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A new subspecies of *Teucrium montanum* (Lamiaceae) from northern Albania

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Abstract

Morphological and anatomical variation within *Teucrium montanum* was examined in 322 individuals from 33 populations, representing the two currently accepted subspecies, subsp. *montanum* and subsp. *helianthemoides*, as well as three populations of a morphologically distinctive group from northern Albania. A total of twenty-two morphological and twenty-three anatomical quantitative characters were analysed using univariate and multivariate methods, and a further analysis was conducted of the qualitative traits of habitus, indumentum and corolla colour. Selected individuals were cultivated ex situ under uniform conditions to assess the stability of diagnostic traits. The multivariate analyses consistently revealed that the Albanian populations were clearly differentiated from both recognised subspecies. They were characterised by an ascending shrub habitus, elongate, linear-lanceolate leaves with a hook-shaped tip, more than 25 idioblasts (oil cells) per leaf cross-section, and a completely white lower corolla lip. These diagnostic characters remained stable under cultivation. On the basis of the congruent morphological and anatomical differentiation, the Albanian plants, endemic to ultramafic substrates of the Prokletije Mountains around Shkodër, are described as a new subspecies, *Teucrium montanum* subsp. *skadarensis* subsp. nov. A key to the subspecies of *T. montanum* is provided.

Keywords: endemism, taxonomy, sect. *Polium*, mountain germander, Balkan peninsula, multivariate statistics

Introduction

With more than 250 species, *Teucrium* is the second largest genus in the subfamily Ajugoideae (Navaro 2020, Stanković 2020) and is widely regarded as one of its most taxonomically challenging groups (Salmaki *et al.* 2016). *Teucrium montanum* Linnaeus (1753: 565) is an evergreen, semi-ligneous dwarf shrub distributed throughout southern and central Europe and Asia Minor, extending to Algeria in North Africa (Tutin & Wood 1972, POWO 2026). Across this range, *T. montanum* exhibits remarkably broad ecological amplitude, occurring in grasslands, rocky and stony slopes, cliff crevices, screes, garrigues, and both deciduous and coniferous woodlands (Zbiljić *et al.* 2023). It grows on calcareous, siliceous and ultramafic bedrock (Lakušić & Lakušić 2014, Zbiljić *et al.* 2023), from sea level (Perrino & Wagensommer 2012) up to the subalpine and alpine belts (Lakušić & Lakušić 2014, Stinca *et al.* 2019, Zbiljić *et al.* 2023). Such extensive habitat tolerance is generally regarded as the main driver of the pronounced morphological plasticity and variability for which the species is well known (Zlatić *et al.* 2023, Zbiljić *et al.* 2023).

On the Balkan Peninsula, this variability is manifested in seven morphological groups (hereafter referred as MGs), which can be consistently distinguished using a combination of quantitative and qualitative morphological traits (Zbiljić *et al.* 2023). A subsequent AFLP-based genetic survey of the Balkan populations revealed that the inferred genetic clusters corresponded only partially to the recognised MGs, indicating that the observed genetic diversification incompletely reflects the morphological diversification of the complex (Zbiljić *et al.* 2024). This incongruence has been attributed to weak reproductive barriers within *T. montanum* s.l., a taxon which is known to hybridise with related

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species of *Teucrium* sect. *Polium*, and this phenomenon is now well documented (Zbiljić *et al.* 2021, Varga *et al.* 2024, Lakušić *et al.* 2024). Such weak reproductive isolation is evident not only between otherwise well-differentiated species, but also among MGs whose ranges came into secondary contacts during the complex geological history of the Balkan Peninsula. Consequently, genetic differences among these groups have become blurred, shaping the genetic structure currently observed within the complex (Zbiljić *et al.* 2024).

Despite its remarkable variability, only two subspecies are currently accepted: subsp. *helianthemoides* (Adamović) Baden (1991: 74), restricted to the Scardo–Pindus mountain system in North Macedonia and Greece, and the typical subsp. *montanum*, which occurs throughout the species' range (Baden 1991, Zbiljić *et al.* 2023).

Among the recognised MGs, "skadarensis" stands out as a particularly well differentiated group, clearly separated from the remaining groups by both quantitative and qualitative morphological characters (Zbiljić *et al.* 2023). However, it has not yet been directly compared with western European populations of *T. montanum* subsp. *montanum*, which correspond to the typical material indicated in the protologue by Linnaeus (1753). In addition, the previous morphometric analyses were based on only one population of the "skadarensis" MG, providing an insufficient basis for assessing the overall variability of this group and for proposing a revised taxonomic treatment.

To address these gaps, the present study aimed to: (1) compare the two currently accepted subspecies of *T. montanum* with several newly collected populations of the "skadarensis" MG, (2) identify the morphological characters most relevant for the morphological diversification of these groups, and (3) propose a revised taxonomic concept within *T. montanum* s.l.

Material & methods

Material

A total of 322 individuals from 33 populations were included in the present study, comprising 24 populations of subsp. *montanum*, six populations of subsp. *helianthemoides*, and three populations representing the "skadarensis" MG (Table 1, Figure 1). The sampling comprised typical populations of subsp. *montanum* from Germany (Linnaeus 1753: 565), together with the typical population of subsp. *helianthemoides* from Mount Olympus, Greece (Adamović 1904: 136). Between eight and 21 individuals were sampled per population for morphometric analysis, and two to ten additional specimens were selected as vouchers and deposited in the Herbarium of the Institute of Botany and Botanical Garden, Faculty of Biology, University of Belgrade (BEOU). Individuals for morphometric analyses were fixed in a mixture of glycerol and 50% ethanol (1:1).

Morphological analyses

All anatomical and morphological quantitative measurements were performed following the protocol described in Zbiljić *et al.* (2023). For anatomical analysis, permanent leaf slides were prepared according to the standard light microscopy methodology described in Lakušić *et al.* (2010). Transverse leaf sections, 26 µm and 65 µm thick, were cut with a Reichert sliding microtome, cleared, stained with safranin and alcian blue, and mounted in Canada balsam. The sections were imaged with an Olympus BX-41 trinocular microscope fitted with an Olympus SC30 camera. A total of 23 anatomical characters were measured, nine on the 65 µm sections and fourteen on the 26 µm sections. For morphological analysis, two leaves, five bracts, one stem and two calyces were dissected per individual, and were mounted on graphoscope foil and scanned at high resolution. Measurements were obtained using Digimizer Image analysis software (MedCalc Software 2005–2011). The percentage of yellow in the corolla (%_yellow) was obtained by analysis of photographs of the plants from their natural habitats according to the protocol described by Zbiljić *et al.* (2023) and Zbiljić (2023). In total, 22 morphometric characters were measured, comprising 20 quantitative traits and two derived ratios. All measured characters with acronyms are listed in Table 2.

For the qualitative morphological traits, habitus characteristics and indumentum types were evaluated. Habitus characteristics were evaluated by analysing plants in their natural habitats. All plants analysed were assigned to one of the two morphological habitus states (decumbent subshrub or ascending shrub) previously defined in Zbiljić *et al.* (2023). Indumentum types were evaluated by analysing the surfaces of leaves, stems and calyces using an SZ61 stereomicroscope. All individuals analysed were assigned to one of the three indumentum states (glabratum, pubescent, lanato-tomentose), which had been previously defined in Zbiljić *et al.* (2023).

