	Albania, Tepelenë	200
48	AL-Vlorë	<i>C. versicolor</i>	versicolor	B2	X	X	BEOU 40066	Albania, Vlorë	20
<i>C. versicolor</i> subsp. <i>tenorei</i>									
49	IT-Matera	<i>C. tenorei</i>	tenorei	B2	X	X	BEOU 41745	Italy, Matera	347

(Continues)

## Appendix 1. Continued.

No.	Locality code	Taxon	Informal name	G	S	M	Herbarium and voucher no.	Country and locality	Alt. (m)
50	IT-Castellaneta	<i>C. tenorei</i>	tenorei	B2	X	X	BEOU 41741	Italy, Castellaneta	223
51	IT-Punta Palascia	<i>C. tenorei</i>	tenorei	B2	X	X	BEOU 41746	Italy, Punta Palascia	55
52	IT-Alessano	<i>C. tenorei</i>	tenorei	B2	X		ZA 30841	Italy, Alessano	9
53	IT-II Ciolo	<i>C. tenorei</i>	tenorei			X	BEOU 41748	Italy, Giuliano del Capo, Il Ciolo	26
54	IT-Leuca	<i>C. tenorei</i>	tenorei			X	BEOU 41749	Italy, Leuca, Santa Maria di Leuca	46
55	IT-Gallipoli	<i>C. tenorei</i>	tenorei	B2	X	X	BEOU 41750	Italy, Gallipoli, Conchiglie–Alto	10

