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ORIGINAL ARTICLE

The Danube is not a border for geophytes: *Ornithogalum refractum* (*Asparagaceae*) discovered in Slovakia

Michal Hroneš[1] · **Alena Uvírová**[1,2]

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Abstract
Current number of species of *Ornithogalum* s. lat. in Slovakia is eight. We here report the discovery of a ninth species, *Ornithogalum refractum* Kit. ex. Willd. The species was first discovered in the vicinity of Štúrovo town in southern Slovakia in April 2023. We used a multi-method biosystematic approach to demonstrate its difference from morphologically similar species *O. divergens* Boreau. Flow cytometry and chromosome counting revealed that pentaploids and hexaploids of *O. refractum* occur in Slovakia. Its residence time in Slovakia is unclear, but we suggest that it is not of a recent origin, and the species occurrence has been overlooked due to its superficial similarity with *O. divergens*. The species occurrence in southern Slovakia represents a continuation of its distribution in northern Hungary and it is probably the northernmost in the entire range.

Keywords Central Europe · *Hyacinthaceae* · New record · Polyploidy · Scilloideae

Introduction

The flora of Slovakia counts about 5300 species (Letz et al. 2024+). The floristic composition of the country is influenced mainly by two floristic regions – the Carpathians and Pannonia (Futák 1984; Ulrych et al. 2019). Pannonian lowland covers a considerable part of southern Slovakia and hosts the most thermophilous vegetation in the country (Fekete et al. 2016; Ulrych et al. 2019). It is an absolute northern distribution limit for many plant taxa (Michalko et al. 1986), including monocot geophytes such as *Allium marginatum* Janka, *Colchicum arenarium* Waldst. & Kit., *Ornithogalum comosum* L. (incl. *O. pannonicum* Chaix ex Vill.) and *Sternbergia colchiciflora* Waldst. & Kit. These species are either Pannonian (sub)endemics or representatives of the pannonian-pontic-submediterranean floristic element (Čeřovský et al. 1999; Kliment 1999; Vojtěchová et al. 2023).

✉ Michal Hroneš
michal.hrones@upol.cz

[1] Department of Botany, Palacký University in Olomouc, Šlechtitelů 27, 77900 Olomouc, Czech Republic

[2] Department of Ecology and Environmental Sciences, Palacký University in Olomouc, Šlechtitelů 27, 77900 Olomouc, Czech Republic

Genus *Ornithogalum* L. (Ornithogaleae, Scilloideae, *Asparagaceae*) is one of the most taxonomically complicated and challenging genera in Europe and western Asia. There is an ongoing debate about the generic concept of Ornithogaleae with two contradictory opinions on the delimitation of genera. Manning et al. (2009) proposed an extremely broad generic concept and recognised only four genera in the whole Ornithogaleae based on the phylogeny of four plastid markers and sampling of 70 species. This view is basically mirrored in the account for *Ornithogalum* in the Plants of the World database (POWO 2025). On the contrary, Martínez-Azorín et al. (2011) proposed to recognise 19 narrowly delimited genera based on a combined data set of five nuclear and plastid markers, morphological matrix using 34 morphological traits and 80 species. The generic delimitation of Ornithogaleae by Martínez-Azorín et al. (2011) overlaps well with the one proposed by Speta (1998) and Pfosser and Speta (1999), and it is more useful in field-based botany as it recognises morphologically well-defined units with fewer species in each genus.

Ornithogalum s. str. [sensu Martínez-Azorín et al. (2011)] is distributed from Morocco to Turkmenistan, and approximately 80 species are currently recognised (POWO 2025). The latest infrageneric classification is based mainly on bulb features and germination type and recognises eight subgenera (Zahariadi 1965, 1980). However, the well-sampled

phylogeny for this genus is still missing, and the monophyly of the subgenera has never been tested. The type subgenus *Ornithogalum* consists of a morphologically uniform group of species with concrescent bulb scales, tepals appressed to fruit after anthesis, ovaries with six obtuse ribs and epigeal germination (Zahariadi 1980). It is a karyologically complicated diploid-polyploid complex with x = 9 and reported ploidy levels ranging from 2n = 2x = 18 to 2n = 10x = 90 (Hrouda 1980; Peruzzi and Passalaqua 2002). The subgenus contains several taxa with wider distribution in Europe – *O. comosum* s. lat., *O. refractum* Kit. ex Willd. and notoriously known *O. umbellatum* aggregate which in Central Europe consists of *O. kochii* Parl., *O. umbellatum* L. and *O. divergens* Boreau (Hrouda 1980; Zahariadi 1980).

While most of the abovementioned species are either diploid or low-ploidy level taxa, two species of *Ornithogalum umbellatum* aggregate with pentaploid and higher ploidy levels are reported from Central Europe (sensu Martínek and Nováček 2023). The widespread *O. divergens* with 2n = 5x = 45 and 2n = 6x = 54 and *O. refractum* until now known from Central Europe from Hungary only with 2n = 5x = 45 (Hrouda 2007, 2010; Speta 2010). Both taxa have a high proportion of vegetative reproduction via underground lenticular bulbils which discriminates them from the rest of the species (Király 2009). *Ornithogalum refractum* can be differentiated from *O. divergens* by scape being either underground for most of its length, pedicels being reflexed from distinct pulvinus, and bracts of the same length to longer than pedicels (Zahariadi 1980; Király 2009).

Current number of recognised species of *Ornithogalum* s. lat. in the flora of Slovakia is eight: two native species of *Loncomelos* Raf. [*L. brevistylum* (Wolfner) Dostál, *L. sphaerocarpum* (A. Kern.) Dostál], one native and one introduced species of *Honorius* Gray [*H. boucheanus* (Kunth) Holub, *H. nutans* (L.) Gray] and four species of *Ornithogalum* s. str. (*O. comosum*, *O. divergens*, *O. kochii*, *O. umbellatum*) from which *O. comosum* is considered extinct, and presence of *O. umbellatum* requires confirmation (Eliáš et al. 2015; Letz et al. 2024+). Here we report an occurrence of the ninth species, *O. refractum*, which was found for the first time in southern Slovakia in spring 2023.

Material and Methods

Plant material and vegetation relevés

Plant material was collected in April 2023 and April 2025 in the vicinity of Štúrovo town and nearby Kamenica nad Hronom village (Nové Zámky district) in southern Slovakia. In total, 42 individuals of *O. divergens* and suspected *O. refractum* from six populations were collected and further used for analyses (Table 1). Several plants were processed as herbarium specimens and deposited in the herbarium of the Department of Botany, Palacký University in Olomouc (OL, Thiers 2024+). The rest was transferred into the departments' greenhouse for further analyses.

To characterise the vegetation with the suspected presence of *O. refractum* in Slovakia, two standard phytocoenological relevés (4 m × 4 m) were recorded on 5 May 2023 and 18 April 2025 in the populations STK and STD, respectively, using the nine-grade Braun-Blanquet scale for the estimation of abundance/dominance (van der Maarel and Franklin 2013). The character of localities in studied populations of *O. divergens* did not permit the recording of relevés due to frequent mowing. The classification of vegetation types represented by the relevés proved difficult using conventional methods and was therefore discussed with Milan Chytrý (Masaryk University, Brno, CZ).

