

бель 40–50 см дл.

7. *V. ciceroidea* Boiss. var. *multijuga* Boiss.

- Ось листа мягкая, тонкая, дугообразно изогнутая, 10–40 мм дл., заканчивается мягким, простым или ветвистым усиком или мягкой щетинкой, реже листочком. Лист состоит из 3–7 пар не отставленных друг от друга листочков 2–10(13)×1–4(5) мм. Венчик малиново-красный, после сушки синий. Флаг 14–22 мм дл., отгиб короче ноготка. Стебель 9–30 см дл.

6. *V. alpestris* L.

29. Зрелые бобы продолговато-ромбические или клиновидные, к основанию суженные, голые, темно- или светло-коричневые, створки жесткие, внутри с остатками губчатой паренхимы, 25–35×5–9 мм. Соцветие обычно рыхлое. Венчик пестрый. Флаг (9)13–18 мм дл., отгиб равен или длиннее ноготка. Семена 3,5–4,5×2,5–3,5 мм, рубчик равен 1/4–1/5 окружности семени. Стебель 40–120 см дл.

8. *V. tenuifolia* Roth.

- Зрелые бобы ассиметрично эллипсовидные, с закругленным основанием, серо-зеленые или светло-коричневые, створки тонкие, без губчатой паренхимы внутри, 15–23×5–7 мм. Соцветие обычно густое. Венчик пестрый, флаг 9–14 мм дл., отгиб равен ноготку. Семена 2,5×3,5 мм, рубчик равен 1/3–1/5 окружности семени. Стебель 30–150 см дл.

9. *V. cracca* L.

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THE GENUS *MERENDERA* (*COLCHICACEAE*) SYSTEMATICS ON THE ANATOMICAL DATA

The arguments showing the separate position of Caucasian species of the genus *Merendera* – *M. eichleri* (Regel) Boiss., *M. raddeana* Regel, *M. mirzoevae* Gabrieljan, *M. greuteri* Gabrieljan, *M. candidissima* Misch. ex Grossh., *M. ghalgana* Otchiauri have been found. As the proofs are used the data on leaf, nectary and anther connective anatomy, the diagnostic significance of which were demonstrated earlier (Oganezova, 1986, 2000). It is possible to include *M. manissadjanii* Aznav. as a synonym into *M. raddeana*. The anatomical data are co-ordinated with karyology and they together point out the Caucasian region, especially Armenian Highland, as an important center of the genus species differentiation and, possibly, as an extant piece of its ancestor forms area, which was wider in the past.

Օգանեզովա Գ. Հ. *Merendera* (*Colchicaceae*) ցեղի կարգաբանությունը անատոմիական տվյալների հիման վրա: Ըստ փերիտի, առջի նեկարիա-նոցի և կապի անարմիական տվյալների, որոնց դիագնոստիկ նշանակությունը *Merendera* և *Colchicum* ցեղերի համար ավելի վաղ ապացույցվել էր (Oganezova, 1986, 2000), գտնվել են լրացուցիչ փաստարկերի ի օգուտ կոկ-կայան *M. eichleri* (Regel) Boiss., *M. raddeana* Regel, *M. mirzoevae* Gabrieljan, *M. greuteri* Gabrieljan, *M. candidissima* Misch. ex Grossh., *M. ghalgana* Otchiauri տեսակների ինքնությունը: Նախադրել է *M. manissadjanii* Aznav. ընդու-նել որպես հոմանիշ *M. raddeana*-ի: Անատոմիական տվյալները համաձայ-նեցվում են տեսակների կարիոտիպի հետ և հանգեցնում են նրան որ կոկ-կայան տարածքը և հարկապես Հայկական լեռնաշխարհի ցեղի տեսակա-յին դիֆերենցիացիայի կարևոր կենտրոն են, և հնարավոր է հնադարում նրա խախտման ձևերի ավելի լայն արեալի մնացորդ:

Оганизация Г. Г. Систематика рода *Merendera* (*Colchicaceae*) по данным анатомии. По данным анатомии листа, тычиночного нектарника и связника, диагностическая значимость которых для родо-*Merendera* и *Colchicum* ранее доказана (Оганизова, 1986, 2000), найдены доказательства самостоятельности кавказских видов *M. eichleri* (Regel) Boiss., *M. raddeana* Regel, *M. mirzoevae* Gabrieljan, *M. greuteri* Gabrieljan, *M. candidissima* Misch. ex Grossh., *M. ghalgana* Otchiauri. Возможно включение *M. manissadjanii* Aznav. в синонимы *M. raddeana* Regel. Данные анатомии согласуются с кариологией видов и указывают на то, что кавказский регион и, особенно, Армянское нагорье являются важным центром видовой дифференциации рода и, возможно, островком более обширного в древности ареала его предковых форм.

Merendera Ramond is one of the disputable genus from the aggregated taxon *Colchicum* L. s. l. Besides the above-mentioned genera, genus *Bulbocodium* L. is included into this complex. The old discussion on the taxonomically status of these three genera is connected with their doubtless morphological similarity. The main difference between them is the presence or absence (partly or completely) of the flower tube. On the other hand, for *Merendera* and *Colchicum* s. str. genera parallel series of species are mentioned, which could be interpreted as a proof of their divergence. So the main essence of the discussion, initiated by B. Stefanov (1926) and K. Persson (1992) who insisted on indivisible genus *Colchicum* s. l., is different interpretation of the divergence level.

The genus *Colchicum* s. str. numbers 65–80 species (Vvedenskii, 1963; Wendelbo, 1985; Feinbrun-Dothan, 1986) and has a rather wide distribution area – Ancient Mediterranean with irradiation to Submediterranean. Separate species occur in Middle and Atlantic Europe. The west boarder is South Scandinavia, the east – the Tibet.

The number of *Merendera* species is about 20 and their distribution area has other boarders.

