



Original Scientific Paper

Taxonomic significance of pollen morphology of *Pterocephalus plumosus* (Caprifoliaceae)

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ABSTRACT:

Comparative palynological studies of Dipsacaceae s.str. show considerable diversity in the pollen grain morphology of its representatives. The aim of this research was to provide more detailed palynomorphological data on selected taxa whose pollen grains are characterised by tricolpate apertures (*Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa*). The pollen morphology of *P. plumosus* was studied using both light microscopy and scanning electron microscopy. The pollen grains are tricolpate, suboblate to prolate; large in size. Their outline in polar view (amb) is subcircular, rarely trilobate. The brevicolpi have a distinct margo and acute ends. The exine sculpture is echinate-microechinate-nanoechinate. The exine structure (columellae) of the pollen grains of *P. plumosus*, *S. pratensis* and *S. inflexa* was analysed for the first time in the current study. Pollen grains in *P. plumosus* are distinguished by long and dense columellae in the mesocolpia, and longer in the apocolpia. Our new palynomorphological data support a close relationship between *S. pratensis* and *S. inflexa* by the presence of shorter sparse columellae throughout the pollen exine. The UPGMA dendrogram shows the distinctive morphometric characters of *P. plumosus* pollen grains, which is thus included as a separate branch.

Keywords:

pollen sculpture and structure, diagnostic characters, taxonomy, SEM microscopy, UPGMA analysis, Scabioseae

UDC: 582.971.1:581.33

Received: 28 February 2022

Revision accepted: 30 June 2022

INTRODUCTION

The genus *Pterocephalus* Vaill. ex Adans. was previously placed in the family Dipsacaceae Juss. (BOBROV 1957; KOTOV 1961; FERGUSON 1976; TAKHTAJAN 2009). According to the latest versions of the Angiosperm Phylogeny Group system (APG III 2009; APG IV 2016), it is included in the extended family Caprifoliaceae s.l. (together with Diervillaceae Pyck, Morinaceae Raf., Valerianaceae Batsch, etc.). The phylogenetic position of Dipsacaceae within the order Dipsacales has been studied extensively (DONOGHUE *et al.* 1992; CAPUTO & COZZOLINO 1994; BELL *et al.* 2001; ZHANG *et al.* 2003; CAPUTO *et al.* 2004; BELL & DONOGHUE 2005; AVINO *et al.* 2009; CARLSON *et al.* 2009; XIANG

et al. 2020; WANG *et al.* 2021; YILDIRIM *et al.* 2022). According to new data, all representatives of Dipsacaceae were assigned to the subfam. Dipsacoideae Eaton (WANG *et al.* 2021; YILDIRIM *et al.* 2022).

Earlier researchers subdivided Dipsacaceae into three tribes: Knautieae Tiegh., Dipsaceae Rchb., and Scabioseae DC. (VAN TIEGHEM 1909; DE CASTRO & CAPUTO 1997–1998; AVINO *et al.* 2009). *Pterocephalus* was usually affiliated with the tribe Dipsaceae (BOBROV 1957; KOTOV 1961). However, MAYER & EHRENDORFER (2013) and MAYER (2016) proposed an improved family classification, with two subfamilies and eight tribes. Based on morphological, anatomical and other data, *Pterocephalus* s.str. is included (together with *Scabiosa* L. and *Sixalix* Raf.) in

the tribe Scabioseae s.str., subfam. Scabiosoideae Burnett (MAYER & EHRENDORFER 2013; MAYER 2016).

Pterocephalus includes approximately 30 species occurring in the Canary Islands, the Mediterranean to Central Asia, the Himalayas and Western China, and NE to E tropical Africa (BOBROV 1957; FERGUSON 1976; MAYER & EHRENDORFER 2000; MAYER 2016). Most of the species of *Pterocephalus* s.str. are perennials and range from shrubs to chamaephytes or polycormic hemicryptophytes, and only two species [*P. brevis* Coult. and *P. plumosus* (L.) F.Dietr.] are annual therophytes. All species are characterised by a lack of floral bracts (MAYER & EHRENDORFER 1999, 2000). The most recent comprehensive taxonomic treatment of the genus *Pterocephalus*, based on morphological, anatomical, palynological, and karyological data, was published by MAYER & EHRENDORFER (2000). The authors divided the taxa of *Pterocephalus* into five groups and placed only *P. plumosus* in the most advanced group V (epicalyx with corona, diaphragma fused with elongated epidiaphragma). According to molecular phylogenetic data, *Pterocephalus* forms a sister clade with *Scabiosa* and *Sixalix* (CAPUTO *et al.* 2004; AVINO *et al.* 2009; CARLSON *et al.* 2009). *Pterocephalus plumosus* is a native member of the flora of Ukraine and adjacent countries (BOBROV 1957; KOTOV 1961; MOSYAKIN & FEDORONCHUK 1999).

It is well known that the morphological characteristics of pollen grains as additional diagnostic features are often used in the taxonomy (e.g., MOSYAKIN & TSYMBALYUK 2015, 2017; BELLONZI *et al.* 2020; ALBACH *et al.* 2021; GASPARINO *et al.* 2021; TSYMBALYUK *et al.* 2021a, b, 2022; etc.). Comparative palynomorphological studies of Dipsacaceae s.str. show great diversity in the pollen grain morphology of its representatives. Several studies have been devoted to the palynomorphological features of Dipsacaceae, which have revealed colpate and porate pollen types of its taxa. In the present study, we will consider the structure and sculpture of colpate pollen grains of selected representatives of Dipsacaceae s.str.

