



# POLLEN MORPHOLOGY OF SOME *CENTAUREA* L., *PSEPHELLUS* CASS. AND *CYANUS* MILLER TAXA

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Received March 9, 2009; revision accepted September 28, 2009

The pollen morphology of 29 taxa, 24 of which are endemic to Turkey, was investigated in detail by light and scanning electron microscopy. LM examination showed pollen grains to be tricolporate, rarely tetracolporate, isopolar, radially symmetrical, subprolate, spheroidal-subprolate, operculate, tectum perforate, scabrate and microechinate. *P. pecho* Albow. and *P. appendicigera* C. Koch resemble the *Montana* type, *C. pichleri* subsp. *pichleri* Boiss. and *C. pichleri* subsp. *extrarocularis* (Hayek & Siehe) Wagenitz resemble the *Cyanus* type, and *C. pseudoscabiosa* subsp. *pseudoscabiosa* Boiss. & Buhse are consistent with the *Dealbata* type, *C. pestalozzae* Boiss. and *C. carduiiformis* subsp. *carduiiformis* DC. with the *Scabiosa* type, and the other taxa with Wagenitz's *Jacea* type.

**Key words:** *Centaurea*, *Cyanus*, *Psephellus*, pollen morphology, LM, SEM.

## INTRODUCTION

The genus *Centaurea* L. is one of the largest genera in Asteraceae. The number of species included in this genus ranges between 200 and 700 species depending on the classification (Bremer, 1994; Helwig 2004; Bancheva and Greilhuber, 2006). Turkey is one of the important centers of diversity for the genus *Centaurea* (Wagenitz, 1986); 172 species and 6 imperfectly known species of *Centaurea* were recognized for *Flora of Turkey* by Wagenitz (1975). Since then, 27 new species have been described (Davis et al., 1988; Agababian, 1997; Güner et al., 2000; Duran and Duman, 2002; Greuter, 2003a,b; Türkoglu et al., 2003; Aytaç and Duman, 2005; Uzunhisarcikli et al., 2005; Vural et al., 2006; Wagenitz et al., 2006; Eren, 2007; Kaya and Vural, 2007; Uysal et al., 2007; Uzunhisarcikli et al., 2007; Aksoy et al., 2008; Uysal et al., 2008; Armağan and Ünal, 2009; Hamzaoglu and Budak, 2009; Uysal and Köse, 2009). In addition, *Centaurea wagenitziana* Bancheva & Kit Tan, *Centaurea cassia* subsp. *dumanii* M.Dinç, A. Duran & B. Bilgili and *Centaurea kaynakiae* Daskin & Yilmaz have been

described (Tan et al., 2009; Dinç et al. 2009; Daskin and Yilmaz, 2009).

As a consequence of the unnaturalness of *Centaurea* s.l., recent approaches have split this taxon into several more natural genera: *Centaurea* s.str., *Cyanus* Miller, *Psephellus* Cassini and *Rhaponticoides* Vaillant (Greuter, 2003a,b; Hellwig 2004). A new species of *Cyanus*, *C. eflanensis* Kaya & Bancheva, is described from Karabük, Turkey (Kaya and Bancheva, 2009).

The genus *Centaurea* presents taxonomic and nomenclatural problems. Palynological studies together with recent molecular approaches and karyological studies are very helpful in solving these problems. Garcia-Jacas et al. (2001) proposed *Centaurea* sections with *Dealbata* pollen classified as *Psephellus*, in addition to morphology and pollen type evolution, ITS and *matK* chloroplast gene phylogenies and karyological data. In other work by Garcia-Jacas et al. (2000, 2006), *Centaurea jacea* group was analyzed by ITS sequence, supported by karyological evidence. The results showed good correlation with the biogeographic distribution of the species.

Pollen grains of some Turkish *Centaurea* taxa have been studied by LM (Wagenitz, 1955; Avetisjan,

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1964; Inceoglu and Karamustafaoglu, 1976; Kaya 1985, 1986), LM, SEM and TEM (Pinar and Inceoglu, 1996; Pehlivan 1994, 1995a,b; Celik et al., 2005). Wagenitz (1955) divided the genus *Centaurea* into eight groups on the basis of exine structure and sculpturing: *Serratula*, *Centaurium*, *Scabiosa*, *Crupina*, *Jacea*, *Dealbata*, *Montana* and *Cyanus*. Avetisyan (1964) defined five pollen types as *Jacea*, *Centaurium*, *Scabiosa*, *Serratula* and *Psephellus*. Pehlivan (1994, 1995a,b) studied endemic Turkish *Centaurea* taxa in detail. Her findings are consistent with Wagenitz's *Jacea* and *Cyanus* types. Pinar and Inceoglu (1996) proposed a palynological solution for the taxonomical problems of *C. triumphettii* All., groups A, B and C. They observed that Group C is distinguished from groups A and B on the basis of pollen shape, size and costae and shows characteristics consistent with Wagenitz's *Montana* type. Villodre and Garcia-Jacas (2000) stated that pollen type is one of the most reliable characteristics for establishing phylogeny in this group.

This paper gives detailed information on the pollen morphology of Turkish *Centaurea*, *Psephellus* and *Cyanus* taxa in order to contribute to their taxonomy.

## MATERIALS AND METHODS

Plant samples were collected from different regions of Turkey during our field investigations. Voucher specimens are listed in Table 1. For morphological analysis, pollen grains were prepared according to Wodehouse (1935) and Erdtman (1960). LM observations of nonacetolyzed pollen grains were made with an Olympus binocular microscope at 1000 $\times$  magnification. Acetolyzed pollen were observed and measured with Kyowa microlux-11 and Leica DM LB2 microscopes. All of the morphological parameters investigated are given in Table 2. Measurements are scored for 50 mature pollen grains per slide (Aytug, 1967). Pollen morphological parameters were measured under a Prior light microscope. Photomicrographs were taken with a Leica DM LB2 photomicroscope at 1000 $\times$  magnification.

For SEM, nonacetolyzed pollen grains were mounted on double-stick tape and pulse sputter-coated for 3.5 min with gold. Pollen grains were examined with a Jeol JSM-6060 LV SEM operated at 15kV. Morphological terminology follows Skvarla and Turner (1966), Skvarla et al. (1977), Walker (1974), Faegri and Iversen (1975).

## RESULTS

Under LM, pollen grains are isopolar, radially symmetrical, spheroidal, subprolate, subprolate-spher-

oidal and operculate. Their apertures are often tricolporate, rarely tetracolporate. The amb is circular and intersemiangular (Figs. 1–22). LM and SEM shows exine sculpture to be scabrate and microechinate, and the tectum is perforate (Tab. 2, Figs. 23–44). Exine sculpture is scabrate when the sculpturing elements are less than 1  $\mu\text{m}$ , and microechinate when 1–2  $\mu\text{m}$  (Wagenitz, 1955). The colpus membrane is granulate, granulate-perforate-reticulate and granulate-perforate. The pollen grains of *C. pseudoscabiosa* subsp. *pseudoscabiosa*, *P. pecho*, *P. appendicigera*, *C. pichleri* subsp. *pichleri* and *C. pichleri* subsp. *extrarosularis* have columellae with two layers and exine acaveate (Figs. 13–22, 49). The remaining 25 taxa have columellae with one layer and well developed cavea (e.g., Figs. 1–12, 45–48). The internal columella at the mesocolpia is scored as 3.33  $\mu\text{m}$  for *P. pecho*, 4.94  $\mu\text{m}$  for *C. pichleri* subsp. *pichleri*, 4.65  $\mu\text{m}$  for *C. pichleri* subsp. *extrarosularis*, 3.65  $\mu\text{m}$  for *C. pseudoscabiosa* subsp. *pseudoscabiosa* and 2.65  $\mu\text{m}$  for *P. appendicigera*. External columella values vary from 1.38 to 3.34  $\mu\text{m}$ . The external columella is thickest for *C. antiochia* var. *antiochia* (3.34  $\mu\text{m}$ ) and thinnest for *C. solstitialis* subsp. *pyracantha* (1.38  $\mu\text{m}$ ). The polar axis (P) ranges from 27.03 $\pm$ 1.53 to 52.65 $\pm$ 2.20  $\mu\text{m}$  (non-acetolyzed pollen, W) and 29.26 $\pm$ 1.33 to 68.30 $\pm$ 2.23  $\mu\text{m}$  (acetolyzed, E); the equatorial axis ranges from 26.52 $\pm$ 1.44 to 43.09 $\pm$ 2.61 (W) and 26.75 $\pm$ 0.95 to 51.22 $\pm$ 2.1  $\mu\text{m}$  (E). The polar axis is longest in *C. antiochia* var. *antiochia* (68.30  $\mu\text{m}$ ) and shortest in *C. cariensis* subsp. *longipapposa* (29.26  $\mu\text{m}$ ); the equatorial axis is longest in *C. carduiiformis* subsp. *carduiiformis* (51.22  $\mu\text{m}$ ) and shortest in *C. cariensis* subsp. *longipapposa* (26.75  $\mu\text{m}$ ). In all taxa examined, the width of the porus (plt) [3.52–14.26  $\mu\text{m}$  (W); 5.46–16.64  $\mu\text{m}$  (E)] is bigger than the width of the colpus (clt) [1.79–10.83  $\mu\text{m}$  (W); 4.61–11.04  $\mu\text{m}$  (E)].

