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Micromorphology of endemic *Centaurea glaberrima* subsp. *divergens* (Asteraceae)

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Abstract – In this study, the micromorphology of the vegetative and reproductive structures of the endemic *Centaurea glaberrima* Tausch subsp. *divergens* (Vis.) Hayek (Asteraceae), using scanning electron microscope (SEM), is presented for the first time. Uniseriate whip-like non-glandular and biseriate glandular trichomes are found on the surface of all aboveground parts (stem, leaves, peduncles, involucral bract). On the adaxial leaf epidermis ribbed thickenings (striation pattern) of outer periclinal cell walls, slightly curved anticlinal cell walls and anomocytic stomata are noticed. Rugose abaxial surface with thorny protuberances of the involucral bract is documented. Corolla is glabrous with longitudinally parallel epidermal cells with distinct straight outline. Isopolar, radially symmetric and tricolporate microechinate pollen grains are seen. Short stylar hairs, without cuticular striations, are present along the outer sides of the style, while the inner sides (abaxial surface) constitute the papillate stigmatic surface. Microcharacters found in cypsela are as follows: slightly ribbed body; rotund base; lateral and concave insertion; short, unicellular curly acute trichomes; smooth epidermis; fine-sulcate ornamentation; rod shaped epidermal cells with short, obtuse end walls and straight anticlinal walls; poorly developed minutely dentate pericarp rim; and dimorphic pappus with bristles of different length and morphology, with pinnules restricted to the margins of the bristles. The results obtained contribute to knowledge about the micromorphology of the studied endemic species and provide features for its better identification. The taxonomic significance of the analyzed characters is discussed. Some well defined microcharacters of the studied species might have taxonomic value.

Keywords: cypsela, involucral bract, inflorescence, leaf, SEM, stem, taxonomy

Introduction

Centaurea L. (Asteraceae, Centaureinae, Cardueae) includes nearly 250 species mainly distributed in Eurasia, especially in the Irano-Turanian and Mediterranean regions. It is formed by annual, biennial or perennial herbs, less often shrubs, with usually unarmed leaves (Susanna and Garcia-Jacas 2007). *Centaurea* is a genus of complex taxonomy. According to Hilpold et al. (2014) the genus can be classified into three well delimited subgenera: *Centaurea*, *Cyanus* (Mill.) Cass. ex Hayek and *Lopholoma* (Cass.) Dobrocz. Subgen. *Centaurea* comprises three clades, partly congruent with their geographic distribution: The Eastern Mediterranean Clade (EMC) comprises species often with spiny bract appendages; the Western Mediterranean Clade (WMC) comprises species with pronounced spiny bract appendages and the Circum-Mediterranean Clade (CMC) comprises species that are predominantly not or only slightly spiny in their bract appendages. Within the CMC clade, the most distinctive characters are also bract appendages (Hilpold et al. 2014). Three extreme forms of bract are recognized: membranaceous, long ciliate-fimbriate, and reduced or missing appendages. The CMC is a large group comprising, among others, the section *Centaurea*, which has the highest species number in the Balkans, with subsections *Centaurea*, *Phalolepis* (Cass.) Garcia-Jacas, Hilpold, Susanna & Vilatersana and *Willkommia* (Blanca) Garcia-Jacas, Hilpold, Susanna & Vilatersana (Hilpold et al. 2014).

Centaurea glaberrima Tausch belongs to the Circum-Mediterranean Clade, sect. *Centaurea*, subsect. *Centaurea*. According to the description given by Dostál (1976) and Šilić (1990), it is a biennial or perennial plant, with erect, rigid, furrowed, glabrous stem up to 80 cm, paniculate branched below. Leaves are green, glabrous, dotted. Lower leaves are petiolate, 2-pinnatisect with subulate linear segments not more than 1 mm wide. Capitula are solitary, ob-

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long-ovate, 10 mm long and 6 mm wide. Involucral bracts are ovoid-conical, glabrous, shiny, with brown appendages, mucronate with a 0.5 mm apex and 3–5 fimbriae 0.5 mm long on each side. Cypselae are 3 mm long, gray-blackish, shiny, slightly hairy, with pappus 1/3 as long as cypsela. Florets are pink. *C. glaberrima* is endemic to the west Balkan Peninsula. It inhabits fields and waste places, as well as rocky cliffs in Croatia, Bosnia and Herzegovina and Montenegro (Dostál 1976). Two subspecies are recognized within the *C. glaberrima*, subsp. *glaberrima* and subsp. *divergens* (Vis.) Hayek, which differ in length and number of fimbriae on the involucral bract appendages (Nikolić 2020).