Nomenclature of both species and vegetation units was unified using FloraVeg.EU database (Chytrý et al. 2024).

Flow cytometry and chromosome counting

Relative genome size, i.e., the ratio of standard and sample peak, of *Ornithogalum* samples was established by flow cytometry. One approximately 2 cm long root without a root tip was co-chopped together with 0.5 cm^2 of leaf tissue of an internal standard. *Vicia faba* L. 'Inovec' (2C = 26.9 pg) served as the primary internal standard. Due to peak overlap with standard in some *O. refractum* individuals, *Secale cereale* L. 'Daňkovské' (2C = 16.19 pg) was used as the secondary standard. The sample was prepared in 1 ml of LB01 buffer supplemented with PVP (polyvinylpyrrolidone, 10 g in 500 ml of buffer) using a sharp razor blade (Doležel and Bartoš 2005; Doležel et al. 2007). Another 500 µl of buffer was added, and the solution was filtered through the nylon mesh and supplemented with 50 µl of DAPI (4′,6-diamidino-2-phenylindole; final concentration 4 µg/ml). Samples were run on Partec ML flow cytometer (Partec GmbH, Münster, Germany) equipped with a Partec UV LED kit (365 nm, 10 mW; Partec GmbH, Münster, Germany). The fluorescence intensity of at least 3000 particles was recorded. The relative nuclear DNA content of analysed plants was assessed by the peak position of the sample relative to an internal reference standard peak using Partec FloMax software. The peak ratios resulting from measurements with *Secale* were multiplied by 0.45 obtained from several measurements of both standards together to harmonise results using *Secale* with samples measured with *Vicia*.

Flow cytometry results for *O. refractum* were calibrated by our own chromosome counts. Two individuals were counted for each of the two populations studied (STD, STK). Actively growing root tips from plants cultivated in greenhouse were pre-treated in 8-hydroxyquinoline for six hours in the dark and at room temperature. Then they were fixed in 96% ethanol : cold acetic acid (3:1) until the squash preparation (at least overnight). Maceration has been done for four minutes

Table 1 List of populations sampled, their taxonomic identity, relative genome size (ratio of sample peak position to peak position of *Vicia faba* L. 'Inovec', 2C = 26.9 pg) acquired by flow cytometry and corresponding ploidy level estimated from chromosome counts. N – number of individuals used for flow cytometry and morphometric analysis; N_C – number of individuals counted for chromosomes and their 2n; MH – Michal Hroneš, AU – Alena Uvírová

Population ID	Locality	Taxon	N	Relative genome size			Ploidy level	N_C
				mean	±SD	min–max		
KAM	Slovakia, Kamenica nad Hronom: road ditch in Nové Vinohrady settlement, E of village, 106 m a.s.l., 47°49′21.9"N, 18°45′16.5"E, 16. 4. 2023, leg. MH							
		O. divergens	5	1.50	0.03	1.45–1.54	6x	-
STC	Slovakia, Štúrovo: *Tilia* stand in front of new cemetery in Novocintorínská street, 123 m a.s.l., 47°47′40.5"N, 18°42′8.9"E, 18. 4. 2025, leg. MH & AU							
		O. divergens	4	1.32	0.01	1.30–1.34	5x	-
STD	Slovakia, Štúrovo: Danube waterfront next to the Mária Valéria bridge, 105 m a.s.l., 47°47′52.8"N, 18°43′37.6"E, 17. 4. 2023 & 18. 4. 2025, leg. MH & AU							
		O. divergens	1	1.34	-	-	5x	-
		O. refractum	9	1.09	0.03	1.07–1.16	5x	2 (2n = 45)
		O. refractum	4	1.37	0.01	1.36–1.38	6x	-
STK	Slovakia, Štúrovo: levee near the confluence of Danube and Hron rivers E of town, 108 m a.s.l., 47°49′5.5"N, 18°44′16.6"E, 16. 4. 2023, leg. MH							
		O. divergens	3	1.29	0.05	1.22–1.34	5x	-
		O. refractum	1	1.12	-	-	5x	-
		O. refractum	6	1.39	0.02	1.36–1.41	6x	2 (2n = 54)
STP	Slovakia, Štúrovo: sandy lawns in Petőfiho street, 112 m a.s.l., 47°47′34.0"N, 18°43′10.7"E, 18. 4. 2025, leg. MH & AU							
		O. divergens	5	1.28	0.05	1.18–1.32	5x	-
STW	Slovakia, Štúrovo: ruderal lawns between road and field in Továrenská cesta street, ca. 500 m E of railway station, 120 m a.s.l., 47°47′54.6"N, 18°41′12.7"E, 20. 4. 2025, leg. MH & AU							
		O. divergens	4	1.32	0.02	1.29–1.34	5x	-

in a solution of 35% hydrochloric acid: 96% ethanol (1:1). Macerated root tips were then placed into a small vial with Fe-acetocarmine and left for four minutes to stain. Then the meristem was gently dissected from the rest of the root tip, and squashes were made in a drop of Fe-acetocarmine. Resulting metaphases were observed under a Carl Zeiss, Axio Scope.A1 light microscope equipped with Axiocam 105 Color camera (both Carl Zeiss AG, Jena, Germany). Flow cytometry results for *O. divergens* were calibrated by chromosome counts of broader sampling from Central Europe prepared in our lab by the same method as described above (see Kovalová 2023).

Morphometric analysis

In order to morphologically distinguish *O. refractum* from *O. divergens* and to characterise Slovak plants of *O. refractum*, 27 quantitative morphological traits were measured and counted in the field. Additional seven ratios were calculated from these traits (for the list of studied traits, ratios and character abbreviations see Table 2). Morphological characters were measured using a measure and digital calliper Extol 3426. All individuals used for flow cytometry investigation, and thus with known ploidy level, were used for morphometric analysis (Table 1).

The resulting morphological matrix was analysed using NCSS 9 (Hintze 2013) and Morphotools 2 (Šlenker et al. 2022) package in R 4.1.2 (R Core team 2017). Morphological differences between groups defined by obtained relative genome sizes were tested using the analysis of variance (ANOVA) test and the Tukey-Kramer multiple comparison test. Traits that were found invariable between the groups by ANOVA (see Table 2) were excluded from the matrix for multivariate analyses. The correlation matrix using the Pearson correlation coefficient was calculated before multivariate analyses. When correlation exceeded $r \geq |0.95|$, one trait from the pair was excluded from the following analyses (Lstinf). We also excluded height (Hbl) and width of bulb (Wbl) as these dimensions may reflect the age of an individual and/or the soil depth in which bulb grows (Trávníček et al. 2009; Howard et al. 2025) and kept only their ratio in the matrix. The resulting matrix with 12 measured morphological characters and their six ratios was then analysed using Ward's clustering analysis with Euclidean distance and principal component analysis (PCA) with Euclidean distance and standardization of traits to a zero mean and unit variance to see the clustering of the individuals in morphospace.

