Stomata and pollen grain characteristics of two endemic lilies: *Lilium bosniacum* and *L. carniolicum* (*Liliaceae*)

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Abstract. The present paper reports palynological and anatomical investigations of two European endemic Turk's-cap lilies *Lilium bosniacum* and *L. carniolicum*. The analyses of exine structure, for both species, did not reveal important differences in size of lumina. Differences in leaf anatomy evidenced that *L. carniolicum* had a hypostomatic leaf type, while surprisingly *L. bosniacum* had a transitional one (from hypostomatic towards the amphistomatic leaf type). The examination of the stomatal density and size among *L. bosniacum* populations exposed statistical important differences for one population from atypical geological peridotite substrate.

Key words: exine structure, leaf anatomy, *Lilium*, pollen, scanning electron microscopy (SEM), stomata

Introduction

The genus *Lilium* includes about 100 species, grouped in seven sections, which are geographically distributed in North America, Europe and Asia (Comber 1949). In Europe this genus includes 10 species and a certain number of taxa with unclear taxonomical status (Matthews 1980). One of them is *L. bosniacum* (Beck) Beck ex Fritsch, a rare and vulnerable taxon from Central Dinaric Alps, included in the list for the "*Red book*" of the Flora of Bosnia and Herzegovina (Šilić 2000). It belongs, together with *L. albanicum* Griseb. and *L. jankae* A. Kern., to the *L. carniolicum* Bernh. ex W.D.J. Koch complex (Matthews 1980). *Lilium carniolicum* is also an endemic species, but with wider distribution, spreading from W Balkan Peninsula to SE Alps.

Lilium bosniacum was described for the first time (Beck 1887) as a variety of *L. carniolicum* and until now its status has been frequently altered from independent species to form rank of *L. carniolicum* (Beck 1887, 1903; Fritsch 1909; Košanin 1926; Hayek 1932–1933; Rohlena 1942; Popova 1981; Matthews 1984). Nevertheless, recent molecular and molecular cytogenetic studies have clearly proved the existence of four distinct species within the *L. carniolicum* complex: *L. albanicum*, *L. bosniacum*, *L. carniolicum* and *L. jankae* (Muratović & al. 2005, 2010a, b).

The most important studies reported until now on *L. bosniacum* and *L. carniolicum* have been related to their morphological (Beck 1903; Košanin 1926; Matthews 1984) or ecological variation (Lakušić & Kutleša 1971; Popova 1981; Lakušić 1987). The "Bosnian lily" is a bulbous, perennial herb with black to purple spotted yellow-

ish Turk's-cap perigons. Its stem is from 40 cm to 80 cm high, all leaves are alternate, the upper 3–10 mm broad with 4–8 veins. The number of flowers grades from one space: to 10. *Lilium carniolicum* possesses from one to six Turk's-cap black spotted, light red to red orange flowers. The stem is from 40 cm to 100 cm high; all leaves are alternate, the upper 4–17 mm broad with 3–9 veins.

According to basic karyotype features *L. bosniacum* (Wolkinger 1966; Medjedović 1976) and *L. carniolicum* (Zucconi 1956) karyotypes consist of 24 chromosomes with different number of secondary constrictions (6 for *L. bosniacum* and 8 for *L. carniolicum)*. Molecular cytogenetic investigations evidently distinguished these two species according to fluorescence *in situ* hybridization (FISH), chromomycin and DAPI bandings (Siljak-Yakovlev & al. 2003; Muratović & al. 2005, 2010a). According to Rešetnik & al. (2007) molecular phylogeny based on the internal transcribed spacer (ITS) was unable to discriminate *L. bosniacum* representatives from the *L. carniolicum* ones. On the contrary, the study of Muratović & al. (2010b) was also based on ITS sequences, but clearly discriminated these two taxa. These authors pointed out that molecular phylogeny could not always resolve complicated taxonomic misunderstandings, especially in cases dealing with only one or two specimens being used as the representatives of closely related species. Furthermore, if reticulate evolution is being involved in diversification of group such as the *L. carniolicum* complex, it is necessary to combine sampling material both from geographically distant populations and overlapping zones for more comprehensive interpretation of phylogenetic and taxonomic relationships (Muratović & al. 2010b).

