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Comparative morphometric and morphological study of the pollen of *Beta trigyna*, *B. vulgaris* and *B. vulgaris* subsp. *maritima* (Chenopodiaceae/Amaranthaceae *sensu* APG IV)

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Key words: Beteae, LM, palynomorphology, sculpture, SEM, structure, UPGMA.

Ključne besede: Beteae, svetlobni mikroskop, palinomorfologija, skulptura, vrstični elektronski mikroskop, struktura, UPGMA.

Abstract

Pollen morphology of *Beta trigyna*, *B. vulgaris* and *B. vulgaris* subsp. *maritima*, last of those studied for the first time, was investigated using light and scanning electron microscopy, based on 10 herbarium specimens. The aim of the study was to provide detailed data on the pollen characteristics of these taxa to identify similarities and differences between them. Pollen grains are pantoporate, spheroidal, circular in outline; small- and medium-sized. Exine sculpture is nanoechinate, tectum is psilate or psilate-perforate. Pore membranes are nanoechinate. Diagnostic relevance of the characters of pollen grains is discussed (pollen and pore diameters, distance between pores and between pore centres, nanoechini size and density, number of nanoechini on pore membranes, structure of columellae). UPGMA dendrograms based on palynological data support the differentiation of *B. trigyna* (section Corollinae), *B. vulgaris* and *B. vulgaris* subsp. *maritima* (section Beta). The obtained characteristics of pollen grains of *Beta* species can be used in spore-pollen analysis, especially in identifying the impact of human economic activity in the past.

Izvleček

S svetlobnim in vrstičnim elektronskim mikroskopom smo na 10 herbarijskih primerkih proučevali morfologijo peloda vrst *Beta trigyna*, *B. vulgaris* in *B. vulgaris* subsp. *maritima*, slednja je proučevana prvič. Namen raziskave je bil pridobiti natančne podatke o značilnostih peloda teh taksonov in izpostaviti podobnosti in razlike med njimi. Pelodna zrna so pantoporatna, sferoidna in okrogle oblike, majhna do srednje velika. Eksina je nanoehinatna, tektum je psilaten ari psilaten-perforaten. Membrane por so nanoehinatne. Obravnavali smo diagnostični pomen lastnosti pelodnih zrn (premere peloda in por, razdaljo med porami in središči por, velikost in gostoto nanoehinijev na membranah por, zgradbo kolumel). Z Dendrogrami UPGMA na osnovi palinoloških podatkov so potrdili razlike med vrstami *B. trigyna* (section Corollinae), *B. vulgaris* in *B. vulgaris* subsp. *maritima* (section Beta). Dobljene lastnosti pelodnih zrn vrst rodu *Beta* lahko uporabimo pri analizah spor in pelodnih analizah, predvsem pri ugotavljanju vpliva človekove gospodarske aktivnosti v preteklosti.

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Introduction

Beta L. belongs to the tribe Beteae (Betoideae, Chenopodiaceae/Amaranthaceae sensu APG IV), and comprises 9–10 species and an uncertain number of subspecies or varieties, which are mainly included in *B. vulgaris* L. (Iamonico, 2019). Wild representatives of the genus are annual, biennial and perennial herbaceous plants occurring from the Atlantic coast of Europe, Macaronesia, Eastern Europe and the Mediterranean Region to West and South Asia including Eastern India and Bangladesh (Ford-Lloyd & Williams, 1975; Ball & Akeroyd, 1993; Kadereit et al., 2006; Iamonico, 2019; POWO, 2023). In the flora of Ukraine and Bulgaria the genus is represented by the taxa *B. trigyna* Waldst. & Kit., *B. vulgaris*, and *B. vulgaris* subsp. *maritima* (L.) Arcang. (Iljin, 1952; Jordanov & Kuzmanov, 1966; Mosyakin & Fedoronchuk, 1999; Yena & Yevseyenkov, 2010). *Beta vulgaris* is a biennial or perennial plant; its native range is in the Azores, Western Europe and Eastern Europe, the Mediterranean Region and eastwards to India (Ford-Lloyd & Williams, 1975; POWO, 2023). This species is of great economic importance as a sugar crop, vegetable and fodder plant. *Beta vulgaris* is also used as medicinal and ornamental plant (Ford-Lloyd & Williams, 1975; POWO, 2023). The perennial sea beat *B. vulgaris* subsp. *maritima* (syn.: *B. maritima* L.) is widespread and native to Macaronesia, Western and Eastern Europe, the Mediterranean Region, the Middle East and extends to India; mainly in maritime locations along the seashores, but inland populations also occur (Ford-Lloyd & Williams, 1975; Letschert, 1994; Stevenato et al., 2001; Biancardi et al., 2012; Richards et al., 2014; Van Dijk & Hautekèete, 2014). *Beta vulgaris* subsp. *maritima* has the Mediterranean as its centre of diversity and, most likely, centre of domestication (Richards et al., 2014). It is estimated to be the wild progenitor of cultivated beet; it is also considered the most important wild source of genetic diversity useful in improvement of cultivated beet, especially sugar beet (Richards et al., 2014; Stevanato et al., 2001). The native range of the perennial species *B. trigyna* is SE Europe to Iran and Turkmenistan (Ford-Lloyd & Williams, 1975; Kadereit et al., 2006; POWO, 2023).

The most comprehensive taxonomic treatment of the genus *Beta* was published by Iamonico (2019). Molecular phylogenetic studies of the genus were carried out by Shen et al. (1998), Hohmann et al. (2006), and Kadereit et al. (2006). *Beta vulgaris* and *B. vulgaris* subsp. *maritima* are included in the section Beta, and *B. trigyna* is included in the section Corollinae (Tranzschel) Ulbr. (Kadereit et al., 2006; Iamonico, 2019). The first two taxa are diploids with $2n = 18$ chromosomes; but *B. trigyna* is a hexaploid with $2n = 54$ (see e.g., Queirós, 1975; Češchmedjiev, 1976; Pastor et al., 1988; Ball & Akeroyd, 1993; Dempsey et al., 1994; Runemark, 1996, etc.). According to the literature, some *Beta* taxa are problematic and need further revision (Kadereit et al., 2006; Iamonico, 2019).

The palynomorphological characters are often used as additional diagnostic features in the taxonomy (Celenk et al., 2008; Albach et al., 2021; Tsymbalyuk et al., 2021, 2022a, 2022b; El Ghazali, 2022) as well as for spore-pollen analysis in the paleopalynology (Monoszon, 1973; Bezusko et al., 2003, 2023; Tsymbalyuk et al., 2005; Lewandowska et al., 2023). Many authors studied and discussed the pollen morphology of *B. trigyna* or *B. vulgaris* using light, scanning and/or transmission electron microscopy (Tsukada, 1967; Monoszon, 1973; Nowicke, 1975; Skvarla & Nowicke, 1976; Kupriyanova & Alyoshina, 1972; Nowicke & Skvarla, 1979; Tsymbalyuk, 2005, 2008; Tsymbalyuk et al., 2005; Angelini et al. 2014). Despite the relatively numerous publications, the knowledge about the morphology of pollen grains in *B. trigyna* and *B. vulgaris* are fragmentary because the available descriptions usually have only briefly addressed the pollen morphology or researchers have analysed a few selected pollen features.

Palynomorphological investigation of *B. trigyna*, *B. vulgaris* and *B. vulgaris* subsp. *maritima* taxa was carried out using light and scanning electron microscopy in order to provide detailed quantitative and qualitative data on their pollen characteristics to identify similarities and differences between them.