## Appendix 2. Specimens examined in this study.

*Campanula versicolor* subsp. *versicolor*. **ALBANIA: Gjirokastër** — Dhëmbel (pers. obs., Lakušić, D. 2012); Gjirokastër (BEOU 31444); Mount Dhëmbel, saddle Dhëmbel (BEOU 32737); Poliçan (BEOU 42510); Tepelenë, Bence gorge (BEOU 34817, BEOU 40065); Tepelenë, Luzat (BEOU 40061); Tepelenë, rocks below fortress (BEOU 40064, ZAGR 39388); Tepelenë (BEOU 40063); Vjosa river, Këlcyrë gorge, between Këlcyrë and Dragot (pers. obs., Lakušić, D. 2012; BEOU 32837, BEOU 40062); **Korçë** — Mali i Thatë, Shëngjergj (BEOU 38307); Prespa Lake, Maligrad (BEOU 38751); **Sarandë** — Bistrica (BEOU 32621); Butrint (BM 001191859); Maja e Dhema, between Ksamil Pasqyra (W 2012-00847); **Vlorë** — Bistrica (pers. obs., Lakušić, D. 2012; BEOU 40060); Dukat (pers. obs., Lakušić, D. 2012); Palasë, below fortress (ZAGR 39389); Vlorë, Dukat i Ri (BEOU 32618); Vlorë (BEOU 31443, BEOU 32617, BEOU 40066). **GREECE: East Central** — Osa (BEOU 27739); **North Central** — Edessa, Edessa–Agras (BP 380965); Kalabaka, Grand Meteora (MNHN P04442298); Kalabaka, Meteora (W 11674); Kastoria, Kastoria Lake (SOM 135684); Kastoria (E 00616299); Kozani, Servia (W 9490); Mt. Olympus, Lithoro, Enipeas (W 2013-04281, E 00616290); Mt. Olympus, Lithoro, Mega Rema (AMD 44175, B 10-0365469, BEOU 22436, BEOU 22439, BEOU 22440, BM 001191866, BM 001191873, BP 142008, BP 389977, L 2997008, LD 1323599, LD 1330319, LD 1331519, LD 1367798, LD 1371473, LE 1017320, LE 1017324, MANCH, MNHN P00177996, MNHN P00177997, MNHN P00177998, MNHN P00177999, MNHN P00185840, MNHN P00185841, PH 0000426, PH 00025238, SOM 72821, SOM 72822, SOM 72824, SOM 75231, W 4240, W 9324, W 9325); Mt. Olympus, Lithoro (L 2997009, L 2997010, W 18988); Mt. Olympus, monastery of St. Dionysius, refuži Stavros (BEO, LD 1323539, LD 1380098, MNHN P00178000, SOM 72825, SOM 75230, W 01254, W 18987); Mt. Olympus, Prionia (BEOU 24729, BEOU 39010, BEOU 40041, BEOU 40042, BEOU 40043, BEOU 40044, BEOU 8045); Mt. Olympus (BP 389975, C, FI 050345, MNHN P00177995); Oros Askion, east of Namata (E 00616301); Oros Askion (BEOU 39009); Mts. Pindhos, Kalabaka, Meteora (SOM 165164); Pineios river, Tempi gorge, Rapsani (W 01148); Pineios river, Tempi gorge (BEOU 28150, BEOU 40044); Prespa Lake, Mikro Prespa (pers. obs., Lazarević, P. & al. 2017); **Ionian islands** — Kefalonia, Argostolion (BM 001191871, FI 050366); Kefalonia, Ainos (BEO); Kefalonia, Poros (E 00616296); Corfu, Ag. Dimitrios (C); Corfu, Lakones (BEOU 44460); Corfu, Makrades (BEOU 44461); Corfu, Pantocrators (W 2004-00954, W 2006-16339); Lefkada, Apolpena (BEOU 40054); Lefkada, Exanthia (BEOU 44458); Lefkada, Nydri, Nydri waterfall (BEOU 44459); Lefkada, from village Kalamitsi toward beach Kavalikefta, W exp. (BEOU 31441); Lefkada (BEOU 40053); **Southern Pindhos** — Mts. Acarnanian, monastery Romvos, between Gdyves and Flamboura summits (W 2008-20961); Klissoura gorge, Chrisobergion, Byzantine church Agia Eleousa (C); Mts. Pindhos, Agrafa, Karoplesi (BM 001191860, E 00616295); Sermeniko, Kokkino Lithari (E 00616291, LD 1374174, MANCH); Mt. Tomaros, Kopani (C); Mt. Tomaros (BM 001191864, FI 050367); Mt. Tzoumerka, Katafigi (BEOU 37023); Mt. Tzoumerka, Strungula (BEOU 32341); Mt. Tzoumerka, Vorea (BEOU 40056); Mt. Tzoumerka (BEOU 40055); **Peloponnese** — Alonistaina (BEOU 40052); Mt. Helmos, Kalavrita, from ski center to the summit (pers. obs., Lakušić, D. & al. 2017); Mt. Helmos, Krioneri, Zarouchla (C); Mt. Helmos (BM 001191867, MNHN P00185837, PI-GUAD); Mt. Kyllini, east of Ano Trikala; along the road towards the summit (pers. obs., Lakušić D. & al. 2017); Mt. Kyllini, Ano Trikala (C); Mt. Kyllini, Trikala (BEO, BM 001191861, BM 001191862, BM 001191872, BP 389971, FI 050362, MANCH, MNHN P00185838, W 62601); Langadia (BEOU 28142); Mt. Mainalo, Levadi, ski center (C); Mt. Mainalo, east of ski center (BEOU 46977); Mt. Mainalo, along the road towards the ski center (pers. obs., Lakušić D. & al. 2017); Mani, Cape Matapan, Porto Kagio (W 9494); Mt. Mavrovouni (BEOU 40049, BM 001191870, C, CGE 25027, FI 050360, LE 017321); Mt. Parnon, Polidroso, drinking fountain (BEOU 46983); Mt. Parnon (BP 142009, BP 389972, FI 050347, FI 050365, GE, LD 1320542, MANCH, MNHN P00185834, MNHN P00185835, MNHN P00185836, MNHN P04444771, W 2186); Mt. Taygetus, Parorio (BEOU 40051); Mt. Taygetus (BEOU 36868, BEOU 40050, BM 001191863, BM 001191869, COI 0054764, E 00616293, E 00616297, E 00616298, E 00616300, FI 050359, LE 1017322, MANCH, MNHN P00185825, MNHN P00185826, MNHN P00185839, NCY 004736, W 8160); Tripoli, Neochori (BEOU 40048); **Northern Pindhos** — Gliki, Aheron river, tunnel (pers. obs., Janković, I., Stevanoski, N. 2016); Ioannina, Mitsikeli (BEOU 39012); Ioannina, Konitsa (C); Ioannina (BEOU 40057); Mitsikeli, Kriovrisi (W 2007-16737); Mt. Tymfi, Astraka (W 9498); Mt. Tymfi, Mikro Papigo (BEOU 39011, BEOU 40059, L 3744198); Mt. Tymfi, Vikos, Kokkoros bridge (BEOU 40058); Mt. Tymfi, Vikos (BEOU 27894); **North East** — Mt. Panagaion Hills, Lofkes (C); **Sterea Ellas** — Chelidona, Palio Mikro Chorio (BP 389370, CGE 25028, GE, W 9852); Chelidona (MNHN P00185832, MNHN P00185833); Delphi, Castalian, Hyampeia (NCY 018637); Delphi, Castalian (NCY 018634, NCY 018635); Mt. Giona (BEOU 28090, BEOU 40047, BEOU 47093, NCY 018633, NCY 018636); Mt. Helicon, Palaeovouni (C); Mt. Helicon, Paliovouna, Koukoura (C); Levadia, Trophonios (U 1181190); Mt. Parnassus, between Amfissa and Karoute (C); Mt. Parnassus, Eptalofos (BEOU 40046); Mt. Parnassus, Gourma (C, FI 050348, L 2996997, MNHN P00185827, MNHN P00185828, MNHN P00185829, PI, W, W 19896); Mt. Parnassus, Langadha (C); Mt. Parnassus, at ski center (BEOU 27700); Mt. Parnassus (BEO, BEOU 31921, BEOU 40045, E 00616292, MNHN P00185824, MPU, U 1181191); Mts. Agrafa, south of the village Petralona, ESE of the peak Svoni, peak Pouli (C); Mts. Pindhos, Mt. Tymfristosi, Sympetherikon (BP 389370, FI 050346, MNHN P00185830, MNHN P00185831, W 17161); Prevezis, between Nikopoleos and Pargas, Kato Mirsini (C); Mt. Vardousia, Vustiniza (BM 001191868, MANCH, MNHN P00185843, MNHN P00185844, MNHN P00185845, MNHN P04444770, BP 142010). *Campanula versicolor* subsp. *korabensis*. **ALBANIA: Dibër** — Mt. Korab, Radomirë, Fuša i Korabit (BEOU 46501); Mt. Korab, Radomirë (pers. obs., Lakušić, D. & al. 2016); **Kukës** — Mt. Gjallica, between Lusen and Kolesjan (BEOU 46503); Mt. Gjallica, Shija river gorge, close to Bicaj (BEOU 46507, NHMR 1094); Mt. Koritnik, Vana-Tal (W 2008-02139); Mt. Paštrik, west side (W 14919); **Lezhë** — Kurbnesh (BEOU 42620). **BULGARIA: Kyustendil** — Mt. Konjevaska (BP 380964); Zemen, Zemen gorge (BEOU 40039, SOM 157675, SOM 75227, SOM 75228); Zemen, Zemenski prolom (BEOU 30450, BEOU 37646); Mt. Zemenska (SOM 102124, SOM 165495). **MACEDONIA: Southeastern region** — Rabrovo (BM 001191865); **Southwestern region** — Black Dri river gorge, Debar Lake, HE Globočica (HMMNH 3825); Black Dri river gorge, Debar Lake, HE Špilje (HMMNH 2235 ⇒ HMMNH 2239); Black Dri river gorge, Lukovo (BEO, BEOU 37573); Debar, between Debar and Izrovi (C); Mt. Galičica, Baba (BEOU 33464, BEOU 37579, BEOU 37614, BEOU 38237, BEOU 40037); Mt. Galičica, Gjura (HMMNH 6986, HMMNH 6987); Mt. Galičica, toward Tomoros (BEO); Mt. Galičica, Ljubaništa (BEOU 37577); Mt. Galičica,

