Wulfenia **25** (2018): 179–208

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Taxonomic revision and morphological analysis of Red Vanilla Orchid, *Nigritella miniata* (Crantz) Janchen 1960 (Orchidaceae-Orchideae) in the Julian and Dinaric Alps (Slovenia)

Igor Paušič, Igor Dakskobler, Boštjan Surina & Branko Dolinar

Summary: Floral morphological characters of Red Vanilla Orchid (*Nigritella miniata*) from the Julian and Dinaric Alps of Slovenia were studied and compared, the population from the Dinaric Alps was evaluated for the first time. 142 individual inflorescences and 114 flowers were examined in total, 18 morphological characters were measured. Based on Welch's ANOVA results and Games-Howell post hoc test, we revealed statistically significant differences between plants from all the observed localities in the majority of the floral characters, and also high morphological variability (standard deviation was observed) both within and between the localities. According to PCA and DFA results, no clear groups corresponding to *N. miniata, N. bicolor* or *N. hygrophila* were formed and a high degree of specimens overlapped. No clear morphological differences, at least between *Nigritella miniata* and *Nigritella bicolor,* were confirmed. Analysed material from the Dinaric Alps belongs to the single taxon, *Nigritella miniata* s. str. Due to the high degree in overlap of the majority of the sampled character values within and between the localities, we could confirm the existence of a single, but highly variable, red flowering taxon for Slovenia – *Nigritella miniata* s. str. The existence of the morphologically poorly separated variety *Nigritella miniata* var. *dolomitensis*, previously known as *Nigritella hygrophila* from the Triglav Lakes Valley, was not sufficiently confirmed in this study. High degree of morphological variability within and between the populations of Red Vanilla Orchid (*Nigritella miniata*) is most probably driven by somatic mutations, which also explain frequent misinterpretations in the field, but also the recent inconsistent nomenclature regarding *Nigritella miniata*.

Keywords: orchids, *Nigritella miniata*, *Nigritella bicolor*, *Nigritella hygrophila*, *Nigritella miniata* var. *dolomitensis*, floral morphological characters, Julian Alps, Dinaric Alps, Slovenia

Members of the genus *Nigritella* (Vanilla Orchids) are well-known to nature lovers and botanists visiting European mountain areas in the early summer. Since most of the *Nigritella* species have a similar habit and exhibit marked similarities in macro-morphological traits, which makes it difficult to identify them in the field (Bournérias et al. 1998; Brütsch 2000), the long-term ongoing interest of the *Nigritella* research was (and still is) the species taxonomy. Studies by Teppner and Klein have greatly contributed to the knowledge of this genus (Teppner 2004; Teppner & Klein 1990, 1993, 1998; Teppner & Ster 1996) but also that of Foelsche (Foelsche 2014, 2015; Foelsche & Zernig 2007; Foelsche & Heidtke 2011; Foelsche et al. 2017).

This genus constitutes a polyploid complex with a center of diversification in the Alps (Hedrén et al. 2000). Chromosome counts show that *Nigritella* comprises a number of diploid taxa with the somatic number $2n = 2x = 40$, and a series of polyploid taxa with chromosome numbers ranging from $2n = 60$ to $2n = 100$ (reviewed in Hedrén et al. 2017). In contrast to the dark flowered 'black' species (not the *N. nigra* complex!), *N. rhellicani*, *N. cenisia, N. gabasiana* and *N. ravnikii* which are diploid and reproduce sexually, taxa from the *N. miniata* complex (*N. miniata* s. lat.) are polyploids and reproduce by means of apomixis (Teppner & Klein

1985a, b). In the late 1980's and 1990's, extensive caryologic and embryologic studies dealing mainly with *Nigritella miniata* s. lat. were published by Teppner & Klein (1985a, b, 1990) in order to prove the existence of some newly described, rare polyploid species from the Eastern Alps such as *N. archiducis-joannis*, *N. stiriaca* and *N. widderi*. In the last years, further new species were described: *N. minor* (Foelsche & Zernig 2007), *N. bicolor* (Foelsche 2010) and *N. hygrophila* (Foelsche & Heidtke 2011).

Red Vanilla Orchid (*Nigritella miniata* s. lat.) is a group of morphologically highly variable (but not well defined!) taxa with a disjunct distribution ranging from the South-Eastern Alps and the Carpathians in the east to the Dinaric Alps in the south (Baumann & Künkele 1982). The Red Vanilla Orchid population in the Dinaric Alps is restricted to only a few localities on slopes of Mt. Snežnik, SW Slovenia. *Nigritella miniata* was and still is differently interpreted by European botanists and orchidophiles causing nomenclatural uncertainties and problems. Our knowledge on the red-flowering *Nigritella* taxa has changed considerably over time. Crantz (1769) provided the first written reports on *Nigritella miniata* from Rax-Schneeberg (Austria) using the name *Orchis miniata* (Lorenz & Perazza 2012). Wettstein (1889) interpreted all *Nigritella* taxa as part of the genus *Gymnadenia* and used the name *Gymnadenia rubra* for the same red-flowering Vanilla Orchids that were renamed to *Nigritella rubra* by Richter (1890). Since Janchen (1959), two names were used, *Nigritella rubra* (*Gymnadenia rubra*) and also *Nigritella miniata*, causing confusion within the scientific community (Lorenz & Perazza 2012). Two polyploids, *Nigritella dolomitensis* (Teppner & Klein 1998) and *Nigritella buschmanniae* (Teppner & Ster 1996), were described from Brenta (Dolomites). Lorenz & Perazza (2004) claim *Nigritella dolomitensis* is a synonym for *Nigritella rubra* s. lat. In the last decades, three new species were described, two of them from Styria: *Nigritella minor* (Foelsche & Zernig 2007) and *Nigritella bicolor* (Foelsche 2010). A third species, *Nigritella hygrophila* was described from the Passo Pordoi in the eastern Dolomites (Italy) (Foelsche & Heidtke 2011). *Nigritella rubra* (Wettst.) K. Richt. is claimed to have a fairly restricted distribution in Austria (Styria and Lower Austria).

Determination of the Red Vanilla Orchids proves to be problematic due to the vague morphological criteria, restricted morphological differences, high morphological variability of numerous floral characters, small floral elements in particular and due to their frequent misinterpretation in the past as almost impossible (Foelsche 2010). These taxa cannot be separated on the basis of their vegetative organs (Lorenz & Perazza 2012). From that point, it is not surprising that authors dealing with the taxonomic problems within the *Nigritella miniata* complex in the past came to different conclusions regarding the taxonomic status of the above mentioned taxa (Baumann et al. 2006; Boillat 2011; Delforge 2006, 2011; Kreutz 2004; Lorenz 2004; Lorenz & Perazza 2004; Perazza 2009; Teppner 2004, 2008; Wenker 2007).

Taxonomic status of some newly described taxa from the *Nigritella miniata* complex such as *Nigritella bicolor* (syn. *N. miniata* var. *bicolor*) and also *Nigritella hygrophila* (syn. *N. miniata* var. *dolomitensis*) remains questionable due to the lack of sufficient morphological or genetic support and still causes a degree of uncertainty among the scientists. *Nigritella bicolor* and *Nigritella hygrophila* were inadequately evaluated and described. Differentiation to other red taxa was provided, but the statistical approach was somewhat vague with a low number of the observed specimens or morphological characters. Lorenz & Perazza (2012) claim that the morphological differences between *Nigritella miniata*, *Nigritella hygrophila* and *Nigritella bicolor* are not significant enough to preserve their species status. They interpret *Nigritella dolomitensis* as a variety of *Nigritella miniata* and *Nigritella minor* as a good species (Lorenz & Perazza 2012).

Foelsche (2014) published an extensive study with new contributions to the *Nigritella miniata* group. The author clearly separates *Nigritella miniata*, *Nigritella hygrophila* and *Nigritella bicolor* based on floral morphology. No statistical analysis was performed in order to adequately evaluate these differences between the taxa which could make determination possible. On the other hand, Lorenz & Perazza (2012) published results of an extensive biometric investigation dealing with the Eastern-Alpine group of *Nigritella miniata* s. lat. Data were processed by multivariate discriminant analysis and evaluated additionally by scatter plot diagrams. As a result, both recently described taxa, *Nigritella bicolor* and *Nigritella hygrophila*, were revealed to be insufficiently differentiated from *Nigritella miniata* and from *Nigritella miniata* var. *dolomitensis* respectively, and to be classified as varieties or higher ranges. Furthermore, authors reveal no statistically significant differences in floral character values between *Nigritella miniata* and *Nigritella bicolor*. The same was applied to newly described *Nigritella hygrophila*.

In Slovenia, *Nigritella miniata* grows scattered across the Julian Alps, Karavanke Mts. (Perko 2004; Foelsche et al. 2017) and Dinaric Alps (Biasoletto 1846). Past reports from Kamnik-Savinja Alps remain unconfirmed. Already in 1967, Tone Wraber (mscr. 28.7.1967) used the name *Nigritella rubra* for specimens found in the area of Mt. Vrbanova Špica (the Triglav mountains in the Julian Alps). Ravnik (1990) provides one of the first distribution maps of the genus *Nigritella* in Slovenia. He mentioned the presence of *Nigritella rubra*, but only for Mt. Snežnik (Dinaric Alps). *Nigritella miniata* was reported in Slovenia for the first time by Martinčič et al. (1984), in the second edition of Mala flora Slovenije. Jogan (2000) and Martinčič et al. (2007) mentioned *Nigritella miniata* on Mt. Snežnik in the Dinaric Alps. The name *Nigritella miniata* was also used in other publications (Wraber 1990; Surina 2005; Dolinar 2015; Hedrén et al. 2017). In the third edition of Mala flora Slovenije (Martinčič et al. 1999) and also in the fourth one (Martinčič et al. 2007), the synonym *N. rubra* (Wettst.) K. Richt. was used. In the last decades, terminology dealing with Red Vanilla Orchids changed. For Slovenia, the occurrence of *Nigritella bicolor* (Foelsche 2010; Foelsche et al. 2017) and *Nigritella hygrophila* (Foelsche 2011) was reported (Foelsche 2010; Dakskobler et al. 2012, 2015; Dakskobler & Dolinar 2016; Dakskobler & Surina 2017; Foelsche et al. 2017) for the Julian and Dinaric Alps.

Biasoletto (1846) provided first records on the existence of Vanilla Orchids on Mt. Snežnik (Dinaric Alps). He named this taxon *Nigritella suaveolens* Koch. Ravnik (personal notice) and Mayer (1954) also noticed red flowering *Nigritella* specimens on southern slopes between summits of Mali and Veliki Snežnik in 1950. According to Surina (2005), Red Vanilla Orchids thrive scattered in four localities in the Mt. Snežnik area. Ravnik (2002) interpreted plants from Snežnik (also from Julian Alps!) as a single taxon, *Nigritella rubra*. The Austrian botanist Foelsche determined Red Vanilla Orchids from Snežnik as *Nigritella bicolor* (Foelsche 2010). Foelsche (2017) provided first information on the existence of two red flowering taxa from Mt. Snežnik, *Nigritella miniata* and *Nigritella bicolor*. *Nigritella bicolor* is, according to Foelsche (2017), rare on Mt. Snežnik. Different opinions on the presence of the two (or a single) red flowering taxa (taxon) in Dinaric Alps have been continued since then, mainly due to the lack of clear morphological criteria (diagnostic morphological values) for *Nigritella bicolor*.