According to our knowledge no data exists about anatomical or palynological characteristics of the two species except a short description of *L. bosniacum* pollen grain by Medjedović (1976). Therefore we focused our attention in this study to: **1**) leaf anatomy and pollen morphology of *L. bosniacum* and *L. carniolicum*; **2**) possible variation of stomata and pollen grain characteristics among *L. bosniacum* populations from contrasting environments.

Material and methods

Pollen grains and leaf materials were collected from three natural populations of *L. bosniacum* and two populations of *L. carniolicum* during June 2005 (Table 1, Fig. 1).

Table 1. Origin of plant material.

Taxa	Localities
L. bosniacum	Mt Crepoljsko, 1200 m, Bosnia and Herzegovina
	Mt Bjelasnica, 1700–1800 m, Bosnia and Herzegovina
	Kladanj-Muske vode, 970 m, Bosnia and Herzegovina
	Nevesinje, 1150 m, Bosnia and Herzegovina (**P**)*
L. carniolicum	Japetic, *ca*. 870 m, Croatia
	Mt Lanaro, Carso Triestino, 500 m, Italy
	Mt Kolusch, Nahas, Staernick, *ca*. 1000 m, near Trieste, Italy (**P**)*

* Studied materials from the Herbarium of the National Museum of Natural History, Paris. The other herbarium vouchers are deposited in National Museum of B&H (SARA), Herbarium of Laboratory for research and protection of endemic resources, Department of Biology, University of Sarajevo.

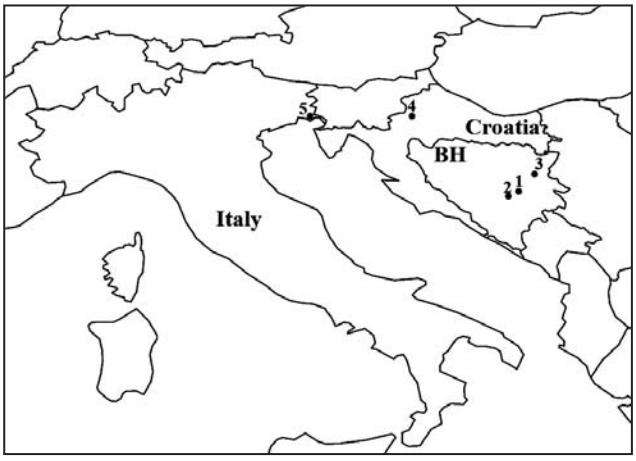

Fig. 1. Distribution of analyzed *Lilium* populations: **1**, Mt Crepoljsko; **2**, Mt Bjelasnica; **3**, Kladanj; **4**, Japetic; **5**, Mt Lanaro.

Lilium bosniacum samples from Bjelasnica and Kladanj populations are situated at a very inclined slope, covered by shallow soil poor in plant nutrients. While population Kladanj is characterized by low altitude (970 m) and specific geological substrate (peridotite), the Bjelasnica population was at relatively extreme altitude and limestone geological substrate (1700–1800 m). These conditions are however not common for *L. bosniacum* and are contrary to the conditions for individuals from the Crepoljsko population (limestone geological substrate, deep soil, altitude 1150–1200 m). In addition, pollen material of *L. bosniacum* and *L. carniolicum* was collected in the herbarium of National Museum of Natural History Paris (P) (Table 1).

Exine surface and structure for both taxa were studied by scanning electron microscopy (SEM) following the method described by Avetissian (1950). Pollen terminology was done according to Punt & al. (2007) and Hesse & al. (2009).

Alexander test (Alexander 1969) was performed for the analyses of *L. bosniacum* interpopulation pollen grains viability and size variation. For each of three investigated populations 20 individuals were collected during the flowering period (June 2005). Alexander test was done immediately after pollen harvesting in the field. The same slides used for detection of aborted and non aborted pollen grains were employed, three months later, for measuring of polar axis (P) and equatorial diameter (E).

Leaf anatomy was studied in a sample of 20 individuals for each population of *L. bosniacum* and 15 individuals for two *L. carniolicum* populations. *Lilium carniolicum* accessions were lesser since those populations were reduced in the number of individuals. Two leaves per individual from the central part of stem were stored in preservation solution (85 ml of 70 % ethanol, 10 ml of 49 % formaldehyde and 5 ml of acetic acid).