Table 2 Morphological differences between the four cytotypes resulted from FCM analysis based on all collected individuals (see Table 1) with results of ANOVA test (F) and Tukey-Kramer multiple comparison test (superscript letters). All values in mm

Taxon		*O. divergens* (5x)^{A}			*O. divergens* (6x)^{B}			*O. refractum* (5x)^{C}			*O. refractum* (6x)^{D}				
Character	abbreviation	mean	±SD	min–max	mean	±SD	min–max	mean	±SD	min–max	mean	±SD	min–max	F	p
height of bulbil	Hbl	5.7	0.7	4.4–6.9	6.1	1.0	4.9–7.6	5.5	0.5	4.9–6.3	6.1	1.0	4.9–7.6	1.08	0.370
width of bulbil	Wbl	4.0	0.5	3.0–4.8	4.1	0.6	3.3–4.9	3.9	0.5	3.3–4.5	4.1	0.6	3.3–4.9	0.55	0.649
height of mature bulb	Hb	24.8^{B}	4.0	18.8–33.7	20.8	4.2	15.8–28.0	21.9	3.4	17.0–26.4	20.8	4.2	15.8–28.0	4.09	**0.013**
width of mature bulb	Wb	19.7^{D}	4.2	13.4–31.0	15.4^{A,B,C}	2.7	10.5–19.7	22.7^{D}	4.4	16.9–30.4	15.4^{A,B,C}	2.7	10.5–19.7	6.25	**0.001**
ratio of height/width of mature bulb	R_HbWb	1.3^{B,C}	0.1	1.1–1.5	1.4^{B,C}	0.2	1.1–1.8	1.0^{A,D}	0.1	0.9–1.1	1.4^{B,C}	0.2	1.1–1.8	20.80	**< 0.001**
number of leaves	Nl	4.5	1.7	3–8	3.2^{B,C}	0.8	2–4	5.9^{D}	1.3	5–8	3.2^{B,C}	0.8	2–4	8.37	**< 0.001**
width of leaf	Wl	3.8^{B}	1.0	2.6–6.1	3.1^{A,C,D}	0.7	2.0–4.0	3.5^{B}	0.7	2.4–4.8	3.1^{B}	0.7	2.0–4.0	7.37	**< 0.001**
width of central leaf stripe	Wstr	0.9	0.2	0.6–1.3	0.8^{B,C}	0.2	0.5–1.0	1.1^{D}	0.3	0.8–1.6	0.8^{B,C}	0.2	0.5–1.0	5.06	**0.005**
ratio of width of central stripe/width of leaf	R_WstrWl	0.2^{C}	0.1	0.2–0.4	0.3	0.1	0.2–0.4	0.3^{A}	0.1	0.2–0.5	0.3	0.1	0.2–0.4	2.89	**0.048**
height of plant (incl. inflorescence)	Lstinf	183.4^{C,D}	47.4	127.0–283.0	112.5^{A,B}	18.7	82.0–135.0	90.2^{A,B}	21.2	63.0–127.0	112.5^{A,B}	18.7	82.0–135.0	20.24	**< 0.001**
length of scape	Lst	113.9^{C,D}	40.3	62.0–217.0	69.9^{A,B}	16.1	43.0–90.0	48.1^{A,B}	11.5	30.0–60.0	69.9^{A,B}	16.1	43.0–90.0	14.40	**< 0.001**
number of flowers	Nfl	9.4	3.9	5–18	7.3^{C}	2.2	4–11	14.4^{D}	7.6	4–27	7.3^{C}	2.2	4–11	3.76	**0.019**
ratio of length of inflorescence/number of flowers^{E}	R_LinfNfl	8.2^{C}	2.3	3.7–12.2	6.3^{C}	1.9	2.9–9.3	3.4^{A,B,D}	1.5	1.8–6.0	6.3^{C}	1.9	2.9–9.3	11.40	**< 0.001**
length of 1st branch of inflorescence	L1b	48.6^{B,C,D}	10.1	35.0–72.0	29.3^{A}	5.5	23.0–40.0	28.6^{A}	4.7	19.0–36.0	29.3^{A}	5.5	23.0–40.0	20.09	**< 0.001**
length of 1st branch bract	L1br	33.4	7.0	24.0–54.0	26.0	7.0	20.0–35.0	28.0	5.0	20.0–37.0	31.1	4.2	25.0–39.0	2.81	0.053
ratio of length of 1st branch bract/length of 1st branch	R_L1brL1b	0.7^{C,D}	0.1	0.5–0.9	0.7^{C,D}	0.1	0.5–0.9	1.0^{A,B}	0.1	0.8–1.2	1.1^{A,B}	0.2	0.9–1.4	23.03	**< 0.001**
length of 2nd branch of inflorescence	L2b	44.6^{C,D}	10.7	31.0–70.0	33.8	7.9	21.0–42.0	27.2^{A}	7.4	16.0–38.0	28.6^{A}	4.7	22.0–35.0	11.79	**< 0.001**
length of 2nd branch bract	L2br	29.1	8.5	16.0–53.0	24.0	7.4	18.0–36.0	26.2	5.6	16.0–33.0	28.1	2.9	23.0–32.0	0.92	0.441
ratio of length of 2nd branch bract/length of 2nd branch	R_L2brL2b	0.7^{C,D}	0.1	0.4–0.9	0.7^{C,D}	0.2	0.5–0.9	1.0^{A,B}	0.1	0.8–1.2	1.0^{A,B}	0.2	0.8–1.4	15.01	**< 0.001**
length of outer tepal	Lot	19.9^{B}	2.4	14.9–23.0	16.8^{A,C}	0.5	16.1–17.4	20.6^{B}	2.4	16.1–22.9	19.5	1.6	17.2–22.3	3.84	**0.017**
width of outer tepal	Wot	7.0	1.1	5.2–9.1	6.2	1.2	4.8–7.6	7.1	0.8	6.0–8.1	6.7	0.5	5.8–7.6	1.29	0.291
length of inner tepal	Lit	17.3	2.0	13.8–20.6	15.4^{C}	0.5	14.7–15.9	18.8^{B}	2.3	15.8–22.3	17.9	1.1	16.2–20.1	4.13	**0.012**
width of inner tepal	Wit	6.1	1.3	4.3–8.6	5.8	0.7	5.0–6.6	6.5	0.9	5.0–7.8	5.8	0.9	4.5–7.1	0.89	0.457
width of stripe of outer tepal	Wostr	4.3^{C}	0.6	2.7–5.2	4.4^{C}	0.8	3.5–5.5	5.4^{A,B,D}	0.4	4.8–6.1	4.5^{C}	0.7	3.7–5.8	8.28	**< 0.001**
ratio of outer tepal stripe/width of outer tepal	R_WostrWot	0.6^{C}	0.1	0.5–0.8	0.7	0.0	0.7–0.8	0.8^{A,D}	0.0	0.7–0.8	0.7^{C}	0.1	0.6–0.8	9.67	**< 0.001**
length of filament	Lfil	7.2	1.5	4.6–8.9	8.2	0.4	7.7–8.7	7.2	0.7	6.2–8.7	6.6	1.4	4.3–9.0	1.90	0.145
width of filament on the base	Wfil	1.5^{B}	0.4	0.9–2.2	2.1^{A,C}	0.4	1.8–2.7	1.7^{B}	0.2	1.4–1.9	1.7	0.2	1.5–2.1	5.33	**0.004**

