

EXAMINATION OF ACHENE ULTRASTRUCTURAL FEATURES OF SOME TAXA BELONGING TO THE SECTIONS *PSEUDOSERIDIA*, *CHEIROLEPIS*, *MICROLOPHUS*, *RHIZOCALATHIUM* AND *PTERACANTHA* (*CENTAUREA*, ASTERACEAE) SECTIONS VIA SCANNING ELECTRON MICROSCOPY

DEMIRELMA, H.

Department of Biology, Faculty of Science, Selçuk University, Konya 42031, Turkey
(e-mail: demirelma@gmail.com; phone: +90-532-635-0305)

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Abstract. The study was carried out to determine the achene surface morphologies of 21 taxa in five sections (sect. *Pseudoseridia*, *Cheirolepis*, *Microlophus*, *Rhizocalathium* and *Pteracantha*) belonging to the genus *Centaurea* L. in Türkiye via SEM. The surface structures of the achenes of each taxon were described in detail, and a dendrogram showing the close relationships of the species was obtained by converting the determined micromorphological features into numerical data with the PRIMER7 programme. The findings show that achene surface morphologies are of great importance in determining the taxonomic relationships of taxa. The structure and length of the pappus also play a critical role among systematic characters and species boundaries. The seed surface morphologies do not support the previous sectional assignments of the genus *Centaurea* in previous research. Particularly, the seed surfaces of some subtaxa of *C. kotschy* and *C. drabifolia* were found to be significantly different, indicating the need for a taxonomic arrangement at the species level. In addition, it was thought that different populations of the *C. isaurica* taxon were differentiated considerably in terms of achene morphology and this might be related to interspecific hybridization. Additionally, the pappus structures were plumose, barbellate and scabrous and they could be simple or double-rowed.

Keywords: fruit surface, micromorphology, taxonomy, Türkiye

Introduction

Centaurea L. (Asteraceae) is an important and relatively large genus for the Flora of Turkey (Wagenitz, 1975), and the genus displays an extensive distribution across Eurasia, especially in Irano-Turanian and the Mediterranean regions (Susanna and García-Jacas, 2007). The genus still includes some taxonomic problems, especially in sectional borders, even though various approaches have been applied to solve these problems within the genus (Garcia-Jacas et al., 2000, 2001, 2006; Romaschenko et al., 2004; Uysal et al., 2009, 2010, 2015, 2016, 2017; Hilpold et al., 2014; Negaresh and Rahiminejad, 2018). Especially, thanks to cytogenetic (chromosome numbers and karyomorphology) and molecular data findings (SDS-PAGE, microsatellites and DNA sequences approaches) analyses were carried out more natural and certain classification of the genus *Centaurea*. Many new species have been discovered recently (Yıldırım, 2012, 2018; Köse and Alan, 2013; Bancheva et al., 2014a; Bancheva and Kaya, 2015; Bona, 2015a, 2016; Negaresh et al., 2015; Yüzbaşıoğlu et al., 2015; Kültür et al., 2016; Pınar, 2016; Uysal et al., 2016, 2017, 2022, 2024; Uysal and Hamzaoğlu, 2017; Behçet et al., 2017; Armağan and Uysal, 2018; Negaresh and Rahiminejad, 2018; Şirin et al., 2019, 2020, 2022; Hamzaoğlu and Koç, 2020; Duman et al., 2021; Özbek, 2021).

It is also seen that there are some doubts and uncertainties about the sections to which new published taxa are assigned and this situation further increases the problems related

to the mentioned sectional boundaries. Thus, different approaches or analyses are needed to produce solutions at least at the sectional level and to gain more information. Recently, SEM-assisted micro morphological analyses have been frequently used to solve similar problems in different taxonomic groups (Çelik et al., 2005, 2008; Uysal et al., 2005; Gömürgeç et al., 2010; Uysal et al., 2010; Potoğlu Erkara et al., 2012; Atasagun et al., 2013; Shabestari et al., 2013; Bona, 2014, 2015b, 2023; Bancheva et al., 2014b; Hayta et al., 2016, 2017; Candan et al., 2016; Ozcan, 2018; Bıyıklıoğlu et al., 2018; Aydın et al., 2019; Yılmaz Çıtak et al., 2019; Başer et al., 2019; Ali et al., 2021; Şirin et al., 2022; Sulborska-Rozycka et al., 2022; Hoşgören, 2024; Tavassol and Attat, 2025). According to the List of Plants of Türkiye (Uysal, 2012), while 194 taxa in Türkiye represent the genus *Centaurea*, this number has currently reached 222 with the latest additions and new records (Uysal, 2012; Hamzaoglu and Koç, 2020; Duman et al., 2021; Özbek, 2021; Şirin et al., 2022; Uysal et al., 2022). Of these taxa, 135 are endemic for Türkiye, the rate being approximately 60%.

In the Flora of Turkey, the genus *Centaurea* was revised by Wagenitz (1975) and, in the taxonomy of the genus, primarily involucre bracts and appendages as well as seed characteristics (pappus and achene shape) were used. In the relevant studies, pappus structures were effectively used especially for the distinction of closely-related taxon groups or some sections. Some of these sections are the subject of this study and it is seen that limited characters were taken into consideration in the distinction of taxa especially in sections *Cheirolepis*, *Pseudoseridia* and *Rhizocalathium*. In this study, I will try to demonstrate how realistic the section boundaries are or how natural they are in terms of taxonomy. For this purpose, seed surfaces of *Cheirolepis* and closely-related sections were investigated and analysed in detail, with at least one species representing each section.

Material and methods

Plant samples belonging to five related sections of the *Centaurea* genus, which forms the basis of the study, were collected from natural habitats by Uysal and Ertuğrul between 2002-2020 in years. The collected samples were dried and pressed according to common herbarium techniques and preserved in the Selçuk University, Faculty of Science, Department of Biology, (KNYA) Herbarium. Apart from this, mature achenes had been taken into special seed paper envelopes for SEM analyses during the field studies. For SEM studies, at least 10 achenes for each taxon were dehydrated in an acetone series, dried using carbon dioxide and double-sided tape was used to mount the achenes on stubs. In order to observe the surface details of the achenes with a ZEISS LS-10 model scanning electron microscope, the surfaces of the achenes were coated with gold (Candan et al., 2009). SEM photographs of the taxa were taken at 120x for the general appearance of the achenes, 1.00kx for the general surface appearance of the achenes and 4.00kx for the appearance of the microstructural features of the achenes. For the terminology of achene surface structures, botanical Latin was used (Stearn, 1983). Measurements are based on average values of at least five achene samples, with seventeen characters being investigated and used in this analysis. Qualitative and quantitative characters were determined for use in the numerical taxonomic study and a data matrix was created in the light of the findings obtained (Tables 1 and 2). A detailed dendrogram and a graphic representing most selective characters were created to decide relationships of species and if possible the section boundaries via PRIMER7 (Plymouth Marine Laboratory, Plymouth, UK; Clarke and Warwick, 1994).

Table 1. The ultrastructural features of seed surface belonging to pseudoseridia, cheirolepis, microlophus, rhizocalathium and pteracantha section (*Centaurea*)

Taxa	Length (mm)	Width (mm)	Shape	Compressed or swollen	Hair status	Pitted or not	Basis shape
<i>Centaurea hermannii</i>	4.5±0.25	2.2±0.05	Obovate-elliptic	Compressed	Pilose	Not pitted	Obtuse
<i>C. cheirolepidoides</i>	5.0±0.25	2.8±0.05	Obovate	Swollen	Glabrous	Pitted	Obtuse
<i>C. odyseii</i>	4.5±0.25	1.82±0.03	Obovate	Compressed	Glabrous	Pitted	Obtuse
<i>C. drabifolia subsp. cappadocica</i>	5.17±0.25	2.32±0.03	Obovate-elliptic	Swollen	Glabrous	Pitted	Obtuse
<i>C. drabifolia subsp. cappadocica</i>	4.87±0.23	1.82±0.03	Narrowly obovate	Swollen	Strigose	Pitted	Obtuse
<i>C. drabifolia subsp. detonsa</i>	5.67±0.23	2.25±0.05	Obovate-oblong	Compressed	Pilose	Pitted	Obtuse
<i>C. drabifolia subsp. austroanatolica</i>	4.62±0.38	1.85±0.01	Obovate-oblong	Compressed	Pilose	Not pitted	Rotund
<i>C. drabifolia subsp. drabifolia</i>	4.12±0.13	1.9±0.05	Obovate-oblong	Compressed	Glabrous	Pitted	Obtuse
<i>C. kotschyi var. kotschyi</i>	6.12±0.13	2.07±0.03	Obovate-oblong	Swollen	Glabrous	Not pitted	Obtuse
<i>C. kotschyi var. decumbens</i>	6.61±0.09	2.9±0.01	Obovate	Compressed	Glabrous	Pitted	Obtuse
<i>C. kotschyi var. floccosa</i>	5.75±0.05	2.62±0.03	Obovate	Swollen	Pilose	Not pitted	Obtuse
<i>C. derderiifolia</i>	8.92±0.03	3.17±0.08	Oblong	Compressed	Glabrous	Pitted	Acute
<i>C. deflexa</i>	5.25±0.05	2.95±0.05	Obovate	Swollen	Puberulent	Pitted	Rotund
<i>C. nivea</i>	4.42±0.02	2.3±0.03	Obovate-oblong	Swollen	Puberulent	Pitted	Obtuse
<i>C. saligna</i>	7.57±0.03	3.03±0.02	Oblong	Compressed	Glabrous	Not pitted	Obtuse
<i>C. armena</i>	4.87±0.03	1.82±0.08	Obovate-oblong	Swollen	Strigose	Pitted	Obtuse
<i>C. thracica</i>	4.62±0.02	2.62±0.03	Elliptic	Swollen	Glabrous	Not pitted	Obtuse
<i>C. cheirolopha</i>	5.0±0.25	2.25±0.05	Obovate-elliptic	Compressed	Pilose	Not pitted	Obtuse
<i>C. isaurica</i>	4.37±0.03	1.8±0.02	Obovate-oblong	Swollen	Pilose	Not pitted	Rotund
<i>C. isaurica</i>	5.0±0.5	2.25±0.25	Obovate-elliptic	Swollen	Glabrous	Pitted	Rotund
<i>C. cf. isaurica</i>	4.7±0.3	2.07±0.15	Narrowly obovate	Compressed	Glabrous	Not pitted	Obtuse

