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Original scientific paper

ANATOMICAL INVESTIGATIONS OF ENDEMIC
SPECIES *CENTAUREA RUPESTRIS* L. AND *C.*
FRITSCHII HAYEK (ASTERACEAE)

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The paper deals with the anatomy of the shoot and the root of the species *Centaurea rupestris* L. and *C. fritschii* Hayek, endemic in the Balkans. The species show great correspondence in the internal structure indicating their close interrelationship. Some anatomical phenomena not described so far were established in the course of these studies. These are: the presence of a bundle sheath in medullary bundles, formation of stem pith hollow by lysigeny, and occurrence of inulin crystals in living plants.

Introduction

The genus *Centaurea* is one of the richest genera in the *Asteraceae* with regard to the number of species. The genus comprises about 600 species (Cronquist 1981), which, according to Hegi (1929), have the main spreading area in the Mediterranean region.

Earlier anatomical investigations within the genus *Centaurea* were performed from two aspects. One aspect of these investigations was aimed at solving some taxonomical and phylogenetical problems (Dormer 1961, 1962, Dittrich 1968, Ninova 1973, 1978 a, b, Singh and Pandey 1984, and others) or was related to ecoanatomical investigations (Korčagina 1965, Arena et al. 1975, Goryšina and Hecuriani 1980, and others). The other aspect concerned fundamental knowledge about the anatomical structure of the members of genus *Centaurea*. Such is the character of the work of Heinricher (1883) and

other investigations resulting in data on some anatomical peculiarities of the genus *Centaurea* (Solleder 1899, Metcalfe and Chalk 1950, 1979, 1985). Anatomical analyses as an introduction to phytochemical investigations of the genus *Centaurea* (Karawya et al. 1974 a, b, c, Kuštrak and Radić 1985, Negrete et al. 1988) can be added to these fundamental investigations.

Analyses of the internal structure of the Illyrian-Adriatic endemic species *C. rupestris* and the Balkan endemic *C. fritschii* were also an introduction to phytochemical analysis of both species. The investigations were performed not only to gain a better insight into the anatomy of the species studied, but also to contribute to the knowledge of the anatomy of the genus *Centaurea* and family *Asteraceae* in general, and to help avoid some earlier incorrect anatomical interpretations.

Material and Methods

Material

C. rupestris was collected in the Adriatic coastal region near Kraljevica (Uvala Scott) and *C. fritschii* in the hills of Samoborsko gorje (Stojdraga) near Zagreb (for distribution see Pavletić and Trinajstić 1983). Both species were sampled during the flowering time. The investigations were conducted on the plant material preserved in FAA fixing fluid (Johansen 1940). The stem was analysed also in living state.

Methods

The anatomy of the species investigated was studied mainly in cross sections made manually by means of a razor blade and analysed by light microscopy. In order to identify the presence and location of some substances and anatomical structures (inulin, oxalate crystals, lignin, cutin, suberin and wax) some conventional histochemical reactions were made according to Behrens (1908) and Johansen (1940). The 1% aqueous solution of alcian blue was used in cellulose wall test.

Photographs were made by means of an Opton light microscope using 22 din ORWO film.

Results

Our investigations have revealed that *C. rupestris* and *C. fritschii* do not show any significant differences in the internal structure of the shoot and root. Therefore, the anatomy described in further text refers to both investigated species. The differences between both species, existing in the structure of epidermal cells and leaf anatomy, will be especially pointed out.

The stem

In *C. rupestris* the uniseriate **epidermis** shows xeromorphic characteristics. The epidermal cells have markedly thick cellulose outside walls with thick striated cuticle. The anomocytic stomata with xeromorphic

guard cells occur in small cavities. *C. fritschii* as a mesomorphic plant has moderately thinwalled epidermal cells with anomocytic stomata and thin cuticle.

The upper edged part of the stem is covered with non-glandular and glandular hairs. Non-glandular uniseriate hairs have 2—3 base cells and a long whip-like terminal cell (Fig. 15) forming a web-like covering. In the projecting parts of the edged stem non-glandular hairs have a character of emergences; they consist of multicellular conical collenchymatous base and one or several long whip-like terminal cells (Fig. 14). The unfrequent glandular hairs contain 2—3 basal cells and a secretory head cell on the top (Fig. 16).

In the peripheral part of the stem **cortex** the lacunar collenchyma which sporadically passes over into lamellar one alternates with chlorenchyma tissue. In the younger edged stem part, the collenchyma is present in projecting and chlorenchyma in depressed parts of the stem (Fig. 1). In the direction towards the lower rounded stem part, the difference between collenchyma and chlorenchyma tissue diminish up to complete disappearance of chlorenchyma. In the cortical parenchyma tissue of the upper stem part, the **cortical bundles** situated under the chlorenchyma are present (Fig. 1). These small collateral vascular bundles have an inverse orientation of xylem and floem and do not possess a proper or clearly defined sclerenchymatic vascular sheath (Fig. 2). The phloem of cortical bundles leans against lignified distal ends of medullary rays or can be inserted in them (cf. Heinricher 1883) and in this way, the bundles protect the soft phloem tissue (Figs. 2, 3, 5). Only some cortical bundles are connected with the outer sclerenchymatic sheaths (»bundle caps«) of the main vascular bundles or are enclosed in them. In the direction towards lower stem part, cortical bundles together with chlorenchyma gradually disappear.