According to the original description of *Nigritella bicolor* (Foelsche 2010), colour of the flowers (Klein 1996), labellum and inflorescence shape are the key characters to be considered. Papillosity of the bracts proves as an unreliable character. Foelsche (2010) points to the dimension of lateral sepals: *Nigritella bicolor* (1.5–2.4 mm, on average 2 mm) and *Nigritella miniata* (1.5–2.0 mm, on average 1.7 mm); petals: *Nigritella bicolor* (1.1–1.7 mm, on average 1.3 mm), *Nigritella miniata* (1.2–1.8 mm, on average 1.5 mm). Sepals and petals have almost the same width as *Nigritella rubra* (*Nigritella miniata*) in contrast to *Nigritella bicolor*, where the relation in width between sepals and petals is almost 2:1 (Foelsche 2010). Foelsche (2010) also points to the length of the spur: *Nigritella bicolor* (1.0–1.9 mm) and *Nigritella miniata* (0.7–1.4 mm). We can clearly see the high degree of overlapping in values of the above stated morphological characters that should divide these two taxa. Brighter, lowermost flowers in the case of *Nigritella bicolor* compared to flowers from the central part of the same inflorescence that are much darker, are also confusing. In the protologue, Foelsche (2010) stated that the different colouration of the flowers (brighter colouration of the lowermost flowers compared to the flowers in the middle of the inflorescence) is not a good, reliable character for *Nigritella bicolor*. One year later, Foelsche & Heidtke (2011) also denied the reliability of the first character, the relation in the width between sepals and petals.

The inflorescence shape is typical of *Nigritella hygrophila*. According to Foelsche (2011), the almost as high as wide inflorescence shape is the key character for *Nigritella hygrophila*. The colour of *Nigritella hygrophila* varies from dark red to dark scarlet red and ranges between *Nigritella miniata* and *Nigritella dolomitensis* (Lorenz & Perazza 2012). According to the authors, a narrow dorsal sepal is characteristic of *Nigritella hygrophila*, including petals which are much narrower than the sepals (Foelsche & Heidtke 2011). Sepals are relatively wide, often more than 2 mm. This taxon apparently thrives in moist, cool places.

Recently, Slovenian botanists have pursued the opinion that two red-flowering Vanilla Orchid taxa appear in Slovenia: the first one *Nigritella miniata* (*Nigritella rubra*) grows on Mt. Snežnik and supposedly also in some areas in the Julian Alps, and the second one, *Nigritella bicolor* sensu Foelsche (2010), is widely distributed in the Julian Alps. According to Dakskobler & Dolinar (2016) and Foelsche (2017), the third taxa, the *Nigritella hygrophila*, is also present in Slovenia. It can be found in the Triglav Lakes Valley (Julian Alps) and in the area of Lazoviški Preval, also in the Julian Alps.

We carried out this research due to the unsolved but still present taxonomic (and nomenclatural) questions in regard to *Nigritella miniata*, unreliable and often impossible determination of taxa with questionable diagnostic values for a specific character that should make the determination in the field (or lab) possible.

The aim of this particular study was:

1) to combine all published (and unpublished) data of Red Vanilla Orchid populations in Slovenia in order to make the first comprehensive distribution map. We plan to reveal how the plants from different localities were attributed in the past;

2) to reveal the degree of morphological variability between (and within) the localities of Red Vanilla Orchid in Julian and Dinaric Alps of Slovenia which could explain current misconceptions regarding the nomenclature of this particular group and also to morphologically evaluate population from the Dinaric Alps for the first time;

3) and to reveal if morphological differences explain the current taxonomic differentiation or just illuminate the geographic differentiation of the taxa. Does current systematics of Red Vanilla Orchid in the Julian and Dinaric Alps correspond with the described taxa? What is the valid nomenclature?

Materials and methods

Searching for data. Various sources, author's personal data, herbaria [LJU, LJM, LJS] and the FloVegSi database of Jovan Hadži Institute of Biology, ZRC SAZU (Seliškar et al. 2003) were searched in order to extract reliable data for *Nigritella miniata* s. lat. localities in Southeastern Calcareous Alps (Julian Alps, Karavanke Mts. and Kamnik-Savinja Alps) and in Dinaric Alps (Mt. Snežnik), Slovenia.

Field sampling and measurements. Six sampling populations were evaluated, four in the Julian and two in Dinaric Alps. Number of flowering specimens at each locality is low, not higher than 20 (40). Field sampling was performed in 2016 and 2017. In order to preserve Red Vanilla Orchid populations, inflorescences were measured in the field. The following two characters were measured: (1) Inflorescence length and (2) inflorescence width. At each locality, one flower per inflorescence was picked from the field. Fully opened, undamaged flowers from the basal ⅓ of the inflorescence were collected and preserved in 70% ethanol. The following sixteen floral characters were measured: labellum length, labellum width, left sepal length, left sepal width, dorsal sepal length, dorsal sepal width, right sepal length, right sepal width, left petal length, left petal width, right petal length, right petal width, ovary length, ovary width, spur length and spur width. Floral characters were examined and measured under the binocular stereoscopic microscope Nikon SMZ 1000 (8–80×). NIS Elements D 4.2 software was used for all the measurements.

Taxa determination based on available literature. We were about to test if, based on our own morphometric data (18 floral characters), the following three taxa could be separated: *Nigritella miniata*, *Nigritella bicolor* and *Nigritella hygrophila*. The following papers with original descriptions were used in order to extract characteristic values of the observed floral characters for those three taxa: Foelsche & Heidtke (2011), Foelsche (2010, 2014) and Lorenz & Perazza (2012).

Data analysis. Morphometric data for individual plants were summarised on an Excel v14.3 spreadsheet. Univariate and multivariate statistics of morphological data (continuous characters) obtained from inflorescences and flowers was performed. From univariate methods, Welch's ANOVA method was performed in order to evaluate differences in means between the sampled groups of plants per locality. Games-Howell post hoc test was used in order to reveal pairs with statistically significant differences ($p<0.05$) between values of the particular floral character. Shapiro-Wilk's test of normality was performed to test and ensure the normal distribution of data. Levene's test for equality of variances between groups of plants (per locality) was used. Mean values plus sample standard deviations for all metric data (characters) were calculated for each locality. Box plots and scatter plots for each character per locality were presented (median values, upper and lower quartiles, maximum and minimum values plus outliers). Multivariate statistics based on continuous characters were used. Multivariate statistics have already been widely performed by solving taxonomic problems on *Dactylorhiza*, *Epipactis*, *Ophrys*, *Platanthera*, *Serapias* (Tyteca & Gathoye 2000; Cristaudo et al. 2009; Lorenz et al. 2011; Lowe 2011) and *Nigritella* (Lorenz & Perazza 2012). Principal component analysis (PCA) based on a correlation matrix (18 reproductive characters) and discriminant function analysis (DFA), also based on a correlation matrix of 18 reproductive characters was performed. For statistical analysis SPSS was used (SPSS Inc. 2006).

Results

Distribution of Red Vanilla Orchid in the Julian and Dinaric Alps

In the territory of Slovenia, Red Vanilla Orchid is locally distributed, mainly across the Julian Alps, Karavanke Mts. and Dinaric Alps. There are also older, but in the last 30 years unconfirmed data available on the presence of taxa on Mt. Porezen (Julian pre-Alps, Cerkno Mts.) and Kamnik-Savinja Alps. In 1944–2017, 230 localities were detected (Supplement 1; Fig. 1). The name *Nigritella rubra* (Wettst.) K. Richt. was used for specimens from 33 localities (Dinaric Alps, Julian Alps and Karavanke Mts.) and *Nigritella miniata* s. lat. for a single locality in the Julian Alps. Authors attributed specimens from 20 localities (Dinaric Alps, Julian Alps and Karavanke Mts.) as *Nigritella miniata*. The name *Nigritella bicolor* was widely used for specimens from 163 localities (Dinaric Alps, Julian Alps and Karavanke Mts.) and *Nigritella hygrophila* for 22 localities (Julian Alps and Karavanke Mts.). The fact that various authors used two to three different names for specimens growing at the same localities in ten cases is very interesting (see Supplement 1).

Sampled localities. Four localities were sampled from Julian Alps (Fig. 2): Mt. Mangart (15 inflorescences and 17 flowers), Veliki Draški Vrh (later on Draški vrh) (24 inflorescences and 24 flowers), the Triglav Lakes Valley (18 inflorescences and 15 flowers) and Mt. Viševnik (17

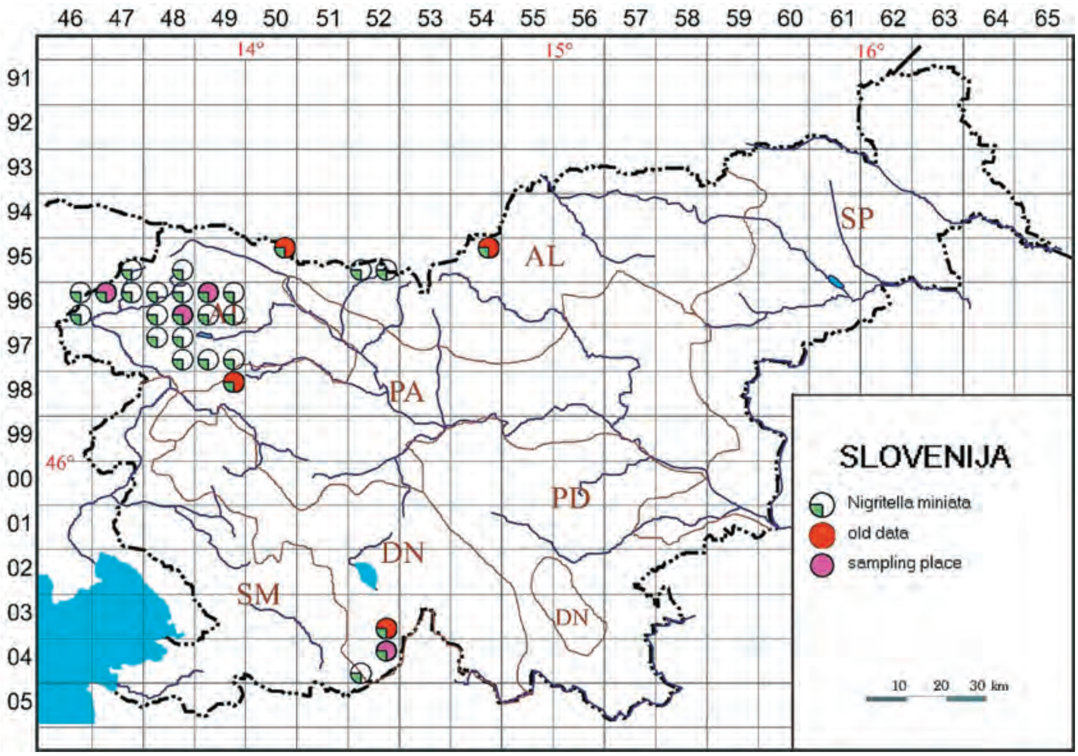

Figure 1. Map of Slovenia representing the distribution of Red Vanilla Orchid (*Nigritella miniata*) together with the sampled localities.

inflorescences and 25 flowers). Although one flower per inflorescence was sampled in the field at each locality; we took 2 flowers per inflorescence (2 inflorescences) at the locality Mangart and Viševnik (4 inflorescences). In the past, plants from the above mentioned localities were interpreted in a different way. Plants from Mangart area were attributed as *Nigritella miniata* (Supplement 1) or *Nigritella bicolor* (Foelsche 2010). Authors interpreted plants from Draški Vrh area as *Nigritella bicolor* or *Nigritella hygrophila*. In the Triglav Lakes Valley area three names were used in the past: *Nigritella miniata, Nigritella bicolor* (Dakskobler et al. 2015) and *Nigritella hygrophila*. For Mt. Viševnik four names were used in the past: *Nigritella rubra*, *Nigritella miniata*, *Nigritella bicolor* and *Nigritella hygrophila*.

