

On three cultivated subspecies of pea (*Pisum sativum* L.)

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The common pea (*Pisum sativum* L.) is an important crop characterised by high diversity, taxonomic fixation of which may be important for selection as it attracts attention to the taxa recognised, although this recognition can be poorly justified. Two subspecies of the common pea, traditionally recognised in Russian botanical and genetical literature, *Pisum sativum* L. subsp. *transcausicum* Makasheva from Transcaucasia and *Pisum sativum* L. subsp. *asiaticum* Govorov from Anterior and Central Asia and North Africa, are considered, as well as their diagnostic characters and arguments in favour of their subspecific status. *P. sativum* subsp. *transcausicum* is characterised by small seeds, three pairs of small diamond-shaped leaflets, vigorous branching and full reproductive compatibility with *Pisum sativum* L. subsp. *sativum* and has a very limited range in Georgia. As a very local landrace it hardly deserves a subspecific status, however it is reasonable to consider it as a variety, *Pisum sativum* L. subsp. *sativum* var. *transcausicum* (Makasheva) Kosterin comb. nov. The subspecies *P. sativum* subsp. *asiaticum* practically misses diagnostic characters which are limited to small flowers with presence of some flavonoid pigmentation in the corolla. In fact, this subspecies has accumulated very diverse landraces from most of the Old World. Absence of reliable diagnostic characters makes it impossible to recognise this subspecies. Thus, *P. sativum* subsp. *asiaticum* is a later synonym of *P. sativum* subsp. *sativum*, to which all cultivated representatives of *P. sativum* L. should be attributed. A peculiar form traditionally cultivated in Egypt was described as the species *Pisum jomardii* Schrank and subsequently considered also in the ranks of subspecies and variety; it would better be considered as *Pisum sativum* L. subsp. *sativum* var. *jomardii* (Schrank) Govorov.

Key words: *Pisum sativum* L. subsp. *sativum*; *Pisum sativum* L. subsp. *transcausicum* Makasheva; *Pisum sativum* L. subsp. *asiaticum* Govorov; *Pisum jomardii* Schrank; *Pisum sativum* L. subsp. *sativum* var. *transcausicum* (Makasheva) Kosterin comb. nov.; *Pisum sativum* L. subsp. *sativum* var. *jomardii* (Schrank) Govorov; pea; subspecies; varieties; landraces.

О трех культурных подвидах посевного гороха (*Pisum sativum* L.)

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Горох (*Pisum sativum* L.) – важная сельскохозяйственная культура, характеризующаяся большой изменчивостью. Ее таксономическое оформление имеет значение для селекции, поскольку привлекает особое внимание к выделяемым таксонам, хотя их выделение не всегда оправданно. Рассмотрены два традиционно выделяемых в отечественной ботанической и генетической литературе культурных подвида посевного гороха – *Pisum sativum* L. subsp. *transcausicum* Makasheva из Закавказья и *Pisum sativum* L. subsp. *asiaticum* Govorov из Передней и Центральной Азии и Северной Африки, их диагностические признаки и аргументация в пользу их выделения. *P. sativum* subsp. *transcausicum* отличается мелкими семенами, тремя парами мелких ромбовидных листочков, усиленной ветвистостью, полной репродуктивной совместимостью с обычным культурным горохом *Pisum sativum* L. subsp. *sativum* и имеет очень ограниченный ареал в Грузии. Такая узколокальная культурная форма вряд ли заслуживает подвидового статуса, однако ее целесообразно рассматривать в качестве разновидности *Pisum sativum* L. subsp. *sativum* var. *transcausicum* (Makasheva) Kosterin comb. nov. Подвид *P. sativum* subsp. *asiaticum* не имеет надежных диагностических признаков, которые сводятся в основном к мелким цветкам с присутствием некоторой флавоноидной пигментации венчика. По сути к этому подвиду были отнесены самые разнообразные местные традиционные формы посевного гороха Старого Света. Отсутствие надежных диагностических признаков также не позволяет признать данный таксон ни в каком ранге. Таким образом *P. sativum* subsp. *asiaticum* является более поздним объективным синонимом *P. sativum* subsp. *sativum*, к которому следует относить все культурные представители вида посевного гороха (*P. sativum* L.). Своеобразная местная форма, традиционно культивировавшаяся в Египте, была первоначально описана в ранге вида *Pisum jomardii* Schrank и впоследствии рассматривалась также в рангах подвида и разновидности в составе азиатского подвида. Представляется целесообразным рассматривать ее как *Pisum sativum* L. subsp. *sativum* var. *jomardii* (Schrank) Govorov.