Materials and methods

In total, pollen grains of 10 specimens belonging to *B. trigyna*, *B. vulgaris* and *B. vulgaris* subsp. *maritima* (henceforth *B. maritima*) taxa 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; the herbarium acronym is given according to Thiers (2023 [continuously updated]).

The methods used in the present study have been described in details earlier (Tsymbalyuk et al., 2023a, 2023b). 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 30 properly developed pollen grains from each specimen were measured, and the measurements included the following parameters: pollen diameter, pore diameter, distance between pores, exine thickness. The distance between pore centres and C/D value (C – pollen diameter, D – distance between pore centres) were calculated (McAndrews & Swanson,

1967). The number of pores was calculated by multiplying the number of pores visible on the surface by two and adding the number of pores at the edge of the pollen grain. For all quantitative characters, descriptive statistics was applied and the range (minimum–maximum), arithmetic mean and standard deviation were calculated using Microsoft Excel software. The slides were deposited in the Palynotheca (reference pollen collection) at the National Herbarium of Ukraine (Bezusko & Tsymbalyuk, 2011).

For SEM studies (JEOL JSM-6060LA), dry and acetolysed 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 nanoechini and columellae were taken on 5–8 pollen grains from each specimen from SEM micrographs and made using the program AxioVision Rel.4.8.2. The numbers of nanoechini per unit area (4 μm²) and on pore membranes were determined. Terminology used in descriptions of pollen grains follows mainly the glossaries of Punt et al. (2007) and Halbritter et al. (2018). Abbreviations of taxon author names follow Brummitt & Powell (1992), with additions available from the continuously updated International Plant Names Index (IPNI, 2023) and from POWO (2023).

Cluster analysis was carried out to determine the phenetic similarities among the investigated taxa. Thirteen quantitative characters were examined: pollen and pore diameter, distance between pores and between pore centres, pore number, C/D value, and exine thickness (Table 1); nanoechini: height, width at the base, number/4 μm², number on pore membranes; columellae: height and thickness (Table 2). Cluster analysis was carried out using the unweighted pair group method with arithmetic mean (UPGMA). The Euclidean distance was used as a similarity index in clustering analyses. PAST (PAleontological STatistics) v. 4.08 was used for the analysis (Hammer et al., 2001). The variability of the characters has been examined by Box plots.

Table 1: Pollen morphometric characters (using LM): the values are presented as Mean ± Standard deviation and Range (minimum-maximum) (all measurements given as μm); 1, 2, 3, 4 – specimen number; G – general specimens' measurements; C – pollen diameter, D – distance between pore centres.

Tabela 1: Morfološke značilnosti peloda (z uporabo LM): vrednosti predstavljajo povprečje ± standardna deviacija in rang (minimum-maksimum) (vse meritve so v μm); 1, 2, 3, 4 – številka primerka; G – glavne meritve primerkov; C – premer peloda, D – razdalja med središčem pore.

Taxon	Pollen diameter	Pore diameter	Distance between pores	Distance between pore centres	Pore number	C/D	Exine thickness
Beta trigyna 1	28.46±2.04 25.27–33.25	3.83±0.46 2.66–5.05	3.29±0.54 2.66–4.65	7.13±0.86 5.32–9.04	30.13±2.06 28–35	0.25±0.03 0.19–0.30	2.62±0.09 2.39–2.79
Beta trigyna 2	27.66±2.07 23.94–31.92	3.87±0.52 2.66–5.32	3.48±0.48 2.66–3.99	7.35±0.84 5.32–9.31	28.90±2.19 26–34	0.26±0.02 0.22–0.31	2.57±0.23 2.39–3.32
Beta trigyna 3	26.82±1.09 23.94–29.26	4.94±0.81 3.99–6.65	3.58±0.48 2.66–4.65	8.52±0.94 6.65–9.97	24.93±1.63 22–29	0.31±0.03 0.25–0.38	2.51±0.13 2.26–2.66
***Beta trigyna* G**	**27.64±1.91 23.94–33.25**	**4.21±0.80 2.66–6.65**	**3.45±0.51 2.66–4.65**	**7.67±1.07 5.32–9.97**	**27.98±2.97 22–35**	**0.27±0.04 0.19–0.38**	**2.57±0.17 2.26–3.32**
Beta vulgaris 1	19.28±0.89 17.29–21.28	2.35±0.31 1.99–3.32	2.24±0.24 1.99–2.66	4.60±0.42 3.99–5.71	29.76±1.54 26–32	0.23±0.01 0.20–0.29	2.38±0.16 1.99–2.66
Beta vulgaris 2	22.52±2.05 18.62–26.60	3.09±0.72 1.99–4.65	2.74±0.45 2.39–3.99	5.83±1.08 4.38–8.37	26.13±2.15 23–32	0.25±0.03 0.20–0.33	2.44±0.22 1.99–2.92
Beta vulgaris 3	18.70±0.90 17.29–19.95	2.39±0.23 1.99–2.66	2.42±0.15 2.26–2.66	4.81±0.32 4.25–5.32	27.26±1.48 26–32	0.25±0.01 0.22–0.29	2.44±0.12 2.26–2.66
***Beta vulgaris* G**	**20.17±2.18 17.29–26.60**	**2.61±0.58 1.99–4.65**	**2.47±0.37 1.99–3.99**	**5.08±0.88 3.99–8.37**	**27.72±2.31 23–32**	**0.25±0.02 0.20–0.33**	**2.42±0.17 1.99–2.92**
Beta maritima 1	21.13±1.34 18.62–23.94	2.79±0.40 2.39–3.99	2.76±0.36 2.39–3.99	5.55±0.65 4.78–7.44	27.07±3.25 24–32	0.26±0.03 0.22–0.36	2.34±0.22 1.99–2.66
Beta maritima 2	19.99±0.93 18.62–22.61	2.50±0.13 2.39–2.66	2.45±0.23 1.99–2.79	4.96±0.31 4.38–5.45	31.76±2.29 28–36	0.24±0.01 0.22–0.28	2.28±0.18 1.99–2.66
Beta maritima 3	18.66±1.00 17.29–19.95	2.35±0.29 1.59–2.66	2.39±0.16 1.99–2.66	4.74±0.39 3.59–5.32	28.26±2.06 25–32	0.25±0.01 0.20–0.28	1.70±0.21 1.33–1.99
Beta maritima 4	20.33±1.45 18.62–23.94	2.61±0.35 1.99–3.32	2.37±0.20 1.99–2.66	4.99±0.41 4.12–5.71	33.85±2.69 29–39	0.24±0.02 0.19–0.28	2.23±0.18 1.99–2.66
***Beta maritima* G**	**20.00±1.49 17.29–23.94**	**2.56±0.34 1.59–3.99**	**2.49±0.29 1.99–3.99**	**5.05±0.54 3.59–7.44**	**30.23±3.73 24–39**	**0.25±0.02 0.19–0.36**	**2.13±0.33 1.33–2.66**

Table 2: Pollen morphometric characters (using SEM): the values are presented as Mean ± Standard deviation and Range (all measurements given as µm); 1, 2, 3, 4 – specimen number; G – general specimens' measurements.
Tabela 2: Morfološke značilnosti peloda (z uporabo SEM): vrednosti predstavljajo povprečje ± standardna deviacija in rang (minimum-maksimum) (vse meritve so v µm); 1, 2, 3, 4 – številka primerka; G – glavne meritve primerkov.