Leaf anatomy was studied at the numerous handmade transverse sections following Šoljan (1982). Epidermal abaxial and adaxial surface prints were striped off and transferred to slides for determination of stomata size and density. Samples were taken from both sides of the epidermis, from the central part of the leaf blade up to its apical end. For each investigated individual the number of stomata was counted for 20 surface areas (each area = mm^2), defining stomatal density. All measurements of stomata size (length and width) were carried out on five closed, randomly selected stomata from abaxial epidermis per individual. All photographs were taken on a Zeiss Axiophot microscope. The measurements of pollen and stomata size were performed under phase contrast light microscope LM (Wild M20).

One-way analysis of variance (ANOVA) was used to analyze mean values of stomata density and pollen traits of *L. bosniacum* populations. Scheffe's test was carried out to detect the differences among populations. Spearman's correlation test was employed to check possible relationships between investigated characters. The correlation test was performed using mean values of all analysed features at individual level. All analyses were run in SPSS (Statistical Package for the Social Sciences) for Windows ver. 15.

Results

SEM results for *L. bosniacum* and *L. carniolicum* pollen grains

The pollen grains of *L. bosniacum* and *L. carniolicum* were anatreme, with a narrow, very deep sulcus by rounded ends, almost as long as the equatorial diameter (Figs 2A, 2D). Ratio between polar axis and equatorial diameter showed that *L. bosniacum* pollen shape was suboblate. The same is the case for the *L. carniolicum*. The exine surface had a rich ornamentation in both taxa. The macroreticulate tectum was formed of the rectangular columellae. The wall thickness for both species ranged from 1 to 2.2 μm (Figs 2E, 2F 2G, 2H). The columellae heads (caput) in *L. bosniacum* were more curved than in *L. carniolicum* (Figs 2E, 2G). Both species possessed two types of lumina (rounded and rectangular). SEM observation showed that the longest rounded lumina diameter for *L. bos-*

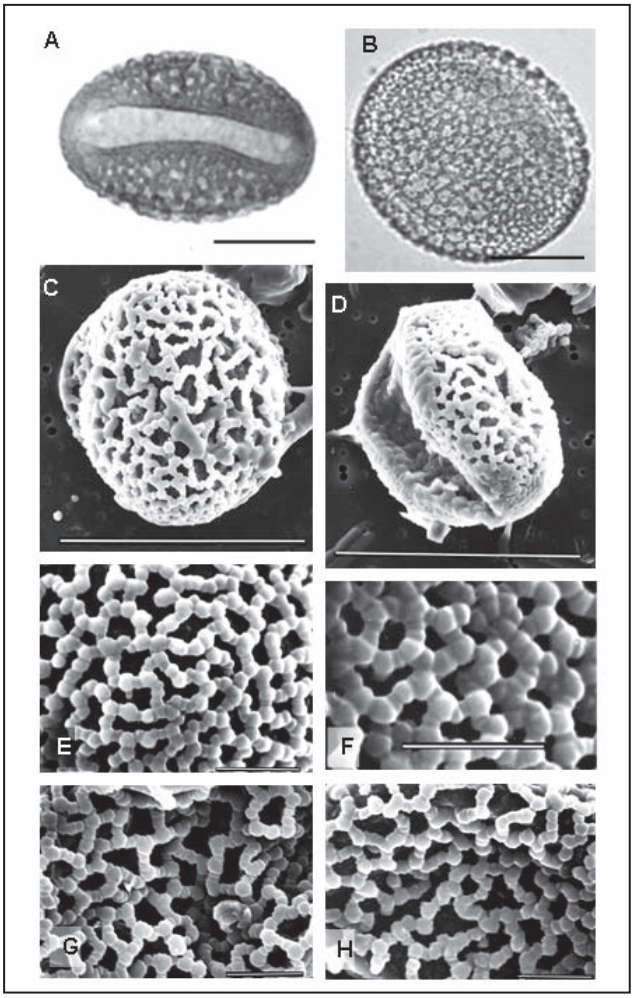

Fig. 2. Alexander test of *L. bosniacum* pollen grain: **A** – polar view, narrow, deep sulcus in front (scale bar = 25 μm); **B** – polar view intersulcate space in front (scale bar = 25 μm);
SEM of *L. bosniacum* pollen grain: **E –** rectangular lumina; **F –** rounded lumina (scale bar = 10 μm);
SEM of *L. carniolicum* pollen grain: **C** – polar view intersulcate space; **D** – narrow, deep sulcus (scale bar = 50 μm); **G –** rounded and rectangular lumina; **H** – the longest dimension of rectangular lumina (scale bar = 10 μm).