Pollen grains of *P. plumosus* have been studied using light microscopy (VINOKUROVA 1959; AL-DOBAISSI *et al.* 2020), scanning electron microscopy (MOSTAFA *et al.* 2017), or both light and scanning electron microscopy (MAYER & EHRENDORFER 2000; KHALIK 2010). Previously, we studied the pollen grains of *Succisa pratensis* Moench and *Succisella inflexa* (Kluk) Beck (TSYMBALYUK *et al.* 2019b). Despite the relatively numerous publications, the knowledge about the morphology of pollen grains in *P. plumosus* is fragmentary because the available descriptions usually only briefly address the pollen morphology of this species, or researchers have analysed only a few selected pollen features.

Our main objective was to perform a more detailed palynomorphological investigation of *P. plumosus* in order to provide an assessment of the taxonomic significance of its pollen morphology and to compare it with *S. pratensis* and *S. inflexa*.

MATERIAL AND METHODS

The pollen grains of *P. plumosus* 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). Herbarium acronyms are given following the *Index Herbariorum* (THIERS 2022). The ten studied specimens are listed in the Appendix. The abbreviations of the names of the taxon authors follow BRUMMITT & POWELL (1992), with additions and updates available from IPNI (2022).

The methods used in the present study have been previously described in detail (TSYMBALYUK *et al.* 2021a, b). The pollen morphology was studied using both light microscopy (LM) and scanning electron microscopy (SEM). For LM studies (Biolar, $\times 700$), the pollen was acetolysed following ERDTMAN (1952), mounted on slides with glycerinated gelatin, analysed and photomicrographed. The morphometric features of 25 properly developed pollen grains from each specimen were measured, and the measurements included the following parameters: polar axis (P), equatorial diameter (E), colpus length and width, and margo and exine thickness. All exine measurements were taken in the mesocolpium and apocolpium regions. In order to determine the pollen shape, the P/E ratio was calculated. For all the quantitative characters, descriptive statistics were applied and the range (minimum and maximum values), arithmetic mean and standard deviation were calculated. The slides were deposited in the Palynothea (reference pollen collection) at the National Herbarium of Ukraine (BEZUSKO & TSYMBALYUK 2011).

For SEM studies (JEOL JSM-6060LA), dry and acetolysed pollen grains (from *P. plumosus*, *S. pratensis* and *S. inflexa*) 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, nanoechini and columellae were taken on five pollen grains from each specimen from SEM micrographs using AxioVision Rel.4.8.2. software. The number of echini/microechini/nanoechini per unit area ($100 \mu\text{m}^2$) was determined. The terminology used in the descriptions of the pollen grains mainly follows 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 *P. plumosus*, *S. pratensis* and *S. inflexa*. Eight quantitative palynomorphological characters (listed in Table 1) were examined. PAST (PAleontological STatistics) software v. 4.08 was used for the analysis (HAMMER *et al.* 2001).

RESULTS

The data on the quantitative and qualitative pollen characters used in this study are summarised in Tables 1–3.

Table 1. A morphometric comparison of the pollen grains of *Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa* (all measurements given as μm).

Taxon	Polar axis	Equatorial diameter	P/E ratio	Colpi length	Colpi width	Margo thickness	Exine (m/a)	Columellae length (m/a)	Columellae thickness (m/a)
<i>Pterocephalus plumosus</i>	88.66±5.97	75.67±4.49	1.17±0.09	32.58±4.74	2.09±0.87	2.17±0.56	8.10±0.68	2.61±0.26	0.78±0.12
	73.15–98.42	66.50–87.78	0.83–1.34	25.27–39.90	0.66–3.99	1.06–2.66	6.65–9.31/ 11.26±0.82 9.31–13.30	2.34–3.07/ 3.88±0.74 2.83–4.66	0.64–1.00/ 1.11±0.37 0.68–1.98
<i>Succisa pratensis</i>	87.91±6.50	83.05±6.28	1.06±0.08	32.31±3.31	3.08±0.90	1.46±0.25	9.24±1.26	2.42±0.30	1.30±0.23
	73.15–98.42*	66.50–98.42*	0.85–1.16*	26.60–39.90*	1.99–5.32*	1.33–1.99*	6.65–10.64*	2.03–2.85	1.03–1.81
<i>Succisella inflexa</i>	72.95±3.37	71.42±3.52	1.02±0.07	27.93±1.33	1.83±1.06	1.10±0.30	7.72±0.88	1.78±0.14	0.80±0.14
	66.50–79.80*	65.17–79.80*	0.87–1.14*	26.60–30.59*	0.66–3.99*	0.66–1.59*	6.65–9.31*	1.47–2.03	0.61–1.01

The values are presented as Mean \pm Standard deviation and Range (min-max); m – mesocolpium; a – apocolpium; *data from TSYMBALYUK *et al.* 2019b)

Table 2. A morphological comparison of the pollen grains of *Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa*.

