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Pollen morphology of selected taxa of *Valeriana* (Caprifoliaceae): taxonomic and evolutionary implications

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Abstract

Pollen morphology of 34 herbarium specimens belonging to 17 taxa of the genus *Valeriana* was studied using light and scanning electron microscopy. The aim of this research was to evaluate the taxonomical value of palynomorphological data for species-specific identification. Pollen grains are monads, radially symmetrical, isopolar, tricolpate, oblate to prolate (P/E = 0.69–1.59); medium- or large-sized (P = 26.60–66.50 µm; E = 23.94–57.19 µm). Colpi are long, medium-length or short, with acute, obtuse or rounded ends. Four types and eight subtypes of exine sculpture were recognised: type I—echinate-verrucate (5 spp.), type II—echinate-nanoechinate-verrucate (10), type III—echinate-microechinate-nanoechinate-verrucate (1), type IV—echinate-microechinate-nanoechinate (1). Additional characters of taxa of *Valeriana* diagnostic at species level for the purposes of taxonomy are: size of pollen and colpi, exine sculpture: presence/absence of verrucae, their form, size and form of echini/microechini/nanoechini, their number, pattern of tectum in areas between echini, exine thickness in mesocolpia and apocolpia. Our palynomorphological data support the results of molecular phylogenetic studies. The close phylogenetic relationships of the species *V. montana*, *V. tripteris*, *V. supina* and *V. pyrenaica* are also supported by their palynomorphological characters, such as exine sculpture (type I). Cluster analysis mainly supports the definition of pollen types and subtypes (based on qualitative data), since species are grouped as five separate branches. The pollen grains of five taxa were analysed for the first time in the current study.

Keywords: Eudicots, exine sculpture, taxonomy, Valerianaceae

Introduction

Valeriana Linnaeus (1753: 31) is a genus of the tribe Valerianeae Höck (1901: 408), subtribe Valerianinae Graebner (1906: 31), family Valerianaceae Batsch (1802: 227), nom. cons. According to the Angiosperm Phylogeny Group (2003, 2009, 2016), Valerianaceae is included in the family Caprifoliaceae Jussieu (1789: 210), nom. cons. The phylogenetic position of Valerianaceae within the order Dipsacales has been studied extensively (Bell *et al.* 2001, Donoghue *et al.* 2001, 2003, Zhang *et al.* 2003, Bell 2004, Hidalgo *et al.* 2004, Xiang *et al.* 2020, etc.). Valerianaceae traditionally has been subdivided into three tribes: Patrinieae Höck (1901: 408), Triplostegieae Höck (1901: 408) and Valerianeae (Bell & Donoghue 2005). In general, tribe Valerianeae is formed by the genera *Plectritis* (Lindley 1827: tab. 1094) Candolle (1830: 631), *Valerianella* Miller (1754: s.p.), *Fedia* Gaertner (1791: 36), nom. cons., *Valeriana* and *Centranthus* DC. in Candolle & Lamarck (1805: 238), with the addition of some small South American genera segregated by some authors (Raymúndez *et al.* 2002, Hidalgo *et al.* 2004, Bell & Donoghue 2005). *Valeriana* is the largest genus in tribe Valerianeae and comprises ca. 200–250 species distributed throughout much of the world (except Australia and New Zealand), mostly at high elevations and with many species in alpine zones (Hidalgo *et al.* 2004, Bell & Donoghue 2005, Jacobs *et al.* 2010, Nagahama & Bonino 2020). Around the world several species of *Valeriana* are used for medicinal purposes, since their underground organs contain various compounds with sedative and relaxing properties (Nagahama & Bonino 2020). Various taxonomic treatments of genus *Valeriana* have been published by Grubov (1958), Katina (1961), Ockendon (1976), Voroshilov (1978), and Holub & Kirschner (1997).

According to molecular phylogenetic data, *Valeriana* is not monophyletic. *Valeriana*, *Plectritis* and *Centranthus* form a sister clade to a clade containing *Fedia* and *Valerianella* (Hidalgo *et al.* 2004, Bell & Donoghue 2005, Bell 2007, Winkworth *et al.* 2008, Bell *et al.* 2012, 2015). The molecular analysis performed by Raymúndez *et al.* (2002) included four European species, which form a separate clade: *V. dioica* Linnaeus (1753: 31), *V. officinalis* Linnaeus (1753: 31), *V. tripteris* Linnaeus (1753: 32), and *V. apula* Pourret (1788: 332). According to Hidalgo *et al.* (2004), the investigated European species of genus *Valeriana* form two clades: one with *V. officinalis* subsp. *tenuifolia* (Vahl 1805: 6) Schübler & Martens (1834: 25), *V. dioica* and *V. jatamansi* Jones (1790: 416), and the other with *V. pyrenaica* Linnaeus (1753: 33), *V. saliunca* Allioni (1785: 3), *V. montana* Linnaeus (1753: 32) and *V. apula*. According to Bell & Donoghue (2005), the small clade (clade III) consisting exclusively of European taxa (*V. supina* Linnaeus (1767: 27), *V. montana*, *V. tripteris*, and *V. pyrenaica*) is placed at the base of the *Valeriana*+*Plectritis* clade and is sister to the rest of this clade. Recent molecular phylogenetic studies support the isolation of this clade (Bell *et al.* 2015).

It is well known that morphological characteristics of pollen grains as additional diagnostic features are often used in the taxonomy (e.g., Mosyakin & Tsymbalyuk 2015, 2017, Tsymbalyuk *et al.* 2019, 2021a, b, 2022, Albach *et al.* 2021, Alcantara *et al.* 2022, etc.). Many authors have studied and discussed the pollen morphology of Valerianaceae, including some *Valeriana* taxa, using light, scanning and/or transmission electron microscopy (e.g., Wagenitz 1956, Clarke & Jones 1977, Clarke 1978, Kupriyanova & Alyoshina 1978, Patel & Skvarla 1979, Diez 1984, Xena de Enrech 1993, Perveen & Qaiser 2007, etc.). Existing descriptions of pollen grains in general have been made at the genus level. Despite the relatively numerous publications, the knowledge about the structure and sculpture of pollen grains in *Valeriana* is fragmentary because the available descriptions usually have only briefly addressed the pollen morphology of few selected taxa, or researchers analysed few selected pollen features.

The aims of the present research were to study and analyse the morphological and morphometric characters of pollen grains of selected *Valeriana* species, to evaluate the taxonomical value of these data for species-specific identification and to compare the palynomorphological results with the molecular phylogenetic data.

Materials and Methods

Pollen grains of 17 taxa (34 specimens) of *Valeriana* were sampled in the National Herbarium of Ukraine [KW – herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine; acronym according to Thiers (2022)]. Plant names and authors were checked from different sources (e.g., Euro+Med (2006–), IPNI 2022, POWO 2022). Author abbreviations follow IPNI (2022). The methods used in the present study are described in details earlier (e.g., Tsymbalyuk *et al.* 2021a, b). Pollen morphology was studied using both light microscopy (LM) and scanning electron microscopy (SEM). For LM studies (Biolar, ×700), the pollen was acetolysed following Erdtman (1952), mounted on slides with glycerinated gelatin, analysed and photomicrographed. Pollen morphometric features of 20 properly developed pollen grains from each specimen were measured, and the measurements included the following parameters: polar axis (P), equatorial diameter (E), colpus length, colpus width, apocolpium diameter, mesocolpium diameter, halo thickness, exine thickness. The P/E ratio was calculated in order to determine the pollen shape. For all quantitative characters, descriptive statistics was applied and the range (minimum and maximum values), arithmetic mean and standard deviation were calculated (see Table 1). The slides were deposited in the Palynotheca at the National Herbarium of Ukraine (Bezusko & Tsymbalyuk 2011).

For SEM studies (JEOL JSM-6060LA), dry and acetolysed (some taxa) pollen grains were treated with 96%-ethanol, then the samples were sputter-coated with gold and investigated at the Centre of Electron Microscopy of the M.G. Kholodny Institute of Botany. The measurements of the echini, microechini and nanoechini were taken on 10 pollen grains from each specimen from SEM micrographs using the program AxioVision Rel.4.8.2. The number of echini/microechini/nanoechini per unit area (100 μm^2) was determined (Table 3). Terminology used in descriptions of pollen grains follows mainly the glossaries of Punt *et al.* (2007) and Halbritter *et al.* (2018).

Cluster analysis, performed by the Unweighted Pair Group Method with Arithmetic Average (UPGMA), was carried out to determine the phenetic similarity between *Valeriana* taxa. Ten quantitative palynomorphogical characters (listed in Table 1) and six qualitative characters (listed in Table 3) were examined. The PAST (PAleontological STatistics) program v. 4.08 was used for the analysis.

TABLE 1. Pollen morphometric characters: mean ± standard deviation, range (min–max) (all measurements given as μm).