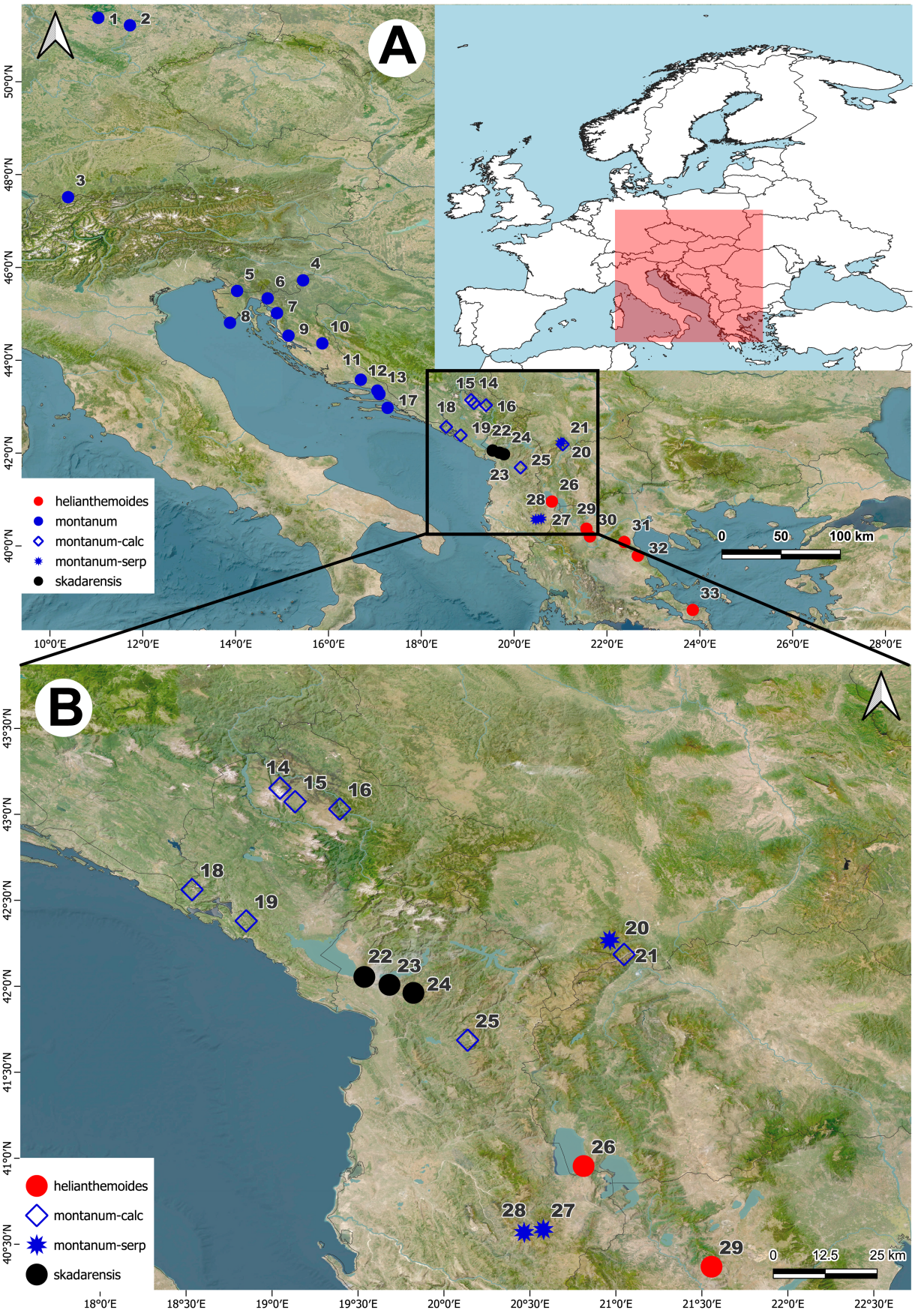


FIGURE 1. Sampled populations analysed in this study. A—All populations, B—populations analysed at the second level of statistical analysis. Population numbers correspond to Table 1.

TABLE 1. Populations analysed in this study. Populations marked with an exclamation mark were included in the multivariate analysis at first level; populations marked with an asterisk were included in the multivariate analysis at the second level. Two-letter country codes defined by the ISO 3166-1 alpha-2 standard. Abbreviations: LAT—latitude; LONG—longitude; mont—subsp. *montanum*, calc—calcareous substrate, serp—serpentinite substrate, skad—morphological group "skadarensis", hel—subsp. *helianthemoides*.

No.	Country	Locality	LAT	LONG	Group	Voucher number
1	DE	Barbarossahöhle !	51.376	11.039	mont	72404
2	DE	Freyburg !	51.215	11.721	mont	72403
3	DE	Bad Oberdorf !	47.512	10.388	mont	72405
4	HR	Žumberak !	45.720	15.452	mont	54019
5	HR	Vodice !	45.492	14.029	mont	54021
6	HR	Fužine !	45.331	14.689	mont	54020
7	HR	Senj !	45.015	14.889	mont	54023
8	HR	Istra !	44.805	13.877	mont	54022
9	HR	Velebit !	44.528	15.137	mont	54024
10	HR	Gračac !	44.362	15.867	mont	54025
11	HR	Trilj !	43.579	16.695	mont	54027
12	HR	Biokovo !	43.344	17.052	mont	54030
13	HR	Biokovo !	43.271	17.097	mont	54031
14	ME	Durmitor, Inđini dolovi *	43.142	19.072	mont-calc	54015
15	ME	Durmitor, Vražja glava *	43.073	19.134	mont-calc	54016
16	ME	Dobrilovina *	43.030	19.394	mont-calc	54014
17	HR	Pelješac !	42.973	17.273	mont	54032
18	ME	Orjen *	42.562	18.534	mont-calc	54017
19	ME	Lovćen *	42.379	18.849	mont-calc	54018
20	RS	Štrbce *	42.228	21.008	mont-serp	54040
21	RS	Brezovica *	42.185	21.048	mont-calc	54039
22	AL	Shkodër ! *	42.054	19.537	skad	72688
23	AL	Maja Boks ! *	42.008	19.683	skad	46619
24	AL	Gomsiqe ! *	41.973	19.781	skad	72687
25	AL	Deja *	41.686	20.138	mont-calc	47262
26	MK	Galičica !	40.954	20.812	hel	54036
27	AL	Gjergjevicë *	40.584	20.578	mont-serp	54037
28	AL	Mali i Ostrovicë *	40.567	20.466	mont-serp	54038
29	GR	Askion !	40.368	21.556	hel	67659
30	GR	Vourinos !	40.203	21.633	hel	67660
31	GR	Olympus !	40.082	22.373	hel	67668
32	GR	Ossa !	39.786	22.664	hel	46622
33	GR	Evia, Dirfi !	38.618	23.848	hel	69457

To test whether plants retain their characteristic morphology, several individuals from each group (subsp. *montanum*, subsp. *helianthemoides* and MG "skadarensis") from several populations were transferred to be cultivated under the same conditions in a private garden in Belgrade. All transplanted individuals were first potted together with soil collected from their native localities and subsequently planted under the same climatic conditions.

TABLE 2. All characters with their acronyms used in this study, with Shapiro–Wilk normality and Kruskal–Wallis (KW) tests performed at two levels. Abbreviations: KW H—H statistic; KW p—p value; I—univariate statistic performed at the first level; II—univariate statistic performed at the second level.