niacum did not exceed 2.5 µm, while the lowest was around 1 µm (Figs 2E, 2F). The values for the longest rectangular dimensions were bellow 2.5 µm and maximum up to 8 µm (Fig. 2E). In *L. carniolicum* the longest rounded lumina diameter were above 3 µm, while the lowest values were smaller than 1 µm (Figs 2C, 2G, 2H). The longest rectangular lumina dimensions started above 3 µm and went beyond 8 µm (Figs. 2C, 2G, 2H), including sporadically occurring of rectangular doubled sized lumina almost 14 µm long (Fig. 2H).

Interpopulation analysis of *L. bosniacum* pollen grains

The percentage of sampled viable pollen grains in the investigated populations varied from 85 to 98 %. There were no significant differences among the investigated populations for polar axis (P), equatorial diameter (E) and P/E ratio (Table 2). However, Bjelasnica population had slightly higher P values (53.45 µm) in comparison to Kladanj (50.52 µm) and Crepoljsko (50.79 µm) accessions.

Table 2. Interpopulation variation of pollen grain size in *L. bosniacum*.

	P[1] in µm	CV[2] (%)	E[3] in µm	CV (%)	P/E
Bjelasnica	53.45 (±3.52)[4]	6.58	61.96 (±2.85)	4. 59	0.86 (±0.02)
Kladanj	50.52 (±1.25)	2.48	62.06 (±0.96)	1.54	0.81 (±0.01)
Crepoljsko	50.79 (±2.64)	5.20	61.26 (±1.06)	1.72	0.83 (±0.03)

[1]Polar axis; [2]Coefficient of variation; [3]Equatorial diameter; [4]Standard deviation in parentheses.

General features of *L. bosniacum* and *L. carniolicum* leaf anatomy traits

The leaves in all studied populations of *L. bosniacum* (Figs 3B, 3D) and *L. carniolicum* had a single epidermal layer with a thick cuticle coating both sides. At the surface view epidermal cells showed extended longitudinal axes and somewhat sinuous anticlinal walls (Figs 3E, 3F, 3G, 3I). No differences in the sinuosity were observed among *L. bosniacum* and *L. carniolicum* populations.

Stomata of both species belonged to anomocytic celled type (Figs 3A, 3E, 3G). The adaxial epidermis of *L. carniolicum* lacked stomata, or there were just few at the apical margin of the leaf blade (Fig. 3I). It might be concluded that *L. carniolicum* had a hypostomatic leaf type. Surprisingly, the stomata were distributed at both epidermal sides in all studied *L. bosniacum* populations. The stomatal density in all investigated populations of *L. bosniacum* at the adaxial epidermis was the highest in the apical part (Fig. 3E) and decreased from the central part of the blade to the leaf base. The basal part of leaf blade was astomatal (Fig. 3F). The abaxial epidermis always had higher stomatal density than the adaxial (Table 3, Figs 3E, 3G). The highest density was found at the central part of leaf blade between the veins (Fig. 3G). The hairs were sporadically present both along the veins and the leaf margins in all studied *L. bosniacum* and *L. carniolicum* populations. They were grouped from four to eight at the apical part of the leaf margins (Figs $3H_1$, $3H_2$). It was evident that hairs were more abundant in *L. carniolicum* than in *L. bosniacum*.

Table 3. Descriptive parameters for analyzed stomata traits.

Population	Trait*	Min	Max	Mean	sd
Bjelasnica	L	77.78	84.26	80.41	1.91
	W	46.52	53.32	49.39	2.08
	SDab	5.00	21.00	11.97	2.93
	SDad	2.00	12.00	5.91	1.45
Crepoljsko	L	69.91	75.99	72.38	1.77
	W	46.74	53.62	49.76	2.15
	SDab	4.00	26.00	12.72	4.19
	SDad	2.00	15.00	5.82	1.98
Kladanj	L	93.34	99.90	96.39	2.05
	W	55.22	61.24	58.58	1.92
	SDab	4.00	18.00	9.84	2.88
	SDad	1.00	12.00	4.65	1.44

***L** – length (µm); **W** – width (µm); **SDab** – stomatal density on abaxial epidermis; **SDad** – stomatal density on adaxial epidermis, apical half of the leaf; **sd** – standard deviation.