Exine was thickest in *C. pichleri* subsp. *extrarosularis* and thinnest in *C. paphlagonica* (Tab. 2). Ektexine/endexine values were calculated at 4/1 for *P. appendicigera*, 3/1 for *P. pecho* and 2/1 for the other examined species. While ektexine thickness decreases at regions close to apertures, endexine becomes thicker. Ektexine at the mesocolpia was thickest (7.16  $\mu\text{m}$ ) for *C. pichleri* subsp. *pichleri* and thinnest (2.27  $\mu\text{m}$ ) for *C. zeybekii*. Ektexine at the aperture was thickest for *C. carduiiformis* subsp. *carduiiformis* (2.91  $\mu\text{m}$ ) and thinnest for *C. zeybekii* (0.81  $\mu\text{m}$ ). In SEM, the number of microspines counted per 5 mm<sup>2</sup> was highest for *C. cariensis* subsp. *longipapposa*, and lowest for *C. babylonica*, *C. paphlagonica*, *C. helenioides*, *C. polyclada*, *C. saligna*, *C. pichleri* subsp. *extrarosularis*, *C. antiochia* var. *antiochia* and *C. stenolepis*. The number of

TABLE 1. List of taxa examined, localities and collectors

Taxa	Date	Collector and herbarium number	Locality
<i>C. zeybekii</i> Wagenitz	08.06.1999	Z.Kaya Y.Genc 681	B1 Izmir: Nif Mt., Ovacik village, 300-450 m., BOF
<i>C. polyclada</i> DC.	07.07.2000	Z.Kaya M.Cetin 482	B1 Izmir: Yamanlar, above Yamanlar, Caparli, roadside, 700 m., BOF
<i>C. cariensis</i> subsp. <i>longipapposa</i> Wagenitz.	28.08.1999	Z.Kaya 605	B/C 3 Isparta: Dede Mt. slope, 1400 m, BOF
<i>C. cariensis</i> subsp. <i>maculiceps</i> (O. Schwarz) Wagenitz	24.05.2001	Z.Kaya M.Agir 1504	C1 Aydın: Buharkent, near geothermal facilities, 200-250 m., BOF
<i>C. consanguinea</i> DC.	27.06.1989	Z. Kaya 312	B7 Elazığ, Karakoçan, 10 km. to Karakoçan, 1200 m
<i>C. aggregata</i> subsp. <i>aggregata</i> Fish.& Mey ex DC.	14.07.1982	Z.Kaya 1170	B7 Elazığ: Kozgediği, 1400 m, BOF
<i>C. cadmea</i> Boiss.	15.07.1999	Z.Kaya 1315	A4 Bartın: Ulus, Ulukaya waterfall at rocky place, 600 m, BOF
<i>C. luschaniana</i> Heimerl	25.05.1999	Z.Kaya 613	C3 Antalya: Termassa Eren Tesis, 800 m, BOF
<i>C. tossiensis</i> Freyn & Sint.	22.09.2000	Z.Kaya 798	A4 Kastamonu: Daday, Agli, Cayozu, open place, 1100 m, BOF
<i>C. stenolepis</i> Kerner	16.08.1999	Z.Kaya 785	A3 Bolu, Mengen, Arak village, open field, 900 m, BOF
<i>C. odyssei</i> Wagenitz	29.08.1994	Z.Kaya F.Hellwig 1741	B1 Balıkesir: Edremit, Baba Mt., Avcılar village, 1450 m, BOF
<i>C. drabifolia</i> subsp. <i>cappadoccica</i> (DC.)Wagenitz	08.07.1990	Z.Kaya 1375	C3 Antalya: Akseki, Yıldızlın, 1800-2400 m, BOF
<i>C. drabifolia</i> subsp. <i>detonsa</i> (Bornm.) Wagenitz	28.08.1999	Z.Kaya 1218	B/C3 Isparta: Dede Mt. slopes, 1600 m, BOF
<i>C. saligna</i> (C.Koch) Wagenitz	24.06.2004	Z.Kaya 703	B7 Elazığ: Alacakaya, 1400-1500 m, BOF
<i>C. helenioides</i> Boiss.	26.08.1992	Z.Kaya 1126	A8 Rize: İkizdere, Anzer, above rocky place, 2200m, BOF
<i>C. paphlagonica</i> (Bornm.) Wagenitz	20.08.1994	Z.Kaya 372	A4 Ankara: Kızılcahamam, Işık Mt., Yukarı cami village, 1400 m, BOF
<i>C. amanicola</i> Hub-Mor.	10.08.1994	R.Binzet 1860	C6 Adana: Osmaniye-Yarpuz road, 1000 m, BOF
<i>C. babylonica</i> (L.) L.	27.06.1991	Z.Kaya F.Hellwig 1275	C5 Hatay: Erzin, Başlamış village, roadside, 600 m, BOF
<i>C. ptosimopappa</i> Hayek	23.06.1999	Z.Kaya F.Hellwig 642	C5 Hatay: Erzin, Başlamış village, 800 m, BOF
<i>C. solstitialis</i> subsp. <i>pyracantha</i> (Bornm.) Wagenitz	19.07.1996	Z.Kaya B.Yaman 723	C3 Antalya: Serik-Antalya road, 20 m, BOF
<i>C. calcitrapa</i> subsp. <i>cilicica</i> (Boiss & Bal) Wagenitz	6.07.1999	Z.Kaya R.Binzet 980	C5 Mersin: Gozne-Sogucak road, 900 m, BOF
<i>C. pestalozzae</i> Boiss.	18.07.1996	Z.Kaya B.Yaman 514	C3 Antalya: Tahtalı Mt., 2100-2200 m, BOF
<i>C. antiochia</i> var. <i>antiochia</i> Boiss.	05.07.2003	M.Bona 1650	C5 Hatay: Habip Neccar Mt., BOF
<i>C. carduiiformis</i> subsp. <i>carduiiformis</i> DC.	06.07.2003	Z.Kaya 760	A4 Ankara: Eymir Lake, 500 m, BOF
<i>C. pseudoscabiosa</i> subsp. <i>pseudoscabiosa</i> Boiss.& Buhse	08.10.2005	K.Kilic 1373	A9 Ardahan, Çıldır Lake 1600 m, BOF
<i>P. pecho</i> Albow.	18.05.2002	Z.Kaya Y.Genc 1867	A8 Artvin: Fistikli village, entrance of Hatilla National Park, 510 m, BOF
<i>P. appendicigera</i> C.Koch	25.08.1994	Z.Kaya F.Hellwig 1114	A8 Rize: İkizdere, Anzer village, Alcagaz locality, 2750 m, BOF
<i>C. pichleri</i> subsp. <i>extrarosularis</i> (Hayek & Siehe) Wagenitz	27.07.2005	A.Cansaran 913	A5 Amasya: Ak Mt., 2050 m, BOF
<i>C. pichleri</i> subsp. <i>pichleri</i> Boiss.	10.06.1999	Z.Kaya 918	A3 Bolu, Mengen, Arak village, open field, 900 m, BOF