No	Characters	Acronym	Shapiro Wilk	KW H I	KW *p* I	KW H II	KW *p* II
1	Central nerve	R_CN	0.00	**30.01**	**0.00**	**16.34**	**0.00**
2	Leaf centre curvature	R_LC	0.83	**43.43**	**0.00**	**7.90**	**0.02**
3	Leaf curvature	R_L_Curv	0.00	**7.67**	**0.02**	**34.24**	**0.00**
4	Area of leaf surface / 1000	A_L	0.77	**8.08**	**0.02**	**12.39**	**0.00**
5	Area of indumentum surface / 1000	A_In	0.03	**19.21**	**0.00**	**11.90**	**0.00**
6	Indumentum adaxial percentage of coverage (%)	C_In-ad	0.00	**143.70**	**0.00**	**90.62**	**0.00**
7	Indumentum abaxial percentage of coverage (%)	C_In-ab	0.00	**40.06**	**0.00**	**43.15**	**0.00**
8	Width of the leaf on cross section	W_L	0.63	**26.53**	**0.00**	**27.90**	**0.00**
9	Thickness of the leaf	T_L	0.46	**31.66**	**0.00**	**47.50**	**0.00**
10	Radius of the oil cell	R_OC	0.00	**98.96**	**0.00**	**93.41**	**0.00**
11	Number of oil cells	No_OC	0.00	**92.93**	**0.00**	**76.43**	**0.00**
12	Number of capitate hairs	No_CH	0.00	**21.40**	**0.00**	**11.76**	**0.00**
13	Number of peltate hairs	No_PH	0.00		ns	**11.62**	**0.00**
14	Radius of peltate hairs	R_PH	0.08	**13.23**	**0.00**		ns
15	Number of stomata	No_Stom	0.00	**22.42**	**0.00**	**13.69**	**0.00**
16	Thickness of adaxial epidermal cells	T_Epi-ad	0.89	**40.37**	**0.00**		ns
17	Thickness of abaxial epidermal cells	T_Epi-ab	0.00		ns		ns
18	Thickness of palisade tissue	T_Pal	0.00	**18.63**	**0.00**	**18.14**	**0.00**
19	Thickness of palisade tissue—adaxial	T_Pal-ad	0.07	**28.69**	**0.00**	**18.01**	**0.00**
20	Thickness of palisade tissue—abaxial	T_Pal-ab	0.00		ns		ns
21	Thickness of spongy tissue	T_Spo	0.00	**25.21**	**0.00**	**20.48**	**0.00**
22	Number of palisade layers	No_Pal_l	0.00		ns		ns
23	Thickness of cuticula	T_Cut	0.00	**21.15**	**0.00**	**22.49**	**0.00**
24	Leaf surface	L_S	0.22	**11.00**	**0.00**		ns
25	Average width of leaf	Avg_w_l	0.99	**18.81**	**0.00**	**30.63**	**0.00**
26	Leaf base width	L_B_L	0.00		ns		ns
27	The widest part of the leaf	w_L	0.85	**27.00**	**0.00**	**40.60**	**0.00**
28	Leaf length	L_L	0.51	**64.48**	**0.00**	**64.58**	**0.00**
29	Relation between the widest part of the leaf and leaf length	W_L/L_L	0.01	**115.80**	**0.00**	**102.52**	**0.00**
30	Distance between leaf base and the widest part of the leaf	D1	0.45	**28.58**	**0.00**	**27.59**	**0.00**
31	Number of teeth on the edge of the leaf	L_T	0.00		ns		ns
32	Relation between distance D1 and leaf length	L_L/D1	0.00	**23.09**	**0.00**	**23.84**	**0.00**
33	Bract length	B_L	0.02	**39.42**	**0.00**	**28.56**	**0.00**
34	Average width of bract	Avg_w_b	0.09	**62.95**	**0.00**	**71.01**	**0.00**
35	Stem height	S_H	0.00	**101.70**	**0.00**	**83.62**	**0.00**
36	Frequency of stipules on stem's nodes	Frequ_S	0.00		ns	**10.70**	**0.00**
37	Average length of first three internodes	Avg_L_F_I	0.19	**66.70**	**0.00**	**26.54**	**0.00**
38	Average length of last three internodes	Avg_L_L_I	0.01	**86.32**	**0.00**	**57.18**	**0.00**
39	Percentage of yellow in corolla lower lip	%_yellow	0.00	**145.10**	**0.00**	**13.37**	**0.00**
40	Distance between calyx base and tooth base	D_Cal_b_T_b	0.06	**40.58**	**0.00**		ns

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TABLE 2. (Continued)

No	Characters	Acronym	Shapiro Wilk	KW H I	KW *p* I	KW H II	KW *p* II
41	Distance between the tooth base and the beginning of the narrow part of the tooth	D_T_b_T_t	0.00	**25.15**	**0.00**	**35.37**	**0.00**
42	Length of narrow part of tooth	L_n_T	0.53		ns	**6.30**	**0.04**
43	Width of tooth	W_T	0.01	**13.09**	**0.00**	**12.19**	**0.00**
44	Number of flowers in terminal inflorescence	No_F_I	0.00	**93.76**	**0.00**	**79.53**	**0.00**
45	Number of terminal inflorescences	No_I	0.00		ns		ns

Data analyses

The normality of the distribution of the measured quantitative characters was assessed using the Shapiro–Wilk test. As most of the analysed characters did not conform to a normal distribution, all quantitative characters were log-transformed before further multivariate analyses. The non-parametric Kruskal–Wallis (KW) test was used to identify the characters that differed most strongly among the three analysed groups. For characters found to be significant in the KW test, Dunn's post hoc test with Bonferroni correction was applied to resolve the pattern of pairwise differences among the groups. Before the multivariate analyses, a Spearman correlation matrix was calculated and, within pairs of highly correlated characters, the character with the lower significance in the KW test was excluded. Principal component analysis (PCA) was performed to assess the overall morpho-anatomical variability among the analysed individuals and the contribution of individual characters to this variability. To test whether the analysed groups differ significantly from one another, permutational multivariate analysis of variance (PERMANOVA) based on Gower distance and 9999 permutations, and linear discriminant analysis (LDA) were performed. All statistical analyses were performed using PAST v.5.3 (Hammer *et al.* 2001). Multivariate analyses were conducted at two hierarchical levels (datasets). At the first level, 23 populations were included to assess the general pattern of discrimination among three a priori defined groups: 14 populations of subsp. *montanum* sampled across western Europe and the north-western Balkans; 6 populations of subsp. *helianthemoides* representing the entire range of the taxon in the southern Balkans; and 3 populations of the "skadarensis" MG from northern Albania. At this level, principal component analysis (PCA) was performed on 42 variables, PERMANOVA was performed on 42 morphological characters based on Gower distances, and linear discriminant analysis (LDA) was performed on 20 variables based on the results of the KW test. At the second level, the analysis was restricted to 13 populations to resolve the degree of discrimination between the "skadarensis" MG and the geographically closest populations of subsp. *montanum*, growing on two different geological substrates. At this level, PERMANOVA was performed on 42 morphological characters based on Gower distances, and linear discriminant analysis (LDA) was performed on 12 variables based on the results of the KW test. To minimise the risk of overfitting and spurious discrimination in the LDA models, a reduced set of variables was used for the analyses at both levels.