3 species occur in the west of Mediterranean (Valdés, 1980; Valdés et al., 1987). Majority of the species is distributed in the north-east of Mediterranean (Balkans), Asia Minor, the Caucasus and in the north part of Iran (Černjachovskaja, 1935; Grossheim, 1940; Valdés, 1980; Brickell, 1984; Wendelbo, 1985; Persson, 1992; Bokeria, 1999; Gabrieljan, 2001). About 11 species occur in this part of the area, 6 of them are in the Caucasus only, mainly in its

south part. And, besides this territory, 2 more species exist in the boundary parts of Turkey and Iran. Three species occur in Central Asia. Two of them are narrow area endemics from the Kopet Dag and Tadzhikistan (*M. jolanthae* and *M. hissarica*), and *M. robusta* has a wider distribution – north part of Iran, Afghanistan, India (Černjachovskaja, 1935; Vvedenskij, 1963; Nikitin, Geldychanov, 1988; Persson, 1992). There is also 1 species distributed in Ethiopia (Gabrielian, 2001).

So, the area of genus *Merendera* in comparison with that of the genus *Colchicum* is more narrow and disjunctive. The major disjunction is the central part and south-west of Mediterranean.

In this group of taxa, distributed mainly on Armenian Highland, the volumes of some species are also discussed. These are *M. raddeana*, *M. manisadjanii*, *M. candidissima*, *M. mirzoevae*, *M. ghalgana*, and *M. eichleri*. Different scientists interpret them in different ways. E. G. Černjachovskaja (1935), A. A. Grossheim (1940), E. C. Gabrieljan (1986, 1999, 2001), M. R. Bokerija (1999) and other, who research the Caucasian species not only in herbaria but in the field too, recognize their separate status. D. Brikell (1984) recognizes only 4 species of *Merendera* for Turkey. He included the species *M. manisadjanii*, *M. raddeana*, *M. eichleri* into *M. trigyna*. The author emphasized the affinity of the species *M. trigyna* and *M. attica*. K. Persson (1992) recognizes genus *Colchicum* s. l., and in "Flora Iranica" adduces 17 species, 6 of which belong to genus *Merendera*. She includes the species *M. candidissima* and *M. ghalgana* in the synonyms of *C. trigyna* (*M. trigyna*). In the comments of *C. eichleri* (*M. eichleri*) Persson supposes its affinity with Armenian endemic *M. mirzoevae* and presumes possibility of their union.

So, Brikell who studied *Merendera* from the western part of Armenian Highland and adjacent territories includes into *M. trigyna* the species with differences both in morphology and ecology. *M. raddeana* and *M. manisadjanii* are high-mountain sub-alpine, alpine species from grasslands. *M. trigyna* is mainly middle- and low-mountain species typical for dry stone places, mountain steppes, sagebrush semi-desert, and phrygas. *M. eichleri* is a low-mountain species, often growing in sandy places on the coast of the Caspian Sea (Grossheim, 1940; Gabrieljan, 2001).

Persson researched species of the genus from the Iranian part of Armenian Highland and adjacent territories. She includes a very specific high-mountain species from the Great Caucasus *M. ghalgana* (sub-alpine meadows) into *M. trigyna* and supposes the possibility to unite *M. mirzoevae* (low, middle and high mountain zones, in plant communities connected with forests) with *M. eichleri*. In the same way she includes three Central Asian species into the volume of *C. robusta* (*M. robusta*). But *M. jolanthae* is an endemic of the Kopet Dag, occurs on clay and gypsous slopes of mountainous Turkmenistan, *M. hissarica* is an endemic of the high-mountainous Tajikistan and a characteristic element of alpine meadows. *M. robusta* sensu Vvedenskij (1963) grows on sandy, clay soils of the lower part of the mountains.

So, to prove the separate status for the disputable species it is necessary to find for them morphological features having phylogenetic adaptive significance (Georgievsky, 1989).

Materials and methods

For the solution of the systematical problems of genus *Merendera*, a possibly large amount of species from different parts of the genus area and from different ecotopes

must be researched and compared. Leaf structure, structure of staminal nectary and anther connective were selected as features with phylogenetic adaptive significance. For the genus *Merendera* as well for the genus *Colchicum* (Oganezova, 2000) the diagnostic significance of these features were revealed earlier (Oganezova, 1986).

Living plants fixed by FAA (l. p.) and herbarium samples of the following species were studied.

M. trigyna (Steven ex Adams) Stapf.: 1) Yerevan environs, Jrvež, sagebrush semi-desert. 20.03.1984. G. Oganezova (l. p.); 2) Yerevan, Botanical Garden of the Botanical Institute. 8.05.1997. G. Oganezova (l. p.); 3) Armenia, Megri district, environ of village (vil.) Vardanidzor. 12.04.1980. K. Tamanjan (l. p.); 4) Circa n. Erevan, p. Jrvež. In pratibus. 13.05.1943. S. Tamamshian & A. Fedorov, ERE 3223; 5) Erevan, pr. P. Avan, fl. Gedar, 23.03.1944. S. Tamamshian & A. Fedorov, ERE 31082; 6) Environ of Tbilisi, Kodžori, near Ker-Ogly. 23.03.1936. Š. Kutateladze, TBI; 7) Georgia, Meschetija, between vil-s. Schvilisi and Phocchovi. 8.05.1965. L. Chintibidze, M. Davlianidze, TBI; 8.) (Determined as *M. caucasica* M. Bieb.) Transcaucasica, Tiflis, prope lacum Tshedinum ju dedissilus graminosis. 16.03.1919. A. Grossgeijm, ERE 31082.

M. sobolifera Fisch. & C. A. Mey.: 9) Armenia, Ararat district, salt marsh near Ararat settlement. 25.05.1978. N. Chandžjan, ERE 124235; 10) same place, 20.03.1979. G. Oganezova, ERE 111252; 11) same place and time – (l. p.) G. Oganezova.