The primary vascular cylinder is split into large **main collateral bundles** which surround the pith (Fig. 1). The bundles are supported by sclerenchymatic sheaths, which are especially strong (»bundle cap«) above the phloem (Fig. 1). The parenchyma of medullary rays soon becomes sclerified, except in the basal part of the stem, where this process takes place after the secondary growth has finished (Figs. 3, 4, 5). In the cortical parenchyma close to each sclerenchymatic »cap« most often three schizogenous **secretory ducts** or canals are present (Fig. 2). Some of them can be incorporated in the »bundle cap«, or even in the lignified parenchyma of medullary rays.

The stem **pith** is composed of two types of parenchyma. Immediately beneath the capitulum, i. e. about 10 mm lengthwise, the stem pith is built of stellate parenchyma cells (Metcalf and Chalk 1979, p. 54) of cellulose walls and large intercellular spaces (Figs. 7, 8). In this area of the pith, **medullary bundles** are present and incorporated in stellate parenchyma (Figs. 7, 8). These bundles are more often incomplete consisting of the phloem only; rarely, they are collateral with poorly developed xylem. Both types of medullary bundles show a clearly differentiated sclerenchymatic bundle sheath (Fig. 8). Close to the capitula the vascular elements of these bundles are gradually reduced and finally end as small rests of sclerenchyma, whereas on the opposite side they seem to end blindly. The number of the bundles varies from a few to about eight.

The stellate parenchyma cells of the pith pass at a lower level into common roundish parenchyma cells from which those in perimedullar

position have slightly lignified walls. The **pith hollow** (canal) present in the lower older part of the stem originates in a particular way. In the middle of the pith the walls of unligified parenchyma cells start strongly to swell, which leads to reduction of cell lumina and to maceration of swollen and mucilaginous cells (Fig. 6). The result of this process is the formation of longitudinal cavity in the pith of older stem part (Fig. 9.) from which a mucilaginous mass flows out.

The **secondary growth**, generally of *Helianthus*-type (K a u s s m a n n and S c h i e w e r 1989, p. 139), takes place in the lower part of the stem. Congruently to that, before the formation of cambium ring, smaller additional bundles occur in the region of some medullary rays (Fig. 4). Aberrations from this way of secondary growth are present sporadically, i.e. in some interfascicular regions the cambium produces only medullary ray parenchyma (Fig. 5) or simultaneously a small amount of secondary xylem and passibly some secondary phloem (Fig. 3). After the secondary growth has finished, the interfascicular cambium and the parenchyma of medullary rays become entirely sclerified (Fig. 4, 5).

The leaf

The anatomy of the segments and petiole of pinnatisect leaves was analysed.

The leaves of *C. rupestris* are **isolateral** (Fig. 11) and amphistomatic with slightly xeromorphic epidermis and anomocytic stomata (Fig. 13). The lamina mesophyll consists of 3—4 layers of palisade parenchyma and of 2—3 layers of spongy parenchyma in the middle (Fig. 11). In contrast, the mesomorphic leaves of *C. fritschii* are **dorsiventral** in their inner structure (Fig. 10), having moderately thinwalled epidermis.

Two types of non-glandular whip-like **hairs** are present on the surface of the leaves. On the margins of the leaf segments, an uniseriate hair base is constituted of 3—6 thickwall cells (Fig. 18) and that of hairs on the very lamina of about ten cells with somewhat thinner walls. In *C. fritschii* the basis of whip-like hairs was generally thicker than those in *C. rupestris*. The glandular hairs were noticed very rarely.

The vascular bundles arranged in the middle of mesophyll are provided with a distinct sheath of parenchyma without chloroplasts (Figs. 10, 11). In addition, the larger veins contain a common sclerenchymatic sheath at least above the phloem. In the parenchymatous sheath of vascular bundles single secretory ducts can be present on the phloic side (Fig. 10). They pass from the base of petiole and rachis to the basal and middle part of leaf segments. The collenchyma situated below the epidermis supports the leaf segments in particular places.

The petioles are also covered with common whip-like hairs. In some places interrupted thickwall hypodermis is present. The hypodermis is followed by alternating regions of chlorenchyma and collenchyma (Fig. 12). Large collateral bundles surrounded with prominent sheaths are inserted in ground parenchyma. On their phloic side above the sheath run the secretory ducts. Small bundles which represent the spurs of cortical bundles of the stem can be observed between main bundles (Fig. 12).

The involuclar bracts and florets

The upper epidermis as well as the hypodermis of involuclar bracts consist of elongated cells with thick and lignified walls. The thinwalled