Taxon	Nanoechini (SEM)				Columellae (SEM)	
	Height	Width at the base	Number/4 µm²	Number on pore membranes	Height	Thickness
Beta trigyna 1	0.14±0.04	0.23±0.03	9.27±1.21	16.61±2.92	0.62±0.06	0.30±0.03
	0.08–0.22	0.18–0.30	7–11	13–22	0.53–0.73	0.23–0.36
Beta trigyna 2	0.12±0.04	0.21±0.03	7.94±1.60	17.41±2.67	0.66±0.04	0.31±0.03
	0.06–0.22	0.16–0.28	6–12	14–22	0.58–0.74	0.25–0.36
Beta trigyna 3	0.13±0.03	0.23±0.03	8.66±1.94	20.12±3.62	0.75±0.09	0.31±0.06
	0.07–0.20	0.18–0.30	6–12	15–27	0.57–0.88	0.22–0.43
***Beta trigyna* G**	**0.13±0.04**	**0.22±0.03**	**8.48±1.69**	**17.91±3.34**	**0.71±0.10**	**0.31±0.05**
	0.06–0.22	**0.16–0.30**	**6–12**	**13–27**	**0.53–0.88**	**0.22–0.43**
Beta vulgaris 1	0.09±0.01	0.15±0.02	14.12±1.36	9.12±1.26	0.54±0.06	0.19±0.02
	0.07–0.12	0.13–0.21	12–16	8–12	0.45–0.63	0.16–0.23
Beta vulgaris 2	0.10±0.02	0.17±0.02	11.04±1.60	13.82±2.60	0.52±0.04	0.20±0.01
	0.06–0.14	0.13–0.21	9–15	8–17	0.45–0.61	0.18–0.23
Beta vulgaris 3	0.10±0.02	0.16±0.02	13.18±1.69	11.17±1.61	0.55±0.05	0.19±0.01
	0.07–0.13	0.13–0.21	10–16	9–15	0.45–0.63	0.17–0.22
***Beta vulgaris* G**	**0.09±0.02**	**0.16±0.02**	**12.21±2.05**	**11.87±2.88**	**0.54±0.05**	**0.19±0.01**
	0.06–0.14	**0.13–0.21**	**9–16**	**8–17**	**0.45–0.63**	**0.16–0.23**
*Beta maritima*1	0.09±0.02	0.18±0.03	12.07±1.57	13.00±2.33	0.47±0.05	0.17±0.01
	0.05–0.14	0.12–0.24	9–15	10–17	0.41–0.58	0.15–0.21
Beta maritima 2	0.09±0.02	0.17±0.03	12.39±1.58	11.40±2.48	0.42±0.04	0.20±0.02
	0.05–0.15	0.11–0.24	10–15	7–16	0.35–0.53	0.16–0.25
Beta maritima 3	0.09±0.02	0.17±0.03	14.11±1.60	10.95±2.69	0.48±0.08	0.21±0.02
	0.05–0.14	0.12–0.24	12–17	6–15	0.35–0.59	0.18–0.26
Beta maritima 4	0.10±0.03	0.18±0.02	12.36±1.49	9.18±1.78	0.45±0.04	0.18±0.01
	0.05–0.15	0.12–0.23	9–15	6–12	0.38–0.55	0.17–0.21
***Beta maritima* G**	**0.09±0.02**	**0.18±0.03**	**12.67±1.71**	**10.92±2.69**	**0.46±0.06**	**0.20±0.02**
	0.05–0.15	**0.11–0.24**	**9–17**	**6–17**	**0.35–0.59**	**0.15–0.26**

Results

The original data on quantitative pollen characters used in this study are summarised in Tables 1, 2. LM and SEM photomicrographs of pollen grains are shown in Figures 1–4. UPGMA dendrograms showing the relationships of pollen grains of studied taxa are presented in Figure 5. Box plots illustrating the variation in pollen diameter, pore diameter, distance between pores and pore centres, pore number, and exine thickness of *B. trigyna*, *B. vulgaris* and *B. maritima* pollen grains are shown in Figure 6.

Description of pollen grains

Beta trigyna (Figures 1a–h; 2a, b; 3a, b; 4a–c)

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, slightly undulated or undulated on the edge; medium-sized: P (Polar axis) = E (Equatorial diameter) = 23.94–33.25 µm; pantoporate, with 22–35 pores evenly distributed on the surface. Pores circular, 2.66–6.65 µm in diameter, with distinct or indistinct margins. Distance between pores 2.66–4.65 µm, between pore centres – 5.32–9.97 µm. C/D = 0.190–0.388. Exine 2.26–3.32 µm thick (Table 1). Sexine thicker than nexine. Columellae distinct or indistinct. LO-analysis: columellae distinct, circular, densely distributed, nanoechini indistinct or invisible.

Figure 1: Pollen grains of *Beta* (LM): a–h – *B. trigyna* (a–d – specimen 2, Ukraine, e–h – specimen 3, Turkey), i–p – *B. vulgaris* (i, j – specimen 1, Ukraine, k, l – specimen 2, Ukraine, m–p – specimen 3, India), q–x – *B. vulgaris* subsp. *maritima* (q–t – specimen 1, France, u – specimen 4, Egypt, v – specimen 3, France, w, x – specimen 2, India). Scale bars = 10 µm. →

Slika 1: Pelodna zrna vrst rodu *Beta* (LM): a–h – *B. trigyna* (a–d – primerek 2, Ukrajina, e–h – primerek 3, Turčija), i–p – *B. vulgaris* (i, j – primerek 1, Ukrajina, k, l – primerek 2, Ukrajina, m–p – primerek 3, Indija), q–x – *B. vulgaris* subsp. *maritima* (q–t – primerek 1, Francija, u – primerek 4, Egipt, v – primerek 3, Francija, w, x – primerek 2, Indija). Merilo = 10 µm. →