Micromorphological characters of leaves (Adedeji and Jewoola 2008, Gavrilović et al. 2019), involucral bracts (Robinson 2009, Gavrilović et al. 2019), flowers (Torres and Galetto 2007, Erbar and Leins 2015, Erbar et al. 2018) and especially those of cypselae (Dittrich 1968, Zhang et al. 2013, Ghimire et al. 2016, Kalmuk et al. 2018, Gavrilović et al. 2019, Ozcan and Akinci 2019) have provided useful information for the taxonomy and phylogeny of particular plant groups in Asteraceae. *Centaurea* taxa were poorly investigated from a micromorphological point of view. Dittrich (1968) performed a morphological investigation on fruits of the subtribe Centaureinae and defined characters (the form of the hilum, the mechanisms for detaching the fruits (elaiosomes or simple parenchymatic tissues), the consistence of the pericarp and the hairiness of the fruit) which are important for the definition of the genera. In addition, several studies have shown importance of cypsela microcharacters (e.g. surface pattern, indumentum, pappus structure) in the Centaurea taxonomy (Bona 2014, Candan et al. 2016, Ozcan and Akinci 2019). Wagenitz (1955) examined pollen morphology of the *Centaurea* taxa and divided the genus into eight subgenera: *Serratula*, *Centaurium*, *Scabiosa*, *Crupina*, *Jacea*, *Dealbata*, *Montana* and *Cyanus*, based on pollen shape, exine ornamentation, internal and external layers of columellae, length of colpus, pore shape and costae. However, there are a few novel studies that evaluate the pollen morphology of *Centaurea* species (Özler et al. 2009, Shabestari et al. 2013, Baser et al. 2019).

Centaurea glaberrima is micromorphologically completely unexplored. The aims of our present study are to examine: (1) the micromorphology of the vegetative and reproductive structures of *C. glaberrima* subsp. *divergens* and (2) particular micromorphological traits that might have possible taxonomic value.

Materials and methods

Plant material

Plant material of *C. glaberrima* subsp. *divergens* was collected in June 2003, during the flowering period, in a natural habitat: Rose, Montenegro (Fig. 1). Plants were identified according to Dostál (1976) and Nikolić (2020), while nomenclature follows Hilpold et al. (2014). Voucher specimens were deposited in the Herbarium of the University of Belgrade - Faculty of Biology, Institute of Botany and Botanical Garden "Jevremovac" (accession number: BEOU 38399). Standard herbarium acronym follows Thiers (2019) +: Index herbariorum (http://sweetgum.nybg.org/science/ih/).

Fig. 1. *Centaurea glaberrima* Tausch subsp. *divergens* (Vis.) Hayek at the habitat.

Micromorphological analysis

No special pre-treatments were applied in preparation for scanning electron microscopy (SEM). Dry plant parts, both vegetative (stem, leaf, peduncle) and reproductive (inflorescence, involucral bracts, petals, pollen, style and cypsela), taken from herbarium specimens, were sputter-coated with gold for 180 s at 30 mA (BAL-TEC SCD 005), and observed using a JEOL JSM-6460LV electron microscope at an acceleration voltage of 20 kV. The terminology of the cypsela microstructure follows Barthlott (1981, 1984), Barthlott et al. (1998) and Zhang et al. (2013), while pappus description follows Small (1919) and Bean (2001).

Results

Stem and peduncle micromorphology

Whip-like uniseriate non-glandular trichomes consisted of a short, upright stalk, composed of several cells, and an elongated, curled terminal cell and they are very sparsely distributed on the stem and peduncle (Fig. 2A-B). Large glandular trichomes of the capitate type, seen as glandular dots, were found on the stem surface (Fig. 2A-B), while their distribution was much more dense on the peduncle surface, especially near the inflorescence (Fig. 3B). Stomata with well developed outer cuticular ledge were also seen on the stem and peduncle (Fig. 2B).