Taxon	Polar axis (P)	Equatorial diameter (E)	P/E ratio	Colpi length	Colpi width	Apocolpium	Mesocolpium	Halo thickness	Exine in poles	Exine thickness
V. montana	51.73 ± 5.81 43.89–66.50	44.28 ± 2.88 37.24–50.54	1.17±0.14 0.92–1.47	29.52 ± 6.00 19.95–39.90	5.58±0.53 5.32–6.65	19.68 ± 1.95 15.96–22.61	33.44 ± 1.34 31.92–35.91	1.42±0.50 0.66–2.39	–	3.52±0.47 2.66–3.99
V. tripteris	40.69 ± 4.47 31.92–53.20	40.76 ± 4.59 31.92–50.54	1.00±0.10 0.82–1.25	26.73 ± 2.41 23.94–30.59	7.04±1.33 5.32–9.31	18.88 ± 2.36 15.96–22.61	31.18 ± 2.57 27.93–35.91	0.42±0.13 0.26–0.66	–	2.26±0.26 1.99–2.66
V. supina	49.80 ± 2.03 46.55–54.53	43.15 ± 3.10 38.57–50.54	1.15±0.06 1.02–1.31	36.04 ± 2.62 31.92–39.90	3.45±0.88 2.66–5.32	16.22 ± 1.86 13.30–19.95	32.45 ± 1.53 29.26–35.91	0.35±0.11 0.26–0.66	–	3.02±0.53 2.66–3.99
V. pyrenaica	47.34 ± 3.10 41.23–51.87	43.29 ± 2.57 37.24–47.88	1.09±0.10 0.88–1.28	34.84 ± 4.28 29.26–39.90	5.98±0.66 5.32–6.65	18.75 ± 2.75 15.96–22.61	28.72 ± 1.53 26.60–31.92	1.06±0.23 0.66–1.33	–	2.91±0.35 2.39–3.32
V. transsilvanica	46.61 ± 2.16 42.56–50.54	48.21 ± 1.96 45.22–51.87	0.96±0.03 0.88–1.02	31.12 ± 2.80 26.60–34.58	9.31±1.57 6.65–11.97	22.21 ± 0.60 21.28–22.61	33.91 ± 1.07 31.92–35.91	0.97±0.18 0.66–1.33	–	3.49±0.55 2.66–3.99
V. dioica	30.59 ± 1.97 26.60–33.25	30.59 ± 2.48 23.94–34.58	1.00±0.10 0.84–1.38	23.00 ± 1.19 21.28–25.27	5.98±1.80 2.66–9.31	12.76 ± 0.65 11.97–13.30	21.54 ±0.99 19.95–23.94	0.74±0.29 0.26–1.06	–	2.23±0.19 1.99–2.39
V. simplicifolia	40.56 ± 3.95 34.58–47.88	35.77 ± 2.84 30.59–39.90	1.13±0.10 0.89–1.29	27.66 ± 1.76 25.27–31.92	6.65±1.97 3.99–10.64	13.16 ± 0.93 11.97–14.63	27.73 ± 1.64 25.27–31.92	1.06±0.36 0.66–1.59	–	2.95±0.49 2.66–3.99
V. wolgensis	47.68 ± 4.63 39.90–55.86	48.21 ± 4.22 39.90–54.53	0.99±0.11 0.81–1.22	36.04 ± 3.05 30.59–39.90	5.71±1.88 2.66–9.31	14.49 ± 1.25 13.30–17.29	31.65 ± 1.90 27.93–34.58	1.10±0.18 0.66–1.33	–	3.99± 0.69 2.66–5.32
V. stolonifera	50.27 ± 2.67 43.89–54.53	40.09 ± 4.21 31.92–46.55	1.26±0.12 1.03–1.50	38.43 ± 3.82 33.25–45.22	4.38±1.03 2.66–5.32	15.02 ± 2.06 11.97–17.29	33.51 ±1.30 31.92–35.91	0.58±0.29 0.26–1.06	–	2.77±0.33 2.39–3.32
V. officinalis	43.09 ± 3.32 38.57–50.54	38.83 ± 5.44 31.92–47.88	1.12±0.16 0.91–1.41	28.46 ± 3.26 23.94–33.25	4.38±1.33 2.66–6.65	14.23 ± 1.78 11.97–17.29	29.45 ± 2.60 25.27–33.25	0.70±0.27 0.26–1.06	–	3.29±0.57 2.66–3.99
V. exaltata	46.28 ± 6.27 38.57–58.52	40.56 ± 6.13 29.26–50.54	1.15±0.16 0.84–1.39	29.26 ± 2.45 26.60–33.25	5.18±1.51 2.66–7.98	17.82 ± 1.59 14.63–19.95	33.58 ± 2.22 29.26–35.91	0.50±0.19 0.26–0.66	–	3.69±0.44 2.66–3.99
V. sambucifolia	56.72 ± 4.59 49.21–66.50	47.54 ± 4.68 39.90–57.19	1.20±0.16 0.90–1.50	39.63 ± 5.03 31.92–46.55	3.99±1.03 2.66–5.32	17.02 ± 2.36 13.30–19.95	38.37 ± 3.39 33.25–43.89	0.70±0.27 0.26–1.06	–	2.79±0.31 2.39–3.32
V. angustifolia	45.28 ± 4.93 37.24–55.86	49.34 ± 3.68 42.56–57.19	0.92±0.14 0.69–1.18	33.11 ± 4.34 26.60–39.90	8.51±2.07 3.99–11.97	15.29 ± 1.80 11.97–17.29	31.18 ± 2.24 27.93–35.91	1.22±0.17 1.06–1.59	–	3.09± 0.43 2.66–3.99
V. grossheimii	48.01 ± 3.80 42.56–55.86	45.02 ± 4.29 34.58–50.54	1.07±0.11 0.88–1.31	30.85 ± 3.40 26.60–37.24	7.44±1.21 5.32–9.31	16.22 ± 0.79 14.63–17.29	31.72 ±1.34 29.26–33.25	0.98±0.28 0.66–1.33	–	3.13±0.59 2.66–3.99
V. rossica	55.46 ± 2.97 49.21–59.85	41.36 ± 2.48 35.91–46.55	1.34±0.08 1.12–1.48	36.90 ± 3.98 29.26–46.55	3.79±0.86 2.66–5.32	15.07 ± 1.25 13.30–17.29	29.65 ± 2.62 26.60–33.25	0.51±0.16 0.26–0.79	3.75±0.28 3.32–3.99	2.46±0.18 1.99–2.66
V. tuberosa	51.16 ± 5.38 39.90–61.18	44.55 ± 4.03 29.26–51.87	1.15±0.12 0.85–1.59	36.40 ± 3.90 30.59–43.89	6.16±1.59 3.99–10.64	16.49 ± 2.69 11.97–22.61	31.76 ± 1.49 29.26–34.58	0.95±0.27 0.66–1.33	–	3.12±0.63 2.39–3.99
V. alliariifolia	39.76 ± 2.81 34.58–43.89	40.36 ± 2.82 31.92–45.22	0.98±0.09 0.84–1.14	25.13 ± 2.33 19.95–27.93	6.25±0.60 5.32–6.65	12.63 ± 1.22 9.31–13.30	27.06 ± 0.86 26.60–29.26	1.71±0.29 1.33–1.99	4.45±0.63 3.99–5.32	2.77±0.27 2.39–3.32

Results

The original data on quantitative and qualitative pollen characters used in this study are summarised in Tables 1–3. Both original and published data on quantitative pollen characters are summarised in Table 4. LM and SEM photomicrographs of pollen grains are shown in Figures 1–6. Box plots showing the variation of polar axis and equatorial diameter are given in Figure 7. UPGMA dendrograms showing the relationships of pollen grains of *Valeriana* species are presented in Figure 8.

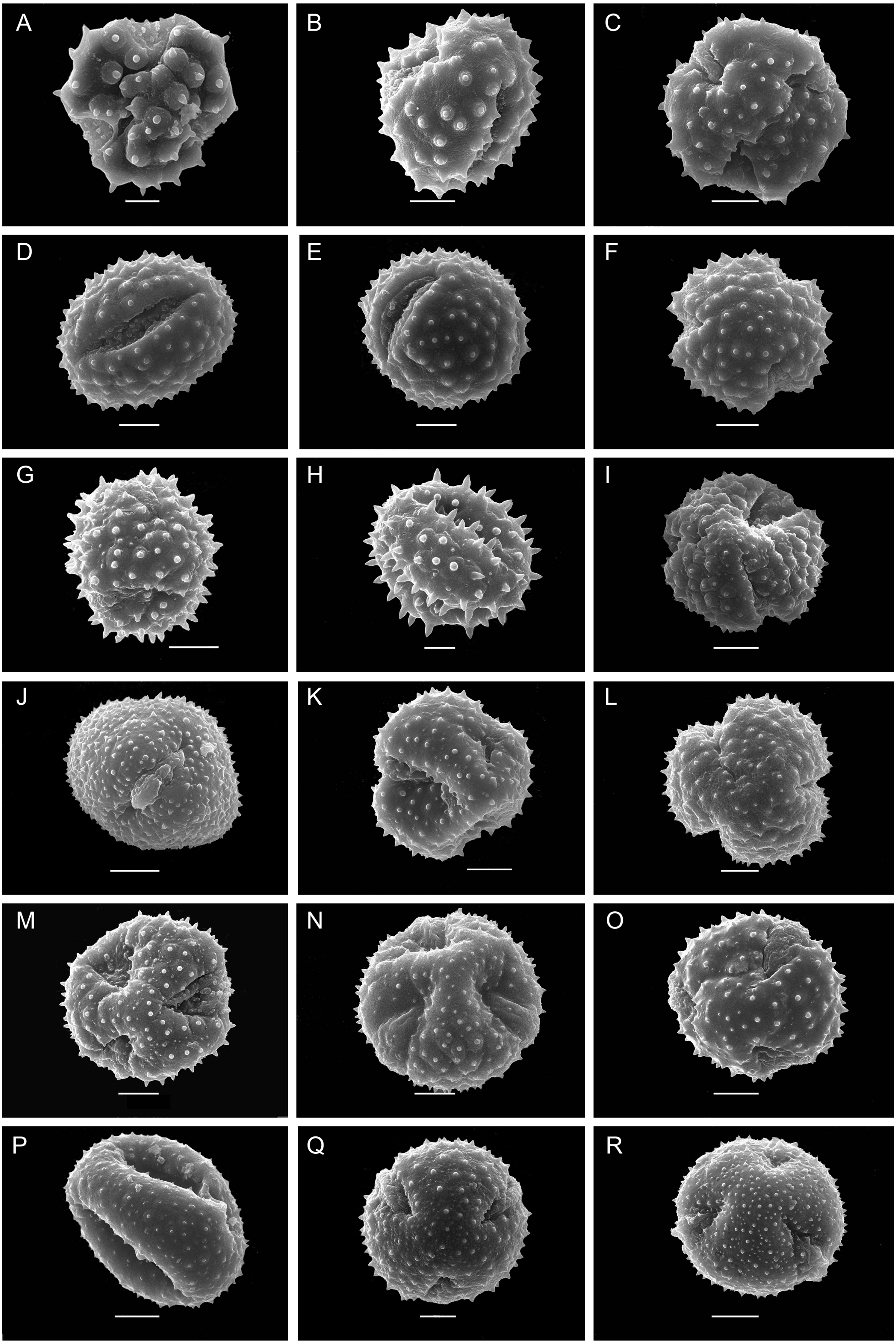


FIGURE 1. Pollen grains of *Valeriana* (SEM). A. *V. montana.* B. *V. tripteris.* C. *V. supina.* D. *V. pyrenaica.* E, F. *V. transsilvanica.* G. *V. dioica.* H. *V. simplicifolia.* I. *V. wolgensis.* J. *V. officinalis.* K. *V. exaltata.* L. *V. sambucifolia.* M. *V. angustifolia.* N. *V. stolonifera.* O. *V. grossheimii.* P. *V. rossica.* Q. *V. tuberosa.* R. *V. alliariifolia.* A, C, F, I, K–O, Q, R. Polar view. B, D, E, G, H, J, P. Equatorial view. Scale bars: 10 µm, except in H: 5 µm.