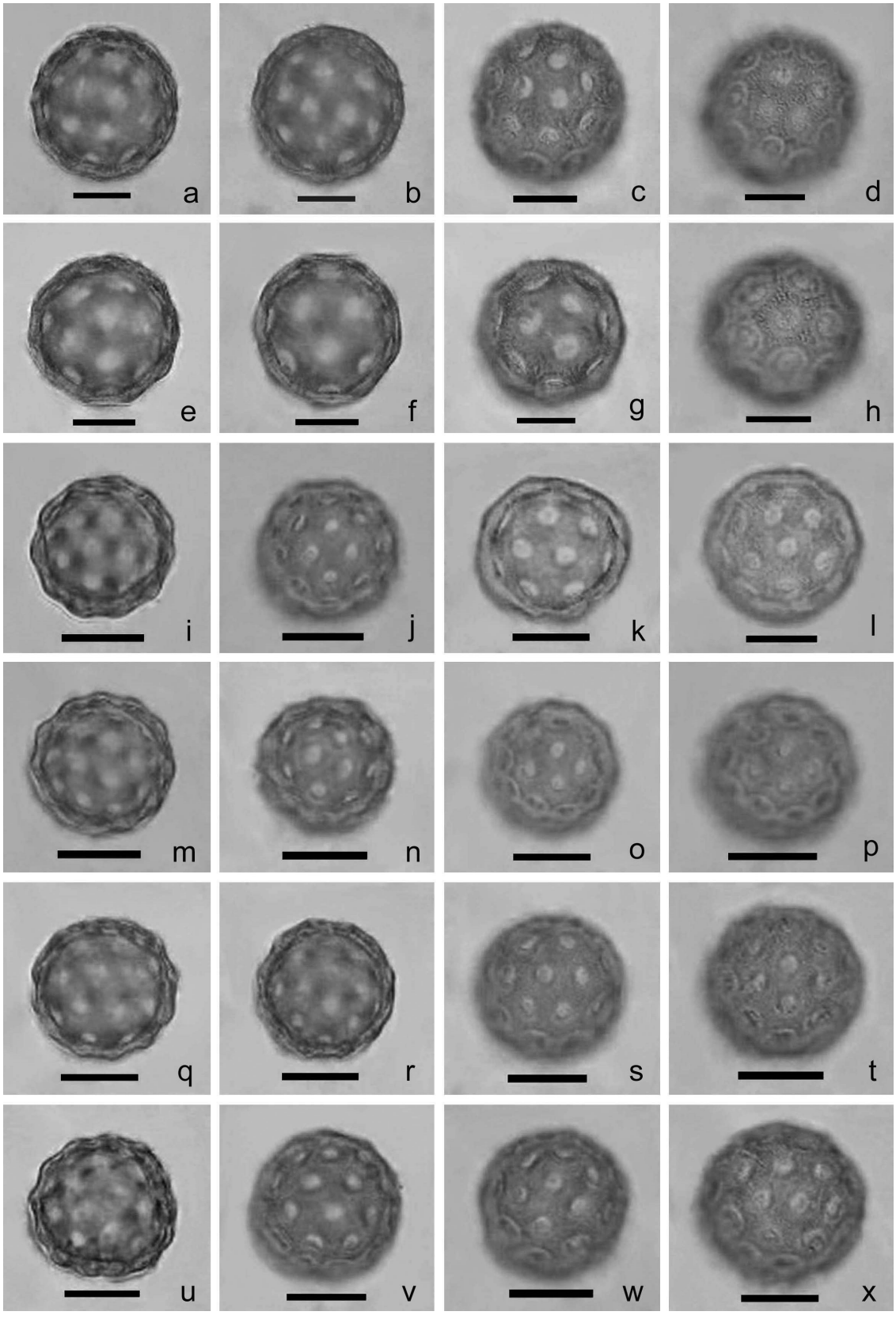

Figure 1

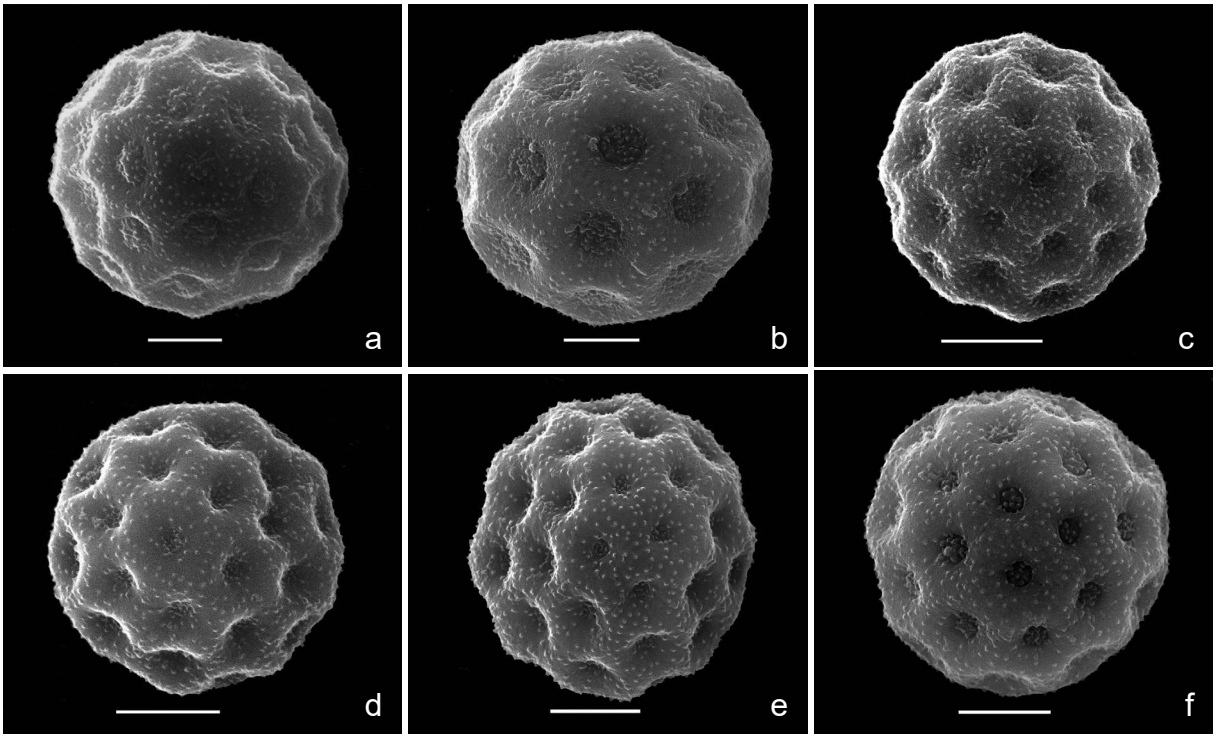

Figure 2: Pollen grains of *Beta* (SEM): a, b – *B. trigyna* (a – specimen 1, Ukraine, dry pollen, b – specimen 3, Turkey, acetolysed pollen), c, d – *B. vulgaris* (c – specimen 1, Ukraine, dry pollen, d – specimen 3, India, dry pollen), e, f – *B. vulgaris* subsp. *maritima* (e – specimen 4, Egypt, dry pollen, f – specimen 4, Egypt, acetolysed pollen). Scale bars = 5 μm.

Slika 2: Pelodna zrna vrst rodu *Beta* (SEM): a, b – *B. trigyna* (a – primerek 1, Ukrajina, suh pelod, b – primerek 3, Turčija, acetoliziran pelod), c, d – *B. vulgaris* (c – primerek 1, Ukrajina, suh pelod, d – primerek 3, Indija, suh pelod), e, f – *B. vulgaris* subsp. *maritima* (e – primerek 4, Egipt, suh pelod, f – primerek 4, Egipt, acetoliziran pelod). Merilo = 5 μm.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.06–0.22 μm high, 0.16–0.30 μm wide at base, sparsely or more densely distributed (6–12/4 μm²); tectum psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 13–27), pores' margin raised or sunken; mesoporia mainly flattened or rarely convex. Columellae medium-length or long, 0.57–0.88 μm long, thick, 0.22–0.43 μm wide, densely or sparsely arranged (Table 2).

Specimens investigated: 1. Crimea, Yayla, Ai-Petri. Rocky slope, in a funnel. 25 July 1974. *O. Dubovik* (KW). 2. Crimea, Belogorsk District, Belaya Skala village, along the Biyuk-Karasu River. 8 June 1978. *O. Dubovik* (KW). 3. Turkey. Ex Herb. Hort. Bot. Reg. Kew. Prov. Erzurum: Kop Dag Pass: weed; alt. 9000 ft. 9 August 1962. Coll. *P. Furse* 3484 (KW).