Results

Univariate statistics

The Kruskal–Wallis (KW) test showed that 36 of the 45 measured characters differed significantly among the three analysed groups (Table 2). The characters that showed the most significant differences between the analysed groups were the percentage of yellow in the lower corolla lip (%_yellow), percentage of adaxial indumentum coverage (C_In-ad), ratio between the widest part of the leaf and leaf length (W_L/L_L), stem height (S_H), the radius of the oil cell (R_OC) and the number of flowers in the terminal inflorescence (No_F_I) (Figure 2A). At the second level, the KW test showed that 35 of the 45 measured characters were significantly different between the analysed groups. The characters that differed most significantly among groups at this level were the ratio between the widest part of the leaf and leaf length (W_L/L_L), the radius of the oil cell (R_OC), the percentage of adaxial indumentum coverage (C_In-ad), stem height (S_H), the number of flowers in the terminal inflorescence (No_F_I) and the number of oil cells (No_OC) (Figure 2B).

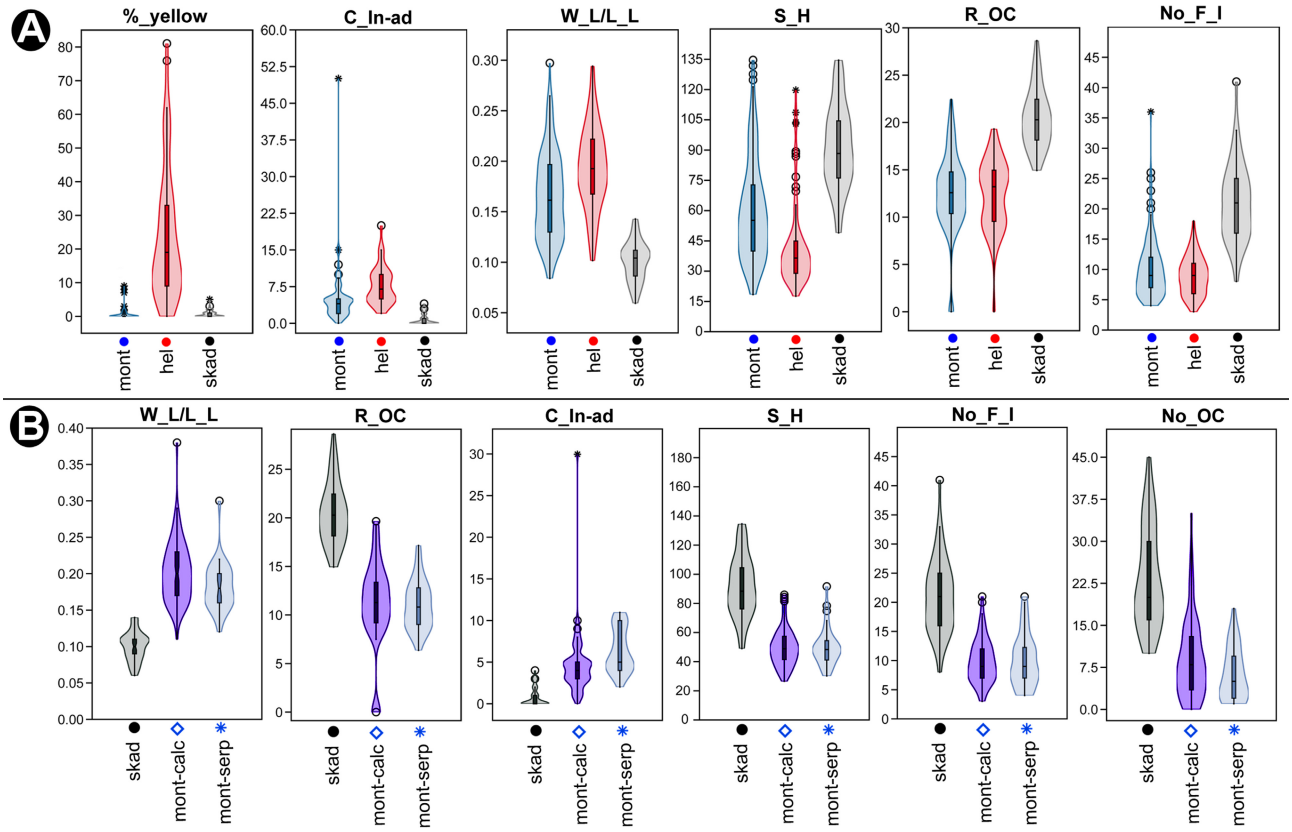


FIGURE 2. Box and violin plots for the most significant characters distinguishing the groups at the first (A) and second (B) level of statistical analyses. The horizontal line shows the median, the box shows the 25th–75th percentiles, and the whiskers show values 1.5 times above and below the box. Values outside the inner whiskers are shown as circles, and values more than three times the box height are shown as stars. The acronyms of the characters correspond to Table 2.

Multivariate statistics

Principal component analysis showed that the first three axes accounted for 50.91% of the total variability, with PCA1, PCA2 and PCA3 explaining 25.92%, 14.08% and 10.91%, respectively. The variables contributing most to the observed variability were %_yellow, T_Pal-ab, No_OC, C_Ind-ad, Avg_L_L_I, Avg_L_F_I, S_H, L_S, R_OC and No_F_I. Along the first and second axes, individuals of subsp. *montanum* occupied a central position in the ordination space, while individuals of the other two groups partially overlapped along the first axis (Figure 3A). PERMANOVA showed statistically significant differences among the three groups in multivariate space (Total sum of squares = 5.497; Within-group sum of squares = 4.613; F = 30.6; p = 0.0001). Linear discriminant analysis (LDA) of the first dataset showed that the first discriminant axis accounted for 79.02% and the second for 20.98% of the total discrimination (Figure 3B). MG "skadarensis" was clearly separated from the other two groups along the first two axes. The two other groups—subsp. *montanum* and subsp. *helianthemoides*—were largely, though not completely, separated in the space of the same axes. The characters that contributed most to the observed discrimination among groups were %_yellow, C_Ind-ad, No_OC, Avg_L_L_I, Avg_L_F_I, No_F_I, S_H and R_OC.

Multivariate analyses of the second dataset included 170 individuals from three groups: subsp. *montanum* from serpentine substrates (34 individuals), subsp. *montanum* from calcareous substrates (89 individuals), and MG "skadarensis" itself. PERMANOVA showed that the three analysed groups differed significantly from one another in multivariate space (total sum of squares = 3.148; within-group sum of squares = 2.406; F = 25.77; p = 0.0001). Linear discriminant analysis, including all 170 individuals of the second dataset showed that the first discriminant axis accounted for 95.99% and the second for 4.01% of the total discrimination. MG "skadarensis" was clearly separated from the other two groups in the space of the first two discriminant axes, whereas the other two groups were overlapped along the same axes (Figure 3C). The characters that contributed most to the observed discrimination among groups in this model were C_In-ad, No_OC, No_F_I, Avg_L_L_I, R_OC, S_H, L_L, and Avg_w_b, listed in order of decreasing contribution.

