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Pollen morphology of *Scabiosa* L. and *Lomelosia* Raf. (Caprifoliaceae) taxa in Türkiye

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Abstract: Pollen morphology of 34 taxa belonging to genera *Scabiosa* and *Lomelosia* were investigated using a light microscope (LM) and scanning electron microscopy (SEM). Pollen grains of *Scabiosa* and *Lomelosia* taxa are tricolpate and triporate, respectively. Pollen shapes vary from oblate to prolate. The exine surface ornamentation can be divided into five types, namely echinate, echinate-microechinate, echinate-gemmate, echinate-microechinate/gemmate and microechinate-gemmate. Pollen grain sizes were classified as very large in three species of *Lomelosia* and large in the rest. Statistical analyses revealed some quantitative morphological features, such as equatorial axes, L (polar view amb), and t (apocolpium) as the primary characters for separating the examined taxa. The taxa were separated from each other by clustering analysis of selected pollen characters, and the investigated species were placed within two clusters. Present findings revealed that some *Scabiosa* species should be transferred to *Lomelosia* depending on palynological characters.

Key words: *Scabiosa*, *Lomelosia*, Pollen characters, PCA, systematic, Türkiye

1. Introduction

Scabiosa L. (Caprifoliaceae) is a genus that contains annual, biennial, perennial herbaceous or shrub-form plants with about 80 species, found mostly in the Mediterranean basin, Asia, Europe, and South Africa (Reveal and Chase, 2011). *Lomelosia* Raf. (Caprifoliaceae) includes about 63 annual and perennial species, scattered across the Mediterranean region. The greatest diversity is concentrated in the eastern Mediterranean and the Middle East, with outliers extending to China and Japan.[1]

Scabiosa was first described by Linnaeus together with the genera *Dipsacus* L. and *Knautia* (Linnaeus, 1753). Later, it was divided into different genera such as *Cephalaria* Schrad. *ex* Roem & Schult., *Pterocephalus* Adans, *Succisa* Haller and *Callistemma* (Adanson, 1763; Haller, 1768). *Scabiosa* species were later introduced into new genera such as *Lomelosia* Raf, *Pseudoscabiosa* Devesa, *Sixalis* Raf, and *Pterocephalidium* G. Lopez. (Devesa, 1984; Lopez-Gonzales, 1986). Greuter and Raus (1985) suggested that this genus be divided into *Scabiosa*, *Lomelosia*, and *Sixalis* genera. In a study conducted by Greuter and Raus (1985), the synonym names of all taxa were determined by considering the genera and taxa that had been separated from *Scabiosa* up to that time.

The *Scabiosa* is a taxonomically complex genus (Christopoulou et al., 2008) that was previously included in the Dipsacaceae family. It was later added to the Caprifoliaceae family as a result of morphological studies and molecular phylogenetic analyses (APG IV, 2016). Due to widespread hybridization, the number of species (and subspecies) reported within the genus is unclear (Bobrov, 1957; Grossman, 1975; Jasiewicz, 1976).

The taxa of the genus *Scabiosa* L. in Türkiye are represented by 3 sections as *Sclerostemma*, *Cyrtostemma*, and *Trochocephalus* and 35 taxa (excluding East Aegean Islands and incompletely known) in the flora of Türkiye and the East Aegean Islands (Matthews, 1972; Duman, 2000; Aksoy et al., 2020). According to the List of Plants of Türkiye, the genus *Scabiosa* is represented by 36 taxa (Göktürk, 2012). In present literature, these sections are evaluated under the genera *Scabiosa* L., *Sixalix* Rafinesque, and *Lomelosia* Rafinesque, due to the differences in their involucel structures (Greuter and Raus, 1985; De Castro and Caputo, 1999; Mayer and Ehrendorfer, 1999). Recent findings show that only 11 of 35 taxa found naturally in Türkiye belong to the genus *Scabiosa*, and the remaining 24 have been evaluated within the genus *Lomelosia* (Greuter and Raus, 1985; Aksoy et al., 2020; IPNI, 2022).

1 POWO (2023). "Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/ [Accessed 14 July 2023].

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The pollen morphology of this family has been investigated by various authors (Ting, 1949; Nowicke and Skvarla, 1979; Feng et al., 2000; Khalik, 2010; Mostafa and Sedigheh, 2016; Mostafa et al., 2017; Tsymbalyuk et al., 2021). Many researchers in plant systematic studies have emphasized the importance of pollen morphology. Stuessy (2009) states that palynological data were useful at all stages of the taxonomic hierarchy. Some studies have proven that pollen morphology played an important role in solving taxonomic uncertainty (Feng et al., 2000; Khalik, 2010; Ozbek et al., 2022). Palynological characteristics may reintroduce several controversial genera and solve problems related to the origin and evolution of numerous taxa (Nair, 1980; Mete et al., 2021).

No studies have been reported on pollen morphology of *Scabiosa* and *Lomelosia* taxa in Türkiye, so the aims of this study are to investigate the pollen morphology of the *Scabiosa* and *Lomelosia* taxa of Türkiye and to evaluate the importance of these characters in the taxonomy of these genera.

2. Materials and methods

Plant specimens were collected from the natural distribution areas of the species during the flowering period (Table 1). Pollen preparations were made from mature pollen grains of the species in accordance with Wodehouse (1935). About 30 pollen grains were used in each preparation. With the use of a Leica DM750 light microscope, polar diameter (P), equatorial diameter (E), number of colpus, length of colpus (clg), diameter of pores, pollen grains of view from the pole (L=AMB diameter), distance between colpi and pore (t), exine and intine thickness were measured. Arithmetic mean (M), minimum and maximum values of these measurements were calculated (Tables 2–4). SEM images were also taken to examine the exine structure and the ornamentation of pollen in more detail (Figures 1–7). Pollen morphological analyses of plant species examined were made with the use of relevant literature (Erdtman, 1969; Faegri and Iversen, 1992; Punt et al., 2007; Hesse et al., 2009).

2.1. Multivariate analysis

Pollen morphological characters of 34 taxa were determined together with their correlation coefficients and species were grouped using clustering analysis method [unweighted pair group method with arithmetic mean (UPGMA), dissimilarity, standardized variables]. Eight quantitative palynological characters (P, E, P/E, L, t, clg-plg, exine and intine) were chosen to differentiate the *Scabiosa* and *Lomelosia* taxa. The average of each selected quantitative character was taken. Cluster analysis was performed based on Euclidian distances and UPGMA clustering method (Sokal 1958; Mete et al., 2021) to group the taxa into clusters according to similarity of all pollen variables (Figure 8).

Principal component analysis (PCA) was used to identify the most important characters for interpreting and summarizing the data. Eigen values were plotted in a two-dimensional scatter plot along the first and second principal components (PC1, PC2), representing the highest pollen variation (Figure 9). Box plots showing the quantitative measurements of each palynological characters were also provided (Figures 10–11). All statistical analyses were generated with R 4.0.2 software (R Core Team 2020).

3. Results

3.1. Size, shape, and symmetry

Pollen grains of all studied taxa were radially symmetrical and isopolar. The pollen grains of *Scabiosa* taxa were prolate and subprolate in shape. The pollen grains of all *Scabiosa* taxa were classified as large.

The largest pollen was observed in *Scabiosa triniifolia* with a size of 69.19–81 × 59.9–70.4 μm. The smallest pollen was found in *Scabiosa velenovskiana* with a size of 57.19–70.06 × 44.5–54.08 μm. Amb was circular, and circular-semitriangular (58.28–70.23 μm) in *Scabiosa* (Table 2, Figures 1–2).

The pollen grains of *Lomelosia* taxa were oblate, suboblate, and oblate-spheroidal in shape. The pollen grains of *Lomelosia caucasica*, *L. balianii* and *Lomelosia olivieri* were classified as very large, while the pollen grains of other *Lomelosia* taxa were classified as large. The largest pollen was observed in *Lomelosia caucasica* with a size of 80.27–89.67 × 103.21–115.84 μm, *Lomelosia balianii* with 55.1–83.66 × 80.34–113.6 μm and *Lomelosia olivieri* with 91.12–92.35 × 98.57–104.74 μm. The smallest pollen was found in *Lomelosia cosmoides* with a size of 41.20–51.70 × 68.94–86.36 μm. Amb was circular, triangular, and circular-semitriangular (59.71–100.8 μm) in *Lomelosia* (Tables 3–4, Figures 3–7).

3.2. Aperture characteristics

Pollen grains had tricolpate aperture in species belonging to *Scabiosa* and triporate aperture in those belonging to *Lomelosia*. Colpi were usually long and narrow (Clg 25.65-36.58 μm) in *Scabiosa* taxa. The shortest colpus was found in *Scabiosa lucida* while the longest was found in *Scabiosa triniifolia*.

Pores were found to be circular or elongate in *Lomelosia* taxa. The pore diameters ranged from 11.43 to 22.87 μm. The largest pore diameter (on average) was found in *L. caucasica*. The smallest pore diameter was observed in *L. divaricata*.

Two types of apertures could be recognized as described by Khalik (2010). Planaperture conveys that the apertures were located in the middle of the edges in a polar view (*Scabiosa*), and angulaperturate means that the apertures were located at the angles of the outline in polar view (*Lomelosia*).

