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STRUCTURAL INVESTIGATION OF THE SECRETORY SYSTEM OF SOME ENDEMIC AND MEDICINAL SPECIES OF APIACEAE FROM UZBEKISTAN

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Middle Asia is one of the major centers of origin and diversity of the family Apiaceae. Secretory system and other anatomical peculiarities of many endemic Apiaceae are still poorly investigated. Comparative anatomical study of plant secretory structures has a great theoretical and practical importance in relation to taxonomy, ecology and pharmacology. The paper provides the results of structural investigation of the secretory system of five endemic and medicinal species of Apiaceae from Middle Asia (*Sphaerosciadium denaense, Ferula foetida, F. varia, F. kyzylkumica, Dorema sabulosum*). It was revealed that different representatives of the family Apiaceae growing in various habitats have a secretory system represented with terpenoid keeping schizogenous secretory ducts. Desert plants (*F. foetida, F. varia, F. kyzylkumica, D. sabulosum*) have larger secretory ducts producing more of terpenoids, than a mesophilous relic mountain species *S. denaense*. The most characteristic structural features of secretory system of *S. denaense* are small diameter of lumen, small epithelial cells, and the absence of ducts around the xylem of the medullary bundles in the stem and petioles. The structural features of secretory system are specific to each of the investigated plants. The topography and dimensions of secretory ducts are a diagnostic character applied in species identification.

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Key words: Middle Asia; Apiaceae*; Ferula; Dorema; Sphaerosciadium*; endemic; medicinal plants; plant anatomy; morphology; secretory system

بررسی ساختمان سیستم ترشحی تعدادی از گیاهان دارویی انحصاری خانواده چتریان از کشور ازبکستان

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آسیای میانه یکی از مراکز بزرگ پیدایش وتنوع گونه های گیاهی خانواده چتریان است. سیستم بافت‌های ترشحی و سایر مشخصات آناتومیکی گیاهان این خانواده کمتر بررسی گردیده‌اند. مطالعات مقایسه‌ای آناتومیکی ساختمان‌های ترشحی دارای ارزش تئوری و عملی در رابطه با تاکزونومی، اکولوژی و داروسازی است. این مقاله نتایج بررسی ساختمان اندام‌های ترشحی پنج گونه گیاه دارویی انحصاری آسیای میانه از خانواده چتریان (Sphaerosciadium denaense, Ferula foetida, F. varia, F. kyzylkumica, Dorema sabulosum) را ارایه می‌نماید.

این مطالعه نشان داد که نمونه‌های مختلفی از گیاهان خانواده چتریان که در رویشگاه‌های متفاوتی میرویند، دارای یک سیستم ترشحی هستند که ترپنوییدها را در مجاری واقع در فضاهای بین سلولی خود جای می‌دهند. گیاهان مناطق بیابانی (F. foetida, F. varia, F. kyzylkumica, D. sabulosum) در مقایسه با گیاه مناطق معتدل کوهستانی *Sphaerosciadium denaense* ، دارای مجاری ترشحی بزرگتری هستند. شاخص‌ترین صفات ساختمان ترشحی S. denaense قطر کم حفره درون سلولی، سلول‌های پوششی کوچک و عدم حضور مجاری دراطراف گزیلم و دستجات مغزی در دمبرگ و ساقه است. مشخصات سیستم‌های ترشحی هر یک از گونه‌های بررسی شده شاخص همان گونه بوده است. ابعاد و توپوگرافی مجاری ترشحی صفت شاخص هر گونه بوده است.

INTRODUCTION

Apiaceae Lindley (Umbelliferae) is a worldwide distributed family of flowering plants represented with 442 genera and 3,575 species (Christenhusz & Byng 2016). Middle Asia is one of the major centers of origin and diversity of this family (Pimenov & Ostroumova 2012). Umbelliferae feature various biologically active substances of a high pharmacological value (coumarins, flavonoids, resins, etc.), widely used in the traditional and folk medicine (Pimenov & Sklyar 1988; Eisenman & al. 2013; Berdimukhammedov 2013; Amiri & Joharchi 2016). Thus, comparative anatomical study of secretory structures has a great theoretical and practical importance in relation to taxonomy and ecology of Apiaceae and their pharmacological use. The topography and dimensions of secretory ducts are diagnostic characters and have been applied in identification of pecies. Terpenoid keeping schizogenous secretory ducts occur in all organs of species of the family Apiaceae, but the structural investigation of secretory system of many Middle Asiatic taxa (especially endemic species, including objects of our research) is still incomplete.

Our research is focused on the comparative anatomical survey of different representatives of the family Apiaceae growing wild in Uzbekistan, in particular, rare, endemic and medicinal plants. Detailed structural investigation of this family is very important for its taxonomic treatment and publishing of the new edition of the Flora of Uzbekistan (Sennikov & al. 2016).

This paper provides the results of structural investigation of the secretory system of five species from the family Apiaceae (*Dorema sabulosum* Litw., *Ferula foetida* (Bunge) Regel, *F. kyzylkumica* Korovin, *F. varia* (Schrenk.) Trautv. and *Sphaerosciadium denaense* (Schischk.) Pimenov & Kljuykov). Two of them are endangered plants endemic to Uzbekistan, two species are endemic to Middle Asia, and one species is endemic to the Iran-Turanian floristic province and widely distributed, dominant of desert vegetation of Middle Asia (Korovin 1959; Pimenov & Kljuykov 1983; Pimenov 2009a, 2009b).

MATERIALS AND METHODS

The plant materials were collected from natural habitats in the southwestern part of Kyzylkum Desert and on the Hissar Range (fig. 1). The specimens were identified using Flora of U.S.S.R. (Shishkin & al. 1950, 1952), Flora of Uzbekistan (Korovin 1959) and Conspectus Florae Asiae Mediae (Pimenov & Kljuykov 1983). The vegetative and generative organs of virginile and mature reproductive plants were fixed in 70° ethanol. For anatomical study, manual cross sections of the roots, stems, petioles, leaves, flowers and fruits were prepared, stained with safranin and methylene blue, sealed with glycerine-gelatine, and examined with a light microscope using the standard technique (Ruzin 1999). Cross sections of ovary of *Ferula* species were made by microtome. A micrometer eyepiece (MOB 1-15x) was used for measurements. The mathematical processing was carried out with the standard statistical methods (Zaitsev 1991). The micro-photographs were taken with a digital camera using a microscope photo adapter. The morphological descriptions are based on surveys of fresh material, herbarium specimens from the Central Herbarium of Uzbekistan (TASH), and examination of literature. The terminology of structural characters was used in accordance with Kljuykov & al. (2004). The herbarium specimens are stored at the Central Herbarium of Uzbekistan (TASH).