Ключевые слова: *Pisum sativum* L. subsp. *sativum*; *Pisum sativum* L. subsp. *transcausicum* Makasheva; *Pisum sativum* L. subsp. *asiaticum* Govorov; *Pisum jomardii* Schrank; *Pisum sativum* L. subsp. *sativum* var. *transcausicum* (Makasheva) Kosterin comb. nov.; *Pisum sativum* L. subsp. *sativum* var. *jomardii* (Schrank) Govorov; горох; подвиды; разновидности; местные культурные формы.

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The common pea (*Pisum sativum* L.) is an important crop with three important applications, as a vegetable, corn and fodder culture (plus a less known application in crop rotation for enrichment of soils with nitrogen). The pea is the first genetical object (Mendel, 1866; Kosterin, 2015) and is characterised by huge accumulated genetic and phenotypical variation (Blixt, 1972). It is not hence surprising that for a long time it has been attracting a thorough attention of various researchers including botanists, resulting in a complicated and discrepant intraspecies taxonomy, the history of which was considered in detail in a comprehensive monograph by R.Kh. Makasheva (1979). This monograph has also presented a taxonomical system of the genus *Pisum* L. in general and the species *P. sativum* in particular, which until recently was universally used in Russia; it was quite close to that by C. Lehmann (1954) which, in turn, until recently was the most used worldwide.

The system of the species *P. sativum* adopted by Makasheva (1979) contains two wild and three cultivated subspecies, wild *P. sativum* subsp. *elatius* (Bieb.) Schmalh. and *P. sativum* subsp. *syriacum* Berger, and cultivated *P. sativum* subsp. *sativum*, *P. sativum* subsp. *asiaticum* Govorov and *P. sativum* subsp. *transcaucasicum* Makasheva. The same three cultivated subspecies are adopted in the taxonomical system by H. Lehmann and S. Blixt (1984), based on genetic factors exhibiting Mendelian segregation. This mini review concerns *P. sativum* subsp. *asiaticum* and *P. sativum* subsp. *transcaucasicum* and argues in favour of considering them to be later synonyms of the autonymic subspecies *P. sativum* L. subsp. *sativum* rather than their recognition at subspecific rank. Besides, ‘Jomard’s pea’ is considered, which was suggested to be another cultivated subspecies of *P. sativum* in one of our earlier papers (Kosterin, Bogdanova, 2008) that we now consider unjustified. It is noteworthy that the system of the genus *Pisum* by N. Maxted and M. Ambrose (2001), most broadly accepted at present, also recognises only one cultivated subspecies of the common pea, *P. sativum* subsp. *sativum*.

For the sake of practical convenience, in this work I proceed considering *Pisum* as a genus, although a recent molecular phylogenetic analysis of the tribe Fabea (Schaefer et al., 2012) suggested to cancel the genus *Pisum* and subsume it, as a section, to the genus *Lathyrus* L. (Coulot, Rabaute, 2016; Kosterin, 2017). Since I do not support a subspecific rank of the taxa considered, treatment of the common pea in the genus *Lathyrus* (under the name *Lathyrus oleraceus* Lamarck) would not demand new combinations.