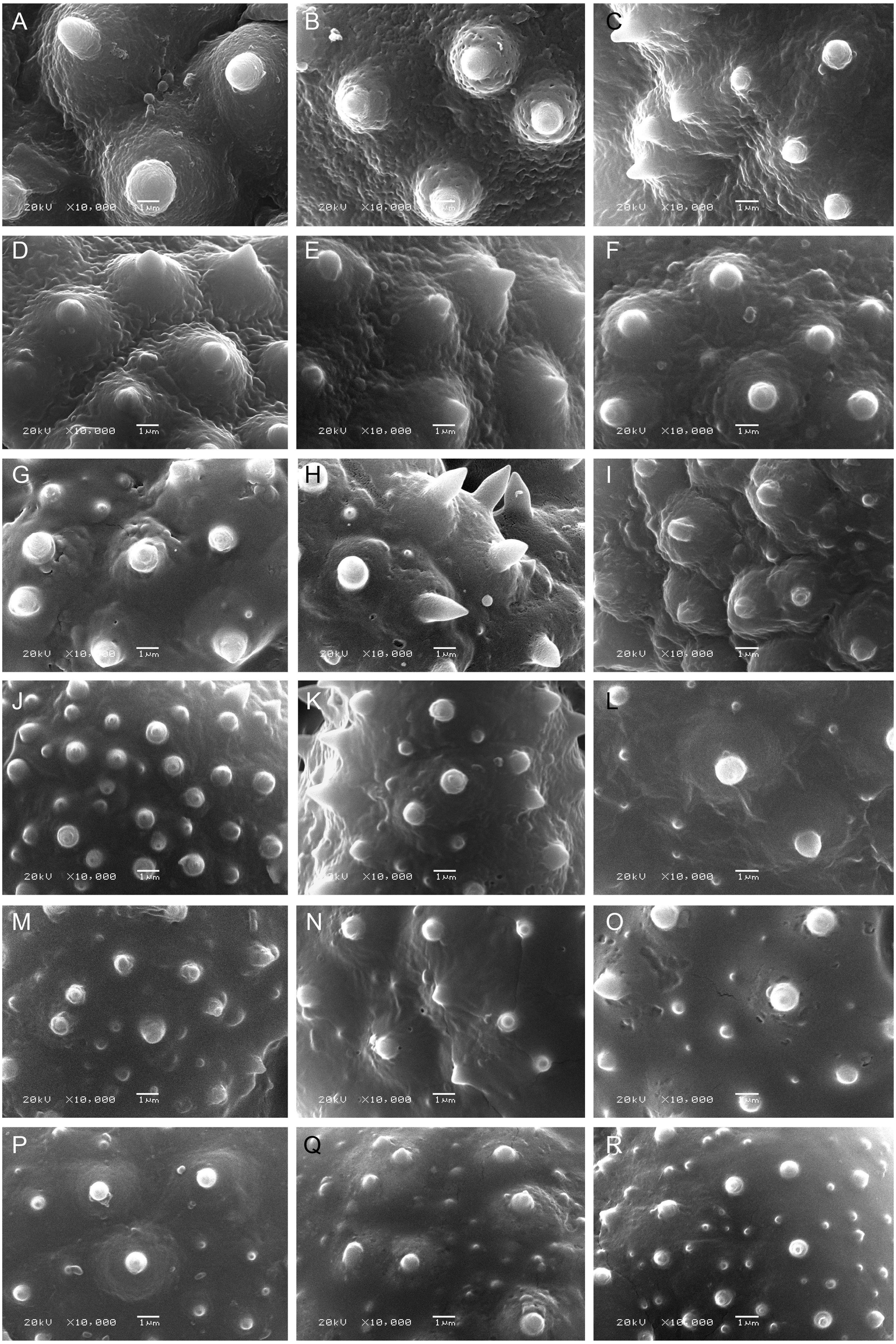


FIGURE 2. Exine sculpture of pollen grains of *Valeriana* (SEM). A. *V. montana.* B. *V. tripteris.* C. *V. supina.* D. *V. pyrenaica.* E, F. *V. transsilvanica.* G. *V. dioica.* H. *V. simplicifolia.* I. *V. wolgensis.* J. *V. officinalis.* K. *V. exaltata.* L. *V. sambucifolia.* M. *V. angustifolia.* N. *V. stolonifera.* O. *V. grossheimii.* P. *V. rossica.* Q. *V. tuberosa.* R. *V. alliariifolia.*

General description of pollen grains of *Valeriana*

Pollen grains in monads, radially symmetrical, isopolar, tricolpate, oblate to prolate (P/E = 0.69–1.59), in equatorial view elliptic or circular, in polar view slightly 3-lobate, 3-lobate or circular (Figs. 1, 4–6); medium- or large-sized: P = 26.60–66.50 µm; E = 23.94–57.19 µm. **Colpi** slightly sunken, long, medium-length or short, 19.95–46.55 µm; narrow, medium-width or wide, 2.66–11.97 µm; with distinct, uneven and more or less straight margins, tapered to acute, obtuse or rounded ends; surrounded by distinct or indistinct, narrow, medium-width or wide **halo**, 0.26–2.39 µm thick. **Mesocolpium** 19.95–43.89 µm, **apocolpium** 9.31–22.61 µm. **Exine** 1.99–5.32 µm thick in mesocolpium and 3.32–5.32 µm thick in apocolpium, **pollen wall** tectate (Tables 1, 2). **Sexine** about two or three times as thick as nexine throughout. **Columellae** prominent in surface view, simple, short or long, unbranched, in some taxa slightly branched in apocolpia, dense, more or less evenly distributed in mesocolpia or slightly longer, more scattered and sometimes coalesced at apocolpia (Fig. 3).

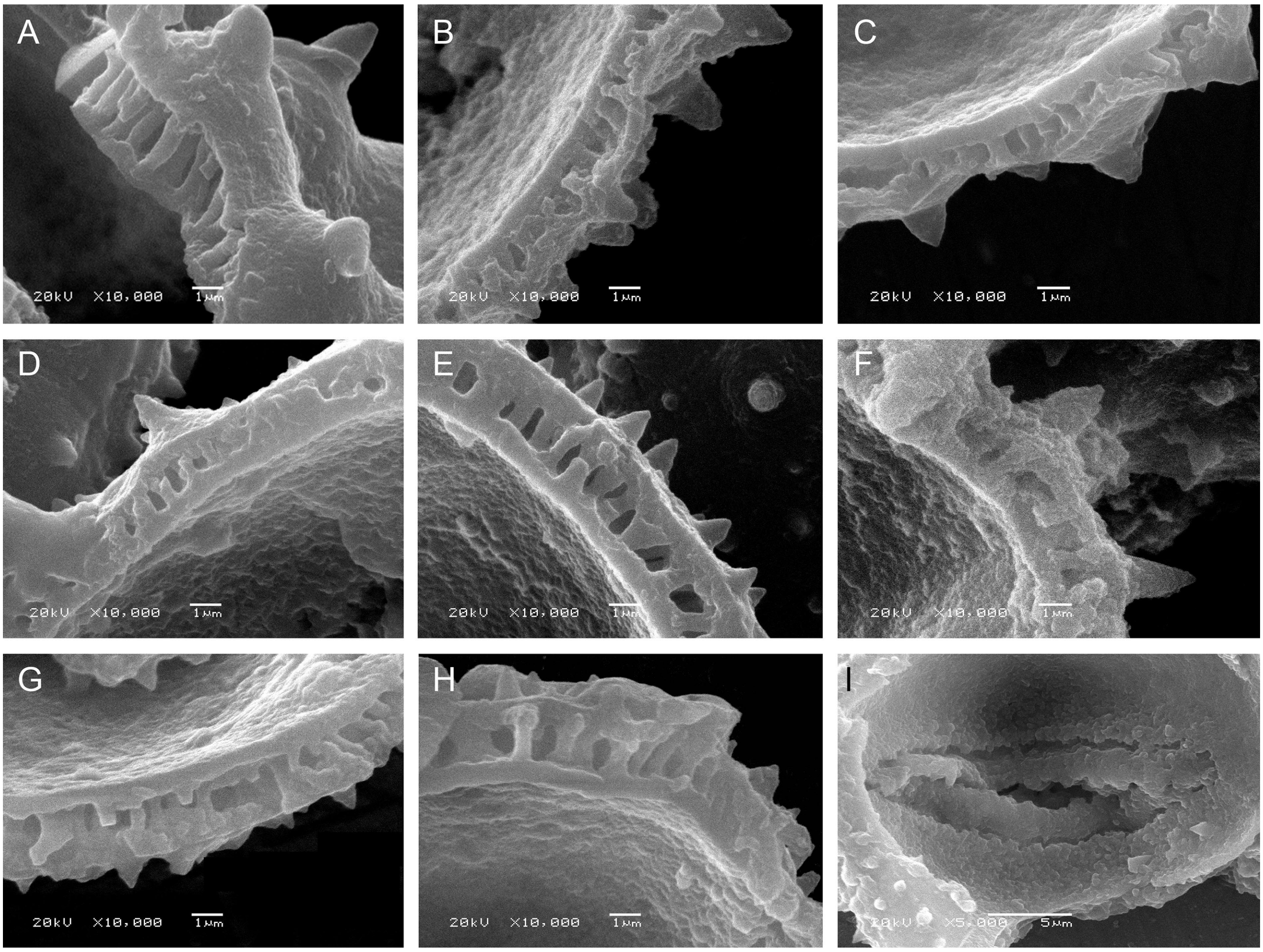


FIGURE 3. Exine structure of pollen grains of *Valeriana* (SEM). A. *V. montana.* B. *V. tripteris.* C. *V. pyrenaica*. D, E. *V. rossica.* F. *V. simplicifolia.* G–I. *V. alliariifolia.* A–D, F, G. Columellae in mesocolpia. E, H. Columellae in apocolpia. I. Colpus with halo.

Exine sculpture echinate-verrucate, echinate-nanoechinate-verrucate, echinate-microechinate-nanoechinate-verrucate, or echinate-microechinate-nanoechinate; **echini** 1–21/100 µm², 1.00–2.71 µm high, 0.82–1.79 µm wide at base; cylindrical or conical, cylindrical echini parallel-sided below, conical above; conical echini with mainly convex and straight sides; apices acute, obtuse or curved; **microechini** 4–15/100 µm², 0.52–0.99 µm high, 0.62–1.33 µm wide at base; **nanoechini** 3–29/100 µm², 0.22–0.41 µm high, 0.31–0.48 µm wide at base (Table 3); **verrucae** more or less circular, prominent, less prominent or flattened, sometimes so close together that they merge; **tectum** psilate or psilate-perforate in areas between echini. **Colpus membranes** irregularly microechinate-granulate or echinate-granulate (Figs. 1, 2).

TABLE 2. Pollen morphological characters.

Taxon	Shape	Equatorial view	Polar view	Colpi margin	Colpi length/width	Halo	Colpus membrane	Exine sculpture	Columellae
V. montana	spheroidal to prolate	elliptic, circular	slightly 3-lobate	uneven	long, medium-length or short, wide, ends acute or obtuse	narrow or wide	microechinate-granulate	echinate-verrucate	distinct
V. tripteris	suboblate to subprolate	circular, elliptic	slightly 3-lobate	uneven	medium-length or short, wide, ends obtuse	narrow	microechinate-granulate	echinate-verrucate	distinct
V. supina	prolate-spheroidal to subspheroidal	circular, elliptic	slightly 3-lobate,3-lobate	uneven	long, medium-length, narrow, ends acute or rounded	narrow	microechinate-granulate	echinate-verrucate	distinct
V. pyrenaica	spheroidal to subprolate	elliptic, circular	slightly 3-lobate,circular	uneven	long, medium-length, wide, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-verrucate	distinct
V. transsilvanica	spheroidal	circular	slightly 3-lobate, circular	uneven	long, medium-length, wide, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-verrucate	distinct or indistinct
V. dioica	suboblate to subprolate	circular	slightly 3-lobate, circular	uneven	medium-length or short, narrow to wide, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	indistinct
V. simplicifolia	subspheroidal	circular	slightly 3-lobate, circular	uneven	long, medium-length, medium-width or wide, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	indistinct
V. wolgensis	suboblate to subprolate	elliptic, circular	3-lobate	uneven	long, medium-length, narrow to wide, ends obtuse	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. stolonifera	prolate-spheroidal to prolate	elliptic	slightly 3-lobate	uneven	long, narrow, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct or indistinct
V. officinalis	spheroidal to prolate	elliptic, circular	3-lobate	straight or uneven	long, medium-length or short, narrow to wide, ends obtuse or acute	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. exaltata	suboblate to prolate	elliptic, circular	3-lobate	straight or uneven	long, medium-length, narrow to wide, ends obtuse or acute	narrow	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. sambucifolia	spheroidal to prolate	elliptic	3-lobate	uneven	long, narrow, ends acute	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. angustifolia	oblate -subprolate	elliptic	3-lobate	uneven	long, medium-length, medium-width or wide, ends obtuse	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct or indistinct
V. grossheimii	subspheroidal	elliptic	3-lobate, slightly 3-lobate	uneven	long, medium-length, wide, ends obtuse or rounded	narrow or medium-width	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. rossica	prolate-spheroidal to prolate	elliptic	3-lobate	uneven	long, narrow, ends obtuse	narrow	microechinate-granulate	echinate-nanoechinate-verrucate	distinct
V. tuberosa	suboblate to prolate	elliptic, circular	3-lobate	straight or uneven	long, medium-length, medium-width or wide, ends acute or obtuse	narrow or medium-width	microechinate-granulate	echinate-microechinate-nanoechinate-verrucate	distinct
V. alliariifolia	suboblate to spheroidal	circular	3-lobate	straight	medium-length or short, wide, ends acute	medium-width or wide	echinate-granulate	echinate-microechinate-nanoechinate	distinct

TABLE 3. Comparison between echini, microechini and nanoechini (all measurements given as µm).