RESULTS AND DISCUSSION

Structural features of each studied species are described below. Morphometric parameters of the secretory system are summarized in tables 1–2. Localization of secretory ducts in vegetative and generative organs is shown in figs 2, 4 & 5.

***Sphaerosciadium denaense* (Schischk.) Pimenov & Kljuykov**

Sphaerosciadium denaense is the only representative of the Middle Asiatic relic monotypic genus *Sphaerosciadium* Pimenov & Kljuykov (fig. 2).

This plant remains one of the most rare and poorly studied species of Middle Asiatic Apiaceae.

Sphaerosciadium denaense was described in 1950 by B.K. Schischkin as *Danaa denaensis* Schischk. (Schischkin & al., 1950). Later it was transferred to the genus *Physospermum* Cusson, and finally, in 1981, it was separated as the monotypic genus by M.G. Pimenov and E.V. Kljuykov (1981). *Sphaerosciadium denaense* is a critically endangered national endemic with restricted habitat, included in the Red Data Book of Uzbekistan (2009). It is a petrophyte species distributed in the Sangardak and Tupalang river basins on the southern slope of the Hissar Range, in Surkhandarya region of Uzbekistan (Pimenov 2009). It is a mesophilous drought-escaping species (ephemeroid) growing on stony slopes and rocks at the altitude of 900–1400 m a.s.l.

Sphaerosciadium denaense is a polycarpic perennial herb up to 1 m high, with a taproot going deep underground and a weakly branching (biaxial) caudex. The taproot is 3-5 cm in diameter, and the caudex is 1-1.3 cm. The primary root is spindle-shaped, slightly thickened in the basal part, with wrinkled brown epidermis. Older parts are covered with a thick layer of fissured and desquamating cork. The cylindrical caudex is also covered with dark brown wrinkled epidermis, fissured and desquamating. The orthotropic stem is straight and glabrous, bearing leaves and spherical, wide, and very lax terminal inflorescence. The radical and stem leaves are situated on long and thick petioles 20-30 cm long and 10-20 cm wide, with fleshy and leathery ear-shaped amplexicaul sheaths up to 3 cm wide. The leaf blade is tripinnatisect, 3-7cm long and 2-4 cm wide; primary and secondary segments are petiolate, terminal lobes are sessile. Umbels are 10-12-rayed, with long (9-12 cm) and widely spreading nearly glabrous rays, bracts and bracteoles are absent. Umbellules are 8-10-flowered. Flowers are white or light pink, with flat and relatively large rhombic petals. Calyx teeth are obsolete. The fruits are didymous; mericarps are equal, orbicular, 3-4 mm long and 3-4 mm wide, dark brown, with filiform ribs, flat stylopodium, and long recurved styles. The plant blooms in April, and fruits ripe in May – June.

The secretory ducts in the underground organs are located in the phloem and in the cortical parenchyma. The old and disintegrating secretory ducts with empty lumen are located near to the cork, while small young ones are situated right below the cambium. The secretory ducts within the primary root are various in size, large and small (table 1, fig. 2, a-b). The secretory ducts of the caudex are uniform and surrounded with tangential epithelial cells (table 1, fig. 2, c). The xylem occupies over 60% in the cross section of the primary root and caudex, and phloem is less developed (fig. 2, a-c).

The above ground axial organs contain vascular bundles of various types and a complex well-developed secretory system with an extensive network of anastomoses. The secretory ducts are located randomly in the cortical parenchyma and in the pith of the basal part of the inflorescence's main axis (table 1). In the cortical parenchyma, they form a circle over bundles, 1 to 3 units surrounded by the phloem of the medullary bundles, and randomly situated in the pith of the main and lateral axes of the inflorescence. Secretory ducts form a circle over the large bundles of the ray of the umbel and umbellule (fig. 2, d-g; table 1). The size of secretory ducts correlates with the size of plant organs; that is, the ducts decrease in size from the basal part of the main axis of the inflorescence towards the rays of umbellules. There are 2 (3) secretory ducts over the central bundle on the abaxial side of the leaf, one large duct on the adaxial side, one duct over and one duct under the lateral bundles, and one duct in the tip of the leaf, on the adaxial side (fig. 2, h-i; table 1). Large vascular bundles of the leaf are accompanied by large secretory ducts, and small ducts are situated over the small bundles. In the petiole, secretory ducts can be found only in surroundings of large vascular bundles, and these ducts are larger than in the leaf (fig. 2, j-l; table 1). The main features of secretory system of the aboveground axial organs of relict species *S. denaense* are small diameter of lumen, small epithelial cells, and the absence of ducts around of the xylem of the medullary bundles in the stem and petioles.

The secretory structures in generative organs of *S. denaense*, includes one median secretory duct in the petal, and two ducts in the anther's connective; the ovary of each carpel contains four vallecular and two commissural vittae (fig. 2, m-o; table 1). On the dorsal side of the mericarp, there are 4-5 long secretory ducts running over the entire surface, 4-5 truncated vittae are situated in furrows, and 2-4 commissural vittae are found on the ventral side (fig. 2, p-q; table 1). Vallecular vittae in the fruit of *S. denaense* are more numerous and larger than in the ovary. Rib secretory ducts are absent.

***Ferula foetida* (Bunge) Regel, *F. kyzylkumica* Korovin, *F. varia* (Schrenk.) Trautv.**

Ferula foetida is a representative of the subgenus *Scorodosma* (Bunge) Drude. It is an Irano-Turanian species common for sandy and clay deserts of Middle Asia. *Ferula foetida* is a valuable medicinal, melliferous, food and forage plant. We studied specimens collected on the southern Piedmont plain of the Kuldzhuktau Range, on sandy soils.

Table 1. The structural features of the secretory system of studied species.