Table 2 (continued)

Taxon		*O. divergens* (5x)[A]			*O. divergens* (6x)[B]			*O. refractum* (5x)[C]			*O. refractum* (6x)[D]				
Character	abbreviation	mean	± SD	min–max	mean	± SD	min–max	mean	± SD	min–max	mean	± SD	min–max	F	p
length of anther	Lant	3.9	0.4	3.5–4.6	3.8	0.3	3.5–4.2	4.1	0.1	3.9–4.3	4.0	0.3	3.5–4.4	1.67	0.189
length of ovary	Lov	6.2	1.1	4.1–7.5	5.8	0.6	4.8–6.3	6.8	0.9	5.2–7.7	6.2	0.6	5.0–7.0	1.82	0.160
width of ovary	Wov	3.0[B,C]	0.4	2.5–3.5	2.5[A,C]	0.4	2.0–3.0	3.5[A,B,D]	0.4	2.9–4.2	3.0[C]	0.3	2.5–3.5	7.96	**< 0.001**
length of style	Lsty	3.4	0.6	2.4–4.3	3.4	0.6	2.6–3.9	3.3	0.3	2.7–3.6	3.2	0.4	2.4–3.7	0.55	0.651
ratio of length of style/length of ovary	R_LstyLov	0.6	0.2	0.3–0.9	0.6	0.1	0.4–0.7	0.5	0.1	0.4–0.7	0.5	0.1	0.4–0.6	1.11	0.356

[A, B, C, D] Significant differences of mean between the taxa based on results of Tukey–Kramer multiple comparison test

[E] Calculated as (height of plant – length of scape)/number of flowers

Results

Ploidy level, chromosome counts and relative genome size

Two ploidy levels corresponding to 2n = 5x = 45 (two plants, population STD) and 2n = 6x = 54 (two plants, population STK) were obtained by chromosome counting (Fig. 1). Four non-overlapping relative genome size groups were observed, two of them corresponding to pentaploids (both *O. divergens* and *O. refractum*) and two to hexaploids (again both *O. divergens* and *O. refractum*, Table 1, Online Resource 1).

Morphological differentiation of *O. refractum* and *O. divergens*

Significant differences (< 0.05) between the groups defined by their genome sizes were found by ANOVA in 21 out of 34 studied morphological traits and ratios (Table 2, Online Resource 2). Tukey-Kramer multiple comparison test further showed that both ploidies of *O. refractum* differ from both studied ploidies of *O. divergens* by shorter overall habit including length of stem and bracts generally of the same length or longer than the respective branch (Table 2, Fig. 2). Pentaploid *O. refractum* further differed from all other three taxa by higher number of flowers per inflorescence length, outer tepals with wider green stripe on its abaxial side and wider ovary. Hexaploid *O. refractum* further differed from all other three taxa by thinner bulbs. For additional differences see Table 2 and Online Resource 2.

Ward's cluster analysis revealed two main groups corresponding to *O. divergens* and *O. refractum*. The finer clustering showed much more intricate structure with individuals of both ploidies intermixed in clusters (Fig. 3a). PCA showed a similar pattern with the first axis explaining 28.3%, the second axis 23.1% and the third axis 14.2% of total variation. Pentaploid *O. refractum* occupied the left side of the ordination space and *O. divergens* individuals of both ploidy levels were positioned in the right part. Hexaploid *O. refractum* filled the space between these two main groups (Fig. 3b). Hexaploid *O. divergens* were separated from the rest along the third axis (Fig. 3c). Characters R_LinfNfl and Wostr were the most correlated ones with the first axis, R_HbWb and Lot were the most correlated ones with the third axis (Online Resource 3).

Habitat of *O. refractum* in Slovakia

Two populations of *O. refractum* in Štúrovo town area were discovered (STD, STK). Pentaploid *O. divergens* was also present in both places. Vegetation of stands in both populations remained unclassified as the species spectrum

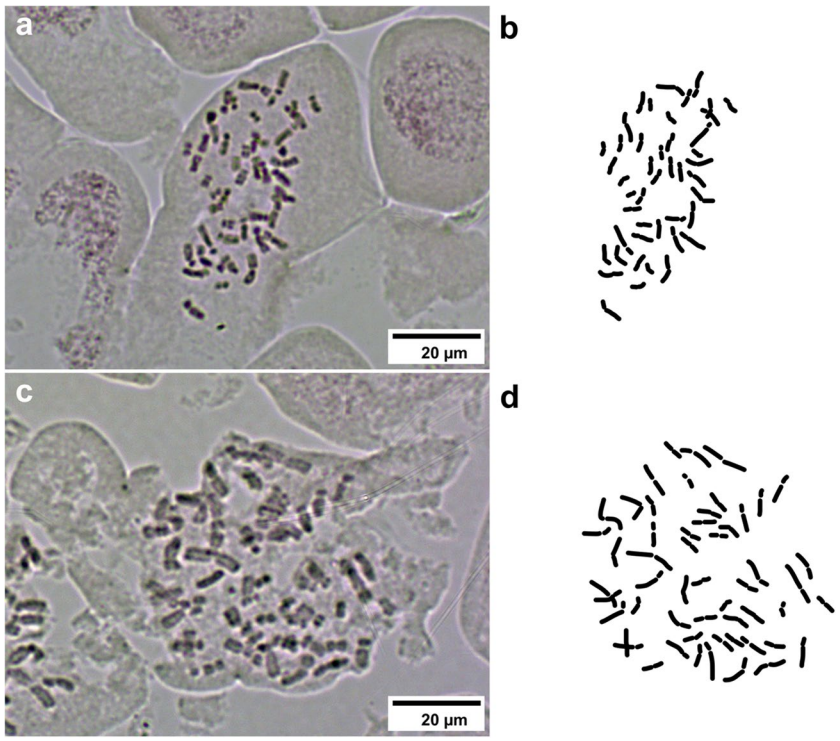


Fig. 1 Chromosome metaphases of *O. refractum* from Štúrovo, Slovakia: **a, b** pentaploid 2n = 45 (population STD); **c, d** hexaploid 2n = 54 (population STK)