M. raddeana Regel; 12) Herbarium Caucasicum, Lawalan. 20 Jun. 1880. Radde, TGM; 13) Georgia, South-Osetian mountain station of the USSR SCI. Academy, place named Ermani, nears the station, 2200-m. a. s. l., moraine. 14.05.1942. V. Darbin, TBI; 14) Georgia, Distr. Leningori, ante Achalgori. In cacumine mont. "Sameba" ad fontes fauc. flum Alevistzkali in pascuis subalpinus supra pag. Kocziani, ad nives. 1.05.1954. Elis Kikodze, TGM 50716; 15) Georgia, Thusheti. In divortium fl. Gometzari & Cancachovani. 31.05.1980. G. Arabuli, G. Ligokeli, TGM 62509; 16) Armenia, Kamo district, spur of Gegham ridge near vil. Baškend. 11.06.1978. E. Gabrielian, ERE 112839; 17) Armenia, Megri district, vil. Kaler environs, mountain Čknavor. 14.05.1979. G. Oganezova (l. p.).

M. manisadjanii Aznav.: 18) Armenia, Zangezur, Kapudžuch mountain, eastearn slope, 2600 m. 28.05.1985. S. Balojan, ERE 130761, 130762; 19) same place, 2600–2900 m., meadows. 28.05.1985. S. Balojan, ERE 135186. 20) Armenia, Aragaž mountain, turfy meadows, 2400 m. 5.05.1997. E. Gabrielian, ERE 144931; 21) Armenia, Megri district, Aijgedzor, Teij vil. environ, right bank of Megrageret river, near the mining galleries. 6.04.1980. A. Sagatelian (l. p.).

M. mirzoevae Gabrielian: 22) Armenia, Dilidžan, Golovino. 20.01.1980. E. Gabrielian (l. p.); 23) same place. 30.03.1980. E. Gabrielian (l. p.);

M. candidissima Misch. ex Grossh.: 24) Armenia, Zangezur, Šikachoch reservation, Nerkin Hand vil. 12.02.1961. M. Grigorijan, ERE 121340. 25) Armenia, Megri district, on road from Švanidzor to Gjumaranc, oak forests. 11.03.1986. G. Oganezova, ERE 130911. 26) Armenia, Sisian district, Šamb vil. environ, Vorotan river canyon, rare juniper forest, 1250–1350 m. 14.03.1990. I. Gabrielyan, ERE 143209.

M. greuteri Gabrielian: 27) Armenia, Talin district, Arteni mountain, vil. Areg environ, 1800–1900 m. 24.04.1980. G. Oganezova, ERE 146798; 28) same place, 6.05.1980. G. Oganezova, ERE 146796, 146797; 29) same place, 9.04.1998. E. Gabrieljan (l. p.); 30) Armenia, Aragac mountain. 9.04.1998. E. Gabrielian (l. p.).

M. eichleri (Regel) Boiss.: 31) Caucasus, Kislowodsk, 2700. 10.06.1897. I. Akiniev, TBI; 32) Charami mountain (1890) to north of Adžikabul (Šemachin district, Baku province). 6.04.1907. Schelkovnikov, Schmidt, TGM 7312; 33) Azerbaidžan, Baku district, near place named Zych (locus classicus). 19.04.1924. P. Gurijiskij, BAK; 34) the Caucasus, Kabardino-Balkaria, right bank of the Čerek Bezengian river, near the place of its flow into Mižergi river. Meadows on sandy soil. Alt. 2000 m. N. Portnier, LE.

M. ghalgana Otshiauri: 35) Georgia, Kazbegian district, right bank of the river Chdiskali, on meadow's. 30.03.1964. E. Chucišvili, D. Očiauri, TBI; 36) Georgia, vil. Kazbegi, place "Cocechi", sub-alpine meadows, pasture, 1750 m. 11.05.1964. E. Chucišvili, TBI;

M. attica (Spruner ex Tommasini) Boiss. & Spruner in Boiss. (syn. *M. rhodopea* Vel.): 37) Bulgaria, Stanimska. 04.1894. V. Stribrny, ERE 6965.

M. pyrenaica (Porret) P. Fourn. (syn. *M. montana* Lange, *M. bulbocodium* Ramond.): 38) Scotland, Dundee, Index Seminum, 1979 (one had send bulbs with dry leaves); 39) Espana, Huesca, base de los Mallos. 23.08.1979. B. Valdēs, SEV.

M. androcymbioides Valdēs: 40) Espana, Malaga. Serania de Ronda. Entre Ronda y San de Alcantara. Suelos calizos, c. 900 m. s. m. Localidad classica. 16.02.1978. B. Cabezudo, J. Pastor, S. Talavera & B. Valdēs, SEV.

M. filifolia Camb.: 41) Espana, Sevilla: cerca de Moron. 19.10.1979. J. Pastor et Valdēs, ERE 62191.

M. robusta Bunge: 42) Turkmenistan, Poltavskoe vil. near Kuška fortress, on hills. 22.03. 1930. A. Butkov, ERE 5430; 43) same place. 27.04.1930. A. Butkov, ERE 67739.

Anatomical structure of the leaf margin and midrib, staminal nectary and anther connective were studied for almost all samples, excluding samples of *M. ghalgana*. Only the leaves of this species were investigated because of the flowers' absence. Common methods for comparative morphological and anatomical study with a light microscope were applied. The whole herbarium materials of the genus *Merendera* from ERE, TBI, TGM, and the Caucasian part LE and partly from BAK were observed.

Results

Anatomy of the leaf. The major diagnostic feature for *Merendera* species is the structure of the main vein – midrib. Sometimes leaf margin and lateral veins structure also served for identification. In this article I restrict the description of the specific features of leaf (staminal nectary and anther connectives also) for different species of *Merendera* because earlier (Oganezova, 1986, 2000) I already gave the whole description of this part of the plant for the both genera – *Merendera* and *Colchicum*.