Leaf micromorphology

Both adaxial and abaxial leaf surfaces of *C. glaberrima* subsp. *divergens* are sparsely covered with non-glandular trichomes, the same type as on the stem and peduncle (Fig. 2C-D). Glandular trichomes of the capitate type, which are sunk-

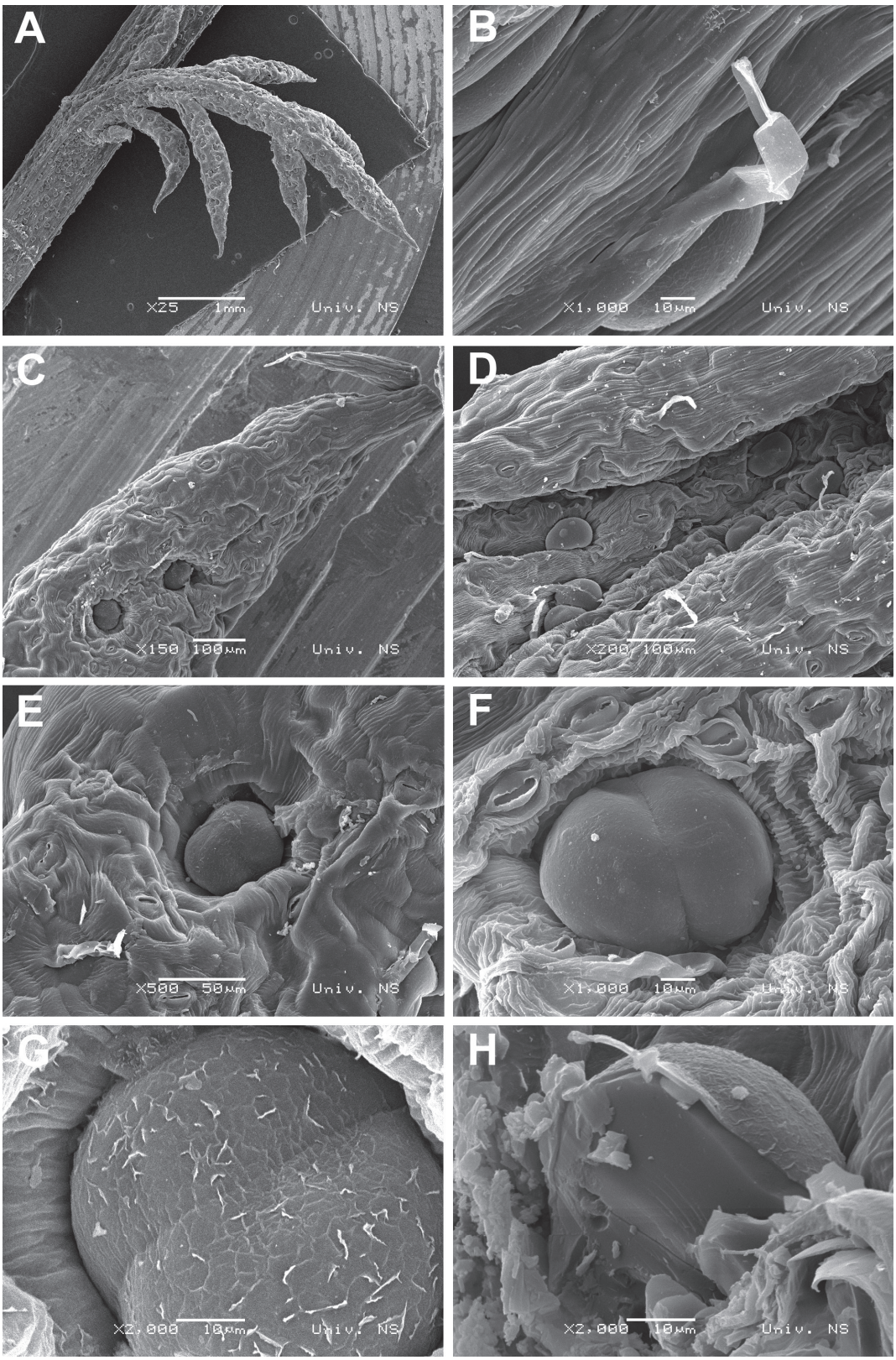

Fig. 2. Stem (A-B) and leaf (C-H) micromorphology of *C. glaberrima* subsp. *divergens*. A – general view of the stem and leaf with numerous glandular trichomes, B – uniseriate non-glandular trichome of stem, C – adaxial leaf side, D – abaxial leaf side, E-F – sunken biseriate glandular trichomes, striation pattern and anomocytic stomata on adaxial leaf side, G – rugose surface of the glandular trichome, H – half of the biseriate glandular trichome.