Table 2. The structural features of seed surfaces

Taxa	Achene					Pappus				Scales
	Fruit coat roughish or	Ornamentation	Cell distinct or not	Cell walls distinct or	Present or not	Type	Color	Length mm	Uniseriate or	Present, slightly or not
<i>Centaurea hermannii</i>	Roughish	Irregular sulcate	Distinct	Distinct	Present	Barbellate	Creamy brown	0.5-10	Biseriate	Slightly
<i>C. cheirolepidoides</i>	Not roughish	Irregular sulcate	Distinct	Distinct	Present	Scabrous	Light straw	0.5-7	Biseriate	Present
<i>C. odysssei</i>	Not roughish	Striate	Distinct	Distinct	Present	Scabrous	Creamy brown	1-5.5	Biseriate	Slightly
<i>C. drabifolia subsp. cappadocica</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Brown	8-10	Uniseriate	Slightly
<i>C. drabifolia subsp. cappadocica</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Straw	7-9	Uniseriate	Present
<i>C. drabifolia subsp. detonsa</i>	Not roughish	Striate	Distinct	Distinct	Present	Barbellate	Cream	8-10	Uniseriate	Present
<i>C. drabifolia subsp. austroasnatolica</i>	Not roughish	Fine sulcate	Distinct	Distinct	Present	Barbellate	Brown	9-10	Uniseriate	Present
<i>C. drabifolia subsp. drabifolia</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Brown	6-8	Uniseriate	Present
<i>C. kotschyi</i> var. <i>Kotschyi</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Plumose	Creamy brown	9-11	Uniseriate	Present
<i>C. kotschyi</i> var. <i>decumbens</i>	Not roughish	Fine sulcate	Not distinct	Not distinct	Present	Plumose	Cream	15-20	Uniseriate	Present
<i>C. kotschyi</i> var. <i>floccosa</i>	Roughish	Irregular sulcate	Distinct	Distinct	Present	Scabrous	Bright brown	9-11	Uniseriate	Present
<i>C. derderiifolia</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Straw	20-25	Uniseriate	Present
<i>C. deflexa</i>	Not roughish	Irregular sulcate	Distinct	Not distinct	Present	Barbellate	Cream	9-11	Uniseriate	Present
<i>C. nivea</i>	Not roughish	Fine sulcate	Distinct	Distinct	Present	Barbellate	Cream	9-11	Uniseriate	Present
<i>C. saligna</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Plumose	Yellowish brown	17-23	Uniseriate	Slightly
<i>C. armena</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Straw	0.5-2	Biseriate	Present
<i>C. thracica</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Barbellate	Brown	0.5-6	Biseriate	Slightly
<i>C. cheirolopha</i>	Not roughish	Regular sulcate	Distinct	Distinct	Present	Scabrous	Light brown-cream	0.5-1.5	Uniseriate	Not present
<i>C. isaurica</i>	Roughish	Fine sulcate	Distinct	Distinct	Present	Scabrous	Purplish brown	1-5	Biseriate	Not present
<i>C. isaurica</i>	Roughish	Fine sulcate	Distinct	Distinct	Present	Scabrous	Purplish brown	0.5-5	Biseriate	Slightly
<i>C. cf. isaurica</i>	Not roughish	Irregular sulcate	Distinct	Distinct	Present	Scabrous	Straw	0.5-6	Biseriate	Present

For statistical analyses, the basic characteristic features of achenes were calculated: arithmetic average (x), maximum and minimum values (max and min), standard deviation (SD), and coefficient of variation (CV). The Kruskal-Wallis test (for $P \leq 0.05$) was used, as a nonparametric alternative to ANOVA (Zar, 1984). The values of the average length-width and coefficients of variation of the seeds of the *Pseudoseridia*, *Cheirolepis*, *Microlophus*, *Rhizocalathium* and *Pteracantha* (*Centaurea*) sections are given in Table 3.

Table 3. Average length-width and coefficients of variation in seeds belonging to the *pseudoseridia*, *cheirolepis*, *microlophus*, *rhizocalathium* and *pteracantha* section (*Centaurea*)

Taxa	Average (length/width)	Coef. var. (length/width)
<i>Centaurea hermannii</i>	4.4740/2.1890	3.24/1.94
<i>C. cheirolepidoides</i>	4.4890/1.8210	4.16/1.11
<i>C. odyseii</i>	4.8920/1.8190	2.93/0.91
<i>C. drabifolia</i> subsp. <i>cappadocica</i>	4.3470/1.8480	2.04/0.43
<i>C. drabifolia</i> subsp. <i>cappadocica</i>	4.9630/2.8030	3.53/1.19
<i>C. drabifolia</i> subsp. <i>detonsa</i>	5.1380/2.3210	3.26/1.04
<i>C. drabifolia</i> subsp. <i>austroanatolica</i>	5.6560/2.2450	2.94/1.35
<i>C. drabifolia</i> subsp. <i>drabifolia</i>	4.1550/1.8990	2.22/1.83
<i>C. kotschyi</i> var. <i>kotschyi</i>	6.1530/2.0660	1.36/1.08
<i>C. kotschyi</i> var. <i>decumbens</i>	6.6030/2.8970	1.02/0.28
<i>C. kotschyi</i> var. <i>floccosa</i>	5.7540/2.6200	0.60/0.70
<i>C. derderifolia</i>	8.9210/3.1650	0.23/1.77
<i>C. deflexa</i>	5.2530/2.8760	0.65/7.09
<i>C. nivea</i>	4.4190/2.2990	0.27/0.88
<i>C. saligna</i>	7.372/3.0360	8.45/0.85
<i>C. armena</i>	4.8640/1.8180	0.38/3.50
<i>C. thracica</i>	4.6230/2.6210	0.25/0.75
<i>C. cheirollopha</i>	5.0000/2.2560	3.85/1.34
<i>C. isaurica</i>	4.3670/1.7990	0.43/0.67
<i>C. isaurica</i>	5.005/2.3050	7.47/6.74
<i>C. cf. isaurica</i>	4.7100/2.0710	4.60/5.26

Results and discussion

In this study, SEM was used to determine the achene surface morphology of 21 taxa belonging to the genus *Centaurea* and to determine detailed seed surface morphology. The seed surfaces of the sections and species discussed in this publication do not provide strong data or concepts in terms of determining the section boundaries. However, it is seen that it supports the relationships between species in a way that is largely consistent with the morphological studies carried out previously and contributes to the clarification of species boundaries. Amongst the micromorphological characters examined, it was determined that especially the features such as pericarp surface shape, indumentum, cell shape, cell wall structure and shape were distinctive. Very detailed information about the structure of the seed surface taxa is given in Tables 4 and 1.