Taxon	Shape	Amb	Colpi margins	Colpi ends	Margo	Colpus membrane	Tectum	Columellae in mesocolpium
<i>Pterocephalus plumosus</i>	suboblate to prolate	trilobate subcircular	straight or uneven	acute	narrow or wide	psilate-granulate	psilate-rugulate	long, dense
<i>Succisa pratensis</i>	suboblate to subprolate*	trilobate subcircular*	irregular*	obtuse or acute*	narrow*	granulate-echinate*	psilate-perforate*	short, sparse
<i>Succisella inflexa</i>	suboblate to spheroidal*	trilobate subcircular*	irregular*	obtuse or acute*	narrow*	granulate-echinate*	rugulate*	short, sparse

*data from TSYMBALYUK *et al.* (2019b)

SEM and LM photomicrographs of the pollen grains are shown in Figs. 1–3. A UPGMA dendrogram showing the relationships between the pollen grains of *P. plumosus*, *S. pratensis* and *S. inflexa* is presented in Fig. 4.

Descriptions of the pollen grains

***Pterocephalus plumosus* (L.) F.Dietr.** (Figs. 1A–D, 2A–D & 3A–D)

LM. The pollen grains are monads, isopolar, tricolpate, suboblate to prolate (P/E=0.83–1.34); in equatorial view elliptic, rarely circular; amb mainly subcircular, rarely 3-lobate; large in size: P=73.15–98.42 μm , E=66.50–87.78 μm . Brevicolpi 25.27–39.90 μm long, 0.66–3.99 μm wide, with distinct, more or less straight margins, rarely slightly uneven, with acute ends and a distinct margo, 1.06–2.66 μm thick; colpus membrane psilate. Exine tectate, 6.65–9.31 μm thick in the mesocolpium, 9.31–13.30 μm in the apocolpium. Tectum thin, three or four times thinner than the infratectum. Columellae distinct, short and dense in the mesocolpium, longer in the apocolpium, branched above. Nexine two times thicker than the tectum. LO-analysis: columellae circular, rarely elongated, densely distributed. Echini indistinct on the surface, indistinct or rarely distinct on the edges, sparsely distributed.

SEM. Exine sculpture echinate-microechinate-nanoechinate. Echini conic, 1.01–1.68 μm high, 0.98–1.48 μm wide

at the base, with straight or convex sides and acute apices; tectum psilate-rugulate in the area between the echini. Microechini 0.68–0.98 μm high, 0.69–1.36 μm wide at the base, with straight or convex sides and acute apices; nanoechini 0.14–0.42 μm high, 0.24–0.59 μm wide at the base. Echini (1–3/100 μm^2) and microechini (1–4/100 μm^2) sparsely distributed, nanoechini (61–118/100 μm^2) densely distributed. Colpus membranes psilate-granulate. Columellae distinct, more simple in the mesocolpium, 2.34–3.07 μm long and 0.64–1.00 μm thick; longer in the apocolpium, often branched above, 2.83–4.66 μm long and 0.68–1.98 μm thick; granules are also observed.

Numerical analysis of the palynomorphological character states

The cluster analysis of *P. plumosus*, *S. pratensis* and *S. inflexa* pollen clearly separates the species. As seen in the UPGMA dendrogram, *P. plumosus* has distinctive pollen morphometric characters and is placed as a separate branch. *Succisa pratensis* and *Succisella inflexa* were grouped into another branch because they had more similar pollen grain features (Table 1, Fig. 4).

DISCUSSION

In general, the data in the present investigation are in agreement with the results of previous LM and SEM studies. The