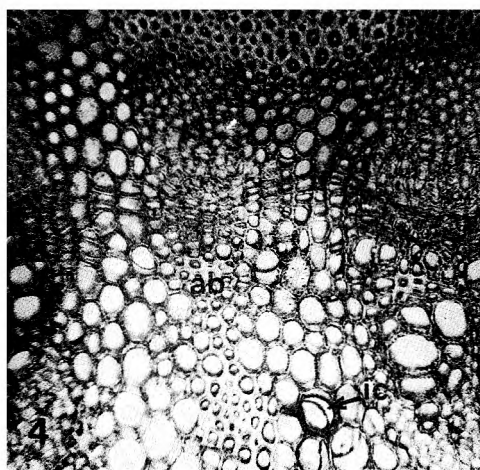
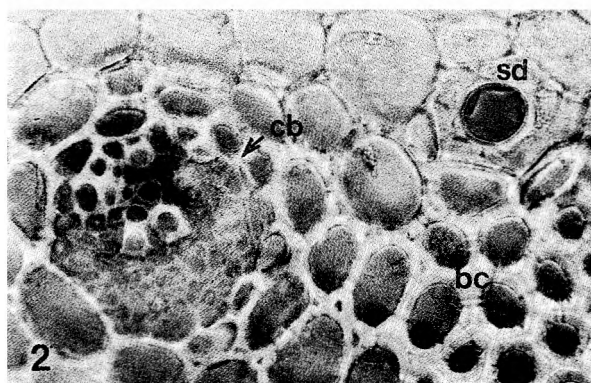
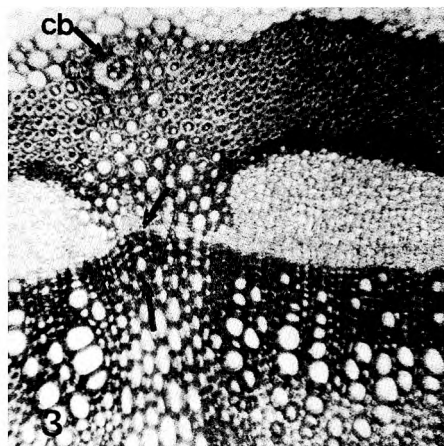
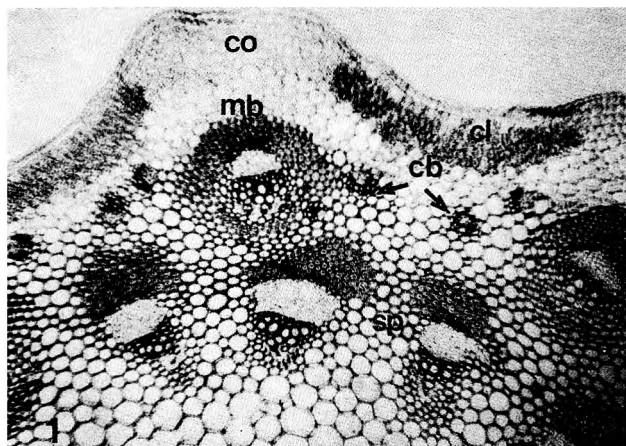
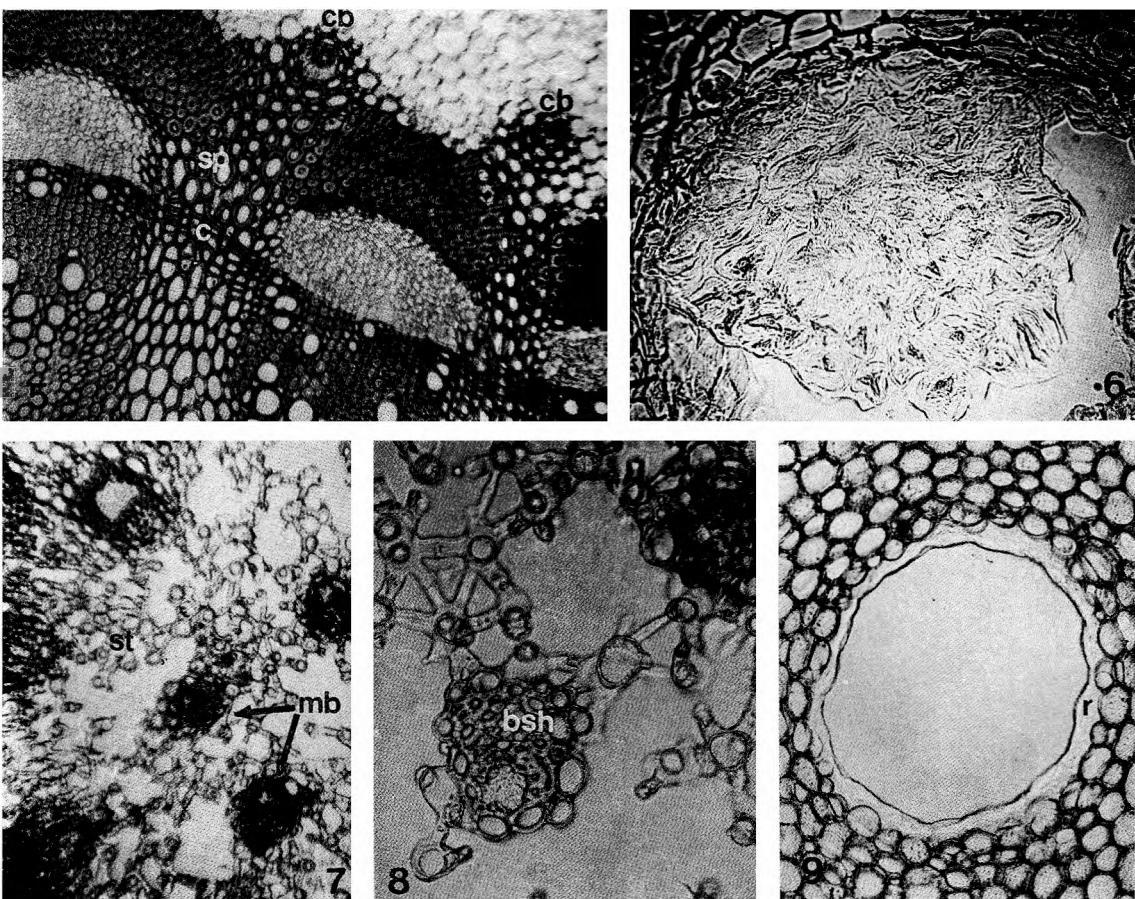


Fig. 1. Cross section through the stem of *Centaurea rupestris* in the primary stage; collenchyma (co), chlorenchyma (cl), small cortical bundles (cb), large main bundles (mb), sclerified parenchyma (sp). 45 : 1.