Taxon	Echini			Nanoechini			Microechini		
	Height	**Width at the base**	**Number/ 100 µm²**	**Height**	**Width at the base**	**Number/ 100 µm²**	**Height**	**Width at the base**	**Number/ 100 µm²**
Type I—Echinate–verrucate									
Subtype Ia. Verrucae prominent									
V. montana	2.48–2.71	1.57–1.79	1–3						
Subtype Ib. Verrucae prominent									
V. tripteris	1.31–1.60	1.21–1.39	3–5						
Subtype Ic. Verrucae flattened									
V. supina	1.37–1.59	1.12–1.27	6–8						
Subtype Id. Verrucae prominent									
V. pyrenaica	1.06–1.21	1.11–1.29	4–6						
V. transsilvanica	1.06–1.18	1.06–1.21	4–6						
Type II—Echinate–nanoechinate–verrucate									
Subtype IIa. Verrucae prominent									
V. dioica	1.57–1.81	1.17–1.38	6–8	0.33–0.39	0.38–0.48	3–14			
V. simplicifolia	1.68–2.05	1.01–1.26	5–8	0.27–0.35	0.36–0.46	6–10			
Subtype IIb. Verrucae prominent									
V. wolgensis	1.22–1.55	1.08–1.19	4–7	0.39–0.40	0.45–0.47	6–10			
Subtype IIc. Verrucae less prominent									
V. stolonifera	1.11–1.36	0.82–1.10	5–8	0.31–0.41	0.42–0.47	5–11			
Subtype IId. Verrucae flattened									
V. officinalis	1.19–1.41	0.98–1.10	4 –21	0.22–0.31	0.40–0.44	8–25			
V. exaltata	1.28–1.48	0.95–1.19	5–9	0.25–0.33	0.38–0.47	9–13			
V. sambucifolia	1.00–1.42	0.89–1.16	3–9	0.25–0.37	0.38–0.46	6–13			
V. angustifolia	1.25–1.66	0.89–1.35	3 –10	0.23–0.31	0.33–0.46	11–25			
V. grossheimii	1.18–1.45	0.96–1.20	3 –10	0.24–0.33	0.33–0.42	6–10			
V. rossica	1.00–1.32	0.81–1.12	2–7	0.24–0.34	0.39–0.44	7–12			
Type III—Echinate-microechinate-nanoechinate-verrucate. Verrucae flattened									
V. tuberosa	1.01–1.34	0.84–1.32	1–4	0.22–0.31	0.31–0.39	9–17	0.87–0.99	0.93–1.33	4–9
Type IV—Echinate–microechinate-nanoechinate. Verrucae absent									
V. alliariifolia	1.01–1.08	0.69–0.97	1–2	0.26–0.34	0.32–0.37	23–29	0.52–0.99	0.62–0.93	10–15

Pollen types and subtypes

The data obtained demonstrated that the pollen grains of *Valeriana* differ in their exine sculpture (Fig. 2). Four types and eight subtypes of exine sculpture were recognised: type I—echinate-verrucate, type II—echinate-nanoechinate-verrucate, type III—echinate-microechinate-nanoechinate-verrucate, type IV—echinate-microechinate-nanoechinate. Both the first and the second types contain four subtypes, segregated according to the form of verrucae, form and size of echini, structure of tectum, number of echini/microechini/nanoechini (Table 3).

Type I. Exine sculpture echinate-verrucate, verrucae prominent or flattened. Species: *V. montana*, *V. tripteris*, *V. supina*, *V. pyrenaica*, *V. transsilvanica* Schur (1866: 290).

Subtype Ia. Species: *V. montana* (Fig. 2A). Verrucae prominent; echini 1–3/100 μm², cylindrical, higher than basal width, 2.48–2.71 μm high, 1.57–1.79 μm wide at base; tectum psilate-perforate in areas between echini.

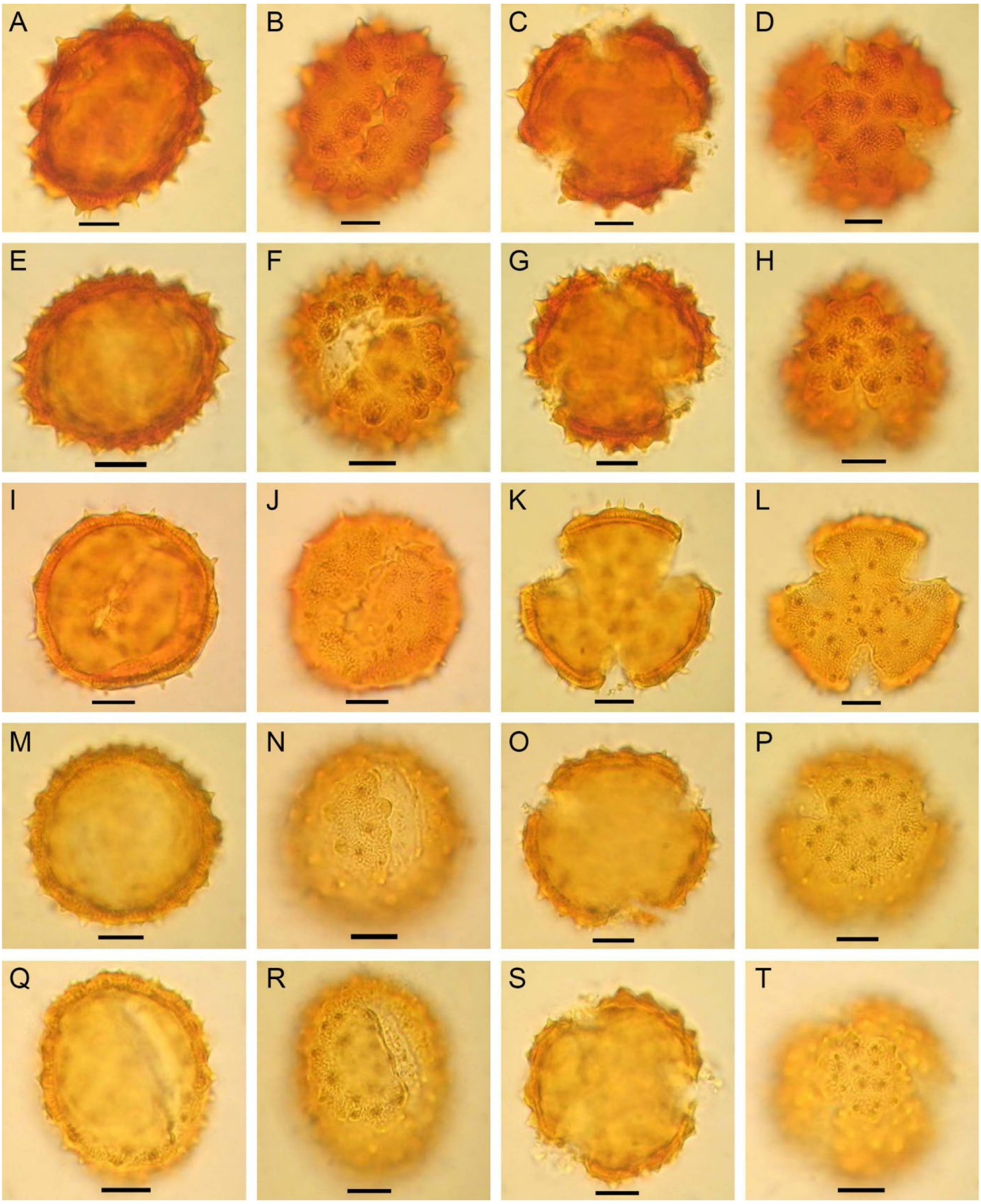


FIGURE 4. Pollen grains of *Valeriana* (LM). A–D. *V. montana*. E–H. *V. tripteris*. I–L. *V. supina*. M–P. *V. pyrenaica*. Q–T. *V. transsilvanica*. A, B, E, F, I, J, M, N, Q, R. Equatorial view. C, D, G, H, K, L, O, P, S, T. Polar view. Scale bars: 10 μm.

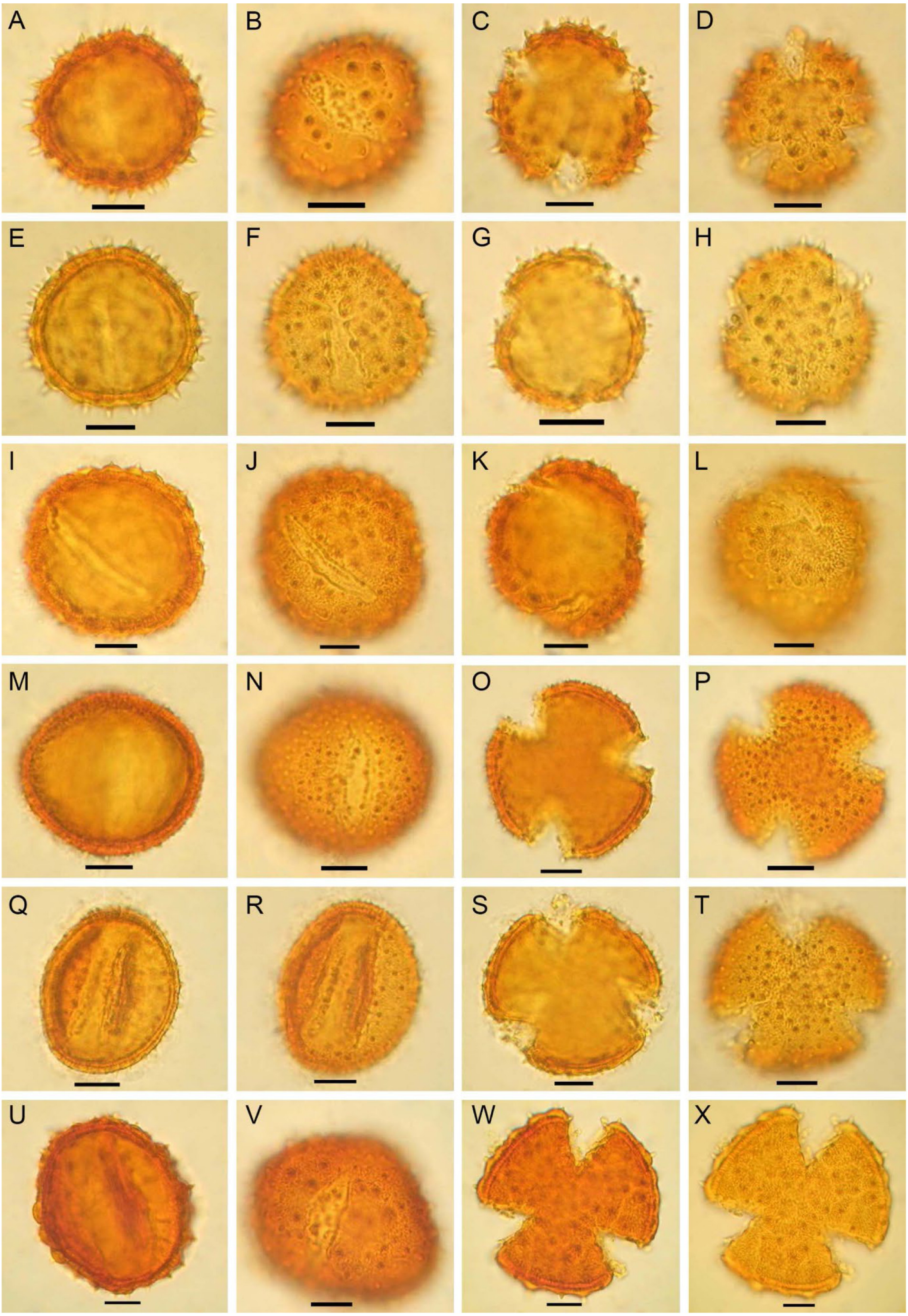


FIGURE 5. Pollen grains of *Valeriana* (LM). A–D. *V. dioica*. E–H. *V. simplicifolia*. I–L. *V. wolgensis*. M–P. *V. officinalis*. Q–T. *V. exaltata*. U–X. *V. sambucifolia*. A, B, E, F, I, J, M, N, Q, R, U, V. Equatorial view. C, D, G, H, K, L, O, P, S, T, W, X. Polar view. Scale bars: 10 µm.