	Sphaerosciadium denaense				*Dorema sabulosum*			
	a	b	c	d	a	b	c	d
1	30.7±1.71	11.6±0.68	20.6±0.79	6-8	106.16±2.72	10.15±0.38	36.54±0.93	7-9
2	17.1±1.1	5.6±0.4	11.2±0.45	6-8	0	0	0	0
3	32.59±0.29	14.42±0.16	15.94±0.22	6-8	34.3±0.02	4.5±0.01	11.6±0.12	12-14
4	26.26±0.30	13.29±0.14	14.66±0.17	6-8	40.8±0.05	3.06±0.02	5.76±0.43	17-24
5	21.29±0.25	8.42±0.16	13.99±0.15	6-8	37.62±0.7	4±0.09	6.2±0.3	16-22
6	16.78±0.25	7.2±0.17	11.23±0.19	6-8	12.75±0.03	2.2±0.01	3.69±0.05	10-15
7	47.28±0.41	12.41±0.20	20.93±0.18	9-11	51.26±0.85	12.49±0.55	21.32±0.63	14-16
8	66.02±1.35	17.96±0.55	27.32±0.62	6-8	60,78±1,25	15,53±0,29	21,41±0,49	11,4±0,18
9	42.82±0.85	19.92±0.34	24.9±0.47	6-7	159.42±1.31	6.06±0.9	17.09±0.15	17-18
10	50.74±0.58	20.76±0.25	23.2±0.46	7-8	87.10±0.78	9.41±0.11	19.53±0.15	11-12
11	0	0	0	0	90.08±0.95	8.26±0.11	20.03±0.17	12-14
12	35.86±0.84	16.84±0.41	19.64±0.77	6-7	196.56±1.85	10.72±0.9	20.54±0.18	23-25
13	23.58±0.28	13.06±0.16	16.48±0.28	6-7	69.29±0.70	7.84±0.9	13.76±0.11	16-18
14	0	0	0	0	26.8±0.23	5.6±0.3	10.64±0.8	6-8
15	175.82±2.59	29.66±0.79	43.38±0.92	10-16	417.04±3.92	-	-	-
16	170.2±2.37	33.02±0.79	43.64±0.86	10-14	0	0	0	0

Table 1 continued.

	Ferula foetida				*F. varia*				*F. kyzylkumica*			
	a	b	c	d	a	b	c	d	a	b	c	d
1	62.8±0.35	16.4±0.11	26.8±0.16	6-9	122.7±0.82	21.6±0.23	38.4±0.24	9-12	73.8±0.4	8.9±0.09	19.6±0.15	11-15
2	0	0	0	0	0	0	0	0	52.5±0.35	9.1±0.1	18.5±0.13	7-11
3	61.1±0.37	15.5±0.15	24.7±0.19	11-14	114.7±0.88	18.5±0.15	29.7±0.29	14-17	50.8±0.33	15.4±0.14	16.4±0.11	10-13
4	49.7±0.31	12.6±0.14	19.5±0.23	11-14	89.63±0.71	14.5±0.15	24.4±0.21	12-15	37.2±0.31	12.1±0.14	14.6±0.17	8-10
5	38.2±0.32	10.5±0.12	16.4±0.13	11-14	66.7±0.55	14.2±0.15	22.3±0.18	12-15	26.9±0.25	8.5±0.12	13.5±0.15	6-8
6	27.4±0.21	9.2±0.11	14.5±0.15	10-12	40.3±0.37	12.5±0.14	20.6±0.18	10-12	20.8±0.25	8.2±0.12	12.4±0.15	6-8
7	49.3±0.47	9.0±0.16	19.9±0.31	10-14	73.3±1.01	8.4±0.17	20.6±0.42	14-17	51.4±0.68	8.5±0.14	17.5±0.26	12-13
8	43.3±0.41	11.6±0.15	18.5±0.22	8-11	60.38±0.34	13.43±0.18	19.72±0.23	10-14	31.56±0.36	8.87±0,08	11.9±0.19	9-13
9	98.6±0.85	20.6±0.25	33.4±0.37	15-17	118±1.05	21.5±0.19	32.7±0.29	14-17	131±1.12	20.5±0.19	34.5±0.31	15-18
10	0	0	0	0	0	0	0	0	55.3±0.48	19.4±0.21	26.4±0.21	11-13
11	0	0	0	0	58.8±0.45	11.2±0.15	19.3±0.21	11-13	60.8±0.55	12.2±0.11	23.3±0.21	11-13
12	32.8±0.34	16.4±0.15	19.6±0.19	6-7	60.8±0.67	20.4±0.21	25.4±0.25	13-15	66±0.59	20.4±0.21	25.4±0.25	14-16
13	28.5±0.28	14.6±0.16	18.4±0.17	6-7	44.5±0.38	19.2±0.21	23.1±0.21	11-13	54±0.52	22.1±0.21	24.1±0.26	11-13
14	0	0	0	0	20.3±0.18	8.5±0.08	12.4±0.15	6-7	22.6±0.24	8.8±0.15	12.6±0.15	6-7
15	0	0	0	0	453.65±2.66	11.85±0.15	20.4±0.41	44-50	583.3±2.34	14.13±0.23	39.08±0.32	39-44
16	0	0	0	0	212.09±1.03	7.96±0.18	14.33±0.36	35-40	263.6±1.73	16.46±0.24	31.56±0.39	17-20

Symbols: 1, main root; 2, caudex; 3, stem (main axis of the inflorescence); 4, lateral axis of order I of the inflorescence; 5, umbels ray; 6, umbellule's ray; 7, main bundles of leaf; 8, petiole; 9, petal; 10, anther; 11, filament; 12, ovary's vallecular vittae; 13, ovary's commissural vittae; 14, ovary's rib; 15, fruit's vallecular vittae; 16, fruit's commissural vittae; a, diameter of lumen of secretory duct μm; b, height of epithelial cells, μm; c, width of epithelial cells, μm; d, number of epithelial cells. (0), secretory duct is absent; (-), epithelial cells obliterate.

