SORBUS ARMENIACA AND THE ORIGIN OF HYBRIDOGENOUS SPECIES OF SORBUS SECTION LOBATAE IN CAUCASUS

On the basis of taxonomical, morphological, anatomical, palynological and other data the problems of origin of next hybridogenous species of Caucasus are discussed: Sorbus armeniaca, S. caucasica, S. tamamschjanae, S. roopiana, S. persica, S. takhtajanii, S. luristanica, S. kuznetzovii and the Central Asian species of S. turkestanica. Each of them has a specific set of various features. Despite their hybrid origin, these forms are so isolated and viable that they have gained an independent area, which means that they turned into real species.

The story of parental pair investigation of *S. armeniaca* species is given in detail. Photographs and drawings are provided.

Sorbus, S. armeniaca, Caucasus, hybridogenous species, anatomical, palynological characters

Գաբրիելյան Է. Ֆ., Բալայան Կ. Վ. Sorbus armeniaca-ն եւ Կովկասի հիբրիդոգեն Sorbus Lobatae սեկցիայի տեսակների առաջացումը: Տաքսոնոմիկ, մորֆոլոգիական, անատոմիական, պալինոլոգիական եւ այլ տվյալների հիման վրա քննարկվում են Կովկասի 8' Sorbus armeniaca, S. caucasica, S. tamamschjanae, S. roopiana, S. persica, S. takhtajanii, S. luristanica, S. kuznetzovii, ինչպես նաեւ միջինասիական S. turkestanica հիբրիրդգեն տեսաների առաջացումը։ Գրանցից ուրաբանչյուրի համար գոյություն ունի տարբեր հատկանիշների առանձնահատուկ շարջ։ Չնայած իրենց հիբրիդային առաջացմանը, այդ ձեւերը այնքան առանձնացած են եւ կենտունակ, որ ձեռք են բերել ինքնուրույն արեալ, այսինքն, դարձել են իրական տեսակներ։

Մանրամասնորեն տրվում է *S. armeniaca* տեսակի ծնողական ձեւի բացահայտման պատմությունը։ Բերվում են լուսանկարներ եւ նկարներ։

Sorbus, S. armeniaca, Կովկաս, իիբրիդոգեն տեսակներ, անատոմիական հատիկանիշներ, պալինոլոգիա

Габриэлян Э. Ц., Балаян К. В. Sorbus armeniaca и происхождение гибридогенных видов секции Lobatae рода Sorbus Кавказа. На основании таксономических, морфологических, анатомических, палинологических и других данных обсуждаются вопросы происхождения следующих гибридогенных видов Кавказа: Sorbus armeniaca, S. caucasica, S. tamamschjanae, S. roopiana, S. persica, S. takhtajanii, S. luristanica, S. kuznetzovii и центральноазиатского вида S. turkestanica. Для каждого из них имеется специфический набор различных признаков. Несмотря на свое гибридное происхождение, эти формы настолько обособлены и жизнеспособны, что приобрели самостоятельный ареал, то есть стали реальными видами.

Детально дается история нахождения родительской пары видов S. armeniaca. Приводятся фотографии и рисунки.

Sorbus, S. armeniaca, Кавказ, еибридогенные виды, анатомические, палинологические признаки.

Despite a monograph written by E. Ts. Gabrielian (1978), the problem of hybridogenous species of *Sorbus* genus of Caucasus flora still needs a modern commentary.

S. armeniaca Hedl. species which was described by Hedlund (1901) is often confused with another of *Sorbus* species which also has lobate leaves. Earlier it was identified as *S. scandica* Fr. or *S. intermedia* (Ehrh.) Pers., later – as *S. caucasica* Zinserl., *S. persica* Hedl., *S. dualis* Zinserl. (= *S. roopiana* Bordz.) and even as a rather distant species *S. kuznetzovii* Zinserl.