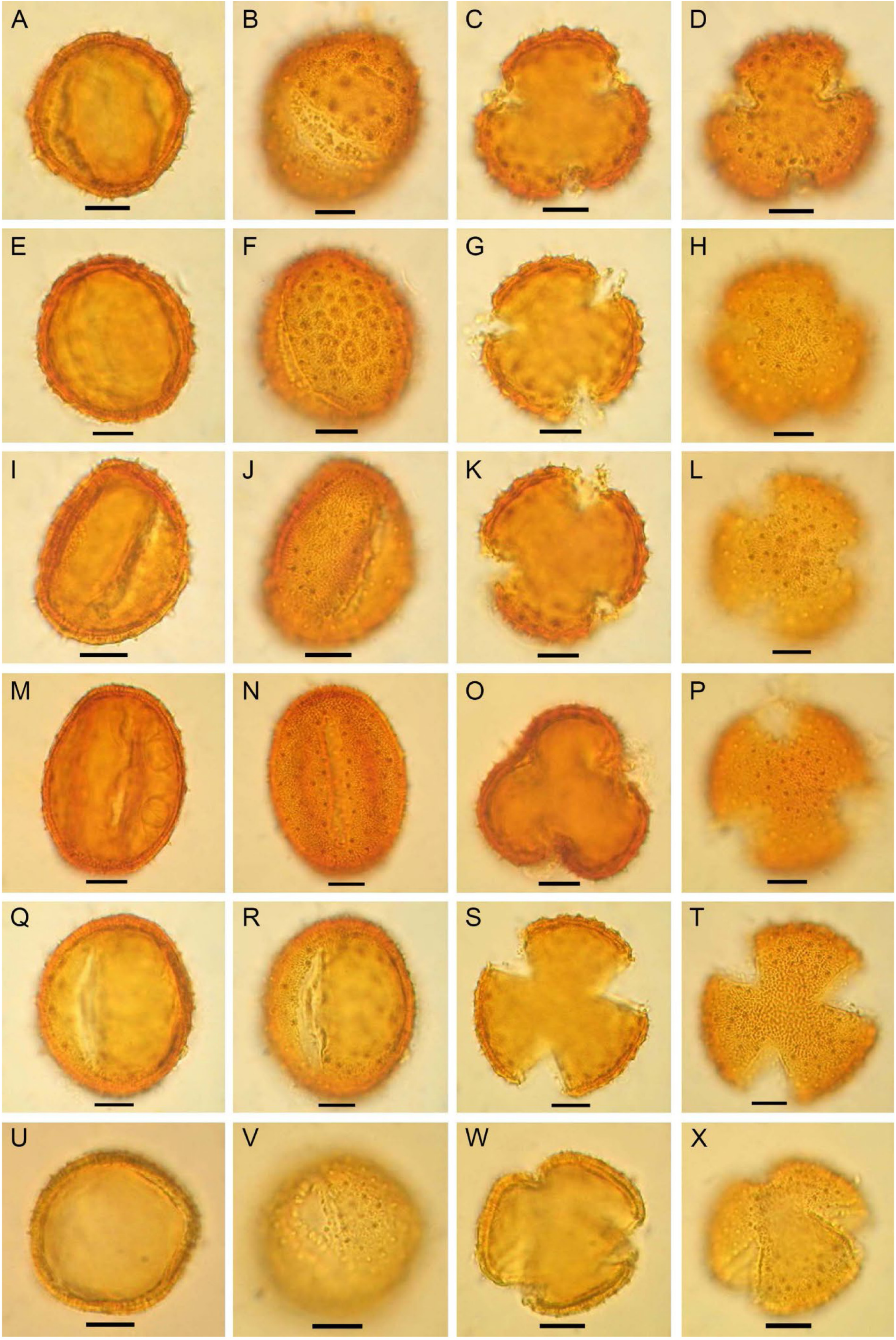


FIGURE 6. Pollen grains of *Valeriana* (LM). A–D. *V. angustifolia.* E–H. *V. stolonifera*. I–L. *V. grossheimii*. M–P. *V. rossica.* Q–T. *V. tuberosa.* U–X. *V. alliariifolia.* A, B, E, F, I, J, M, N, Q, R, U, V. Equatorial view. C, D, G, H, K, L, O, P, S, T, W, X. Polar view. Scale bars: 10 µm.

Subtype Ib. Species: *V. tripteris* (Fig. 2B). Verrucae prominent; echini 3–5/100 μm², conical, higher than basal width, 1.31–1.60 μm high, 1.21–1.39 μm wide at base; tectum psilate-perforate in areas between echini.

Subtype Ic. Species: *V. supina* (Fig. 2C). Verrucae flattened; echini 6–8/100 μm², conical, higher than basal width, 1.37–1.59 μm high, 1.12–1.27 μm wide at base; tectum psilate-perforate in areas between echini.

Subtype Id. Species: *V. pyrenaica* (Fig. 2D), *V. transsilvanica* (Fig. 2E, F). Verrucae prominent; echini 4–6/100 μm², conical, about as wide as high, 1.06–1.21 μm high, 1.06–1.29 μm wide at base; tectum psilate-perforate in areas between echini.

Type II. Exine sculpture echinate-nanoechinate-verrucate, verrucae prominent or flattened. Species: *V. dioica*, *V. simplicifolia* (Reichenbach 1823: 48, tab. LIX, fig. 120) Kabath (1846: 37), *V. wolgensis* Kazakevicz (1922: 61), *V. stolonifera* Czernajew (1845: 133, in nota), *V. officinalis, V. exaltata* Pohl (1809: 41), *V. sambucifolia* Pohl (1809: 41), *V. angustifolia* Host (1827: 36) [non Mill. 1768], *nom. illeg.* (≡*V. stolonifera* subsp. *angustifolia* Soó (1972: 208)), *V. grossheimii* Voroschilov (1953: 12 sec. IPNI 2022) (≡*V. armena* (Smirnov 1946: 71) subsp. *grossheimii* (Voroschilov) Voroschilov (1975: 41)), *V. rossica* Smirnov (1925: 9 sec. IPNI 2022).

Subtype IIa. Species: *V. dioica* (Fig. 2G), *V. simplicifolia* (Fig. 2H). Verrucae prominent; echini 5–8/100 μm², cylindrical, higher than basal width, 1.57–2.05 μm high, 1.01–1.38 μm wide at base; nanoechini 3–14/100 μm², 0.27–0.39 μm high, 0.36–0.48 μm wide at base; tectum psilate-perforate in areas between echini.

Subtype IIb. Species: *V. wolgensis* (Fig. 2I). Verrucae prominent; echini 4–7/100 μm², conical, higher than basal width, 1.22–1.55 μm high, 1.08–1.19 μm wide at base; nanoechini 6–10/100 μm², 0.39–0.40 μm high, 0.45–0.47 μm wide at base; tectum psilate in areas between echini.

Subtype IIc. Species: *V. stolonifera* (Fig. 2N). Verrucae less prominent; echini 5–8/100 μm², conical, higher than basal width, 1.11–1.36 μm high, 0.82–1.10 μm wide at base; nanoechini 5–11/100 μm², 0.31–0.41 μm high, 0.42–0.47 μm wide at base; tectum psilate in areas between echini.

Subtype IId. Species: *V. officinalis* (Fig. 2J), *V. exaltata* (Fig. 2K), *V. sambucifolia* (Fig. 2L), *V. angustifolia* (Fig. 2M), *V. grossheimii* (Fig. 2O), *V. rossica* (Fig. 2P). Verrucae flattened; echini 2–21/100 μm², conical, higher than basal width, 1.00–1.66 μm high, 0.81–1.35 μm wide at base; nanoechini 6–25/100 μm², 0.22–0.37 μm high, 0.33–0.47 μm wide at base; tectum psilate in areas between echini.

Type III. Exine sculpture echinate-microechinate-nanoechinate-verrucate. Species: *V. tuberosa* Linnaeus (1753: 33) (Fig. 2Q). Verrucae flattened; echini 1–4/100 μm², conical, higher than basal width to about as wide as high, 1.01–1.34 μm high, 0.84–1.32 μm wide at base; microechini 4–9/100 μm², 0.87–0.99 μm high, 0.93–1.33 μm wide at base; nanoechini 9–17/100 μm², 0.22–0.31 μm high, 0.31–0.39 μm wide at base; tectum psilate in areas between echini.

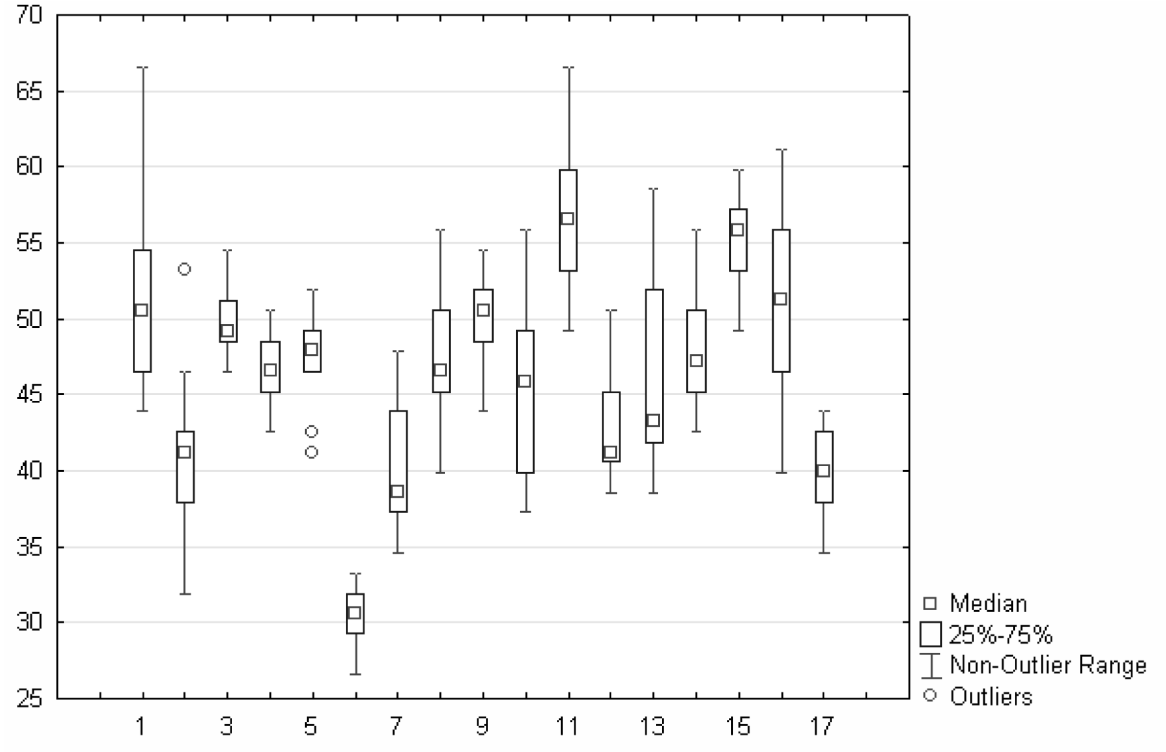
Type IV. Exine sculpture echinate-microechinate-nanoechinate. Species: *V. alliariifolia* Vahl (1805: 11) (Fig. 2R). Verrucae absent; echini 1–2/100 μm², conical, higher than basal width, 1.01–1.08 μm high, 0.69–0.97 μm wide at base; microechini 10–15/100 μm², 0.52–0.99 μm high, 0.62–0.93 μm wide at base; nanoechini 23–29/100 μm², 0.26–0.34 μm high, 0.32–0.37 μm wide at base; tectum psilate in areas between echini.