Ferula foetida (Bunge) Regel is a monocarpic perennial herb up to 1-1.5 m high (fig. 3, A). The taproot is thickened, tuberous, turnip-shaped, 10–12 cm in diameter. The stem is single (rarely more than one), thick and stout, pubescent, and branching in the upper third. The lower branches are alternate, the upper ones are verticillate. The leaves are soft and fast-fading, usually glabrous on the upper side and softly pubescent from the underside, wide, tripinnatisect; terminal lobes are large, entire, oblong, oblong-lanceolate or lanceolate, 8-11.5 cm long and 3-3.5 cm wide; sheaths are large, inflated, outside densely covered with hairs. The inflorescence is a dense spherical panicle. Umbels are compact, 25-rayed; umbellules are 15-flowered and densely pubescent. Bracteoles are absent.

Ferula kyzylkumica Korovin belongs to the sect. *Xeronarthex* Korovin of subgenus *Peucedanoides*. It is a rare endemic species growing on outcrops of variegated beds of the relic insular mountains of the Kyzylkum, and a national endemic included in the Red Data Book of Uzbekistan (2009).

Ferula kyzylkumica is a polycarpic perennial herb 30-50 cm high (fig. 3, B), with a vertical taproot 1.5 cm in diameter and a well-developed caudex. Stem is single, covered at the base with fibrous remains of petioles, in the middle part branching in a narrow panicle; the branches are alternate. The leaves are tripinnatisect, wide rhombic in the outline; segments are bipinnate; terminal lobes are elliptic, serrate, 0.8-1.8 cm long and 0.5-1 cm wide, covered with tiny aciculae on both sides. Sheaths are elliptical, amplexicaul. Central umbels are almost sessile, 7-10-rayed; lateral umbels are situated on long peduncles. Umbellules are 10-flowered, without bracteoles.

Ferula varia (Schrenk.) Trautv. belongs to subgenus *Peucedanoides* (Boiss.) Korovin, sect. *Macrorhiza* Korovin. It is a species endemic to Middle Asia, sporadically distributed in sandy and clay deserts, relic mountains and foothills. We investigated specimens from rocky slopes of the Kuldzhuktau Range.

Ferula varia is a monocarpic perennial herb up to 1 m high (fig. 3, C). The taproot is tuberous, turnip-shaped, 10–12 cm in diameter. The stem is single (rarely more than one), glabrous, relatively thick and stout, branching in upper part; the lower branches are alternate, and upper ones are verticillate. The leaves are soft, fast-fading, glabrous, tripinnatisect, triangular in outline; terminal lobes are narrow linear-lanceolate, 4.5-6.5 cm long and 0.2-0.3 cm wide. Sheaths are glabrous, coriaceous, oval-lanceolate. The inflorescence is a dense spherical panicle. Umbels are 10-15(25)-rayed, umbellules are 13-18-flowered. Bracteoles are absent or small, scale-shaped.

Ferula foetida blooms in March – April, and fruits ripe in April – May. *F. varia* blooms in April – May, and produces fruits in May – June; *F. kyzylkumica* blooms in May, and fruits ripe in June. *Ferula kyzylkumica* is a drought-resistant plants with long growing period; *Ferula foetida* and *F. varia* are drought-escaping species (ephemeroids).

Roots of all studied species of the genus *Ferula* have a dark brown, wrinkling and easily peeling epidermis. The older parts are covered with a thick layer of fissured and peeling cork. The phloem is well-developed, multi-layered and thin walled. The cortical parenchyma contains numerous secretory ducts; the larger ones are located in the upper and middle part, while the smaller ones are concentrated in the lower part of the parenchyma (fig. 4, i-k; table 2). Lumens of secretory ducts are largest in the primary root of *F. varia* and smallest in the caudex of *F. kyzylkumica*. In general, tuberous taproots of monocarpic species (*F. foetida, F. varia*) are distinguished by well-developed phloem tissue with numerous secretory ducts.

The anatomy of the stem, leaf and mericarp of *F. foetida* has been studied by Iranian scientists (Ashena & al. 2014); anatomical structure of vegetative organs of *F. foetida* and mericarps of *F. foetida* and *F. varia* were investigated in Kazakhstan (Safina & Pimenov 1984; Safina 2012; Imanbayeva & al. 2015). In our study, we specified the structural parameters of the secretory system of these species, and identified certain differences between specimens of *F. foetida* from Uzbekistan and Iran.

The cross section of stem displayed following differences in the structure of secretory system of studied species. *Ferula foetida* has a thicker stem with a greater number of secretory ducts than *F. varia* and *F. kyzylkumica*. The secretory ducts in the stem of *F. varia* are distinguished by the largest diameter of the lumen and numerous epithelial cells around them. In the epidermal parenchyma, the secretory ducts are located above of the vascular bundles (table 2, fig. 4, f, g, h). There are 5-6 secretory ducts near each of the vascular bundles in the pith of *F. foetida*. One to two secretory ducts are located near each of the vascular bundles in the pith of *F. varia;* the diameter of the secretory ducts is significantly larger than in the other studied species of *Ferula*. In the pith of *F. kyzylkumica*, there are one or two secretory ducts near each of the vascular bundles.

The cross section of mature leaves of three studied species shows following topography of the secretory system. In the leaves of *F. foetida*, secretory ducts are located above and below the bundles throughout the

lobes. There is one secretory duct on the abaxial side of the large central vascular bundle, two on the adaxial side, one over and one under the small central bundle. The lateral bundles are numerous, schizogenous ducts can be found on the phloem and the xylem side of the bundles (fig. 4, a). In the leaves of *F. varia,* one large secretory duct is found on the abaxial side of the central vascular bundle and one small secretory duct is situated on the adaxial side. Each lobe of the leaf contains two large and two small bundles accompanied by secretory ducts on the abaxial side. Two large ducts runs along the edges of the leaf blade and one is situated below the primary vein (fig. 4, b). In the terminal lobes of *F. kyzylkumica,* solitary secretory ducts are located over and under the central bundle; each of the lateral bundles also is accompanied by secretory duct situated on the abaxial side of the leaf. *Ferula foetida* is distinguished by wider segments of leaves with more secretory ducts than in *F. varia* and *F. kyzylkumica*. The large secretory ducts of *F. varia* are considerably wider, and the number of epithelial cells is greater, but the lumens of the small ducts are larger in the leaves of *F. foetida* than in the other species.