(Continues)

## Appendix 2. Continued.

saddle (BEOU 21848, BEOU 40036); Mt. Galičica, old ski lift (BEOU 37620); Mt. Ilinska planina, village Golemo Ilino, summit Liska (BEOU 37582, BEOU 37611, HMMNH 7027, HMMNH 7043 ⇒ HMMNH 7045); Mt. Ilinska planina, village Golemo Ilino (BEOU 29700, BEOU 40035); Mt. Ilinska planina, Železnec (BEOU 37610); Makedonski Brod, Pešnica river gorge, at the cave (BEOU 38464); Mt. Momina čuka (BRNM 13254/36, BRNM 13261/36); Ohrid Lake, Peštani (BEOU 27924, BEOU 37574, BEOU 37575); Poreče, Breznica (BEO); Stogovo, Gari, above village (HMMNH 2234); Suhu Dol, Kičevo (BEO); Treska river, Kozjak Lake, Zdunje (BEOU 30005, BEOU 37601); Treska river, Poreče, Kapina (BEO); Treska river, Poreče, Selišta (BEO); **Pelagonia** — Kičevo (BEOU 22437); Prespa Lake, Oteševo (BEOU 37623, BEOU 46665); Prespa Lake, Oteševo–Carina (BEOU 46666); Prespansko jezero, Stenje (BEOU 46667, BRNM 13255/36, HMMNH 6985); **Polog Region** — Mt. Bistra, Galičnik, between Janče and Galičnik (BEOU 37569, BEOU 37570); Mt. Bistra, Galičnik (BEOU 30785, BEOU 37602); Mt. Bistra, summit Maskarovec (HMMNH 2240 ⇒ HMMNH 2251); Radika river gorge, Adžina reka (BEOU 40038); Radika river gorge, between Debar and Mavrovi anovi, crossroad for Nichpur (C); Radika river, Barič gorge (BEOU 33441, BEOU 33442, BEOU 37567); Radika river, Rec gorge (BEOU 33459, BEOU 37566); Radika river, Sence (BEOU 33439, BEOU 33440, BEOU 37568); **Northeastern region** — Kumanovo, village Pčinja (BEOU 37598, BEOU 38516); **Skopje** — Katlanovo, Katlanovo spa (BEOU 37605, HMMNH 2843 ⇒ HMMNH 2865); Katlanovo, Kožle, Prnar (BEO); Katlanovo, Kožle (BEOU 37604, HMMNH 2866 ⇒ HMMNH 2893); Mts. Sharr, Kobilica (BP 389973, BP 389974); Mts. Sharr, Raduša (BEO); Skopje, quarry Govrlevo (BEOU 37609); Mt. Skopska Crna Gora, Banjani, monastery of St. Ilija (BEOU 37600, HMMNH 2106 ⇒ HMMNH 7026); Mt. Skopska Crna Gora, Ostruga (BEOU 37599); Treska, HE Matka (BEO, BEOU 27448, HMMNH 2225 ⇒ HMMNH 2229, HMMNH 2947, HMMNH 2950 ⇒ HMMNH 2970, HMMNH 4413 ⇒ HMMNH 7024, HMMNH 7028 ⇒ HMMNH 7042); Treska river, monastery of St. Nikola Šiševski (BEO); Treska river, Matka canyon, monastery of the Holy Mother of God (BEO, HMMNH 2898 ⇒ HMMNH 2921, HMMNH 2947 ⇒ HMMNH 2949, HMMNH 2966); Treska river, Matka canyon (BEOU 37606); Treska river (JE 00007087); **Vardar** — Demir Kapija, Beli Kamen (BEO); Demir Kapija, Kadovo gorge (BEOU 25040); Demir Kapija (BEO, BEOU 33715, BEOU 37593, E 00113261, W 1995-06892); Drenovo gorge, between Kvardarci and Prilep, Raec (BEOU 30306, BEOU 37591); Mt. Flora (BRNM 13256/36, BRNM 13258/36); Mt. Klepa (pers. obs., Zlatković, B. 2018); Mt. Kožuf, Dudica (BRNM 13260/36); Mt. Kožuf, Pržigrad (BRNM 13259/36); Veles, Babuna river, Pešti gorge (HMMNH 2230 ⇒ HMMNH 2233); Veles, Babuna river gorge (BEO, BEOU 37594, BEOU 38590); Veles, Mladost Lake (BEOU 37596, BEOU); Veles, Navičanska reka (BEO); Veles, Topolka river (BEOU 22438, BEOU 37595); Veles, Vardar river gorge, close to railroad station “Pčinja” (HMMNH 2210, HMMNH 2211); Veles, Veles, Vardar river gorge (BEOU 25035, SOA 18768); Veles (BEOU 27450, BEOU 27451). **SERBIA: South** — Preševo (BEO, BEOU 40040, BEOU 40192); **Kosovo** — White Drin river canyon, Našec (BEOU 1855); Mt. Kodža Balkan (BEOU 2545); Prizren, Duvska Klisura gorge (BEOU 2581); Prizren, Prizrenska Bistrica river (BEOU 40190); Prizren, Prizrenska Bistrica river gorge, Dušanov Grad (BEOU 24520, BEOU 28087); Prizren, Prizrenska Bistrica river gorge, Kaljaja (BEO); Prizren, Prizrenska Bistrica river gorge (BEOU 2893); Prizren, Sinan Pasha mosque (BEOU 31446); Mt. Sharr, Brod selo – Gradski kamen (BEOU 2316/91); Mt. Sharr, Drven grad (BEO); Mt. Sharr, Globočki kamen (BEOU 22710); Mt. Sharr, village Gotovuša (BEOU 33143); Mt. Sharr, Gotovuška river gorge (BEOU 7792); Mt. Sharr, Kokošnje, Ljuboten (slopes toward village Gotovuša) (BEOU 7826); Mt. Sharr, Kule, towards Lešačka Bistrica river valley (BEOU 1308/92); Mt. Sharr, Tumba peak (BEOU 7811). **Campanula versicolor** subsp. **tenorei**. **ITALIA: Apulia** — Brindisi (K 00814350); Castellana (BEOU 41741); Gallipoli, Conchiglie-Alto, Montagna Spaccata (BEOU 41750, FI 050351); Gallipoli, Madonna Dell’Alto Mare (BM 001191882); Gallipoli, Rupì di San Mauro (BM 001191882); Gallipoli (RO); Guliano del Capo, Il Ciolo (BEOU 41748); Laterza, gravina di Laterza (BEOU 41739, BEOU 41740); Leuca, Santa Maria di Leuca (BEOU 41749, PignS982: 692); Marina Serra (BEOU 41747); Massafra, gravina della Madonna della Scala (BEOU 41751); Mottola, gravina di Petruscio (BEOU 41743); Otranto (FI 050364); Palagianello, gravina San Biagio (BEOU 41742); Porto Miggiano, Santa Cesarea Terme (pers. obs., Vydrova, A., Grulich, V. 2014); Punta Palascia (BEOU 41746, BM 001191874, BM 001191875, BM 001191876, BM 001191877, BM 001191878, BM 001191879, BM 001191880, BM 001191881, BM 001191883, BM 001191885, BP 380969, E 00616303, FI 050352, FI 050353, FI 050354, GE, MNHN P00185822, PI-GUAD, RO); Taranto, Murgie di Leucaspidi (K 00814351); Palagianello, Gravina di Palagianello (RO). **Basilicata** — Matera, gravina di Matera (BEOU 41744), Matera (BEOU 41745, FI 050356, FI 050357, FI 050358, RO).