S. armeniaca was described according to Szovits' collections from Nagorno-Karabakh¹.

When E. Ts. Gabrielian worked in Leningrad (S. Petersburg) on her dissertation "Caucasian representatives of *Sorbus* species" in 1952–1955, she came to a conclusion that Caucasian herbarium did not have enough material to make a complete picture of *S. armeniaca*. Moreover, when T. Hedlund (1901), described this species, he noted that he had very modest material from Szovits' collection at his disposal, and it was not enough to judge about the variability of the species. And indeed, Hedlund's description can't be considered complete. Later, in LE general herbarium two specimens of plants which had been collected by Szovitz from Kirs mountain were found, which completely coincided with the image and the description given by Hedlund.

V. I. Lipsky (1899), in "Flora of Caucasus", in chapter 2, indicates that a manuscript by C. A. Meyer «Notizen über das Herbarium Szovitzianum angefertigt von C. A. Meyer» is kept in the archival materials of the Library of the Academy of Science (Leningrad). In chapter 3, which is titled "Information on botanical collections of Caucasus" and is very important for researchers of the Flora of Caucasus (p. 126–129), under \mathbb{N} 105 he describes the routes of Szovits' collections of plants in 1828-1830 (p. 153-155). After a long search, Gabrielian found a manuscript which had been written by Meyer himself in Gothic scripts. It is still a question whether it was incomplete or unfinished, but, luckily, a part of Szovits' route to Karabakh was preserved, in particular to the mountain Kirs in September 1829. At that time Karabakh still belonged to Armenia, therefore Hedlund gave it the epithet "armeniaca". It hardly exists in modern Armenia. S. armeniaca was collected only once by N. Gurvich in June 1937 in the forest not far from Dilijan (North Armenia). Gabrielian's searches undertaken in 1952 and later, in that area were not successful. Only two specimens of this rare species were discovered on the mountain Kirs, that is in its locus classicus, in the course of an expedition to Nagorno-Karabakh that took place in 1962. It turned out that they were completely identical to Szovits' samples, especially with isolectotype, which were discovered in the archival materials of the British Museum (BM!). Their leaves were wider than the samples from Leningrad and than the leaves on the image made by Hedlund. One of these trees reaches 12 meters in height and 30 cm. in diameter of the trunk. It is the first time when such large tree with such thick trunk can be found among the representatives of Lobatae section. Perhaps, it is this tree that Szovits collected his herbarium from more then a century ago. In any case, the samples collected from this tree in the vicinity of the peak of Kirs mountain should be considered as the topotypes of S. armeniaca.

Then and there, in the oak-hornbeam forest another species, *S. aucuparia* L., with pinnate leaves also was collected (photo 1). Supposedly that was one of the parents of hybridogenous species *S. armeniaca*. But the second parent, which presumably should be with simple leaves, hasn't been found.

In connection with the study of flora of Nagorno-Karabakh, K. V. Balayan has thoroughly studied the contents of the oak-hornbeam forest in locus classicus of S. armeniaca and its vicinity on Lysogorsk pass. This species was collected in the same place by Lomakin (LE!, TBI!, TGM!), T. Geideman (BAK!, LE!, MW!), Chadarin (BAK!, LE!, MW!). In addition to S. armeniaca (photo 3), Balayan also discovered a simpleleaf samples of S. graeca (Spach) Lodd. ex Schauer (photo 2) In addition to these two species and basic forest species (Quercus macranthera Fisch. & C. A. Mey. and Carpinus betulus L.), Balayan noted the following accompanying species: Acer platanoides L., Pinus kochiana Klotzsch, Pyrus caucasica Fed., Malus orientalis Uglizk., Crataegus orientalis Pall., Salix caprea L., Viburnum lantana L., Rubus buschii (Rosan.) Grossh., Rosa canina L. etc, which were founded between the heights of 1800 meters and 2300 meters and on rocky slopes of the top borders of the forest.

It is known about two finds of *S. subfusca* Ledeb. in the vicinity of Lysogorsk: 21.8.1931. T. Geideman (LE!) and in the same place, in the vicinity of Isak-Bilakh, 10.6.1936. N. Gurvich (BAK!, ERE 14556!, LE!). Usually this species has pink anthers. Interestingly, one of *S. graeca* species, which was collected by Balayan in the same place, had pink anthers, and this "S. graeca" indeed occured *S. subfusca* species (photo 4).