Beta vulgaris (Figures 1i–p; 2c, d; 3c, d; 4d–f)

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, slightly undulated or undulated on the edge; small and medium-sized: P = E = 17.29–26.60 μm; pantoporate, with 23–32 pores evenly distributed on the surface. Pores circular, 1.99–4.65 μm in diameter, with indistinct or distinct margins. Distance between pores 1.99–3.99 μm, between pore centres – 3.99–8.37 μm. C/D = 0.200–0.331. Exine 1.99–2.92 μm thick (Table 1). Sexine thicker than nexine. Columellae indistinct or invisible. LO-analysis: columellae indistinct or rarely distinct, circular, densely distributed, nanoechini invisible.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.06–0.14 μm high, 0.13–0.21 μm wide at base, sparsely or more densely distributed (9–16/4 μm²); tectum psilate or psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 8–17), pores' margin sunken or raised; mesoporia mainly convex or rarely flattened. Columellae medium-length, 0.45–0.63 μm long, thin, 0.16–0.23 μm wide, densely arranged (Table 2).

Specimens investigated: 1. [Ukraine] Donetsk Region, Makiivka, Novo-Kalynove village, gardens along the road to the mine. 30 June 1982. *R.I. Burda, A.E. Kuskov* (KW). 2. [Ukraine] Kozatske village in the Shevchenkiv region. Cultivated. July 1920. *M. Pidoplichko* (KW). 3. [India] Delhi University Campus. 15 February 1957. *Manahar Lal* (KW).

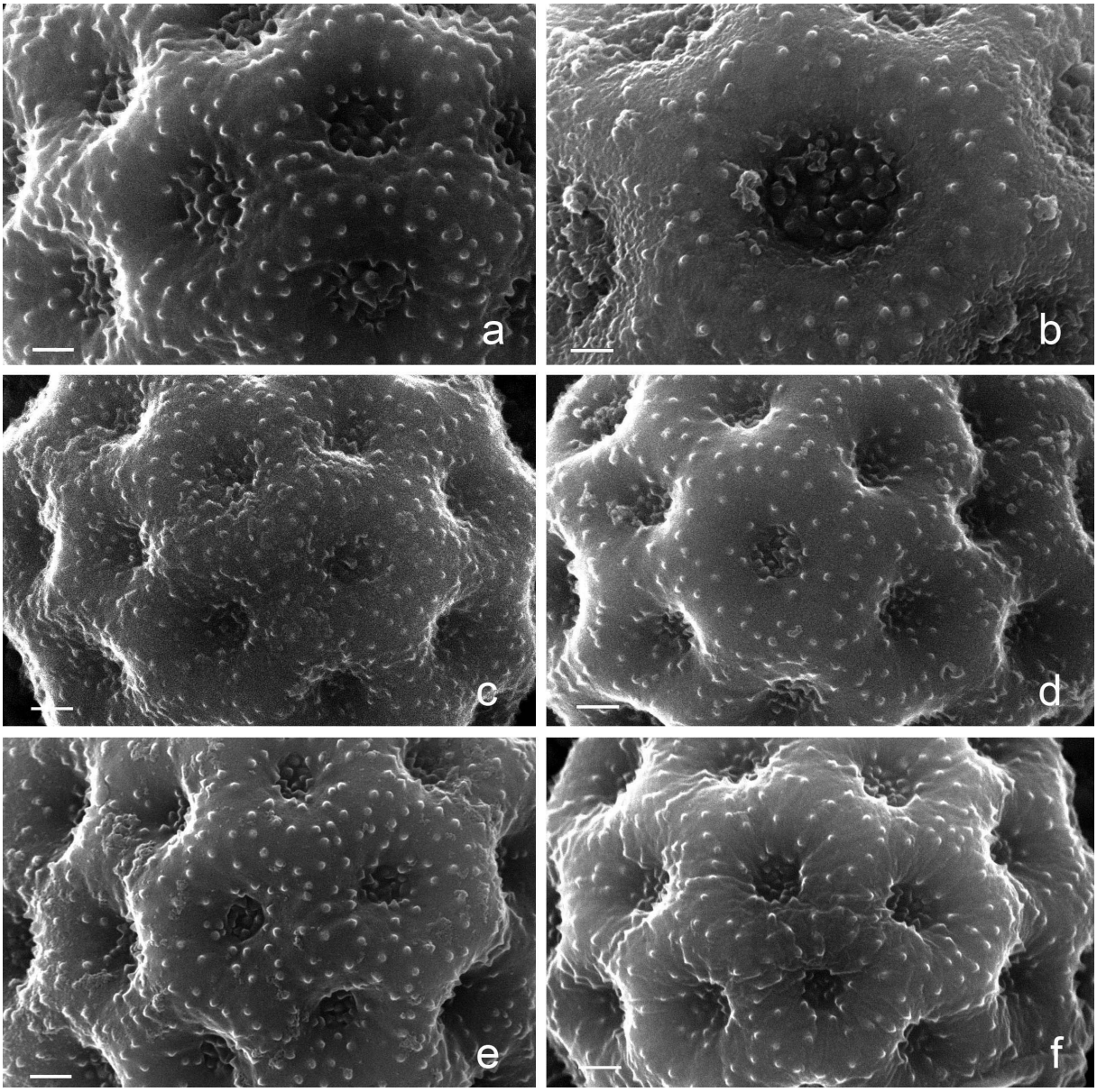

Figure 3: Exine sculpture of pollen grains of *Beta* (SEM): a, b – *B. trigyna* (a – specimen 1, Ukraine, dry pollen, b – specimen 3, Turkey, acetolysed pollen), c, d – *B. vulgaris* (c – specimen 1, Ukraine, dry pollen, d – specimen 3, India, dry pollen), e, f – *B. vulgaris* subsp. *maritima* (e – specimen 4, Egypt, dry pollen, f – specimen 2, India, dry pollen). Scale bars = 1 μm.

Slika 3: Eksina pelodnih zrn vrst rodu *Beta* (SEM): a, b – *B. trigyna* (a – primerek 1, Ukrajina, suh pelod, b – primerek 3, Turčija, acetoliziran pelod), c, d – *B. vulgaris* (c – primerek 1, Ukrajina, suh pelod, d – primerek 3, Indija, suh pelod), e, f – *B. vulgaris* subsp. *maritima* (e – primerek 4, Egipt, suh pelod, f – primerek 2, Indija, suh pelod). Merilo = 1 μm.

***Beta maritima* (= *B. vulgaris* subsp. *maritima*)** (Figures 1q–x; 2e, f; 3e, f; 4g–i)

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, slightly undulated or undulated on the edge; small and medium-sized: P = E = 17.29–23.94 μm; pantoporate, with 24–39 pores evenly distributed on the surface. Pores circular, 1.59–3.99 μm in diameter, with indistinct or distinct margins. Distance between pores 1.99–3.99 μm, between pore centres – 3.59–7.44 μm. C/D = 0.193–0.366. Exine 1.33–2.66 μm thick (Table 1). Sexine thicker than nexine. Columellae indistinct or invisible. LO-analysis: columellae indistinct or rarely distinct, circular, densely distributed, nanoechini invisible.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.05–0.15 μm