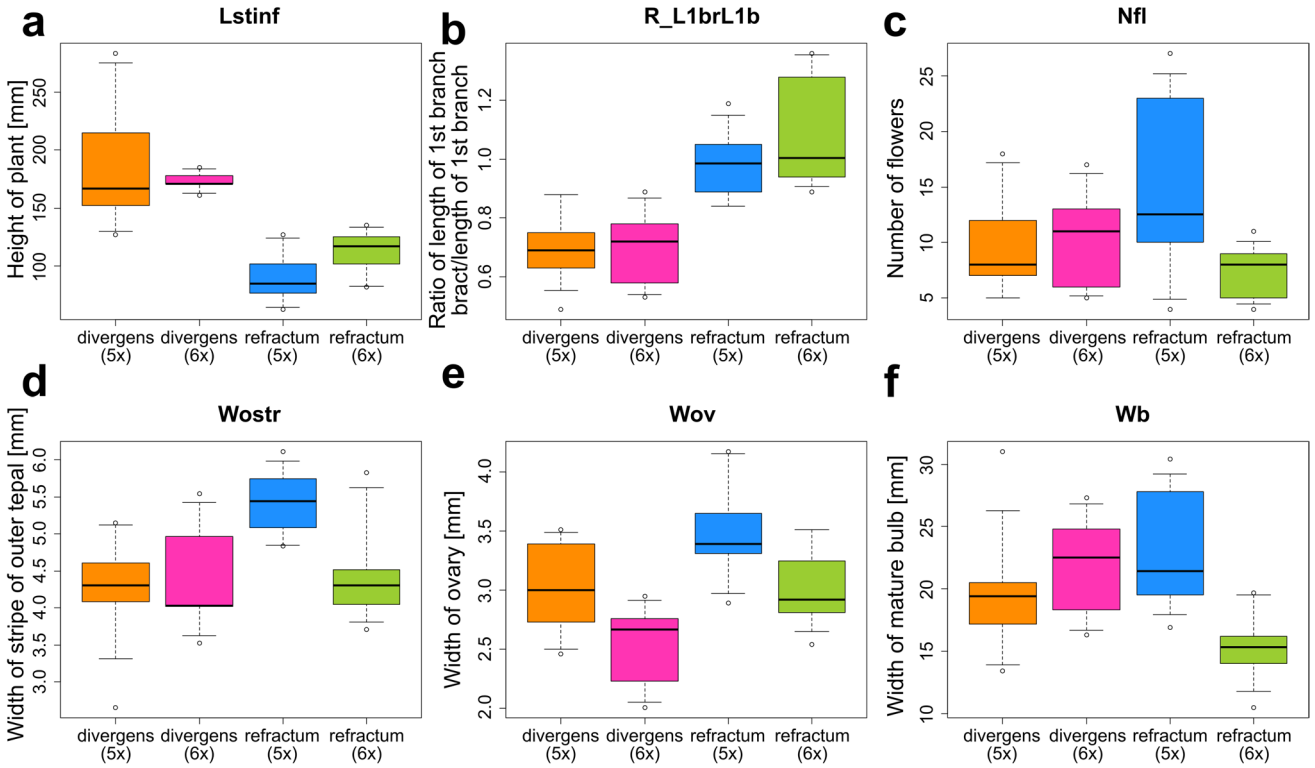


Fig. 2 Morphological differentiation in selected traits of pentaploid and hexaploid *O. refractum* and *O. divergens* based on all collected individuals (see Table 1). For character abbreviations see Table 2. Boxes define the 25th and 75th percentiles, horizontal lines show the median, whiskers are from the 10th to 90th percentiles, circles show extreme values

consisted of local species assemblage not characteristic of any particular vegetation type (M. Chytrý, pers. comm.). Population STD occurred in a regularly mown city lawn with the occurrence of some thermophilous species on the Danube waterfront. Population STK occurred on the levee of the Hron River in thermophilous weedy vegetation with dominant occurrence of therophytes and geophytes. In both stands, species characteristic of *Stellarietea mediae* and *Artemisietea vulgaris* classes dominated, but thermophilous species of order *Festucetalia valesiacae* and some mesophilous species of order *Arrhenatheretalia elatioris* occurred also with high frequencies. Vegetation on both stands is illustrated by the following phytocoenological relevés:

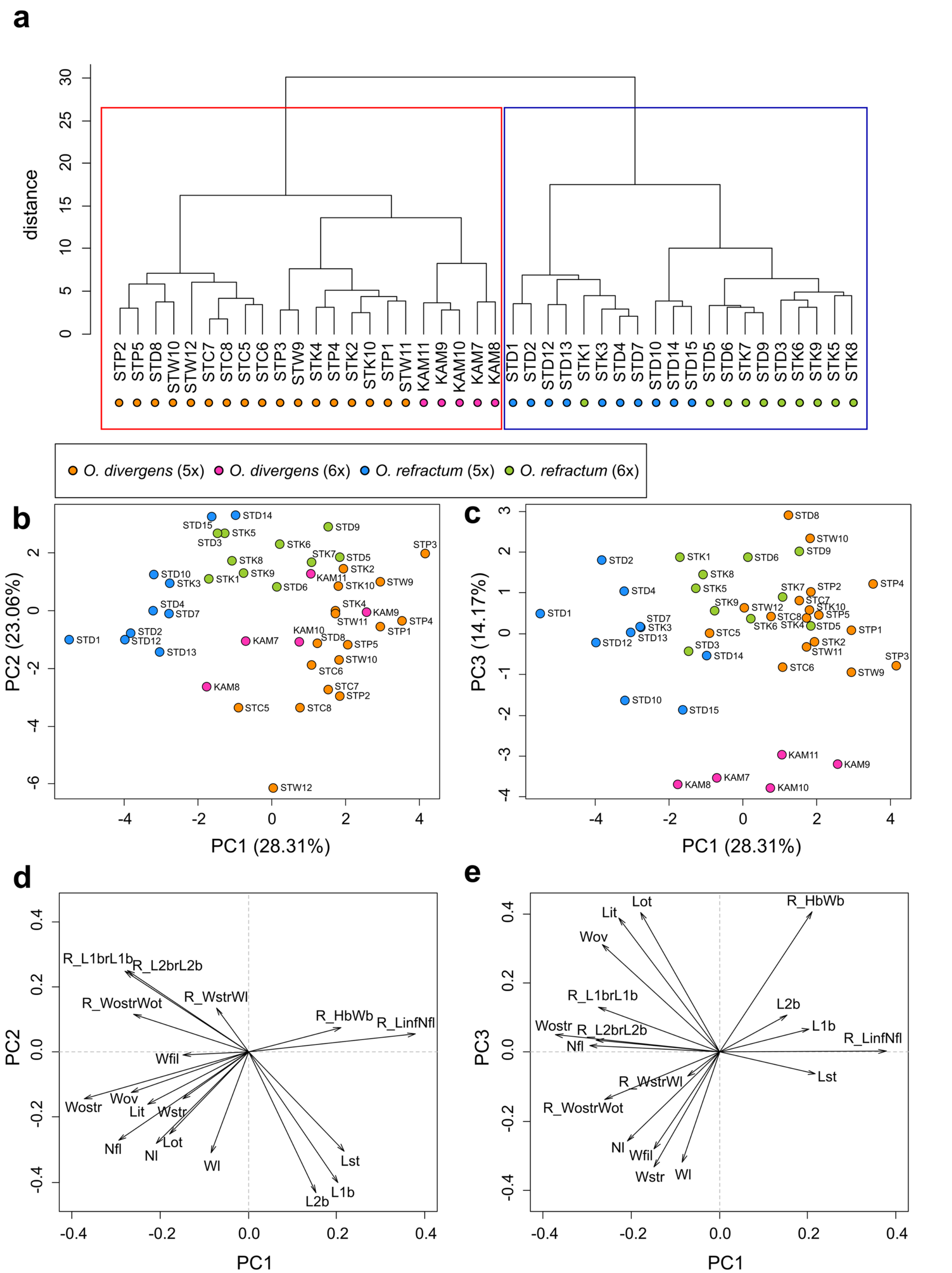
SK, Štúrovo town (distr. Nové Zámky): levee near the confluence of Danube and Hron rivers E of town, 47°49′5.5"N, 18°44′16.6"E, 108 m a. s. l., population STK, relevé size 4 m×4 m (16 m^2), slope 30°, orientation SW, 5. 5. 2023, *M. Hroneš, A. Uvírová*.
E_1 (40%): *Erodium cicutarium* 2b, *Bromus tectorum* 2a, *Medicago minima* 2a, *Carex praecox* 2m, *Euphorbia cyparissias* 2m, *Anchusa officinalis* 1, *Arenaria serpyllifolia* 1, *Dianthus deltoides* 1, *Poa bulbosa* 1, *Allium scorodoprasum* +, *Alyssum alyssoides* +, *Bromus hordeaceus* +, *Bromus sterilis* +, *Capsella bursa-pastoris* +, *Centaurea stoebe* subsp. *stoebe*. +, *Cerastium glutinosum* +, *Cichorium intybus* +, *Convolvulus arvensis* +, *Conyza canadensis* +, *Elymus repens* +, *Geranium pusillum* +, *Lamium purpureum* +, *Microthlaspi perfoliatum* +, *Muscari neglectum* +, *Ornithogalum divergens* +, *Ornithogalum refractum* +, *Plantago lanceolata* +, *Poa angustifolia* +, *Potentilla argentea* +, *Rumex thyrsiflorus* +, *Silene conica* +, *Silene vulgaris* +, *Veronica arvensis* +, *Vicia grandiflora* +, *Viola arvensis* +, *Viola kitaibeliana* +, *Myosotis arvensis* r, *Silene latifolia* subsp. *alba* r, *Tragopogon orientalis* r, *Valerianella locusta* r, *Vicia hirsuta* r, *Vicia lathyroides* r, *Vicia sativa* r. – E_0 (10%).
SK, Štúrovo town (distr. Nové Zámky): Danube waterfront next to the Mária Valéria bridge, 47°47′52.8"N, 18°43′37.6"E, 105 m a. s. l., population STD, relevé size 4 m×4 m (16 m^2), slope 20°, orientation W, 18. 4. 2025, *M. Hroneš, A. Uvírová*.
E_1 (60%): *Carex stenophylla* 3, *Erodium cicutarium* 2b, *Stellaria pallida* 2b, *Festuca pratensis* 2a, *Malva sylvestris* 2a, *Anchusa officinalis* 2m, *Plantago lanceolata* 2m, *Medicago minima* 1, *Ornithogalum divergens* 1, *Poa angustifolia* 1, *Achillea millefolium* agg. +, *Carex praecox* +, *Cerastium glutinosum* +, *Ficaria calthifolia* +, *Geranium pusillum* +, *Lamium amplexicaule* +, *Lamium purpureum* +, *Medicago sativa* +, *Muscari neglectum* +, *Ornithogalum refractum* +, *Poa bulbosa* +, *Potentilla argentea* +, *Senecio vulgare* +, *Silene vulgaris* +, *Valerianella locusta* +, *Veronica arvensis* +, *Veronica filiformis* +, *Veronica hederifolia* +, *Veronica polita* +, *Capsella bursa-pastoris* r, *Convolvulus arvensis* r, *Taraxacum* sect. *Taraxacum* r. – E_0 (20%).

Discussion

We have shown that *Ornithogalum refractum* occurs at two localities with dozens of individuals in Slovakia. Both populations are mixed-ploidy with co-occurring 5x and 6×cytotypes. Its populations in Štúrovo are the northernmost known populations in the Pannonian Basin, and they represent a continuation of species distribution in northern Hungary. As discussed below, we do not consider its occurrence to be a consequence of a recent introduction but rather a result of overlooking.

As showed by Speta (2010), the type locality of *O. refractum* should be traced to Budapest. The species is distributed from Hungary through the Balkan Peninsula to Italy and Türkiye, and around the Black Sea coast in Romania to Crimea (Zahariadi 1980; Rat 2019). However, some reports of its occurrence, especially in southern parts of its range, may represent misidentifications (Speta 2010). The centre of its distribution in Hungary is located in the hilly areas (Buda, Gerecse, Pilis and Visegrádi-hegység) in the north of the country, south of the right bank of the Danube River in the area between Győr and Esztergom (Rat 2019; Bartha et al. 2021+). Therefore, it would not be surprising to discover additional populations in southern Slovakia, especially in the area between Komárno and Štúrovo, and in the wider vicinity of Burda hills, i.e. the area which is separated only by the Danube River from the current known range of *O. refractum*. In this respect, our findings fit well with this expectation.

The karyology of *O. refractum* is complicated. Most of the authors report it as a polyploid species with x = 9 and 2n = 6x = 54 (Markova et al. 1972; Raamsdonk 1986; Lovka 1995; Dalgıç and Özhatay 1997). However, a wide range of chromosome counts for this species has been reported from Italy: 2n = 4x = 36, 2n = 5x = 45, 2n = 6x = 54, 2n = 8x = 72 and 2n = 10x = 90 (partly reported as *O. brutium* Terrac.; Peruzzi and Passalaqua 2002). Other counts based on x = 7 (Šopova and Sekovski 1981) were disproved by Peruzzi and Passalaqua (2002) as belonging to *O. sibthorpii* Greuter s. lat. In this respect, we consider counts with 2n = 28 presented by Dalgıç and Özhatay (1997) also erroneous. Speta (2010) counted 2n = 45 in plants from Budapest which agrees with one of our counts from Štúrovo. The presence of pentaploids and hexaploids in the Pannonian Basin, hexaploids in the Balkan Peninsula and Türkiye, and even higher polyploids in southern Italy and Sicily may indicate a complicated cytogeographical structure which is quite common in other monocot polyploid complexes (Vestek et al. 2019; Duchoslav et al. 2020; Horák et al. 2023; Mtileni et al. 2024). On the contrary, some of the higher ploidy level reports may be


a
distance
0 5 10 15 20 25 30
STP2 STP5 STD8 STW10 STW12 STC7 STC8 STC5 STC6 STP3 STW9 STK4 STP4 STK2 STK10 STP1 STW11 KAM11 KAM9 KAM10 KAM7 KAM8
STD1 STD2 STD12 STD13 STK1 STK3 STD4 STD7 STD10 STD14 STD15 STD5 STD6 STK7 STD9 STD3 STK6 STK9 STK5 STK8
O. divergens (5x) O. divergens (6x) O. refractum (5x) O. refractum (6x)
b
PC2 (23.06%)
PC1 (28.31%)
c
PC3 (14.17%)
PC1 (28.31%)
d
PC2
PC1
R_L1brL1b R_L2brL2b R_WostrWot R_WstrWl R_HbWb R_LinfNfl Wfil Wostr Wov Lit Wstr Nfl Nl Lot Wl Lst L2b L1b
e
PC3
PC1
Lot Lit Wov R_HbWb R_L1brL1b L2b Wostr R_L2brL2b L1b Nfl R_LinfNfl R_WstrWl Lst R_WostrWot Nl Wfil Wstr Wl