BOF – herbarium sheet from the Faculty of Forestry of Bartın University

TABLE 2. Pollen morphological parameters of taxa examined

Taxa	P	E	P/E	L	clg	clt
<b>Section Acrolophus</b>						
<i>C. zeybekii</i> (W)	29.62±1.96	28.41±1.02	1.04	27.01±1.14	25.68±1.14	7.14±1.21
<i>C. zeybekii</i> (E)	31.40±3.03	29.21±1.67	1.07	28.90±1.84	27.79±2.97	6.31±1.11
<i>C. polyclada</i> (W)	28.05±1.15	28.21±0.41	0.99	25.64±1.3	24.93±1.61	5.63±1.21
<i>C. polyclada</i> (E)	34.97±1.55	30.86±1.46	1.13	31.85±1.30	30.60±1.65	7.21±0.89
<i>C. cariensis</i> subsp. <i>longipapposa</i> (W)	30.76±1.63	30.63±1.45	1.00	28.13±1.37	25.34±1.13	7.64±0.93
<i>C. cariensis</i> subsp. <i>longipapposa</i> (E)	29.26±1.33	26.75±0.95	1.09	27.23±1.20	26.69±1.41	4.61±0.79
<i>C. cariensis</i> subsp. <i>maculiceps</i> (W)	28.41±1.65	29.25±1.68	0.97	26.75±1.63	23.52±1.58	5.98±1.10
<i>C. cariensis</i> subsp. <i>maculiceps</i> (E)	37.40±2.43	30.47±1.63	1.22	31.57±5.14	31.71±2.32	6.16±1.50
<i>C. consaguinea</i> (W)	28.53±1.34	27.43±1.67	1.04	26.07±1.36	23.94±1.96	9.18±1.28
<i>C. consaguinea</i> (E)	33.90±2.75	32.19±1.56	1.05	30.92±1.87	27.15±3.16	7.79±1.40
<i>C. aggregata</i> subsp. <i>aggregata</i> (W)	27.27±1.29	26.25±1.34	1.03	26.04±0.28	20.56±0.88	6.10±0.67
<i>C. aggregata</i> subsp. <i>aggregata</i> (E)	35.57±2.24	31.08±1.98	1.14	32.33±1.30	30.38±1.95	8.00±1.02
<b>Section Phalolepis</b>						
<i>C. cadmea</i> (W)	30.14±1.33	29.09±1.25	1.06	27.56±1.03	23.76±1.02	7.03±0.24
<i>C. cadmea</i> (E)	33.84±3.62	30.29±2.25	1.17	30.37±3.04	29.76±3.42	7.52±1.19
<i>C. luschaniana</i> (W)	32.85±2.25	31.18±2.37	1.05	29.18±0.81	25.83±1.13	7.45±1.21
<i>C. luschaniana</i> (E)	38.26±2.09	36.20±1.84	1.05	35.78±1.70	33.94±1.67	10.11±1.05
<i>C. tossiensis</i> (W)	27.03±1.53	26.52±1.44	1.01	24.42±1.72	21.08±1.46	9.07±1.21
<i>C. tossiensis</i> (E)	43.06±2.28	40.67±2.68	1.05	38.12±1.53	35.71±1.62	6.12±1.19
<b>Section Jacea</b>						
<i>C. stenolepis</i> (W)	29.19±2.44	30.74±1.68	0.95	29.33±1.14	25.16±3.59	9.91±1.30
<i>C. stenolepis</i> (E)	42.62±2.18	39.95±1.89	1.07	40.09±1.65	34.59±2.45	10.04±1.48
<b>Section Pterocantha</b>						
<i>C. odyssei</i> (W)	30.49±1.58	30.54±1.33	0.99	28.92±0.82	25.85±1.08	8.95±1.84
<i>C. odyssei</i> (E)	46.51±3.03	38.60±1.97	1.2	40.93±2.68	36.76±2.13	8.56±1.14
<b>Section Cheirolepis</b>						
<i>C. drabifolia</i> subsp. <i>capadoccica</i> (W)	31.74±2.46	32.29±1.89	0.98	30.33±1.51	27.16±1.02	6.02±0.89
<i>C. drabifolia</i> subsp. <i>capadoccica</i> (E)	44.60±2.11	37.49 ±1.81	1.18	39.88±2.09	37.49±2.81	7.15±1.29
<i>C. drabifolia</i> subsp. <i>detonsa</i> (W)	34.75±1.43	34.11±1.47	1.02	32.43±1.11	27.43±0.91	8.77±1.11
<i>C. drabifolia</i> subsp. <i>detonsa</i> (E)	45.59±2.46	37.39±1.29	0.03	42.10±2.50	40.06±3.01	7.70±1.08
<i>C. saligna</i> (W)	41.06±1.83	40.45±1.88	1.01	39.18±1.23	38.17±0.98	1.79±0.50
<i>C. saligna</i> (E)	48.11±2.96	43.67±2.76	1.10	44.37±3.27	40.02±2.39	9.93±1.24
<b>Section Grossheimia</b>						
<i>C. helenioides</i> (W)	40.97±2.25	41.06±3.03	0.99	36.79±2.03	33.92±2.48	10.63±1.67
<i>C. helenioides</i> (E)	51.79±2.40	41.64±2.40	1.24	44.41±3.27	41.72±2.15	7.97±1.77
<b>Section Plumosipappus</b>						
<i>C. paphlagonica</i> (W)	37.28±2.62	37.48±1.47	0.99	38.76±1.54	31.82±1.80	8.38±0.59
<i>C. paphlagonica</i> (E)	53.55±3.03	39.27±2.68	1.36	41.38±4.88	44.07±3.12	6.40±1.03
<b>Section Cynaroides</b>						
<i>C. amanicola</i> (W)	35.42±1.57	31.75±2.43	1.12	29.58±1.11	27.23±0.96	3.52±0.47
<i>C. amanicola</i> (E)	41.08±2.81	38.33±1.94	1.07	38.13±3.29	34.21±2.56	6.89±1.03
<b>Section Microlophus</b>						
<i>C. babylonica</i> (W)	34.59±1.73	31.48±1.82	1.10	30.13±1.25	29.10±1.23	6.03±0.15
<i>C. babylonica</i> (E)	43.90±2.37	35.74±2.27	1.23	38.77±2.20	37.94±2.66	7.27±1.20
<b>Section Ptosimopappus</b>						
<i>C. ptosimopappa</i> (W)	30.04±2.11	29.68±1.97	1.01	28.13±1.14	23.79±1.56	6.27±0.93
<i>C. ptosimopappa</i> (E)	43.02±2.55	36.96±1.44	1.16	38.31±1.23	33.45±3.11	6.77±0.96

plg	plt	plg/ plt	plt...clt	t	Exine	Intin	costae	dh	dt	Orn.
8.16±1.41	8.57±1.12	0.95	plt>clt	6.76±1.18	1.47±0.46	0.5±0.11	not-meas	not-meas	not-meas	S
5.74±0.98	7.50±1.66	0.76		6.67±1.03	2.80±0.25	Absent	2.23±0.45	0.83±0.16	1.69±0.27	
7.08±0.6	7.81±0.41	0.90	plt>clt	6.17±2.12	1.06±0.2	0.82±0.04	not-meas	not-meas	not-meas	S
7.52±1.00	8.86±1.35	0.84		7.75±1.28	2.81±0.35	Absent	1.86±0.16	0.94±0.10	2.02±0.40	
7.61±0.87	8.35±0.93	0.91	plt>clt	9.38±0.64	2.42±0.42	0.52±0.07	not-meas	not-meas	not-meas	S
4.50±0.89	5.46±1.21	0.82		5.73±0.79	2.83±0.42	Absent	2.34±0.53	0.60±0.19	1.52±0.34	
5.57±1.23	6.22±1.17	0.89	plt>clt	6.14±0.78	2.80±0.63	0.63±0.11	not-meas	not-meas	not-meas	S
6.35±1.00	6.75±1.91	0.94		6.46±0.95	2.88±0.48	Absent	2.11±0.38	0.55±0.18	1.22±0.38	
10.09±1.59	9.18±1.28	1.10	plt>clt	6.80±0.54	1.80±0.10	0.54±0.11	not-meas			S
10.40±2.37	11.70±1.70	0.89		6.97±1.30	3.75±0.56	Absent	2.88±0.44	<1µm	-	
5.71±0.97	5.88±0.96	0.97	plt>clt	7.10±0.58	2.45±0.63	0.88±0.66	not-meas.			S
8.38±1.23	11.18±1.59	0.75		7.33±1.19	3.33±0.34	Absent	2.39±0.47	<1µm	-	
6.60±1.25	7.73±1.24	0.85	plt>clt	7.42±0.41	2.45±0.34	0.74±0.15	not-meas	not-meas	not-meas	S
6.70±1.39	8.76±1.91	0.76		7.78±1.34	2.91±0.27	Absent	2.24±0.45	0.70±0.20	1.39±0.45	
7.70±1.14	7.45±1.04	1.03	plt>clt	5.99±0.61	3.67±0.63	0.80±0.09	not-meas.			S
10.63±1.18	12.07±1.10	0.88		7.18±1.03	2.98±0.26	Absent	2.44±0.49	<1µm	-	
9.18±1.44	9.24±1.27	0.99	plt>clt	8.22±1.01	1.76±0.47	0.44±0.06	not-meas	not-meas	not-meas	S
5.17±1.11	7.14±1.35	0.72		6.32±1.28	3.18±0.46	Absent	2.24±0.51	0.91±0.25	2.04±0.35	
7.53±0.99	8.07±1.28	0.86	plt>clt	7.35±0.78	2.07±0.35	0.5±0.11	not-meas.	1.10±0.09	1.30±0.09	M
8.67±1.15	12.61±1.36	0.69		8.99±1.47	3.59±0.46	Absent	2.99±0.51	1.76±0.35	4.05±0.74	
9.02±2.67	8.95±1.84	1.01	plt>clt	9.02±1.08	1.92±0.07	0.52±0.07	not-meas	0.94±0.09	1.39±0.10	S
8.86±1.14	12.55±1.63	0.71		8.69±1.44	3.77±0.40	Absent	2.81±0.39	not-meas	not-meas	
6.45±1.23	6.69±1.12	0.96	plt>clt	7.69±0.78	1.65±0.37	0.74±0.11	not-meas.	0.52±0.18	1.42±0.77	S
7.45±1.59	6.91±1.59	1.07		9.69±1.20	2.91±0.26	Absent	2.72±0.51	0.93±0.14	2.14±0.43	
6.12±0.85	7.08±0.99	0.86	plt>clt	7.85±0.71	2.34±0.31	0.88±0.08	not-meas.	0.61±0.18	1.32±0.31	S
8.03±1.34	9.10±1.52	0.88		7.39±1.40	2.97±0.29	Absent	2.20±0.50	0.97±0.18	1.85±0.28	
10.74±1.20	9.27±1.20	1.15	plt>clt	9.52±1.15	1.18±0.13	1.06±0.14	not-meas.	0.65±0.18	1.12±0.11	S
9.60±1.25	13.42±1.60	0.72		10.34±1.81	3.78±0.22	Absent	2.86±0.41	not-meas	not-meas	
11.16±2.09	11.78±1.67	0.94	plt>clt	10.81±1.30	2.75±0.64	0.74±0.14	not-meas	0.92±0.15	1.38±0.11	M
8.07±1.54	8.40±1.91	0.96		7.85±1.50	3.13±0.48	Absent	2.69±0.63	1.64±0.38	3.36±0.78	
8.29±1.33	8.38±0.59	0.99	plt>clt	7.42±0.53	1.89±0.39	0.51±0.09	not-meas	0.91±0.33	2.06±0.53	M
9.53±1.16	9.60±1.68	0.99		2.53±0.65	2.48±0.47	Absent	Absent	1.25±0.37	2.56±0.65	
3.21±0.48	3.52±0.47	0.91	plt>clt	5.97±0.48	2.52±0.41	0.92±0.09	not-meas.	0.67±0.02	1.53±0.10	S
7.68±0.83	9.89±1.13	0.78		7.94±1.22	4.55±0.52	Absent	4.02±0.63	0.95±0.13	2.04±0.37	
6.15±0.12	8.15±0.63	0.75	plt>clt	6.23±1.11	2.14±0.31	0.41±0.23	not-meas.	1.00±0.13	1.96±0.50	M
7.63±1.22	9.28±1.74	0.82		7.85±1.14	3.26±0.50	Absent	3.18±0.50	1.09±0.22	2.26±0.56	
5.66±0.89	6.27±0.93	0.90	plt>clt	7.65±1.06	2.90±0.53	0.80±0.16	not-meas.	1.16±0.18	1.91±0.58	M
7.30±0.84	8.92±1.38	0.82		7.37±1.16	3.88±0.50	Absent	2.78±0.48	1.86±0.21	3.99±0.52	