The petioles of *F. foetida* and *F. varia* are terete in transverse section, with an adaxial groove. The petiole of *F. kyzylkumica* is terete in section, without a groove. Vascular bundles are collateral, large and small, with random orientation. Secretory ducts are situated between the collenchyma and vascular bundles. In petioles of *F. foetida,* there are up to 5-6 ducts around the vascular bundle; one duct above the phloem and two ducts around the xylem are found in petioles of *F. varia* and *F. kyzylkumica*. The secretory ducts in the ribs are larger than the internal ones (fig. 4, c-e).

All studied species of the genus *Ferula* have pentamerous flowers with reduced calyx teeth. The petals of *F. foetida* are light yellow, ovate, obtuse. The petals of *F. varia* are yellow, oblong-elliptical with attenuate and incurved tip. *Ferula kyzylkumica* has yellow petals, hairy from the dorsal side, ovate, attenuate and incurved on the tip, with a thickened central vein.

The secretory ducts are located only in the petals and ovary wall in the flower of *F. foetida,* in the petals, ovary wall and filaments in the flower of *F. varia,* in the petals, filaments, anther connective, ovary wall, anthers and ovules in the flower of *F. kyzylkumica* (fig. 4, l-n). The flower of xerophilous *F. kyzylkumica* contains more secretory ducts, than drought-escaping *F. foetida* and *F. varia* (table 2). During the two-cell pollen phase commissural, dorsal and rib secretory ducts form in the ovary of *F. kyzylkumica*. This fact indicates that certain substances present in the secretory ducts are involved in the formation of the generative structures, which corresponds to the data provided by Saidhodzhaev & al. (1993) on the maximum accumulation of ester compounds in *F. kyzylkumica* during the flowering period.

The anatomy of secretory structures in the fruits of the examined *Ferula* species is specific. The mericarps of *F. foetida* are 16.4 mm long and 11.4 mm wide, rounded-oval or elliptic in outline, strongly compressed dorsally in transverse section, covered on the dorsal side by unicellular trichomes, with broadly winged lateral ribs (fig. 4, q). We found, that the ovary of *F. foetida* contains vallecular and commissural secretory ducts, but in the mature fruit these ducts are obliterated. L.K. Safina (2012) provided similar data for plants from Kazakhstan, but F.A. Ashena & al. (2014) reported that vallecular and commissural ducts are seen only in fruits of *F. foetida* from Iran. We can suppose that in conditions of the Kyzylkum desert plant fully consumes the biologically active compounds containing in the flower for the development of the embryo.

Ferula varia has elliptical strongly compressed mericarps, 12.9 mm long and 9.1 mm wide, with 3 slightly prominent ribs and 4 vallecular vittae on the dorsal side, and with 2-3 commissural vittae on the ventral side (table 2, fig. 4, r). The mericarps of *F. kyzylkumica* are oblong-oval, strongly compressed from the ventral side, slightly convex from the dorsal side, 7.5 mm long and 4.5 mm wide. The secretory system is represented with 4 vallecular and 5-6 commissural vittae, 3-4 rib, secretory ducts in the lateral ribs, and 3 ducts in the dorsal ribs (table 2). The vallecular vittae in mericarps of *F. kyzylkumica* and the commissural vittae of *F. varia* have the largest diameter of lumen. The most complex secretory structures are developed in the fruits of *F. kyzylkumica*; it is associated with species drought resistance and its advanced phylogenetic position.

Dorema sabulosum Litw.

Dorema sabulosum is a psammophyte species, endemic to Middle Asia. It is a medicinal, ornamental, melliferous, food and forage plant growing on the sand dunes of the southwestern Kyzylkum. The genus *Dorema* with 12-16 species is widespread in Middle and South-Western Asia. It was considered as affined with *Ferula* (Pimenov 1988). The results of serological and molecular phylogenetic analyses (Ajani & al. 2008; Panahi & al. 2015) reveals that *Dorema* should be transferred to *Ferula,* but a full taxonomic treatment of these taxa has not been performed and a new nomenclatural combination for *Dorema sabulosum* has not been validly published to date. According to the rules of the "International code of nomenclature for algae, fungi, and plants" (Melbourne Code) (McNeill

& al. 2012; Wiersema & al. 2015), *Dorema sabulosum* Litw. is an accepted name.

Dorema sabulosum is an ornamental, fodder and melliferous plant, which also contains resin. Local people in Middle Asia use this resin as a styptic plaster; a liquid extract from young sprouts is used for the treatment of gastric diseases, and tincture of the stem is used for heart diseases (Larin & al. 1956). The Turkmen folk medicine uses the milky latex from the roots as an anaesthetic, diuretic, styptic, wound healing, antipyrotic and anthelmintic (Berdymukhamedov 2013).

Dorema sabulosum is a monocarpic herb 1-1.2 m high (fig. 5). It has a vertical thickened turnip-shaped taproot 8-10 cm in diameter. The stem is single, thick and stout, pubescent, covered at the base with fibrous remains of petioles, terete in transverse section, ribbed and branched from the middle. The basal leaves of *D. sabulosum* are large, petiolate, greyish-green, pubescent; sheaths are adpressed, semi-amplexicaul. Petioles are covered with papilloma trichomes. The leaf blade is wide triangular in outline, tri-pinnatisected, with lanceolate, acuminate terminal lobes, 7-9 cm long and 1.5-2.5 cm wide. The inflorescence is a pyramidal panicle, and its structure distinguishes *Dorema* from other genera of Apiaceae (Pimenov 1988). Umbellules are 8-12-flowered, with filiform bracteoles. Flowers are situated on thin pedicels up to 5 mm long. Calyx teeth are obsolete. Petals are greenish-yellow with a dark central vein, 2.5 mm long, oblong-ovate with an incurved tip. The ovary is semi-inferior, cylindrical and densely pubescent; there are two carpels containing two ovules inside. The stylopodium is patelliform; the style has a truncated stigma up to 2 mm long. The fruits are elliptic, 15 mm long and 9 mm wide. The mericarp is compressed dorsally and slightly twisted, with whitish margins 1 mm wide, and with filiform dorsal and winged lateral ribs. The plant blooms in April, and fruits ripe in May – June.