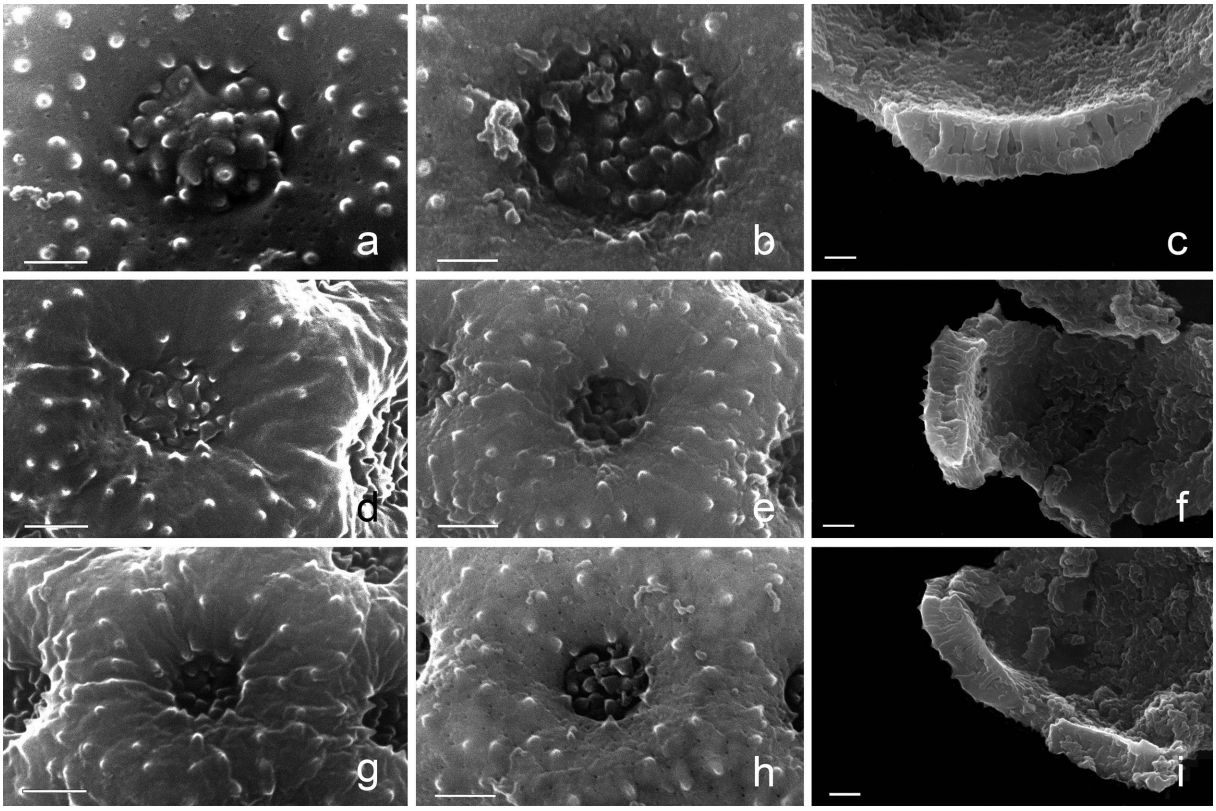

Figure 4: Pores and exine structure of pollen grains of *Beta* (SEM): a–c – *B. trigyna* (a – specimen 1, Ukraine, dry pollen, b, c – specimen 3, Turkey, acetolysed pollen), d–f – *B. vulgaris* (d – specimen 1, Ukraine, dry pollen, e, f – specimen 3, India, acetolysed pollen), g–i – *B. vulgaris* subsp. *maritima* (g – specimen 2, India, dry pollen, h – specimen 2, India, acetolysed pollen, i – specimen 1, France, acetolysed pollen); a, b, d, e, g, h – pores, c, f, i – columellae. Scale bars = 1 µm.

Slika 4: Pore in struktura eksine pelodnih zrn vrst rodu *Beta* (SEM): a–c – *B. trigyna* (a – primerek 1, Ukrajina, suh pelod, b, c – primerek 3, Turčija, pelod v acetonu), d–f – *B. vulgaris* (d – primerek 1, Ukrajina, suh pelod, e, f – primerek 3, Indija, pelod v acetonu), g–i – *B. vulgaris* subsp. *maritima* (g – primerek 2, India, suh pelod, h – primerek 2, Indija, pelod v acetonu, i – primerek 1, Francija, pelod v acetonu); a, b, d, e, g, h – pore, c, f, i – kolumele. Merilo = 1 µm.

high, 0.11–0.24 µm wide at base, sparsely or more densely distributed (9–17/4µm²); tectum psilate or psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 6–17), pores' margin sunken or raised; mesoporia mainly convex or rarely flattened. Columellae short and medium-length, 0.35–0.59 µm long, thin, 0.15–0.26 µm wide, densely arranged (Table 2).

Specimens investigated: 1. France, Charente-Inférieure [nowadays Charente-Maritime]. Pointe d'Yves, rocailles. 4 Juin 1929. Herbier *J. Charrier* (KW). 2. [India] Herb. Ind. Or. Hook. fil. F. Thomson. Hab. Punjab. Cult. Regio. hop. Coll. *I.I.* (KW-TURCZ: Turczaninow historical herbarium in Kyiv). 3. [France] Ajaccio – Corsica (KW-TURCZ). 4. [Egypt] prope Cahiram in pratis. Unio itiner. leg. Januario 1833. Dr. *A. Wiest* 77 (KW-TURCZ).

Numerical analysis of the palynomorphological characters

Cluster analysis of all 10 studied specimens clearly distinguished the three specimens of *B. trigyna* (Table 1; Figure 5a). The specimens with similar larger pollen diameter, pore diameter, distance between pores and pore centres, number of pores, C/D value and exine thickness belonging to *B. trigyna* are placed into a separate branch. On the other hand, *B. vulgaris* and *B. maritima* specimens with the smallest measurements of pollen grain features are placed in another branch (Figure 5a). In general, the variation range in the characteristics of pollen grains between the different specimens of *B. trigyna* is small (see Figure 6); no significant discontinuity within species was observed. The samples of *B. trigyna* from Ukraine had most similar characters. However, an exception is the *B. trigyna* specimen collected in Turkey, which had larger

mean pore diameter, pore centre distance, C/D value, and pore number, which is also confirmed by the dendrogram (Figure 5a). Specimens with comparable average measurements of pollen grain features, belonging to *B. vulgaris* and *B. maritima*, are grouped together and placed in a separate branch (Figure 5a).

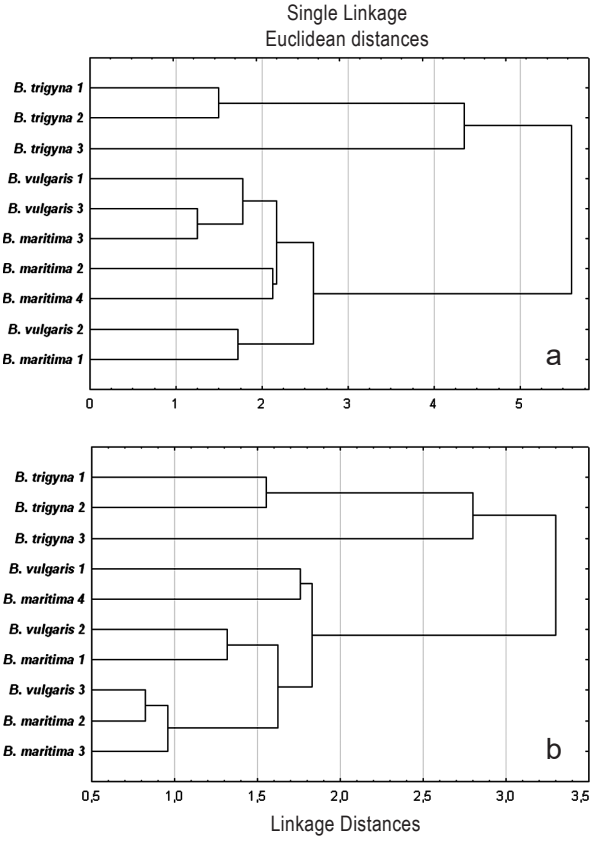

Figure 5: UPGMA dendrograms showing the relationships of pollen grains of *B. trigyna*, *B vulgaris* and *B. vulgaris* subsp. *maritima* taxa: a – quantitative characters (see Table 1), b – quantitative characters (see Table 2).