en under the surface, are evident on both leaf surfaces (Fig. 2C-F). Glandular trichomes are biseriate (Fig. 2F-H). Surface of the glandular trichome is rugose (Fig. 2G). Cells of the adaxial epidermis are polygonal in shape (Fig. 2E). Outer periclinal cell walls are convex (Fig. 2E) and with strongly ribbed thickenings (striation pattern) (Fig. 2E-F). Anticlinal cell

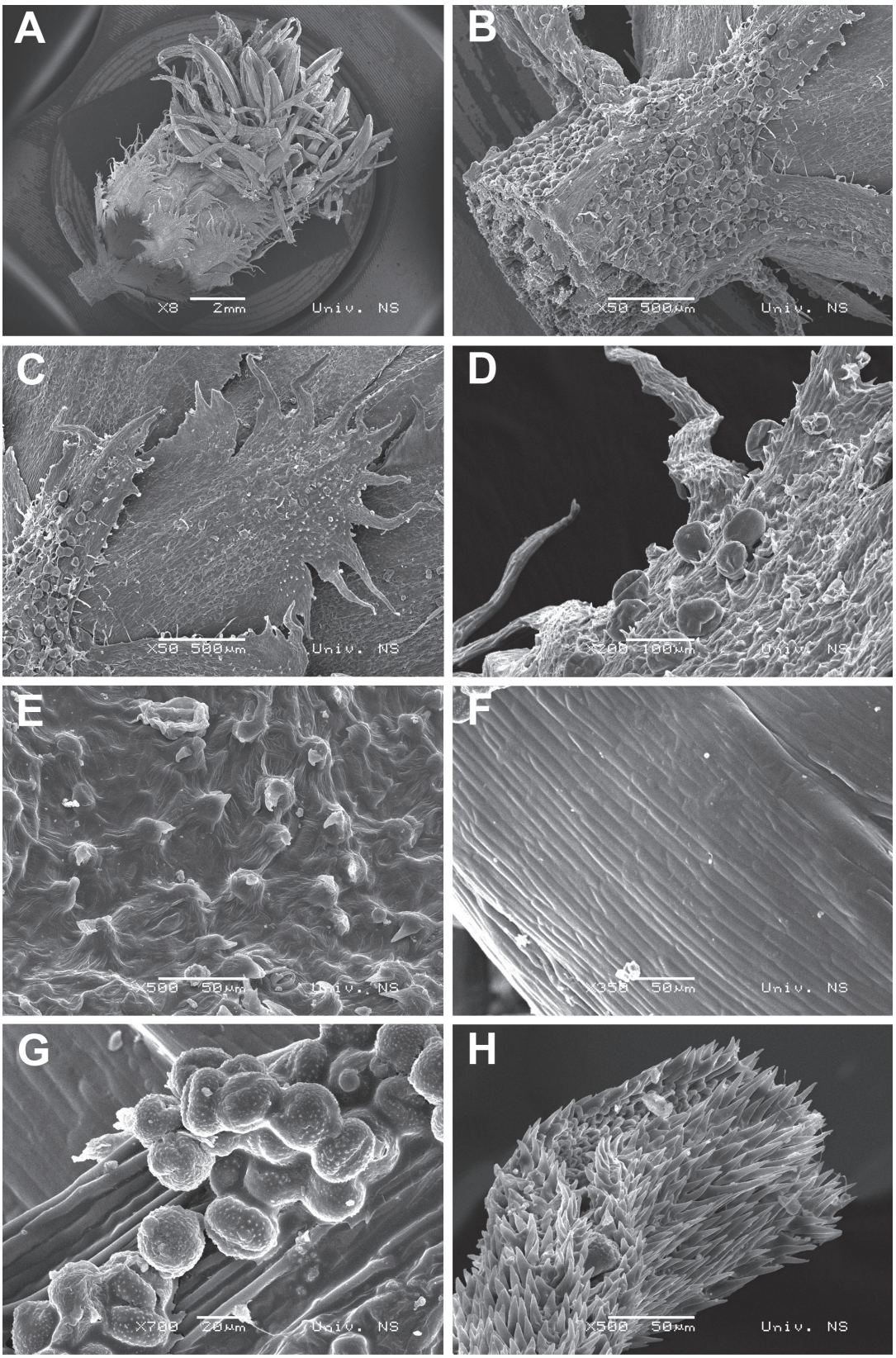

Fig. 3. Inflorescence micromorphology of *C. glaberrima* subsp. *divergens*. A – general view of the inflorescence, B – peduncle with glandular trichomes, C-D – middle involucral bract with glandular trichomes, E – rugose surface with thorny protuberances of the involucral bract, F – glabrous corolla surface, G – microechinate pollen grains, H – short stylar hairs, without cuticular striations.

walls are slightly curved (Fig. 2E). Anomocytic stomata, with well developed outer cuticular ledge, were observed on the adaxial and abaxial leaf surfaces (Fig. 2C-F).