**Appendix 3.** Descriptive statistics of morphological characters of *Campanula versicolor* s.l. (Max = maximum value; Min = minimum value; Std. Dev. = standard deviation; CV = coefficient of variation).

Character code	Character	Min (mm)	Mean (mm)	Max (mm)	Std. Dev.	CV (%)
Corolla						
Co-H	Length	9.4	15.2	26.2	3.0	19.8
Co-De	Depth	3.5	6.0	10.1	1.4	23.4
CoL-H	Corolla lobe length	5.5	10.1	17.8	2.2	21.5
CoL-h	Distance from maximal width of the lobe base to the corolla base	3.4	6.0	11.0	1.5	24.9
CoL-W	Width of the corolla lobe base	4.7	7.0	10.9	1.2	17.5
CoL-Wm	Maximal width of the corolla lobe	4.6	7.3	11.7	1.3	17.8
Co-Per	Base perimeter	4.6	10.3	16.7	2.0	19.6
Co-Di	Height of connate part	2.6	5.1	9.7	1.4	26.5
Calyx						
CaD-W	Width of the teeth base	1.1	1.9	3.0	0.4	19.9
CaD-L	Teeth length	2.6	6.5	13.3	2.0	30.4
Ca-H	Height	1.5	2.5	4.3	0.4	16.6
CaPe-L	Pedicel length	0.2	2.9	13.6	1.7	59.0

(Continues)