Comparative pollen morphology

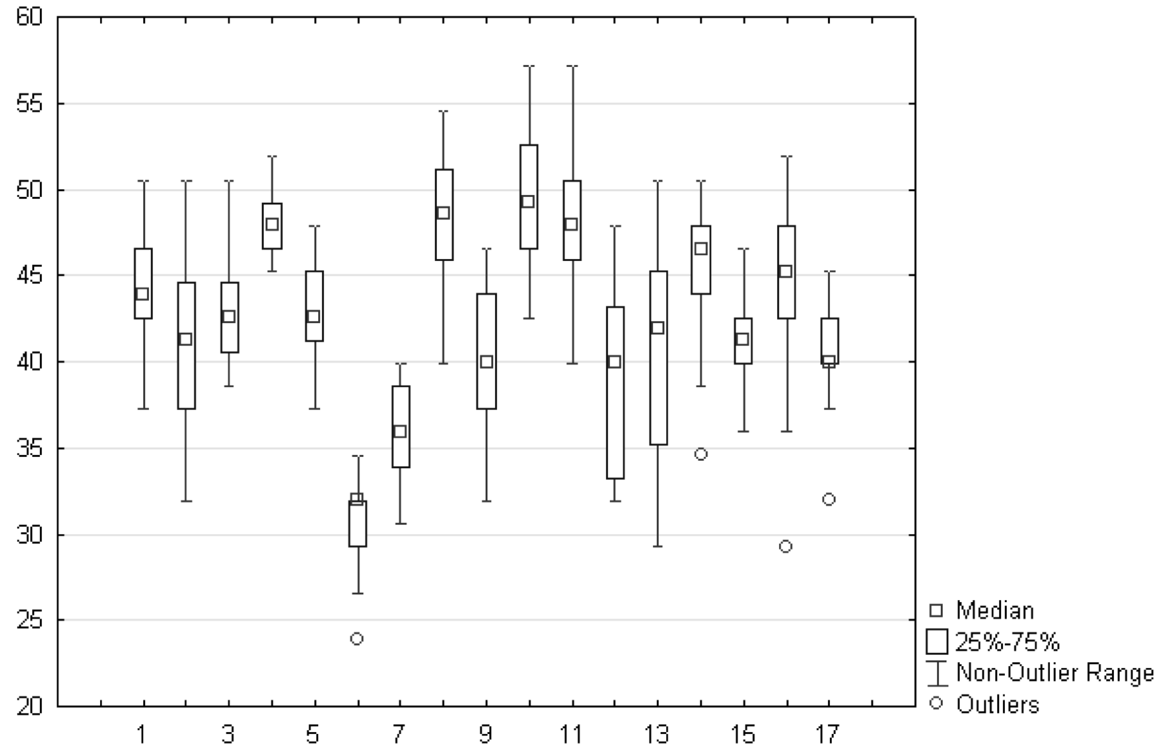
Shape:—According to P/E ratio (0.69–1.59), pollen grains are oblate to prolate in shape. The smallest value of P/E ratio was in *V. angustifolia* (0.69), and the largest in *V. tuberosa* (1.59). The outline in equatorial view is elliptic or circular, in polar view—slightly 3-lobate, 3-lobate or rarely circular (Figs. 1, 4–6).

Size:—Most *Valeriana* species have overlapping size ranges (Fig. 7A, B). The smallest pollen grains were observed in *V. dioica* (26.60–33.25 × 23.94–34.58 μm) (Fig. 7A), while the largest pollen grains were measured in *V. sambucifolia* (49.21–66.50 × 39.90–57.19 μm) and *V. montana* (43.89–66.50 × 37.24–50.54 μm) (Fig. 7A). But some species in this study differed in pollen size. For example, *V. dioica* and *V. simplicifolia*, which are included in subtype IIa (Table 3; Fig. 7A, B).

Apertures:—Pollen grains of all species investigated have three apertures. Longer colpi were characteristic for *V. sambucifolia*, *V. stolonifera* and *V. rossica* (29.26–46.55 μm), while shorter and medium-length colpi were observed in *V. alliariifolia*, *V. tripteris* and *V. dioica* (19.95–30.59 μm). All other species were characterised by medium-length and long colpi (e.g., *V. simplicifolia* and *V. tuberosa*, 25.27–43.89 μm), however the most variable colpi in length were present in *V. officinalis* (23.94–33.25 μm) and *V. montana* (19.95–39.90 μm). Narrow colpi were characteristic for *V. supina*, *V. sambucifolia*, *V. stolonifera*, and *V. rossica* (2.66–5.32 μm), wide colpi were characteristic for *V. montana*, *V. tripteris*, *V. transsilvanica*, *V. pyrenaica*, *V. grossheimii*, and *V. alliariifolia* (5.32–11.97 μm), medium-width and wide for *V. simplicifolia*, *V. angustifolia* and *V. tuberosa* (3.99–11.97 μm), while most variable narrow, medium-width and wide colpi were observed in *V. officinalis*, *V. exaltata*, *V. dioica*, and *V. wolgensis* (2.66–9.31 μm). In all species colpi were surrounded by a halo (Fig. 3I). Pollen grains of *V. tripteris*, *V. supina*, *V. exaltata*, and *V. rossica* had



A



B

FIGURE 7. Box plots illustrating the variation of polar axis (A) and equatorial diameter (B) of *Valeriana* pollen grains. 1. *V. montana.* 2. *V. tripteris.* 3. *V. supina.* 4. *V. transsilvanica.* 5. *V. pyrenaica.* 6. *V. dioica.* 7. *V. simplicifolia.* 8. *V. wolgensis.* 9. *V. stolonifera.* 10. *V. angustifolia.* 11. *V. sambucifolia.* 12. *V. officinalis.* 13. *V. exaltata.* 14. *V. grossheimii.* 15. *V. rossica.* 16. *V. tuberosa*. 17. *V. alliariifolia.*

distinct or indistinct narrow halo (0.26–0.66 (–0.79) µm). Pollen grains of *V. transsilvanica*, *V. pyrenaica*, *V. dioica*, *V. simplicifolia*, *V. officinalis*, *V. sambucifolia*, *V. stolonifera*, *V. angustifolia*, *V. grossheimii*, *V. wolgensis*, and *V. tuberosa* had distinct, narrow and medium-width halo (0.26–1.33 (–1.59) µm), while *V. alliariifolia* had medium-width or wide halo (1.33–1.99 µm), and *V. montana* had narrow and wide halo (0.66–2.39 µm).

Exine:—More or less constant exine thickness throughout the pollen grain was present in all *Valeriana* species. On average, the exine was the thinnest in *V. tripteris* (mean 2.26 µm) and *V. dioica* (mean 2.23 µm) along the entire pollen grain, while the thickest one occurred in *V. wolgensis* (mean 3.99 µm). Two species, *V. rossica* and *V. alliariifolia*, had thicker exine in apocolpia (Table 1). Columellae in all species were mainly short, simple, unbranched and dense, regularly spaced in the mesocolpia and apocolpia. Pollen grains of *V. montana* (Fig. 3A) had longer columellae in the mesocolpia and apocolpia. In pollen grains of *V. dioica* and *V. simplicifolia* (Fig. 3F), columellae were indistinct. In pollen grains of *V. rossica* (Fig. 3E) and *V. alliariifolia* (Fig. 3H), columellae were longer in apocolpia.

Sculpture:—Pollen grains of the studied species are divided into four types and eight subtypes of exine sculpture (Tables 2, 3). Pollen grains in *V. montana*, *V. tripteris*, *V. supina*, *V. pyrenaica*, *V. transsilvanica*, and *V. simplicifolia* were characterised by small perforations in the tectum areas between the echini, all other species had psilate tectum. The highest echini were found in *V. montana* (subtype Ia); they were sparsely distributed (1–3/100 µm²) (Fig. 2A). In *V. pyrenaica* and *V. transsilvanica* (subtype Id; Figs. 2D–F), the echini were about as wide as high, while in *V. tripteris* and *V. supina* their height was usually more than their width (Figs. 2B, C). In *V. supina*, echini had a curved apex (Fig. 2C). The species *V. tripteris* (subtype Ib) and *V. supina* (subtype Ic) also differed in the number of the echini per unit area (3–5/100 µm² and 6–8/100 µm², respectively). Five species, *V. montana*, *V. tripteris*, *V. supina*, *V. pyrenaica* and *V. transsilvanica*, demonstrated almost complete absence of nanoechini. Our results showed that the echini size and number in *V. dioica* and *V. simplicifolia* (subtype IIa) were overlapping. Echini of *V. dioica* tended to be smaller than those of *V. simplicifolia* (Table 3). Also, *V. dioica* had higher nanoechini. Among species of the subtype IId, *V. angustifolia* tended to have bigger echini (Fig. 2M). Also, in this species, the nanoechini were more densely distributed, which is similar to the pollen of *V. officinalis*. Most similar were the pollen grains of *V. exaltata* and *V. officinalis*. The structure of echini and nanoechini of *V. exaltata* and *V. officinalis* was overlapping among specimens attributed to either taxon. *Valeriana grossheimii* and *V. rossica* had very flattened verrucae. Pollen grains of *V. wolgensis* (subtype IIb; Fig. 2I) had larger distinct prominent verrucae than *V. stolonifera* pollen (subtype IIc; Fig. 2N). According to the structure of echini/microechini and the presence of verrucae, *V. tuberosa* belonged to a separate type III. According to the structure of echini/microechini, their number, and the absence of verrucae, *V. alliariifolia* belonged to a separate type IV. Pollen grains of all but one species investigated had irregularly microechinate-granulate colpus membrane. Only *V. alliariifolia* had echinate-granulate colpus membranes. Echini were long, located at edges of colpus membrane.

Numerical analysis of the palynomorphological character states

The cluster analysis of *Valeriana* pollen clearly separated the species. As seen in the UPGMA dendrograms (Fig. 8), species had distinctive pollen morphometric characters (Table 1). The species *V. officinalis* and *V. simplicifolia* were included in the same group because they had similar values of P/E and colpi length; *V. wolgensis* and *V. angustifolia* had similar values of apocolpium and mesocolpium; *V. supina* and *V. tuberosa* had similar values of P/E, colpi length, apocolpium and exine thickness (Fig. 8A). On the other hand, *Valeriana* taxa had distinctive qualitative morphological characters of pollen grains and were grouped as five separate branches: I—*V. montana*; II—*V. tripteris*, *V. transsilvanica*, *V. pyrenaica*, *V. dioica*, *V. simplicifolia*, *V. supina*; III—*V. wolgensis*, *V. stolonifera*, *V. angustifolia*, *V. sambucifolia*, *V. officinalis*, *V. exaltata*, *V. grossheimii*, *V. rossica*; IV—*V. tuberosa*; V—*V. alliariifolia* (Table 3, Fig. 8B).