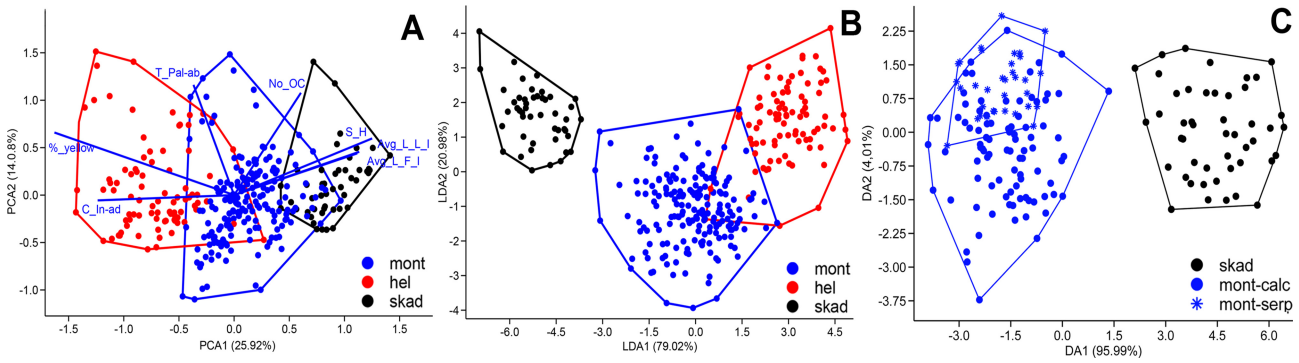


FIGURE 3. Scatterplots of multivariate statistical analyses at the first and second levels. A—Principal component analysis displayed along the first and second axes, including only populations at the first level of statistical analysis; B—Linear discriminant analysis including only populations at the first level of statistical analysis, with three a priori groups consisting of two accepted subspecies and MG "skadarensis"; C—Linear discriminant analysis including only populations at the second level of statistical analysis, with three a priori defined groups: subsp. *montanum* from limestone, subsp. *montanum* from ultramafic bedrock, and MG "skadarensis". Abbreviations of the groups correspond to Table 1.

Qualitative morphological characters: habitus, indumentum type and corolla colour

Although indumentum-related traits were also captured through the quantitative characters R_PH, No_PH and No_CH, which refer to glandular trichomes, the type of indumentum formed by non-glandular trichomes—which constitute the dominant component of the indumentum—was not quantitatively assessed. Similarly, while the colour of the lower corolla lip was captured through the quantitative character %_yellow, the colours of the remaining corolla parts were not quantified. Habitus, indumentum type and corolla colour proved to be stable characters within populations, although the growth form could vary slightly depending on the microtopography of the habitat. All individuals within populations of MG "skadarensis" were characterised by an ascending shrub habitus (Figure 4, A and B; Figure 7 A, Figure 8 A), whereas individuals from all populations of subsp. *montanum* and subsp. *helianthemoides* predominantly displayed a decumbent subshrub habitus, except for individuals growing on extremely steep terrain, which instead developed a pendent, cushion-like habitus (Figure 4 C, D, E and F). As with growth habitus, the type of indumentum was a highly stable character within a population, showing no variation among individuals. In populations of subsp. *montanum*, the indumentum was dominated by uniseriate, unbranched, appressed, curled non-glandular trichomes and was assessed as pubescent (Figure 5. A, Figure 6. subsp. *montanum* A, B, C and D). In populations of subsp. *helianthemoides*, the indumentum was dominated by uniseriate, unbranched, protruding, more or less straight hairs and was assessed as lanato-tomentose (Figure 5. B, Figure 6. subsp. *helianthemoides* A, B, C and D). In populations of MG "skadarensis", the indumentum was dominated by the same trichome type as in subsp. *montanum* and was likewise assessed as pubescent (Figure 5. C, Figure 6. MG "skadarensis" A, B, C and D). Leaf and calyx indumentum were densest in subsp. *helianthemoides* (sparsely lanato-tomentose), followed by subsp. *montanum*, and least dense in MG "skadarensis", which were evaluated as glabratum indumentum types. In individuals from populations of subsp. *montanum*, corolla colour was predominantly white, with the modified upper lip gradually transitioning from white to dark brown (Figure 5 A). In individuals from populations of subsp. *helianthemoides*, the lower corolla lip was light yellow to yellow, while the modified upper lip was dark yellow distally, becoming brown (Figure 5 B). In individuals from populations of MG "skadarensis", the lower corolla lip was entirely white, while the modified upper lip was white proximally, gradually becoming dirty white distally (Figure 5 C, Figure 7 B, Figure 8 B1 and B2).

Morphology of cultivated plants

Most of the transplanted individuals did not survive. The ones that did survive originated from Fužine (Croatia), representing subsp. *montanum*; from Mount Olympus (Greece), representing subsp. *helianthemoides*; and from Maja Boks (Albania), representing two individuals of the "skadarensis" MG. All individuals that survived the first growing season continued to grow for several additional seasons—the Fužine and Olympus samples for four years, and the Maja Boks sample for three years. After several years of cultivation, all individuals fully retained their qualitative morphological characters of habitus, indumentum and corolla colour. Morphological traits of the cultivated plant from MG "skadarensis" are presented in Figure 7.