Table 4. Collection data of the studied taxa

Taxa	Locality	Endemic
<i>Centaurea hermannii</i>	A2 Bursa: Yalova, Armutlu, Fıstıklı village, 570 m, 20.06.2018, Uysal 3744	*
<i>C. cheirolepidoides</i>	C3 Antalya: Elmalı, Teke-Çiğlikara, 1500 m, 28.06.2002, Uysal 1000	*
<i>C. odyseii</i>	B1 Balıkesir: Kaz Mountain National Park, Sarıkız Hill, 1700 m, 16.07.2003, Uysal 520	*
<i>C. drabifolia</i> subsp. <i>cappadocica</i>	B5 Yozgat: Deveci Mountain, Artova Yeşilyurt road, Kunduz stream, 1120 m, 26.07.2003, Uysal 525	*
<i>C. drabifolia</i> subsp. <i>cappadocica</i>	C5 Niğde: Bolkar Mountain, Bulgar mine, 1900 m, 28.07.2004, Uysal 854	*
<i>C. drabifolia</i> subsp. <i>detonsa</i>	C4 Karaman: Ermenek-Kazanç village, Kırkkuyu, 1800 m, 13.07.2003, Uysal 517	
<i>C. drabifolia</i> subsp. <i>austroanatolica</i>	B2 Balıkesir: Harmancık-Bursa road, Pinus forest clearing, stony, rocky slopes, 1050 m, 30.06.2004, Uysal 565	*
<i>C. drabifolia</i> subsp. <i>drabifolia</i>	A2 Bursa: Uludağ summit, on rock, 2000-2100 m, 30.07.2004, Uysal 569	*
<i>C. kotschyi</i> var. <i>kotschyi</i>	C4 Konya: Karapınar, Protection Research Area, 1800 m, 27.07.2003, Uysal 535	
<i>C. kotschyi</i> var. <i>decumbens</i>	C4 Karaman: Between Ermenek and Tekeçatı, Akpınar roadside, ca. 1500 m, 13.07.2003, Uysal 514	*
<i>C. kotschyi</i> var. <i>floccosa</i>	B6 Kahramanmaraş: Kayseri-Göksun road, 12 km before to Göksun, steppe plains, 1465 m, 08.08.2020, Uysal 4126	*
<i>C. derderiifolia</i>	B6 Kayseri: Gürün-Divriği road, 18 km, 1500-1600 m, 26.07.2003, Uysal 530	*
<i>C. deflexa</i>	C4 Konya: Taşkent-Ermenek road, 22 km, 1660 m, 13.07.2003, Uysal 512	*
<i>C. nivea</i>	B3 Eskişehir: Mihalçık, Mihalpu-Alpu road, 19-20 km, 900-950 m, 15.07.2003, Uysal 519	*
<i>C. saligna</i>	B9 Erzurum: Karayazı-Göksu road, as you descend into the Göksu valley, the stream bed, 2200 m, 30.07.2004, Uysal 891	*
<i>C. armena</i>	B6 Sivas: North east of Mescidli village, steppe, limestone slopes, 1400 m, 08.06.2020	*
<i>C. thracica</i>	B2 Balıkesir: Dursunbey, 502 m, 29.06.2004, Uysal 539	*
<i>C. cheirolopha</i>	C5 Adana: Osmaniye, Yarpuz road, forest openings, 800 m, 26.07.2003, Uysal 534	
<i>C. isaurica</i>	C5 Karaman: Ayrancı, northern slopes of Avdan Mountain, 1500 m, 22.07.2000, Ertuğrul 2310	*
<i>C. isaurica</i>	C4 Konya: Bozkır, Sorkun, lower Sorkun Plateau, above the summit rocks, 2000 m, 13.07.2003, Uysal 509	*
<i>C. cf. isaurica</i>	C5 Karaman: Ayrancı, northern slopes of Avdan Mountain, 1500 m, 22.07.2000, Ertuğrul 2309	*

Sect. *Pseudoseridia* Wagenitz

Centaurea hermannii F. Hermann: Achenes 4.5 × 2.2 mm, obovate-elliptic, compressed, pericarp slightly pilose hair, brown and longitudinally with yellowish stria. The achene colour noticeably turns to yellow towards the apical part, not pitted, obtuse at the base. Seed coat slightly roughish, ornamentation irregular sulcate and superficially slightly rugose. Cell and cell walls distinct and cells are edged and thick, short edges of

cells are irregular, cell surface slightly rugose. Pappus, scabrous, double serial inner pappus ca. 0.5–1.5 mm, outer pappus 8–10 mm, not deciduous. Hilum subapical, prominent open and rugose, scales weakly present (*Fig. 1 G-I*).

Centaurea cheirolepidoides Wagenitz: Achenes 5×2.8 mm, obovate, swollen, pericarp glabrous, cream, shiny, pitted, obtuse at the base. Seed coat not rough, ornamentation irregular sulcate. Cell and cell walls distinct, short edges of cells are swollen and irregular serial, arranged in a slightly imbricate pattern, cell surface slightly rugose. Pappus scabrous, double serial inner pappus 0.5–0.75 mm, outer pappus 7 mm, light straw-coloured, not deciduous. Hilum subapical, prominent open, no hairs, scales present (*Fig. 1 M-O*).

Centaurea isaurica Hub.-Mor.: (Ertuğrul 2310). Achenes 4.37×1.8 mm, obovate-oblong, swollen, slightly pilose hairy, pericarp ivory colour; not pitted, rotund at the base. Seed coat roughish, ornamentation fine sulcate, cell and cell walls distinct, short edges of cells are irregular, arranged slightly in an imbricate pattern. Pappus scabrous, double serial, inner pappus 1 mm, outer pappus 4–5 mm, purplish-brown, not deciduous. Hilum subapical, slightly open, scales absent (*Fig. 1 A-C*).

Centaurea isaurica Hub.-Mor.: (Ertuğrul 2309). Achenes 5×2.25 mm, obovate-elliptic, swollen, pericarp glabrous, ivory; slightly pitted, rotund at the base. Seed coat roughish, ornamentation fine sulcate, cell and cell walls distinct, short edges of cells are slightly irregular, arranged in a slightly imbricate pattern. Additionally, there are openings between the short edges of the cells in the same series that touch each other and pits are observed near the ends of the short sides. Pappus scabrous, double serial, inner pappus 0.5–1.5 mm, outer pappus 4–5 mm purplish-brown, not deciduous. Hilum prominent open and subapical, scales weakly present (*Fig. 1 D-F*).

Centaurea cf. *isaurica* Hub.-Mor.: (Uysal 509). Achenes 4.7×2.07 mm, narrowly obovate, compressed, pericarp glabrous, ivory colour, slightly brown-striped not pitted, obtuse at the base. Seed coat not rough, ornamentation irregular sulcate. Cell and cell walls slightly distinct, short edges of cells are slightly swollen and irregular, arranged in a slightly imbricate pattern. Pappus scabrous, double serial, inner pappus 0.5–0.6 mm, outer pappus 5–6 mm, outer pappus straw-coloured, inner pappus brown, not deciduous. Hilum subapical, prominent open, scales present (*Fig. 1 Ö-R*).

Centaurea cheirolapha (Fenzl) Wagenitz: Achenes 5×2.25 mm, obovate-elliptic, compressed, pericarp slightly pilose hairy, brown straw-coloured, not pitted, obtuse at the base. Seed coat not roughish, ornamentation regular sulcate. Cell and cell walls distinct and cell surface slightly rugose, short edges of cells are slightly irregular. Additionally, there are gaps between the short edges of the cells in the same series that touch each other and swellings are observed near the ends of the short sides. Pappus scabrous, uniseriate, 0.5–1.5 mm, light brown-cream, deciduous. Hilum subapical, prominent open and slightly rugose and hairy, scales absent (*Fig. 1 J-L*). The distribution of taxa is given in *Figure 2*.

***Sect. Pteracantha* Wagenitz**

Centaurea odyssei Wagenitz: Achenes 4.5×1.82 mm, obovate, compressed, pericarp glabrous, pitted, cream, obtuse at the base. Seed coat not roughish, ornamentation striate. Cell and cell walls distinct, cells edges thickened, cell surface slightly rugose, short edges angled and pitted. Pappus scabrous, double serial, inner pappus 1 mm, outer pappus 5–5.5 mm cream-brown colour, not deciduous. Hilum subapical and aperture prominent, scales slightly present (*Fig. 3 A-C*). The distribution of taxa is given in *Figure 4*.