Sorbus armeniaca is included in Lobatae Gabrielian section. When this section was established (Gabrielian,

¹ I. O. Szovits, was a pharmacist from Odessa; in 1828-1830 he collected significant amount of plants in Armenia, Karabakh, in various areas of Georgia, on the shores of the Black Sea to the south of river Rion and also in South-West of the Persian Province of Azerbaijan. Fisher and Meyer described many new species on the basis of these wonderful collections made by Szovits.

1978), all species which had more or less lobate leaves, i.e. hybridogenous ones, mostly stabilized hybrids, were included into it. Diploid *S. aucuparia*, is very polymorphic and the only species with pinnate leaves in the Caucasus and one of diploid species with simple leaves which is characteristic to the Caucasus must have been the parents of the hybrids of this section. This assumption was confirmed during a joint caryological study (Gabrielian, 1978; Jankun, Gabrielian, 1979). All Armenian and Caucasian species with lobate leaves proved to be tetraploid (2n=68), and only *S. tamamschjanae* Gabrielian was a triploid. (2n = 51).

These caryological studies were initiated by a number of works by Hedlund (1901, 1907, 1948). On the basis of morphological, palynological and genetical studies of *Sorbus* species, he came to a conclusion that several primary, i.e. diploid species with distinct features and fertile pollen grains later, in the process of hybridization, bred many species with sterile pollen grains. Hedlund believes that in Europe the primary species are *S. aucuparia*, *S. aria* (L.) Crantz, *S. torminalis* (L.) Crantz, *S. chamaemespilus* (L.) Crantz. In his opinion, the rest are derivates from this four species.

Cytoembryological studies which Liljefors conducted for many years (1934, 1953, 1955) confirmed the assumptions made by Hedlund regarding the origin and development of this species in Scandinavia. All primary species proved to be diploids and the rest – triploids and tetraploids.

The optimal level of polyploidy in *Maloideae* subfamily is tetraploid (2n=68). Liljefors established a clear correlation between *S. aucuparia's* and *S. aria's* macromorphology and embryology. Liljefors expanded Hedlund's experiments in castration, isolation, and pollination of flowers and came to a conclusion that a mature (fully developed) seed can't appear without pollination and that pollination is necessary for seed formation of agamospermous *Sorbus* species. Though these species' pollination doesn't cause double fertilization, it induces ovule division – these species are pseudogamous.

Gabrielian conducted a similar experiment on Armenian species of the genus (1978). The experiments took three years, which were rather complicated and included castration, isolation and pollination of Armenian Sorbus species. They demonstrated that the fruits of some species (*S. hajastana* Gabrielian, *S. persica* Hedl., *S. tamamschjanae*, *S. takhtajanii* Gabrielian, *S. kuznetzovii* Zinserl.) were kerned but normal seed were hardly formed. All these species proved to be tetraploids, with an exception of *S. tamamschjanae*, which is triploid.

This leads to a conclusion that only *S. aucuparia*, which has pinnate leaves and *S. graeca*², *S. subfusca* and *S. velutina* (Albov) Schneid. with simple leaves can be considered primary or diploids in the Caucasus, which means that they are the parents of the rest of Caucasian and Armenian species, in particular, of *S. armeniaca*. It is interesting that the aforementioned simple-leaved diploid species are also characterized by polyploidy. In addition to 2n=34, this group also includes tetraploid species.

Not all hybrid species have sterile pollen grains and are unfruitful (Gabrielian, 1975, 1978). For instance, *S. roopiana* has a relatively low percentage of pollen grains sterility (30-35 %) and this species bears fruit wonderfully, whereas the percentage of pollen grains sterility of *S. tamamschjanae* equals 75%, and this species doesn't bear fruit well.