Two localities on Mt. Snežnik were sampled from the only known population in the Dinaric Alps: Mali Snežnik (17 inflorescences, 15 flowers) and Grčovsko sedlo (51 inflorescences, 15 flowers). In the past, specimens from Dinaric Alps were interpreted as *Nigritella rubra*, *Nigritella miniata* or *Nigritella bicolor* (Supplement 1; Foelsche 2010).

Morphometric analyses

Table 1 shows mean values and standard deviation of 18 floral characters for each *Nigritella miniata* locality. In the case of 8 characters, the standard deviation within localities was greater than the total amount of variation between localities (inflorescence width, right sepal length, left sepal width, left petal width, right petal width, spur length, ovary length and ovary width).

Statistically significant differences in a specific morphological character between the localities are provided in Table 2 (Welch ANOVA $p \leq 0.01$ in all cases, Games-Howell post hoc test $p < 0.05$). Specimens from Draški Vrh (Julian Alps) have significantly different values of the inflorescence length compared to specimens from the other five localities. Specimens from the Triglav Lakes Valley have significantly different values of the width of the inflorescences compared to the other

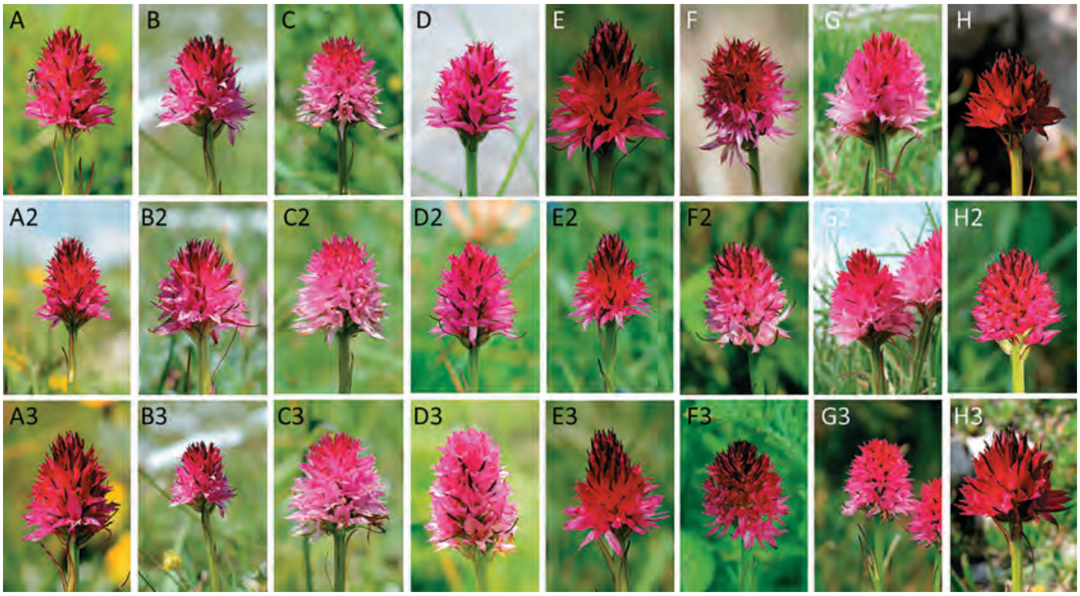

Figure 2. *Nigritella miniata*, variability of the inflorescence shape, colour and labellum shape. Specimens from various localities are presented: A – Mt. Snežnik (Dinaric Alps); B – Mangart (Julian Alps); C – Košutnikov Turn (Karavanke Mts.); D – Triglav Lakes Valley (Julian Alps); E – Planina Klek (Julian Alps); F – Viševnik (Julian Alps); G – Tosc (Julian Alps); H – Lazoviški Preval (Julian Alps).

Table 1. *Nigritella miniata* Morphological values for 6 localities, means and sample standard deviation (SD) for 18 morphometric characters. All values are in mm. R = right, L = left, D = dorsal.

Locality	1–6 together		1 Mangart		2 Veliki Draški Vrh		3 Mali Snežnik		4 Grčovsko Sedlo		5 Triglav Lakes Valley		6 Viševnik	
N (inflorescences/florets)	142/114		15/17		24/24		17/15		51/15		18/15		17/25	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Character														
Infloresc. length	21.87	4.07	18.60	3.46	26.67	2.29	19.29	2.49	22.63	3.34	21.00	2.20	21.47	3.66
Infloresc. width	15.41	3.11	15.80	3.41	14.75	1.51	14.17	3.36	16.47	3.31	19.29	2.58	14.88	3.22
R sepal length	6.45	0.91	5.34	0.55	7.41	0.55	6.05	0.78	6.17	0.51	6.14	0.49	6.95	0.66
R sepal width	1.67	0.40	1.50	0.39	2.08	0.31	1.29	0.34	1.55	0.29	1.57	0.17	1.75	0.31
L sepal length	6.52	0.91	5.55	0.68	7.42	0.56	6.07	0.78	6.11	0.40	6.17	0.50	7.17	0.63
L sepal width	1.65	0.38	1.42	0.44	1.99	0.26	1.33	0.38	1.49	0.22	1.63	0.21	1.80	0.24
D sepal length	6.16	0.96	4.97	0.63	7.16	0.50	5.73	0.82	5.96	0.33	5.74	0.67	6.76	0.60
D sepal width	1.53	0.30	1.35	0.26	1.78	0.21	1.26	0.27	1.41	0.25	1.58	0.25	1.63	0.21
L petal length	5.61	0.85	4.66	0.74	6.62	0.43	5.14	0.68	5.22	0.36	5.45	0.38	5.92	0.56
L petal width	1.29	0.31	1.10	0.42	1.51	0.18	1.10	0.34	1.20	0.23	1.29	0.18	1.35	0.24
R petal length	5.67	0.82	4.81	0.48	6.67	0.41	5.21	0.62	5.20	0.46	5.44	0.39	6.05	0.63
R petal width	1.29	0.29	1.12	0.28	1.45	0.24	1.17	0.37	1.21	0.19	1.31	0.13	1.37	0.31
Labellum length	7.06	0.89	6.20	0.59	8.07	0.40	6.35	0.50	6.57	0.41	7.11	0.88	7.34	0.69
Labellum width	3.67	0.71	2.99	0.69	4.49	0.29	3.30	0.64	3.45	0.34	3.41	0.32	3.87	0.49
Spur length	1.33	0.21	1.16	0.16	1.42	0.14	1.19	0.24	1.23	0.18	1.53	0.14	1.38	0.12
Spur width	0.98	0.19	0.92	0.18	1.07	0.14	0.81	0.19	0.85	0.13	1.13	0.16	1.00	0.13
Ovary length	3.27	0.32	2.96	0.19	3.47	0.33	3.26	0.36	3.21	0.29	3.41	0.17	3.22	0.28
Ovary width	1.59	0.31	1.88	0.35	1.64	0.27	1.37	0.18	1.40	0.13	1.68	0.29	1.54	0.26

Table 2. Welch's ANOVA results, statistically significant differences in morphological characters between Red Vanilla Orchid populations. Legend: 1 – Mangart, 2 – Draški Vrh, 3 – Mali Snežnik, 4 – Grčovsko Sedlo, 5 – Triglav Lakes Valley, 6 – Viševnik.

Character	Welch ANOVA	Games-Howell post hoc (p<0.05)
Inflorescence length	p≤0.01	1-2, 2-3, 2-4, 2-5, 2-6
Inflorescence width	p≤0.01	1-5, 2-5, 3-5, 4-5, 5-6
R sepal length	p≤0.01	1-2, 1-4, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-6, 4-6, 5-6
R sepal width	p≤0.01	1-2, 2-3, 2-4, 2-5, 2-6, 3-5, 3-6
L sepal length	p≤0.01	1-2, 1-5, 1-6, 2-3, 2-4, 2-5, 3-6, 4-6, 5-6
L sepal width	p≤0.01	1-2, 2-3, 2-4, 2-6, 3-5, 3-6, 4-6
D sepal length	p≤0.01	1-2, 1-4, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-6, 4-6, 5-6
D sepal width	p≤0.01	1-2, 1-5, 1-6, 2-3, 2-4, 2-6, 3-5, 3-5, 3-6
L petal length	p≤0.01	1-2, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-6, 4-6
L petal width	p≤0.01	1-2, 2-3, 2-4, 2-5, 2-6,
R petal length	p≤0.01	1-2, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-6, 4-6
R petal width	p≤0.01	1-2, 2-4
Labellum length	p≤0,01	1-2, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-5, 3-6, 4-6
Labellum width	p≤0.01	1-2, 1-6, 2-4, 2-3, 2-5, 2-6,
Spur length	p≤0.01	1-2, 1-5, 1-6, 2-3, 2-4, 3-5, 4-5
Spur width	p≤0.01	1-5, 2-3, 2-4, 3-5, 3-6, 4-5, 4-6
Ovary length	p≤0.01	1-2, 1-5, 1-6, 2-6
Ovary width	p≤0.01	1-3, 1-4, 2-3, 2-4, 4-5, 4-6, 3-5, 3-6

five localities. Considering petals, specimens from the Dinaric Alps and from Draški Vrh are significantly different from the other three localities, but no clear conclusions can be made due to numerous statistically significant pairs (Table 2). Specimens from Mangart, Mali Snežnik and Viševnik proved to be statistically different from most of the other localities. Considering labellum shape (both length and width) again, locations Mangart and Draški Vrh significantly differ from the other sites. By analysing spur dimensions, we see numerous statistically significant pairs of localities. In regard to ovary width, both localities from the Dinaric Alps seem the most specific.

Both the PCA (Table 3, Fig. 3A) and discriminant function analysis (Table 4, Fig. 3B) were performed on all characters and localities gave similar results. No clear groups (corresponding to *N. miniata*, *N. bicolor* or *N. hygrophila*) were formed, the majority of specimens overlapped. In PCA, taxa were not separated along the first and second axis in the ordination graph, which represents 50.79% and 12.13% of the total variation among localities. The majority of the quantitative floral characteristics contributed almost equally to division along the first axis, as seen from the eigenvector values (Table 3). Canonical discriminant function analysis shows that there is not enough information in quantitative characters for clear and unequivocal separation of taxa. The first canonical axis (55.70% of variation) is most closely correlated with characters: inflorescence length, left petal length and left sepal width (Table 4). The second canonical axis

Table 3. Eigenvectors expressing correlation of characters with principal components (axes 1–3) in morphometric analysis of six localities of *Nigritella miniata*.