Fig. 2. Detail of cortical bundle (cb), enclosed in sclerified ray parenchyma, and of schizogenous secretory duct (sd) above the »bundle cap« (bc). 385 : 1.

Figs. 3—4. Details of cross section through the stem of *C. rupestris* in the stage of secondary growth. Fig. 3. Secondary xylem and phloem in the interfascicular region (arrows); cortical bundle (cb). 75 : 1. Fig. 4. Small additional bundle (ab) in the interfascicular region; inulin crystals (ic). 160 : 1.



- Fig. 5. Detail of cross section through the stem of *Centaurea fritschii* in the stage of secondary growth; sclerified ray parenchyma (sp) and cambium (c) in the interfascicular region; cortical bundles (cb). 75 : 1.
- Fig. 6. Maceration of swollen and mucilaginous pith parenchyma cells followed by development of pith hollow in the older stem part of *C. fritschii*. 135 : 1.
- Fig. 7. Medullary bundles (mb) of stem incorporated in stellate parenchyma cells (st) cross sectioned immediately beneath the capitulum of *C. rupestris*. 60 : 1.
- Fig. 8. Detail of medullary bundle with clearly differentiated sclerenchymatic bundle sheath (bsh). 145 : 1.
- Fig. 9. Cross section through the pith hollow of older stem of *C. rupestris*. The rest of swollen cell wall (r) is seen. 91 : 1.

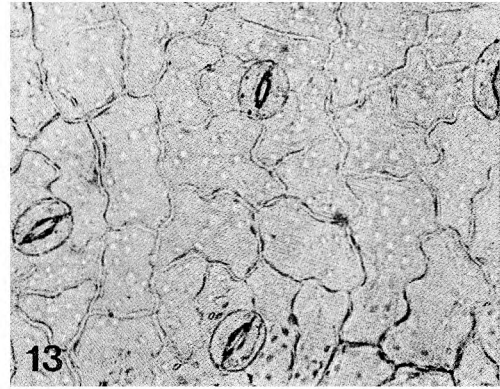
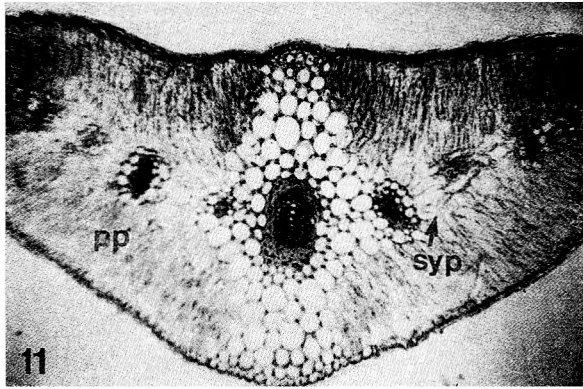
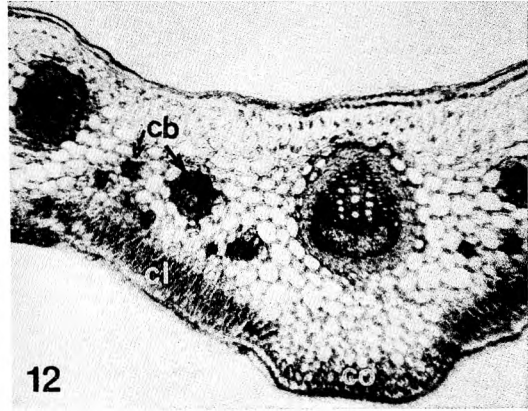
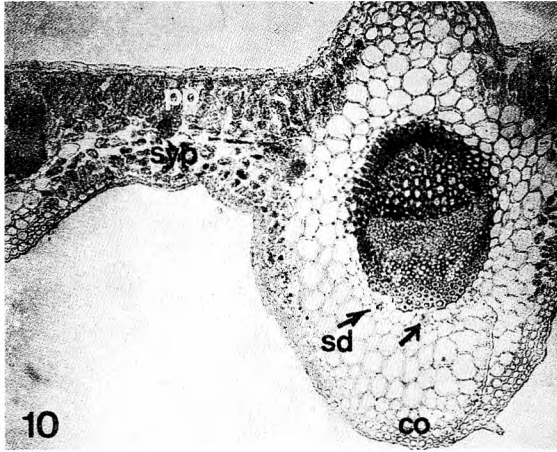


Fig. 10. Cross section through the segment of dorsiventral leaf of *Centaurea fritschii*; palisade parenchyma (pp.), spongy parenchyma (syp), secretory ducts (sd), collenchyma (co) 70.:1.

Fig. 11. Cross section through the segment of the isolateral leaf of *C. rupestris*; palisade parenchyma (pp), spongy parenchyma (syp). 41 : 1.

Fig. 12. Cross section through the petiole of *C. rupestris*; cortical bundles (cb), chlorenchyma (cl), collenchyma (co). 45 : 1.