◂**Fig. 3** Morphological differentiation of studied individuals of *O. refractum* and *O. divergens* based on all collected individuals (see Table 1): **a** results of Ward's cluster analysis, two main clusters belong to both ploidy levels of *O. divergens* (red rectangle) and both ploidy levels of *O. refractum* (blue rectangle); **b, d** PCA scatterplot with the first and second axis displayed; **c, e** PCA scatterplot with the first and third axis displayed

based on different species. Speta (1994) described hexaploid plants morphologically similar to *O. refractum* from Northern Macedonia as a new species, *O. lychnite* Speta. It is not clear if he considered all reports of hexaploids from the Balkan and Türkiye as *O. lychnite*, however, some indirect mentions may confirm this (see Speta 2010). Disentangling the cytogeography of *O. refractum* and deciding whether it consists of only pentaploids or also other cytotypes should be a matter of larger study.

We found both populations of *O. refractum* in Štúrovo to occur in sympatry with pentaploid *O. divergens* which has the same number of chromosomes (Hrouda 2007). However, the species differ in their relative genome size, probably due to different amounts of transposable elements, indicating different evolutionary pathways of both pentaploids. Raamsdonk (1986) found in hexaploid *O. refractum* quite isolated karyotype which was not directly related to any other studied species, including *O. divergens* (as *O. umbellatum* in the study). However, as noted above, Raamsdonk may have based his observations on different morphologically similar species (cf. Speta 2010). While the studied populations possessed non-overlapping relative genome sizes, the relative genome size variation in pentaploids and hexaploids of *O. divergens* is almost continuous when studied on larger scale (Kovalová 2023). Therefore, relative genome size itself does not separate hexaploids of *O. refractum* from both ploidies of *O. divergens* and cannot be used as a sole discriminating character.

Morphologically, *O. refractum* is distinct among Pannonian species by the combination of the following traits: mature bulb globose with concrescent scales, surrounded by numerous leafless bulbils, stem hypogeous for most of its part, bracts as long as inflorescence branches and pedicels in fruit distinctly reflexed. Other European *Ornithogalum* species with at least partly hypogeous stem and reflexed pedicels in fruit, i.e. *O. excapum* s. lat. and *O. sibthorpii* s. lat., have free scales of mature bulb without bulbils. Members of both species complexes also have much lower counts of chromosomes (Speta 1990; Peruzzi and Passalaqua 2002; Rat and Bogdanović 2021). The most similar species by the bulb morphology and the presence of leafless bulbils is therefore *O. divergens*, especially its pentaploid cytotype which is characterised by a lower number of bulbils with leaves. Both taxa can be distinguished by a series of characters (see Tab. 2), but the overall appearance may be misleading for the regular florists. Other facts, which may contribute to the overlooking of *O. refractum* in Slovakia, are its sympatric occurrence with *O. divergens* and only slightly earlier phenology. Similarly, populations of *O. sibthorpii* were overlooked in Croatia (Rat and Bogdanović 2021).

Ornithogalum refractum inhabits (semi-)ruderal places on "stony or cultivated ground" (Zahariadi 1980) or "scrubs and steep slopes" (Krashennikov 1935). In Hungary, it grows mainly in lawns in city parks, dry disturbed places and cemeteries (Speta 2010; Molnár et al. 2017; Löki et al. 2020). While the character of its stands in Hungary is certainly human induced, there is an uncertainty whether the species itself is native or an archaeophyte (Csiky et al. 2023). Cemeteries and ruderalised dry lawns may serve as refugia for thermophilous steppe flora (Molnár et al. 2017; Löki et al. 2020), including other geophytes such as *Iris pumila* L., *Loncomelos brevistylum* and *Sternbergia colchiciflora* (Molnár et al. 2017, 2018, 2020). Analogically, the more widespread and ecologically similar *O. divergens* is not listed as alien in Slovakia, and there are doubts whether it is native or an archaeophyte in Hungary (Medvecká et al. 2012; Csiky et al. 2023). The two populations of *O. refractum* found in Slovakia inhabit semi-ruderal vegetation with frequent occurrence of therophytes, geophytes and thermo- and xerophilous native species, either on periodically mown city lawns or less extensively managed places such as levees. The character of vegetation with occurrence of numerous native species, at least in the second population, suggests that our recent findings of *O. refractum* are not of very recent origin. However, additional data (including the herbaria revision) need to be collected to decide whether *O. refractum* is native, archaeophyte or neophyte in the flora of Slovakia.

Species description based on Slovakian plants

Ornithogalum refractum **Kitaibel ex Willdenow**, Enum. Pl. Suppl. 18 (1814). Figure 4

Bulbous, glabrous geophyte, 6.0–13.0 cm tall (from base of bulb to uppermost flower). Mature bulbs 1–2, 1.6–2.8 cm long, 1.1–3.0 cm in diameter, almost globose to widely ovoid, bulb scales concrescent, outer tunic light brown, surrounded by numerous (up to 65) lenticular leafless bulbils and usually also few (up to 5) bulbils with single tubular leaf. Bulbils ca 0.5 cm long and 0.4 cm wide. Leaves 4–8, 0.2–0.5 cm wide, linear, slightly canaliculate, much longer than stem and inflorescence together, dark green, adaxially with silver, 0.5–1.3 mm wide stripe covering 1/3–1/2 of leaf width. Scape for the most part hypogeous, 3.0–9.0 cm long. Inflorescences epigeous or only on up to 2.0 cm long scape above ground, widely corymbose, with 4–27 flowers; two lowermost branches of the inflorescence 1.6–4.0 cm long; bracts 1.6–3.9 cm long, usually of almost the same length or slightly longer than respective