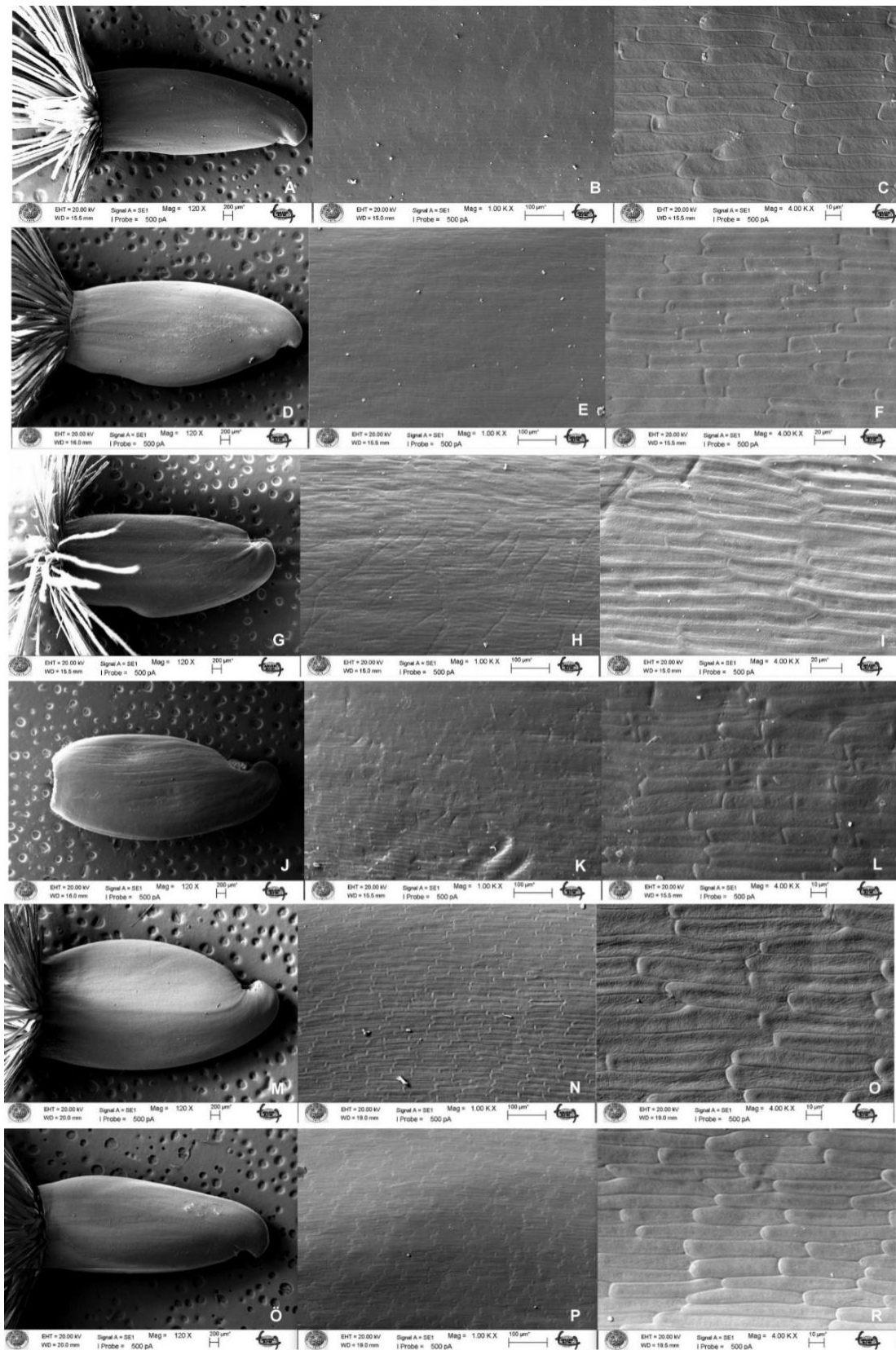


Figure 1. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea isaurica* (A–C), *Centaurea isaurica* (D–F), *Centaurea hermannii* (G–I), *Centaurea cheirolapha* (J–L), *Centaurea cheirolepidoides* (M–O), *Centaurea* cf. *isaurica* (Ö–R)

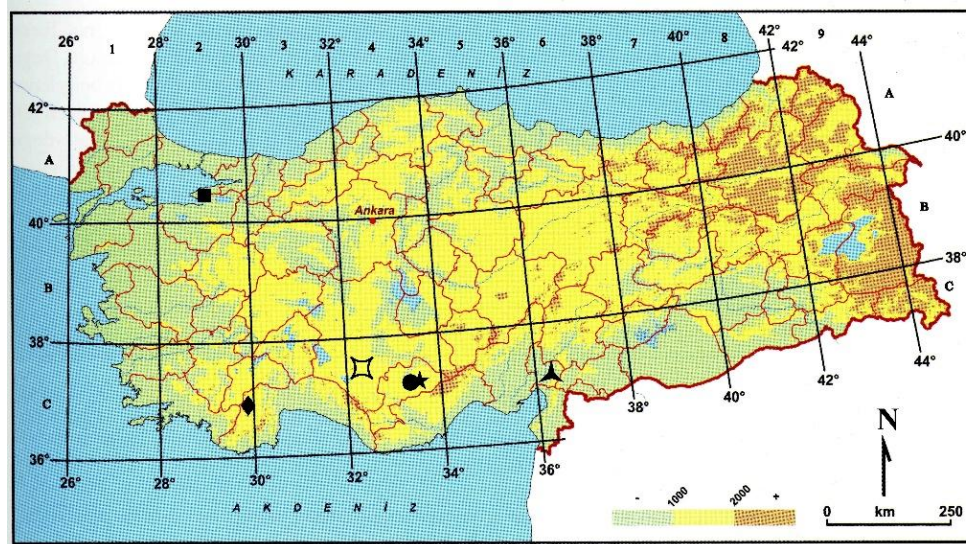


Figure 2. Distribution map of *Centaurea hermannii* (■), *Centaurea cheirolepidoides* (◆), *Centaurea isaurica* (●), *Centaurea isaurica* (✕), *Centaurea cf. isaurica* (★), *Centaurea cheirololpha* (▲)

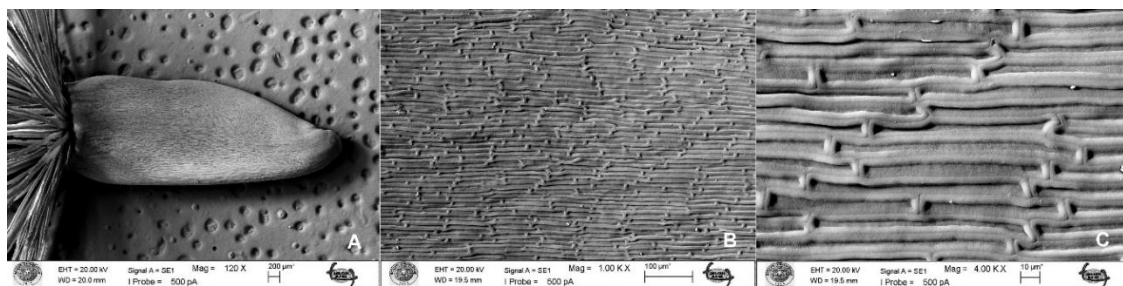


Figure 3. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea odyseii* (A-C)

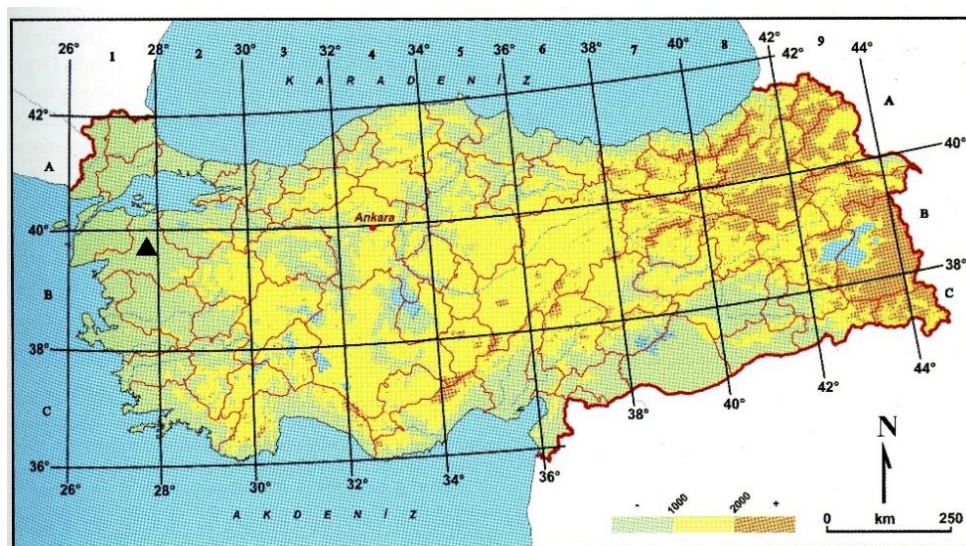


Figure 4. Distribution map of *Centaurea odyseii* (▲)

Sect. *Rhizocalathium* Tzvelev

Centaurea armena Boiss.: Achenes 4.87×1.82 mm, obovate-oblong, swollen, pericarp scattered strigose, cream, grey-brown stripes, pitted, obtuse at the base. Seed coat not rough, ornamentation regular sulcate. Cell and cell walls distinct, cell edges distinct and slightly thickened, short edges of cells are irregular, pits are observed near the ends of the short sides, cell surface slightly rugose. Pappus barbellate, double serial, inner pappus 0.5–1 mm, outer pappus 1.5–2 mm, not deciduous. Hilum subapical, prominent open and hairy, scales present (Fig. 5 A-C). The distribution of taxa is given in Figure 6.