Fig. 13. Anomocytic type of stomata on the leaf of *C. rupestris*. 465 : 1.

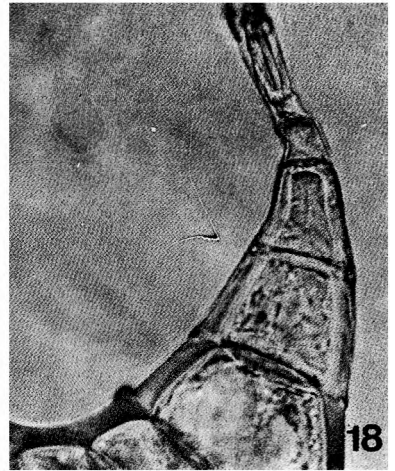
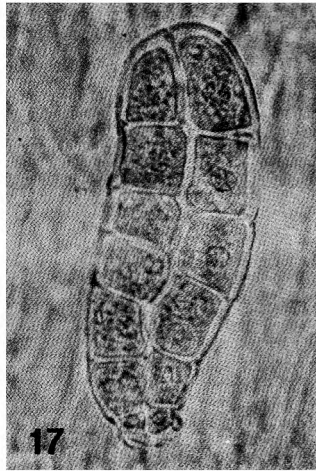
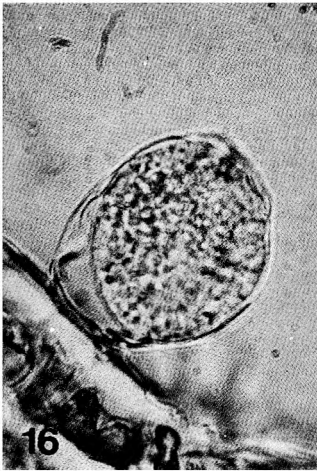
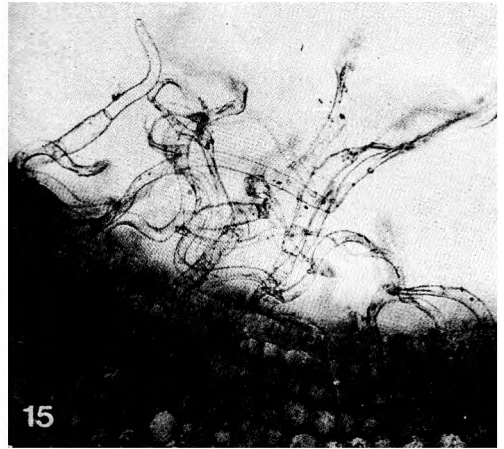
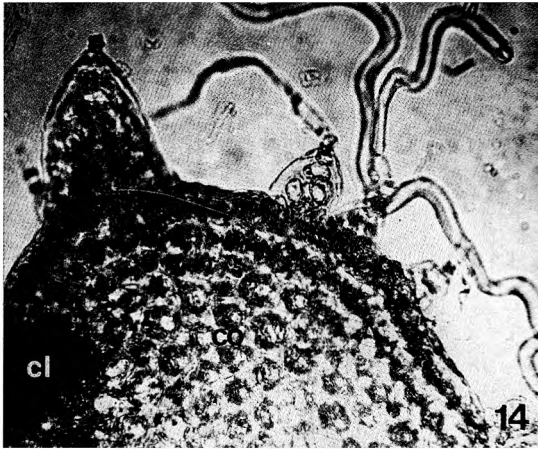


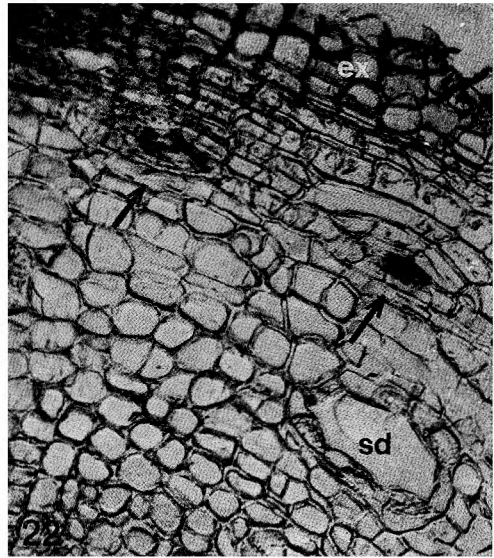
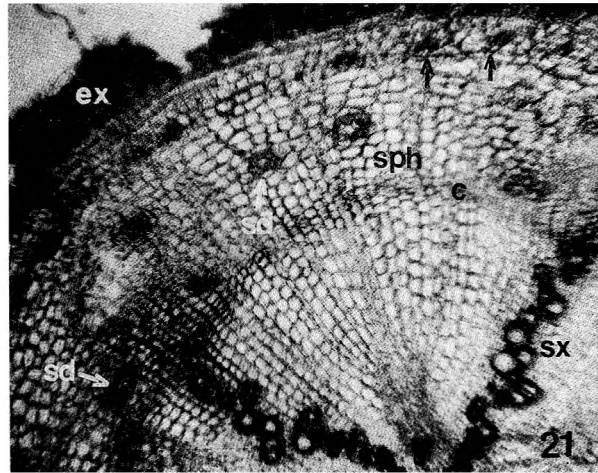
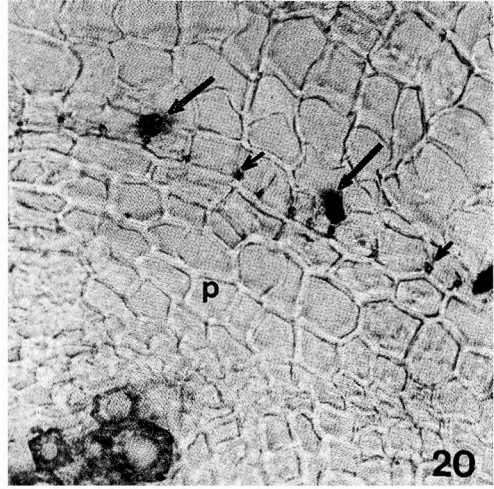
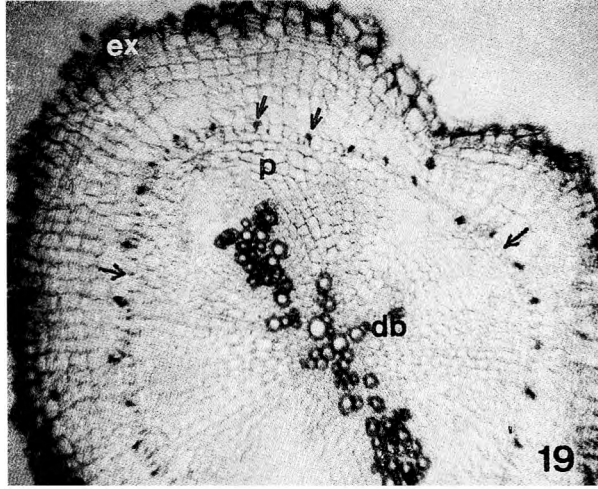
Fig. 14. Emergences with whip-like terminal cells on the projecting part of the edged stem of *Centaurea rupestris*; chlorenchyma (cl), collenchyma (co). 210 : 1.