Involucral bract micromorphology

The *C. glaberrima* subsp. *divergens* inflorescences subtended an involucre of overlapping bracts with several fim-

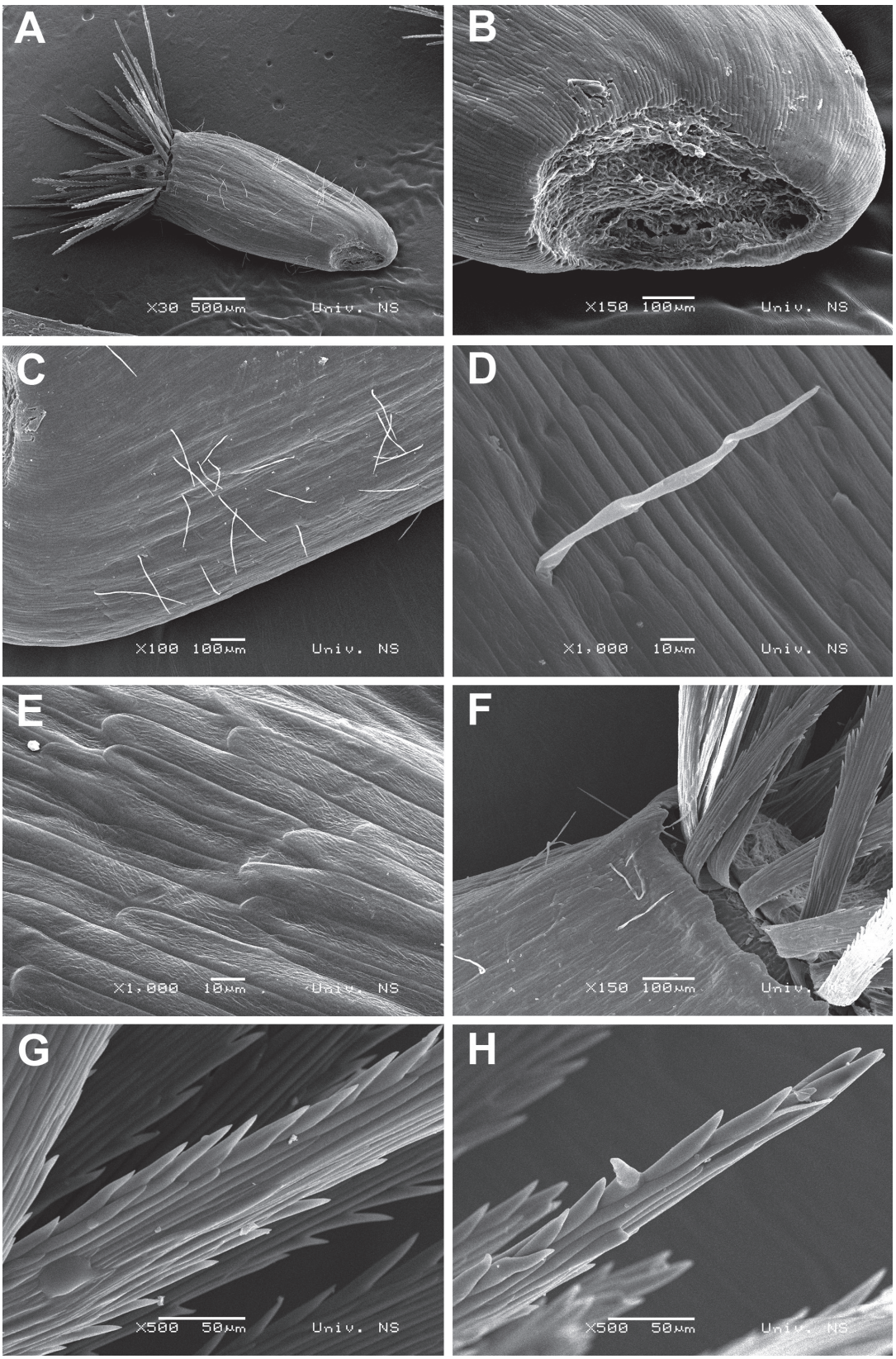

Fig. 4. Cypsela micromorphology of *C. glaberrima* subsp. *divergens*. A – general view of the cypsela, B – lateral concave insertion, C-D – short, unicellular curly acute trichomes, D-E – fine-sulcate ornamentation of the cypselae, F – minutely dentate apical pericarp rim and dimorphic barbate-aristate pappus, G – lateral insertion of the pinnules, H – acute apex of the bristle.

briae (length more than 1 mm) on each side (Fig. 3A-C). The outermost involucral bracts are very densely covered with glandular trichomes of the biseriate capitate type, seen as glandular dots, as well as with sparsely distributed non-glandular trichomes (Fig. 3A-C). Middle involucral bracts are sparsely covered with both types of trichomes (Fig. 3C-

D). Abaxial surface of the involucral bracts (especially seen on the middle bracts) is rugose with thorny protuberances (Fig. 3E). Small protuberances are seen over the entire surface (Fig. 3E). Stomata with well developed outer cuticular ledge are also observed (Fig. 3E).

Corolla, pollen and style micromorphology

Corolla is glabrous. Epidermal cells are longitudinally parallel to the long axis of the corolla. Corolla lacks trichomes. The outline of the epidermal cells is distinct (Fig. 3F). Epidermal cells are rod shaped with short, obtuse end walls. The cell boundaries are very thin and the centers of the cells are higher than the boundaries. The anticlinal walls of the epidermal cells are straight (Fig. 3F). Exploring inflorescence micromorphology, we observed isopolar, radially symmetric and tricolporate pollen grains. Surface of the pollen grains is microechinate (Fig. 3G). Style is distinctly bifid (branches obtuse), short-pilose above a collar of long sweeping hairs at the bifurcation point (not shown herein). Acute (expanded at the base and pointed at the upper