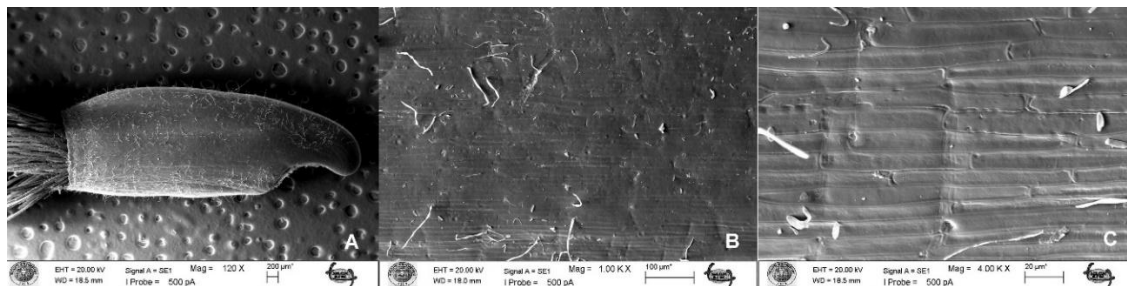


Figure 5. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea armena* (A-C)

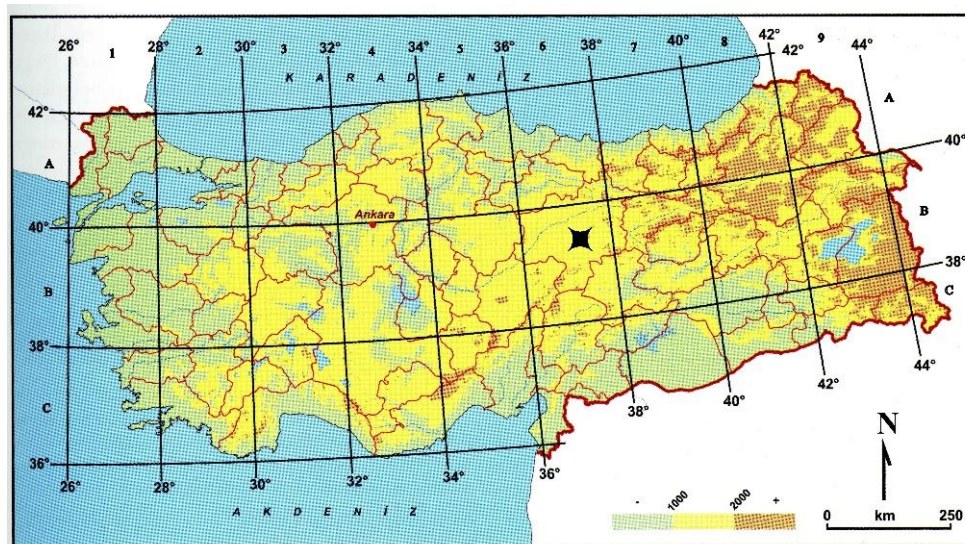


Figure 6. Distribution map of *Centaurea armena* (✱)

Sect. *Microlophus* (Cass.) DC.

Centaurea thracica Janka ex Gugler: Achenes 4.62×2.62 mm, elliptic, swollen, pericarp glabrous, creamy, white-striped, not pitted, obtuse at the base. Seed coat not roughish, ornamentation regular sulcate. Cell and cell walls distinct, short edges of cells irregular and slightly swollen are observed near the ends, cells bordered, cell surface slightly rugose. Pappus barbellate, double serial, inner pappus 0.5 mm, outer pappus 5–6 mm, brown at the base and light brown towards the tip, not deciduous. Hilum subapical, prominent open, scales weakly present (Fig. 7 A-C). The distribution of taxa is given in Figure 8.

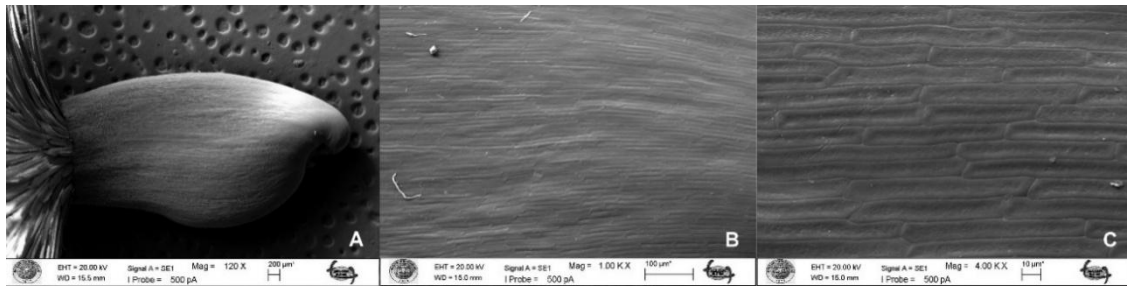


Figure 7. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea thracica* (A-C)

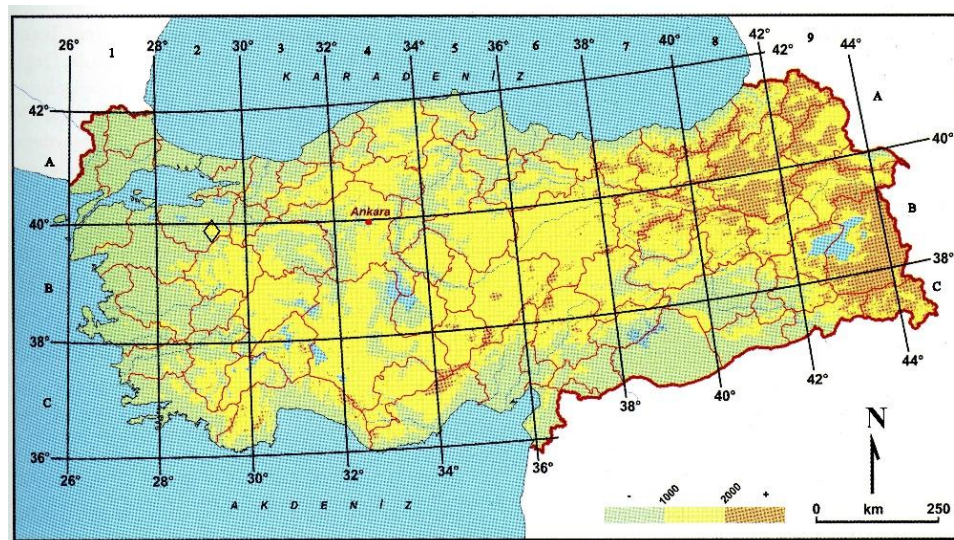


Figure 8. Distribution map of *Centaurea thracica* (◊)

Sect. *Cheirolepis* (Boiss.) O. Hoffm.

Centaurea drabifolia subsp. *cappadocica* Wagenitz: (Uysal 525). Achenes 4.87×1.82 mm, obovate-elliptic, swollen, pericarp glabrous, scattered strigose, brown, white-striped, pitted, obtuse at the base. Seed coat not rough, ornamentation regular sulcate. Cell and cell walls distinct, short side ends swollen, cells borders irregular thick, cell surface rugose. Pappus barbellate, uniseriate, 7–9 mm, straw-coloured, deciduous, scales present (Fig. 9 C1-C3).

Centaurea drabifolia subsp. *cappadocica* Wagenitz: (Uysal 854). Achenes 5.17×2.32 mm, obovate, swollen, pericarp, glabrous, brown, cream-striped and black-spotted, pitted, obtuse at the base. Seed coat not roughish, ornamentation regular sulcate. Cell distinct, cell walls not distinct, cell surface slightly rugose, short edges of cells are slightly swollen and irregularly serial. Pappus barbellate, uniseriate, 8–10 mm, deciduous. Hilum subapical and its aperture is not very prominent, scales present. (Fig. 9 F1-F3).

Centaurea drabifolia subsp. *detonsa* Wagenitz: Achenes 5.67×2.25 mm, obovate-oblong, compressed, pericarp sparse pilose, pitted, creamy, obtuse at the base. Seed coat not roughish, ornamentation striate. Cell and cell walls distinct and cell edges thickened and surrounded by deep hollow cells, irregular serial and cells surfaces slightly rugose. Pappus barbellate, uniseriate, 8–10 mm, cream, not deciduous. Hilum subapical and its aperture is prominent and hairy, scales present (Fig. 10 G1-G3).

Centaurea drabifolia subsp. *austroanatolica* Wagenitz: Achenes 4.62×1.85 mm, obovate-oblong, compressed, pericarp sparse pilose hairy, cream, black-striped, not pitted, rotund at the base. Seed coat not roughish, ornamentation fine sulcate. Cell and cell walls distinct, cell edges not thickened, slightly rugose, short edges slightly swollen, irregular serial and slightly imbricate. Pappus barbellate, uniseriate, 9–10 mm, brown, not deciduous. Hilum subapical and aperture prominent, scales present (Fig. 10 H1-H3).