TABLE 2. continued

Taxa	P	E	P/E	L	clg	clt
<b>Section Mesocentron</b>						
<i>C. solstitialis</i> subsp. <i>pyracantha</i> (W)	30.62±1.30	26.14±1.32	1.17	25.12±1.11	24.01±1.02	7.21±0.52
<i>C. solstitialis</i> subsp. <i>pyracantha</i> (E)	40.06±2.56	32.69±2.09	1.23	35.23±2.48	35.84±2.66	6.79 ±1.60
<b>Section Calcitrapa</b>						
<i>C. calcitrapa</i> subsp. <i>cilicica</i> (W)	27.81±1.08	27.70±0.67	1.00	27.04±2.71	22.84±0.63	5.61±1.05
<i>C. calcitrapa</i> subsp. <i>cilicica</i> (E)	38.86±2.44	29.90±1.57	1.29	34.77±2.06	30.57±3.13	5.98±1.30
<b>Section Acrocentron</b>						
<i>C. pestalozzae</i> (W)	47.73±3.72	37.57±2.22	1.27	35.07±2.49	34.65±1.23	8.47±1.13
<i>C. pestalozzae</i> (E)	59.86±5.01	44.73±3.27	1.34	46.08±3.49	44.94±5.37	7.52±1.16
<i>C. antiochia</i> (W)	52.65±2.20	41.71±2.60	1.26	39.71±1.07	44.03±1.02	10.83±1.74
<i>C. antiochia</i> (E)	68.30±2.23	49.48±1.72	1.38	55.07±2.05	48.34±3.18	6.82±1.32
<i>C. carduiiformis</i> subsp. <i>carduiiformis</i> (W)	39.14±2.93	40.98±1.96	0.95	51.41±0.63	30.37±1.72	4.82±1.59
<i>C. carduiiformis</i> subsp. <i>carduiiformis</i> (E)	67.57 ±2.46	51.22±2.1	1.32	52.30±4.00	46.00±3.05	7.80±1.31
<i>C. pseudoscabiosa</i> subsp. <i>pseudoscabiosa</i> (W)	33.15±1.39	34.14±1.20	0.97	32.47±1.40	29.02±2.03	7.79±1.69
<i>C. pseudoscabiosa</i> subsp. <i>pseudoscabiosa</i> (E)	39.99±2.02	42.45±1.46	0.94	39.97±1.84	31.12±2.32	9.79±1.58
<i>Phsephellus</i>						
<i>P. pecho</i> (W)	40.60±1.23	36.76±1.16	1.10	34.68±1.17	33.68±1.62	8.16±1.44
<i>p. pecho</i> (E)	55.80±1.98	43.22±1.51	1.29	48.44±2.07	43.08±2.56	8.84±1.19
<i>P.appendicigera</i> (W)	37.12±1.43	35.34±2.53	1.05	33.04±1.15	26.32±1.84	8.63±1.58
<i>P.appendicigera</i> (E)	45.53±3.05	42.22±2.40	1.07	41.06±2.82	36.55±3.16	11.04±1.34
<i>Cyanus</i>						
<i>C. pichleri</i> subsp. <i>extrarosularis</i> (W)	42.20±1.63	40.16±2.39	1.05	38.53±2.84	35.92±2.21	8.86±1.68
<i>C. pichleri</i> subsp. <i>extrarosularis</i> (E)	65.03±3.95	46.63±2.16	1.39	51.20±2.51	52.06±3.77	10.23±2.19
<i>C. pichleri</i> subsp. <i>pichleri</i> (W)	44.54±1.78	40.52±1.76	1.10	39.71±1.12	35.01±2.21	8.12±2.12
<i>C. pichleri</i> subsp. <i>pichleri</i> (E)	65.96±2.86	48.78±2.46	1.35	55.53±2.87	51.22±3.16	10.52±2.22

perforations was highest for *C. pichleri* subsp. *extrarosularis*, *C. cariensis* subsp. *longipapposa*, *C. odyseyi* and *C. pestalozzae*. The distance between spines ranged from 0.28 µm (*C. cariensis* subsp. *longipapposa*) to 2.02 µm (*C. paphlagonica*). Operculum diameter ranged from 4.49 µm (*C. odyseyi*) to 10.61 µm (*C. pichleri* subsp. *extrarosularis*).

## DISCUSSION

In recent taxonomic revisions of the genus *Centaurea* (Wagenitz and Hellwig, 2000; Greuter, 2003a,b; Hellwig, 2004), several of our investigated species were excluded from this genus and shifted to the genus *Psephellus* (*C. appendicigera*, *C. pecho*) and to the genus *Cyanus*, [*C. pichleri* subsp. *pichleri* Boiss., *C. pichleri* subsp. *extrarosularis* (Hayek and Siehe) Wagenitz]. In Turkey, the first detailed morphological analyses of pollen grains in *Centaurea* were made by Wagenitz (1955) and Avetisian (1964) in an attempt to solve phylogenetic problems in this genus. Wagenitz (1955) typified *Centaurea* pollen grains by morphological features. He used the following features to group acetolyzed pollen: pollen shape, exine ornamentation, internal and external layers of columellae, length of colpus,

pore shape and costae. *Serratula*, *Crupina* and *Centaureum* pollen types were recognized as the most primitive, *Dealbata*, *Cyanus* and *Montana* as intermediate, and *Scabiosa* and *Jacea* as the most advanced types.

Some authors have asserted that the presence of single or double layers of columellae of the pollen wall can be used as principal criteria in taxonomic arguments (Wagenitz, 1955; Skvarla et al., 1977). Here we used some additional features such as apocolpium and intine thickness. Pollen grains of 22 taxa analyzed in this study represent Wagenitz's *Jacea* pollen type based on the following characters: spheroidal-subprolate, costae, scabrate and microechinate ornamentation, long colpus, and the presence of cavea, (Tab. 2, Figs. 1–8, 23–28, 45–48).