part) stylar hairs are present along the outer side of the stigma (Fig. 3H). No stylar cuticular striations were found on the hairs. Thus, the upper part of the style and the outer part of the dichotomous stigma formed a secondary pollen presenter. Only the inner side of the stigma (abaxial surface) was covered with papillate stigmatic surface (Fig. 3H).

Cypsela micromorphology

The fruit of *C. glaberrima* subsp. *divergens* is differentiated into cypsela and pappus (Fig. 4A). The cypsela is slightly ribbed and rotund at the base. Insertion of the cypsela is lateral and concave (Fig. 4A-B). Carpopodium is absent (Fig. 4A-B). Short, unicellular, curly acute trichomes are sparsely present on the cypsela surface (Fig. 4C-D). Cypsela lacks glandular trichomes. The elongated epidermal cells are longitudinally parallel to the long axis of the cypsela (Fig. 4D-E). The cypsela coat is not roughish, the epidermis is smooth. Ornamentation of the cypsela is fine-sulcate (Fig. 4D-E). The outline of the epidermal cells of the cypsela is distinct. Epidermal cells are rod shaped with short, obtuse end walls (Fig. 4E). The cell boundaries are very thin and the centers of the cells are higher than the boundaries (Fig. 4E). The anticlinal walls of the epidermal cells are straight (Fig. 4E). Epicuticular secretion is undeveloped. The apical pericarp rim is minutely dentate, poorly developed, and the pericarp crown is totally absent (Fig. 4F). At the upper portion of cypsela, a dimorphic barbate-aristate pappus, consisting of free, numerous bristles of different size and shape, shorter than cypsela, is present (Fig. 4A, F). The outer pappus is pluriseriate, formed by short triangular bristles and long narrow, subulate, barbellate bristles, while the inner pappus is very reduced, almost vestigial, formed by triangular bristles (Fig. 4F). Pinnules (pectines) are restricted to the margins of the bristles. Both the ventral and dorsal bristle surfaces are smooth (Fig. 4G). Apex of the bristle is acute (Fig. 4H).