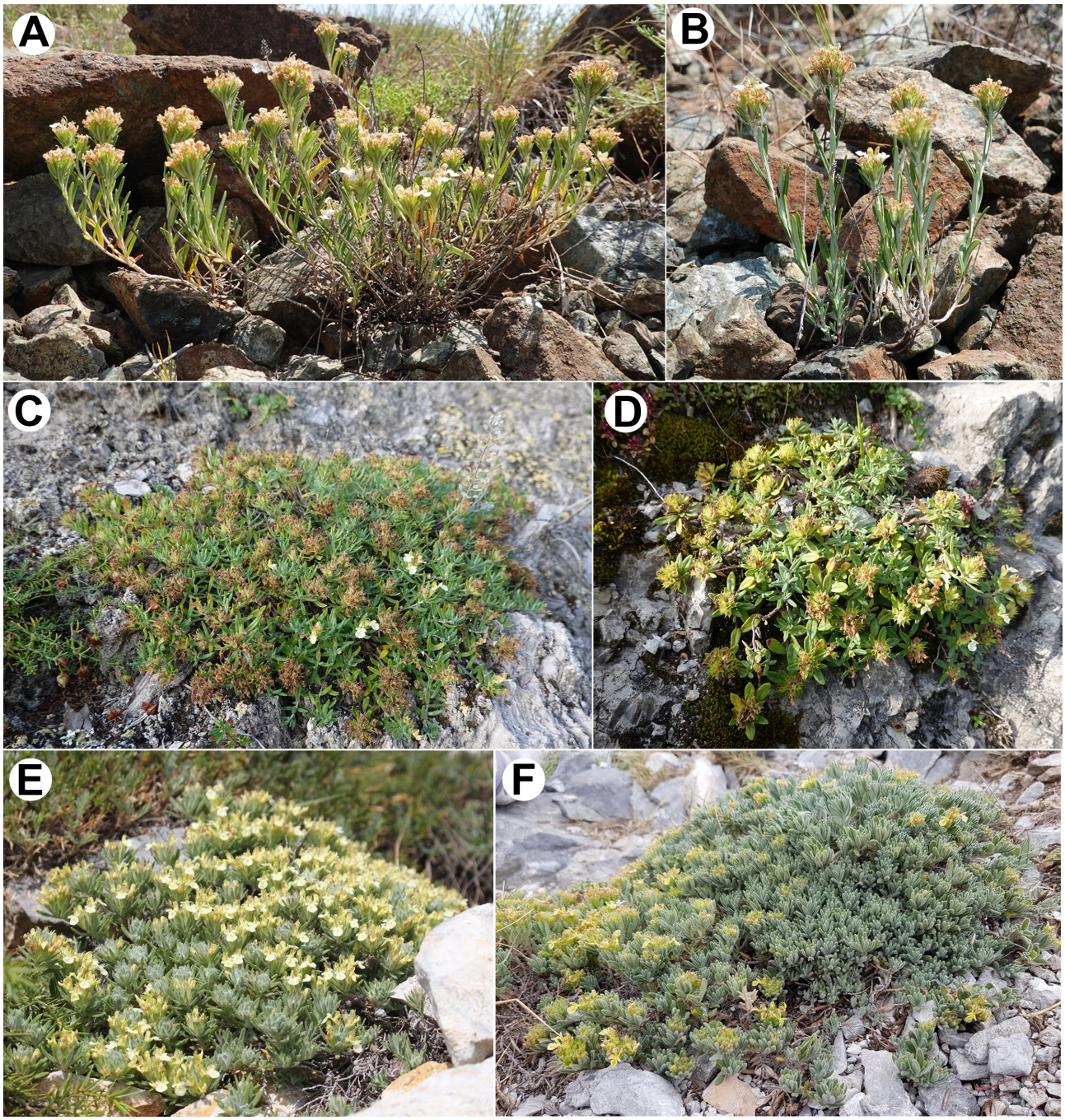


FIGURE 4. Two types of habitus (ascending shrub and decumbent subshrub) identified in the analysed populations. A, B—ascending shrub type of habitus of MG "skadarensis" from Albania, Shkodër (population 22); C—decumbent subshrub type of habitus from the typical population of subsp. *montanum* from Germany, Barbarossahöhle (population 01); D—decumbent subshrub type of habitus from the typical population of subsp. *montanum* from northern Germany, Bad Oberdorf (population 03); E—decumbent subshrub type of habitus from the northernmost sampled population of subsp. *helianthemoides* from North Macedonia, Mount Galičica (population 26); F—decumbent subshrub type of habitus from the southernmost population of subsp. *helianthemoides* from Greece, Mount Dirfi (population 33).

Discussion

Most characters that differed significantly among groups at the first level were also significant at the second, with No_PH, T_Epi-ad, R_PH, and Frequ_S constituting exceptions to this rule. Overall, the slightly higher KW H-statistics and PERMANOVA results at the first level indicate stronger differentiation among the broader groups than among the more closely related groups compared at the second level. This finding is consistent with the inclusion of two groups

belonging to subsp. *montanum* and geographically proximate populations of MG "skadarensis", where historical gene flow may have promoted morphological similarity. In general, the significant characters identified in this study correspond well with previous Balkan-wide analyses of *T. montanum* (Zbiljić *et al.* 2023), except for leaf-margin teeth (L_T), which were important in that study but were scarcely recorded and statistically non-significant in this study.



FIGURE 5. Inflorescence and indumentum of the two accepted subspecies and MG "skadarensis". A—Plant from a typical population of subsp. *montanum* from Germany, Barbarossahöhle (population 01), terminal head-like inflorescence with white lower corolla lip and the modified upper lip gradually transitioning from white to dark brown, and pubescent indumentum on stem and leaf abaxial side; B—plant from the southernmost population of subsp. *helianthemoides* from Greece, Mount Dirfi (population 33), head-like inflorescence with yellow corolla lip and the modified upper lip gradually transitioning from yellow to brown, and lanato-tomentose indumentum on stem and leaf abaxial side; C—plant from the MG "skadarensis" from Albania, Maja Boks (population 23), terminal head-like inflorescence with almost completely white corolla, and pubescent indumentum on stem and leaf abaxial side.

Multivariate analyses confirmed significant morphological differentiation among the analysed groups, despite the presence of a few outlying individuals. Given the high degree of morphological plasticity exhibited by *T. montanum* (Stevanović & Stevanović 1985, Lakušić & Lakušić 2014, Zlatić *et al.* 2023), the occurrence of such exceptions is not unexpected and does not compromise the overall pattern. The distinctiveness of MG "skadarensis" is supported by both quantitative and qualitative traits, particularly habitus, stem height, internode length, corolla colour, and indumentum characters (Figures 3–8). In comparison with subsp. *montanum*, MG "skadarensis" has fewer non-glandular trichomes on the upper leaf surface, but a similar pubescent indumentum type. Conversely, subsp. *helianthemoides* is clearly distinguished by its dense lanato-tomentose indumentum. MG "skadarensis" also differs in its ascending shrub habitus, with laterally rising peripheral shoots, contrasting with the cushion-like habitus of the two accepted subspecies.

The cultivation of plants under uniform conditions further supports the stability and reliability of the most diagnostic traits. Although *T. montanum* is known to exhibit ecological plasticity, especially in leaf and stem characters, indumentum and corolla colour remained stable over several growing seasons. As demonstrated in the research by Baden (1991), a comparable level of stability has been observed in subsp. *helianthemoides*, thereby underscoring the significance of these taxonomic characteristics.

The complex geological history of the Balkan Peninsula has promoted diversification within *T. montanum sensu lato*, but genetic, ecological, and morphological patterns correspond only partly (Zbiljić *et al.* 2024). Broad ecological tolerance, secondary contact, and gene flow within sect. *Polium* have likely contributed to this mismatch. Consequently, genetic evidence alone is insufficient for taxonomic delimitation in this complex. The present results demonstrate that MG "skadarensis" is morphologically well differentiated from both subsp. *montanum* and subsp. *helianthemoides*, despite the genetic affinities reported in previous studies. The combination of the following morphological characteristics is indicative of adaptation to the hot, dry summers, wet mild winters, and ultramafic substrates of northern Albania: erect stems, long internodes, narrow leaves and a distinctive habitus. In addition, regarding anatomical features, the large and numerous "oil cells" in the leaf mesophyll may represent a further adaptation to the dry summer period. The function of these structures has already been investigated in the phylogenetically closely related species *T. polium* (= *T. capitatum*) from Greece (Christodoulakis *et al.* 2010), which showed that they do not perform the secretory function previously proposed by Fahn and Cutler (1992), but most probably serve as water reservoirs. These findings support the interpretation that MG "skadarensis" represents a morphologically distinct lineage deserving independent taxonomic status.