Transcaucasian Pea (*Pisum sativum* L. subsp. *transcaucasicum* Makasheva)

The subspecies *P. sativum* subsp. *transcaucasicum* Govorov nom. illeg., including nine groups of varieties (‘proles’) was erected by L.I. Govorov (1937, p. 242) in the first edition of the ‘Cultivated Flora of the USSR’, with the following note: “We isolate the endemic forms of Transcaucasia into a new subspecies ssp. *transcaucasicum* and attribute it to the species of cultivated forms, *P. sativum*” (here and on the Russian text is translated into English by the author of this paper). Govorov (1937, p. 283) provided it with the following diagnosis: “Differs drastically from other subspecies by oblong, acute, always whole-edged leaflets. The habitus of the

entire plant is vetch-like. The flowers are moderately large. The alae are usually dark-violet. The carina always is more or less coloured with anthocyanin. The stems do not branch or are scarcely branching at base, moderately high. The pods are narrow, from small to medium-sized, always with a parchment layer. The seeds are small, usually of an angulate shape, pigmented”. (An example of such plant is shown in Figure, b.) He also provided the following geographical range: “Central Transcaucasia, North Caucasus and south-eastern European part of the Union”. Govorov (1937, p. 295) reported seven varieties of this subspecies. No information on the origin of the type is given but the names of most varieties and their groups were formed from toponyms, among which we find Bakuriani, Akhalkalaki, Dzhavakheti, Volga, Saratov, the three former ones referring to the territory of Georgia and the two latter to the present-day Russia.

The descriptions of the subspecies, varieties and their groups were given only in Russian that contradicted the rules of botanical nomenclature and made those names illegal. The situation was corrected by R.Kh. Makasheva (1979) who repeated the descriptions by Govorov in Latin, with some update including comparative diagnoses and information of the types, and some change of the system of varieties: in her treatment the subspecies had five varieties, two of which were split into two, and one into three subvarieties. This made R.Kh. Makasheva the actual author of these taxa as validly published. In particular she (Makasheva, 1979, p. 71) for the first time provided the comparative diagnosis of the subspecies: “Differs from a close subspecies *asiaticum* Govorov by 3–4-paired narrow leaflets (2–2.5 times as long as wide)”. Information about the types of varieties and subvarieties (that for the nominotypical var. *transcaucasicum* is missing) gives us an idea of the provenance of the Transcaucasian pea materials at Makasheva’s disposal. It is striking that for as many as eight recognised taxa there are only two geographical localities – “near Bakuriani and Mitrab village” (*locus classicus* of three varieties and four more subvarieties) and “Saratov Province, in a vetch field”! That is, extensive taxonomical formalisation was undertaken for polymorphism observed just in two local populations!

P.M. Zhukovskiy (1964, p. 333) added the subspecies “*P. sativum* subsp. *transcaucasicum* Govorov” to the second edition of his monograph ‘Cultivated plants and their relatives’ with the following characteristics: “Small-seeded, anthocyanin-coloured forms in meadow herbage of the subalpine zone of Transcaucasia”. Here one can recognise indication to growing in the wild, that by no means corresponds to both the earlier opinion of the taxon’s author, L.I. Govorov (1937, p. 242), who attributed it to “the species of cultivated forms”, and to the later opinion by R.Kh. Makasheva (1979, p. 71): “The forms cultivated for fodder in Central Transcaucasia and North Caucasus, field weedy forms in vetch and lentil fields (before [19]30s years) in the south-eastern European part of the USSR”. More recent and/or detailed information on cultivation or spontaneous growing of these forms in the Caucasus and Transcaucasia is missing, but their non-dehiscing pods imply them to be cultivated.

Another phenotypical peculiarity of the Transcaucasian pea is a rare allelic electromorph 2 of the subtype 6 of histone H1 (Berdinkov et al., 1989, 1993; Kosterin et al., 1994) resulting



Pisum sativum subsp. *sativum* var. *transcausicum* (Govorov) Kosterin, com. nov., accession VIR4871 (Bakurian): a – seeds; b – branches of the upper part of the plant.

from a substitution of proline to hystidine in the C-terminal domain of the protein (Kosterin et al., 2012). It is noteworthy that the same electromorph is found in accession VIR1851 from Georgia (Tbilisi Botanical Garden), originally identified in the N.I. Vavilov All-Union Institute of Plant Breeding, St-Petersburg (VIR) as wild subspecies *P. sativum* subsp. *elatius* (Bieb.) Shmalh. but actually missing the key characters of a wild pea, dehiscent pods and gritty seed testa, and with ‘normal’, by no means vetch-like habitus (Berdnikov et al., 1993).