Centaurea drabifolia subsp. *drabifolia* Wagenitz: Achenes 4.12×1.9 mm, obovate-oblong, compressed, pericarp glabrous, brown, pitted, obtuse at the base. Seed coat glabrous, not roughish, ornamentation regular sulcate. Cell and cell walls distinct, cell edges thickened and cell surfaces rugose, short edges slightly pitted, irregular serial. Pappus barbellate, uniseriate, 6–8 mm, brown, deciduous. Hilum subapical and aperture prominent, scales weakly present (Fig. 10 I1-I3).

Centaurea kotschyi var. *kotschyi* Boiss.: Achenes 6.12×2.07 mm, obovate-oblong, swollen, pericarp glabrous, brown, cream-striped, not pitted, obtuse at the base. Seed coat not roughish, ornamentation regular sulcate. Cell and cell walls slightly distinct, short edges of cells irregular and slightly swollen are observed near the ends, cell surface slightly rugose; additionally, there are gaps between the short edges of the cells in the same series that touch each other. Pappus plumose uniseriate, 9–11 mm, creamy-brown, not deciduous. Hilum apical-subapical, hilum slightly open and slightly rugose, scales present (Fig. 9 B1-B3).

Centaurea kotschyi var. *decumbens* Wagenitz: Achenes 6.61×2.9 mm, obovate, compressed, pericarp glabrous, brown, pitted, obtuse at the base. Seed coat not roughish, ornamentation fine sulcate. Cell and cell walls not distinct, cell edges thickened and incurved, slightly rugose, cells irregular and, if intertwined, short cell edges pitted. Pappus plumose, uniseriate, 15–20 mm, cream, not deciduous. Hilum apical aperture not deep and rugose, scales present (Fig. 10 K1-K3).

Centaurea kotschyi var. *floccosa* (Boiss.) Wagenitz: Achenes 5.75×2.62 mm, obovate, swollen, pericarp pilose hairy, bright brown, not pitted, obtuse at the base. Seed coat rough, ornamentation irregular sulcate. Cell and cell walls distinct and thickened rugose, short edges of cells are swollen and irregular serial, cell wall is thickened in some cells, in some cells, the cell wall not clearly visible. Pappus scabrous, uniseriate, 9–11 mm, not deciduous. Hilum apical and rugose, scales present (Fig. 9 E1-E3).

Centaurea derderiifolia Wagenitz: Achenes 8.92×3.17 mm, obovate-elliptic, compressed, pericarp glabrous, brown and usually cream-striped, distinct keel, pitted, slightly acute at the base. Seed coat not roughish, ornamentation regular sulcate. Cell and cell walls distinct, arranged in a slightly imbricate pattern, short edges of cells are swollen and irregular serial, cell surface distinct rugose. Pappus barbellate, uniseriate, 20–25 mm, brown, deciduous. Hilum subapical, not hairy, prominent open and rugose, scales weakly present (Fig. 9 D1-D3).

Centaurea deflexa Wagenitz: Achenes 5.25×2.95 mm, obovate, swollen, pericarp puberulent, creamy-brown, cream-striped, pitted, rotund at the base. Seed coat not roughish, ornamentation irregular sulcate. Cell distinct, cell walls not distinct and not thickened; cell irregular, short edges not thickened, in some cells the short edges not distinct and, if intertwined and slightly pitted, cell surface rugose. Pappus barbellate, uniseriate, 15–20 mm, cream and not deciduous. Hilum subapical, rugose and aperture not deep, scales present (Fig. 10 L1-L3).

Centaurea nivea (Bornm.) Wagenitz: Achenes 4.42×2.3 mm, obovate-oblong, swollen, pericarp puberulent, brownish-black, slightly pitted, obtuse at the base. Seed coat not roughish, ornamentation fine sulcate. Cell and cell walls distinct, cell edges thickened,

cell surface rugose, cell short edges irregular and slightly pitted. Pappus barbellate, uniseriate, 9–11 mm, creamy-brown, deciduous. Hilum subapical and aperture not deep, scales present. (Fig. 10 J1-J3).

Centaurea saligna (K. Koch) Wagenitz: Achenes 7.57×3.03 mm, oblong, compressed, pericarp glabrous, straw-coloured, brown stripes, not pitted, obtuse at the base. Seed coat not roughish, ornamentation regular sulcate. Cell and cell walls distinct, cells are edged and thick, cells bordered and slightly swollen at the tip, cell surface slightly rugose and grooved, short edges of cells are slightly irregular. Pappus plumose, uniseriate, 17–23 mm, yellowish-brown, not deciduous. Hilum at the tip, prominent open, scales weakly present (Fig. 9 A1-A3). The distribution of taxa is given in Figure 11.

The surface structure, shape, pappus morphology and micromorphological characteristics of the seeds of the genus *Centaurea* are of great importance in distinguishing the species from one another and in taxonomic classification. The findings showed that a striate surface texture is generally dominant; however, variations in surface patterns (such as imbricate, smooth and roughish, the presence of pits, shape of the hilum at the base, cell shape and wall structure) have proven to be decisive for systematic differentiation. Therefore, we can indicate that seed surface ornamentation has too importance for determination of *Centaurea* taxa. The structure and length of the pappus also play a critical role amongst systematic characters.

The nonparametric Kruskal-Wallis test was used to statistically test differences among the species of the genus *Centaurea*. This test determined that the characters and their characteristics were decisive in distinguishing between taxa. The statistical analyses, based on coefficients of variation, indicated that the taxa examined generally exhibited low variation in achene length and width, unlike of pappus shape and length. The taxa with the highest variation in seed traits were *C. deflexa* and *C. saligna*, while the taxa with the lowest variation were *C. derderiifolia* and *C. kotschyi* var. *decumbens*. In the phenetic tree constructed using Primer 7 based on seed surface analysis, *C. hermannii* appears to be significantly differentiated from other species. This taxon is particularly distinguished by its achene base and surface shape as well as pappus length. Among the characters examined, the outer pappus length was found to have the highest variation. The presence or absence of a distinct cell wall was found to have the lowest value. Furthermore, the general shape of the seed and the presence of hairs on the pericarp were found to be important in separating taxa into main clades.

Dittrich (1968) conducted morphological studies on achenes of the genus *Centaurea* and found that the sections had typical achene structures and that there were significant differences between the sections. Interestingly, it is seen that taxa are not grouped within the clade according to achene characteristics, and we assume that the infrageneric classification previously made based on these features is artificial. Moreover, the detailed examination shows that, although the achene structure contains similarities between taxa within the same section, it is not sufficient to form section boundaries and, at least, it shows that it is not correct to evaluate the sections in question as different sections. *C. thracica* is a member of *Microlophus* section and it is placed together with *C. armena* (*Rhizocalathium*) in the dendrogram (Fig. 12). Similarly, chromosomal and molecular studies (Garcia-Jacas et al., 2006; Uysal et al., 2009) indicate that *C. thracica* is a taxon of the *Cheirolepis*-*Pseudoseridia* section rather than the *Microlophus* section. This situation supports previous molecular reports that the borders amongst *Cheirolepis*, *Pseudoseridia* and *Rhizocalathium* is not natural; it would be more accurate to combine these sections and small ones with limited species numbers in their surroundings under a single section.