All studied species of *Merendera* are divided into two groups according to the features of leaf structure. The first group consists of *M. filifolia*, *M. ghalgana*, *M. attica*, *M. trigyna*. These species have structural peculiarities, which stress the adaxial part of leaf near midrib. The second group consists of the rest studied species. For these species the whole area of midrib is structurally distinguished. Both groups are divided into subgroups.

Group 1. 1a. Lower epidermal cells in midrib area have extremely thickened walls and size (*M. attica*). **1b.** Epidermal cells near midrib area are almost unchanged, but above them one-layered thin-walled hypoderma (*M. ghalgana*, *M. filifolia*) is developed. These two species differ from each other by the following features of leaf. *M. ghalgana* (Fig. 1, a, b) develops two layered true palisade tissue and leaf margin

with group of collenchyme cells, which is standard for the majority of species. *M. filifolia* hasn't margin collenchyme; palisade tissue isn't normally expressed. **1c.** A considerable group of hypodermic cells with the thickened walls develops below the midrib (Fig. 1, c, d – *M. trigyna*). Samples N 3 (Fig. 1, d) and N 8 of this polymorphic species differ a little from each other and from the rest samples, which allows to see the interspecies variability amplitude. The differentiation is in quantitative features (number of cells, their size, etc.). Similar distinctions were revealed on the leaf margin of these samples.

Group 2. 2a. The epidermal cells of the both surfaces develop extremely thickened cell walls and have significant increase in the midrib area. Two groups of hypodermic cells develop above and below the midrib. The upper hypoderma consists of a few cells, the lower is more effused (*M. candidissima*, *M. greuteri*, *M. pyrenaica*). Leaf margin of these species are without any peculiarities (Fig. 1, e, f). **2b.** A 2 or 3-layer hypoderma is strongly developed in adaxial and abaxial parts of leaf midrib (Fig. 1, g). Leaf margins of these species have not any peculiarities (*M. androcymbioides*) or contain only a few collenchyme cells (*M. sobolifera*). **2c.** Hypoderma is developed on both adaxial and abaxial sides of the midrib area and consists of one (Fig. 2, b – *M. manisadjanii*) or two layers (Fig. 2, a – *M. raddeana*). Sometimes hypoderma is thin-walled (*M. manisadjanii*). Hypoderma is in contact with the midrib at abaxial part only. Palisade tissue (*M. raddeana*) or parenchymatous sheath of bundle (*M. manisadjanii*) is developed between adaxial hypoderma and midrib. Leaf margin has no peculiarities; sometimes the cell walls here looked thinner than usual. **2d.** This subgroup is similar to the preceding one, but both adaxial and abaxial groups of hypoderma haven't contact with midrib. An increase in both epidermis cells and significance thickening of their walls (Fig. 2, c – *M. eichleri*) was revealed in this part of leaf. **2e.** Adaxial hypoderma is big-celled, noticeably developed and hasn't contact with vascular bundle. In contrast, abaxial is more compact and has such a contact (Fig. 2, d – *M. mirzoevae*). **2f.** Increase in cells and cell walls thickening of both epidermal layers is observed in midrib area. One-layered adaxial and abaxial hypoderma with thickening cell walls develops as well. It hasn't contact with midrib. The same type of hypoderma develops on several big lateral bundles area too. Leaf margins are of common type (Fig. 2, e, f – *M. robusta*).

So, Mediterranean and Minor Asian and Caucasian species of *Merendera* form mixed sub-groups, but Iranian-Central-Asian species *M. robusta* has separate sub-group.

Staminal nectaries. The study of the new species of *Merendera* (Oganezova, 1986) allowed to specify the diagnostic significance of the features of nectaries structure. The research revealed the special importance of: development character of superficial secretory tissue; comparative position of vascular bundles (the number of vascular bundles and secretory tissue may vary for different samples of the same species); presence or absence of schizogenetic cavities (serving for nectar storage). Due to these features *M. filifolia*, *M. pyrenaica*, *M. androcymbioides* and, especially, *M. robusta*, sharply differ from other species. *M. filifolia* (Fig. 3, a) has one vascular bundle in the central part of nectary. The secretory tissue is weakly differentiated into a more dense superficial and more crumbly (with a developed intercellular space) central part. Schizogenetic cavities lack. *M. pyrenaica* and *M. androcymbioides* (Fig. 3, c, b) have similar structure of nectary's vascular system, but the investigated material was in bad condition and it was difficult to make conclusions about some details. The tissue that

surrounded the bundle was destroyed. For *M. androcymbioides* were noted cavities in the margin parts of the nectaries (if they aren't the result of the materials' bad conservation). *M. robusta* (Fig. 3, d, e) besides micro-morphological peculiarities in nectaries structure has also macro-morphological peculiarities. Nectaries fuse with petals along all their length (for other species such fusion is noted only for the basal part of nectaries). So the free surface of nectaries is smaller than in other species. In the inner structure the exact differentiation between the superficial and central part of the secretory tissue lacks. But a few superficial layers of it are distinguished as more dense and about 5 vascular bundles are in contact with them. One of the bundles is bigger than others. In the central part of the nectary dense and crumbly types of secretory tissue are mixed. A few nectar-storage cavities develop only in apical part of nectaries.