## Appendix 3. Continued.

Character code	Character	Min (mm)	Mean (mm)	Max (mm)	Std. Dev.	CV (%)
Pistil						
Pi-L	Length	8.7	15.4	22.8	3.1	20.4
Pi-Sy	Style length	3.6	7.1	10.8	1.4	20.2
Pi-St	Length of hairy part of pistil	4.2	8.3	13.1	2.0	23.8
Stamen						
StB-H	Base height	1.8	3.2	5.0	0.7	21.0
StF-L	Filament length	0.7	1.7	3.5	0.4	25.4
StA-L	Anther length	3.1	6.3	10.5	1.5	23.4
StB-W	Width of the base	1.3	2.1	3.4	0.4	18.2
StB-Wm	Maximal width of the base	1.6	2.5	3.8	0.5	18.5
StB-h	Distance from maximal width to the base	0.5	1.0	2.1	0.3	27.1
StB-Ar	Base area	2.2	5.8	14.7	2.2	38.9
StB-Pe	Base perimeter	5.7	9.1	14.5	1.7	19.1
Habitus						
Pl-H	Height of the plant	78.0	478.9	1220.0	210.0	43.8
Inf-L	Inflorescence length	30.0	195.7	760.9	129.4	66.1
Stem-H	Stem height	23.0	287.8	1070.0	155.0	53.9
Basal leaf (Fb)						
Fb-Lm	Lamina length	20.4	58.3	133.3	20.4	35.1
Fb-Wm	Width of left side	3.8	13.5	36.0	4.8	35.3
Fb-L	Distance from maximal width to the base of the lamina	5.3	17.8	44.0	7.5	41.9
FbPe-L	Petiole length	5.6	51.7	149.7	28.7	55.6
FbPe-Wb	Petiole base width	0.5	4.1	7.9	1.1	27.0
FbPe-W	Petiole width	0.5	2.1	4.6	0.6	29.4
Fb-Ar	Lamina area	134.3	1172.1	6119.6	817.9	69.8
Fb-Pe	Lamina perimeter	53.7	139.4	327.1	46.8	33.6
Middle leaf (Fm)						
Fm-Lm	Lamina length	13.1	44.1	113.9	15.0	33.9
Fm-Wm	Width of left side	2.7	10.6	26.0	3.9	36.8
Fm-L	Distance from maximal width to the base of the lamina	4.2	15.2	45.1	5.7	37.2
FmPe-L	Petiole length	0.8	17.7	100.6	12.3	69.4
FmPe-Wb	Petiole base width	0.4	3.5	6.3	0.9	25.0
FmPe-W	Petiole width	0.8	2.3	4.6	0.6	28.6
Fm-Ar	Lamina area	52.5	684.5	2805.8	462.4	67.6
Fm-Pe	Lamina perimeter	30.5	104.7	245.3	34.7	33.2
Upper leaf (Fu)						
Fu-Lm	Lamina length	7.7	29.2	73.3	10.7	36.8
Fu-Wm	Width of left side	1.6	6.4	16.5	2.7	41.6
Fu-L	Distance from maximal width to the base of the lamina	2.0	11.2	36.7	4.6	41.3
FuPe-L	Petiole length	0.0	5.1	40.0	4.3	85.1
FuPe-Wb	Petiole base width	0.0	2.7	5.7	1.1	42.6
FuPe-W	Petiole width	0.0	2.1	4.6	0.9	43.8
Fu-Ar	Lamina area	17.4	276.5	1678.2	216.4	78.3
Fu-Pe	Lamina perimeter	18.4	67.6	166.8	24.3	35.9

**Appendix 4.**  $F_{ST}$  values between all pairs of 41 × 21 (**Table A**) and 41 × 20 (**Table B**) populations of *Campanula versicolor* s.l. (lower diagonal) with pairwise significance after sequential Bonferroni corrections (upper diagonal). No. = population numbering; ns = non-significant value; \* = significant at  $P < 0.05$ ; \*\* = significant at  $P < 0.01$ ; \*\*\* = significant at  $P < 0.001$ . Population numbering and details are listed in Appendix 1.