Fig. 15. Non-glandular hairs with whip-like terminal cell in the depressed part of the edged stem of *C. fritschii*. 93 : 1.

Fig. 16. Glandular hair on the young stem of *C. rupestris*. 1050 : 1.

Fig. 17. Biseriate glandular hair on the floret of *C. fritschii*. 475 : 1.

Fig. 18. Non-glandular hair with thickwalled base cells from the margin of the leaf segment of *C. fritschii*. 370 : 1.



Figs. 19—20. Cross section through the root of *Centaurea rupestris* in primary stage. Fig. 19. Diarch bundle (db), multiseriate pericycle (p), biseriate endodermis (arrows), exodermis (ex). 58 : 1. Fig. 20. Detail of biseriate endodermis with endodermal resin ducts without epithelium (large arrows) and Casparian strips (small arrows), pericycle (p). 235 : 1.

Figs. 21—22. Cross sections through the root of *C. rupestris* at the beginning of secondary growth. Fig. 21. Secondary xylem with ray parenchyma (sx), cambium (c), secondary phloem (sph), secretory ducts with epithelium (sd), endodermis with resin ducts (arrows), exodermis (ex). 46 : 1. Fig. 22. Detail of Fig. 21; secretory ducts with epithelium (sd), endodermis with resin ducts (arrows), exodermis (ex). 145 : 1.

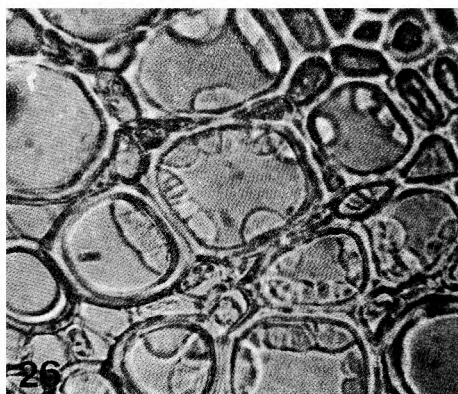
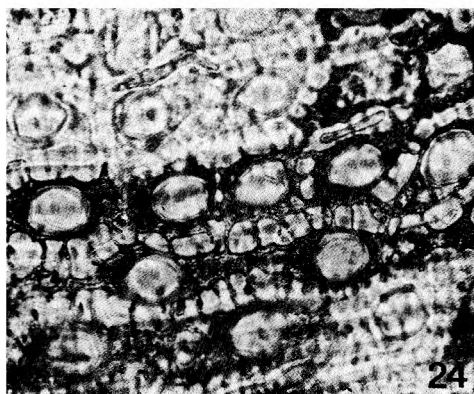
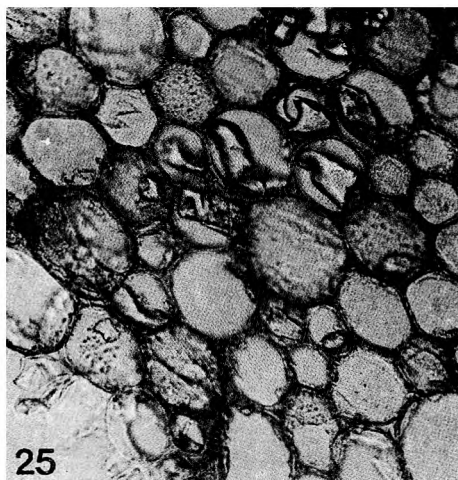
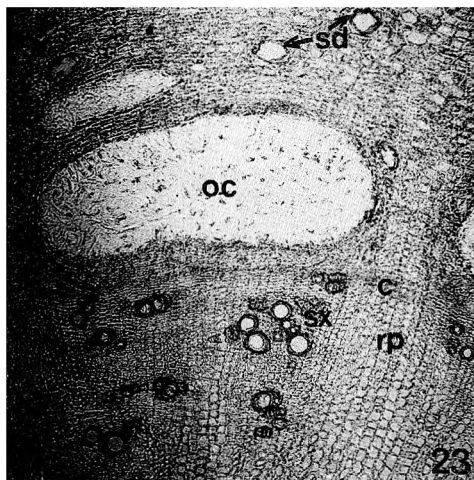