The nectaries of the rest species have structural similarity – differentiated into dense superficial (cavities may develop here) and crumbly, netlike central part of secretory tissue. Vascular bundles develop in the central part. Species-specific features are as follows. *M. trigyna* (Fig. 3, f) has the standard type of nectaries structure, without cavities. As for leaf, polymorphism of this species is revealed in nectaries quantitative features – the number of vascular bundles. In the basal part their numbers vary from 6–7 (in most of the samples) to 19–20 (sample N 3). Commonly, one bigger bundle has central position and the others form a semicircle above it. The central bundle isn't almost revealed for sample N 3. For all samples (as well as for majority of other species) is noted a slow fusion of all bundles near the filaments. *M. mirzoevae*' nectaries structure (Fig. 3, g) is almost similar to the preceding species. *M. attica* nectaries (Fig. 3, h) are similar too, but have schizogenetic cavities. *M. raddeana* nectaries (Fig. 3, i) differ by poly-layered superficial secretory tissue, which is in contact with numerous (~8–10) small vascular bundles. The central bundle is slightly revealed. Cavities are absent. Nectaries of *M. sobolifera* are similar to those of the preceding species. Nectaries of *M. greuteri* (Fig. 3, j) have following peculiarities. Superficial dense secretory tissue of some samples cover not only the adaxial (which is common), but the whole surface of nectary. The small vascular bundles (~10–14) are immersed in it. A large bundle is revealed, but it forms a circle with the other ones. For this species an extreme development of the nectar-storage cavities is specific. They develop gradually and depending on the flower's development. Nectaries of *M. manisadjanii* (Fig. 3, k) have few-layered superficial secretory tissue, all vascular bundles form a circle, the central bundle isn't almost revealed, cavities are present. *M. candidissima* (Fig. 3, l) has a similar structure of nectaries but without cavities. *M. eichleri* (Fig. 3, m) has few-layered superficial secretory tissue; the central bundle is much larger, little bundles surround it, cavities are present.

It is evident from Figures that there are differences in sizes and contours of nectaries, but it is difficult to consider the significance of these features because the alive fixed and dry herbarium materials were investigated.

So, the Central-Asian species *M. robusta* is vividly distinguished according to its nectaries structure, *M. filifolia*, *M. pyrenaica* and *M. androcymbioides* differ as well. Other species are grouped in the following way. *M. trigyna* unites with *M. mirzoevae* and *M. attica*; *M. raddeana* with *M. sobolifera*; *M. manisadjanii* with *M. candidissima*; *M. greuteri* and *M. eichleri* remain alone. Morphological groups formed by nectaries features do not agree with groups, formed on the base of leaf structure.

Anther connectives. The differences in this structure are mainly connected with the position and number of vascular bundles before and behind their contact with filament. For the studied species of the genus *Merendera* 2 types of the connectives were noted: 1) continues in filament – connectivum filamento continuum (Artjushenko, Fedorov, 1975) – *M. robusta*, *M. androcymbioides*; 2) connected with filament by articulation – connectivum articulatione distinctum – the rest of the studied species. In the first case anther is absolutely immobile related to filament. In the second – anthers are mobile, pendulous. However, this mobility may differ depending on the place of articulation. There exist two variants of the articulation place: to the basal (basifixed – *M. filifolia*, *M. pyrenaica*) or middle (dorsifixed – other investigated species) part of anther. Surfaces of anther and connective are usually naked, but in case of *M. robusta* simple hairs cover it. The basal part of connective is wider than the apical one.

The only vascular bundle of filament is prolonged along the whole connectives in case of *M. robusta* and *M. androcymbioides* (Fig. 4, a, b).

The other investigated species are divided in two groups according to the number of vascular bundles and their position in connectives. The first group includes *M. greuteri*, *M. pyrenaica*, *M. eichleri*, *M. manisadjanii*, *M. raddeana* (Fig. 4, c, d, e, g, h). They are characterized by only one vascular bundle behind the place of articulation to the apical part of connective. The basal part lacks the bundle. *M. raddeana* has some specific features. Behind the articula-

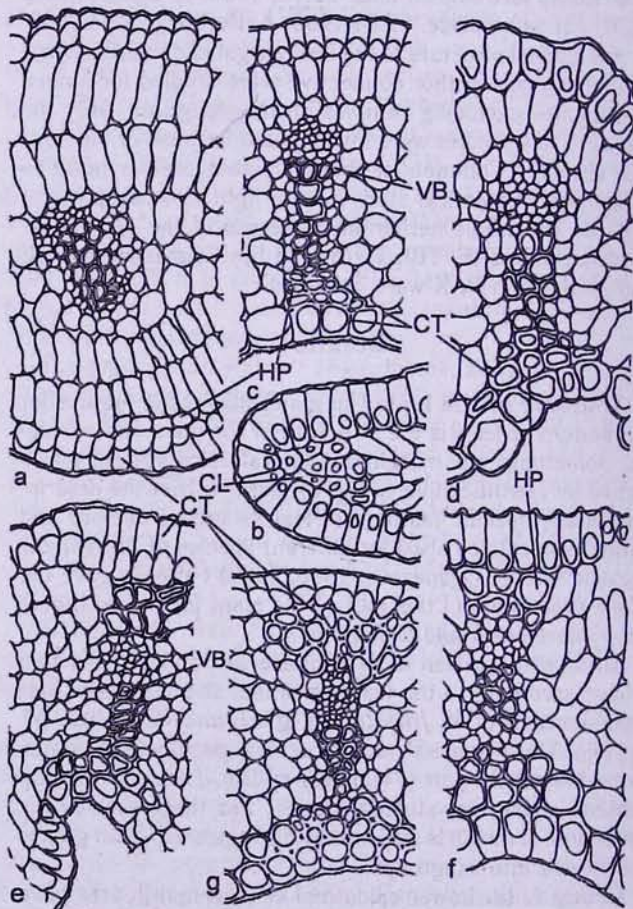


Fig. 1. Cross-section of *Merendera* species leaf midribs (a, c–g) and margins (b); *M. ghalgana* (a, b), *Merendera trigyna* – common type (c), sample N 3 (d), *M. candidissima* (e), *M. greuteri* (f), *M. sobolifera* (g). CL = leaf margin collenchyme; CT = cell walls thickening; HP = hypodermis; VB = vascular bundle. $\times 120$.