Pehlivan (1996) and Çelik et al. (2005) placed pollen grains of *C. consanguinea* in the *Jacea* type. In recent taxonomy, *C. pecho* and *C. appendicigera* have been transferred to genus *Psephellus* (Wagenitz and Hellwig, 2000; Greuter, 2003a,b; Hellwig, 2004). Our results show that the pollen grains of the two taxa resemble the *Montana* type in such characters as long colpus and thick costae, subprolate-prolate shape, and being acaveate (Figs. 15–18, 37–40, 49), rather than the *Psephellus* pollen type. Pollen grains of *C. pseudoscabiosa* subsp. *pseudoscabiosa* (Sect.

plg	plt	plg/ plt	plt>clt	t	Exine	Intin	costae	dh	dt	Orn.
5.98±1.02	7.21±0.52	0.82	plt>clt	6.32±0.48	0.90±0.12	0.69±0.10	not-meas.	0.63±0.22	1.02±0.23	S
7.35±1.13	8.93±1.40	0.82		7.44±1.06	2.95±0.35	Absent	2.55±0.54	0.95±0.13	2.04±0.37	
4.79±1.04	7.61±1.05	0.61	plt>clt	7.34±0.72	2.19±0.27	0.41±0.17	not-meas.	not-meas.	not-meas.	S
6.19±0.77	6.20±1.60	1.22		5.76±0.98	2.82±0.43	Absent	2.12±0.56	0.89±0.12	1.69±0.50	
8.16±1.15	8.47±1.65	0.96	plt>clt	not-meas.	2.70±0.95	0.82±0.31	not-meas.	<1µm	-	S
9.41±1.48	11.19±1.59	0.84			4.10±0.81	Absent	3.32±0.61			
9.69±1.79	9.10±1.90	1.06	plt>clt	not-meas.	3.06±1.02	Absent	not-meas.	<1µm	-	S
11.35±1.74	8.14±1.58	1.39			4.27±0.57		3.68±0.73			
5.79±1.88	5.11±1.72	1.16	plt>clt	7.58±1.06	3.11±0.66	0.55±0.06	not-meas.	not-meas.	not-meas.	S
10.49±1.90	8.06±1.78	1.30		12.60±2.52	4.85±0.57	Absent	3.87±0.57	0.87±1.78	1.67±0.24	
11.52±1.96	12.21±1.79	0.94	plt>clt	6.13±1.24	2.03±0.42	not-meas.	not-meas.	<1µm	-	S
13.32±1.90	14.25±1.89	0.93		8.41±1.60	4.08±0.52	Absent	2.59±0.46			
6.12±1.14	11.22±1.64	0.54	plt>clt	11.22±1.92	2.55±0.59	0.80±0.12	not-meas.	<1µm	-	S
10.10±1.11	13.07±1.61	0.77		11.37±1.91	4.28±0.49	Absent	2.42±0.65			
8.03±1.32	10.63±1.58	0.75	plt>clt	8.05±1.43	3.86±0.86	1.24±0.07	not-meas.	not-meas.	not-meas.	M
12.72±1.72	14.24±2.06	0.89		10.44±1.91	5.29±0.49	Absent	2.76±0.57	1.03±0.13	1.97±0.51	
11.68±1.45	14.26±2.32	0.85	plt>clt	7.69±1.96	3.57±0.23	0.91±0.63	not-meas.	<1µm	-	S
13.77±2.56	16.64±3.30	0.83		10.20±2.09	5.87±0.56	Absent	4.07±0.72			
9.23±1.35	13.13±1.96	0.70	plt>clt	8.01±0.91	4.05±0.44	0.87±0.55	not-meas.	<1µm	-	S
11.73±1.68	15.43±2.36	0.76		10.28±1.75	4.94±0.49	Absent	3.67±0.80			

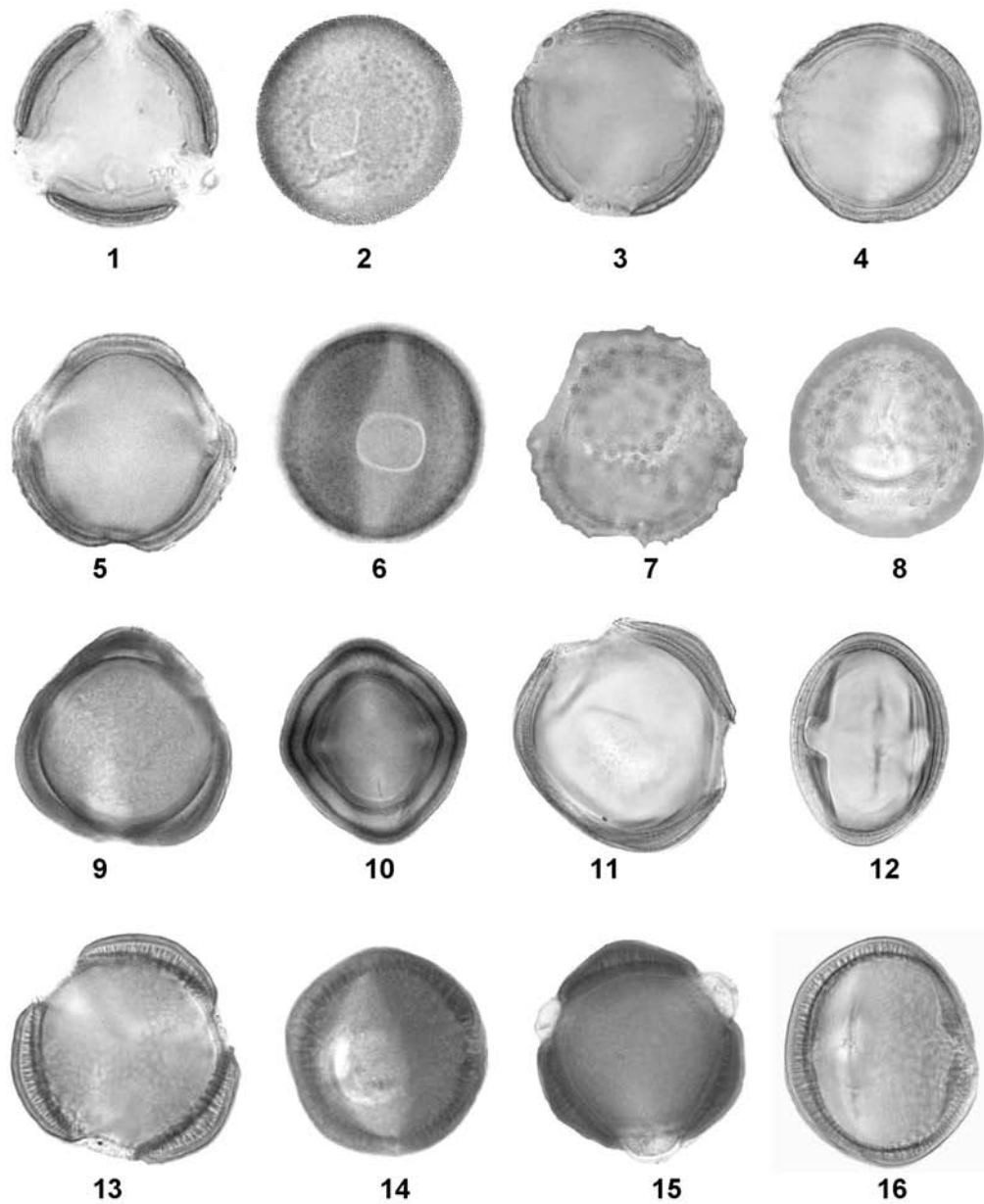
W – Non-acetolyzed pollen grains; E – Acetolyzed pollen grains; P – Polar axis; E – Equatorial axis; L – Equatorial contour diameter; clg – Length of colpus; clt – Width of colpus; plg – Length of porus; plt – Width of porus; t – Length of one side of triangular polar area (apocolpium); dh – Length of spine; dt – Width of spine; Orn – Ornamentation (Exine sculpture); S – Scabrate; M – Microechinate.

*Acrocentron*) should be evaluated as *Dealbata* type (spheroidal pollen shape, short colpus length and small size) (Figs. 13, 14, 35, 36). Although pollen grains of *C. pseudoscabiosa* subsp. *pseudoscabiosa* represent the *Dealbata* pollen type according to Wagenitz's classification, it was not included in genus *Psephellus*. The *Dealbata* pollen type is a diagnostic feature of genus *Centaurea*, which was classified as genus *Psephellus* by Wagenitz and Hellwig (2000) and Garcia-Jacas et al. (2001). Wagenitz and Hellwig (2000) stated that the same pollen type was found in several sections of *Centaurea* centered in eastern Turkey, Caucasia and northwest Iran.

Pollen shape in *C. pichleri* subsp. *extrarosularis* and subsp. *pichleri* is subprolate with a long colpus, strong costae, and acaveate, resembling the *Cyanus* type (Figs. 19–22, 41–44), while pollen of *C. pestalozzae* and *C. carduiiformis* subsp. *carduiiformis* (Sect. *Acrocentron*) better fits the *Scabiosa* type based on cavea character, subprolate pollen shape, scabrate ornamentation and thick costae (Figs. 9–12, 29, 30, 33, 34). The *Cyanus* and *Montana* pollen types are limited to *Centaurea* sect. *Cyanus*, and the *Scabiosa* type is

characteristic of sect. *Acrocentron* in its broadest sense (Garcia-Jacas et al., 2000). Pehlivan (1994, 1995a,b, 1996) determined that the pollen grains of the studied taxa are consistent with the *Jacea* and *Cyanus* pollen types. Although Pinar and Inceoglu (1996) found some morphological differences (e.g., pollen shape and size, costae features) between group C and groups A and B of *Centaurea triumfettii* All., they evaluated all pollen grains of the investigated taxa as belonging to the *Montana* type of Wagenitz (1955).