Fig. 23. Cross section through the root of *Centaurea rupestris* in the later stage of secondary growth; secondary xylem (sx), ray parenchyma (rp), cambium (c), oval cavity (oc) and secretory ducts with epithelium (sd) in secondary phloem. 70 : 1.

Fig. 24. Polyhedral oxalate crystals in square sclerenchyma cells below the lower epidermis of involuclar bracts of *C. rupestris*. 365 : 1.

Fig. 25. Irregular inulin crystals in the pith parenchyma cells of living stem of *C. rupestris*. 145 : 1.

Fig. 26. Inulin spherocrystals in the tracheary elements of fixed stem of *C. fritschii*. 485 : 1.

lower epidermis of the bracts consists of isodiametric cells with slightly wavy anticlinal walls and anomocytic stomata. It is covered with »cobweb« originating from whip-like hairs. Below the lower epidermis are present several layers of sclerenchymatic supporting tissue with thick and lignified cell walls and pronounced pits. The first subepidermal layer of this tissue is composed of square cells containing single polyhedral oxalate crystals (Fig. 24) and below are mainly supporting fibers. Above the phloem of the vascular bundles, located in the green mesophyll, secretory ducts can also be noticed.

On the surface of the floret corolla, large biseriate glandular hairs made of stalk and head can be observed (Fig. 17). In the epidermis of corolla, bundles of needle-shaped colourless crystals, probably of oxalate nature, are present.

The root

In the primary structure of the young root the rhizodermis is soon substituted for multiseriate **exodermis** (Fig. 19). This protecting tissue is formed by suberization of the outer part of cortical parenchyma cells arranged in orderly radial rows. On the boundary of the cortex and central cylinder, **biseriate endodermis** occurs (Figs. 19, 20). It contains Casparian strips on the radial walls of the inner layer and resin ducts without epithelium in intercellular spaces (Fig. 20). The **pericycle** placed beneath the endodermis seems to be multiseriate (Figs. 19, 20).

The **primary vascular structure** of the root is most often diarch (Fig. 19), frequently becoming triarch or even tetrarch at higher levels of the root. During the **secondary growth** (Figs. 21, 23) the formed vascular cambium produces, towards the interior of the root, in the greatest quantity, radially arranged nonlignified woody and ray parenchyma and between them, in a smaller amount, tracheary elements and patches of sclerenchyma, which both also have a tendency of radial orientation. In the secondary phloem, produced by combium in the opposite direction of secondary xylem, the first secondary secretory ducts lined with epithelium appear (Fig. 22). In the later stage of secondary growth (Fig. 23) further considerable changes appear in the root: the endodermal resin ducts move apart from each other by radial divisions of endodermal and other living cells (dilatation growth); secondary secretory ducts in the secondary phloem continue to develop; obliterated primary phloem becomes sclerified sporadically; in the thick secondary phloem oval cavities form, originating in the same way as those in the stem pith, i. e. by a process of lysigeny; the process of suberization of cortical parenchyma reaching the endodermis continues to secondary phloem.

The appearance of inulin

In plant material preserved in fixing fluid FAA containing 70% ethanol (Johansen 1940, p. 188) inulin crystals were present in all parts of the vegetative body (Fig. 26) except the leaf blade. But, unexpectedly, in some specimens of *C. rupestris* inulin crystals were also observed in unfixed living stem (Fig. 25). They were situated inside the pith parenchyma cells in the form of roundish or irregularly shaped crystalline inclusions (Fig. 25), and as true spherocrystals inside the lumina of tracheary elements (unpublished data). In the living tissue of *C. fritschii* inulin crystals were never observed.

Discussion

The main known facts about the anatomy of the genus *Centaurea* (Heinricher 1883, Solereder 1899, Metcalfe and Chalk 1950, 1979, 1985) have been confirmed by the results of our anatomical investigations of *C. rupestris* and *C. fritschii*. They are: the presence of whip-like and glandular hairs, alternations of chlorenchyma and collenchyma in the stem cortex and leaf petioles, the presence of cortical and medullary vascular bundles and occurrence of secretory ducts.

The presence of cobwebby hairs is somewhat more pronounced in xeromorphic *C. rupestris*, but the glandular hairs are rare in both species. According to the literature, the presence of glandular hairs in the genus *Centaurea* is variable. K a r a w y a et al. (1974 a, b) have not noticed their presence on the shoot of *C. calcitrapa*, while Kuštrak and Radić (1985) have found them often on the shoot of *C. gloriosa*. The isolateral structure of leaves noticed in *C. rupestris* has been recorded in many xeromorphic species, and also in some species of the genus *Centaurea* (F a h n 1982, p. 211).