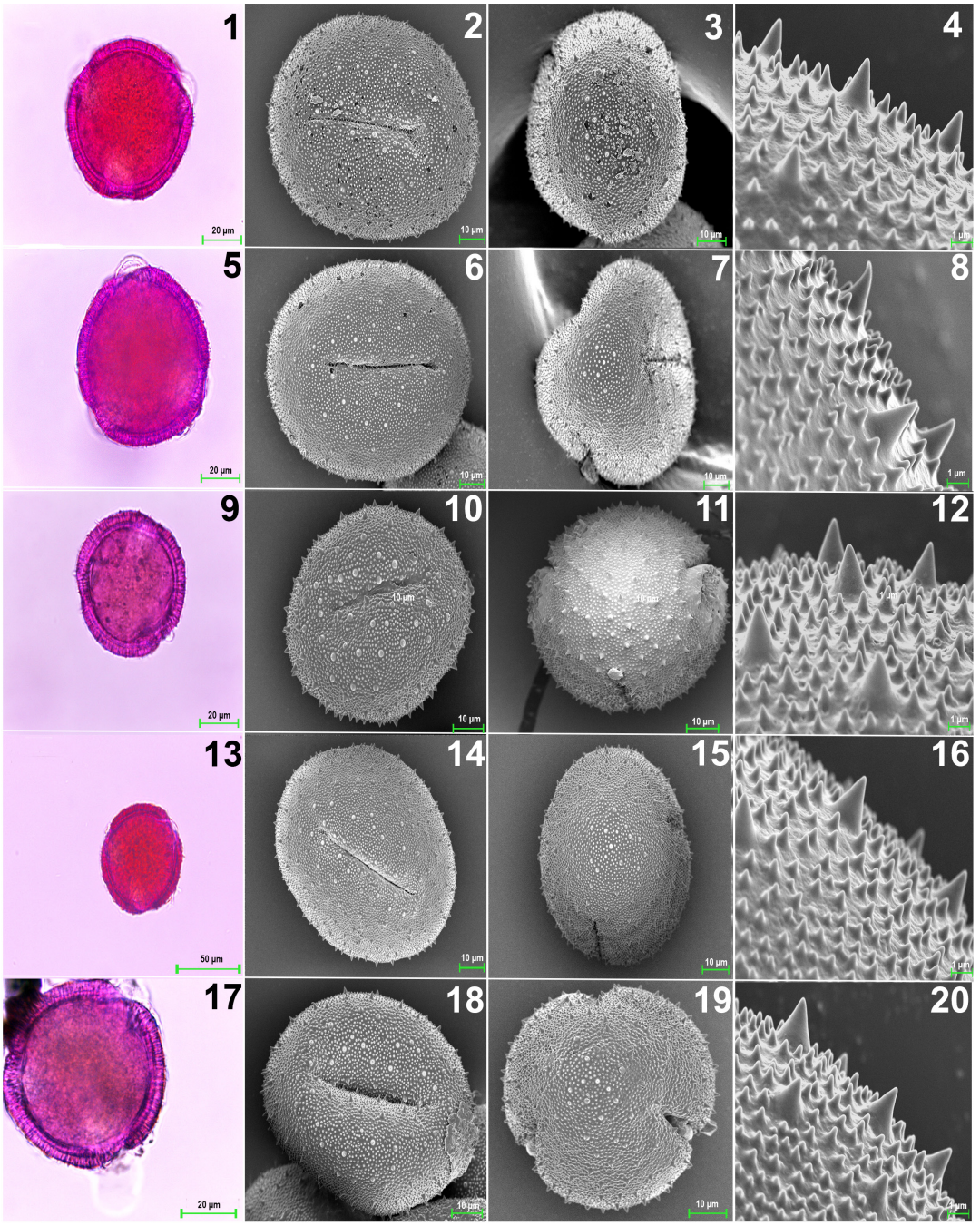


Figure 1. LM and SEM micrographs of *Scabiosa* pollen. 1–4. *S. columbaria* subsp. *columbaria* var. *columbaria*. 5–8. *S. columbaria* subsp. *columbaria* var. *intermedia*. 9–12. *S. columbaria* subsp. *ochroleuca* var. *ochroleuca*. 13–16. *S. columbaria* subsp. *ochroleuca* var. *webbiana*. 17–20. *S. columbaria* subsp. *paphlagonica*.

3.3. Exine, intine and ornamentation

The exine was tectate or subtectate and its thickness ranged from 4.46 to 5.64 µm in *Scabiosa*. The thinnest exine on average was observed in *Scabiosa sosnowskyi*, while the thickest exine overall was found in *S. atropurpurea*. The thickness of intine ranged from 2.20 to 2.52 µm.

The exine was tectate or subtectate and its thickness ranged from 5.13 to 8 µm in *Lomelosia*. The thinnest exine on average was observed in *Lomelosia bicolor*, while the thickest overall exine was found in *L. solymica*. The thickness of intine ranged from 1.93 to 3.75 µm.

The exine ornamentation was echinate or echinate-

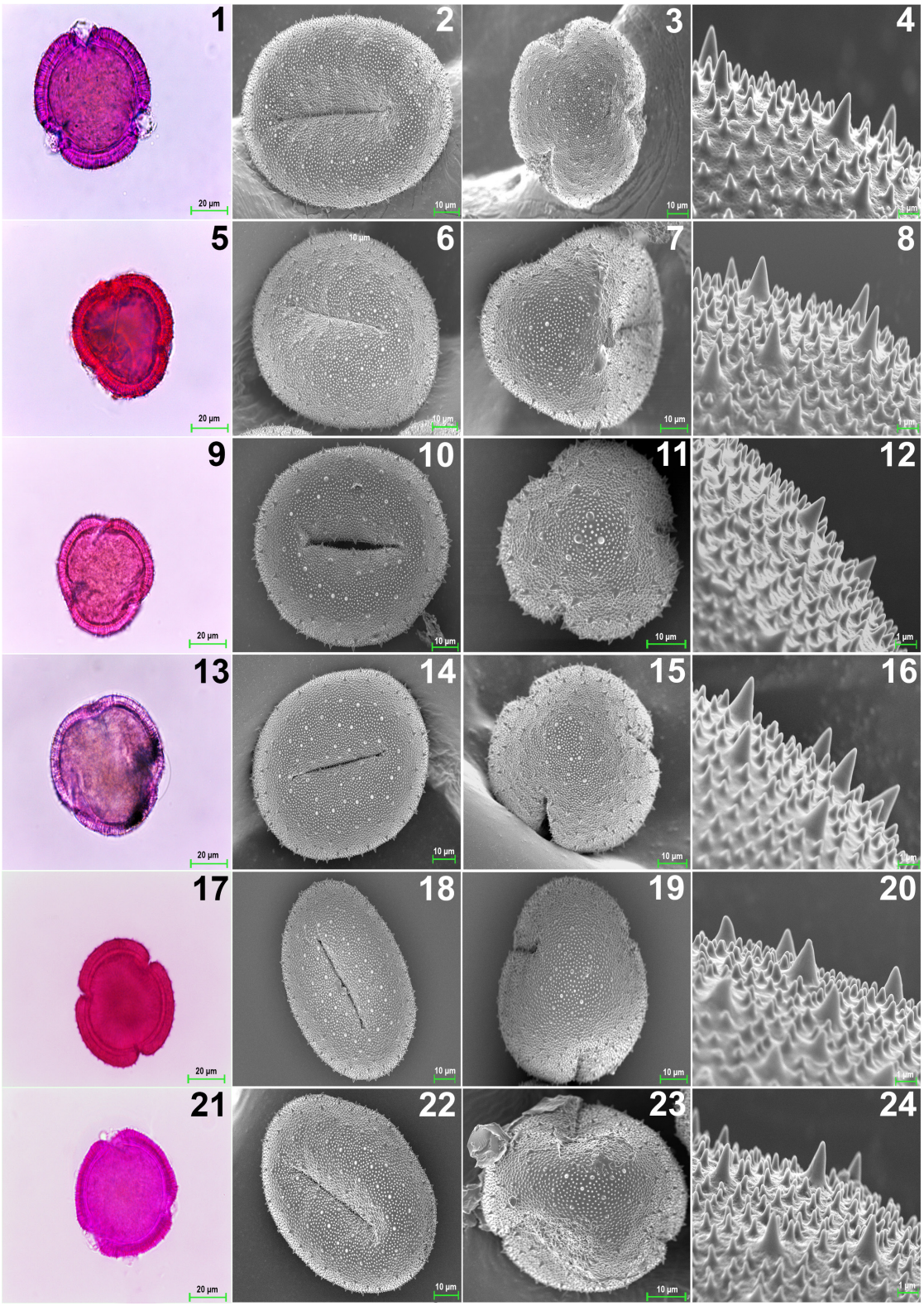


Figure 2. LM and SEM micrographs of *Scabiosa* pollen. 1–4. *S. velenovskiana*. 5–8. *S. crinita*. 9–12. *S. sosnowskyi*. 13–16. *S. triniifolia*. 17–20. *S. lucida*. 21–24. *S. atropurpurea*.