Avetisjan (1964) divided the *Jacea* type into six subgroups based on morphological variations she determined in this pollen type. She also combined the *Dealbata*, *Montana* and *Cyanus* types into one big group, *Psephellus*. In the *Jacea* pollen type the spines are reduced, are subprolate-spheroidal, and there are caveae between the basal layer and columellae. The *Scabiosa* type, with cavea, is more advanced than *Centaurium* with no cavea. In the *Dealbata* type the pollen grains are small with subprolate-spheroidal shape, while in *Montana* and *Cyanus* the pollen is subprolate-prolate. On the basis of her typification, the pollen of *P. pecho*, *P. appendisigera*,

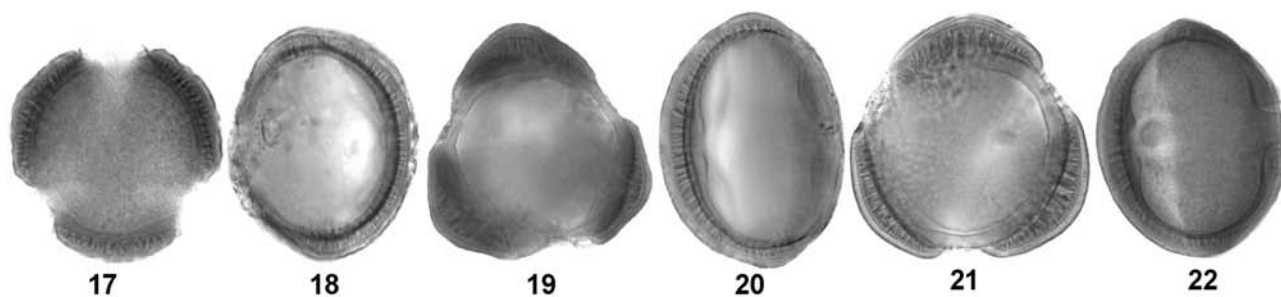


**Figs. 1–16.** Pollen grains of *Centaurea* taxa. **Figs. 1, 2.** *C. cariensis* subsp. *maculiceps*, polar view (Fig. 1) and equatorial view (Fig. 2). **Figs. 3, 4.** *C. cariensis* subsp. *longipapposa*, polar view (Fig. 3) and equatorial view (Fig. 4). **Figs. 5, 6.** *C. consanguinea*, polar view (Fig. 5) and equatorial view (Fig. 6). **Figs. 7, 8.** *C. drabifolia* subsp. *capadoccica*, polar view and ornamentation (Fig. 7) and equatorial view and ornamentation (Fig. 8). **Figs. 9, 10.** *C. pestalozzae*, polar view (Fig. 9) and equatorial view (Fig. 10). **Figs. 11, 12.** *C. carduiiformis* subsp. *carduiiformis*, polar view (Fig. 11) and equatorial view (Fig. 12). **Figs. 13, 14.** *C. pseudoscabiosa* subsp. *pseudoscabiosa*, polar view (Fig. 13) and equatorial view (Fig. 14). **Figs. 15, 16.** *P. pecho*, polar view (Fig. 15) and equatorial view (Fig. 16). Bar = 10 µm. Figs. 1, 3–5, 7, 8, 11–13, 16 – acetolyzed pollen grains; Figs. 2, 6, 9, 10, 14, 15 – nonacetolyzed pollen grains.

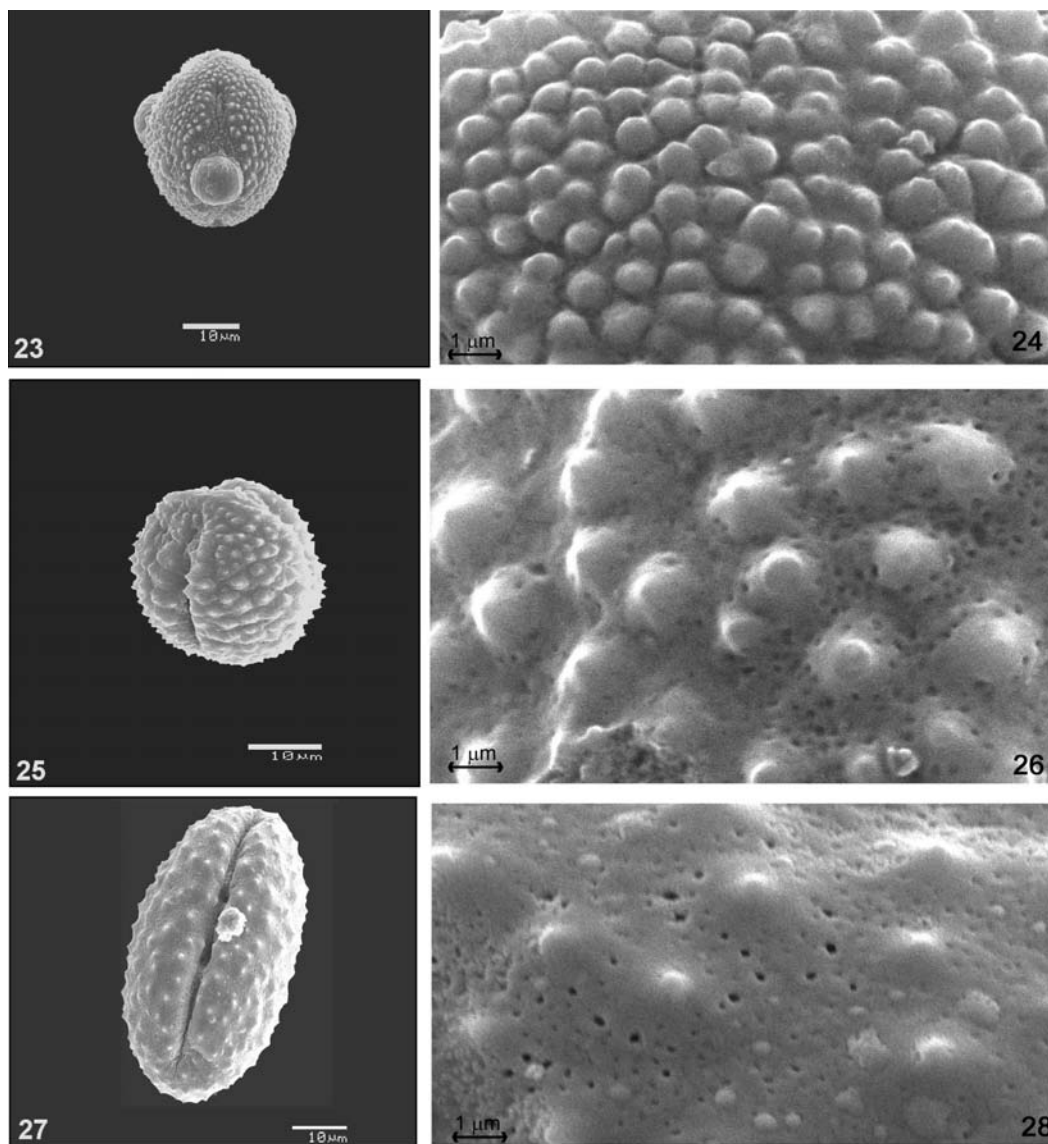
*C. pichleri* subsp. *pichleri*, subsp. *extrarosularis*,  
*C. pseudoscabiosa* subsp. *pseudoscabiosa* is  
*Psephellus* type (Figs. 13–22).