**Table A.**

No.	1	3	4	5	7	8	9	10	11	12	14	15	16	18	19	21	23	25	26	28	29	
1	**																					
3	0.652	**			*	**	**	**	**	**	**	**	*	**	ns	**	**	**	**	**	**	*
4	0.587	0.477	**		ns	**	**	**	**	**	**	**	ns	**	ns	**	**	**	**	**	*	ns
5	0.536	0.328	0.281	**	ns	**	**	**	*	**	**	*	ns	**	ns	*	**	**	*	**	*	ns
7	0.543	0.392	0.212	0.148	ns	ns	**	**	*	**	**	*	ns	*	ns	ns	*	ns	*	ns	*	ns
8	0.559	0.465	0.256	0.253	0.133	**	**	**	**	**	**	**	**	**	ns	**	**	**	**	**	**	**
9	0.520	0.351	0.329	0.187	0.179	0.236	**	**	**	**	**	**	**	**	ns	**	**	**	**	**	**	**
10	0.519	0.409	0.251	0.263	0.179	0.181	0.185	**	**	**	**	**	**	**	ns	**	**	**	**	**	**	**
11	0.568	0.505	0.431	0.394	0.359	0.419	0.364	0.376	**	**	**	**	**	**	ns	**	**	**	**	**	**	**
12	0.422	0.328	0.260	0.195	0.141	0.235	0.176	0.193	0.281	**	**	**	*	**	ns	**	**	**	**	**	**	**
14	0.583	0.417	0.402	0.376	0.317	0.423	0.302	0.340	0.430	0.165	**	**	**	**	ns	**	**	**	**	**	**	**
15	0.609	0.440	0.416	0.324	0.307	0.400	0.277	0.348	0.409	0.174	0.172	**	**	**	ns	**	**	**	**	**	**	**
16	0.471	0.327	0.233	0.217	0.184	0.258	0.246	0.210	0.335	0.085	0.274	0.266	**	**	ns	*	**	**	**	**	*	ns
18	0.491	0.354	0.209	0.207	0.141	0.164	0.141	0.136	0.276	0.165	0.319	0.298	0.208	0.208	ns	**	**	**	**	**	**	**
19	0.598	0.421	0.212	0.184	0.043	0.113	0.113	0.084	0.391	0.154	0.353	0.355	0.210	0.074	0.074	ns	ns	ns	ns	ns	ns	ns
21	0.669	0.472	0.469	0.399	0.367	0.419	0.354	0.411	0.475	0.213	0.391	0.407	0.280	0.357	0.427	**	**	**	**	**	**	**
23	0.644	0.460	0.423	0.354	0.288	0.361	0.335	0.307	0.451	0.175	0.276	0.323	0.291	0.270	0.348	0.380	**	ns	**	**	**	**
25	0.534	0.379	0.335	0.229	0.150	0.251	0.205	0.201	0.314	0.102	0.231	0.245	0.206	0.178	0.192	0.283	0.042	ns	**	**	**	**
26	0.594	0.533	0.494	0.408	0.398	0.487	0.405	0.441	0.444	0.329	0.452	0.441	0.353	0.398	0.456	0.541	0.487	0.382	**	**	**	**
28	0.604	0.444	0.402	0.359	0.364	0.451	0.397	0.387	0.438	0.240	0.374	0.385	0.199	0.354	0.399	0.474	0.452	0.367	0.328	**	**	*
29	0.491	0.413	0.333	0.279	0.244	0.334	0.291	0.279	0.332	0.151	0.289	0.252	0.177	0.251	0.269	0.416	0.365	0.267	0.287	0.240	**	**
30	0.500	0.429	0.405	0.352	0.314	0.405	0.350	0.310	0.345	0.229	0.315	0.276	0.244	0.334	0.353	0.453	0.390	0.305	0.291	0.252	0.089	**
31	0.360	0.361	0.289	0.289	0.252	0.323	0.288	0.241	0.280	0.180	0.306	0.305	0.148	0.225	0.252	0.376	0.356	0.279	0.350	0.234	0.127	**
33	0.517	0.338	0.330	0.224	0.264	0.355	0.301	0.292	0.315	0.183	0.251	0.258	0.177	0.253	0.288	0.399	0.360	0.271	0.350	0.244	0.133	**
34	0.458	0.388	0.323	0.281	0.267	0.339	0.314	0.298	0.333	0.190	0.276	0.252	0.182	0.268	0.284	0.395	0.358	0.287	0.304	0.270	0.110	**
35	0.493	0.392	0.361	0.292	0.300	0.373	0.320	0.327	0.375	0.205	0.284	0.279	0.248	0.295	0.304	0.398	0.370	0.306	0.322	0.277	0.146	**
37	0.488	0.383	0.325	0.263	0.280	0.342	0.293	0.298	0.349	0.190	0.284	0.250	0.194	0.269	0.298	0.399	0.374	0.306	0.344	0.256	0.125	**
38	0.419	0.388	0.263	0.245	0.211	0.286	0.279	0.286	0.294	0.164	0.308	0.278	0.156	0.233	0.229	0.366	0.335	0.265	0.312	0.270	0.113	**
39	0.507	0.402	0.344	0.313	0.322	0.389	0.322	0.310	0.394	0.240	0.299	0.276	0.254	0.295	0.337	0.443	0.408	0.351	0.406	0.322	0.130	**
42	0.469	0.315	0.366	0.277	0.298	0.373	0.275	0.281	0.326	0.225	0.297	0.250	0.234	0.251	0.301	0.426	0.382	0.305	0.387	0.313	0.177	**
43	0.602	0.407	0.443	0.372	0.391	0.445	0.341	0.408	0.473	0.225	0.313	0.251	0.307	0.350	0.407	0.465	0.435	0.373	0.493	0.423	0.232	**
44	0.400	0.330	0.241	0.206	0.177	0.273	0.213	0.216	0.262	0.129	0.253	0.201	0.118	0.168	0.196	0.341	0.306	0.220	0.282	0.191	0.081	**
45	0.534	0.429	0.368	0.333	0.309	0.344	0.298	0.298	0.404	0.224	0.360	0.321	0.243	0.292	0.293	0.450	0.433	0.345	0.388	0.320	0.139	**

(Continues)

Appendix 4. Continued.