When one studies hybrids or stabilized hybrids, such as *S. roopiana*, *S. armeniaca*, *S. caucasica*, it is important to pay attention to the fact that they have two kinds of characters: the ones that were inherited from the parental species

and completely new characters which were not typical to the parents. Only in rare cases it is possible to encounter a hybridogenous species which bears the whole complex of parental morphological, anatomical and palynological characters. An interesting example of such a species is S. turkestanica (Franch.) Hedl., which is characterized by a rather high percentage of pollen grains sterility, almost 98%. Nevertheless it is widely spread from North-East Afghanistan and Turkmenistan, through Uzbekistan, Kazakhstan, and Kirgizia it reaches Tajikistan, where it is particularly widely met. Zinserling (1939) and Gabrielian (1978) believe that this species' parents are S. tianschanica Rupr. and S. persica. The fact that this hybrid possesses specific anatomical and carpological characters (Gabrielian, 1958 a,b,c, 1978) confirms the fact that the choice of parental pair was correct. S. turkestanica has inherited features of anatomical structures of wood, nodes, petioles, fruits, seed-coats, in different combinations. Very primitive parental features: pentamerous apocarpic gynoecia, striate ectexine, characteristic only to S. tianschanica with pinnate leaves, were also inherited by this species. The following are completely new features which were not characteristic to the parents: rather thickened walls of mezocarp cells content tannin, as well as a different shape of stone cells of endocarp.

The following hybridogenous species are included into *Lobatae* Gabrielian section.

S. armeniaca Hedl. **Lectotypus** (Gabrielian 1978: 130): "Karabach orient. in extremo margine sylvarum versus cacumen m. Kirs. 18.9.1829. Szovits" (LE! Isolectotypus, BM!). 2n=68.

In comparison to other hybridogenous species in the Caucasus *S. armeniaca* is rather rare. It can be encountered in the middle forest belt and on the top forest boundary, on rocky lit slopes and on heights of 1500-2300 meters above the sea level.

It is distributed on northern and southern slopes of the eastern part of the Greater Caucasian Range, in East Transcaucasus, in Nagorno-Karabakh (Lysogorsk, Kirs Mountain), in North-West Iran (Kara Dag, Kalibar (Ahar) ranges 1900 m, 26.6.1941. Parsa 32 (K!).

As has been noted, in Armenia it was found only ones, in the vicinity of Dilijan, in the forest, on 12.6.1937 r. by N. Gurvich (BAK! ERE 98460! LE!). Interestingly, that she collected also *S. graeca* with unripe fruits (BAK!) in the same place, on the same day, the same year. The same story occurred with Alekseenko – he collected *S. armeniaca* in Azerbaijan, in the vicinity of Kuba, in the ravine above village Jemi, on the height of 1590 m., on 13.7.1899. He also collected *S. graeca* (LE!) on the same day, near a spring on the rocks above Jemi.

S. armeniaca is distinctly different from close species of *Lobatae* section. It is distinguished from *S. caucasica* in the shape of the leaf and its smaller size, the shape of the leaf base and leaf top, lobes are less deep and on both sides are denticulate; ripe fruits with persistent calyx (the lobes of *S. caucasica* reach two thirds of leaf blade semi-width; inner side of deep lobes not denticulate, ripe fruits have a deciduous calyx).

Pollen grains of *S. armeniaca*, differ from all these species by oblate shape of a pollen grains, also the ends of colpi of 4-colp-pore-orate pollen grains anastomosed at the poles and forming the parasyncolporate apertures, even though they were included into *Takhtajania*³ palynological subtype along with *S. takhtajanii*, *S. persica* and *S. caucasica*.

² The number 2n=34 characteristic to *S. graeca* var. *orbiculata* Gabrielian, which Gabrielian fixed in Vanadzor (North Armenia) and which were established by A. Jankun was not included into a two-volume edition under the editorship of A. Takhtajan (1993) "Chromosome numbers in the flowering plants in the USSR".

³ The pollen of Sorbus genus belongs to Sorbus type. Nevertheless the difference between separate species or groups of them appeared to be so clear that it was necessary to single out a number of morphological subtypes of pollen grains.



Photo 1. Sorbus aucuparia L. Karabagh, Kirs mt. Photo K. Balayan.



Photo 3. Sorbus armeniaca Hedl. Karabagh, Kirs mt. Photo K. Balayan.