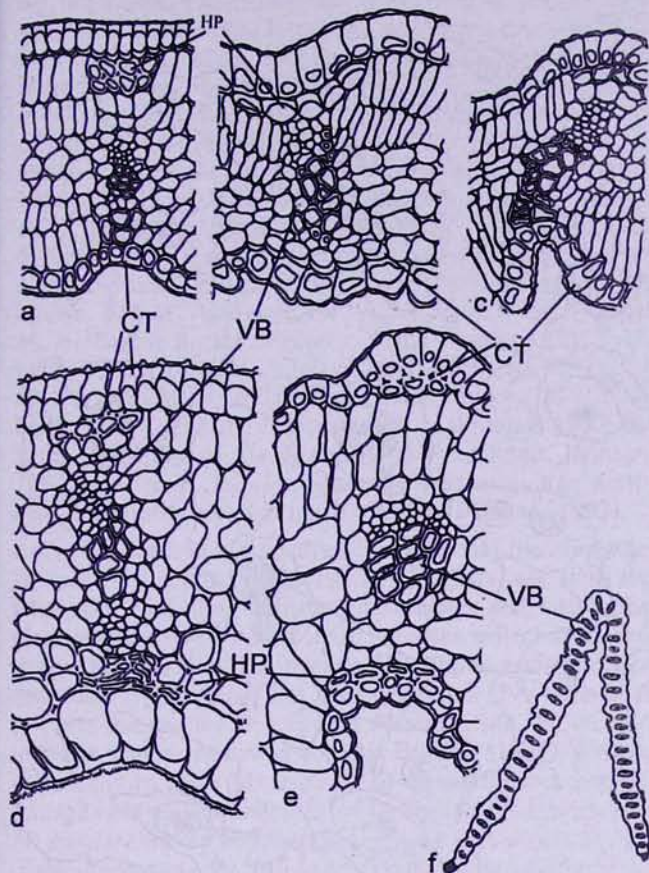


Fig. 2. Cross-section of *Merendera* species leaf (f) and leaf midribs (a-e): *M. raddeana* (a), *M. manisadjanii* (b), *M. eichleri* (c), *M. mirzoevae* (d), *M. robusta* (e, f). $\times 120$.

tion place the bundle branches into three parallel bundles and in this condition continues towards the apical part. In case of *M. manisadjanii* it seems that such branching isn't completed. The second group consists of *M. sobolifera*, *M. candidissima*, *M. attica*, *M. trigyna*, *M. filifolia*, *M. mirzoevae* (Fig. 4, f, j, k-m). In this case filament's bundle behind the articulation with connective is bifurcating and continues both to the apical and basal parts of the connective. The polymorphic species *M. trigyna* demonstrates variability regarding these features too. It is remarkable that for sample N 8 the bifurcation is noted already in the filament and in the connective the basipetal part of the vascular bundle is very short. Actually, *M. attica* doesn't have any bifurcation, a single basipetal bundle is noted at a small distance from the place of articulation.

Discussion

The interspecies differences of *Colchicum* in leaf midrib and surrounding mechanical tissue structure are correlated with the size of leaves and their position in the living plant, with species ecology as well. In other words, *Colchicum* leaf structure is connected with species belonging to different plant communities and different lighting conditions (Oganezova, 2000). For *Merendera* such difference of ecological conditions isn't specific. This genus is not distributed in real forest communities. All its species exist in good lighting condition and have leaves usually clasped to ground. The above mentioned correlation specific for *Colchicum* species' leaf structure is noted for *Merendera*, but only as a tendency, not as a rule. *M. filifolia* (exists in open dry places, on sandy soils) has not large-sized leaves (~ 10 cm in length and 1-2,5(3) cm in width) and mechanical tissue is practi-

cally absent. *M. ghalgana* (high-mountain species, leaves aren't large either) has mechanical tissue weakly developed in the midrib area, but normally developed on the leaf margins. Besides the marginal collenchyme, for *M. attica* (sizes of leaves in fruitage time are $\sim 3,5$ cm in length, ~ 18 cm in width) is specific the increase in epidermal cells and thickening of their walls near the midrib area. *M. trigyna* mainly occurs from low to middle mountainous zones. Sizes of leaves are $\sim 7-9$ cm in width, and 8-10 cm in length. In addition to marginal collenchyme the group of hypodermal cells with thickened cell walls develops below the midrib. *M. sobolifera* (from low to high mountain zones, moist, marshy places), *M. candidissima* (low and middle mountain zones, dry stony places), *M. pyrenaica* (similar conditions), *M. greuteri* (middle zone, exists in similar conditions), *M. androcymbioides* (low part of mountains, dry places) have the marginal collenchyme and develop significant groups of hypodermis both above and below the midrib. The leaves of the first two species have very large sizes (accordingly $\sim 1,4-1,8$ cm in width, 15-18 cm in length and 0,8-1 cm in width, 12-15 cm in length). The leaves of *M. pyrenaica* and *M. androcymbioides* have sizes comparable with those of the leaves of *M. trigyna* and *M. attica*. The leaves of *M. greuteri* in flowering period are narrow, but in fruitage period they become similar in size to those of *M. trigyna*.

M. eichleri, *M. raddeana*, *M. manisadjanii*, *M. robusta* develop hypodermis in the same way as the preceding group, but hypodermis is not so significant either in character of the cell walls thickening, or in the number of their layers. The above-mentioned should be especially noted for high-mountain species *M. raddeana* (length of leaf $\sim 0,8-1$ cm, width ~ 13 cm) and *M. manisadjanii* (width $\sim 1-1,2$ cm, length $\sim 7-10$ cm). The leaves of the two last species in fruitage period are a little bigger in comparison with the leaves of *M. trigyna*. I think it isn't a contradiction, but a demonstration of the specific for high-mountain species tendency to structural reduction. It is noted both for vegetative and generative parts of plant and is explained by their short vegetation period (Oganezova, 1984).

M. robusta is a species with vigorous, large leaves; this peculiarity is reflected in the name. *M. robusta* between midrib structure and leaf size hasn't any contradiction either. The leaves of this species have additional supporting system in the strengthening lateral veins.