Character	Axis 1	Axis 2	Axis 3
Inflorescence length	0.675	0.179	0.458
Inflorescence width	-0.025	0.753	0.239
Ovary length	0.401	0.110	0.643
Ovary width	0.022	0.740	0.106
Labellum length	0.790	-0.118	0.067
Labellum width	0.836	-0.280	0.014
L sepal length	0.838	-0.247	-0.051
L sepal width	0.760	0.190	0.018
D sepal length	0.866	-0.294	0.038
D sepal width	0.755	0.306	-0.037
R sepal length	0.859	-0.218	0.095
R sepal width	0.784	0.158	0.034
L petal length	0.884	-0.227	-0.023
L petal width	0.760	0.052	-0.217
R petal length	0.891	-0.202	0.049
R petal width	0.644	0.223	-0.259
Spur width	0.522	0.570	-0.311
Spur length	0.640	0.336	-0.378

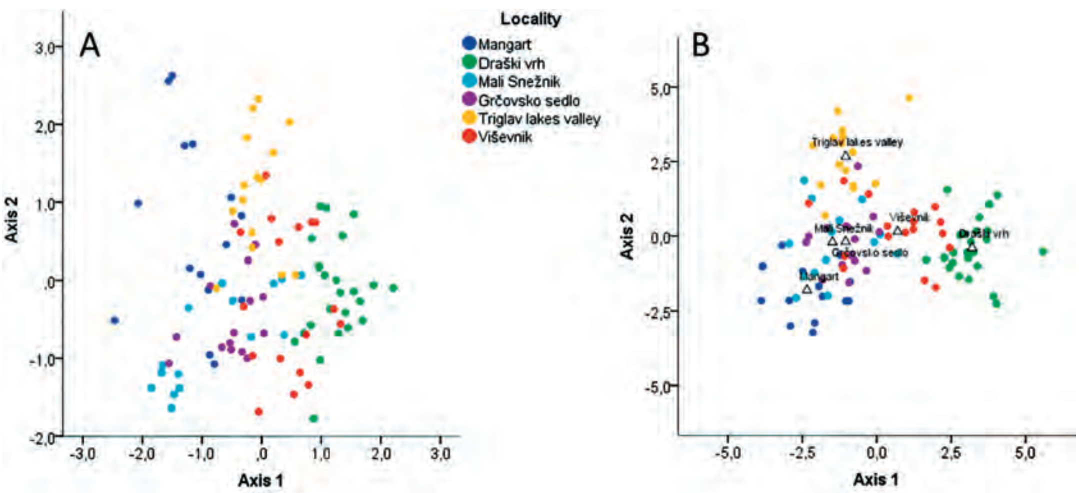

Figure 3. A – Principal components analysis of *Nigritella miniata* localities from the Julian and Dinaric Alps based on 18 morphological characters (Table 1). Axes 1 and 2 explain 50.79% and 12.13% respectively of the total variation. B – Discriminant function analysis of *Nigritella miniata* localities from the Julian and Dinaric Alps based on 18 morphological characters (Table 4). Axes 1 and 2 explain 55.70% and 22.30% respectively of the total variation.

Table 4. Total canonical structure expressing correlation of morphological characters with canonical axes in discriminant analysis of six localities of *Nigritella miniata*.

Character	Axis 1	Axis 2	Axis 3
Inflorescence length	0.614	-0.307	-0.345
Inflorescence width	-0.306	0.971	0.233
Ovary length	0.029	0.505	-0.228
Ovary width	0.057	-0.631	0.537
Labellum length	0.214	0.306	0.396
Labellum width	0.008	0.146	0.060
L sepal length	0.189	-0.189	-0.462
L sepal width	0.436	-0.229	0.334
D sepal length	-0.133	0.160	-0.408
D sepal width	0.160	0.072	0.188
R sepal length	-0.168	0.141	-0.399
R sepal width	0.046	-0.462	0.307
L petal length	0.562	0.056	0.160
L petal width	-0.386	-0.023	0.314
R petal length	0.338	-0.384	0.483
R petal width	-0.123	0.273	-0.672
Spur width	-0.161	-0.028	0.584
Spur length	-0.036	0.819	-0.344

(22.30% of variation) is most closely correlated with the following characters: inflorescence width, spur length and ovary width. In order to show the variability of the most discriminant characters, we have performed graphic tests (box-plots) for median comparisons (Figs 4, 5).

Regarding nomenclature, how many taxa are *miniata*, *hygrophila* or *bicolor*?

Past decisions regarding the nomenclature were inconsistent mainly due to the high morphological diversity of the observed characters within localities which could be, as already presented, even higher than between localities, but also due to the certain amount in overlapping of character values. In the past, two or even three different taxon names were in use literally for the same groups of plants at the same localities (Supplement 1). Certain characters, such as inflorescence shape, labellum shape, spur shape, width and length of sepals and petals should have taxa-specific values (Table 5) in order to enable the determination.

Figure 6A represents width of sepals and petals. According to literature, this ratio should enable the differentiation of at least *Nigritella miniata* and *Nigritella bicolor*. Two lines are shown: the upper one (y = x) meaning that both characters are of the same width which is, according to literature, a characteristic ratio of *Nigritella miniata* and the lower line (y = 0.5*x), the ratio characteristic of *Nigritella bicolor*.

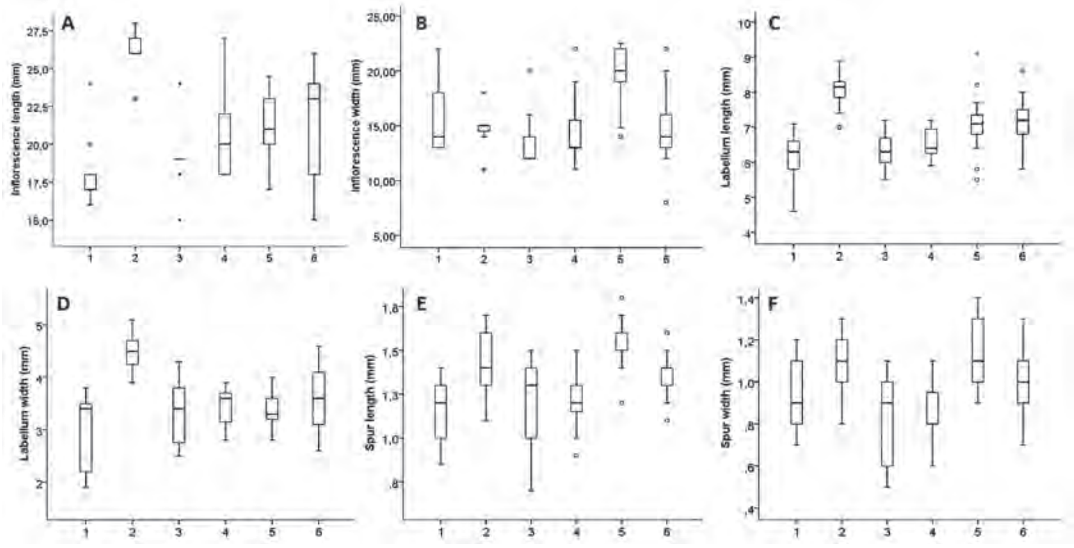

Figure 4. Boxplots representing values for *Nigritella miniata*. Floral characters from six localities (x-axis): 1 – Mangart (Julian Alps); 2 – Draški Vrh (Julian Alps); 3 – Mali Snežnik; 4 – Grčovsko Sedlo; 5 – Triglav Lakes Valley (Julian Alps); 6 –Viševnik (Julian Alps). Rectangles show 25th and 75th percentiles, bold lines show medians and whiskers show 10th to 90th percentiles.

According to literature, petals are much narrower than sepals in *Nigritella hygrophila*. Sepals could reach 2 mm in width in *Nigritella hygrophila*, but are narrower than 2 mm in *Nigritella miniata*. In *Nigritella bicolor*, sepals reach a wider spectrum: 1.3–2.6 mm in width. Width of sepals also varies greatly within the same locality (Fig. 6A). Vast majority of the analysed specimens have ratios between these two lines. Specimens from all six surveyed localities (Red Vanilla Orchids native to Slovenia) exhibit ratios that are located in the close proximity to both lines, but the majority

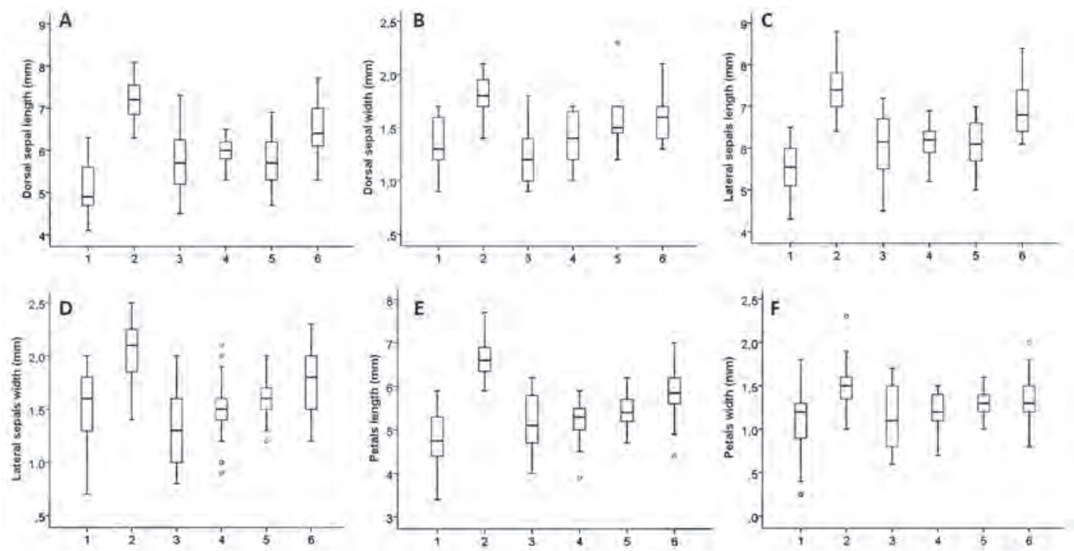

Figure 5. Boxplots representing values for *Nigritella miniata*. Floral characters from six localities (x-axis): 1 – Mangart (Julian Alps); 2 – Draški Vrh (Julian Alps); 3 – Mali Snežnik; 4 – Grčovsko Sedlo; 5 – Triglav Lakes Valley (Julian Alps); 6 –Viševnik (Julian Alps). Rectangles show 25th and 75th percentiles, bold lines show medians and whiskers show 10th to 90th percentiles.

Table 5. Characteristical values of *Nigritella miniata*, *Nigritella bicolor* and *Nigritella hygrophila* according to Foelsche & Heidtke (2011), Foelsche (2010, 2014) and Lorenz & Perazza (2012).

Character	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Inflorescence	15(28) × 13(20) mm	16(32) × 13(23) mm	17(29) × 15(23) mm
Lateral sepals	5.2(7.0) × 1.3(2.5) mm	5.5(7.7) × 1.3(2.6) mm	6.0(6.2) × 1.9(2.2) mm
Dorsal sepal	5.2(6.7) × 1.2(2.0) mm	5.1(7.0) × 1.5(2.2) mm	6.0(6.1) × 1.9(2.2) mm
Petals	4.8(6.0) × 1.2(2.0) mm	4.4(6.4) × 1.0(1.7) mm	5.6(5.7) × 1.0(1.5) mm
Labellum	6.1(8.2) × 2.6(4.7) mm	6.2(7.6) × 3.6(5.2) mm	7 × 3.0 (4.4) mm
Spur	0.9–1.4 mm	1.0–1.8 mm	1.0(1.2)–1.0(1.1) mm
Ovary	2.8 × 4.2 mm	3.0(4.5) × 2.2(2.7) mm	3 mm

of the samples lie in between these lines. This ratio varies considerably within each locality and between localities. Width of sepals and petals clearly does not provide distinction between the previously mentioned three taxa.