Studies of wood anatomy⁴ of *S. armeniaca* from locus classicus (mountain Kirs), reveal that on the transverse section it has ring-porous structure, boundaries of annual layers are distinctly seen; on radial sections there are numerous heavily heterogenous rays (features inherited from *S.graeca*).

Thus, it can be assumed with certainty that *S. aucuparia* and *S. graeca* (2n=34) were this species' parents.

S. caucasica Zinserl. **Holotypus**: "Caucasus. Mons Beschtau 4000', 23.5.1887, leg. Akinfiev" (LE!). 2n=68.

It grows in the middle and in the upper part of the forest belt, on rocks, on limestone, on the height of 900-2200 above the sea level.

It is mainly distributed in the North Caucasus (on the Greater Caucasian Range), Western, Central, and Eastern Transcaucasia (Dagestan, Georgia, Azerbaijan), and rarely in Lazistan and Southern Transcaucasia (Armenia). On this vast territory *S. caucasica* mostly grows side to side with *S. aucuparia* and *S. subfusca*.

S. caucasica is morphologically isolated and all its features are constant. Special searches of other species on Beschtau mountain (*S. caucasica* is described from there) and other places around Kislovodsk have revealed *S. aucuparia* alone.



Photo 2. Sorbus graeca (Spach) Lodd. ex Schauer L. Karabagh, Kirs mt. Photo K. Balayan.



Photo 4. Sorbus subfusca Ledeb. Lysogorsk pass. Photo K. Balayan.

Nevertheless, if we take into consideration its wide natural habitat, it is obvious that interbreeding between *S. aucuparia* and *S. subfusca* could occur in a different place.

According to anatomical structure of *S. caucasica* fruits mostly resemble the structure of *S. subfusca* fruits. However the endocarp of this species consists only of sclerenchyma cells while at *S. caucasica* between small parenchyma cells scattered stony cells with thin walls. Both of these species have ring-porous wood structure with gradual transition from younger wood into older one. On radial section one can see weak heterogenous rays.

Most probably S. caucasica's parents are S. aucuparia and S. subfusca.(2n=34).

S. tamamschjanae Gabrielian. **Holotypus**: "Armenia, in vicinitate Khosrov, supra ruinas pagi Manghjuk, ad ripam sinistram fl. Qjusus, in sylva, 1800 m, 17.6.1968. Gabrielian (ERE!Isolectotypi E! K! LE!)(2n=51).

Armenian Highlands endemic is met solitary in mixed forests or in bush thickets, usually on north slopes on the height of 1500–2600 mm above the sea level. It is a rather rare species. It is described from Khosrov State Reserve. Mostly can be encountered in the vicinity of Garni, Mankuk river gorge, in Vajkh (Eghegis, Jermuk) and one collection from Sisian area, on the shore of Vorotan river in Zangezur. It was also collected in Turkish Armenua from Karakurt and Kars in 1886 by Massalski. (LE!).

⁴ *Maloideae* wood anatomy is very unvaried which can't be said about *Sorbus* genus. Its species differ clearly from each other in such essential features as diffuse-porous wood, homogenous rays, and others (characteristics for section *Aucuparia*) or ring-porous wood, heterogenous rays (at representatives sections *Aria*) Gabrielian (1954).

Previously this species was identifies as *S. scandica*, *S. armeniaca*, *S. roopiana*. In contrast to them it has yellow or bright-orange (and not red) fruits and other morphological characters as well as nodal, petiole and seed-coat anatomy.

What is also interesting about *S. tamamschjanae* is that it inherited from *S. aucuparia* diffuse-porous wood with boundaries of annual layers which are hardly seen and almost homogenous rays. Palynologically this species is very peculiar and separated into subtype *Tamamschjanae*. Only this species has pollen grains in compact tetrads; the solitary pollen grain 3-colpate, almost spheroidal, colpi wide, long, with obtuse end (Gabrielian, 1954, 1973b, 1975b).

Among all Armenian species also only *S. persica*, *S. luristanica* and *S. takhtajanii* have yellow or bright orange fruits. The latter has very peculiar fruits which do not resemble any of other species.