The leaf mesophyll for both taxa consisted of adaxial lobed palisade and spongy tissue layers (Figs. 3B and 3D). The palisade cells for all studied *L. bosniacum* and *L. carniolicum* populations were in a single layer elongated and lobed, while spongy mesophyll appeared in several layers with large intercellular spaces. Vascular tissue, for both species, created collateral veins (Fig. 3C).

Lilium bosniacum interpopulation variation of stomata size and density

A considerable interpopulation variation for *L. bosniacum* was detected in the stomatal density and their size (Table 3). Performed Sperman's correlation test did not disclose significant correlations between investigated characters with exception of abaxial epidermis stomatal density and their length. Namely, the increase of stomata density on the abaxial epidermis were followed by significantly moderate decrease of their length ($r = -0.520$, $N = 30$, $p \leq 0.05$).

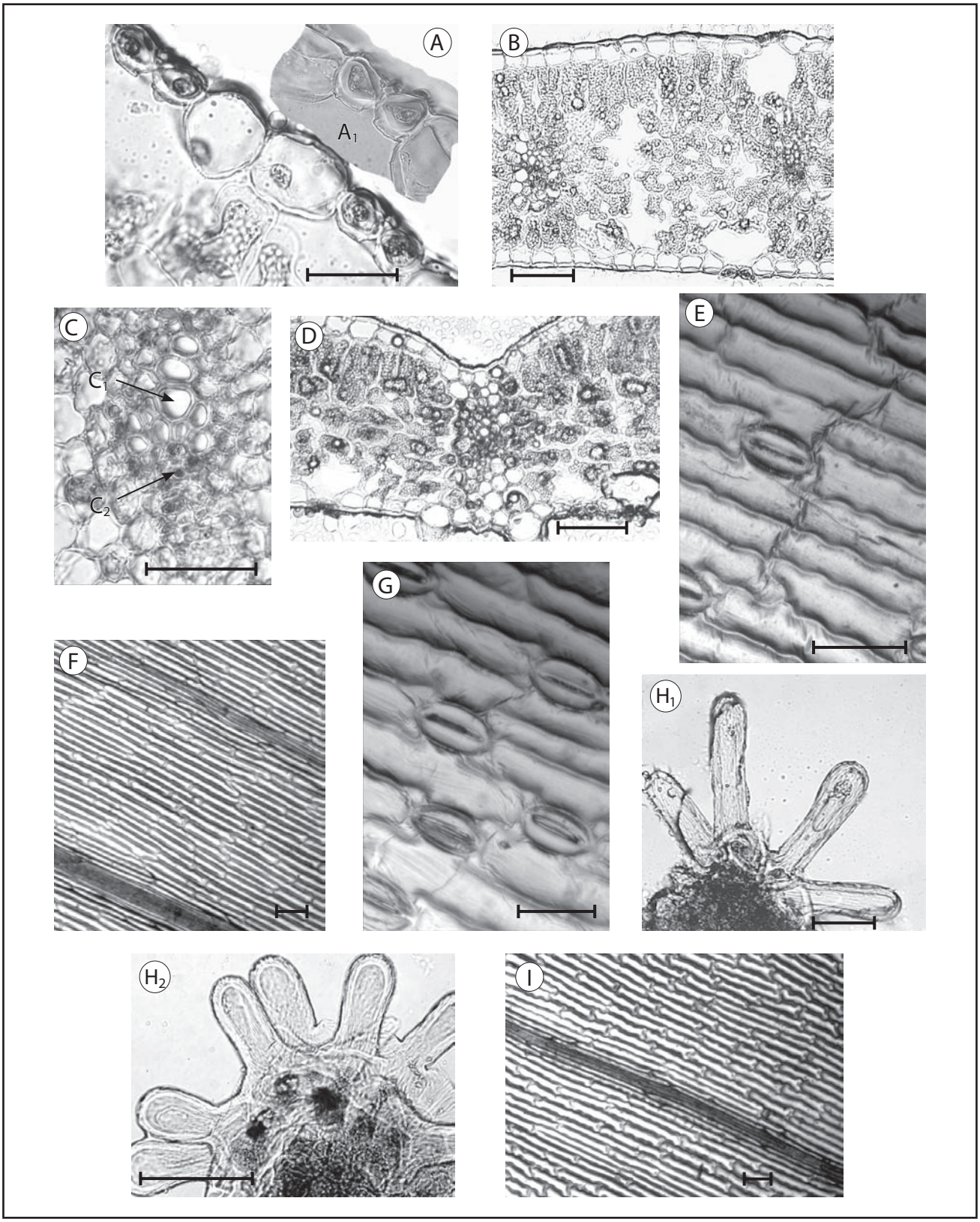

Fig. 3. ***L. bosniacum:*** **A** – single layer of epidermis with thick cuticle and stomata (Kladanj); $\mathbf{A_1}$ – detail; **B** – apical part of leaf blade, amphistomatic (Crepoljsko); **C** – collateral vein (Crepoljsko), $\mathbf{C_1}$ xylem, $\mathbf{C_2}$ phloem; **D** – basal part of leaf blade, hypostomatic with single layer, lobed palisade mesophyll (Crepoljsko); **E** – adaxial epidermis – apical part (Kladanj); **F** – adaxial epidermis, basal part (Kladanj); **G** – abaxial epidermis (Kladanj); $\mathbf{H_1}$ and $\mathbf{H_2}$ – trichomes (Bjelasnica); ***L. carniolicum***: **I** – adaxial epidermis.
Scale bars (F and I = 200 μm; B, D, E, G, = 100 μm; A, C, H_1, H_2 = 50 μm).