Discussion

Data in the present investigation are, in general, in agreement with the results of previous LM and SEM studies (Wagenitz 1956, Clarke & Jones 1977, Kupriyanova & Alyoshina 1978, Patel & Skvarla 1979, Diez 1984). Clarke & Jones (1977) reported larger *V. dioica* pollen than the data obtained in this study. According to Patel & Skvarla (1979), pollen grains of *V. officinalis* were characterised by large size. Data in the present study and that one of Clarke & Jones (1977) showed that pollen grains of *V. officinalis* were characterised by a smaller size. Smaller pollen grains of *V. tuberosa* were reported in Diez's work (1984), but the author also indicated that most of the pollen grains were larger than 40 µm, however some were found to be 30 × 20 µm (Table 4). In the present investigation, wide colpi were characteristic for *V. tripteris* (5.32–9.31 µm), while medium-width and wide ones were observed in *V. tuberosa* (3.99–

10.64 µm). Kupriyanova & Alyoshina (1978) reported narrower *V. tripteris* (1.20–2.40 µm) and *V. tuberosa* (3.00–3.60 µm) colpi than in this study (Table 4). Our survey showed that more or less constant exine thickness throughout the pollen grain was present in all *Valeriana* species. Kupriyanova & Alyoshina (1978) reported variable exine thickness in *V. tripteris* pollen (1.20–4.20 µm) and thicker exine in *V. stolonifera* (3.00–4.80 µm) than in the current study. Clarke & Jones (1977) reported thicker exine in *V. dioica* pollen than our observation (Table 4).

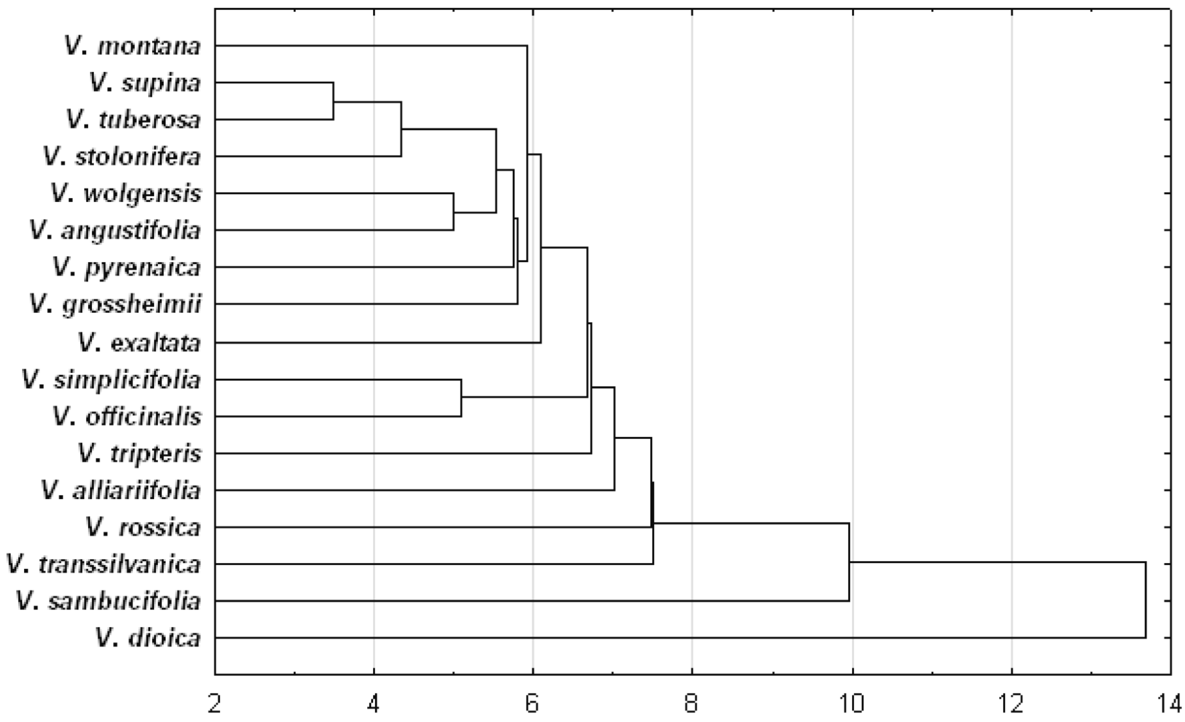
TABLE 4. Summary of pollen morphometric measurements (original and literature data; all measurements given as µm).

Taxon	Polar axis	Equatorial diameter	P/E ratio	Colpi length	Colpi width	Apocolpium	Mesocolpium	Exine thickness
V. tripteris	31.92–53.20	31.92–50.54	0.82–1.25	23.94–30.59	5.32–9.31	15.96–22.61	27.93–35.91	1.33–2.66
V. tripteris (Kupriyanova & Alyoshina 1978)	46.40–55.20	48.00–54.00			1.20–2.40	14.40–15.60	18.00–19.20	1.20–4.20
V. pyrenaica	41.23–51.87	37.24–47.88	0.88–1.28	29.26–39.90	5.32–6.65	15.96–22.61	26.60–33.25	2.39–3.32
V. pyrenaica (Clarke & Jones 1977)	35.00–43.00	37.00–49.00	0.84–1.13					
V. dioica	26.60–33.25	23.94–34.58	0.84–1.38	21.28–25.27	2.66–9.31	11.97–13.30	19.95–23.94	1.99–2.39
V. dioica (Clarke & Jones 1977)	32.00–40.00	35.00–43.00	0.85–1.00					3.00–4.00
V. stolonifera	43.89–54.53	31.92–46.55	1.03–1.50	33.25–45.22	2.66–5.32	11.97–17.29	31.92–35.91	2.39–3.32
V. stolonifera (Kupriyanova & Alyoshina 1978)	48.00–49.20	40.80–42.00			3.00–4.20	14.40–15.60	12.00–14.40	3.00–4.80
V. officinalis	38.57–50.54	31.92–47.88	0.91–1.41	23.94–33.25	2.66–6.65	11.97–17.29	25.27–33.25	2.66–3.99
V. officinalis subsp. *officinalis* (Clarke & Jones 1977)	35.00–45.00	37.00–51.00	0.86–1.05					
V. officinalis (Patel & Skvarla 1979)	65–78	48–65	1.2–1.3	36.00–52.00				4.40
V. sambucifolia	49.21–66.50	39.90–57.19	0.90–1.50	31.92–46.55	2.66–5.32	13.30–19.95	33.25–43.89	2.39–3.32
V. officinalis subsp. *sambucifolia* (Clarke & Jones 1977)	46.00–57.00	46.00–60.00	0.84–1.12					
V. tuberosa	39.90–61.18	29.26–51.87	0.85–1.59	30.59–43.89	3.99–10.64	11.97–22.61	29.26–34.58	2.39–3.99
V. tuberosa (Clarke & Jones 1977)	40.00–54.00	43.00–53.00	0.87–1.10					
V. tuberosa (Kupriyanova & Alyoshina 1978)	54.00–57.60	58.80– 61.20			3.00–3.60	14.40–20.40	19.20–25.20	1.80–3.60
V. tuberosa (Diez 1984)	30.00–52.00	20.00–44.00	1.13–1.50		4.00		20.00–30.00	2.00–3.00

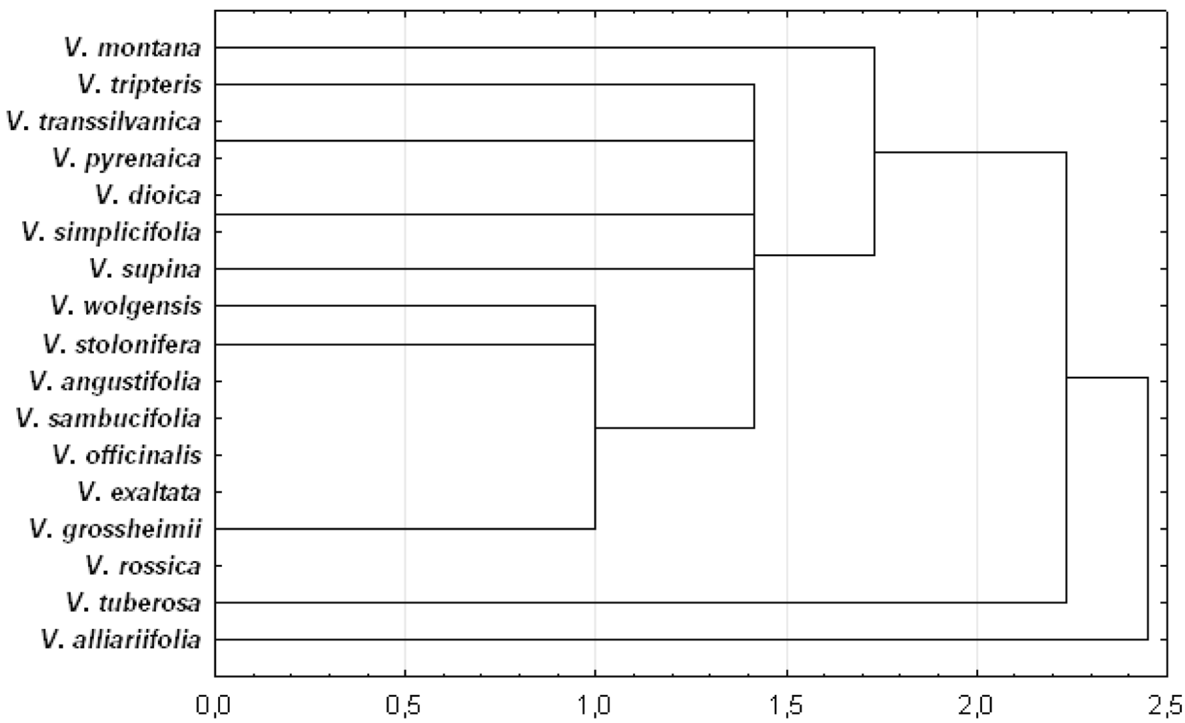
Our data are in good agreement with the data of Wagenitz (1956). The author used the height of the echini as a defining characteristic to distinguish the types of pollen. According to Wagenitz (1956), correct identification of species by pollen is possible if other characteristics are also used.

In the cluster analysis (Fig. 8B) we observed that the studied species formed five groups based on qualitative data (Table 3). In general, the cluster analysis supports the definition of pollen types and subtypes. An exception are both species *V. dioica* and *V. simplicifolia* (type II), which are grouped together with the species of type I.

According to molecular phylogenetic data, the species *V. supina*, *V. montana*, *V. tripteris*, and *V. pyrenaica* form a separate clade (Bell & Donoghue 2005, Bell *et al.* 2015). In the present investigation, the species of this group also differ palynomorphologically from the other studied species. All of these species are of type I, they are characterised by echini and verrucae, and do not have microechini and nanoechini. The echinate-verrucate exine sculpture probably is a synapomorphy in a clade that includes *V. supina*, *V. montana*, *V. tripteris*, and *V. pyrenaica*. The species *V. dioica* and *V. officinalis* are of type IIa and IId respectively, and have nanoechini. They were placed in different groups in the dendrograms (Fig. 8A, B). The species *V. tuberosa* and *V. alliariifolia* that are represented in the samples of molecular studies carried out by Bell *et al.* (2015), have distinctive palynomorphological features and are included in different types (III and IV, respectively), which also supports the cluster analysis (Fig. 8B). Our data showed that pollen grains of *V. alliariifolia* (type IV) are similar to those of representatives of the genus *Centranthus* in the exine sculpture, colpi membrane, and thickening of the exine in the apocolpia (Tsymbalyuk *et al.* 2021b).