**Table A.**

No.	1	3	4	5	7	8	9	10	11	12	14	15	16	18	19	21	23	25	26	28	29
46	0.498	0.312	0.304	0.257	0.259	0.345	0.245	0.287	0.299	0.150	0.193	0.147	0.181	0.234	0.277	0.354	0.323	0.250	0.337	0.233	0.125
47	0.563	0.420	0.407	0.322	0.325	0.420	0.344	0.376	0.408	0.242	0.314	0.252	0.297	0.336	0.373	0.463	0.410	0.342	0.424	0.368	0.134
48	0.484	0.357	0.318	0.280	0.226	0.358	0.310	0.304	0.367	0.211	0.240	0.227	0.218	0.282	0.301	0.411	0.336	0.269	0.277	0.248	0.101
49	0.736	0.555	0.577	0.516	0.514	0.566	0.489	0.486	0.589	0.363	0.336	0.342	0.450	0.497	0.560	0.601	0.500	0.417	0.521	0.516	0.311
50	0.685	0.529	0.546	0.468	0.472	0.540	0.455	0.467	0.547	0.344	0.282	0.337	0.433	0.458	0.518	0.555	0.458	0.397	0.518	0.509	0.315
51	0.573	0.458	0.418	0.364	0.364	0.431	0.353	0.378	0.440	0.279	0.297	0.315	0.319	0.336	0.385	0.489	0.462	0.376	0.437	0.359	0.186
52	0.631	0.513	0.427	0.408	0.380	0.469	0.354	0.417	0.497	0.286	0.249	0.299	0.367	0.360	0.416	0.516	0.483	0.410	0.483	0.416	0.289
55	0.718	0.579	0.545	0.513	0.488	0.536	0.413	0.440	0.557	0.315	0.352	0.317	0.431	0.432	0.502	0.567	0.508	0.426	0.500	0.462	0.310

**Table B.**

No.	30	31	33	34	35	37	38	39	42	43	44	45	46	47	48	49	50	51	52	55	
1	**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
3	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
4	**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
5	**	*	ns	**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
7	**	ns	ns	**	**	**	*	**	**	**	**	*	**	**	**	*	**	**	**	*	**
8	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
9	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
10	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
11	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
12	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
14	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
15	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
16	**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
18	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
19	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
21	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
23	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
25	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
26	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
28	**	**	*	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
29	**	**	*	**	**	**	**	**	**	**	ns	**	**	**	**	**	**	**	**	**	**
30	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
31	0.181	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
33	0.198	0.172	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**

(Continues)



Appendix 4. Continued.

**Table B.**

No.	30	31	33	34	35	37	38	39	42	43	44	45	46	47	48	49	50	51	52	55
34	0.171	0.158	0.09		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
35	0.19	0.201	0.132	0.096		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
37	0.19	0.168	0.11	0.08	0.077		**	**	**	**	**	**	**	**	**	**	**	**	**	**
38	0.215	0.158	0.159	0.127	0.141	0.119		**	**	**	**	**	**	**	**	**	**	**	**	**
39	0.238	0.243	0.19	0.2	0.212	0.158	0.216		**	**	**	**	**	**	**	**	**	**	**	**
42	0.195	0.193	0.197	0.194	0.204	0.173	0.217	0.187		**	**	**	**	**	**	**	**	**	**	**
43	0.32	0.331	0.282	0.248	0.24	0.222	0.246	0.247	0.258		**	**	**	**	**	**	**	**	**	**
44	0.126	0.116	0.131	0.128	0.152	0.11	0.119	0.176	0.114	0.221		**	**	**	**	**	**	**	**	**
45	0.222	0.218	0.203	0.185	0.125	0.123	0.167	0.214	0.223	0.254	0.101		**	**	**	**	**	**	**	**
46	0.171	0.202	0.151	0.153	0.157	0.141	0.175	0.158	0.161	0.155	0.1	0.184		**	**	**	**	**	**	**
47	0.24	0.3	0.203	0.222	0.215	0.152	0.233	0.129	0.227	0.218	0.171	0.211	0.125		**	**	**	**	**	**
48	0.146	0.226	0.145	0.161	0.171	0.168	0.193	0.151	0.199	0.251	0.118	0.196	0.135	0.137		**	**	**	**	**
49	0.299	0.428	0.31	0.281	0.282	0.282	0.38	0.302	0.359	0.361	0.315	0.371	0.256	0.291	0.191		**	**	**	**
50	0.356	0.431	0.26	0.332	0.317	0.316	0.374	0.282	0.351	0.375	0.338	0.408	0.285	0.267	0.22	0.226		**	**	**
51	0.278	0.272	0.151	0.204	0.256	0.225	0.243	0.237	0.276	0.338	0.223	0.298	0.211	0.243	0.205	0.347	0.297		**	**
52	0.341	0.37	0.248	0.288	0.308	0.288	0.328	0.249	0.327	0.334	0.264	0.364	0.239	0.282	0.231	0.425	0.288	0.204		**
55	0.3	0.407	0.329	0.306	0.315	0.295	0.398	0.295	0.375	0.364	0.304	0.359	0.264	0.326	0.269	0.323	0.336	0.347	0.307	