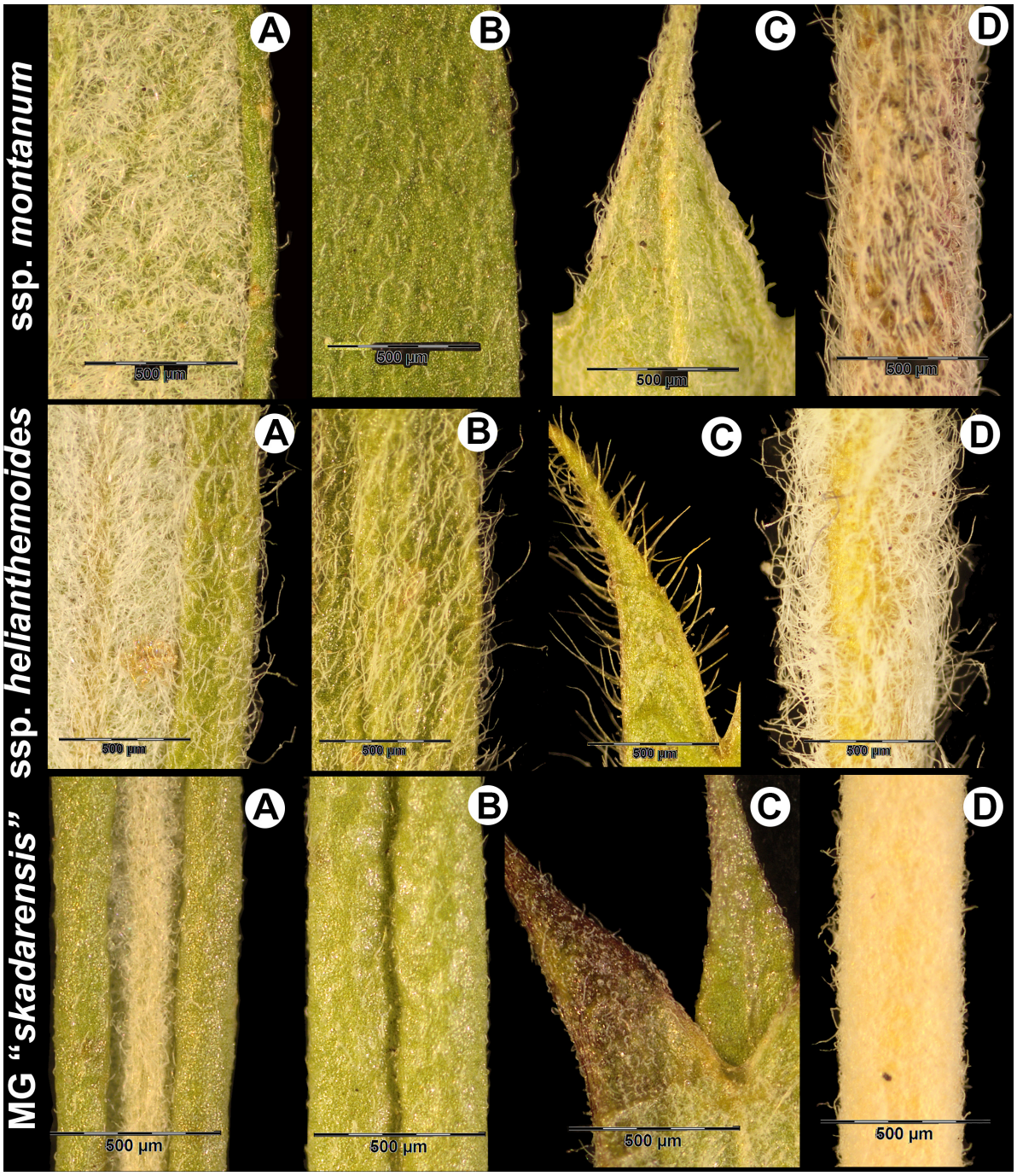


FIGURE 6. Leaf, calyx and stem indumentum of two accepted subspecies and MG "skadarensis". A—leaf abaxial surface; B—leaf adaxial surface; C—calyx; D—stem. Subspecies *montanum* A = pubescent, B = almost glabrous, C = almost glabrous, and D = pubescent indumentum types. Subspecies *helianthemoides* A = lanato-tomentose, B = a less dense lanato-tomentose, C = a less dense lanato-tomentose, and D = lanato-tomentose indumentum types. Morphogroup "skadarensis" A = pubescent, B = glabrous, C = almost glabrous, and D = pubescent indumentum types.

The clear morphological distinctiveness of the MG "skadarensis" populations is evident in their morphology, and when combined with their closer genetic affinity to subsp. *helianthemoides* (Zbiljić *et al.* 2024) but a greater morphological resemblance to the typical subsp. *montanum* (Figures 3 and 5), indicates that they represent a natural entity that cannot be adequately assigned to either of the two currently recognized subspecies. At the same time, the observed morphological differences are not sufficiently pronounced to justify recognition at the species level within sect. *Polium*. We therefore propose that the populations from northern Albania be described as a new subspecies of *T. montanum*, here named *Teucrium montanum* subsp. *skadarensis*, and formally described below.

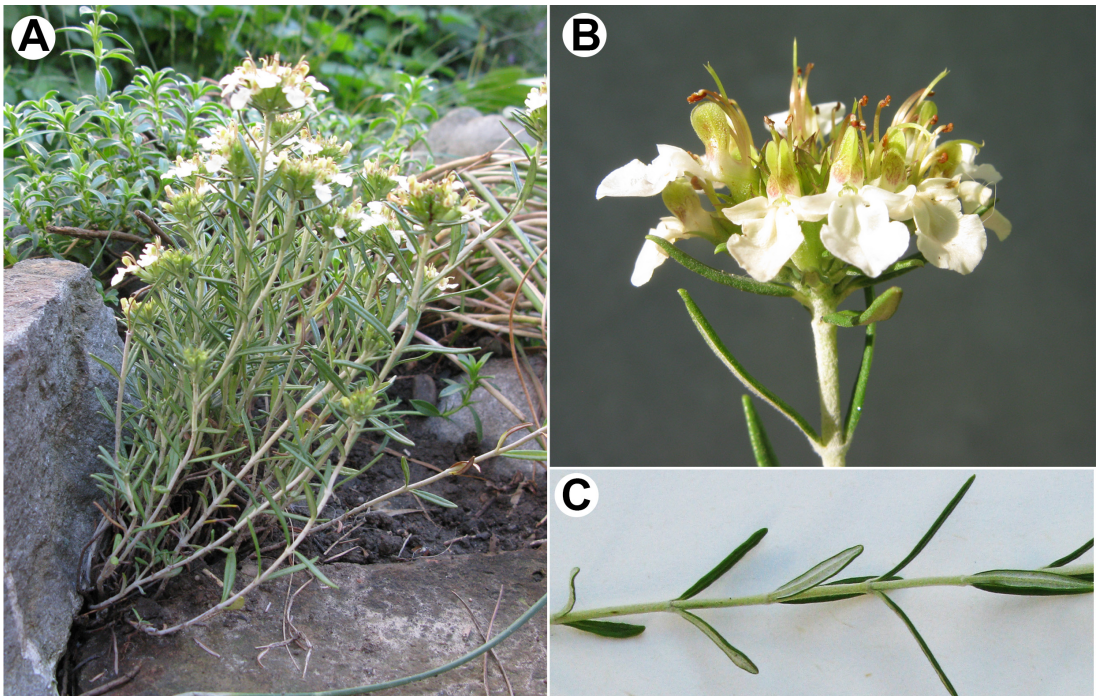


FIGURE 7. Ex situ cultivated plant of MG "skadarensis" originating from Albania, Maja Boks population (population 23). A—ascending shrub habitus; B—head-like terminal inflorescence with an almost completely white corolla; C—long internodes with long, narrow leaves.



FIGURE 8. *Teucrium montanum* subsp. *skadarensis* Zbiljić & D. Lakušić, subsp. nova. A—ascending shrub habitus, individual from natural habitat Maja Boks (population 23); B1—flower, lateral view; B2—flower, frontal view; C—leaf cross-section with numerous idioblasts in the leaf mesophyll, arrows indicate some of the numerous idioblasts.