The taproot of *D. sabulosum* is covered with the multi-layered and wrinkled cork containing phellogen and phelloderm. The multi-layered parenchyma of the secondary cortex contains old secretory ducts. Under the cortex, there is a wide layer of thin walled phloem with numerous radiating secretory ducts (fig. 5, a). The cross section of the stem shows that large and small alternating peripheral vascular bundles accompanied by secretory ducts are found in the epidermal parenchyma. Nearby each vascular bundle in the pith, there are 3-4 secretory ducts.

The secretory ducts are located along the main axis of the leaf; the large duct is on the abaxial side, and the small one on the adaxial side (fig. 5, b). In the cross section of the petiole, there are 14 secretory ducts situated in the periphery and forming a circle over the vascular bundles, and 9 small secretory ducts are situated in the central part of the petiole (fig. 5, c).

The large secretory duct occupies 1/3 of the petal; it is located under the central vascular bundle on the adaxial side (table 1, fig. 5, e). One secretory duct is in the anther connective. Another duct takes up ¼ of the filament; it is situated near the phloem part of the vascular bundle. In the ovary, 8 large vallecular and 4 commissural vittae, 6 dorsal and 4 lateral rib ducts are observed (table 1, fig. 5, f).

The vallecular vittae are only present in the fruit of *D. sabulosum*; two larger lateral vittae and two smaller central ones can be observed in the mesocarp. These vittae are strongly compressed in the tangential direction, and their epithelial cells are obliterated (table 1, fig. 5, g, h).

CONCLUSION

Different species of the family Apiaceae (*Sphaerosciadium denaense, Ferula foetida, F. varia, F. kyzylkumica, Dorema sabulosum*) growing in various habitats have a secretory system represented with terpenoid keeping schizogenous secretory ducts. It was revealed that desert plants (*F. foetida, F. varia, F. kyzylkumica, D. sabulosum*) have more developed secretory system with larger ducts producing more terpenoids than a mesophilous mountain species like *S. denaense*. All studied monocarpic desert species (*F. foetida, F. varia, D. sabulosum*) have similar quantitative parameters of the secretory system.

The secretory ducts of the underground organs are located in the secondary phloem and epidermal parenchyma. The taproots of monocarpic desert species (*F. foetida, F. varia, D. sabulosum*) are characterized by a well-developed phloem tissue and a larger number of secretory ducts than the underground organs of polycarpic species *F. kyzylkumica* and *S. denaense*. The tuberous roots of monocarpic species accumulate large amount of terpenoids and other biologically active compounds which are necessary for plant survival and reproduction in the arid environment.

In the stem, secretory structures are found over the phloem of the peripheral vascular bundles, around the phloem and xylem of the medullary bundles, in the parenchyma of the pith and epidermis. All studied desert species have secretory ducts on the phloem and xylem side of the vascular bundles in the stems and petioles. Well-developed secretory system in the roots and aboveground axial organs of desert Apiaceae is a typical feature of xeric adapted plants. Main structural peculiarities of secretory system of the aboveground organs of relict mountain species *S. denaense* are small diameter of lumen, small epithelial cells, and the

absence of ducts around of the xylem of the medullary bundles in the stem and petioles.

The topography and dimensions of secretory ducts in the aboveground vegetative organs are a diagnostic character, applied in species identification.

The secretory structures in the generative organs are specific to each of the investigated plants. There are only vallecular vittae in petals and in the anther's connective of *S. denaense*, while vallecular and commissural vittae are developed in the ovary and fruit, but rib ducts are absent. The ovary of *F. foetida* contains vallecular and commissural secretory ducts, but in the mature fruit these ducts are obliterated. *Ferula varia* has vallecular and commissural vittae in the flower and fruit. Vallecular and commissural vittae and rib ducts are also found in flowers and fruits of *F. kyzylkumica*. The flower of *D. sabulosum* contains vallecular and commissural vittae, and rib ducts, but only vallecular vittae without epithelial cells remain in the fruit. More developed secretory structures are found in generative organs of *F. kyzylkumica* flowering and fruiting in xerothermic period. Other representatives of the section *Xeronarthex* have the similar complicated structure of secretory system in the generative organs which corresponded to the advanced evolutionary position of this group (Sharipova 2017).

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Fig. 1. Map of the study area.