A



B

FIGURE 8. UPGMA dendrograms showing the relationships of pollen grains of *Valeriana* species. A. Quantitative characters. B. Qualitative characters.

Previously, Clarke (1978) indicated that a trend can be recognised in pollen morphology in Valerianaceae from large, verrucate, prominently echinate grains with thick exine and long columellae to grains which are smaller, have no verrucae, and have small echini and thin exine with very short columellae.

Xena de Enrech (1993) studied the pollen grains of 16 *Valeriana* species that occur in Venezuela. The author found that there are different combinations between pollen size and exine sculpture, and six types of pollen grains were identified based on these features. In a few species, pollen grains were small (types D, E, F), many of them were medium and large (types A, B, C) for the genus, some of them had sizes typical of the primitive type (more than 40 µm). On the other hand, all Venezuelan species did not have verrucae, which generally allowed the author to attribute the pollen of these species as an advanced type within the genus *Valeriana* according to Clarke (1978) and Patel & Skvarla (1979).

In our study, type I pollen found in the species *V. montana*, *V. tripteris*, *V. supina*, *V. pyrenaica*, and *V. transsilvanica* combines the presence of verrucae and echini and rather large sizes. Among these species, pollen from *V. montana* is the largest and has verrucae, thick exine, and longer columellae. On the other hand, the pollen of *V. tripteris*, *V. supina*, *V. pyrenaica*, and *V. transsilvanica* has a thinner exine and shorter columellae. Type II pollen found in *V. dioica*, *V. simplicifolia*, *V. wolgensis*, *V. stolonifera*, *V. angustifolia*, *V. sambucifolia*, *V. officinalis*, *V. exaltata*, *V. grossheimii*, and *V. rossica* combines the presence of verrucae, echini and nanoechini and has a large size. The exception is *V. dioica* which had a smaller size, as well as *V. rossica* which had a thickening of the exine at the poles, which is characteristic of the advanced Valerianaceae genera. The type III pollen found in *V. tuberosa* also combines the presence of verrucae, echini, microechini and nanoechini and is large in size. The type IV pollen found in *V. alliariifolia* is smaller, has a thickening at the poles, has no verrucae, which is also characteristic of the advanced Valerianaceae genera.

If we compare the general characteristics of the pollen grains studied by us with the features of *Valeriana* pollen in general, e.g. the absence or presence of verrucae, and pollen size, then these features allow us to attribute the pollen of European *Valeriana* species to both a primitive and a more advanced type within the genus.

The data in the current study showed that the pollen morphology of *Valeriana* species allows the establishment of hypotheses regarding the evolution of exine sculpture. In particular, we suggest that there is an evolutionary trend towards a decrease in the size of echini, loss of verrucae, and an increase in the number of nanoechini.

Conclusions

Our study, based on the highest number of European *Valeriana* species (17 taxa) analysed so far, allowed more detailed descriptions of the pollen features and confirmed the view that the morphological and morphometric characters are an important additional source of information for taxonomic differentiation of the species, in particular within *Valeriana*. The research results presented here revealed that the diagnostic features of *Valeriana* species pollen grains comprised: size of pollen and colpi, size, form and number of echini, microechini and nanoechini, presence/absence of verrucae, form of verrucae, pattern of tectum in areas between echini, and exine thickness in mesocolpia and apocolpia. The present study provided the first pollen grains descriptions for *V. transsilvanica*, *V. wolgensis*, *V. exaltata*, *V. grossheimii*, and *V. rossica*. Moreover, the pollen characteristics described here may be used in future studies aiming at completing the knowledge on all European *Valeriana* species and at elucidating the evolution of pollen morphology in Valerianaceae.

Specimens examined

Valeriana alliariifolia Vahl

GEORGIA. Herbarium of the Sukhum Botanical Garden of the Academy of Sciences of the Georgian SSR. Abkhazia: 2 km from Ritsa to Auadhara, 22 July 1982, coll. *Selivanova, Vepreva*, leg. *V.S. Kolakovskaya s.n.* (KW).

Valeriana angustifolia Host

UKRAINE. Transcarpathian Region, Uzhhorod District, Antonivka village, "Chertyshi" tract, near the road, 500 m, 9 July 1948, *G. Bilyk s.n.* (KW 007635); Odessa Region, Izmail District, near Vilkovo, on the road to Primorskoe, 1 June 1966, *M. Klokov s.n.* (KW 007639).

Valeriana dioica L.

POLAND. Flora Silesiaca. Śląsk Dolny, Czechnica koło Wrocławia, Łaki – Silesia Inferior, Prata in Czechnica ad Wratislaviam, 26 May 1963, *W. Berdowski s.n.* (KW). COUNTRY UNKNOWN. Prope Sareptamlecta, *s.n.* (KW).

Valeriana exaltata Pohl

UKRAINE. Poltava Region, near Dikanka village, "Karnaukhovo" tract, near Vorskla River, alder, *M. Kotov s.n*. (KW 007641).

Valeriana grossheimii Vorosch.

UKRAINE. Crimea: nature park "Okhotnich'ye khozyaystvo", mountain Roman-Kosh, 1350 m, 19 July 1955, *M. Kotov s.n*. (KW); Crimea: road Ai-Petrinskaya yayla – Sokolinoe, 28th km, at the upper bounds of the forest, 24 July 1974, *O. Dubovik s.n*. (KW).

Valeriana montana L.

AUSTRIA. F. Schultz, herbarium normale. Cent. 11. Forêts des Alpes calcaires à 1900 m, près de Windisch-garsten (Haute-Autriche), 24 Juin 1868, *Oberleitner s.n*. (KW).

Valeriana officinalis L.

UKRAINE. Chernivtsi Region, Kitsman District, near Vytylivky village, wet meadow in the valley of Sovitsa River, 17 June 1954, coll. *I.B. Artemchuk*, leg. *M.V. Klokov s.n*. (KW). RUSSIA. Leningrad [Saint Petersburg] Region, neighborhood of Leningrad, near Dachnoe village, 10 July 1920, *R. Rozhevitz s.n*. (KW 062212). FINLAND. Satakunta (St), Rauma, alder (*Alnus glutinosa*) grove in the southern part of Rekisaari island (61°12'N, 21°26'E), east of Sorkka village, 22 Aug 1975, *Ilmari Kause & Unto Laine s.n*. (KW).

Valeriana pyrenaica L.

FRANCE. Herbier de Georges Desplantes à Flavigny sur Ozerain (Côte d'Or). Pyrénées – Orientales: Vallée de St. Vincent, lieux humides, vers 700 m, Juin 1935, *G. Desplantes s.n*. (KW).

Valeriana rossica P.A.Smirn.

UKRAINE. Sumy, near the campus of the Agrarian University, steppe meadow, slope of the 3rd exposition in the valley of Strilka River, 18 June 1999, *S.M. Panchenko s.n*. (KW 072136); Ivano-Frankivsk Region, Halytskyi District, Bovshev village, Kasova mountain, 23 July 1977, *J. Didukh, G. Kukovytsia & Hryshenko s.n.* (KW). RUSSIA. Bashkiria: Karaidel District, Ust-Baika village, left bank of Ufa River, forest, 15 July 1942, coll. *D. Zerov & A. Lypa*, leg. *M. Kotov s.n.* (KW 00100030).

Valeriana sambucifolia Pohl

UKRAINE. Transcarpathian Region, Rakhiv District, Pip Ivan mountain, Chernogorsky, in the water near the stream, the upper reaches of Beltazul River, an area with *Pinus mugus*, 1700 m, 02 July 1947, *M. Kotov s.n*. (KW). Ivano-Frankivsk Region, Kosiv District, near Burkut village, rocky slopes, 15 July 1954, *A.I. Barbaric, S.V. Topcharov & M. Kukalo s.n*. (KW 011450). FINLAND. Ex Herb. Univ. Ouluensis. Pohjois – Pohjanmaa: Oulu, seashore meadow by side of road to airport, 13 July 1962, *Paavo S. Jokela s.n*. (KW).

Valeriana simplicifolia (Rchb.) Kabath

UKRAINE. Lviv Region, Mostyskyi District, Knyazhiy Most village, 1 km to the north-east, liquid moist mixed forest, 10 May 2002, *V.I. Honcharenko VH 192* (KW 031279); Lviv region, Brody District, Khmelevoe village, Khmelevskoe forestry, sedge swamp, 14 May 1987, *A.V. Shumilova s.n.* (KW 096738). POLAND. Flora Silesiaca Exsiccata. Śląsk Dolny, Stawno koło Milicza, woj. dolnośląskie, podmokłałąka w dolinie Baryczy, 06 June1997, leg. *Edward Kozioł s.n.* (KW 044110).

Valeriana stolonifera Czern.

UKRAINE. Kirovograd Region, Malovyskov District, Onykieve village, on the edge of the forest, 16 June 1949, *F. Green s.n*. (KW); Ternopil Region, Monastyrsky District, near Dobromyshl village, glade in a beech-hornbeam forest, 15 June 1974, *B.V. Zaverukha s.n*. (KW 001231).

Valeriana supina L.

ITALY. Herbarium Prof. Dr. ing. e. h. Dr. techn. h. c. V. Engelhardt. Flora von Italien. Standort: Geröll an der Kölner–Hütte, Rosengartengebiet – Dolomiten, July/August 1926, *V. Engelhardt s.n*. (KW).

Valeriana transsilvanica Schur

UKRAINE. Ivano-Frankivsk Region, Nadvirna District, Chornohora, north-western slope of Danzer mountain, along the stream, 1670 m, 25 June 1999, *R.I. Dmitrakh s.n*. (KW 013793).

Valeriana tripteris L.

UKRAINE. Zakarpattia Region, Rakhiv District, Yasinya village, "Zimir" tract, spruce forest, 09 June 1953, *W. Commendar s.n*. (KW 013864); Zakarpattia Region, Rakhiv District, Svydovets ridge, Blyznytsia mountain, "komyny" 3, 09 July 2005, *S.M. Ziman & O.V. Bulakh s.n*. (KW 00105197). POLAND. Dupla ex herbario Instituti botanici. Academiae Scientiarum Polonae – Cracoviae. Dolina Będkowska ad Zabierzów, Distr. Kraków, Polonia merid., ad vivum, 12 May 1957, leg. *A. Jasiewicz s.n*. (KW).

Valeriana tuberosa L.

UKRAINE. Luhansk Region, Melovsky District, "Streletskaya steppe" reserve, plateau, 02 May 1955, *Z. Sarycheva s.n*. (KW); Donetsk Region, Volodarskyi District, near Nazarivka village, "Kam'yani mohyly", in the steppe, 29 Apr 2013, *V.P. Kolomiychuk s.n*. (KW 00107777). FRANCE. Herbier de Georges Desplantes à Flavigny sur Ozerain (Côte-d'Or). Côte-d'Or: Gevrey, plateau de Château-Renard, calcaire – alt. 320 m, Mai 1930, *G. Desplantes s.n*. (KW).

Valeriana wolgensis Kazak.

UKRAINE. Donetsk Region, Artemovskiy District, Serebryanka, on chalk slopes, 05 June 1962, *O. Dubovik s.n*. (KW). RUSSIA. Bashkiria: near Ufa, government dacha, floodplain of Ufa River, 29 July 1942, *D.Ya. Afanasyev s.n*. (KW).

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