Taxonomic treatment

Key to the subspecies of *Teucrium montanum*

1a The lower lip predominantly white, white-cream, or cream; indumentum consisting of short, intertwined, appressed non-glandular hairs **2**

1b The lower lip light yellow to yellow; indumentum consisting of long, straight, protruding, erect non-glandular hairs ..... ***T. montanum* subsp. *helianthemoides***

2a A decumbent, cushion-like subshrub with narrowly to broadly elliptical leaves; the upper surface of the leaf is nearly glabrous to sparsely hairy; in leaf cross-section, fewer than 25 idioblasts in the mesophyll; the lower lip white to cream-coloured ..... ***T. montanum* subsp. *montanum***

2b An ascending shrub with linear-lanceolate leaves ending in a hook-like tip; the upper surface of the leaf nearly glabrous; in leaf cross-section, more than 25 idioblasts in the mesophyll; the lower lip completely white ..... ***T. montanum* subsp. *skadarensis*** subsp. nova

Teucrium montanum subsp. *skadarensis* Zbiljić & D.Lakušić, subsp. nova

TYPE:—ALBANIA. Shkodër, Badanjort, 42.069670 N, 19.571530 E, Seslerio-Pinetum, serpentinite, 177 m, 24 June 2011, *Lakušić, D., Kuzmanović, N., Lazarević, P., Alegro, A.* (holotype BEOU 32425!).

Diagnosis: Closest to subsp. *montanum*, from which it differs in habitus (ascending shrub vs. decumbent, cushion-like subshrub); leaf shape and dimensions (long, linear-lanceolate leaves with a hook-shaped tip vs. shorter, narrowly to broadly elliptical leaves with a blunt or slightly pointed tip); the number of idioblasts in the leaf mesophyll (always more than 25 in cross-section vs. significantly fewer than 25); and the colour of the lower corolla lip (completely white vs. white to cream).

Description: Perennial, erect, rarely prostrate subshrub with an ascending habitus. Root strong, spindle-shaped. Stem woody at the base, highly branched from the base; lateral shoots gradually rising from the substrate, rounded, covered with dense, curly, appressed, non-glandular trichomes. Stem occasionally reaching up to 25 cm in height in exceptional individuals; internodes from the middle of the stem (1.1–) 1.2–1.9 (–2.1) cm long, slightly shorter than the leaves; internodes in the inflorescence often longer than the leaves. Leaves almost linear-lanceolate to narrowly lanceolate, tapering gradually into a short petiole, often with a hook-shaped tip, (22.7–) 24.3–31.4 (–34.9) mm long, (2.2–) 2.3–3.3 (–3.7) mm wide, with a strongly recurved margin, dark green and nearly glabrous above, completely white and densely hairy beneath. Bracts resembling vegetative leaves in shape, the largest equalling vegetative leaves in size, the smallest up to 4 times smaller. Flowers gathered in capitate dichasia, occasionally branching terminally; pedicels longer on the outer flowers of the inflorescence, very short or absent on the inner flowers. Calyx bell-shaped, more or less bulging at the base, with 5 teeth, one of which may be larger, the teeth tapering to a sharp point, (9.3–) 9.9–12 (–12.9) mm long from base to tip. Corolla zygomorphic, apparently bilabiate, composed of 5 corolla lobes fused at the base into a corolla tube usually twice as long as the calyx. Lower lip completely white, consisting of 3 fused corolla lobes, the central one largest, the two lateral ones smaller and positioned perpendicular to it. Modified upper lip white in the proximal part, gradually becoming dirty white distally. Stamens longer than the corolla, dark green to brown. Flowering from May to July.

Distribution and Ecology: This subspecies is distributed on the slopes of the Prokletije Mountains in Albania, around the city of Shkodër in the north-western part of the country. It grows on ultramafic rocky terrain (*Halacsyetalia sendtneri*) in the hilly and mountainous zones.

Etymology: The subspecific epithet skadarensis refers to the Skadar region (Shkodër in Albanian) in north-western Albania, where the type material was collected and to which the taxon is endemic.

Note: The information about the morphological specificity of the populations from Skadar region has been introduced at the symposium of the 15th Symposium on the flora of southeastern Serbia and neighboring regions (Zbiljić *et al.* 2025). However, no formal description has been provided, nor has the holotype been cited. Therefore, the subspecies has not been validly published at the symposium (ICN, Art. 38).

The subspecies has been recorded at the following localities:

ALBANIA: Shkodër—Shkodër, Badanjort, 42.069670 N, 19.571530 E, *Seslerio-Pinetum*, serpentinite, 177 m, 24 June 2011, *Lakušić, D., Kuzmanović, N., Lazarević, P., Alegro, A.* (BEOU 32425); Shkodër, Badanjort, 42.06963 N, 19.56222 E, rocky ground, *Festuco-Brometea*, serpentinite, 86.9 m, 18 May 2012, *Lakušić, D., Tomović, G., Kuzmanović, N.* (BEOU 34843); Shkodër, Badanjort, 46.9 m, 42.05445 N, 19.53789 E, rocky ground (*Genistetum hassertianae*), serpentinite, 22 June 2015, *Lakušić, D., Kuzmanović, N., Đurović, S., Janković, I.* (BEOU 42161);

Shkodër, Badanjort, 27 m, 42.054378 N, 19.540138 E, rocky ground (*Genistetum hassertianae*), serpentinite, 22 June 2015, *Lakušić, D., Kuzmanović, N., Đurović, S., Janković, I.* (BEOU 42151); Shkodër, Badanjort, 21 m, 42.053381 N, 19.534787 E, rocky ground (*Genistetum hassertianae*), serpentinite, 22 June 2015, *Lakušić, D., Kuzmanović, N., Đurović, S., Janković, I.* (BEOU 42135); Shkodër, Maja Boks, 42.008210 N, 19.683620 E, rocky ground (*Halacsyetalia sendtneri*), serpentinite, 305 m, 24 June 2011, *Lakušić, D., Kuzmanović, N., Lazarević, P., Alegro, A.* (BEOU 32415); Shkodër, Maja Boks, 42.008273 N, 19.683218 E, rocky ground, serpentinite, 300 m, 26 August 2014, *Lakušić, D., Kuzmanović, N., Janković, I.* (BEOU 40181); Shkodër, Maja e Boks, 327.7 m, 42.00854 N, 19.68287 E, rocky ground (*Festuco-Brometea*), serpentinite, 22 June 2015, *Lakušić, D., Kuzmanović, N., Đurović, S., Janković, I.* (BEOU 42199); Shkodër, Maja e Boks, dry rocky grassland (*Halacsyetalia sendtneri*), serpentinite, 42.0082 N, 19.683196 E, 313 m, 9 June 2017, *Lakušić, D., Kuzmanović, N., Milekić, T., Zbiljić, M.* (BEOU 46619); Shkodër, Bokat e Rančit 3: 10 m [CM75], 42.054519 N, 19.540752 E, 31.1 m a.s.l., rocky ground (*Halacsyetalia*), serpentinite, 9 July 2017, *Lakušić, D., Kuzmanović, N., Janković, I.* (BEOU 47172); Albania, Shkodër, 42.05428 N, 19.537172 E, 26 m a.s.l., rocky ground (*Halacsyetalia*), serpentinite, 18 June 2025, Zbiljić, M., Mladenović, Ž., (BEOU 72688); Albania, Gomsiqe, 41.9739447 N, 19.7813979 E, 450 m a.s.l., rocky ground (*Halacsyetalia*), serpentinite, 18 June 2025, *Zbiljić, M., Mladenović, Ž.* (BEOU 72687);

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