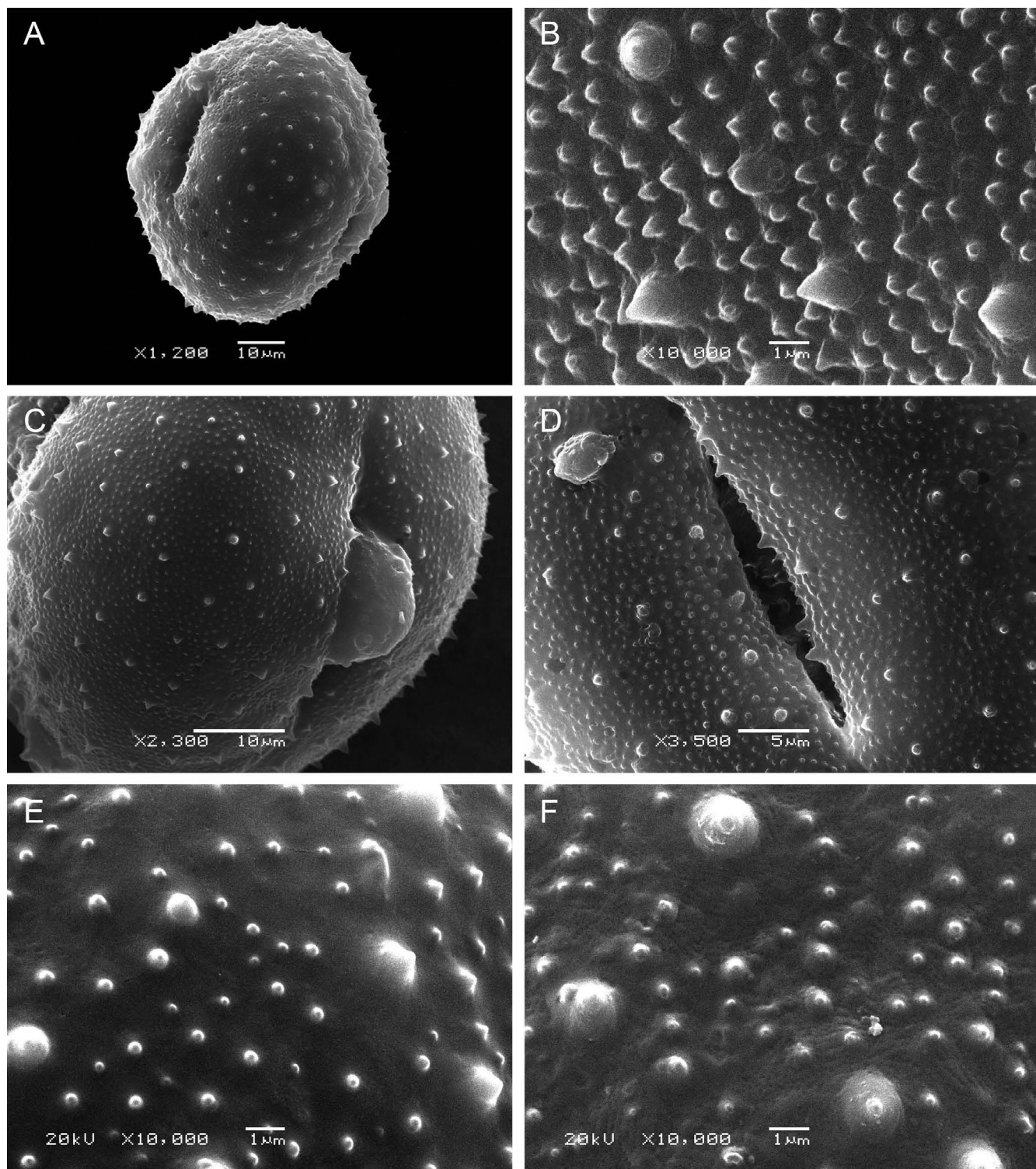


Fig. 1. Pollen grains of *Pterocepalus plumosus*, *Succisa pratensis* and *Succisella inflexa* (SEM). **A–D** – *P. plumosus*, **E** – *S. pratensis*, **F** – *S. inflexa*; **A** – Equatorial view, **B, E, F** – Exine sculpture (**B** – Acetylated pollen); **C, D** – Colpi membranes.

pollen grain sizes obtained are comparable to previously published data. The pollen sizes of *P. plumosus* were given by KHALIK (2010) as $P=68$ (57–75) μm and $E=62$ (50–70) μm . MOSTAFA *et al.* (2017) and AL-DOBAISSI *et al.* (2020) presented only the mean pollen grain sizes of *P. plumosus*

as $P=78.51$ μm , $E=54.93$ μm , and $P=68.9$ μm , $E=67.6$ μm , respectively. VINOKUROVA (1959) reported $P=E=60$ – 61 μm for the pollen grains of this species. MAYER & EHRENDORFER (2000) provided a general description of the pollen grains of the genus *Pterocepalus*, which demonstrates

Table 3. A comparison of echini, microechini and nanoechini (all measurements given as μm).