Thus, the leaf mechanical system distinguishes the disputable species *M. ghalgana*, *M. mirzoevae*, *M. raddeana*, and *M. candidissima* and characterizes the new species *M. greuteri*. I would like to emphasize a slight difference between the leaf structure of the closely related species *M. raddeana* and *M. manisadjanii*. The mentioned features are similar to those of morphologically restricted species *M. candidissima* and *M. greuteri*. I think that leaf structure with reliably authenticity proves the divergence between disputable species of *Merendera*. Some doubts remain for very similar species *M. raddeana* and *M. manisadjanii*. The differences revealed between these species probably are intraspecific variability of the polymorphic *M. raddeana*.

M. robusta sharply differs by the nectaries structure. It has specification both in macro- and micro-morphology of this part of flower. The structure of *M. filifolia*, *M. pyrenaica*, *M. androcymbioides* nectaries has also specific enough – they have only a single vascular bundle. The tendency of correlation of the rest species nectaries structure is connected with their ecology. Nectar-storage cavities are more characteristic for the species from dry places of low and middle mountains zones. It is possible that this factor reveals synergetic evolution between nectaries and pollina-

tors. The pollinators are significant more in spring than in autumn. The latter might explain the similarity between the nectaries structure of autumn-flowering species of different genera – *M. filifolia*, *M. pyrenaica*, *C. umbrosum* (Oganezova, 2000). But similar nectaries structure of the spring-flowering species *M. androcymbioides* make questionable such suppositions. But if the cavities noted in the studied materials of *M. androcymbioides* aren't the artefact (the result of the material's decay) but they are in fact nectar-storage cavities, the contradiction disappears. It might be reasonable to trace the correlation between this event and the tendency towards forming unisexual flowers noted in the Armenian population of *M. trigyna* (Tonjan, 1949; Gabrieljan, 2001) or with intensity of the vegetative breeding. For example, the vegetative breeding of *M. sobolifera* is more intensive because its corm has stolons. Of course, nectaries structure and function are connected with the whole breeding system and here a multi-variant correlation is possible. If we compare this structure of the genera *Colchicum* (Oganezova, 2000) and *Merendera*, we notice that the latter one has a stronger intraspecific variability and a slighter correlation with the habitat conditions of the taxon.

The investigation of anther connectives allowed to define the exact peculiarities of its fixation. The latter is under special attentions of B. Valdés (1980). *M. robusta* and *M. androcymbioides* differ from other species by the type of their anther fixation, which causes their immobility. But anthers "basifixed" type, mentioned by Valdés (1980) for

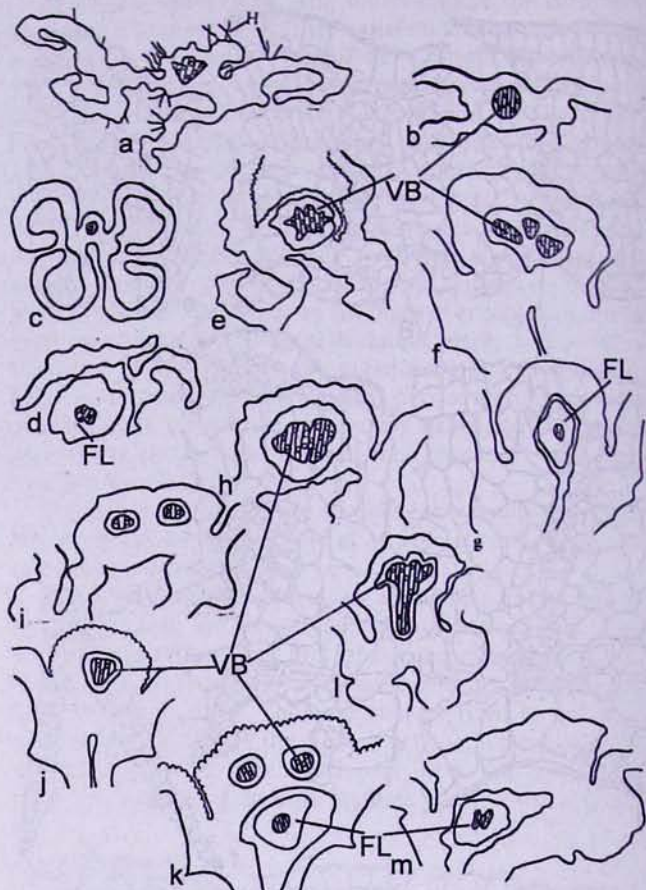


Fig. 4. *Merendera* species connectives in cross-section: before articulation place (d, f, h, j, l, n), upper this place (others); *M. robusta* (a), *M. androcymbioides* (b), *M. pyrenaica* (c, d), *M. eichleri* (e), *M. raddeana* (g, h), *M. candidissima* (i, j), *M. trigyna* (k, l – common type; m – N 8). VB=vascular bundle; FL=filament; H=hair. $\times 20$

M. filifolia, *M. sobolifera*, *M. pyrenaica* is a variant of "connectivum articulatione distinctum", but not "connectivum filamento continuum". For some of the rest species, for example *M. trigyna*, *M. mirzoevae*, *M. candidissima*, *M. raddeana* these features serve as additional distinguishable traits. It is interesting that in case of species, habitant in dry places, their anther connective develops the vascular system along the whole length, on the both sides from the articulation place. Unilateral (acropetal) development type of the vascular system occurs for the species from different ecological conditions. The double-sided (base-acropetal) type of the vascular system provides considerable mobility of the anthers and is another proof of the synergetic evolution with pollinators. The species with immobile type of the anthers are distributed on the edges of the genus area and possibly they could be interpreted as a way to self-pollination. It is known that the self-pollination phenomenon develops more often in the following conditions – on the edges of the area of the species as a method of its extension (Aga-djanjan, 1987, 1992).