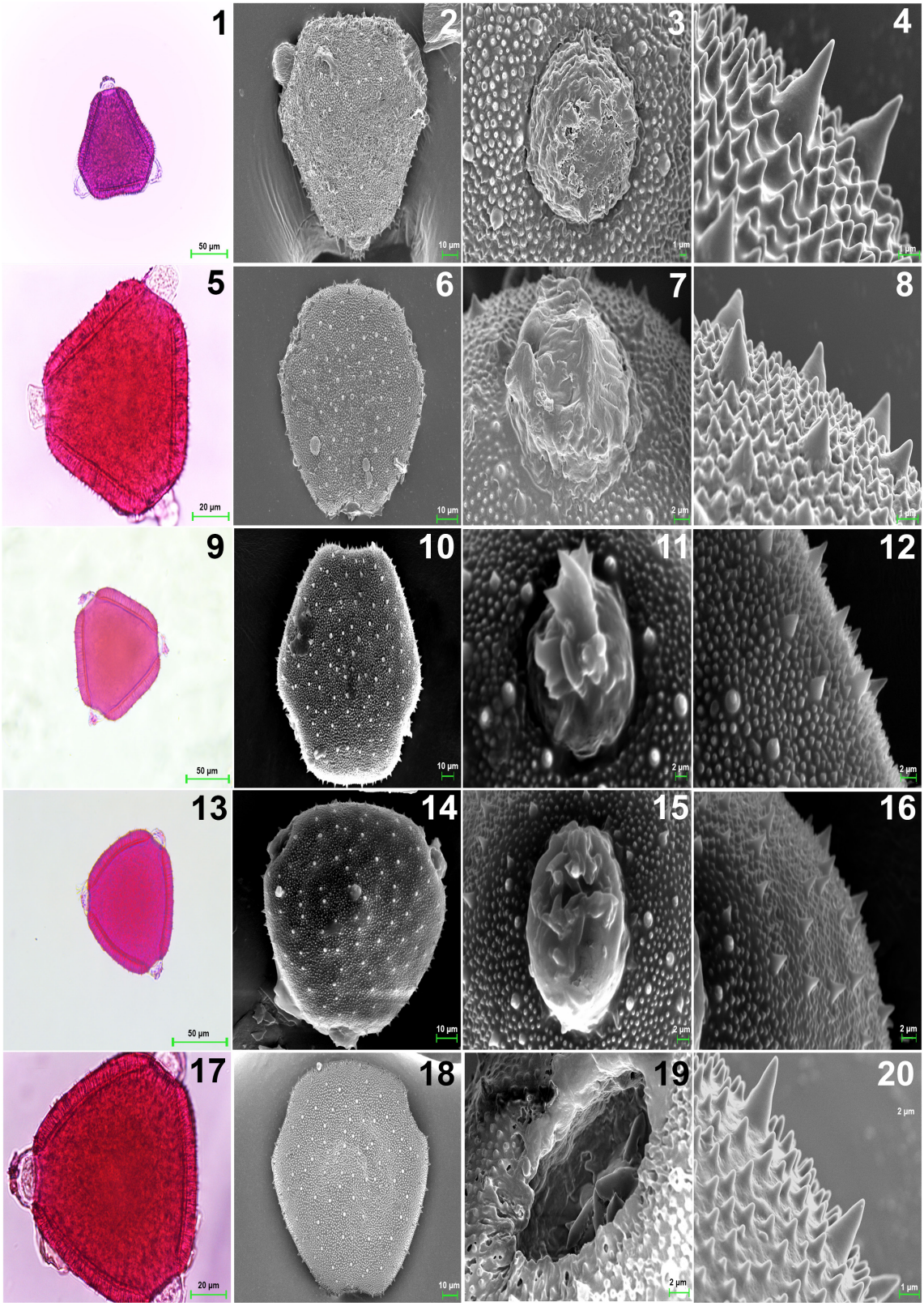


Figure 3. LM and SEM micrographs of *Lomelosia* pollen. 1–4. *L. caucasica.* 5–8. *L. sulphurea.* 9–12. *L. balianii.* 13–16. *L. variifolia* 17–20. *L. kurdica.*

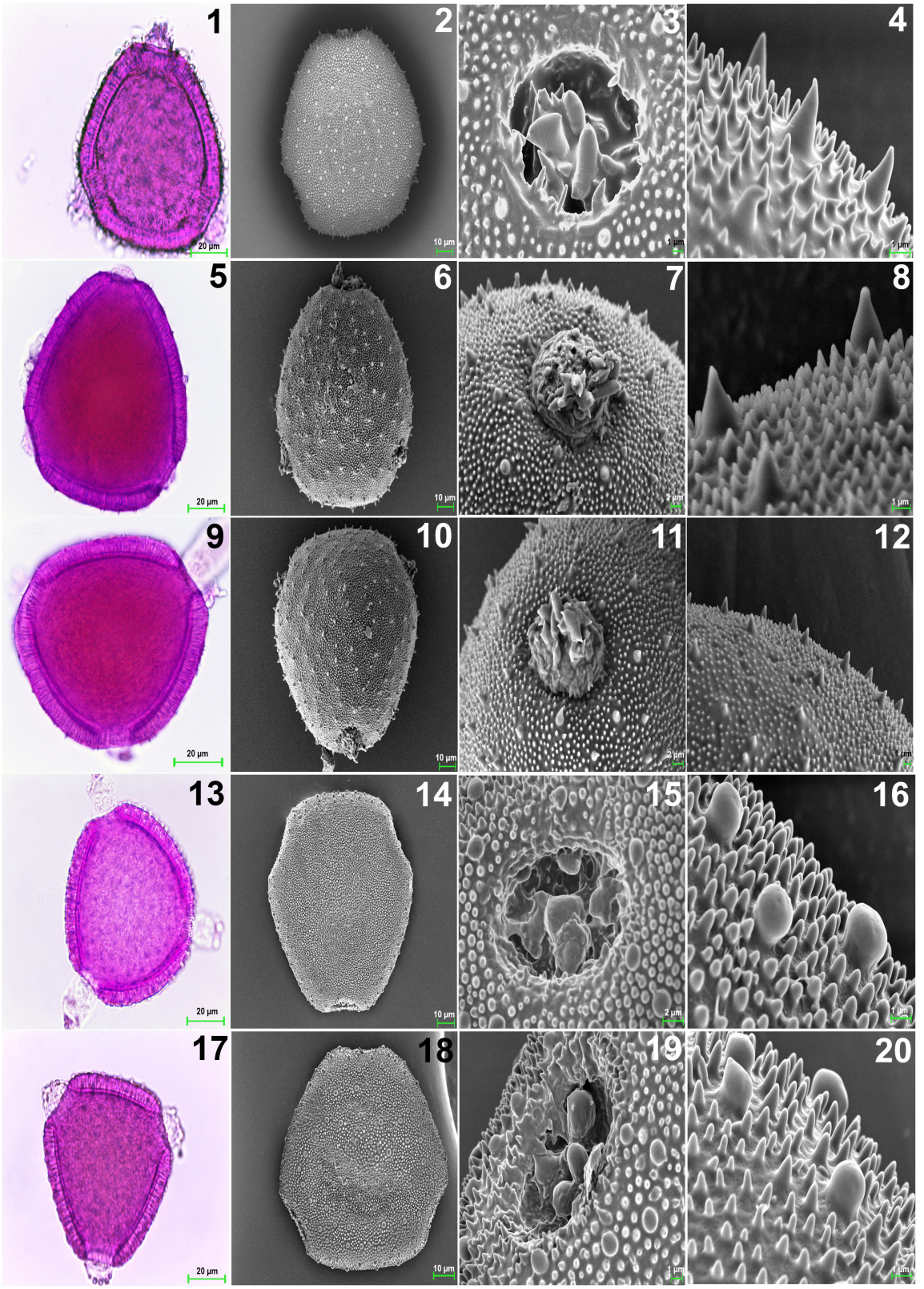


Figure 4. LM and SEM micrographs of *Lomelosia* pollen. 1–4. *L. paucidentata.* 5–8. *L. hololeuca.* 9–12. *L. pseudograminifolia.* 13–16. *L. argentea.* 17–20. *L. polykratis.*