Discussion

We have shown here that the studied species possesses sparsely distributed uniseriate non-glandular and numerous biseriate glandular trichomes on the aboveground vegetative parts, although the species name of this taxon derived from Latin word *glaber* (hairless, smooth) which means without indumentum. Non-glandular trichomes in Asteraceae exhibit a wide range of structural types. Rahiminejad et al. (2010) noted that the type and density of leaf and stem epidermal indumentum were of particular taxonomic value for *Centaurea* species. Metcalfe and Chalk (1972) described uniseriate trichomes with a long terminal cell characteristic for *Centaurea,* which is in accordance with our results. However, two types of non-glandular trichomes, with thick-walled and thin-walled basal cells, were recorded on the leaves of *C. sadleriana* Janka (Luković et al. 2013), *C. rupestris* L. and *C. fritschii* Hayek (Rusak et al. 1992) and *C. cyanus* L. (Haratym et al. 2020). In addition, Haratym et al. (2020) documented two types of non-glandular multicellular trichomes on the stem surface of *C. cyanus*.

Capitate trichomes are found on stem, peduncle and on both leaf sides of the examined species. According to Robinson (2009) the presence of glandular trichomes of the short-stalked capitate type is a widely distributed microcharacter in Asteraceae. Biseriate trichomes are very common within the family (Gavrilović et al. 2018, 2019). Glandular trichomes are found in other *Centaurea* species (Rusak et al. 1992, Luković et al. 2013, Haratym et al. 2020). These trichomes are the main sites of production and accumulation of sesquiterpene lactones (Gavrilović et al. 2018). Cnicin, a biologically active sesquiterpene lactone, has been reported as a constituent of *C. glaberrima* (Tešević et al. 2007).

We found ribbed thickenings (striations) on the surface of the adaxial leaf epidermis of the studied species which might have taxonomic value as was previously stated by several authors (Adedeji and Jewoola 2008, Gavrilović et al. 2019). Rugose cuticle was observed on the lamina epidermis of *Centaurea sadleriana* (Luković et al. 2013). Four types of stomata have been reported in Asteraceae: anomocytic, brachyparacytic, anisocytic and diacytic (Adedeji and Jewoola 2008). We observed the anomocytic type of stomata in the examined species which was also found in *C. sadleriana* (Luković et al. 2013), *C. rupestris* and *C. fritschii* (Rusak et al. 1992). Slightly curved anticlinal cell walls of dorsal epidermis observed in the studied species are found also in *C. rupestris* (Rusak et al. 1992).

Our results showed that the microcharacters of involucral bracts (rugose surface with thorny protuberances, presence of glandular and non-glandular trichomes) might have taxonomic value. Hilpold et al. (2014) stated that the main morphological character used for systematics within *Centaurea* is the form of the scarious bract appendages. For the first time, our results provide information about such a surface of the *C. glaberrima* subsp. *divergens* involucral bracts. Haratym et al. (2020) found numerous pointed unicellular non-glandular trichomes on the edges of each tooth of the

bract of *C. cyanus*. Also on the bract abaxial surface they found two types of non-glandular trichomes as well as biseriate glandular trichomes. Glandular trichomes are also found on *Xeranthemum cylindraceum* Sm., but not on *X. annuum* L. involucral bracts (Gavrilović et al. 2017).

The taxonomic significance of epidermal and cuticular structures of the corolla has been pointed out by Baagøe (1977). Häffner (2000) stated that the patterns of the dorsal epidermis are usually homogeneous within the genera, whereas the ventral epidermis is more variable. We found a glabrous and smooth surface of the dorsal corolla epidermis of the studied species. Haratym et al. (2020) have shown a crested pattern on the epidermal surface of the ligulate flowers of *C. cyanus*. We documented straight anticlinal cell walls of the corolla epidermis in contrast to the undulate cell walls in all Centaureinae members that Häffner (2000) investigated.

General morphology of pollen of the studied species is found to be in agreement with previous comprehensive palynological studies of *Centaurea* taxa (Wagenitz 1955, Özler et al. 2009, Baser et al. 2019). Wagenitz (1955) stated that almost all *Centaurea* species belonging to the sect. *Acrolophus* possess *Jacea* pollen type with reduced spines which is in accordance with our results. However, further methods (acetolysis technique, tansmission electron microscopy (TEM)) and investigation of *C. glaberrima* subsp. *divergens* pollen is needed to determine additional features (e.g., shape, exine structure, the presence of single- or double-layer columellae) which proved to have value in *Centaurea* taxonomy (Wagenitz 1955, Shabestari et al. 2013, Özler et al. 2009, Baser et al. 2019).