According to literature, a short hemispheric inflorescence is typical of *Nigritella hygrophila*. Also, the inflorescences of both *Nigritella miniata* and *Nigritella bicolor* should be more or less elongated (clearly longer than wide). According to some authors, the inflorescence shape, almost as high (long) as wide is the key character (also shape of the labellum and colour) for *Nigritella hygrophila*. In *Nigritella miniata* and *Nigritella bicolor*, short inflorescences also occur regularly. Line y = x in Fig. 6B indicates same inflorescence length and width. The vast majority of specimens has

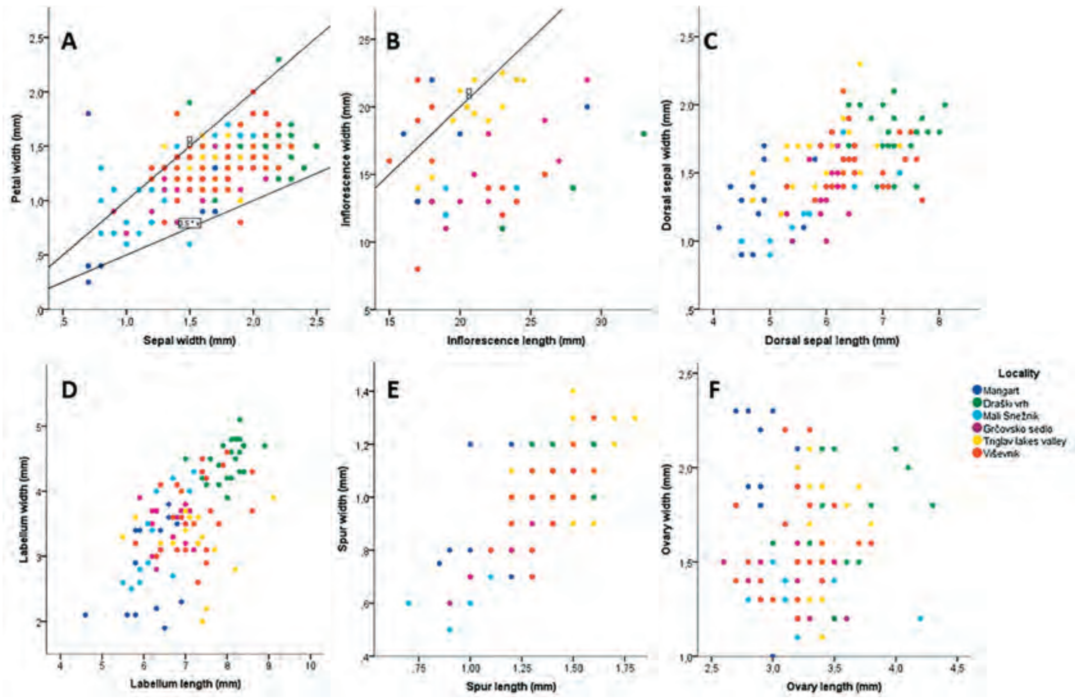

Figure 6. Scatter diagram graphs representing data for measured floral characters from six Red Vanilla Orchid (*Nigritella miniata*) populations.

elongated inflorescences, typical of *Nigritella miniata* and *Nigritella bicolor*. We see that in the proximity of this line, specimens from the Triglav Lakes Valley are almost aggregated. Specimens from other localities also exhibit globular, hemispheric shape of inflorescences: specimens from Viševnik, Mangart and Mali Snežnik. In the localities Mangart, Draški Vrh and Viševnik, we have both specimens with hemispherical and elongated inflorescences growing side by side.

Characteristic values of dorsal sepals overlap to a high degree in all three taxa. Specimens with short and narrow dorsal sepals (Fig. 6C) were detected in the Dinaric Alps (both localities), but also in plants from the Julian Alps (Viševnik, Triglav Lakes Valley and Draški Vrh). On the other hand, plants from the same localities (Mangart, Triglav Lakes Valley, Viševnik and Draški Vrh (but also from the Dinaric Alps) have long (and wide) dorsal sepals. Again, dorsal sepal proves to be an unreliable character in order to separate taxa from *Nigritella miniata* complex.

Labellum shape (Fig. 6D) proved to be a reliable and taxonomically important feature in *Nigritella*. In *Nigritella miniata,* labellum reaches 6.1–8.2 mm in length and is 2.6–4.7 mm wide. Lip is 6.2–7.6 mm long and (3.6)4.0–5.0 mm wide in *Nigritella bicolor* and 7.0 mm long and 3.0–4.4 mm wide in *Nigritella hygrophila*. Like other analysed characters, there is a high degree of overlap of measured values of labellum length and width between the analysed 6 localities, no clear groups are shown in Fig. 6D. In the case of labellum shape in particular, we expected a clear differentiation between the taxa.

Another taxonomically important character of *Nigritella* (Fig. 6E) are the proportions (especially the length) of the spur. According to literature, the spur should be somewhere between 1–1.2 mm long and 1.0–1.1 mm wide in *Nigritella hygrophila*, 0.9–1.4 mm long in *Nigritella miniata* and 1.0–1.8 mm long in *Nigritella bicolor*. We analyzed specimens with short and long spurs growing alongside, growing on the same localities. The dimension of the spur (length and width) proves to be a problematic, questionable character in order to make clear conclusions on the taxonomic status.

Discussion

Variation in organisms attracts the attention of biologists since it provides clues about evolutionary processes (Bernardos et al. 2005). The presence of ploidy variation within plant genera and, in some cases, among populations of single species raises major ecological questions (Lewis 1980). In genus *Nigritella* in particular, a polyploid complex is (was) often associated with vexing taxonomic problems (Ståhlberg 1999). Although apomictic lineages such as tetraploid *Nigritella miniata* lack the recombination, segregation, syngamy and gene flow characteristic of sexual species, populations may still express a certain degree of variability as they are often composed of somewhat divergent lineages (Hedrén et al. 2017). Clones of apomicts can be recognized by small (but constant) differences in morphological characters, and may even be recognized as a separate species (Templeton 1989; Hedrén et al. 2017). As a consequence, some authors have applied more relaxed, inconsistent species delimitation principles, which has resulted in several new species of *Nigritella* with restricted distributions and unclear status (Hedrén et al. 2017).

According to our Welch's ANOVA results (and Games-Howell post hoc test), specimens of *Nigritella miniata* from the analysed six localities (populations) vary significantly in the majority of the observed characters in a statistically significant manner. We revealed a large proportion of variance of numerous characters within the specimens from the same localities, growing close to each other. In the case of 8 observed morphological characters, standard deviation within localities was greater than the total amount of variation between localities (inflorescence width, right sepal length, left sepal width, left petal width, right petal width, spur length, ovary length and ovary width).

Hedrén et al. (2017) described overall genetic differentiation patterns within *Nigritella miniata* and proved a phylogeographic structure: different genotypes within localities are on average more closely related than different genotypes at different localities. This could be confirmed based on morphology. DFA results revealed aggregations of the specimens from each locality. At the same time, a high percentage of specimens overlapped with those from other localities. Differences became larger with increasing distance between the localities being compared, demonstrating that many genotypes are of local and regional origin. Because polyploid *Nigritella miniata* reproduce apomictically, individuals within localities are not connected by gene flow, and species do not comply with the biological species concept (Hedrén et al. 2017). Although the *Nigritella miniata* group may have originated from a single polyploidization event, the group still exhibits an apparent morphological diversity which has become manifested in the segregation into several new taxa at or below species level (Hedrén et al. 2017).

In Slovenia, the name *Nigritella bicolor* is widely used, since the species was described in 2010. Numerous authors report the existence of this taxon in the Julian and Dinaric Alps. *Nigritella miniata* was reported on the same localities. The morphological criteria for *Nigritella bicolor* overlap with the values characteristic of *Nigritella miniata* in a high degree. According to Hedrén et al. (2017), *Nigritella bicolor* is genetically heterogeneous relative to the remainder of *Nigritella miniata*. The authors highlight the need for further evidence whether such an emended taxon is possible to be separated from *Nigritella miniata* on the basis of morphology or any other biologically relevant data. PCA and DFA results in this study based on all 18 floral characters were similar. No clear groups corresponding to *Nigritella miniata* and *Nigritella bicolor* were formed. The majority of the specimens from different localities overlapped. Canonical discriminant function analysis shows that there is not enough information in quantitative characters for clear and unequivocal separation of taxa. *Nigritella miniata* is apparently an old apomict, which has become widely distributed in time, and during its expansion it has gradually accumulated somatic mutations with the effect that regional 'populations' have become genetically (and also morphologically!) differentiated from each other (Hedrén et al. 2017). Mutations on a local scale must have affected the morphology of the species. That is why we can observe significant regional and local differences in the majority of the observed floral characters.

According to the present study, local, geographical variation of the studied floral characters disable determination of the taxa, based on published morphological criteria. Specimens from some localities express a low degree in variability of certain characters in contrast to the specimens from other localities. The generally weak morphological differentiation of the studied polyploid taxa supports the hypothesis of a group of close allies as already mentioned by different authors (Lorenz & Perazza 2002; Hedrén et al. 2017) and reflects in the results of the morphometric analysis. In the field, scientist should focus on the whole spectrum of morphological variability of specimens within a specific locality rather than just isolating a single one and determining it using published (but vague!) criteria which often bring us to different, not well supported conclusions.

In this study, one qualitative character was not included in the analyses, inflorescence colour. Presumed *Nigritella miniata* var. *dolomitensis* from the Triglav Lakes Valley (also present on

Lozoviški preval, Julian Alps, Fig. 1H) exhibits darker colour than specimens from other localities across the Julian and Dinaric Alps. This character, the darker red colouration, is not present in all the observed specimens from this locality! Specimens also grow in more mesic/hygrophilous sites. Its inflorescences are (but not always!) hemispherical. Such groups of plants from Julian Alps (Triglav Lakes Valley and Lazoviški preval area) were determined as *Nigritella hygrophila* (Dakskobler & Dolinar 2016; Foelsche 2017) in the past, prior to the study of Hedrén et al. 2017. According to Hedrén et al. (2017) molecular data did not distinguish *N. hygrophila* from other *N. miniata* morphotypes at *locus classicus* – Passo Pordoi (Dolomites), but rather indicated that the taxon is polyphyletic relative to the reminder of *N. miniata* at the local scale (Hedrén et al. 2017). *Nigritella miniata* var. *dolomitensis* (*Nigritella hygrophila*) that is apparently present but rare in the Julian Alps and differs from plants growing in other localities could not be fully confirmed based on our results. In some localities (Mangart, Viševnik and Mt. Snežnik), specimens with almost white flowers in the lower half of the inflorescences occur. This character does not have any taxonomic importance considering high morphological variation and instable values of all the other evaluated floral characters. Also in *Nigritella lithopolitanica*, a South-eastern Alpine endemic (Ravnik 1978), inflorescences with almost white lowermost flowers frequently occur among specimens with uniform coloured inflorescences.

The results of the present morphological study (based on quantitative data only) support the recognition of a single species of Red Vanilla Orchid for Slovenia: *Nigritella miniata* s. str. The morphologically poorly separated variety, *Nigritella miniata* var. *dolomitensis*, previously known as *Nigritella hygrophila* (Foelsche 2011) could not be sufficiently supported in this study. Blažič (2017) distinguishes between two red-flowering taxa from *Nigritella miniata* s. lat. for Slovenia based on vegetative and reproductive morphological characters: *Nigritella miniata* s. str. and a second one from the Triglav Lakes Valley, but the author does not provide any name for this second taxon. According to this author, the differentiation of these two taxa based on morphological criteria is highly problematic if not impossible. Our results support some previous studies (Lorenz & Perazza 2012): no statistically significant morphological differences were confirmed in the observed 18 floral characters between the three taxa mentioned for Slovenia in previous studies, especially not between *Nigritella miniata* and *Nigritella bicolor*. High degree of morphological variability is caused by somatic mutations which also explain frequent misinterpretations in the field and also recent inconsistent nomenclature regarding *Nigritella miniata*. Morphological differences (variability of the observed floral characters) within and between the localities could not explain the current taxonomic differentiation of *Nigritella miniata* and *Nigritella bicolor*, they just illuminate geographically differentiation of the single taxon, *Nigritella miniata* s. str.