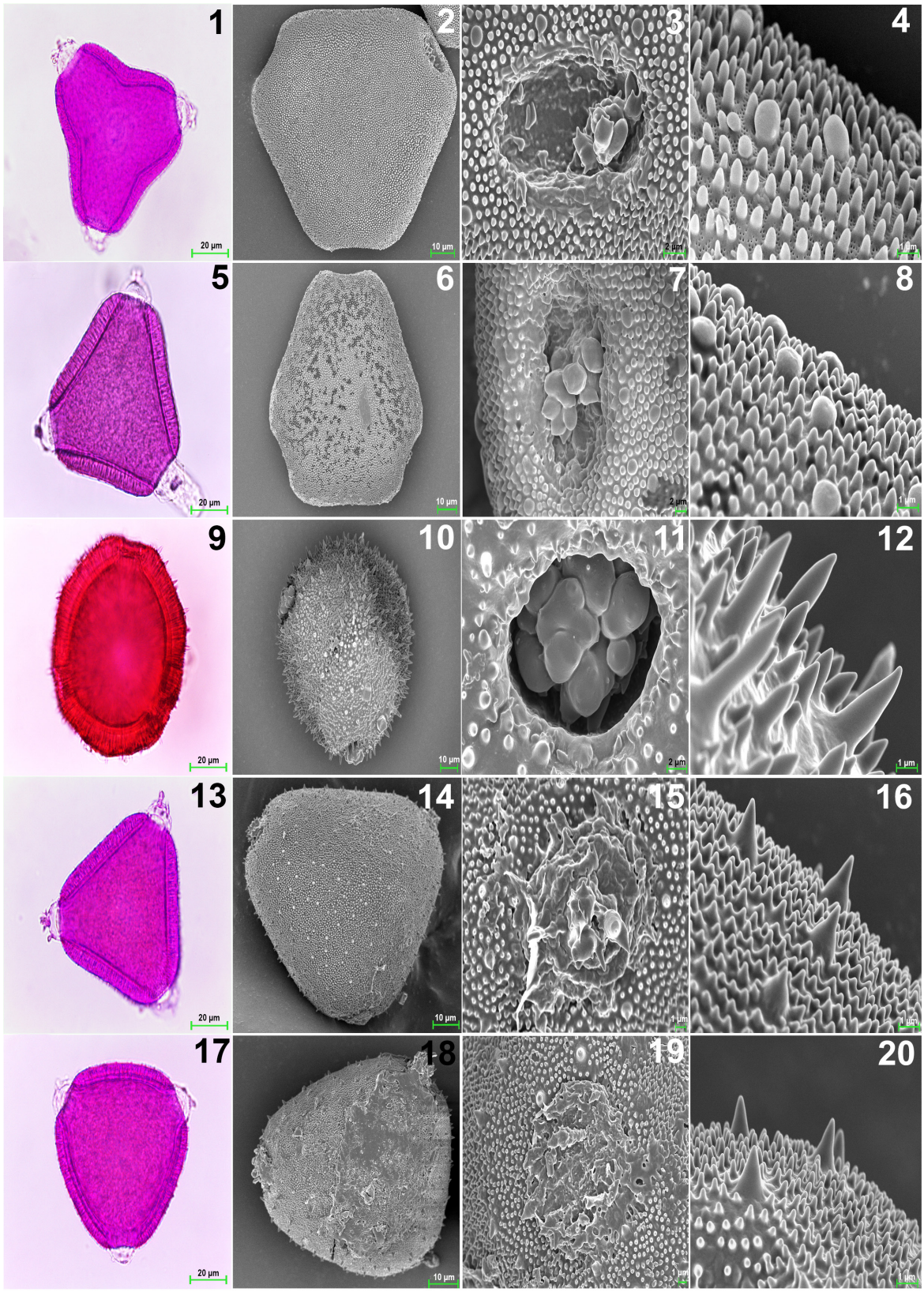


Figure 5. LM and SEM micrographs of *Lomelosia* pollen. 1–4. *L. cosmoides.* 5–8. *L. hispidula.* 9–12. *L. olivieri.* 13–16. *L. reuteriana.* 17–20. *L. micrantha.*

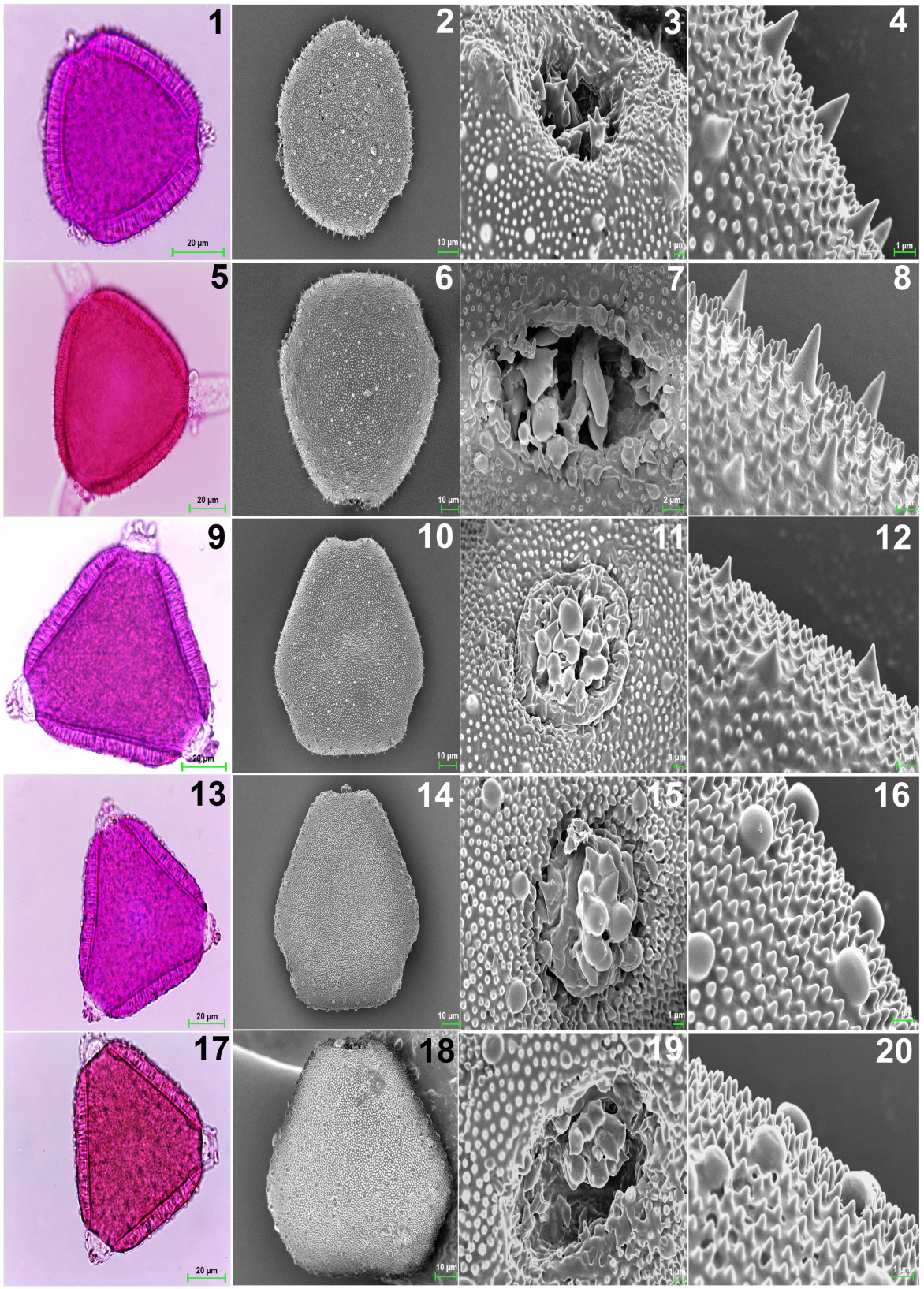


Figure 6. LM and SEM micrographs of *Lomelosia* pollen. 1–4. *L. divaricata.* 5–8. *L. bicolor.* 9–12. *L. prolifera.* 13–16. *L. calocephala.* 17–20. *L. persica.*