Individuals from Bjelasnica population had the highest stomatal density on adaxial (5.91) epidermis, Crepoljsko on abaxial (12.72), while individuals from Kladanj population had the lowest (abaxial 9.84; adaxial 4.65, Table 3). ANOVA test showed that populations significantly differed in abaxial ($F_{2, 59} = 15{,}007$, $p \leq 0.05$) as well as in adaxial ($F_{2, 59} = 126{,}402$, $p \leq 0.05$) stomatal density. Scheffe's test confirmed that only Kladanj population had both abaxial and adaxial stomatal density significantly diverse from the other two populations.

Individuals from Kladanj population had the higher mean value of stomata size (length 96.39 µm; width 58.58 µm) in comparison to population Crepoljsko (length 72.38 µm; width 49.76 µm) and Bjelasnica (length 80.41 µm; width 49.39 µm). Significant differences among investigated *L. bosniacum* populations were observed by ANOVA test in guard cells length ($F_{2,29} = 408.42$, $p \leq 0.05$ and 0.01) and their width ($F_{2,29} = 64.25$, $p \leq 0.05$ and 0.01). Scheffe's test confirmed that only Kladanj population had both stoma length and width significantly different from the other two populations, while stomata for Bjelasnica and Crepoljsko only differed significantly in length.

Discussion

According to our results pollen grains of *L. bosniacum* and *L. carniolicum* belonged to monosulcate pollen type. These results were in agreement with the findings of Kosenko (1999) for most of the investigated species of *Lilium.* Thickness of the columella wall for both species ranged from 1 to 2.2 µm (Figs 2E and 2G). These results also agreed with those found by Kosenko (1999) for genus *Lilium* (1.0–3.4 µm). *Lilium bosniacum* and *L. carniolicum* pollen grains had rectangular columellae.

The columellae heads (caput) in *L. bosniacum* were more curved than those of *L. carniolicum* (Figs 2E, 2G). Following its morphology, Baranova (1985) classified pollen grains of genus *Lilium* into three types: *martagon*, *callose* and *concolo*r. The pollen grains of *L. bosniacum* and *L. carniolicum* might be placed, with slight modification, into the *martagon* type.