As shown by Lorenz & Perazza (2012), there are no significant morphological differences between *Nigritella miniata* from *locus classicus* and investigated samples from other areas including Styria attributed as *Nigritella miniata* or *Nigritella bicolor* by different authors. According to Hedrén et al. (2017), most of the red *Nigritella* samples from these areas and also the few from Slovenia do not show sufficient genetic differences to justify a separation on species or subspecies level based on analysis of microsatellites of non-coding regions of the genome (nuclear as well as plastid genome). Only samples from a restricted area in Styria including the *locus classicus* of *Nigritella bicolor* s. strictiss. from Trenchtling show a recognizable genetic differentiation from *Nigritella miniata*, for which however no distinct morphological differentiation from other bicoloured entities, genetically attributable to *Nigritella miniata*, has been reported. On the contrary, they have been classified as morphologically belonging to presumed *Nigritella bicolor* from the whole *Nigritella miniata* area, including Julian and Dinaric Alps. Concerning *Nigritella hygrophila* from *locus classicus*, genetic investigations reported in Hedrén et al. (2017) did not reveal reliable genetic differences from other populations of *Nigritella miniata* var. *dolomitensis* (*Nigritella dolomitensis*) collected in the Dolomites, to justify a separation of it. This corresponds completely with the above mentioned morphological studies based on extensive biometric evaluations. However, for all the Dolomite populations together, segregation from *Nigritella miniata* seems to be genetically supported. Based on morphology, the subspecies level may be more suitable than the variety level, as formerly favoured by Lorenz & Perazza (2012).

The problem of the correct name, *Nigritella miniata* or *Nigritella rubra,* which has been differently seen by European botanists and orchidophiles for a long time, now also seems to be resolved as the NCVP did not recommend the proposal to conserve *Gymnadenia rubra* over *Orchis miniata*, confirming *Nigritella miniata* – in this context lecto- and epitypified – as a correct name (Applequist 2012; Baumann & Lorenz 2011). The available genetic data in Hedrén et al. (2017) from Slovenian samples support our recent morphometric study by the hitherto investigated red-flowering *Nigritella* populations from Slovenia attributing to a single taxon, Red Vanilla Orchid *Nigritella miniata* s. str.

Acknowledgements

We thank ARSO for permission needed in order to be able to take flowers of *Nigritella miniata* from the habitat (ARSO no. 35603-2/2013-4, 25.5.2013). Sincere thanks to V. Postružnik and A. Šegula for their assistance during measurements of the observed characters and Ž. Cenc for his assistance in the field. Sincere thanks to P. Strgar for pictures from his collection (Fig. 2G, H) and to F. Poljšak for pictures from his collection (Fig. 2E). We thank B. Vreš (Jovan Hadži Institute of Biology, ZRC SAZU) for his help in preparation of Fig. 1. Sincere thanks to A. Žnidaršič for the information on the locality Sleme below Veliki Snežnik. Thanks to B. Anderle, V. Leban, M. Lipovšek, F. Poljšak, I. Papež, J. Peroš, V. Schein, J. Stergaršek, P. Strgar, M. Šenica, M. Tišler, A. Trnkoczy and B. Zupan for their help and support in the field.

References

Applequist W. L. (2012): Report of the Nomenclature Committee for Vascular Plants: 64. – Taxon **61**(5): 1108–1117.

Baumann H. & Künkele S. (1982): Die wildwachsenden Orchideen Europas. – Stuttgart: Franckh.

Baumann H., Künkele S. & Lorenz R. (2006): Die Orchideen Europas mit angrenzenden Gebieten. – Stuttgart: Ulmer.

Baumann H. & Lorenz R. (2011): Proposal to conserve the name *Gymnadenia rubra* (*Nigritella rubra*) against *Orchis miniata* (Orchidaceae). – Taxon **60**(6): 1775–1776.

Bernardos S., Crespi A., Del Rey F. & Amich F. (2005): The section Pseudophrys (*Ophrys*, Orchidaceae) in the Iberian Peninsula: a morphometric and molecular analysis. – Bot. J. Linn. Soc. **148**: 359–375.

Biasoletto B. (1846): Escursioni botaniche sullo Schneeberg (monte nevoso) nella Carniola. – Trieste: I. Papsch & Comp.

Blažič B. (2017): Taksonomsko-morfološka analiza murk (*Nigritella* spp.) v Sloveniji. – Master thesis: Univ. v Ljubljani, Biotehniška fakulteta, Študij ekologije in biodiverzitete.

Boillat V. (2011): *Nigritella rubra*: Eine andere Deutung des Wettstein-Artikels „Untersuchungen über *Nigritella angustifolia*" von 1889. – J. Eur. Orch. **43**(4): 847–862.

Bournérias M., Demange M., Démares M., Engel R., Gerbaud O., Melki F., Quentin P. & Tyteca. D. (1998): *Nigritella* L.C.M. Richard. – In: Bournérias M. [ed.]: Les Orchidées de France, Belgique et Luxembourg. – Paris: Parthénop.

Brütsch J. P. (2000): Die Gattung Nigritella Rich. – Bauhinia **14**: 21–32.

Crantz H. J. N. (1769): Stirpium Austriacarum, Fasciculi VI, pars 2, ed. 1. – Wien: Ioannis Paulis Kraus.

Cristaudo A., Galesi G. & Lorenz R. (2009): Über zwei stabilisierte Hybridpopulationen aus der Gattung *Serapias* auf Sizilien. – J. Eur. Orch. **41**(3/4): 587–610.

Dakskobler I., Dolinar B., Zupan B., Iskra R., Strgar P. & Trnkoczy A. (2012): *Nigritella widderi* Teppner & E. Klein, a new species in the flora of Slovenia. – Folia Biol. Geol. (Ljubljana) **53**(1–2): 25–43.

Dakskobler I., Dolinar B., Zupan B., Poljšak F. & Strgar P. (2015): Fitocenološka oznaka rastišč vrste *Nigritella archiducis-joannis* v dolini Triglavskih jezer (Julijske Alpe, Slovenija). – Folia Biol. Geol. (Ljubljana) **56**(1): 105–114.

Dakskobler I. & Dolinar B. (2016): Razširjenost in nahajališča kukavičevk v Bohinju. – Acta Triglevensia **4**: 5–15.

Dakskobler I. & Surina B. (2017): Phytosociological analysis of alpine swards and heathlands (pioneer patches) on ridges and peaks in the Julian Alps (NW Slovenia). – Hacquetia **16**(1): 49–171.

Dolinar B. (2015): Kukavičevke v Sloveniji. – Podsmreka: Pipinova knjiga.

Delforge P. (2006): Orchids of Europe, North Africa and the Middle East. – London: Timber Press.

Delforge P. (2011): *Gymnadenia rubra* Wettstein 1889 et la taxonomie des nigritelles apomictiques. – Naturalistes Belges **92** (Orchid. 24): 87–116.

Foelsche W. (2010): *Nigritella bicolor*, ein neues apomiktisches Kohlröschen der Alpen, des Dinarischen Gebirges und der Karpaten. – J. Eur. Orch. **42**(1): 3–82.

Foelsche W. (2014): Bestimmungsschlüssel für die Arten und Unterarten der Gattung *Nigritella*. – Museum Joanneum Graz: https://www.museum-joanneum.at/fileadmin/user_upload/Stundienzentrum_Naturkunde/Botanik/BotanikNews/2014_BotNews/Nigritella/Foelsche_2014_Bestimmungsschluessel_Nigritella.pdf [accessed: 7.3.2018]

Foelsche W. (2015): *Nigritella hygrophila* und die Kohlröschen im Gebiet des Pordoijochs (Dolomiten) aus der Sicht von 2014. – Ber. Arbeitskreis. Heimische Orchid. **32**(1): 65–96.

Foelsche W. & Zernig K. (2007): *Nigritella minor* spec. nova (Orchidaceae), ein neues Kohlröschen aus der Steiermark. – Joannea Botanik (Graz) **6**: 5–22.

Foelsche W. & Heidtke U. H. J. (2011): *Nigritella hygrophila* spec. nov. und die roten Kohlröschen am Pordoijoch in den östlichen Dolomiten (Italien). – J. Eur. Orch. **43**(1): 131–160.

Foelsche W., Wüest R., Dolinar B., Dakskobler I. & Paušič I. (2017): *Nigritella kossutensis* und *Nigritella ravnikii,* zwei neue, diploide Arten auf der slowenischen Seite der Karawanken. – J. Eur. Orch. **49**(3–4): 501–577.

Hedrén M., Klein E. & Teppner H. (2000): Evolution of polyploids in the European orchid genus *Nigritella*: Evidence from allozyme data. – Phyton (Horn) **40**(2): 239–275.

Hedrén M., Lorenz R., Teppner H., Dolinar B., Giotta C., Griebl N., Hansson S., Heidtke U., Klein E., Perazza G., Ståhlberg D. & Surina B. (2017): Evolution and systematics of polyploid *Nigritella* (Orchidaceae). – Nord. J. Bot. doi: 10.1111/njb.01539.

Janchen E. (1959): Beiträge zur Benennung, Verbreitung und Anordnung der Farn- und Blütenpflanzen Österreichs. – Phyton (Horn) **8**(3–4): 230–240.

Jogan N. (2000): Naše orhideje. Ključ za določanje kukavičevk divjerastočih v Sloveniji. – Ljubljana: Samozaložba.

Klein E. (1996): Die Blütenfärbung in der Gattung *Nigritella* (Orchidaceae–Orchideae) und ihre taxonomische Relevanz, inkl. einer Neukombination. – Phyton (Horn) **36**(1): 53–62.

Kreutz C.A.J. (2004): Kompendium der Europäischen Orchideen / Catalogue of European Orchids. – Landgraaf: Kreutz Publishers.

Lewis W.H. (1980): Polyploidy in species populations. – In: Lewis W.H. [ed.]: Polyploidy: biological relevance: 103–144. – New York: Plenum.

Lorenz R. (2004): Zu den Gattungen *Epipactis* und *Nigritella* in Südtirol. – 3. Tagung Zoologische und botanische Forschung in Südtirol: 3–32. – Bozen: Naturmuseum Südtirol.

Lorenz R., Madl H., Obrist E., Sölva A. & Stockner W. (2011): Zur Artengruppe von *Epipactis helleborine* (Orchidaceae) in Südtirol (Italien). – Gredleriana (Suppl.) **11**: 45–70.

Lorenz R. & Perazza G. (2004): Studio sulla sistematica delle *Nigritella* rosse nelle Dolomiti. – GIROS, Notizie **27**: 1–9.

Lorenz R. & Perazza G. (2012): Beiträge zur Kenntnis der Blütenmorphologie der Artengruppe *Nigritella miniata* s.l. (Orchidaceae) in den Ostalpen. – Gredleriana **12**: 67–146.

Lowe M.R. (2011): Studies in *Ophrys* L. sectio *Pseudophrys* Godfery – II. *Andrena flavipes* Pz. pollinated taxa. – J. Eur. Orch. **43**(3): 455–497.

Mayer E. (1954): Prispevki k flori slovenskega ozemlja. V. – Biol. Vestn. **3**: 91–101.

Martinčič A., Sušnik F., Ravnik V., Strgar V. & Wraber T. (1984): Mala flora Slovenije: praprotnice in semenke. 2 popravljena in dopolnjena izdaja: 755–756. – Ljubljana: Državna založba Slovenije.

Martinčič A., Wraber T., Jogan N., Podobnik A., Ravnik V., Turk B., Vreš B. (1999): Mala flora Slovenije: ključ za določanje praprotnic in semenk. 3. dopoljnena in spremenjena izdaja. – Ljubljana: Tehniška založba Slovenije.

Martinčič A., Wraber T., Jogan N., Podobnik A., Ravnik V., Turk B., Vreš B., Frajman B., Strgulc-Krajšek S., Trčak B., Bačič T., Fischer M.A., Eler K., Surina B. (2007): Mala flora Slovenije: ključ za določanje praprotnic in semenk. – Ljubljana: Tehniška založba Slovenije.