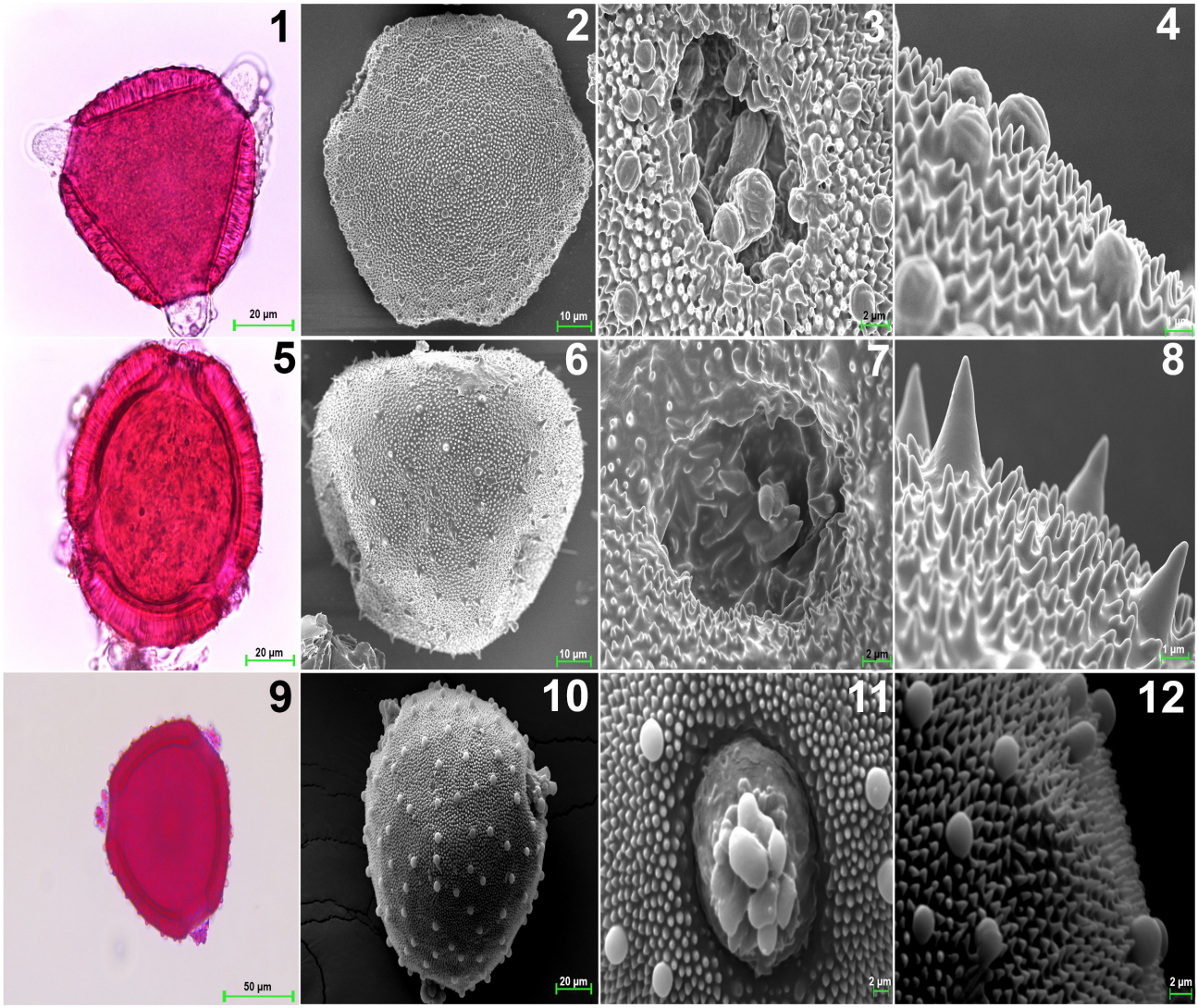


Figure 7. LM and SEM micrographs of *Lomelosia* pollen. 1–4. *L. rotata.* 5–8. *L. solymica.* 9–12. *L. brachiata.*

microechinate in *Scabiosa* taxa, while *Lomelosia* taxa had echinate, echinate-microechinate, echinate-gemmate, echinate-microechinate/gemmate, and microechinate-gemmate pollen grains.

3.4. Multivariate analysis

The phenetic relationships of *Scabiosa* and *Lomelosia* taxa, showed in pollen morphological variation, were specified by two statistical analyses. A dendrogram of Turkish *Scabiosa* and *Lomelosia* taxa was created based on eight palynological characters of 34 taxa by cluster analysis.

Cluster analysis revealed two principal clusters, A and B. The first cluster (A) and the second cluster (B) are divided into two groups. The first cluster included *Lomelosia* taxa, while the second cluster included *Scabiosa* taxa. The first cluster was subsequently split into two subgroups. Both subgroups were mixed, including members of *Lomelosia* (Figure 8).

PCA analysis was used to determine which variables were more important in explaining the total variability. The PCA graph shows the projections of pollen characters in a multidimensional space, where the first two components accounted for 79.7% of the observed variance (Figure 9). The first principal component explained 59.3% of the total variation in the taxa studied. Equatorial axes (E), L (amb), and t (apocolpium) were identified as the most important variables in the first principal component (PC1) because they had the highest relative variation rate. The second principal component (PC2) explained 20.4% of the variation and was associated with the polar axes, and colpus length-pores length (Clg-plg). The third principal component (PC3) explained 9.84% of the total variation and was related to the exine and intine (Table 5).

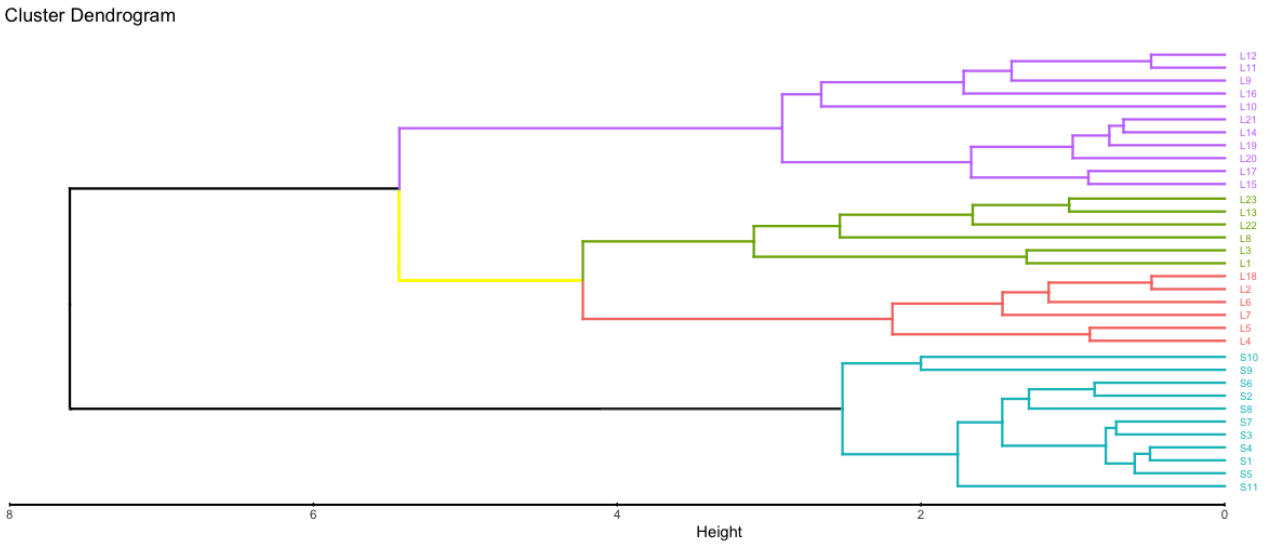


Figure 8. Cluster dendrogram of studied taxa based on pollen morphological data. The taxa names corresponding to the numbers can be seen in Table 1.