Wagenitz (1955, 1976) put forward the idea that  
reduction of the spine and inner columellae, lengthening  
of the colpus and thickening of the costae are

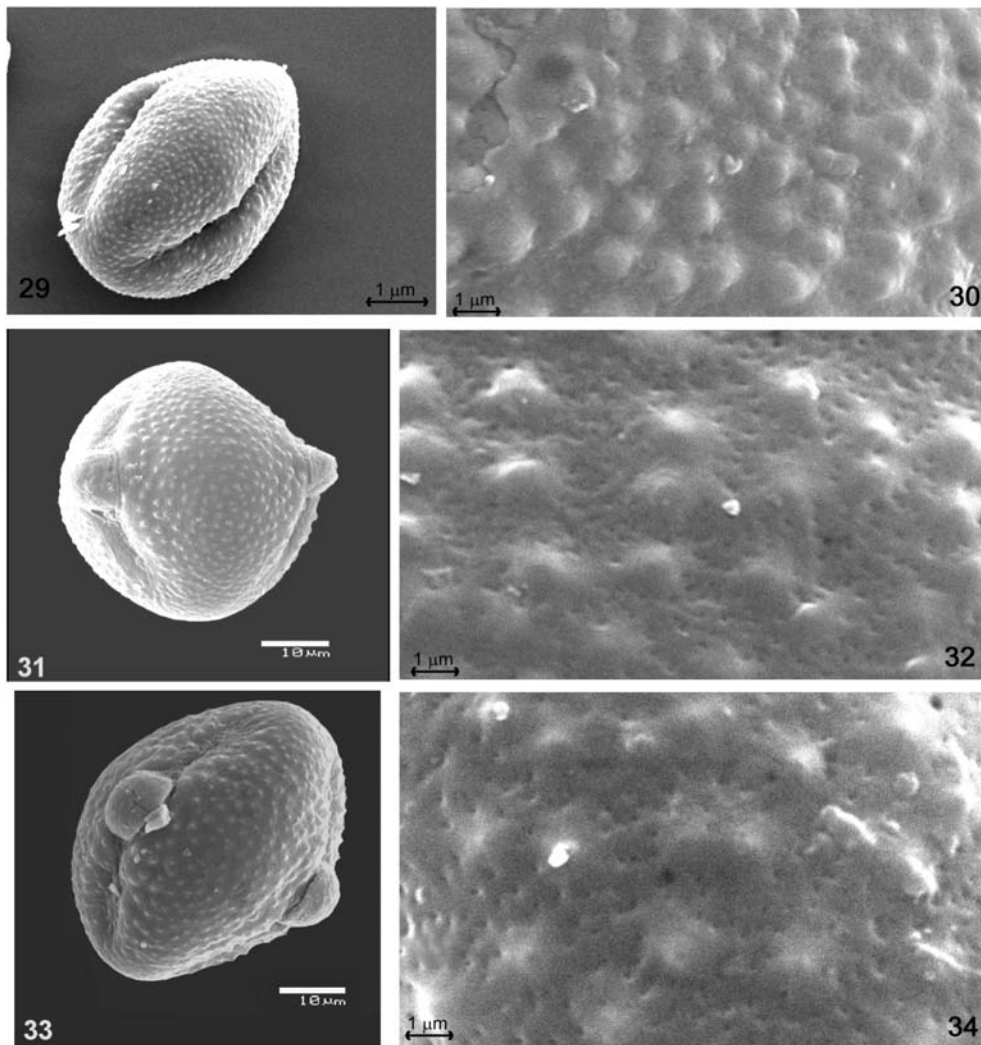




**Figs. 17–22.** Pollen grains of *Psephellus* and *Centaurea* taxa. **Figs. 17, 18.** *P. appendicigera*, polar view (Fig. 17) and equatorial view (Fig. 18). **Figs. 19, 20.** *C. pichleri* subsp. *extrarosularis*, polar view (Fig. 19) and equatorial view (Fig. 20). **Figs. 21, 22.** *C. pichleri* subsp. *pichleri*, polar view (Fig. 21) and equatorial view (Fig. 22). Bar = 10  $\mu$ m. Figs. 18–21 – acetolyzed pollen grains; Figs. 17, 22 – nonacetolyzed pollen grains.



**Figs. 23–28.** Pollen grains of *Centaurea* taxa in SEM. **Figs. 23, 24.** *C. consanguinea*, equatorial view (Fig. 23) and scabrate exine surface (Fig. 24). **Figs. 25, 26.** *C. stenolepis*, equatorial view (Fig. 25) and microechinate exine surface (Fig. 26). **Figs. 27, 28.** *C. paphlagonica*, equatorial view (Fig. 27) and microechinate exine surface (Fig. 28).



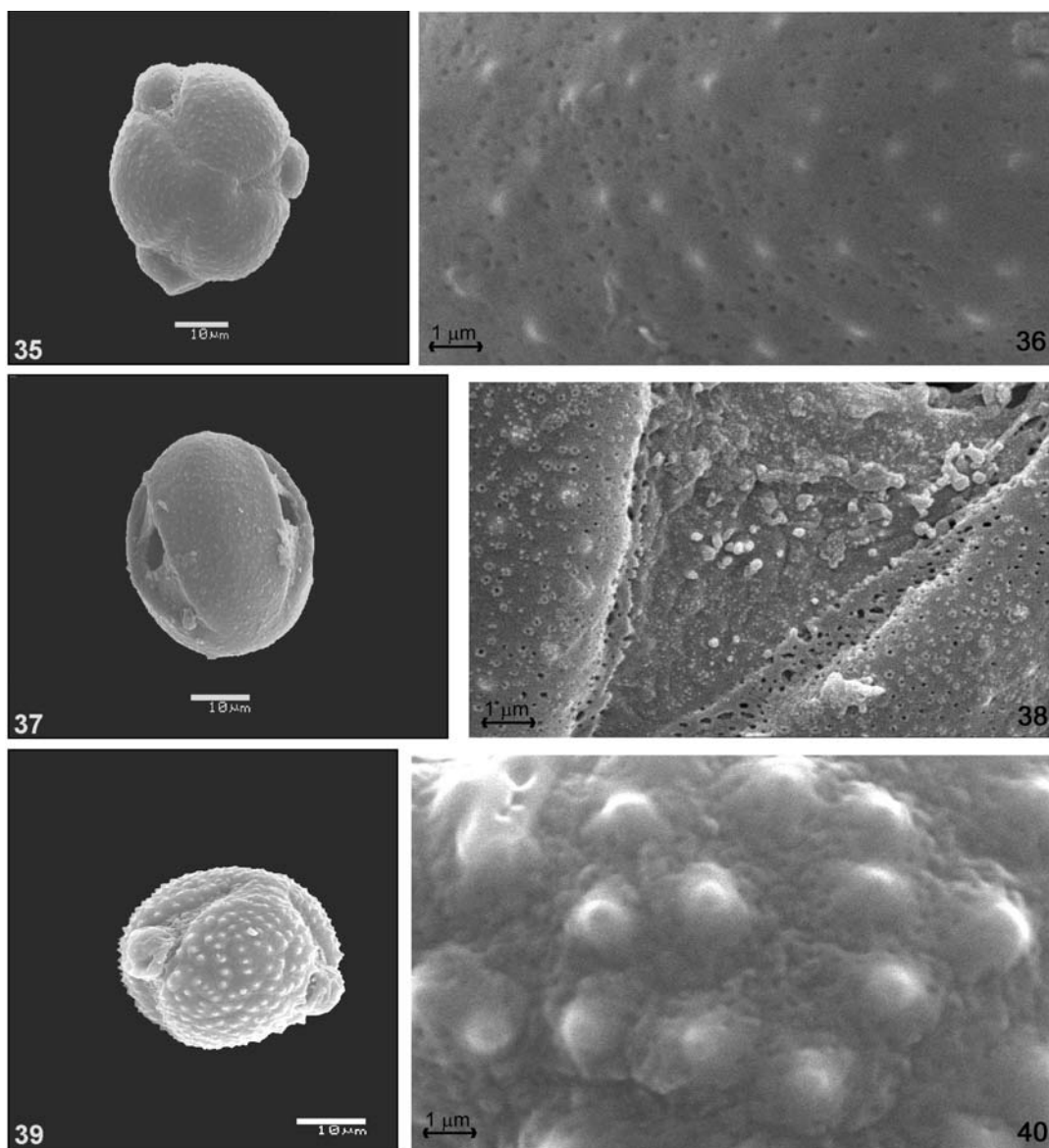
**Figs. 29–34.** Pollen grains of *Centaurea* taxa in SEM. **Figs. 29, 30.** *C. pestalozzae*, equatorial view (Fig. 29) and scabrate exine surface (Fig. 30). **Figs. 31, 32.** *C. antiochia*, equatorial view (Fig. 31) and scabrate exine surface (Fig. 32). **Figs. 33, 34.** *C. carduiformis* subsp. *carduiformis*, equatorial view (Fig. 33) and scabrate exine surface (Fig. 34).

progressive characteristics in the Asteraceae family. We determined that, apart from *P. appendicigera*, *C. helenioides*, *C. stenolepis*, *C. paphlagonica*, *C. babylonica*, *C. ptosimopappa*, in the taxa we studied the spines are shorter than 1  $\mu\text{m}$ . The costae in *C. amanicola* and *C. pichleri* subsp. *extrarosularis* are quite thick (Tab. 2).

Skvarla et al. (1977) divided Asteraceae pollen by exine structure into four different groups: Helianthoid, Senecioid, Arctotoid and Anthemoid. We determined that apart from *C. pseudoscabiosa* subsp. *pseudoscabiosa*, *P. pecho*, *P. appendicigera*, *C. pichleri* subsp. *pichleri* and *C. pichleri* subsp. *extrarosularis* all the taxa have single-layered columellae, a thin

cavea and a thinner internal columellae, therefore resembling the Helianthoid type. *C. pseudoscabiosa* subsp. *pseudoscabiosa*, *P. pecho*, *P. appendicigera*, *C. pichleri* subsp. *pichleri* and subsp. *extrarosularis* belong to the Anthemoid type with their two-layered columellae and being acaveate (Figs. 13–22, 49). Pehlivan (1994, 1995 a, b, 1996) found that the pollen of the species she examined show consistency with the Anthemoid and Helianthoid types.