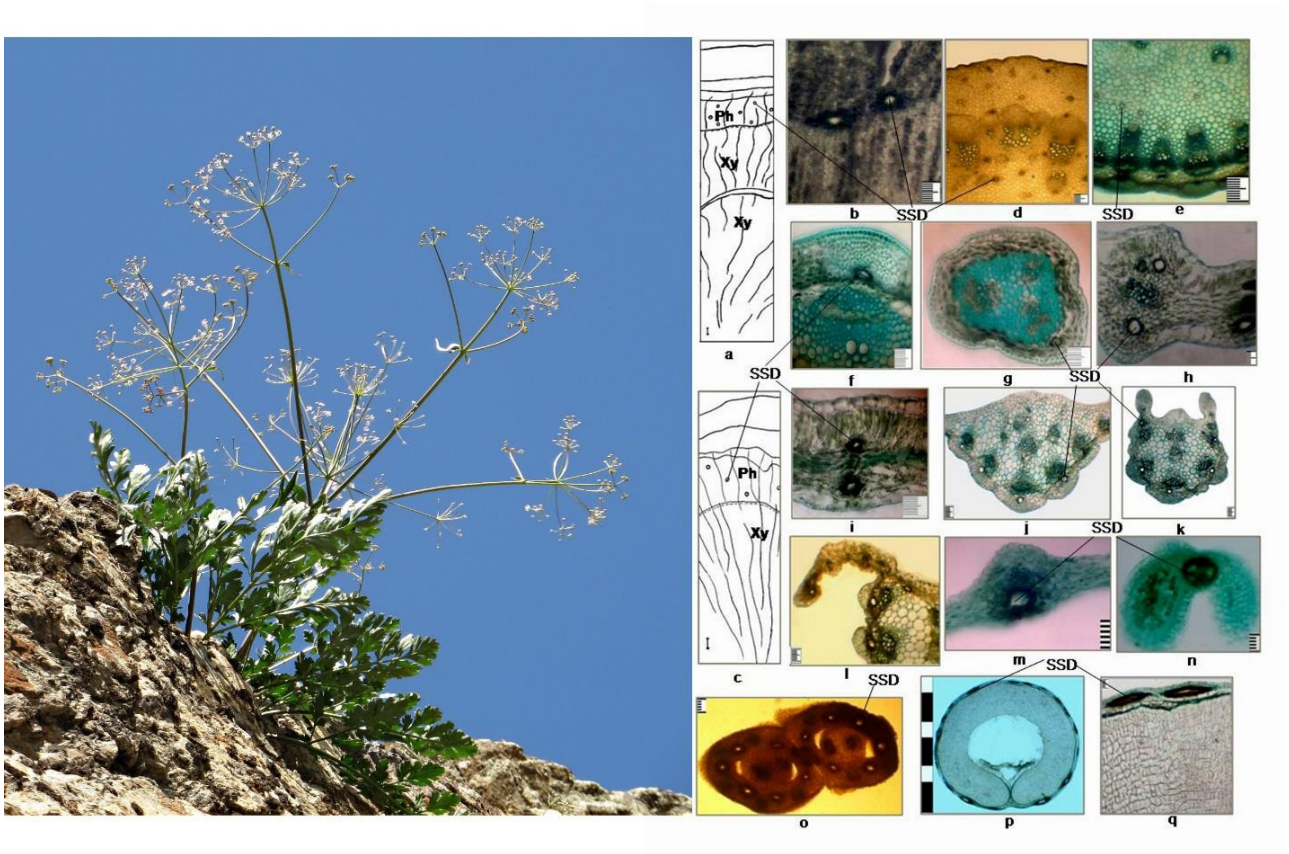

Fig. 2. A general view of *Sphaerosciadium denaense* (Schischk.) Pimenov & Kljuykov and cross sections of its vegetative and generative organs: a- b, main root; c, caudex; d, main axis of the inflorescence (basal part); e, main axis of the inflorescence (middle part); f, lateral axis of 1st order of the inflorescence; g, umbellule's ray; h, main bundles of the leaf; I, lateral bundles of the leaf; j, the basal part of the petiole; k, the middle part of the petiole; l, the upper part of the petiole; m, petal; n, filament; o, ovary; p, pericarp; q, fruit's vallecular duct. Symbols: Ph, phloem; SSD, schizogenous secretory duct; Xy, Xylem. Drawing scale: a-i, q, 100 µm, m, n, o, 50 µm; p, 1 mm.

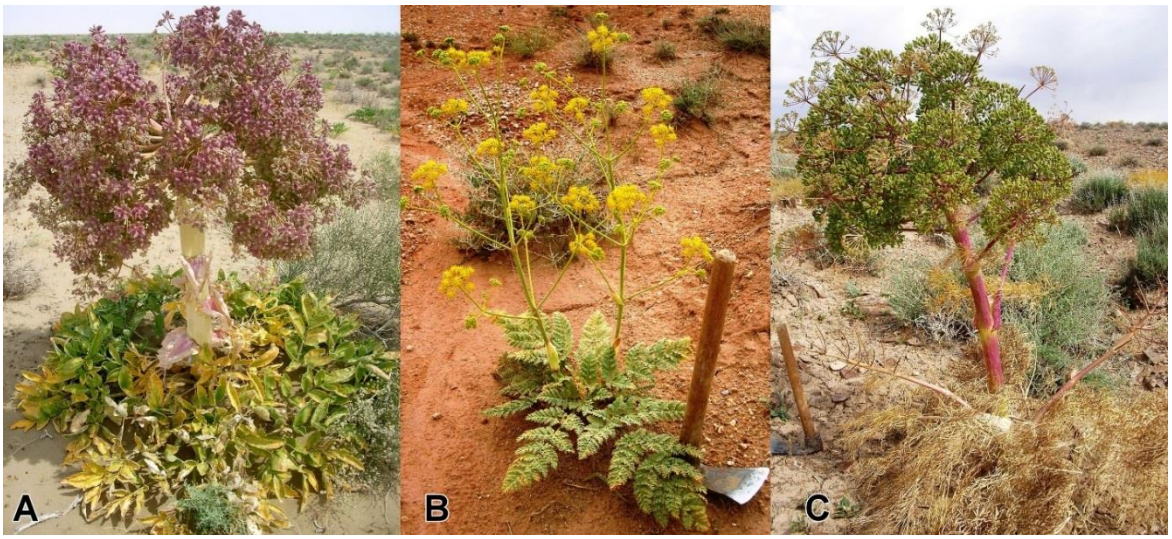

Fig. 3. Studied species of *Ferula*: A, *F. foetida* (Bunge) Regel; B, *F. kyzylkumica* Korovin; C, *F. varia* (Schrenk.) Trautv.