All anatomical characteristics concerning the occurrence of cortical bundles and chlorenchyma quoted by Heinricher (1883) were noticed in the stem of *C. rupestris* and *C. fritschii*, too.

Our findings concerning medullary bundles, the occurrence, location and the flow of the bundles in investigated *Centaurea* species, as well as their structure with regard to arrangement of vascular elements are in agreement with the anatomy of medullary bundles quoted by Metcalfe and Chalk (1950, 1979, p. 79). However, in contrast to the above mentioned authors, we have found that medullary bundles can possess a sclerenchymatic bundle sheath. A marked variation in the number of medullary bundles in *C. rupestris* and *C. fritschii* corresponds to the statement by Metcalfe and Chalk (1950) that even inside the same species, samples with or without medullary bundles can exist.

The finding of schizogenous secretory ducts in the endodermal region of stems of our *Centaurea* species is congruent with reports by Solereder (1899), Metcalfe and Chalk (1950), Ninova (1978b), and Kuštrak and Radić (1985). The endodermal resin ducts without epithelium, characteristic of root in *Asteraceae* (Solereder 1899, Metcalfe and Chalk 1950), have been noticed also in the species investigated.

In the stem of *C. rupestris* and *C. fritschii* the endodermis is not morphologically especially pronounced. Solereder (1899) and Metcalfe and Chalk (1950) do not mention endodermis in the stem of *Centaurea* species, either. However, this fact cannot really exclude its presence because endodermis can be distinguished from neighbouring parenchyma cells only with regard to its physiology (Esau 1965, pp. 375—376, Metcalfe and Chalk 1979, pp. 171—172). Sclerenchymatic »bundle caps« above the phloem of main vascular bundles can be considered as pericycle only with reservation because their possible nonprocambial or nonphloic origin was not investigated and proved (see Esau 1965, pp. 376—377, Metcalfe and Chalk 1979, p. 181). The only thing beyond doubt is that the sclerosed part of the »cap« close to the phloem can be of phloic origin.

The pith hollow, as known from the literature (Mauseth 1988, p. 211, Fahn 1982, p. 197) originates because the pith cells stop early to grow and are torn apart. However, we have established that the central hollow in the stem pith can develop by swelling and maceration of pith

parenchyma cells. As observed, of the same origin are the cavities in the secondary phloem of the root, where the secondary growth also provokes tensions. These facts lead to the conclusion that the hollows or cavities in the tissues caused by tensions, due to longitudinal growth or/and accumulation of secondary tissues, do not form only by breaking of cells (rhexigenously) but by lysigeny, as well.

The primary structure of the root of the species investigated corresponds generally to main facts of primary structure of the root in *Asteraceae* presented by Solereder (1899) and Metcalfe and Chalk (1950). The literature data concerning the changes by secondary thickening are rather poor (comp. Solereder 1899, Metcalfe and Chalk 1950, Karawya et al. 1974a).

It was especially surprising and unexpected to find inulin crystals in the living stem tissue of *C. rupestris*, because it is well known that inulin appears in the cell vacuoles only in solution, and with any dehydration of cells inulin precipitates, mostly in the form of spherocrystals. The presence of inulin crystals in the living stem of *C. rupestris* is very probably caused by excessive desiccation of cells due to climate and soil conditions in the Mediterranean area of distribution of this species. The presence of oxalate crystals in bracts of *C. rupestris* and *C. fritschii* does not seem to be rare because they were observed in bracts of *C. calcitrapa*, too (Karawya et al. 1974b).

The concordance found in the internal structure of *C. rupestris* and *C. fritschii* also indicates a close relationship between these two species. The small differences in the anatomy of these species are caused by different ecological conditions in their habitats. The anatomical investigations described present a contribution to the plant anatomy in general through some anatomical phenomena and structures not described earlier, i.e. the presence of bundle sheath in medullary bundles, the formation of cavity in the stem pith by lysigeny and occurrence of inulin crystals in living plants.

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SAŽETAK

ANATOMSKA ISTRAŽIVANJA ENDEMIČNIH VRSTA *CENTAUREA RUPESTRIS* L.
I *C. FRITSCHII* HAYEK (ASTERACEAE)

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Endemične vrste roda *Centaurea* balkanske regije u anatomskom su i kemijskom pogledu gotovo potpuno neistražene. Anatomska istraživanja ilirsko-jadranske endemične vrste *C. rupestris* i balkanskog endema *C. fritschii* poduzeta su kao uvod fitokemijskim istraživanjima i obuhvaćaju analizu anatomije izdanka i korijena navedenih vrsta. Rezultati tih istraživanja pružaju cjelovitu sliku o unutarnjoj građi istraživanih vrsta, ukazujući na njezinu gotovo potpunu podudarnost, što predstavlja još jednu potvrdu srodnosti dviju navedenih vrsta. Malobrojne razlike u pogledu anatomske građe između vrste *C. rupestris* i vrste *C. fritschii* odraz su različitih ekoloških uvjeta u područjima u kojima te biljke imaju areal svog rasprostranjenja. Pri ovim istraživanjima utvrđene su i neke anatomske strukture i pojave koje dosad nisu zabilježene u literaturi, pa stoga predstavljaju doprinos i anatomiji bilja u cjelini. To su: pojava mehaničkog žilnog ovoja kod medularnih žila, postanak centralne šupljine u srčiki stabljike na lizigeni način te pojava kristala inulina u živim biljkama.

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