An operculum found on the aperture area is accepted as a progressive evolutionary characteristic (Pehlivan, 1994). In our study an operculum was identified in all examined taxa (Figs. 6, 10, 18).



**Figs. 35–40.** Pollen grains of *Centaurea* and *Psephellus* taxa in SEM. **Figs. 35, 36.** *C. pseudoscabiosa* subsp. *pseudoscabiosa*, polar view (Fig. 35) and scabrate exine surface (Fig. 36). **Figs. 37, 38.** *P. pecho*, equatorial view (Fig. 37) and granulate-perforate colpus membrane surface with reticulate colpus margin (Fig. 38). **Figs. 39, 40.** *P. appendicigera*, equatorial view (Fig. 39) and microechinate exine surface (Fig. 40).

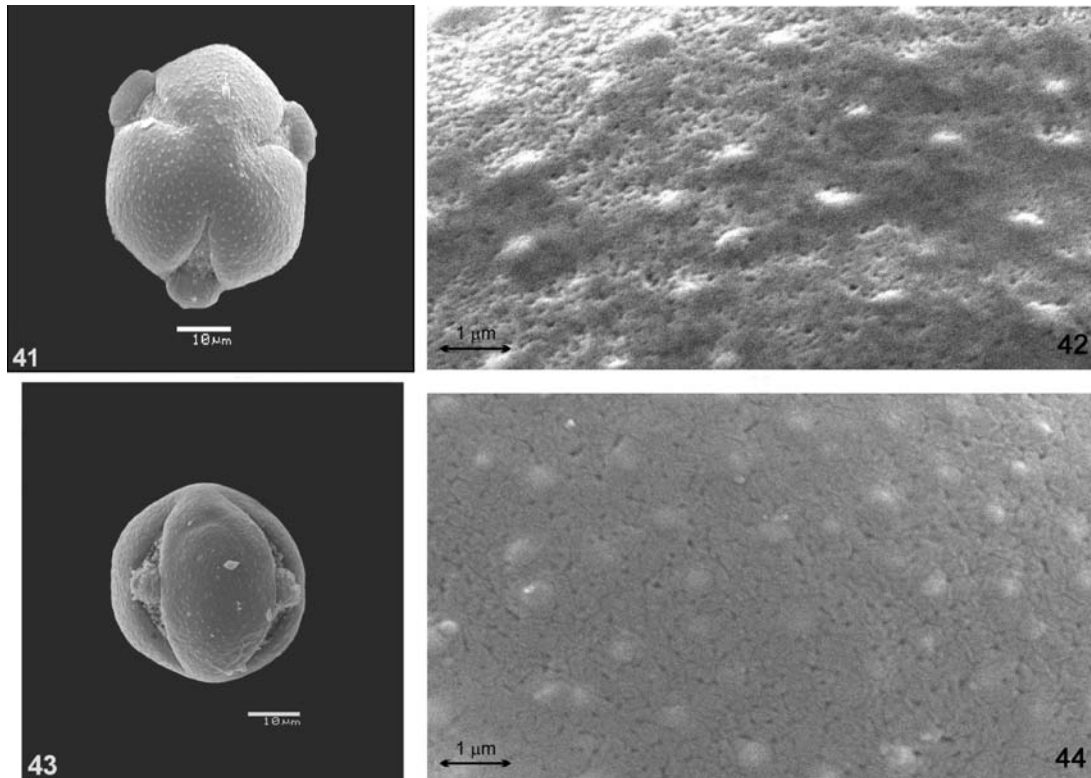
Skvarla et al. (1977) and Stix (1960) claimed that subapical holes in the spine base in Asteraceae are a good taxonomic character for discriminating taxa. Subapical holes in the spine base were observed in all investigated taxa (Figs. 24, 26, 28, 30, 32, 34, 36, 38, 40, 42, 44).

In this study, pollen characters (pollen shape, exine structure, the presence of single- or double-layer columellae, costae thickness and sculpturing) proved to be useful classification characters.

Further morphological, karyological, palynological and molecular studies will help solve problems related to the taxonomy of these genera.

#### ACKNOWLEDGEMENTS

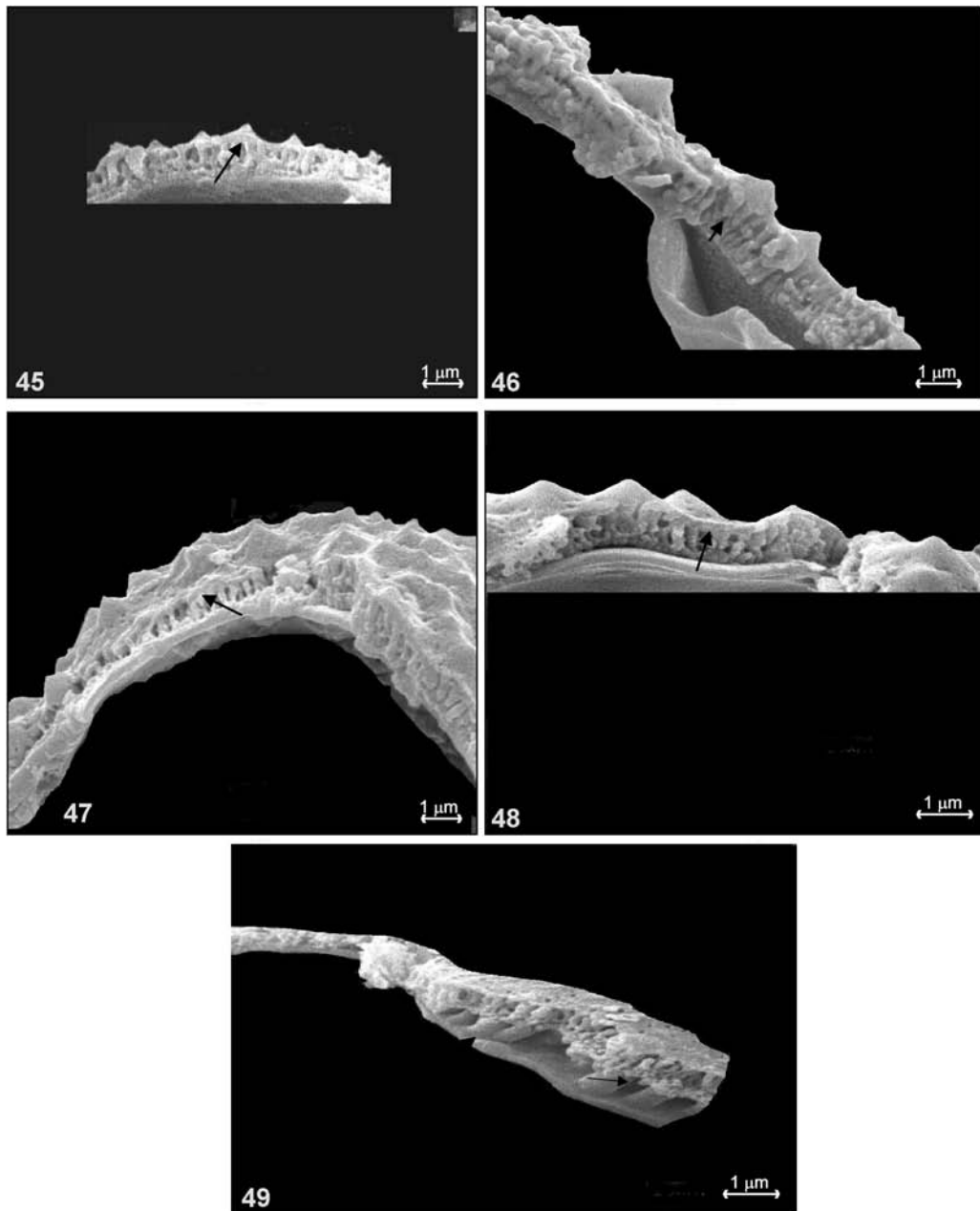
We thank Prof. Dr. Mecit Vural and Bilal Sahin, Ph.D., for verifying plant materials, and Evren Cabi and Umut Toprak for helping to edit the manuscript.



**Figs. 41–44.** Pollen grains of *Centaurea* taxa in SEM. **Figs. 41, 42.** *C. pichleri* subsp. *extrarosularis*, polar view (Fig. 41) and scabrate exine surface (Fig. 42). **Figs. 43, 44.** *C. pichleri* subsp. *pichleri*, equatorial view (Fig. 43) and scabrate exine surface (Fig. 44).

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**Figs. 45–49.** Exine structure in SEM. Single-layered columellae (arrows) in *C. cadmea* (Fig. 45), *C. helenoides* (Fig. 46), *C. babylonica* (Fig. 47), *C. ptosimopappa* (Fig. 48) and two-layered columella (arrow) in *P. pecho* (Fig. 49).

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