Perazza G. (2009): Genere *Nigritella*. – In: Grünanger P. [ed.]: Orchidee d'Italia. – Il Castello, Cornaredo (MI): GIROS.

Perko M.L. (2004): Die Orchideen Kärtnens. – Klagenfurt: Arge NATURSCHUTZ.

Ravnik V. (1978): Beiträge zur Kenntnis der Gattung *Nigritella* Rich. IV. *Nigritella lithopolitanica* V. Ravnik spec. nov. – Acta Bot. Croat. **37**: 225–228.

Ravnik V. (1990): Rod *Nigritella* L.C. Richard v jugovzhodnih apneniških Alpah. – Razprave IV. Razreda SAZU **31**: 272–290.

Ravnik V. (2002): Orhideje Slovenije. – Ljubljana: Tehniška založba Slovenije.

Richter K. (1890): Plantae Europaeae, Tom. 1. – Leipzig: Wilhelm Engelmann.

Seliškar T., Vreš B. & Seliškar A. (2003): FloVegSi 2.0. Računalniški program za urejanje in analizo bioloških podatkov. – Ljubljana: Biološki inštitut ZRC SAZU.

SPSS Inc. (2006): SPSS Base 15.00 User's Guide. Chicago, IL: SPSS Inc.

Ståhlberg D. (1999): Polyploid evolution in the European orchid genus *Nigritella*: evidence from DNA fingerprinting. – Lund University, unpublished: 1999-01-01.

Surina B. (2005): Some novelties in the flora and vegetation of Mt. Snežnik (SW Slovenija, Liburnian karst). – Acta Bot. Croat. **64**(2): 341–356.

Templeton A. (1989): The meaning of species and speciation. – In: Otte D. & Endler J.A. [eds]: Speciation and its consequences: 3–27. – Sunderland, Mass.: Sinauer.

Teppner H. (2004): A review of new results in *Nigritella* (Orchidaceae). – Spraw. Posiedzeń Kom. Nauk. **46**(2): 111–116.

Teppner H. (2008): Kohlröschen, Kohlröserl, (schw.:) „Männertreu" / *Nigritella*. – In: Fischer M., Oswald K. & Adler W. [eds]: Exkursionsflora für Österreich, Liechtenstein und Südtirol [3rd ed.]: 1058–1060. – Linz: Land Oberösterreich, Biologiezentrum der Oberösterr. Landesmuseen.

Teppner H. & Klein E. (1990): *Nigritella rhellicani* spec. nova und *N. nigra* (L.) Rchb. f. s. str. (Orchidaceae – Orchideae). – Phyton (Horn) **31**(1): 5–26.

Teppner H. & Klein E. (1993): *Nigritella gabasiana* spec. nova, *N. nigra* subsp. *iberica* subsp. nova (Orchidaceae – Orchideae) und deren Embryologie. – Phyton (Horn) **33**(2): 179–322.

Teppner H. & Klein E. (1985a): Karyologie und Fortpflanzungsmodus von *Nigritella* (Orchidaceae – Orchideae), inkl. *N. archiducis-joannis* spec. nov. und zweier Neukombinationen. – Phyton (Horn) **25**(1): 147–176.

Teppner H. & Klein E. (1985b): *Nigritella widderi* spec. nov. (Orchidaceae – Orchideae). – Phyton (Horn) **25**(2): 317–326.

Teppner H. & Klein E. (1998): *Etiam atque etiam*: *Nigritella* versus *Gymnadenia*: Neukombinationen und *Gymnadenia dolomitensis* spec. nova (Orchidaceae – Orchideae). – Phyton (Horn) **38**(1): 220–225.

Teppner H. & Ster T. (1996): *Nigritella buschmanniae* spec. nova (Orchidaceae – Orchideae) und eine Biographie für Frau Adolfine Buschmann. – Phyton (Horn) **36**(2): 277–294.

Tyteca D. & Gathoye J. L. (2000): Morphometric analyses of the *Dactylorhiza majalis* group in France and Western Europe − with description of *Dactylorhiza parvimajalis* Tyteca & Gathoye spec. nov. – J. Eur. Orch. **32**(3/4): 471–511.

Wenker D. (2007): Die Gattung *Nigritella* – Rückkehr zu taxonomischer Stabilität. – Jahresber. Naturwiss. Vereins Wuppertal **60**: 177–250.

Wettstein R. von (1889): Untersuchungen über *Nigritella angustifolia* Rich. – Ber. Deutsch. Bot. Ges. **7**: 306–317.

Wraber T. (1990): Sto znamenitih rastlin na Slovenskem. – Ljubljana: Prešernova družba.

Addresses of the authors:

Igor Paušič (corresponding author)
Department of Biology, Faculty of Natural Sciences and Mathematics
University of Maribor
Koroška c. 160
SI-2000 Maribor
Slovenia
E-mail: igor.pausic@um.si

Igor Dakskobler
Jovan Hadži Institute of Biology
Scientific Research Centre of the Slovenian Academy of Sciences and Arts
Regional Research Unit Tolmin
Brunov drevored 13
SI-5220 Tolmin
Slovenia

Boštjan Surina
Faculty of Mathematics, Natural Sciences and Information Technologies
University of Primorska
Glagoljaška 8

SI-6000 Koper
Slovenia,
Natural History Museum Rijeka
Lorenzov prolaz 1
51000 Rijeka
Croatia

Branko Dolinar
Bizjanova 21
SI-1107 Ljubljana
Slovenia

Supplementum 1 ►

Supplementum 1.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Dinaric Alps	Snežnik. Zatreb	Surina B.	45.542	14.408	x		x		
Dinaric Alps	Snežnik. Grčovsko sedlo	Dolinar B.	45.586	14.456	x				
Dinaric Alps	Snežnik. Gašperjev hrib	Dolinar B.	45.586	14.456	x				
Dinaric Alps	Snežnik. clearing above 'kapetanova bajta'	Dolinar B.	45.586	14.456	x				
Dinaric Alps	Snežnik. Mali Snežnik	Dolinar B.	45.590	14.448	x				
Dinaric Alps	Snežnik. Tri kaliči	Avčin F.	45.600	14.454			x		
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.586	14.456				x	
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.588	14.458				x	
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.588	14.457				x	
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.587	14.456				x	
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.587	14.456				x	
Dinaric Alps	Snežnik. Veliki Snežnik	Dakskobler I.	45.590	14.448				x	
Dinaric Alps	Snežnik. Mali Snežnik	Dolinar B.	45.590	14.447			x		
Julian pre-Alps, Cerkno Mts.	Porezen	Terpin R.	46.176	13.980	x				
Julian Alps	Bala. under Mt. Morež	Dakskobler I.	46.394	13.644	x		x		
Julian Alps	Krn Mts. Velika Baba	Surina B.	46.294	13.714			x		
Julian Alps	Kanin Mts. Skripi	Dakskobler I.	46.358	13.486			x		
Julian Alps	Kanin Mts. Lopa	Dakskobler I.	46.371	13.500	x				
Julian Alps	Kanin Mts. Lopa	Dakskobler I.	46.371	13.500	x				
Julian Alps	Kanin Mts. Rupa under Vrh Ribežnov	Dakskobler I.	46.371	13.532	x				
Julian Alps	Bala. Spodnji Lepoč	Dakskobler I.	46.397	13.658	x				
Julian Alps	Črna prst	Veber I.	46.231	13.935	x				
Julian Alps	Dolina between Kaluder and Konj	Dakskobler I.	46.308	13.713	x				
Julian Alps	Dolina between Kaluder and Konj	Dakskobler I.	46.302	13.714	x				
Julian Alps	Kanin Mts.	Dakskobler I.	46.371	13.503	x				
Julian Alps	Kanin Mts.	Dakskobler I.	46.370	13.495	x				

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Planina Tosc (Tošc)	Anderle B.	46.349	13.880	x				
Julian Alps	between planina Dedno polje and Slatna	Dakskobler I.	46.325	13.807	x				
Julian Alps	Lazovški preval	Dakskobler I.	46.339	13.833	x				
Julian Alps	Debeli vrh	Dakskobler I.	46.341	13.825	x				
Julian Alps	Lazovški preval-Ogradi	Dakskobler I.	46.337	13.836	x				
Julian Alps	Ogradi	Dakskobler I.	46.335	13.838	x				
Julian Alps	Jerebica	Dakskobler I.	46.399	13.570	x				
Julian Alps	Mangart-Jarečica	Anderle B.	46.436	13.649	x				
Julian Alps	Rudno polje. Miščovec	Dolinar B.	46.344	13.917	x				
Julian Alps	Krn Mts.	Vreš B.	46.286	13.694				x	
Julian Alps	Planina Klek. Zgornji Klek	Dakskobler I.	46.393	13.970				x	
Julian Alps	Planina Klek. Spodnji Klek	Dakskobler I.	46.393	13.965				x	
Julian Alps	Lazovški preval. Planina v Lazu	Dolinar B.	46.339	13.833	x				
Julian Alps	Lazovški preval. Planina v Lazu	Dakskobler I.	46.339	13.833				x	
Julian Alps	Lazovški preval. Planina v Lazu	Dakskobler I.	46.339	13.833				x	
Julian Alps	Lazovški preval. Planina v Lazu	Dakskobler I.	46.339	13.833				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.339	13.833				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.339	13.831				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.339	13.832				x	
Julian Alps	Ogradi	Dakskobler I.	46.332	13.839				x	
Julian Alps	Ogradi	Dakskobler I.	46.336	13.836					x
Julian Alps	Ogradi	Dakskobler I.	46.335	13.839				x	
Julian Alps	Ogradi	Dakskobler I.	46.335	13.838				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.337	13.833				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.336	13.833				x	
Julian Alps	Ogradi	Dakskobler I.	46.336	13.836				x	
Julian Alps	Ogradi	Dakskobler I.	46.333	13.839				x	

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Planina Klek	Dakskobler I.	46.393	13.970				x	
Julian Alps	Planina Klek. Zgornji Klek	Dakskobler I.	46.394	13.970				x	
Julian Alps	Planina Klek	Dakskobler I.	46.397	13.962				x	
Julian Alps	Planina Klek	Dakskobler I.	46.394	13.964				x	
Julian Alps	Mišelj vrh	Dakskobler I.	46.357	13.839				x	
Julian Alps	Mišelj vrh	Dakskobler I.	46.357	13.838				x	
Julian Alps	Mišelj vrh	Dakskobler I.	46.357	13.837					x
Julian Alps	Mišeljska dolina	Dakskobler I.	46.353	13.838				x	
Julian Alps	Mišeljska dolina	Dakskobler I.	46.352	13.838				x	
Julian Alps	Mišeljska dolina	Dakskobler I.	46.352	13.841				x	
Julian Alps	Mišelj vrh	Dakskobler I.	46.357	13.842				x	
Julian Alps	Mišeljska dolina	Dakskobler I.	46.353	13.837				x	
Julian Alps	Mišeljska dolina	Dakskobler I.	46.356	13.839				x	
Julian Alps	Mišeljska dolina	Dakskobler I.	46.354	13.839				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.356	13.849				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.354	13.846				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.355	13.848				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.355	13.849				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.356	13.849				x	
Julian Alps	Koštrunovec	Dakskobler I.	46.356	13.848				x	
Julian Alps	Mišelj vrh	Dakskobler I.	46.354	13.847				x	
Julian Alps	Planina Klek	Dakskobler I.	46.393	13.968				x	
Julian Alps	Plaski Vogel	Strgar P.	46.338	13.755					x
Julian Alps	Kanin Mts. - Velika Črnelska špica	Anderle B.	46.372	13.524	x				
Julian Alps	Veliki Jelenk	Dakskobler I.	46.384	13.672				x	
Julian Alps	Triglav lakes / Triglavska jezera	Zelesny H.	46.338	13.786				x	
Julian Alps	Krn lakes / Krnska jezera	Poljšak F.	46.274	13.705				x	