Taxon	Echini (SEM)			Microechini (SEM)			Nanoechini (SEM)		
	Height	Width at the base	Number/100 μm^2	Height	Width at the base	Number/100 μm^2	Height	Width at the base	Number/100 μm^2
<i>P. plumosus</i> 1	1.29±0.19 1.01–1.65	1.26±0.14 1.00–1.43	1–3	0.85±0.09 0.74–0.98	1.17±0.16 0.92–1.36	1–3	0.26±0.05 0.19–0.37	0.48±0.10 0.31–0.59	61–76
<i>P. plumosus</i> 2	1.22±0.21 1.02–1.68	1.28±0.14 1.02–1.46	1–3	0.86±0.06 0.81–0.95	1.02±0.15 0.80–1.17	1–2	0.26±0.08 0.14–0.38	0.37±0.09 0.24–0.53	82–110
<i>P. plumosus</i> 3	1.17±0.12 1.02–1.40	1.14±0.16 0.98–1.40	1–3	0.82±0.11 0.68–0.97	0.96±0.20 0.69–1.31	1–4	0.29±0.08 0.17–0.42	0.42±0.10 0.28–0.58	85–101
<i>P. plumosus</i> 4	1.20±0.17 1.01–1.53	1.17±0.17 0.98–1.48	1–3	0.91±0.04 0.87–0.96	1.05±0.07 0.98–1.12	1–4	0.27±0.06 0.18–0.36	0.48±0.08 0.29–0.58	85–118
<i>P. plumosus</i> 5	1.29±0.17 1.02–1.56	1.17±0.13 0.98–1.38	1–3	0.77±0.06 0.68–0.88	1.03±0.09 0.92–1.20	1–4	0.25±0.07 0.16–0.35	0.39±0.06 0.30–0.49	98–107
<i>P. plumosus</i> G	1.24±0.18 1.01–1.68	1.21±0.16 0.98–1.48	1–3	0.82±0.09 0.68–0.98	1.03±0.16 0.69–1.36	1–4	0.27±0.07 0.14–0.42	0.43±0.10 0.24–0.59	61–118
<i>S. pratensis</i> 1	1.25±0.15 1.13–1.47	1.37±0.05 1.29–1.43	1–2	0.92±0.06 0.84–0.99	1.22±0.13 1.12–1.41	1–3	0.24±0.06 0.18–0.35	0.36±0.09 0.27–0.53	31–49
<i>S. pratensis</i> 2	1.28±0.15 1.08–1.49	1.32±0.14 1.13–1.48	1–2	0.78±0.07 0.68–0.87	1.11±0.19 0.92–1.43	1–3	0.28±0.07 0.18–0.36	0.41±0.10 0.25–0.54	28–38
<i>S. pratensis</i> 3	1.24±0.15 1.05–1.53	1.31±0.10 1.14–1.44	1–2	0.86±0.09 0.76–0.98	1.22±0.19 0.94–1.39	1–2	0.33±0.06 0.19–0.39	0.49±0.03 0.42–0.53	32–49
<i>S. pratensis</i> G	1.26±0.15 1.05–1.53	1.32±0.11 1.13–1.48	1–2	0.84±0.09 0.68–0.99	1.17±0.18 0.92–1.43	1–3	0.29±0.07 0.18–0.39	0.42±0.09 0.25–0.54	28–49
<i>S. inflexa</i> 1	1.10±0.03 1.06–1.14	1.22±0.09 1.10–1.37	1–2	0.83±0.06 0.67–0.98	1.14±0.16 0.79–1.39	4–6	0.24±0.06 0.16–0.36	0.41±0.08 0.24–0.56	61–88
<i>S. inflexa</i> 2	1.06±0.02 1.02–1.09	1.24±0.05 1.18–1.32	0–1	0.83±0.11 0.74–0.99	1.07±0.06 0.98–1.14	4–5	0.22±0.05 0.18–0.31	0.39±0.08 0.31–0.53	55–60
<i>S. inflexa</i> G	1.08±0.03 1.02–1.14	1.23±0.08 1.10–1.37	1–2	0.83±0.07 0.67–0.99	1.13±0.15 0.79–1.39	4–6	0.23±0.06 0.16–0.36	0.40±0.08 0.24–0.56	55–88

The values are presented as Mean \pm Standard deviation and Range (min-max). 1, 2, 3, 4, 5 – specimen number; G – general specimens' measurements

that "...pollen of all *Pterocephalus* s.str. species is tricolpate and longiaxial. The exine is densely sculptured with few long and numerous small, sharply pointed echini. Semi-thin sections show that the exine is rather thick and exhibits very dense columellae".

The analysis of our original palynomorphological data and literature records demonstrated that the pollen grains of *P. plumosus* are characterised by tricolpate type of apertures (see also MAYER & EHRENDORFER 2000; KHALIK 2010; MOSTAFA *et al.* 2017). The pollen grains of *P. plumosus* are similar to those of *S. pratensis* and *S. inflexa* in their pollen type (TSYMBALYUK *et al.* 2019b). In contrast, the representatives of the genera *Knautia* L., *Dipsacus* L. and *Cephalaria* Schrad. usually have apertures of the triporate type (CLARKE & JONES 1981; PERVEEN & QAISER 2011; MOSTAFA *et al.* 2017; TSYMBALYUK *et al.* 2018, 2019a, 2021a). Also, the present study demonstrated differences between *P. plumosus* and the two other species, *S. pratensis* and *S. inflexa* (Tables 1–3).

Apertures. The pollen grains of the three species investigated have three apertures (brevicolpi). The longest colpi are characteristic of *P. plumosus*, slightly shorter in *S. pra-*

tensis, while short ones are observed in *S. inflexa* (Table 1). Wide colpi are characteristic of *S. pratensis*, while narrow colpi are observed in *P. plumosus* and *S. inflexa* (Table 1). In all the species the colpi are surrounded by a margo. The pollen grains of *P. plumosus* have a wider margo in comparison to *S. pratensis* and *S. inflexa* which have narrower ones (Table 1).

Shape and size. According to the P/E ratio (Tables 1 & 2), the pollen grains are suboblate to prolate (*P. plumosus*), suboblate to subprolate (*S. pratensis*) and suboblate to spheroidal (*S. inflexa*) in shape. The smallest pollen grains are observed in *S. inflexa*, while the largest pollen grains are measured in *P. plumosus* and *S. pratensis*.