Our findings indicate that the style morphology of *C. glaberrima* subsp. *divergens* resembles that of other Cardueae members: a ring of sweeping hairs on the shaft below the style bifurcation and internal stigmatic surface is a general character which is shared by all Cardueae species (Susanna and Garcia-Jacas 2009). Torres and Galetto (2007) suggested that style morphological characteristics of Asteraceae are far more diverse and represent a highly complex system. Erbar and Leins (2015) observed and described five different cuticular patterns on stylar hairs which could be helpful in phylogenetic classification of Asteraceae. However, we did not observe any of the described patterns in the *C. glaberrima* subsp. *divergens* style. Even though a longitudinal cuticular pattern was detected on the stylar hairs in *C. cyanus* (Haratym et al. 2020), many members of the Cardueae have no stylar cuticular striations (Erbar and Leins 2015). In addition, Erbar et al. (2018) examined style morphology in all Carduoideae tribes and determined 10 new style types in view of shape, bifurcation and distribution of stylar hairs and stigmatic tissue. It was shown that all of the *Centaurea* species, except *C. macrocephala* Muss. Puschk. ex Willd., possess *Centaurea* type styles, which is in accordance with our results.

Although, cypselae are glabrous in most representatives of the Centaureinae (Herrando-Moraira et al. 2019) we found sparsely distributed uniseriate trichomes on the cypselae surface, which is in agreement with Dittrich (1977) who pointed out that *Centaurea* taxa possess cypselae with monocellular trichomes of different length, which are directly fixed on the pericarp epidermis. In addition, Candan et al. (2016) documented hairy pericarp of cypselae of the investigated species of sect. *Acrolophus* (Cass.) DC (*Centaurea*). Susanna and Garcia-Jacas (2009) stated that majority of genera in Centaureinae possess concave, lateral-adaxial insertion areole, often with an elaiosome, which is in accordance with our results (although we did not observed elaiosome, it was probably fallen out). Subbasal-lateral insertion was also found by Dittrich (1968) and Ozcan and Akinci (2019) for all investigated *Centaurea* species. A character that is evident in the subtribe Centaureinae is the presence of a smooth pericarp (Herrando-Moraira et al. 2019, Ozcan and Akinci 2019) which is in accordance with our study. It was shown that the different cellular patterns found in *Centaurea* pericarp might have diagnostic value (Candan et al. 2016, Ozcan and Akinci 2019). Rod shaped epidermal cells found in examined species are also found in all investigated *Centaurea* taxa (Ozcan and Akinci 2019). Minutely dentate apical pericarp rim found in studied species are also present in *C. melitensis* L. and *C. solstitialis* L. (Bean 2001). Pappus usually in two structurally different rows (double pappus) are common in Centaureinae (Dittrich 1968, Susanna and Garcia-Jacas 2009). In the examined species pappus is dimorphic: the outer is pluriseriate and the inner very reduced, almost vestigial, formed by triangular bristles. However, Ozcan and Akinci (2019) have shown that all investigated *Centaurea* taxa possess the same structures of the pappus bristles, only the bristle lengths in the outer and inner row are different. Candan et al. (2016) documented scabrous or barbellate pappus bristles in *Centaurea* taxa from the sect. *Acrolopus*. Häffner (2000) classified genera into three groups based on the bristle cross section and the location of the pinnules on the bristles. Pappus bristles of the examined species belong to the third type, which is characterized by dorsoventrally compressed bristles with rows of pinnules (pectines) at the margins, while both surfaces are smooth. However, Bean (2001) found pinnules borne laterally and dorsally in bristles of *C. melitensis* and *C. solstitialis*.

The present study is the first, and a comprehensive, report on the micromorphology of endemic *Centaurea glaberrima* subsp. *divergens*. Micromorphological features of the leaf epidermis (striation pattern, slightly curved anticlinal cell walls, uniseriate non-glandular and biseriate glandular trichomes), involucral bracts (rugose surface with thorny protuberances, uniseriate non-glandular and biseriate glandular trichomes), corolla (glabrous surface and straight anticlinal cell walls), style (absence of cuticular striations of stylar hairs) and cypsela (minutely dentate apical pericarp rim, dimorphic pappus with reduced inner pappus, lateral insertion of the pinnules) might have taxonomic value and contribute to better species identification. Micromorphological studies of other related *Centaurea* taxa should be continued in order to evaluate their phylogenetic importance.

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