Well known is the interest of cytologists to the Caucasian species of the genera *Merendera* and *Colchicum*, because the diploid kind of their species are concentrated in this region. In my opinion, the comparison of the obtained data with number of chromosomes, known from the literature, makes sense. The number of chromosomes was defined for 13 species of the genus, but only 11 species of this amount have been investigated in the present work. A high level of polyploidy is mentioned for the West Mediterranean species (*M. filifolia* – $2n=42, 54$; *M. pyrenaica* – $2n=54+0-$

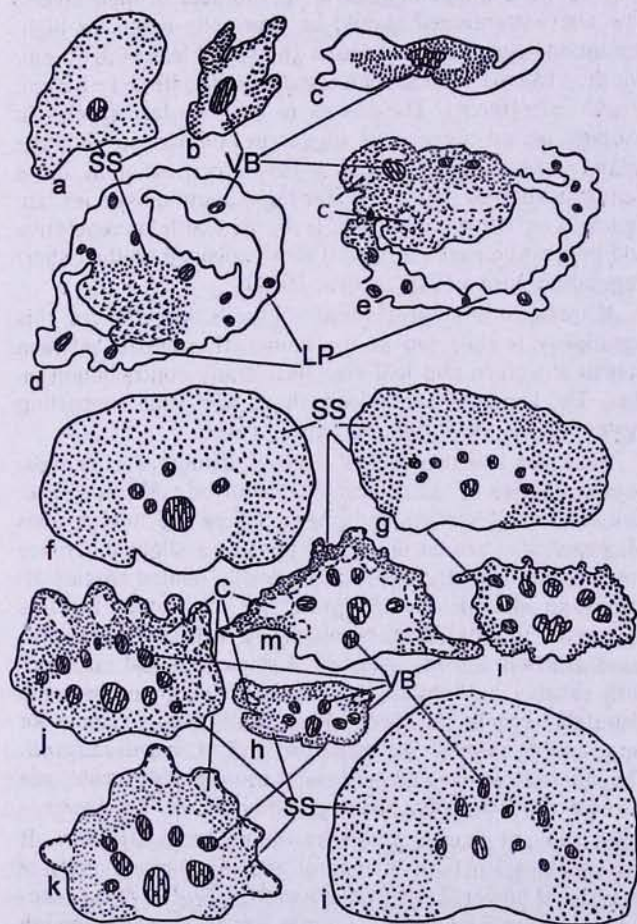


Fig. 3. *Merendera* species nectaries in cross-section: basal part (d), middle part (other); *M. filifolia* (a), *M. pyrenaica* (b), *M. androcymbioides* (c), *M. robusta* (d, e), *M. trigyna* (f), *M. mirzoevae* (g), *M. altica* (h), *M. raddeana* (i), *M. greuteri* (j), *M. manisadjanii* (k), *M. candidissima* (l), *M. eichleri* (m); SS = superficial secretory tissue; C=cavity; VB=vascular bundles; LP=limb of perianth. FS=fissure-like space. $\times 22$.

6B, 60; Valdés, 1980; Goldblatt, 1981, 1990, Goldblatt, Johnson, 1991), East Mediterranean *M. attica* (2n=54; Fedorov, 1969; Goldblatt, Johnson, 1991) and for widespread Irano-Turanian *M. sobolifera* (2n=42, 54; Fedorov, 1969; Moore, 1973; Valdés, 1980). The similar situation is characteristic for two species distributed on the eastern part of the genus area – *M. robusta* (2n=54; Fedorov, 1969; Moore, 1973; Takhtajan, 1990) and *M. jolanthae* (2n=36; Moore, 1973; Takhtajan, 1990). For the species, restricted in their distribution by the Caucasus and, especially, by the Armenian Highland, the following chromosome numbers are known. For *M. raddeana*, *M. eichleri*, *M. candidissima*, *M. mirzoevae* 2n=18 (Fedorov, 1969; Moore, 1973; Takhtajan, 1990; Goldblatt, Johnson, 1991; Pogosjan, 1997). For *M. trigyna* 2n=18, 20 (Fedorov, 1969; Moore, 1973; Goldblatt, 1981; Goldblatt, Johnson, 1991; Takhtajan, 1990; Bokeria, 1999). For *M. ghalgana* 2n=24 (Goldblatt, Johnson, 1991) and for *M. kurdica* (Anatolia southeast, Iraq northeast, Iran northwest and north) 2n=20 (Persson, 1992).

On the bases of the results I conclude that the *Merendera* species accepted by Caucasian scientists are separate, with restricted area, with specific macro- and micro-morphological features, which in some cases reflect their ecological peculiarities. The species *M. trigyna* and *M. attica* are close to each other but very delimited. It is impossible to unite the species *M. trigyna*, *M. raddeana*, *M. eichleri* into one species as it was done by Brickell (1984). Neither is possible to unite *M. trigyna*, *M. candidissima* and *M. ghalgana* (Persson, 1992) into one species. The alliance of *M. eichleri* and *M. mirzoevae* proposed by Persson (1992) is also impossible. Doubtful seems only the separation of *M. manisadjanii*. Morphologically it is closely related to *M. raddeana*, its area is questionable (the Central Anatolia, and East, South-East of Armenia). It is likely to be demonstration of the latter polymorphism.

The diploid number of chromosomes known for the Caucasian species is combined with the concentration of all the revealed morphological types of midrib, nectary and anther connective in this part of genus area. So, the genus *Merendera* is characterized by the following peculiarities. The polyploide species of *Merendera* occur outside the Caucasus only (excluding the widespread *M. sobolifera*). Unisexual flowers of some samples of species of *Merendera* were found in the Caucasus. And, as a contradiction to the above-mentioned, the phenomenon of self-pollination possibly exists on the edges of the genus area. Furthermore, the morphological variability (Richards, 1986) of the Caucasian species is added. All these traits prove that the Caucasus, especially the Armenian Highland is an important modern node of the genus differentiation. It is possible that it is a piece remained from the ancestor area which was larger in the past.

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