Sculpture. The pollen grains of the investigated species have echinate-microechinate-nanoechinate exine sculpture. The pollen grains in *S. pratensis* (Fig. 1E) are characterised by very small perforations in the tectum area between the echini; *P. plumosus* (Fig. 1B) and *S. inflexa* (Fig. 1F) have a rugulate tectum in the area between the echini. The highest echini are found in *P. plumosus* (up to 1.68 μm); the echini are sparsely distributed (1–3/100

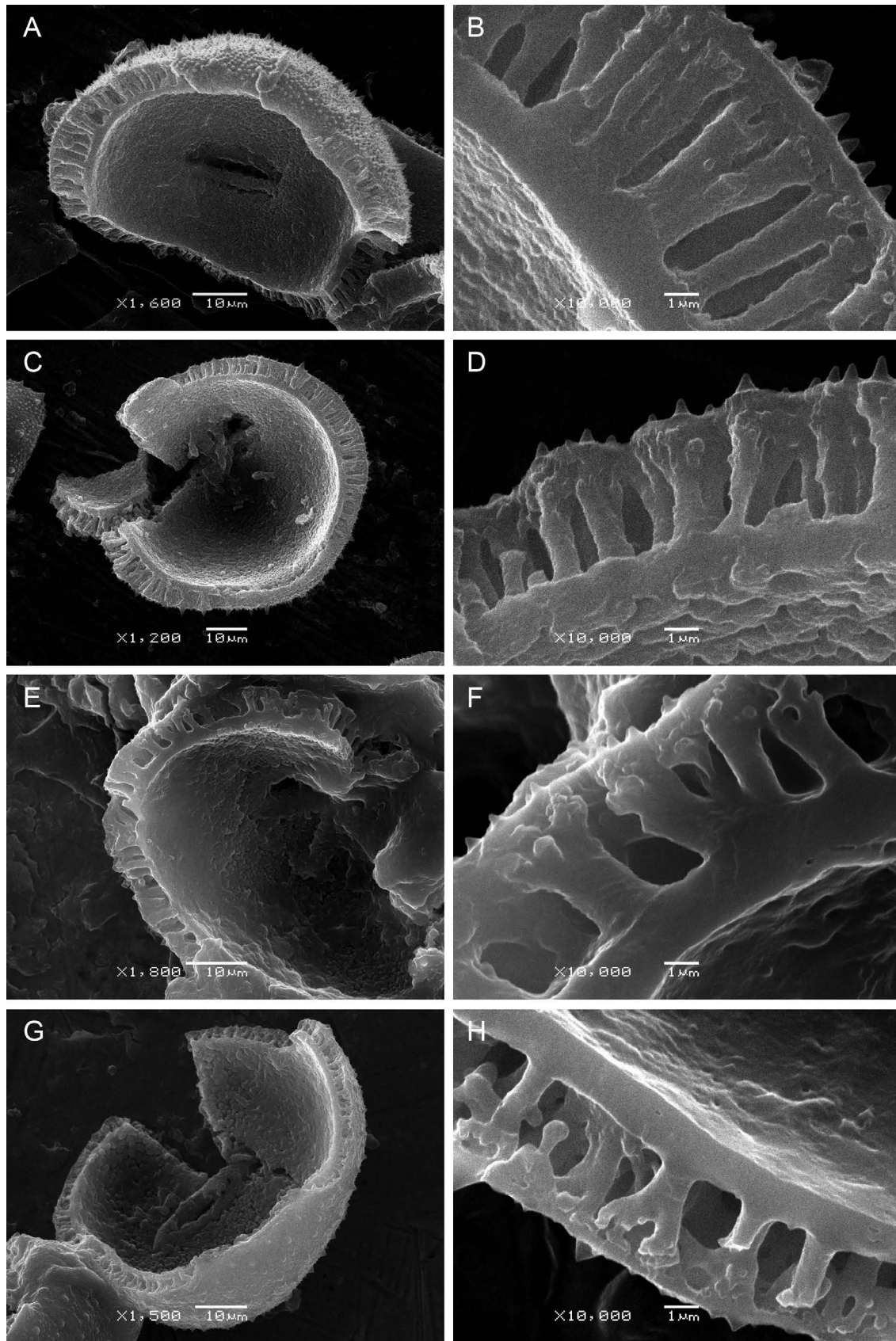


Fig. 2. Exine structure of *Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa* (SEM). **A-D** – *P. plumosus*, **E, F** – *S. pratensis*, **G, H** – *S. inflexa*; **A-H** – Broken exine of acetolysed pollen grains; **B, F** – Columellae in the apocolpium, **D, H** – Columellae in the mesocolpium; **A, G** – Colpus with margo.