Both taxa presented two types of lumina (rounded and rectangular) with no important differences in lumina size. SEM observation illustrated that for *L. bosniacum* both lumina types ranged from 1 to 8 µm (Fig. 2E, 2F). *Lilium carniolicum* lumina values mainly corresponded to this range other than the sporadic occurrence of rounded lumina less than 1 µm and longest rectangular lumina dimensions nearly 14 µm (Fig. 2C, 2G, 2H). The existence of two types of lumina in *L. bosniacum* and *L. carniolicum* could be explained by joining of rounded lumina into one rectangular friquently twice as long. *Lilium bosniacum* and *L. carniolicum* lumina sizes did not fall completely within their range for the genus *Lilium*. According to Kosenko (1999) sizes of lumina in the genus *Lilium* range from 1.7 µm to 17 µm.

Although, two of three *L. bosniacum* populations (Kladanj and Bjelasnica) belonged to habitats with atypical ecological conditions (see material and methods), there was no significant differences in size of pollen grains. Typical environmental conditions for *L. bosniacum* sites were described by Lakušić & Kutleša (1971): limestone or sometimes dolomite geological substrates, deep soils rich in nutrients, and altitudinal optimum from 1200 m to 1300 m. Our earlier studies found existence of B chromosomes in genomes of both Kladanj and Bjelasnica populations (Muratović & al. 2005). The molecular cytogenetic and molecular analyses revealed distinct genomic patterns for Kladanj population which are likely the consequence of adaptation to peridotite-serpentine soils (Muratović 2007; Muratović & al. 2010b). In addition, a high percentage of non-aborted pollen (85 % to 98 %) was observed, suggesting regular meiosis in all investigated populations.

Leaf anatomy investigations did not reveal any important differences in structure of epidermal, mesophyll layers and vascular tissue between *L. bosniacum* and *L. carniolicum* investigated populations. Stomata of both species belonged to the anomocytic type (Fig. 3A), but their distribution formed two distinct leaf types in these two species. While *L. carniolicum* had hypostomatic leaves with no stomata at adaxial epidermis (Fig. 2I), *L. bosniacum* had transitional ones, from hypostomatic to amphistomatic leaf type (Figs 2B, 2D, 2E, 2F, 2G). *Lilium bosniacum* populations had stomata on both epidermal sides although on adaxial epidermis stomata density decreased from the central part of the blade to the leaf base (Figs 2E, 2F). Differences between the two species were also evident in abundance of the trichomes. Košanin (1926) concluded that, also confirmed by our findings, in *L. carniolicum* trichomes were more abundant than in *L. bosniacum*.

The variation of stomata density and size among *L. bosniacum* populations revealed statistically significant differences. Our findings showed significantly lower density of abaxial and adaxial epidermis stomata in Kladanj population relative to other two populations (Table 3). This lower stomatal density might be explained by specific life conditions associated to a geological substrate (peridotite) that is not common for this species (Lakušić & Kulteša 1971). While stomatal density is low, stomata size in Kladanj population is significantly larger in relation to the other two populations (Table 3). The demonstration of significantly longer stomata of Kladanj and Bjelasnica populations in relation to Crepoljsko is consistent with the total DNA amount being slightly higher in Kladanj (68.06 pg) and Bjelasnica (67.97 pg) in comparison to Crepoljsko (67.71 pg), although these values are not significantly different (Muratović & al. 2010b). According to Hodgson & al. (2010) stomata size, as an ecologically important attribute that varies with life conditions, is positively correlated with genome size across a wide range of major angiosperm plant taxa. Earlier investigations about anatomical adaptations of plant species growing on serpentine or peridotite also showed that the populations from serpentine have larger stomata diameter compared to populations from other geological substrates (Ritter-Studnička 1963, 1964). Higher stomata density and lower stomata size were also confirmed for species *Commelina communis* L. by Smith & al. (1989). Performed Spearman's correlation test in this study additionally confirmed significant, moderate, negative correlation between the abaxial epidermis stomata density and their length.

Concluding remarks

The presented results emphasize stomata and pollen grain characteristics of two endemic species *L. bosniacum* and *L. carniolicum*. A significant differentiation in leaf types (hypostomatic – *L. carniolicum*, transitional /hypostomatic to aphistomatic/ – *L. bosniacum*) supported the treatment of both taxa as separate species (Fritsch 1909; Lakušić & Kutleša 1971; Muratović & al. 2005, 2010a, b). The examination of the stomata density and size among *L. bosniacum* populations confirmed stomata characters fluctuate with diverse life surroundings.

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