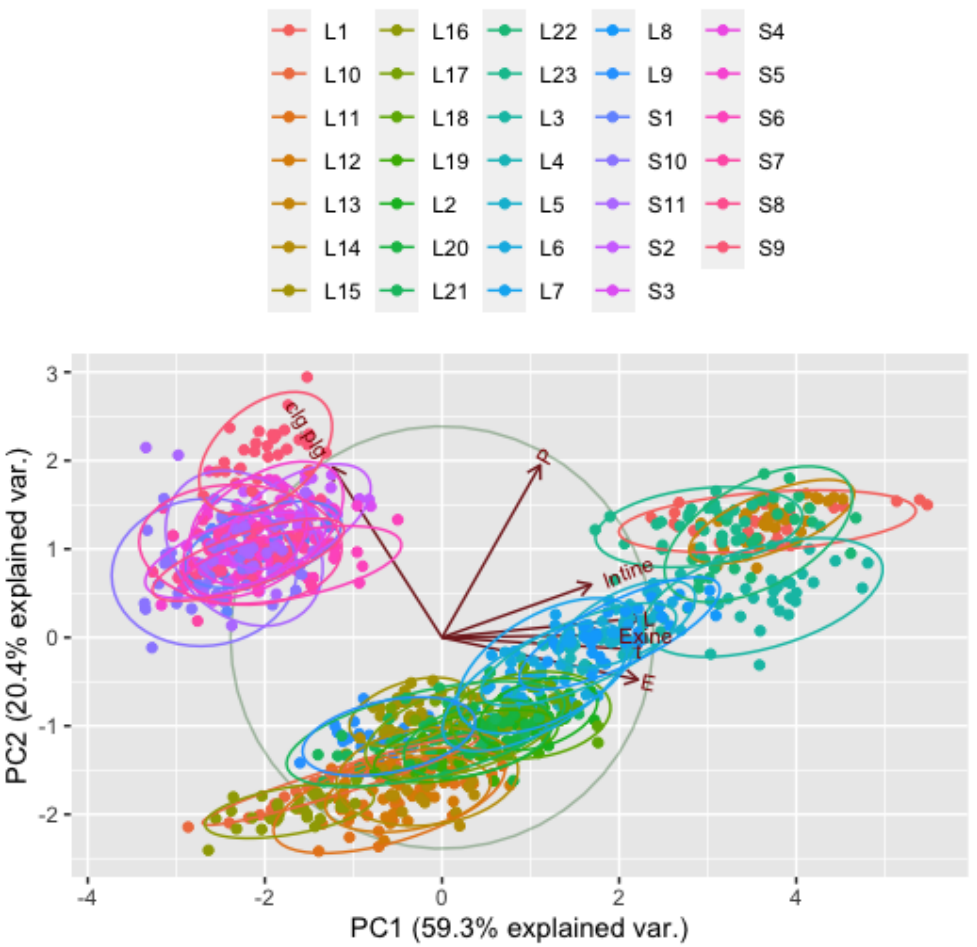


Figure 9. PCA analysis of pollen morphological characteristics

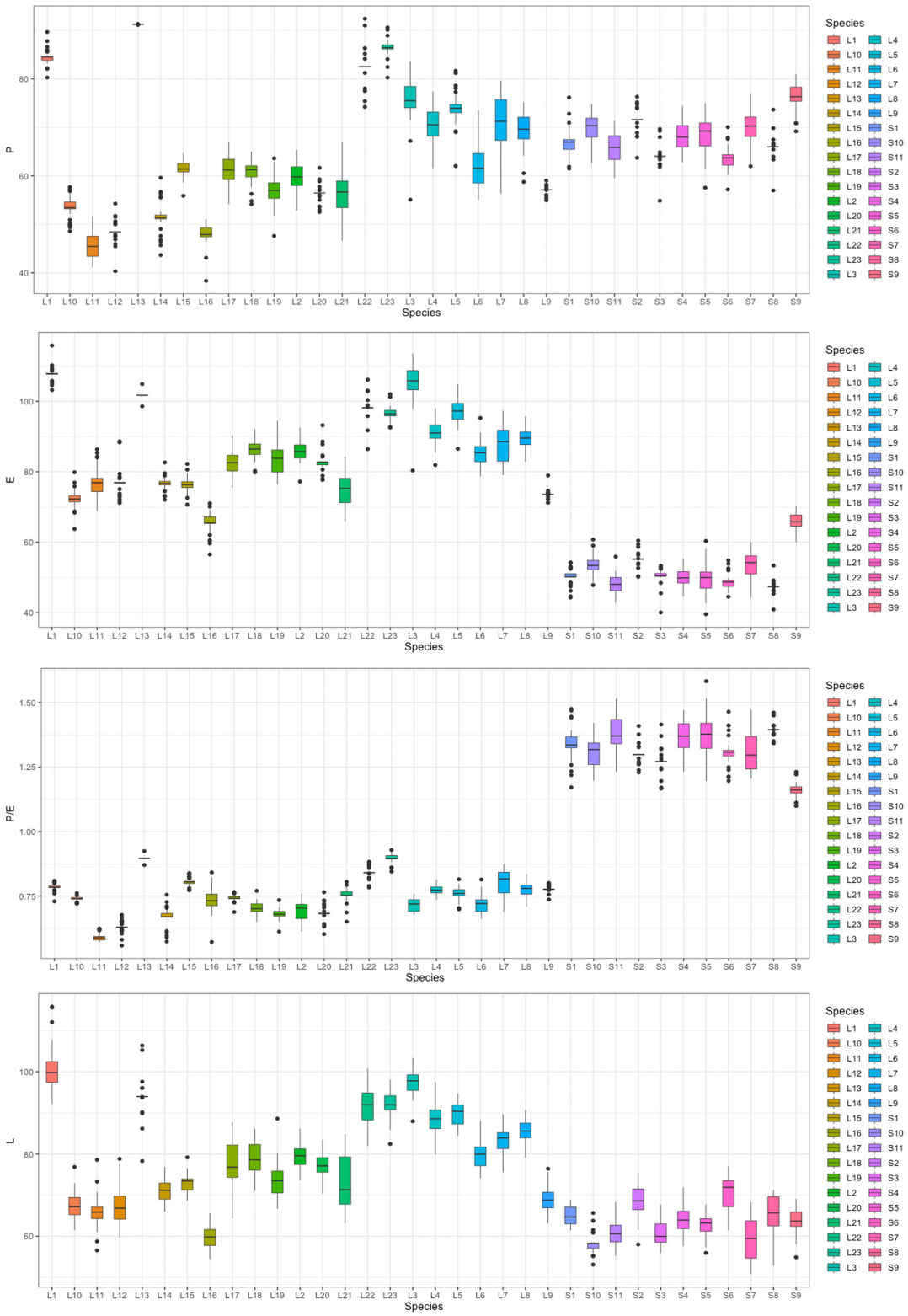


Figure 10. Box plots graph of examined taxa for P, E, P/E, and L.

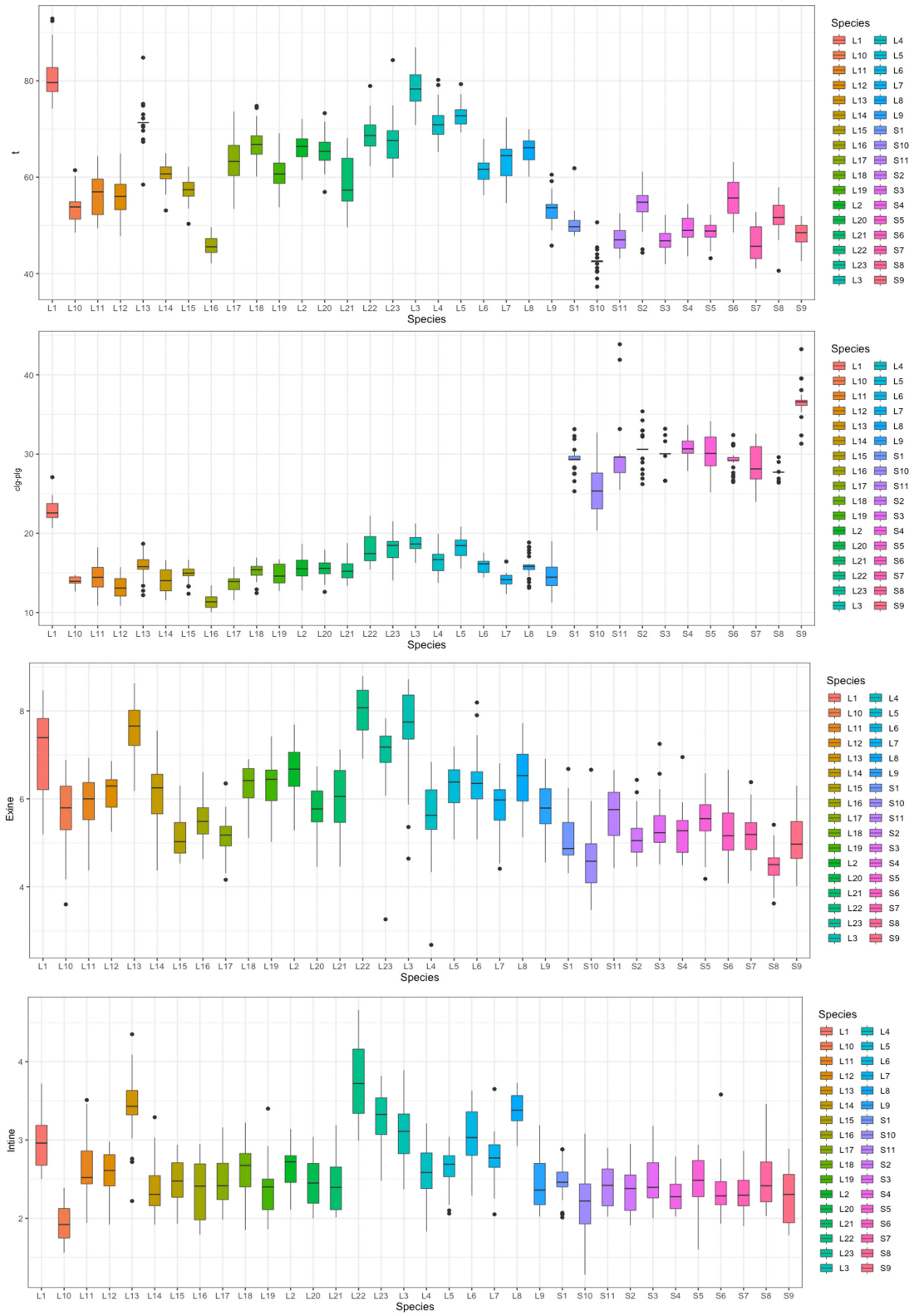


Figure 11. Box plots graph of examined taxa for t, clg-plg, exine, and intine.