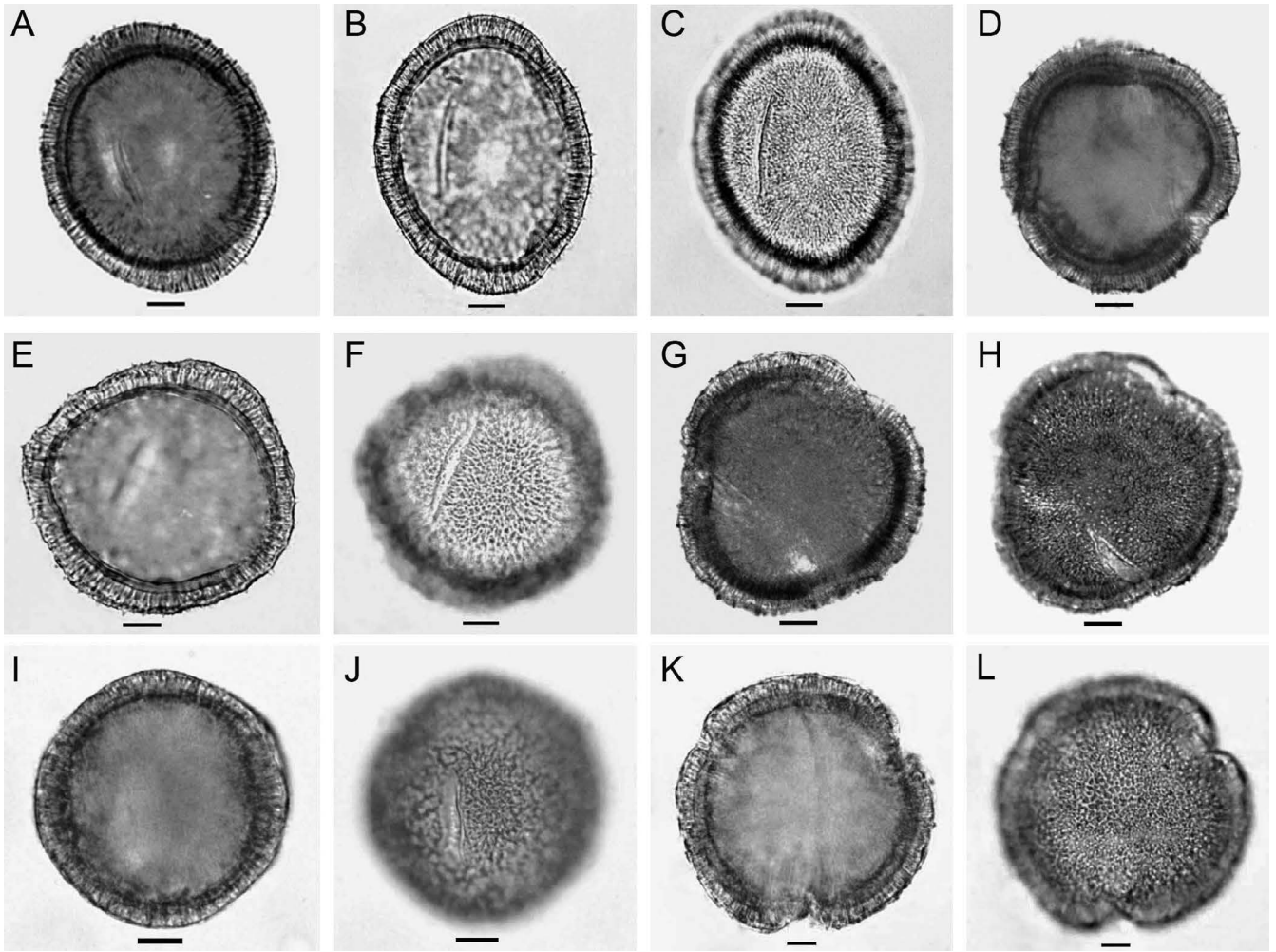


Fig. 3. Pollen grains of *Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa* (LM). A–D – *P. plumosus*, E–H – *S. pratensis*; I–L – *S. inflexa*; A–C, E, F, I, J – Equatorial view; D, G, H, K, L – Polar view; B, F, J – Colpi. Scale bars = 10 μm .

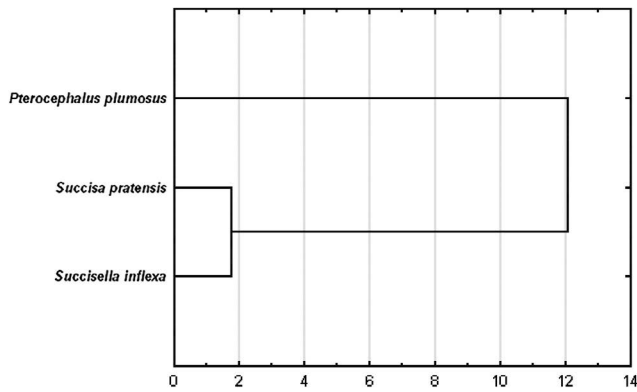


Fig. 4. A UPGMA dendrogram showing the relationships between the pollen grains of *Pterocephalus plumosus*, *Succisa pratensis* and *Succisella inflexa* based on quantitative characters.

μm^2) (Figs. 1B–D). In *S. pratensis* and *S. inflexa* the width of the echini is bigger than their height, while in *P. plumosus* their height is usually bigger than the width (Table 3). Our results show that the size of the echini and their num-

ber in *P. plumosus* and *S. pratensis* overlap. However, these species clearly differ in the distribution of nanoechini (61–118/100 μm^2 and 28–49/100 μm^2 , respectively). The pollen grains of *P. plumosus* have a psilate-granulate colpus membrane, and those of *S. pratensis* and *S. inflexa* one which is granulate-echinate.

Exine. *P. plumosus* has a thickening exine at the apocolpium, whereas *S. pratensis* and *S. inflexa* have exines of uniform thickness throughout (Table 1). The columellae in *P. plumosus* are long and dense in the mesocolpium (Fig. 2D), and longer in the apocolpium (Fig. 2B), while in *S. pratensis* (Figs. 2E & F) and *S. inflexa* (Figs. 2G & H) they are shorter, and sparsely arranged in the mesocolpium and the apocolpium. The exine structure of the pollen grains of *P. plumosus*, *S. pratensis* and *S. inflexa* was analysed for the first time in the current study.