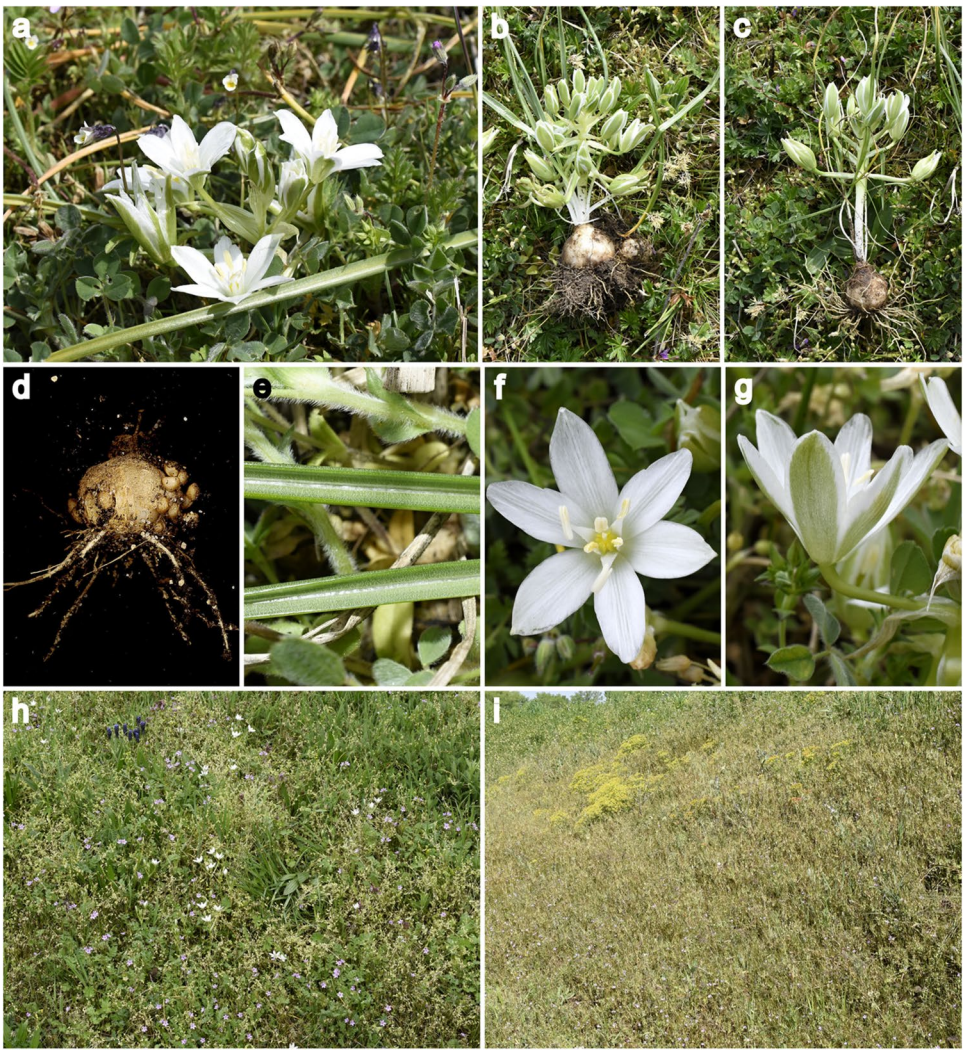


Fig. 4 *Ornithogalum refractum* from Štúrovo: **a** habit of a hexaploid plant with epigeous inflorescence (population STK); **b, c** overall habit of pentaploid plants with ovoid to globose bulbs, hypogeous whitish scape and epigeous inflorescence, lower pedicels becoming deflexed in **b** (population STD); **d** Globose mature bulb with lenticular bulbils (population STD); **e** detail of leaves with central stripe (population STD); **f** detail of flower viewed from above (population STD); **g** side view of flower with distinct short pedicel and wide green stripe on outer tepal (population STD); **h** vegetation in STD population in mid-April with *Cerastium glutinosum*, *Erodium cicutarium*, *Muscari neglectum* and *O. divergens*; **i** vegetation in STK population in mid-May with dominant *E. cicutarium*, *Euphorbia cyparissias* and *Bromus* spp. All photographs by M. Hroneš

branch, long triangular, membranaceous, beige. Flowers with 6 tepals in two whorls, adaxially white, abaxially white with green central stripe. Outer tepals 1.6–2.3 cm long and 0.6–0.8 cm wide, with abaxial green stripe 0.4–0.6 cm wide, covering 60–80% of tepal width; inner tepals 1.6–2.2 cm long and 0.5–0.8 cm wide. Filaments 4.3–9.0 mm long and 1.2–1.4 mm wide at base, triangular, white. Anthers 3.5–4.4 mm long. Ovary 5.0–7.7 mm long and 2.5–4.2 mm wide, cylindrical, with six prominent ribs; stigma 2.4–3.7 mm long. Fruiting pedicels distinctly reflexed, basally with a distinct pulvinus. Capsules of at least the lower flowers epigeous.

Distribution Overall range is unclear due to unresolved taxonomy. With certainty, it is occurring in Hungary and the northern parts of the Balkan Peninsula. The identity of plants from Italy, the southern Balkan Peninsula, the Black Sea coast and Türkiye needs to be confirmed by a biosystematic study. In Slovakia, so far only known from Štúrovo area.

Habitat and phenology Regularly mowed lawns and thermophilous semi-ruderal vegetation. Flowering usually in the second half of April, fruiting in the first half of May.

Preliminary key for *Ornithogalum* subgen. *Ornithogalum* taxa occurring or reported from Slovakia

Due to ongoing research on nomenclature and taxonomy of *Ornithogalum* from Central Europe, some taxa are presented in the following key in wide sense (sensu lato).

1. Leaves almost flat, glaucous, without the distinct white or silver central stripe, usually with distinct cilia along the margins; scape well-developed above the soil; bracts usually of almost the same length or slightly longer than respective branch; ovary with rounded low ribs. Ploidy level 2x. Extinct …..... *O. comosum* s. lat.

— Leaves canaliculate, dark green, with distinct white or silver central stripe, glabrous; scape well-developed above the soil or hypogeous for the most part; bracts usually shorter than the respective branch (when longer, then scape hypogeous for the most part); ovary with obtuse distinct ribs … 2

2. Mature bulbs almost globose, ovoid, pyriform, long pyriform to almost cylindrical, usually longer than wide, without lenticular bulbils; all bulbils (if present) with leaves …..... 3

— Mature bulbs almost globose to widely ovoid, usually as long as wide, or wider than long, surrounded by numerous lenticular bulbils; at least some bulbils without leaves … 4

3. Bulbs solitary or in loose tufts, ovoid to pyriform, without bulbils or with low number of bulbils (up to 12) similar to mature bulbs but smaller, bulbil leaves tubular, without white stripe; leaves surpassing the top of the inflorescence. Ploidy levels 2x, 4x …..... *Ornithogalum kochii* s. lat.

— Bulbs numerous, in dense tufts, long pyriform to almost cylindrical, with 5–25 bulbils similar to mature bulbs but smaller, all usually developing leaves with distinct central white stripe; leaves not surpassing the top of the inflorescence. Ploidy levels 3x, 4x. Doubtfully present … .....*O. umbellatum* L.

4. Scape mostly hypogeous; ratio of lowermost branch bract length/lowermost branch length 0.8–1.4. Ploidy levels 5x, 6x … .....*O. refractum* Kit. ex Willd.

— Scape mostly well-developed above the soil; ratio of lowermost branch bract length/lowermost branch length 0.5–0.9. Ploidy levels 5x, 6x …..... *O. divergens* Bor.

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Author's contribution Conceptualisation, initial fieldwork, data analysis and draft preparation: MH. Both authors later collected data in field and in laboratory and participated on writing of the final version of the manuscript.

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Data availability Primary data are available from the corresponding author upon request.

Declarations

Ethical approval N/A.

Informed consent N/A.

Conflict of interest We declare no conflict of interest.

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