S. tamamschjanae is encountered with such widely spread species as *S. persica* and *S. kuznetzovii* which even grow in its *locus classicus*.

Most probably, in addition to *S. aucuparia* its second parent is *S. persica*.

S. roopiana Bordz. **Holotypus**: "Kars, distr. Kaghyzman, ad rivulum in decliviis montis Kesza-czi, 31.7.1910. T. Roop" (LE!). 2n=68.

It is encountered in oak forests and juniper sparse forests, on forest edge and on the upper forest boundaries, on rocky slopes, on the height of 1200–2400 meters above the sea level.

It is distributed in East Great Caucasus (in Kuba region), in Eastern (Nukha, Geokchai, Shemakha) and Southern Transcaucasia (Sevan, Zanzegur, Meghri, Southern-Karabakh), Nakhichevan, Talysh; Turkish Armenia.

One can often meet *S. aucuparia* and *S. graeca* on the territory of the natural habitat. Undoubtedly, these two species were the parents of *S. roopiana*, Anatomical structure of *S. roopiana* fruits confirms this assumption. There is no starch content cells in *S. aucuparia* fruits, but there are tannin content cells and the pulp turns black under the influence of FeCl₃ on the cross section of *S. aucuparia* fruits, whereas *S. graeca* fruits have a group of tannin content cells, which scattered in mass of minor uncolored starch containing cells. *S. roopiana* fruits have both cells but the amount of starch content cells is so low, that they either do not create a pattern which characterizes *Aria* section, or it is hardly outlined and its pulp blackens almost like the one of *S. aucuparia*. The cells of *S. roopiana* endocarp resemble those of *S. graeca*.

Pollen grains of *S. roopiana* are also peculiar and separated into *Roopiana* subtype as 3-colp-porate with short, wide colpi; pores elongated in the equatorial plane and extended beyond the colpi.

The amount of sterile grains doesn't exceed 35 %. Only this species represents this subtype.

S. persica Hedl. **Lectotypus** (Gabrielian 1978: 135): "Persia borealis in m. Elburs, pr. pagum Passgala, 21.V.1843, Kotschy 187" (LE! Isolectotypi BM!G!LE!W!). 2n=68.

It grows on open slopes or in bush thickets, oak forests or in juniper sparse forests, as a rule solitary, in Central Asia in clearings, and sometimes it forms independent stands, on the height of 700–2500 m above the sea level.

It is widely distributed in Armenia, in Aragatz, Erevan, Sevan (on the North-Eastern (Areguny) shore of Lake Sevan), in Darelegis, Zangezur, Meghri floristic regions, as well as Nakhichevan, Southern Karabakh, in Southern and Eastern Anatolia, Nothern and Western Iran, Khorosan, in Central Asia on Kopetdag, in Pamiro-Alay, Tian Shan.

It is a very polymorphic species. Samples from Central Asia are distinguished by small leaves which are less white pubescent beneath.

Transverse sections of the basal and middle parts of the petioles of this species and many of other anatomical and morphological characters clearly distinguished from other Caucasian representatives of *Lobatae* section. Another features which makes it different from other species of this section could be seen on the transverse section of fruits with small round groups of tannin content cells, equal in size to starch content cells in mesocarp and an absolutely peculiar endocarp, which consists of a numerous large, elongated, thick-walled stone cells.

S. *persica* is also strongly distinguished by the wood anatomy, which has a tendency to ring-porous wood and 1-2-3 rows of weakly heterogenous rays on the transverse section.

Due to the uniqueness of anatomical and morphological features it is rather hard to define the possible parents of this species.

S. takhtajanii Gabrielian. **Holotypus**: «Армянская ССР, Даралагез, окрестности Джермука, левый берег р. Арпа, в лесу, 2200 м над ур. м. 15.IX.1952, Э. Габриэлян» (ERE! Isotypi E!K!LE!). 2n=68.

As a rule, it grows in groups or solitary in oak forests on the height of 1200–2200 meters above the sea level.

It can be encountered on Mount Arailer, in Darelegis, Zangezur, Nakhichevan, as well as in Iran.