According to MAYER (2016), *Succisa* and *Succisella* are placed in the tribe Succiseae. The palynomorphological data in this study also suggest a close affinity between these taxa and confirm their placement in the Succiseae

because they have a similar pollen type, shape, size, colpus membrane, exine sculpture and structure (Tables 1–3, Figs. 1–3). *Pterocephalus plumosus* is placed in tribe Scabioseae (MAYER 2016). Our analysis of the P/E ratio showed that the pollen grains of *P. plumosus* have the largest P/E, while *S. pratensis* and *S. inflexa* have a smaller P/E, showing a significant difference between them (Table 1). They also differ in the structure of the echini and columellae, and in the distribution of nanoechini (Tables 1 & 3, Figs. 1–3). The cluster analysis of *P. plumosus*, *S. pratensis*, and *S. inflexa* also supports these findings (Fig. 4).

CONCLUSION

Pollen morphology proved to be an important additional source of information for species-specific identification between *Pterocephalus*, *Succisa* and *Succisella*. The species could be identified based on morphological and morphometric pollen features, and especially based on the size of the pollen, the structure of the colpi and margo, the exine thickness, the exine structure, the size and form of the echini, the distribution of nanoechini, as well as the pattern of the tectum in the areas between the echini. The pollen characteristics described here may be used in future studies aimed at completing the knowledge on Scabioseae species and at understanding the evolution of pollen morphology in Dipsacoideae in general.

Acknowledgements – The authors express their gratitude to Natalia M. Shyian, Head Curator of the National Herbarium of Ukraine (KW; herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine). The helpful cooperation of Dmytro O. Klymchuk, Head of the Center of Electron Microscopy (M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine), is greatly appreciated.

Specimens examined:

***Pterocephalus plumosus*:** 1. Crimea, districts around the village of Simeiz, on a rocky slope, 6 June 2001, leg./det. O.N. Konoplya (KW 063029); 2. Crimea, 4 July 1902, leg./det. Golde (KW); 3. Herbarium Universitatis Imperialis Sancti Wladimiri. Kiew, Transcaucasia, Elizavetpol District, 12 June 1893, leg./det. V. Lipsky (KW); 4. Editio Horti Botanici Imperialis Petropolitani. Karabagh, in collibus prope Chan-Kendy, July 1990, leg. S. Fedossejew, det. N. Busch (KW); 5. Dagestan, Petrovsk, 2 July 1891, leg./det. V. Lipsky (KW).

***Succisa pratensis*:** 1. Ukraine, Zhytomyr Region, Volodarsk-Volynsky District, St. Turchanka, a pasture in the birch-alder forest, 30 July 1949, leg./det. A. Zapytova (KW); 2. Ukraine, near Vinnitsa [Vinnitsya], a wet meadow north of the railway in the direction of Sosenka (Kalinovka), 24 August 1927, leg./det. K.S. Yankovsky (KW); 3. Ukraine, Chernihiv Region, Lyubech District,

Lyubech village, floodplain of the Dnipro [Dnieper] River, 28 July 1952, leg./det. D. Afanasyev (KW).

***Succisella inflexa*:** 1. Ukraine, Volyn' Region, Kovel District, the village of Ugli, floodplain of the Stohod [Stokhid] River, peat meadows, 3 August 2007, leg./det. T.L. Andriyenko (KW 083618); 2. Belarus, Kamenyuki village, Kamenetsk District, Brest Region, 26 July 1972, leg./det. O. Dubovik (KW).

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REZIME

Taksonomski značaj morfologije semena kod *Pterocephalus plumosus* (Caprifoliaceae)

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Komparativne palinološke studije Dipsacaceae s.str. pokazuju veliki diverzitet morfologije polenovih zrna kod njenih predstavnika. Cilj ovog istraživanja bio je da se dobiju detaljniji palinomorfološki podaci o odabranim taksonima čija se polenova zrna karakterišu trikolporatnim tipom otvora (*Pterocephalus plumosus*, *Succisa pratensis* i *Succisella inflexa*). Morfologija polena *P. plumosus* je proučavana korišćenjem svetlosne mikroskopije i skening elektronske mikroskopije. Polenova zrna su trikolporatna, delimično spljoštena do prolatna, velikih dimenzija. Njihove konture u polarnom položaju su delimično kružne, retko trilobatne. Brevikolpe su sa izraženim marginama i oštrim krajevima. Skulptura egzine je ehinatno-mikroehinatno-nanoehinatna. Struktura egzine polenovih zrna *P. plumosus*, *S. pratensis* i *S. inflexa* je analizirana po prvi put u ovoj studiji. Polenova zrna *P. plumosus* se razlikuju po dugačkoj i gustoj strukturi egzine u mezokolpiumu, i dužoj u apokolpiumu. Naši novi palinomorfološki podaci podržavaju blisku vezu između *S. pratensis* i *S. inflexa* prema prisustvu kraćih retkih kolumela u celoj polenskoj egzini. UPGMA dendrogram potvrđuje da *P. plumosus* ima karakteristične morfometrijske karakteristike polenovih zrna i da je uključen kao posebna grana.

Ključne reči: skulptura i struktura polena, dijagnostički karakteri, taksonomija, SEM mikroskopija, UPGMA analize, Scabiosae