Slika 5: UPGMA dendrogrami, ki prikazujejo podobnosti peloda med vrstami *B. trigyna*, *B vulgaris* in *B. vulgaris* subsp. *maritima*: a – kvantitativni znaki (glej Tabelo 1), b – kvantitativni znaki (glej Tabelo 2).

Pollen samples from Ukrainian *B. trigyna* had the most similar nanoechini and columellae measurements and are clustered into one branch (Table 2; Figure 5b). However, pollen grains of the Turkish *B. trigyna* specimen had bigger nanoechini number on the pore membrane. But in general, as seen in the UPGMA dendrogram, *B. trigyna* has distinctive pollen morphometric features (larger nanoechini, more nanoechini on the pore membrane, sparse distribution of nanoechini on the surface, longer and thicker columellae) and is placed in a separate cluster (Figure 5b). Specimens with a similar number of nanoechini per unit area, number of nanoechini distributed on pore membrane, and comparative size of the columellae, belonging to *B. vulgaris* and *B. maritima*, are grouped together and form a separate branch (Figure 5b).

Discussion

In general, our data are in agreement with the results of previous LM studies (Tsukada, 1967; Kupriyanova & Alyoshina, 1972; Monoszon, 1973; Angelini et al., 2014).

Pollen diameter – The pollen size range for *B. trigyna* was given by Kupriyanova & Alyoshina (1972) as 25.2–27.6 µm, and by Monoszon (1973) as 25.0–30.3 µm. Their data are close to our pollen diameter measurements, although the range in our study is slightly larger. The pollen sizes for *B. vulgaris* were given by Monoszon (1973) as 16.0–18.3 µm. Tsukada (1967) presented only the mean pollen diameter of *B. vulgaris* as 19.5 µm. Angelini et al. (2014) reported pollen grain diameters for *B. vulgaris* ssp. *cicla* (L.) Schübl. & G.Martens (= *B. vulgaris* var. *cicla* L.) [19.71 (18.48–20.02) µm], *B. vulgaris* var. *rubra* L. [20.08 (18.48–21.56) µm], and *B. vulgaris* var. *altissima* Döll (= *B. vulgaris* subsp. *vulgaris*) [20.08 (18.48–21.56) µm]. These reports are similar to those for *B. vulgaris* and *B. maritima* found in the current study (Table 1).

Pore diameter – Kupriyanova & Alyoshina (1972) reported *B. trigyna* pore diameter of 2.4–3.6 µm. Monoszon (1973) reported *B. trigyna* pollen grains that had diameter of pores of 3.5–4.0 µm, and those of *B. vulgaris* – 2.8–3.8 µm, which falls in the range of our data. Angelini et al. (2014) reported pollen grains of *B. vulgaris* ssp. *cicla* (2.31–3.08 µm), *B. vulgaris* var. *rubra* (2.31–3.39 µm), and *B. vulgaris* var. *altissima* (2.31–3.08 µm), in which the diameter of pores is comparable to those of *B. vulgaris* and *B. maritima* reported in the current study (Table 1).

Distance between pores – Kupriyanova & Alyoshina (1972) reported *B. trigyna* pollen grains that had distances between pores of 3.6–4.2 µm, which is in line with the values obtained in this study. Angelini et al. (2014) reported pollen grains of *B. vulgaris* ssp. *cicla* [2.52 (2.00–3.08) µm], *B. vulgaris* var. *rubra* [2.78 (2.31–3.08) µm], and *B. vulgaris* var. *altissima* [3.08 (2.77–3.85) µm], in which the distances between pores are comparable to those of *B. vulgaris* and *B. maritima* in the present study (Table 1).

Distance between pore centres – Monoszon (1973) reported pollen grains with 7.6–9.0 µm distances between centres of pores in *B. trigyna*, and 4.0–5.1 µm in *B. vulgaris* which is consistent with our data (Table 1).

Pore number – Kupriyanova & Alyoshina (1972) reported a greater number of pores on pollen of *B. trigyna* (30–40) than the values found in our study. Monoszon (1973) reported pollen grains of *B. trigyna* with 23–29