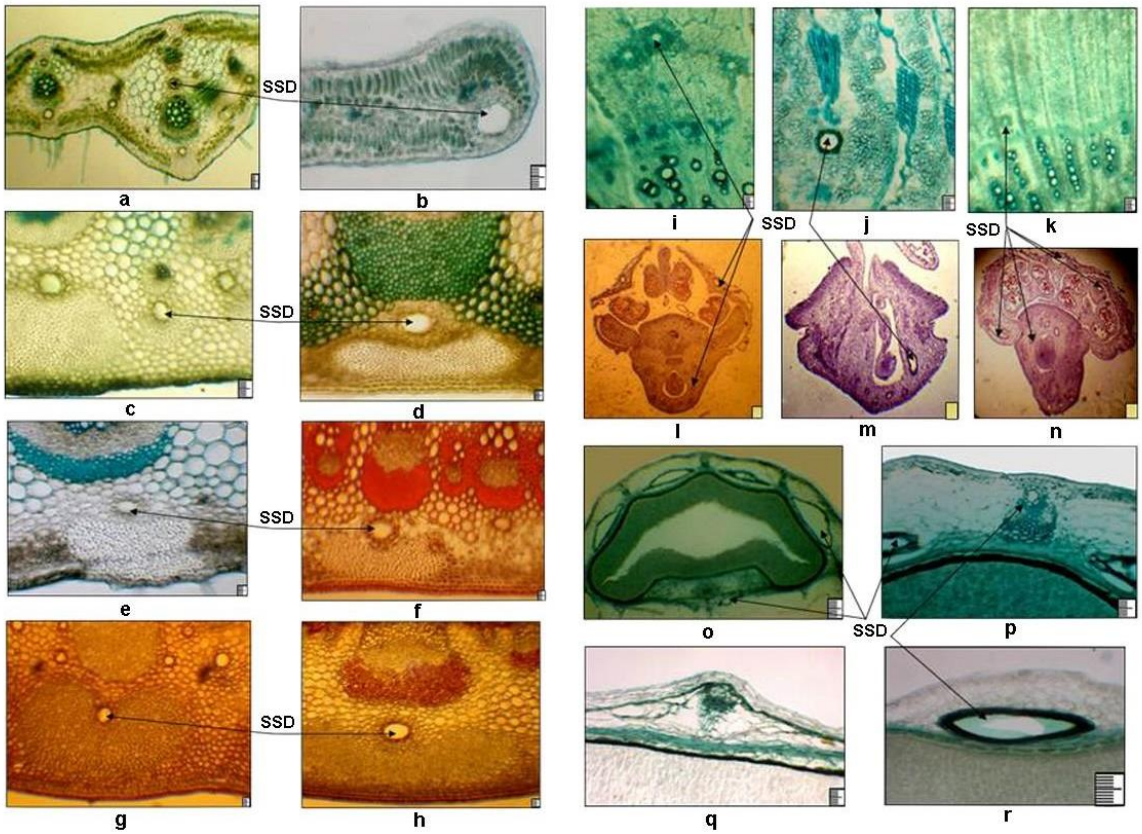

Fig. 4. Cross sections of the vegetative and generative organs of *Ferula* species.
Leaf: a, *F. foetida*; b, *F. varia*. Basal part of the petiole: c, *F. foetida*; d, *F. varia*; e, *F. kyzylkumica*. Stem: f, *F. kyzylkumica*; g, *F. foetida*; h, *F. varia*. Main root: I, *F. foetida*; j, *F. varia*; k, *F. kyzylkumica*. Ovary: l, *F. foetida*; m, *F. varia*; n, *F. kyzylkumica*. Fruit's vallecular vittae: o, p, *F. kyzylkumica*; q, *F. foetida*; r, *F. varia*. Symbols: SSD, schizogenous secretory duct. Drawing scale: a-j, 100 µm.

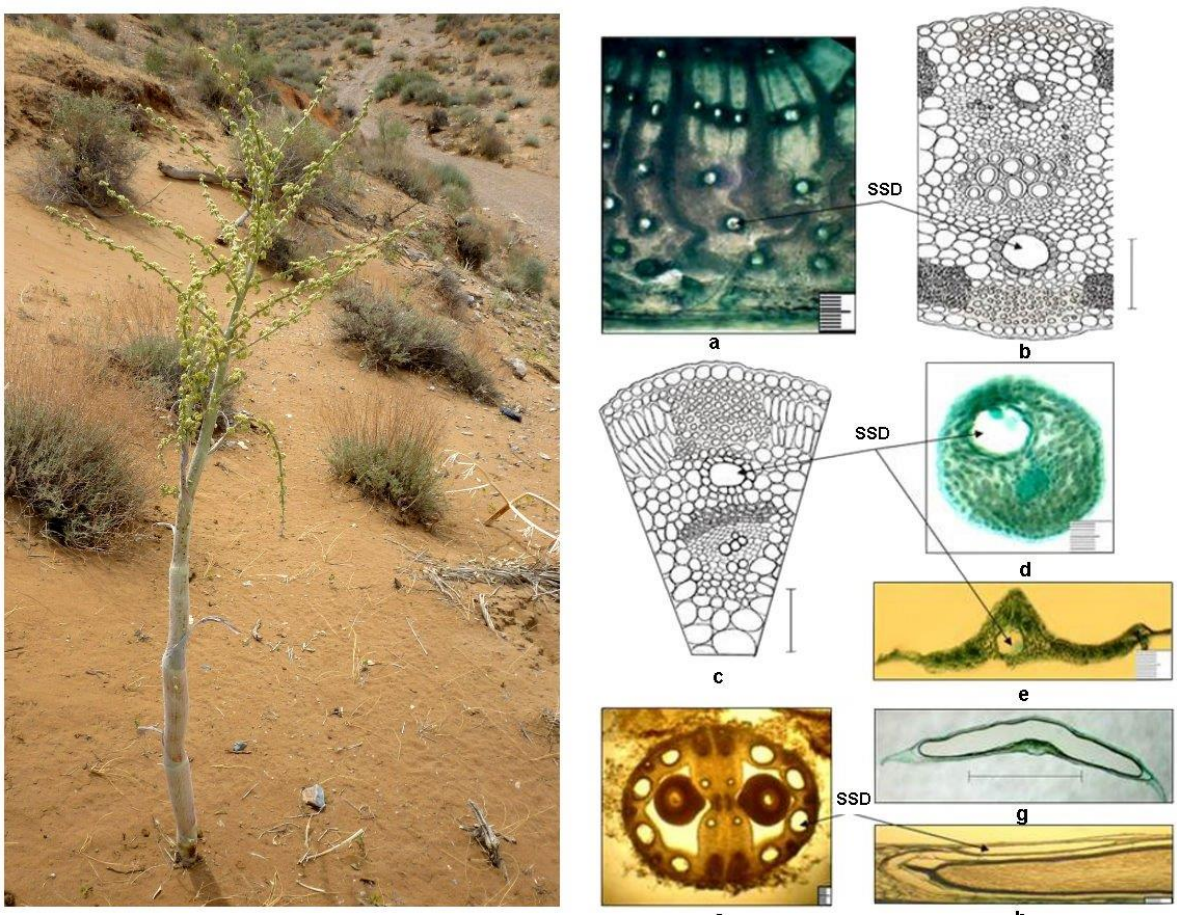

Fig. 5. A general view of *Dorema sabulosum* Litw. and cross sections of its vegetative and generative organs: a, main root; b, main bundles of the leaf; c, the middle part of the petiole; d, filament; e, petal; f, ovary; g, pericarp; h fruit's vallecular vittae. Symbols: SSD, schizogenous secretory duct. Drawing scale: a-f, h, 100 µm, g, 1 mm.

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