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Kriški podi	Završnik K.	46.402	13.809				x	
Julian Alps	Kanin Mts. under Vrh Laške planje	Dakskobler I.	46.342	13.462				x	
Julian Alps	Pokljuka-Viševnik	Dolinar B.	46.358	13.905				x	
Julian Alps	Planina Klek	Dolinar B.	46.394	13.964	x				
Julian Alps	Mangartski podi	Trnkoczy A.	46.442	13.648				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.334	13.742				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.336	13.749				x	
Julian Alps	Plaski Vogel	Dakskobler I.	46.338	13.755				x	
Julian Alps	Plaski Vogel	Dakskobler I.	46.338	13.753				x	
Julian Alps	Travnik	Dakskobler I.	46.338	13.749				x	
Julian Alps	Plaski Vogel	Dakskobler I.	46.338	13.755				x	
Julian Alps	Plaski Vogel	Dakskobler I.	46.338	13.755				x	
Julian Alps	planina Konjščica	Kocjan M.	46.350	13.903				x	
Julian Alps	Triglav lakes / Triglavska jezera	Zupan B.	46.338	13.786				x	
Julian Alps	Vernar. 2190 m	Dakskobler I.	46.361	13.868				x	
Julian Alps	Črna prst	Dakskobler I.	46.231	13.938					x
Julian Alps	Tolminski Migovec	Dakskobler I.	46.251	13.764				x	
Julian Alps	Pokljuka. Viševnik	Dolinar B.	46.359	13.906				x	
Julian Alps	Viševnik	Dolinar B.	46.358	13.905				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.328	13.732				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.330	13.736					x
Julian Alps	Travniška dolina	Dakskobler I.	46.332	13.740				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.332	13.740				x	
Julian Alps	Travniška dolina	Dakskobler I.	46.337	13.748				x	
Julian Alps	Plaski Vogel	Dakskobler I.	46.338	13.755				x	
Julian Alps	Mišeljski preval	Dakskobler I.	46.347	13.840				x	

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Mišeljski preval	Dakskobler I.	46.350	13.837				x	
Julian Alps	Mišeljski konec	Dakskobler I.	46.355	13.831				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.341	13.832				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.341	13.832				x	
Julian Alps	Kanin Mts. Kotel-Jezički	Dakskobler I.	46.367	13.512				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.519				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.519				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.519				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.519				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.520				x	
Julian Alps	Velika Črnelska špica	Dakskobler I.	46.377	13.519				x	
Julian Alps	Mišeljski preval	Dakskobler I.	46.347	13.839				x	
Julian Alps	Mišeljska glava-Mišeljski konec	Dakskobler I.	46.356	13.829				x	
Julian Alps	Mišeljska glava	Dakskobler I.	46.356	13.829				x	
Julian Alps	Velo polje	Dakskobler I.	46.356	13.861				x	
Julian Alps	Mišeljska Planina	Dakskobler I.	46.350	13.851				x	
Julian Alps	Mišeljski preval - Lazovški preval	Dakskobler I.	46.344	13.834				x	
Julian Alps	Mišeljski preval - Lazovški preval	Dakskobler I.	46.343	13.834				x	
Julian Alps	Mišeljski preval - Lazovški preval	Dakskobler I.	46.343	13.833				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.341	13.832				x	
Julian Alps	Lazovški preval	Dakskobler I.	46.341	13.832				x	x
Julian Alps	Ogradi	Dakskobler I.	46.333	13.839				x	
Julian Alps	Ogradi	Dakskobler I.	46.335	13.837				x	
Julian Alps	Ogradi	Dakskobler I.	46.329	13.839				x	
Julian Alps	Ogradi	Dakskobler I.	46.327	13.843				x	
Julian Alps	Ogradi	Dakskobler I.	46.326	13.843				x	
Julian Alps	Vršič-Police	Zwander H.	46.423	13.754			x		

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Mangart. Mali vrh	Dakskobler I.	46.433	13.644				x	
Julian Alps	Rdeči Rob	Dakskobler I.	46.252	13.700				x	
Julian Alps	Triglav lakes / Triglavska jezera	Zupan B.	46.338	13.786				x	
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.335	13.786				x	x
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.338	13.786				x	
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.338	13.786				x	
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.339	13.787				x	
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.337	13.787				x	
Julian Alps	Triglav lakes / Triglavska jezera	Dakskobler I.	46.333	13.787				x	
Julian Alps	Viševnik	Anderle B.	46.358	13.906	x				
Julian Alps	Malo Špičje. Zadnja Lopa	Dakskobler I.	46.354	13.790					x
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.359	13.881				x	
Julian Alps	Tolminski Migovec	Dakskobler I.	46.259	13.764				x	
Julian Alps	Mišeljski konec. 2344 m	Strgar P.	46.356	13.828				x	
Julian Alps	Spodnje Ledine above Velo polje	Dakskobler I.	46.367	13.838				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.354	13.791				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.353	13.791					x
Julian Alps	Malo Špičje	Dakskobler I.	46.350	13.786				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.352	13.789				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.352	13.787				x	
Julian Alps	Malo Špičje-Goriški rob	Dakskobler I.	46.347	13.781				x	
Julian Alps	Malo Špičje-Goriški rob	Dakskobler I.	46.346	13.777				x	
Julian Alps	Malo Špičje-Goriški rob	Dakskobler I.	46.347	13.781				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.350	13.786				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.350	13.787				x	
Julian Alps	Malo Špičje	Dakskobler I.	46.352	13.788				x	
Julian Alps	Viševnik	Dakskobler I.	46.359	13.906				x	x

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Viševnik	Dakskobler I.	46.359	13.906				x	x
Julian Alps	Viševnik	Dakskobler I.	46.359	13.901				x	
Julian Alps	Mali Draški vrh	Dakskobler I.	46.362	13.890				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.883				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.885					x
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.883				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.882				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.881				x	
Julian Alps	Vrbanova špica - Spodnja Vrbanova špica	Wraber T.	46.394	13.870	x				
Julian Alps	Pokljuka - Viševnik	Dolinar B.	46.359	13.905			x		
Julian Alps	Pokljuka - Viševnik	Dolinar B.	46.359	13.906			x		
Julian Alps	Rudno polje	Dolinar B.	46.344	13.917			x		
Julian Alps	between Tosc and Veliki Draški vrh	Strgar P.	46.358	13.878				x	x
Julian Alps	Triglav lakes / Triglavska jezera	Poljšak F.	46.333	13.786				x	x
Julian Alps	Planina na Kalu	Dakskobler I.	46.243	13.760				x	
Julian Alps	Planina na Kalu	Dakskobler I.	46.244	13.761				x	
Julian Alps	Vrh Planje (between Tolminki Kuk and Mahavšček)	Dakskobler I.	46.265	13.758				x	
Julian Alps	Vrh Planje (between Tolminki Kuk and Mahavšček)	Dakskobler I.	46.264	13.758				x	
Julian Alps	Vrh Planje (between Tolminki Kuk and Mahavšček)	Dakskobler I.	46.264	13.758				x	
Julian Alps	Vrh Planje (between Tolminki Kuk and Mahavšček)	Dakskobler I.	46.264	13.758				x	
Julian Alps	Vrh Škrli	Dakskobler I.	46.274	13.751				x	
Julian Alps	Mahavšček	Dakskobler I.	46.277	13.741				x	
Julian Alps	Zaplanja under Triglav	Dakskobler I.	46.381	13.831					x

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Triglav lakes / Triglavska jezera	Zupan B.	46.348	13.796				x	
Julian Alps	Velika Zelnarica	Zupan B.	46.341	13.796				x	
Julian Alps	Mala Zelnarica-Kopica	Zupan B.	46.334	13.794				x	
Julian Alps	Raskovec - Novi vrh	Zupan B.	46.228	13.886				x	
Julian Alps	Rodica	Zupan B.	46.231	13.871				x	
Julian Alps	Velika Zelnarica	Anderle B.	46.342	13.795	x				
Julian Alps	Viševnik	Dolinar B.	46.359	13.905			x		
Julian Alps	between Velika and Mala Zelnarica	Dakskobler I.	46.342	13.795				x	
Julian Alps	between Velika and Mala Zelnarica	Dakskobler I.	46.343	13.795				x	
Julian Alps	Mahavšček	Dakskobler I.	46.278	13.741				x	
Julian Alps	Mahavšček	Dakskobler I.	46.277	13.742				x	
Julian Alps	Veliki Lemež	Surina B.	46.288	13.684		x			
Julian Alps	Planina Razor	Dakskobler L.	46.239	13.804				x	
Julian Alps	Viševnik	Dolinar B.	46.358	13.905			x		
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.885				x	
Julian Alps	between Mali and Veliki Draški vrh	Dakskobler I.	46.361	13.886				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.885				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.359	13.883				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.361	13.880				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.360	13.877				x	
Julian Alps	Planina Konjščica	Dakskobler I.	46.357	13.894				x	
Julian Alps	Veliki Draški vrh	Dakskobler I.	46.360	13.882				x	
Julian Alps	between Veliki Draški vrh and Tosc	Dakskobler I.	46.360	13.877				x	
Julian Alps	between Veliki Draški Vrh and Tosc	Dakskobler I.	46.359	13.875				x	
Julian Alps	Mangart	Dolinar B.	46.439	13.645			x		
Julian Alps	Mangart	Dolinar B.	46.441	13.648			x		
Julian Alps	Mangart	Dolinar B.	46.443	13.643			x		

Supplementum 1. cont.

Region	Area	First Author	Longitude	Latitude	*Nigritella rubra*	*Nigritella miniata* s. lat.	*Nigritella miniata*	*Nigritella bicolor*	*Nigritella hygrophila*
Julian Alps	Pokljuka. Rudno polje	Dolinar B.	46.344	13.917			x		
Julian Alps	Triglav lakes / Triglavska jezera	Zupan B.	46.351	13.801					x
Julian Alps	Mali Raskovec	Dakskobler I.	46.232	13.886				x	
Julian Alps	Mali Raskovec	Dakskobler I.	46.232	13.886				x	
Julian Alps	Veliki Raskovec	Dakskobler I.	46.228	13.885				x	
Julian Alps	Veliki Raskovec	Dakskobler I.	46.228	13.885				x	
Julian Alps	Veliki Raskovec	Dakskobler I.	46.228	13.885				x	
Julian Alps	Veliki Raskovec	Dakskobler I.	46.228	13.886				x	
Julian Alps	Ogradi	Dolinar B.	46.334	13.834	x				
Julian Alps	Kriški podi	Poljšak F.	46.400	13.807			x		
Julian Alps	Mangart	Wraber T.	46.436	13.650			x		
Julian Alps	Možic	Dakskobler I.	46.243	14.000			x		
Karavanke mountain range	Tegoška gora- Macesje	Dolinar B.	46.441	14.392					x
Karavanke mountain range	Mala Peca	Seliškar A.	46.494	14.796	x				
Karavanke mountain range	Tegoška gora	Dolinar B.	46.436	14.385				x	
Karavanke mountain range	Tegoška planina	Dolinar B.	46.431	14.381					x
Karavanke mountain range	Tegoška gora	Dolinar B.	46.434	14.382					x
Karavanke mountain range	Tegoška gora	Dolinar B.	46.437	14.390			x		x
Karavanke mountain range	Tegoška planina	Dolinar B.	46.435	14.385					x
Karavanke mountain range	Košutnikov turn	Dolinar B.	46.443	14.425					x
Total					33	1	20	163	22