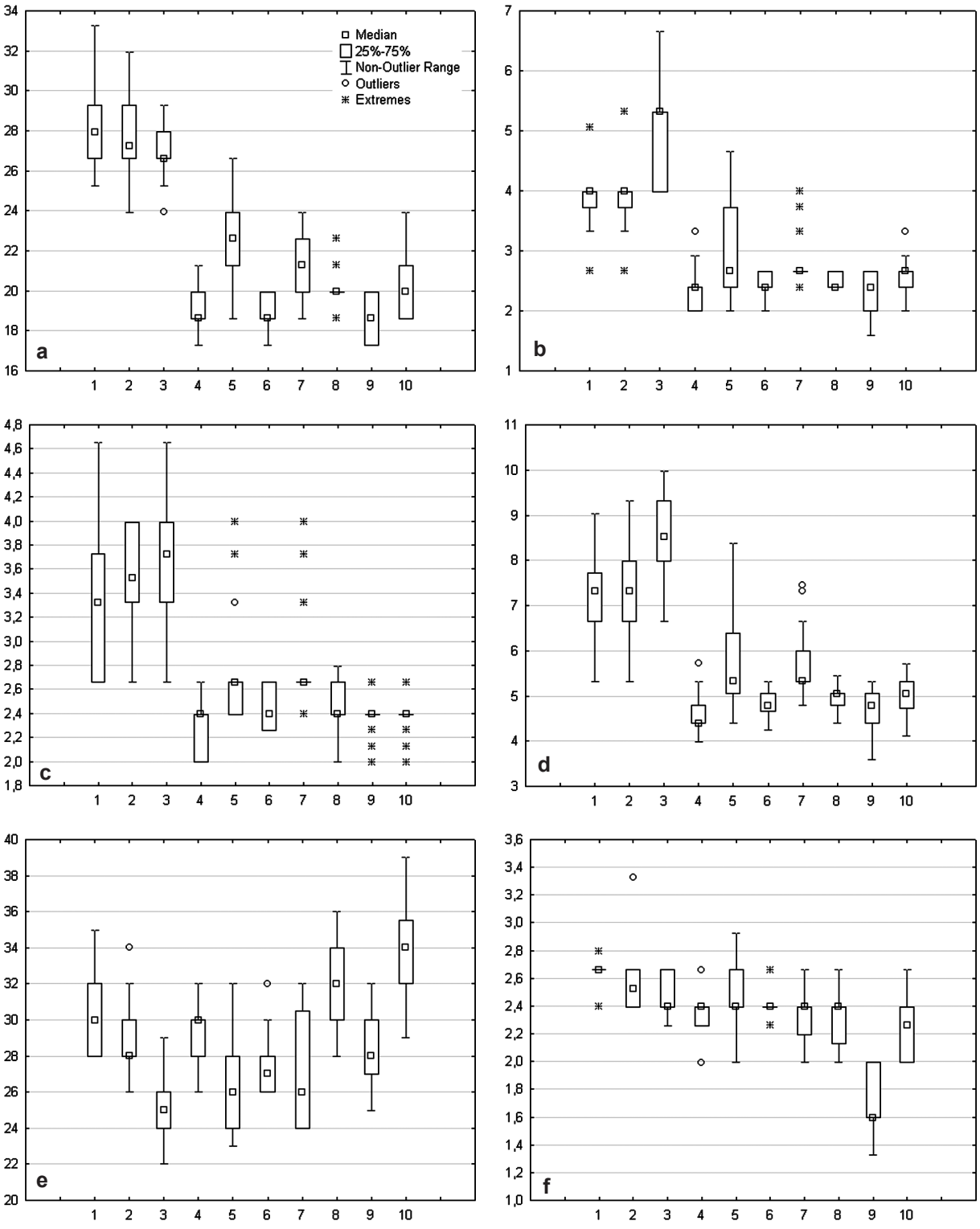

Figure 6: Box plots of *Beta* pollen grains: a – pollen diameter, b – pore diameter, c – distance between pore, d – distance between pore centres, e – pore number, f – exine thickness; 1–3 – *B. trigyna*, 4–6 – *B. vulgaris*, 7–10 – *B. vulgaris* subsp. *maritima.*

Slika 6: Škatle z brki pelodnih zrn vrst rodu *Beta*: a – premer peloda, b – premer pore, c – razdalja med porami, d – razdalja med središči por, e – število por, f – debelina eksine; 1–3 – *B. trigyna*, 4–6 – *B. vulgaris*, 7–10 – *B. vulgaris* subsp. *maritima.*

pores and of *B. vulgaris* with up to 30 pores. Tsukada (1967) reported a total number of 32–40 pores per grain for *B. vulgaris*. Possibly, the observed variation is due to differences in pore counting approaches. Angelini et al. (2014) reported pollen grains of *B. vulgaris* ssp. *cicla* (44–67), *B. vulgaris* var. *rubra* (40–58), and *B. vulgaris* var. *altissima* (35–49), which had more pores than *B. vulgaris* and *B. maritima* counted in the current investigation. Our data showed that the C/D values are very similar in all taxa investigated, since the pollen grains have a similar or at least comparable number of pores (Table 1).

Exine – Kupriyanova & Alyoshina (1972) reported pollen grains of *B. trigyna* that had thinner exine (1.8–2.4 µm) than the values recorded in this study. The exine of the pollen grains of *B. vulgaris* ssp. *cicla* [1.77 (1.54–2.31) µm], *B. vulgaris* var. *rubra* [2.02 (1.54–2.77) µm], and *B. vulgaris* var. *altissima* [1.86 (1.54–2.31) µm], reported by Angelini et al. (2014), is generally thinner than the exine of *B. vulgaris* and *B. maritima* measured in our study (Table 1).

Exine sculpture – Tsukada (1967) presented the mean nanoechini number per unit area in *B. vulgaris* (12.8/4 µm²), which is consistent with our data (Table 2).

The data obtained in the present study show that *B. trigyna* had larger pollen grains than the other two taxa. *Beta vulgaris* and *B. maritima* had overlapping size ranges. This is also supported by the cluster analysis and box plots (Figures 5a, 6a). *Beta trigyna* had fewer pores, while *B. vulgaris* and *B. maritima* had bigger pore numbers (Figure 6e). The largest diameter of pores was observed in *B. trigyna*, while pores with a smaller diameter were found in *B. vulgaris* and *B. maritima* (Figure 6b). Larger distances between pores and between centres of pores were characteristic for *B. trigyna*, while shorter ones were observed in *B. vulgaris* and *B. maritima* (Figure 6c, d). *Beta trigyna* had a thicker exine, while *B. vulgaris* and *B. maritima* had a thinner exine (Figure 6f).

Our data demonstrate the relationship between the pore size and the number of nanoechini on the pore membrane (Tables 1, 2). The pollen grains of *B. trigyna* had a larger pore diameter and a greater number of nanoechini on the pore membrane (Figure 4a, b). Respectively, the pollen grains of *B. vulgaris* and *B. maritima* had a smaller pore diameter and fewer nanoechini on the membrane of pores (Figure 4d, e, g, h).

There are several palynomorphological characters that overlap. For example, pollen grains in all taxa were slightly undulated or undulated on the edge, which also agrees with the data of Kupriyanova & Alyoshina (1972) and Monoszon (1973). According to the mesoporial exine level, pores in *B. trigyna*, *B. vulgaris* and *B. maritima* were sunken or raised. Pollen grains of all taxa had convex or slightly flattened mesoporia and psilate-perforate tectum (Figures 3, 4). Since these characters are similar in all taxa, their usefulness for distinguishing of the taxa is limited.

Some authors have observed a correlation between the ploidy level and the pollen size in members of Chenopodiaceae family: polyploidy may result in larger pollen (e.g., Bassett et al., 1983; Olvera et al., 2006). The latter authors noted also that the number of pores is another pollen character to compare with the chromosome counts in Chenopodiaceae (Olvera et al., 2006). In our study, smaller pollen grains were found in *B. vulgaris* and *B. maritima* which are diploids and possess chromosome numbers of $2n = 18$. The largest pollen grains were found in the hexaploid *B. trigyna* with a chromosome number of $2n = 54$. The data obtained corroborate the relationship between the number of chromosomes and the pollen size. A greater number of chromosomes clearly correspond to an increase in the size of pollen grains. Our studies showed that *B. trigyna* pollen had a larger diameter but fewer pores, whereas *B. vulgaris* and *B. maritima* had a smaller diameter but more numerous pores.

Bezusko et al. (2023) analysed the species composition of the palynofloras of Late Holocene sediments of eight sections located on the territory of the Left Bank of the modern Forest-Steppe zone of Ukraine. The obtained data showed that the composition of palynofloras of Subatlantic–3 Holocene sediments of two sections (Loshchyna and Lopanske) included pollen grains of *B. vulgaris*. The radiocarbon date 550±40 BP records the appearance of pollen grains of *B. vulgaris* in the palynoflora of the investigated deposits of the Lopanske section.

The results of the analysis of paleofloristic materials indicate the cultivation of *B. vulgaris* in the Kharkiv region (Bohodukhivskyi and Dergachivskyi Districts), starting from the second half of the Subatlantic–3 Holocene time. Thus, *B. vulgaris* had its own history of cultivation in the studied area.

Conclusions

The description of the pollen grains of *B. maritima* is provided for the first time in this study. Also, for the first time, a description and comparison of the exine structure using SEM of *B. trigyna*, *B. vulgaris* and *B. maritima* is provided. The most significant characters for the diagnosis of these taxa are: pollen and pore sizes, distance between pores and between pore centres, structure of columellae, nanoechini size and density, number of nanoechini on pore membranes, and exine thickness. The taxa *B. vulgaris* and *B. maritima* are quite similar in pollen grain characters. Pollen grains of *B. trigyna* (section Corollinae) differ in these characters from those of *B. vulgaris* and

B. maritima (section Beta). The presented quantitative and qualitative characteristics of pollen grains and their photomicrographs can be used for pollen identification in paleopalynology for spore-pollen analysis, especially for identifying the impact of human economic activity in the past. When identifying pollen grains, it is possible to use a complex of features of *B. vulgaris* since *B. maritima* grows mainly on sea coasts. The pollen characteristics described here may also be used in future studies aiming at completing the knowledge on Beteae species and Chenopodiaceae/Amaranthaceae in general.

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