Table 1. The collections data of the investigated taxa

No	Taxa	Locality	Voucher number
S1	*Scabiosa columbaria* subsp. *columbaria* var. *columbaria* L.	Artvin: Şavşat, 1297 m, 19 vii 2017	A. Aksoy 2775 & J. Çelik
S2	*Scabiosa columbaria* subsp. *columbaria* var. *intermedia* (Post) Matthews	Adana: Karaisalı, 635 m., 26 vii 2018	A. Aksoy 2961 & J. Çelik
S3	*Scabiosa columbaria* subsp. *ochroleuca* var. *ochroleuca* (L.) Čélak.	İstanbul: Pendik, 92 m., 14 vii 2018	A. Aksoy 2896 & J. Çelik
S4	*Scabiosa columbaria* subsp. *ochroleuca* var. *webbiana* (Don) V.A.Matthews	Kütahya: Gediz, 1524 m., 16 vii 2018	A. Aksoy 2909 & J. Çelik
S5	*Scabiosa columbaria* subsp. *paphlagonica* (Bornm.) V.A.Matthews	Kastamonu: Ilgaz mountain, 1840 m., 17 viii 2018	A. Aksoy 2980 & J. Çelik
S6	*Scabiosa velenovskiana* Bobrov	Artvin: Artvin-Borçka road, 242 m., 24 vii 2018	A. Aksoy 2949 & J. Çelik
S7	*Scabiosa crinita* Kotschy & Boiss.	Erzurum: Oltu, 2095 m., 22 vii 2018	A. Aksoy 2932 & J. Çelik
S8	*Scabiosa sosnowskyi* Sulak.	Rize: Fırtına stream, 10 m., 24 vii 2018	A. Aksoy 2953 & J. Çelik
S9	*Scabiosa triniifolia* Friv.	Kırklareli: Kofçaz, 310 m., 13 vii 2018	A. Aksoy 2889 & J. Çelik
S10	*Scabiosa lucida* Vill.	Gümüşhane: Mount Zigana, 2060-2150 m., 25 vii 2018	A. Aksoy 2958 & J. Çelik
S11	*Scabiosa atropurpurea* L.	Çanakkale: From Kabatepe to Conkbayırı, 1 m., 13 vii 2018	A. Aksoy 2881 & J. Çelik
L1	*Lomelosia caucasica* (M.Bieb.) Greuter & Burdet	Ardahan: Göle, 2100 m., 22 vii 2018	A. Aksoy 2934 & J. Çelik
L2	*Lomelosia sulphurea* (Boiss. & A.Huet) Greuter & Burdet	Erzurum: Palandoken Mountain, 2608 m., 22 vii 2018	A. Aksoy 2976 & J. Çelik
L3	*Lomelosia balianii* (Diratz.) Greuter & Burdet	Gümüşhane: Torul, 2350 m., 29 viii 2020	A. Aksoy 3167 & J. Çelik
L4	*Lomelosia variifolia* (Boiss.) Greuter & Burdet	Antalya: Kaş, 207 m., 08 v 2020	A. Aksoy 3122 & J. Çelik
L5	*Lomelosia kurdica* (Post) Greuter & Burdet	Hatay: Erzin, 1018 m., 14 viii 2018	A. Aksoy 2986 & J. Çelik
L6	*Lomelosia paucidentata* (Hub.-Mor.) Greuter & Burdet	Antalya: Finike-Elmalı road, 805 m.,04 viii 2018	A. Aksoy 2972 & J. Çelik
L7	*Lomelosia hololeuca* (Bornm.) Greuter & Burdet	Kütahya: Tavşanlı, 1120 m., 03 viii 2018	A. Aksoy 2966 & J. Çelik
L8	*Lomelosia pseudograminifolia* (Hub.-Mor.) Greuter & Burdet	Sivas: Kangal-Gürün road junction, 1561 m., 19 vii 2018	A. Aksoy 2914 & J. Çelik
L9	*Lomelosia argentea* (L.) Greuter & Burdet	Isparta: Kızıldağ National Park, 1368 m., 12 vi 2018	A. Aksoy 2860 & J. Çelik
L10	*Lomelosia polykratis* (Rech.f.) Greuter & Burdet	Denizli: Acıpayam, 1508 m., 27 vii 2018	A. Aksoy 2963 & J. Çelik
L11	*Lomelosia cosmoides* (Boiss.) Greuter & Burdet	İzmir: Bozdağ-Salihli road, 292 m., 14 vi 2018	A. Aksoy 2863 & J. Çelik
L12	*Lomelosia hispidula* (Boiss.) Greuter & Burdet	Aydın: Dilek Peninsula National Park, 200 m., 25 v 2018	A. Aksoy 2824 & J. Çelik
L13	*Lomelosia olivieri* (Coult.) Greuter & Burdet	Van: Gürpınar, 2247 m., 21 vii 2018	A. Aksoy 2925 & J. Çelik
L14	*Lomelosia reuteriana* (Boiss.) Greuter & Burdet	Aydın: Karacasu, 680 m., 14 vi 2017	A. Aksoy 2821 & J. Çelik
L15	*Lomelosia micrantha* (Desf.) Greuter & Burdet	Kayseri: Yahyalı, 1487 m., 18 vi 2017	A. Aksoy 2830 & J. Çelik
L16	*Lomelosia divaricata* (Jacq.) Greuter & Burdet	Burdur: Seydiköy, 875 m., 24 v 2018	A. Aksoy 2812 & J. Çelik
L17	*Lomelosia bicolor* (Boiss.) Greuter & Burdet	Bitlis: From Reşadiye to Pelli, 2172 m., 13 vii 2019	A. Aksoy 3055 & J. Çelik
L18	*Lomelosia prolifera* (L.) Greuter & Burdet	Hatay: Arsuz, 28 m., 28 iv 2017	A. Aksoy 2662 & J. Çelik
L19	*Lomelosia calocephala* (Boiss.) Greuter & Burdet	Mersin: Tarsus, 851 m., 11 vi 2018	A. Aksoy 2855 & J. Çelik
L20	*Lomelosia persica* (Boiss.) Greuter & Burdet	Malatya: Doğanşehir, 1023 m., 11 vi 2018	A. Aksoy 2854 & J. Çelik
L21	*Lomelosia rotata* (M.Bieb.) Greuter & Burdet	Kayseri: Yahyalı, 1487 m., 09 vi 2018	A. Aksoy 2831 & J. Çelik
L22	*Lomelosia solymica* Parolly, Ö.Eren & Nordt	Antalya: Kemer, 1700 m., 02 ix 2018	A. Aksoy 2984 & J. Çelik
L23	*Lomelosia brachiata* (Sm.) Greuter & Burdet	Denizli: Bozkurt, 600 m., 22 v 2020	A. Aksoy 3124 & J. Çelik

Table 2. Pollen morphological characters of the studied taxa of *Scabiosa* (S1–S11).

Species	P (µm)			E (µm)			P/E	L (µm)			t (µm)			clg (µm)	Exine (µm)	Intine (µm)	Shape	Aperture type	Ornamentation	Size
	Min.	Max.	Mean	Min.	Max.	Mean		Min.	Max.	Mean	Min.	Max.	Mean	Mean	Mean	Mean				
S1	61.5	76.18	66.97	44.28	58.23	50.14	1.34	61.4	68.83	64.89	47.82	61.85	50.24	29.33	5.15	2.46	Prolate	Tricolpate	Echinate	Large
S2	63.73	76.32	71.59	50.15	60.45	55.15	1.3	58.75	75.47	68.61	44.32	61.15	54.1	30.6	5.15	2.36	Subprolate	Tricolpate	Echinate	Large
S3	54.87	69.66	64.06	40.05	55.3	50.37	1.28	55.89	67.62	60.57	41.94	52.2	46.79	30.04	5.37	2.46	Subprolate	Tricolpate	Echinate	Large
S4	62.75	74.43	68.44	44.54	55.31	50.02	1.37	57.79	71.87	64.14	43.57	54.4	49.4	30.66	5.24	2.30	Prolate	Tricolpate	Echinate	Large
S5	57.56	75	68.52	39.55	61.36	50.03	1.38	55.93	67.7	62.68	43.18	52.2	48.64	30.12	5.56	2.47	Prolate	Tricolpate	Echinate	Large
S6	57.19	70.06	63.69	44.5	54.8	48.7	1.31	61.43	77	70.23	48.54	63.11	55.73	29.17	5.25	2.36	Subprolate	Tricolpate	Echinate	Large
S7	61.99	76.88	69.9	44.25	60.11	53.53	1.31	50.81	68.3	59.41	41.02	52.74	46.35	28.45	5.23	2.33	Subprolate	Tricolpate	Echinate	Large
S8	56.98	73.65	66	40.87	53.37	47.33	1.4	52.9	71.2	65.2	40.58	57.9	51.78	27.7	4.46	2.52	Prolate	Tricolpate	Echinate	Large
S9	69.19	81	76.31	59.9	70.4	65.74	1.16	54.88	69.1	63.94	42.57	51.92	48.05	36.58	5.06	2.29	Subprolate	Tricolpate	Echinate-microechinate	Large
S10	62.61	74.82	69.79	47.82	60.73	53.62	1.3	53.1	65.66	58.28	37.28	50.63	42.61	25.65	4.50	2.20	Subprolate	Tricolpate	Echinate-microechinate	Large
S11	59.53	71.41	65.84	42.79	55.88	48.04	1.37	55.19	68.25	60.96	43.12	52.54	60.96	29.62	5.64	2.43	Prolate	Tricolpate	Echinate-microechinate	Large

(P: Polar axis. E: Equatorial axis. L=AMB: Diameter of pollen at the polar view. t: apocolpium. clg: colpus length)

Table 3. Pollen morphological characters of the studied taxa of *Lomelosia* (L1–L12).

Sp.	P (µm)			E (µm)				L (µm)			t (µm)			plg (µm)	Exine (µm)	Intine (µm)	Shape	Aperture type	Ornamentation	Size
	Min.	Max.	Mean	Min.	Max.	Mean	P/E	Min.	Max.	Mean	Min.	Max.	Mean	Mean	Mean	Mean				
L1	80.27	89.67	84.52	103.21	115.84	107.81	0.78	92.16	115.84	100.80	74.25	81.80	80.89	22.87	7.09	2.97	Suboblate	Triporate	Echinate	Very large
L2	52.84	65.37	59.67	77.21	92.56	85.82	0.70	73.60	86.19	79.32	59.42	72.06	65.84	15.68	6.67	2.67	Oblate	Triporate	Echinate-microechinate	Large
L3	55.10	83.66	75.31	80.34	113.60	105.12	0.72	87.97	103.38	97.40	70.83	86.95	78.56	18.73	7.59	3.13	Oblate	Triporate	Echinate-microechinate	Very large
L4	61.59	77.39	70.53	81.93	98.02	91.07	0.77	79.89	97.51	88.36	65.19	80.18	71.38	16.42	5.69	2.60	Suboblate	Triporate	Echinate-microechinate	Large
L5	62.03	81.67	73.94	86.53	104.87	97.27	0.76	84.43	94.71	89.85	69.27	79.31	72.70	18.20	6.28	2.64	Suboblate	Triporate	Echinate-microechinate	Large
L6	55.10	73.48	61.58	78.50	95.28	85.39	0.72	74.12	88.05	79.57	56.27	68.00	61.61	15.84	6.33	3.03	Oblate	Triporate	Echinate-microechinate	Large
L7	56.36	79.65	70.35	79.03	97.33	87.69	0.80	75.56	89.68	83.19	54.63	73.12	63.85	14.06	5.94	2.81	Suboblate	Triporate	Echinate-microechinate	Large
L8	58.74	75.22	69.44	82.80	95.69	89.25	0.78	79.16	90.69	85.41	60.07	69.97	65.74	15.81	6.71	3.48	Suboblate	Triporate	Echinate-microechinate	Large
L9	54.96	59.03	57.12	71.28	74.01	73.59	0.78	63.18	76.41	69.05	45.80	60.52	53.31	14.51	5.82	2.46	Suboblate	Triporate	Echinate-gemmate	Large
L10	48.58	57.68	53.44	63.77	79.86	72.27	0.74	61.50	76.84	67.48	48.51	61.45	53.72	14.17	5.68	1.93	Oblate	Triporate	Echinate/ microechinate-gemmate	Large
L11	41.20	51.70	45.44	68.94	86.36	76.90	0.59	56.55	78.79	65.89	49.39	64.41	56.60	14.43	5.94	2.61	Oblate	Triporate	Echinate-gemmate	Large
L12	40.33	54.28	48.45	71.18	88.63	76.93	0.63	59.98	78.72	67.52	47.76	64.92	55.74	13.14	6.18	2.58	Oblate	Triporate	Microechinate-gemmate	Large