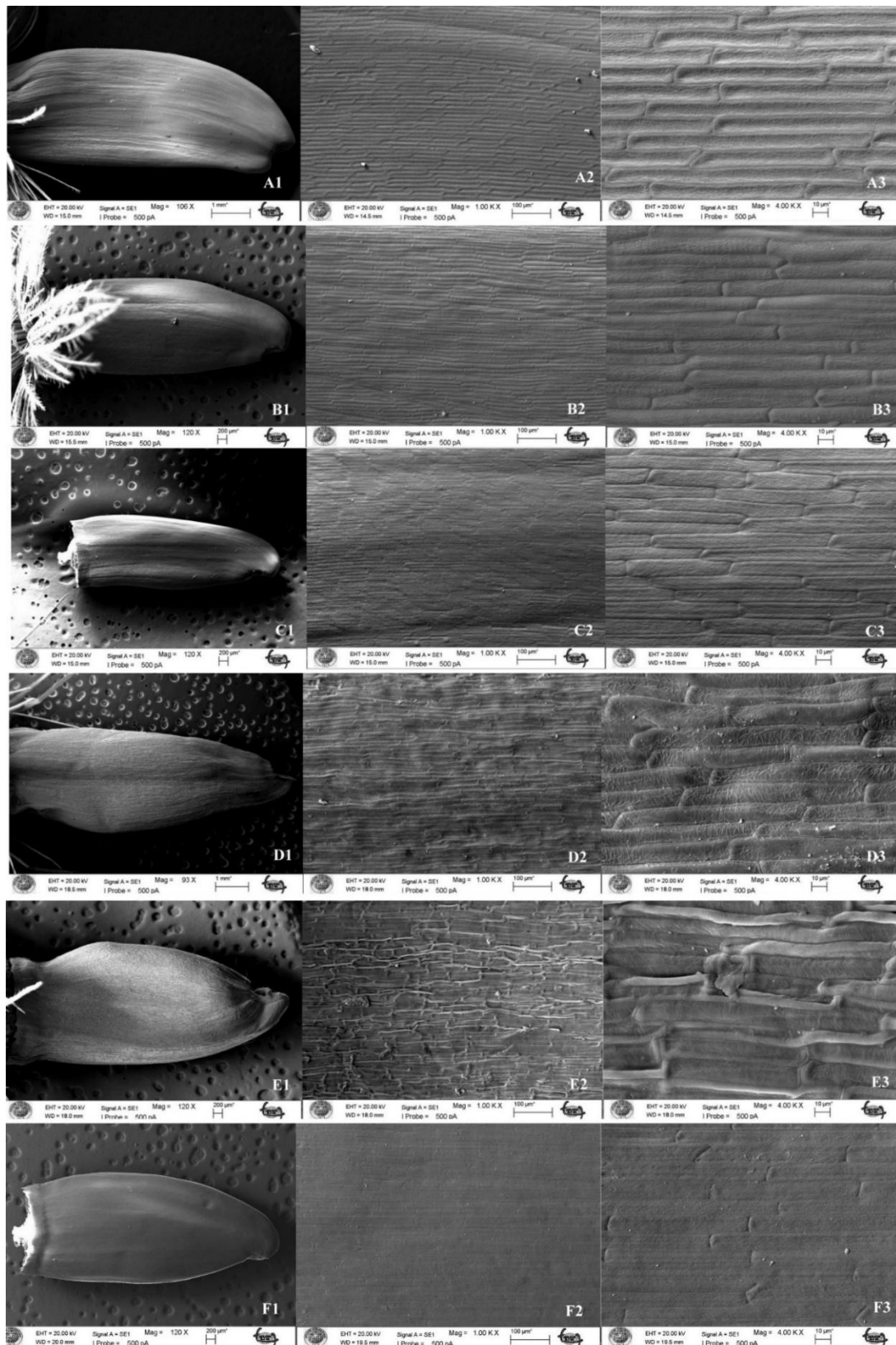


Figure 9. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea saligna* (A1-A3), *Centaurea kotschy* var. *kotschy* (B1-B3), *Centaurea drabifolia* subsp. *cappadocica*, (C1-C3), *Centaurea derderifolia* (D1-D3), *Centaurea kotschy* var. *floccosa* (E1-E3), *Centaurea drabifolia* subsp. *cappadocica* (F1-F3)

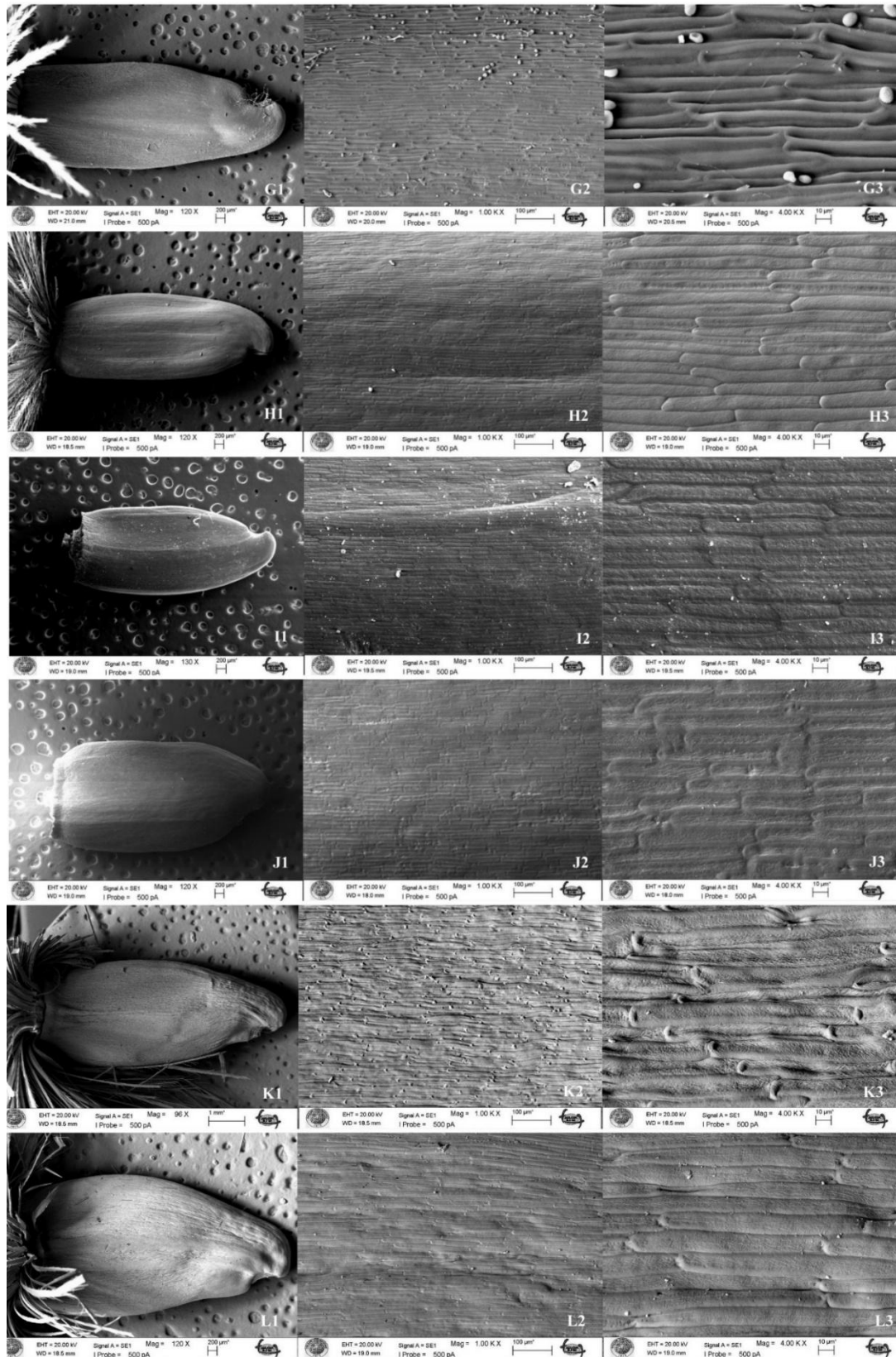


Figure 10. Scanning electron micrographs of the investigated *Centaurea* taxa: *Centaurea drabifolia* subsp. *detonsa* (G1-G3), *Centaurea drabifolia* subsp. *austroanatolica* (H1-H3), *Centaurea drabifolia* subsp. *drabifolia* (I1-I3), *Centaurea nivea* (J1-J3), *Centaurea kotschy* var. *decumbens* (K1-K3), *Centaurea deflexa* (L1-L3)

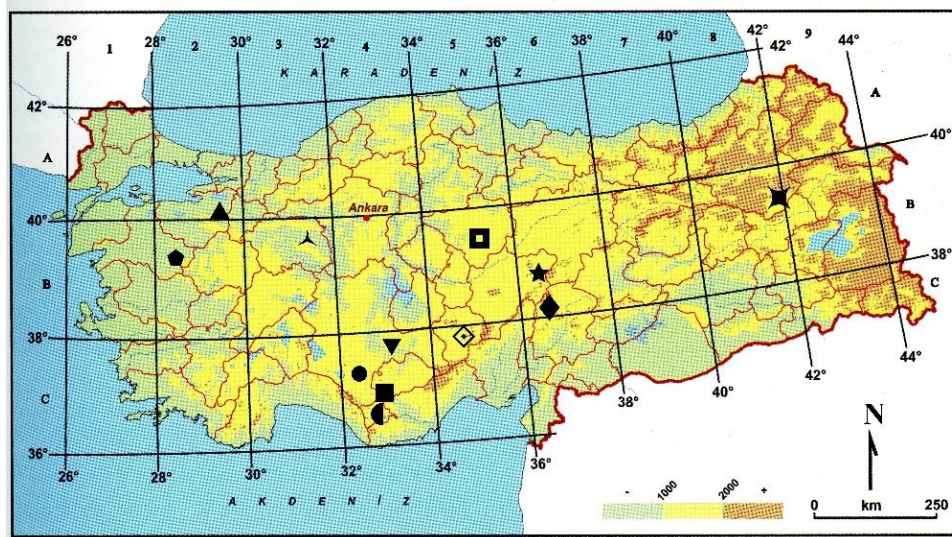


Figure 11. Distribution map of *Centaurea drabifolia* subsp. *cappadocica* (◻), *Centaurea drabifolia* subsp. *Cappadocica* (◊), *Centaurea drabifolia* subsp. *detonsa* (●), *Centaurea drabifolia* subsp. *austroanatolica* (●), *Centaurea drabifolia* subsp. *drabifolia* (▲), *Centaurea kotschy* var. *kotschy* (▼), *Centaurea kotschy* var. *decumbens* (■), *Centaurea kotschy* var. *floccosa* (◆), *Centaurea derderiifolia* (★), *Centaurea deflexa* (●), *Centaurea nivea* (▲), *Centaurea saligna* (★)