Rhomboid-elliptical short pointed leaves, dark green above and greenish-white beneath, the shape of inflorescence and others, distinguish it from more or less close to it *S. persica;* other distinctive features are size, shape, color of fruits, in particular of very specific lenticels, their size and distribution on the fruit surface; anatomy of petioles and seed-coat, as well as the wood structure(it is ring-porous with a gradual transition from younger wood to older one and strongly heterogenous rays.

Most likely, its parental pair is *S. aucuparia* and *S. persica*.

S. luristanica (Bornm.) Schönb.-Tem. **Holotypus**: Luristan, "Schuturunkuh" (m. Oshtoran Kuh), 7.1904, Strauss" (JE, isotypi E!G!LE!). 2n=68.

It grows in oak forests, on forest edges, on rocky slopes, forest clearings, on the height of 1600-2400 meters above the sea level.

It is distributed in Armenia on Mount Aragats, on the North-Eastern (Areguny) shore of Lake Sevan, in Khosrov State Reserve, in Darelegis, Meghri floristic regions, in Nakhichevan, Anatolia: Hakkari; in Iran: Kurdistan, Bakhtiari; Sultanabad; Middle Asia (Kopetdag).

As a rule, taxonomically this species is approached to *S*. *persica*. However, palynologically, it clearly differs from it and is separated into a different subtype *Luristanica*. Pollen grains 3(4-5)-colp-poroidate, spheroidal, the outline in polar view is 3-4-5- rounded-angular. Colpi long, narrow, poroid area slightly elongated in the equatorial plane and slightly extended beyond the colpi.

The number of sterile grains reaches 70-80 %.

Fruits anatomical structure brings *S. luristanica* somewhat closer to *S. persica*; it is distinguished from it by narrow endocarp and larger stone cells which do not form such dense groups.

This species is often encountered with *S. kuznetzovii* and *S. persica*. It is possible that these two species are the parental pair of *S. luristanica*.

S. kuznetzovii Zinserl. **Holotypus**: "Западный Кавказ, Кавказский государственный заповедник и его охранная полоса. Скалы и лужайки на южном склоне г. Закан. 12.VII.1930. А. Лесков." (LE!). 2n=68. As a rule, it grows in oak forests and juniper sparse forests, on open rocky slopes, in bush thickets, on the height of 1200–2400 m above sea level.

It is encountered in the North Caucasus, in Western, South-Western, and Eastern Transcaucasia and is widely distributed in Armenia, on Mounts Aragatz and Arailer, on the North-Eastern (Areguny) shore of Lake Sevan, in Vajkh, in Khosrov State Reserve; in Anatolia.

S. kuznetzovii is often confused with *S. hajastana*, *S. graeca* and other species.

Palynologically this species differs from other *Sorbus* species and is separated into an independent subtype *Kuznetzovii*. Pollen grains 3(4)-colp-poroidate, spheroidal, the outline in polar view is circular. Colpi narrow, very long, almost merge at the poles; the colpi membrane is sculptured. There is some thinning of the membrane in the equatorial zone of the colpi, which serves as the site of pollen tube exit.

Anatomically, the wood of *S. kuznetzovii* is close to *S. graeca*, as it has a ring-porous annual ring with a gradual transition from younger wood into older one and well-defined heterogeneous rays. The fruit transverse section and its structure, location of groups with tannin content cells in the mesocarp and the structure of endocarp also reminds of *S. graeca*.

Unlike *S. graeca*, which hardly has any lenticels, *S. kuznetzovii* fruits are densely covered with small and large lenticels the structure of which reminds of unique lenticels of *S. takhtajanii*. Taking into account that *S. kuznetzovii* is often growing together with *S. graeca*, in particular in Jermuk, wherefrom *S. takhtajanii* was also described, it is logical to assume that this species' parents must have been *S. graeca* and *S. takhtajanii*.

Thus, the majority of the Caucasian hybridogeneous species have set of constant morphological, anatomical, palynological, and other characters, unique for each species.

Despite its hybrid origin, these forms have become so distinct and viable that they have gained an independent natural area, which means that they turned into real species.

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