(P: Polar axis. E: Equatorial axis. L=AMB: Diameter of pollen at the polar view. t: apocolpium. plg: pore diameter)

Table 4. Pollen morphological characters of the studied taxa of *Lomelosia* (L13–L23).

Sp.	P (µm)			E (µm)				L (µm)			t (µm)			plg (µm)	Exine (µm)	Intine (µm)	Shape	Aperture type	Ornamentation	Size
	Min.	Max.	Mean	Min.	Max.	Mean	P/E	Min.	Max.	Mean	Min.	Max.	Mean	Mean	Mean	Mean				
L13	91.12	92.35	91.24	98.57	104.91	101.74	0.9	78.29	10.38	93.95	58.46	84.81	71.32	15.78	7.55	3.43	Oblate-Spheroidal	Triporate	Echinate	Very Large
L14	43.65	59.62	51.36	72.04	82.66	76.68	0.67	66.02	76.83	71.14	53.09	64.96	60.55	14.09	6.11	2.41	Oblate	Triporate	Echinate-microechinate	Large
L15	55.89	64.69	61.42	70.67	82.23	76.27	0.81	68.62	79.2	72.89	50.32	62.13	57.4	14.85	5.17	2.49	Suboblate	Triporate	Echinate-microechinate	Large
L16	38.34	51.08	47.89	56.52	71.02	65.43	0.73	54.5	65.57	59.71	42.13	49.64	45.76	11.43	5.54	2.36	Oblate	Triporate	Echinate-microechinate	Large
L17	56.55	67.1	61.21	75.49	90.27	82.57	0.74	64.26	87.78	78.08	53.43	73.62	63.68	13.69	5.13	2.49	Oblate	Triporate	Echinate-microechinate	Large
L18	54.14	64.95	60.76	79.81	92.08	86.45	0.7	71.05	86.12	78.8	60.11	74.79	67.01	15.2	6.30	2.63	Oblate	Triporate	Echinate-microechinate	Large
L19	47.6	63.62	57	76.42	94.55	83.83	0.68	66.6	88.6	73.65	53.76	69.13	61.13	14.82	6.34	2.37	Oblate	Triporate	Echinate-gemmate	Large
L20	52.54	61.67	56.46	77.7	93.2	82.76	0.68	70.25	83.51	77.24	56.93	73.29	65.45	15.54	5.83	2.47	Oblate	Triporate	Echinate-gemmate	Large
L21	46.6	67.07	56.67	66.04	84.26	75.28	0.75	63.19	84.86	73.13	49.6	68.13	59.07	15.36	5.94	2.44	Suboblate	Triporate	Echinate-gemmate	Large
L22	74.23	92.41	82.54	86.44	106.13	98.18	0.84	81.91	100.82	91.89	62.28	78.92	68.63	18.11	8.00	3.75	Suboblate	Triporate	Echinate	Large
L23	80.26	90.61	86.43	92.56	102	96.44	0.9	82.4	98.09	92.19	59.91	84.29	67.43	18.2	7.00	3.32	Oblate-Spheroidal	Triporate	Echinate-gemmate	Large

(P: Polar axis. E: Equatorial axis. L=AMB: Diameter of pollen at the polar view. t: apocolpium. plg: pore diameter)

Table 5. Principal component analysis (PCA) variable loadings for the first 3 components.

Variables	PC1	PC2	PC3
P	0.228	0.683	-0.204
E	0.455	-0.167	-0.183
L	0.461	0.078	-0.311
t	0.447	-0.048	-0.361
Clg-plg	-0.253	0.673	-0.039
Exine	0.38	0.01	0.524
Intine	0.347	0.21	0.65
Percentage	59.3	20.4	9.84

4. Discussion

Taxonomy of the genera *Scabiosa* and *Lomelosia* is highly controversial and these genera have been the subject of various taxonomic studies. Because the morphological similarities between the *Scabiosa* and *Lomelosia* species are very high, their taxonomic classification is still unresolved (Mostafa and Sedigheh, 2016). Various palynological studies on different Dipsacaceae species have confirmed the importance of pollen characteristics for distinguishing taxa. Khalik (2010) examined the pollen characteristics of nine species belonging to four genera of Dipsacaceae and stated that the pollen character could be used to delimit species.

In this study, LM and SEM were used to observe pollen morphological features of *Scabiosa* and *Lomelosia* taxa of Türkiye. Aperture types are one of the most important pollen characteristics. Present findings revealed that the *Scabiosa* taxa had tricolpate aperture, while *Lomelosia* taxa had triporate aperture. Therefore, the aperture type was found to be useful in distinguishing the genus between *Lomelosia* and *Scabiosa*, and defining the taxa. Clarke and Jones (1981) and Erdtman (1952) examined the pollen morphology of the Dipsacaceae family, and defined two types of pollen apertures: porate and colpate. In regard to the position of the apertures, Khalik (2010) defined three particular types, namely circumaperturate, angulaperturate, and planaperturate. He stated that *Lomelosia* pollen grains were classified as angulaperturate and *Scabiosa* pollen grains were classified as planaperturate. These study results are consistent with the present findings.

Mostafa and Sedigheh (2016) examined the pollen morphology of six *Scabiosa* species, and found that the pollen grains of *S. columbaria* were tricolpate and the other five species were triporate. Mostafa et al. (2017) investigated the pollen morphology of nine species belonging to the family Dipsaceae. The results showed that pollen grains were triporate and tricolpate, and so it was suggested that some *Scabiosa* species be transferred to *Lomelosia* genus depending on the palynological features.

The results of current study revealed that pollen shape of the *Scabiosa* taxa was prolate or subprolate, whereas the *Lomelosia* taxa showed different pollen shapes (oblate, suboblate, oblate-spheroidal). Similar pollen shapes were also reported in previous studies (Mostafa and Sedigheh, 2016; Mostafa et al., 2017).

Pollen ornamentation is often one of the most important features that can be used to distinguish taxa (Pinar et al., 2009; Tsymbalyuk et al., 2021). Khalik (2010) explained that exine ornamentation was also useful for distinguishing closely related genera such as *Scabiosa* and *Lomelosia*. Unlike other studies, in the present study, exine ornamentation did not give a clear distinction to limit the studied species, since, with the exception of a few gemmate species, most of the species had echinate or echinate-microechinate ornamentation.

Pollen grains were classified into 6 groups according to their size by Erdtman (1952): perminuta, minuta, media, magna, permagna, and giganta. According to this classification system, pollen grains of *Lomelosia caucasica*, *L. balianii*, and *L. olivieri* were categorized as permagna and pollen grains of all the remaining taxa were considered magna. Khalik (2010) reported the pollen grains of nine species represented four genera of the Dipsacaceae as magna. Likewise, Mostafa et al. (2017) stated that pollen grains of the Dipsaceace species were magna. Present findings on pollen size are consistent with the results of previous studies.

The findings of this study also revealed that characteristics of pollen morphology such as equatorial axes, L (polar view amb), and t (apocolpium) provided easy and reliable features for taxonomic studies of *Scabiosa* and *Lomelosia*. These results are consistent with other palynological studies on different genera within the family (Khalik, 2010; Mostafa and Sedigheh, 2016; Mostafa et al., 2017).

5. Conclusion

The member of genus *Scabiosa* sensu lato were eurypalynous and pollen grains differed in pollen shape, diameter,

and aperture types. Present analyses conducted for pollen morphological characteristics showed that the interspecies differences within the studied genera were generally insignificant, but there were considerable differences between the various genera. Statistical analysis showed that equatorial axes, L (polar view amb), and t (apocolpium) were the most significant variables in distinguishing the taxa studied. Consequently, these pollen characteristics could assist in taxonomically constraining closely related species. These results indicate the transfer of some *Scabiosa* species to *Lomelosia* based on palynological characters.

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