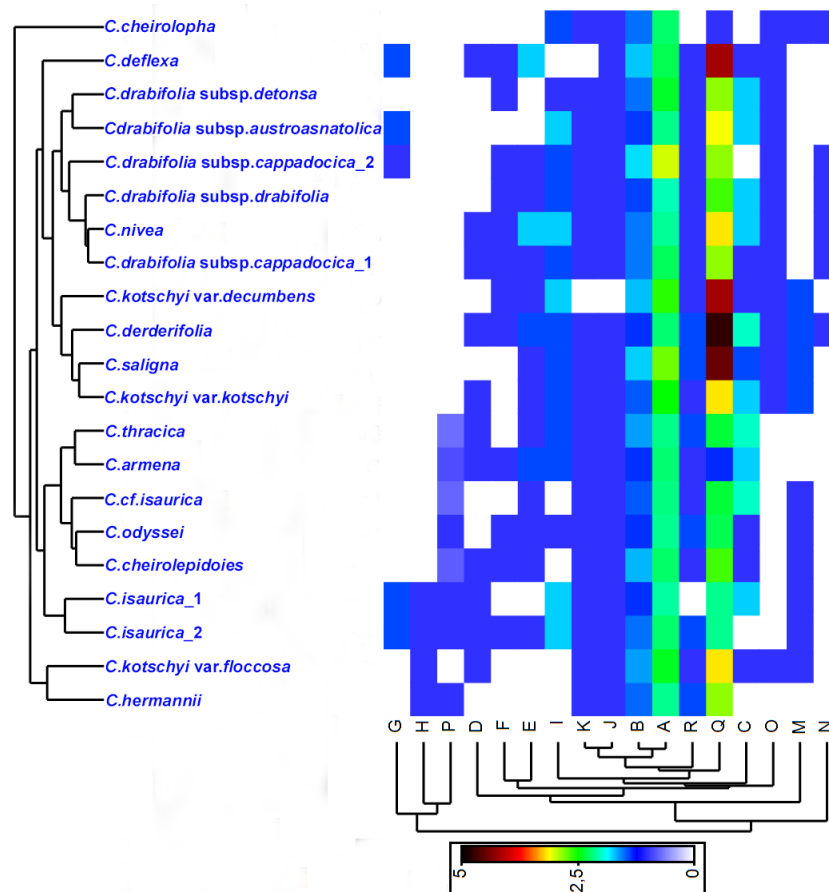


Figure 12. The dendrogram showing relationships between samples and variables

As well many taxonomical studies having been undertaken on a wide range of topics related to the *Centaurea* genus and its taxa, recently, studies have focused on seed surface morphology in order to reveal the relationships between taxa (Çelik et al., 2008; Shabestari et al., 2013; Bancheva et al., 2014b; Bona, 2015; Candan et al., 2016; Hayta et al., 2017; Ozcan, 2018; Bıyıklıoğlu et al., 2018; Başer et al., 2019; Aydın et al., 2019; Şirin et al., 2022; Tavassol and Attar, 2025). Although the conducted seed surface morphology studies are not complete studies in targeting different genera and taxa, they have reported that seed surface morphology is taxonomically important for *Centaurea* and closely-related *Cyanus* and *Psephellus* genera. Unlike of the general conclusion of this paper, previous works comprising relatives show that achene characteristics could be useful for sectional classification of the genus *Psephellus* (Bona, 2015b). Besides with this information, seed surface analyses are not every time determinative for the other close genera. It has been claimed that there is no specific achene and pappus shape for the genus *Cyanus*, all the studied taxa have smooth or smooth-globulate achene surface patterns. Similar conclusions with (Bona, 2014; Candan et al., 2016) can be applied to achene characteristics, including achene length and colour, pappus length and colour, that might be helpful to distinguish more taxa. The micromorphology of the vegetative and generative structures of *Centaurea glaberrima* Tausch subsp. *divergens* (Vis.) Hayek (Asteraceae) has been documented for the first time using scanning electron microscopy (SEM) by Gavrilović and Janačković (2022). In the reported article, the micro morphological features found on the cypsela are reported as follows: Slightly ribbed body, rounded base, lateral and concave insertion zone, short, unicellular, curved and pointed hairs, smooth epidermis, finely grooved surface ornamentation, short, blunt-tipped rod-shaped epidermal cells with straight anticlinal walls, poorly developed, finely toothed pericarp margin, and dimorphic pappus (setae of different lengths and morphologies, and pinnules confined to the edges of the setae). These findings had supplied new information on the micromorphology of this endemic species and contribute to its more accurate description. Additionally, it was stated that some well-defined microcharacters may have taxonomic value for *C. glaberrima*. Involucrum and cypsela structures that can be useful in the classification of six different taxa (*C. carduiformis* DC. subsp. *carduiformis* var. *carduiformis*, *C. drabifolioides* Hub.-Mor. (endemic), *C. glastifolia* L., *C. jacea* L., *C. helenioides* Boiss. (endemic) and *C. polypodiifolia* Boiss. var. *polypodiifolia*) located in different sections within the genus *Centaurea* were examined in detail in terms of morphological and micro morphological features and morphometric analyses were carried out. It was determined that the characters were important in the separation of the taxa (Öztürk and Ergen Akçil, 2025).

Taxonomic studies based on seed and fruit surfaces are frequently used not only within the genus *Centaurea* and its relatives within the Asteraceae, but also operated in different genera and taxonomic groups. These demonstrate a wide range of applications in determining taxon boundaries, including infra- and intergeneric classifications. A study on the macromorphological and micromorphological characters of the seeds (achenes) of species of the genus *Artemisia*, distributed in Türkiye, reported that fruit surface ornamentation and groove-like structures were particularly distinctive (Karaismailoğlu et al., 2024). In another study by Uzun and Palabas Uzun (2024), fruit traits of taxa belonging to the genera *Dittrichia*, *Tragopogon*, and *Jurinea* within the same family were characterized according to their weight and size. The study concluded that the largest fruits belonged to *Tragopogon*, the smallest to *Dittrichia*, and the heaviest to *Jurinea*. In this study on the seed surface of the genus *Pulicaria*, macro- and micromorphological

characteristics of fruits belonging to six *Pulicaria* species from Türkiye were determined using stereomicroscopy and scanning electron microscopy. Achene coloration ranges from light brown to brown. Shapes range from obovate to elliptic. The pappus is persistent in all studied species. All except *P. sicula* have two rows of pappus hairs. In *P. sicula*, the pappus consists of only a single row of hairs. In the other species, the outer row becomes a small crown, while the inner row consists of hairs. While all taxa have glandular hairs, *P. arabica* lacks them (Gürdal and Özdemir Nath, 2025). In the study, the achenes of *C. saligna*, *C. derderiifolia*, and *C. kotschy* var. *decumbens* have particularly large pappus having one series is much longer than the remaining taxa. Among these taxa, *C. derderiifolia* and *C. kotschy* var. *decumbens* exhibit similarities in terms of achene and pappus characteristics, and also their creeping and clump-forming stem structures are noteworthy. Of the analysed taxa, *C. hermannii*, *C. nivea*, and *C. odyseii* have the smallest achenes, but their pappus can vary in length and series as remaining taxa. As a general conclusion, it can be said that the length gradually shortens in a spectrum ranging from plumose to barbellate and scabrous, and taxa with double rows of pappus have shorter achene and pappus.

Some of the taxa investigated in this study are quite locally distributed and morphologically unique species (*C. nivea*, *C. derderiifolia*, *C. deflexa*, *C. hermannii*, *C. odyseii*) and are clearly distinguished from the others in terms of their seed surfaces. However, *C. drabifolia* and *C. kotschy* taxa, which have many subspecies, need more intensive taxonomic studies and their taxonomic status needs to be clarified, because the number of stems, spinules and cilia have been used as limited characters in the separation of subtaxa. SEM analysis of the samples collected from different localities and a possible population of *C. isaurica* showed that there were minor differences in terms of achene shape between the populations thought to be *C. isaurica*, but there was a significant similarity in terms of pappus features. *C. isaurica*, which was thought to be a probable species, appeared quite different and *C. odyseii* appeared to be more related to *C. cheirolepidoides* in terms of seed surface. Based on the field observations and examinations of our University Researchers Uysal and Ertuğrul between 2000-2020 in years, since the presence of individuals belonging to *C. cheirolepidoides* was detected in the area where the relevant population was distributed, it was thought that these samples might belong to a hybrid population between *C. isaurica* and *C. cheirolepidoides*.

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