Such a characteristic of the Transcaucasian pea as three pairs of whole-margined leaflets is found also in the accession WG26109 of wild pea *P. sativum* subsp. *elatius*, also from Georgia (Kvemo-Kartli, Trialeti Mountain Range, 7 km N of Partsklisi) belonging to the evolutionary lineage A, as different from cultivated subspecies which belongs to the lineage B (Zaytseva et al., 2017). However in this accession, the leaflets have another, oblong ovoid shape and they are soft and somewhat curving inside, while in the Transcaucasian pea they are elongate-diamond-shaped, subacute, flat (Figure, b) and very stiff. Perhaps Zhukovskiy (1964, p. 333) implied plants resembling accession WG26109 as “growing in the subalpine zone of Transcaucasia”. It is noteworthy that on a phylogenetic tree reconstructed by Ellis et al. (1998), the four accessions of *P. sativum* subsp. *transcausicum* formed a distinct cluster branched off near the cluster of ‘*P. elatius*’. One could suppose formation of the Transcaucasian pea through a past introgression of wild (resembling WG26109) and cultivated peas in Georgia.

However, our experiments on crossing a typical accession of Transcaucasian pea VIR4871 with WG26109 and testerline WL1238 representing *P. sativum* subsp. *sativum*, carried out in the greenhouse of the Institute of Cytology & Genetics SB RAS, Novosibirsk, in the 2016 autumn vegetation and the 2017 spring vegetation, did not support this assumption. Reciprocal crosses VIR4871 × WL1238 and WL1238 × VIR4871 were carried out; two hybrid plants of the first generation of the former cross and five from the latter cross were grown out and fertility of their pollen was analysed according to Singh (2003). F₁ hybrids of both reciprocal crosses had fully fertile pollen: 98.3 ± 2.6 % filled pollen grains (the number of flowers analysed, *n* = 9) in hybrids WL1238 × VIR4871 and 96.2 ± 10.3 % (*n* = 10) in hybrids VIR4871 × WL1238, that evidenced for the absence of reproductive barriers between the Transcaucasian pea and a typical representative of *P. sativum* subsp. *sativum*, via either reciprocal translocation(s) or a nuclear-cytoplasmatic conflict. We failed to obtain hybrid plants in the cross VIR4871 × WG26109, while in the reciprocal cross WG26109 × VIR4871, pollen fertility was analysed in eleven F₁ obtained and appeared to be 51.4 ± 9.5 % (*n* = 31). Similar values of pollen fertility was found also in eleven F₁ hybrids in the cross WG26109 × WL1238 (54.6 ± 15.3 %, *n* = 30) and in ten obtained reciprocal hybrids WL1238 × WG26109 (38.3 ± 12.0 %, *n* = 26).

Hence a representative of the Transcaucasian pea, VIR4871, showed complete reproductive compatibility with a representative of *P. sativum* subsp. *sativum*, WL1238, but both exhibited only partial compatibility with a Georgian wild pea (*P. sativum* subsp. *elatius* s. l.) accession WG26109 with three leaflet pairs, the F₁ hybrids with which had semifertile pollen, that is the two former peas are related to each other but both unrelated to the third one.

Earlier we recognised the subspecies *P. sativum* subsp. *transcausicum* (Berdnikov et al., 1989, 1993; Kosterin, Bogdanova, 2008), later evasively called it ‘a subspecies of doubtful validity’ (Zaytseva et al., 2012, 2015).

The main problem of the taxonomical status of the Transcaucasian pea is whether it is reasonable to ascribe the subspecific rank to some local cultivated form (landrace) which is endemic for a very small region and has distinct diagnostic characters. If this were a wild plant, the answer would surely be positive, and perhaps this form would be considered even at a species rank. However, we deal with a local traditionally cultivated form, the range of which is inevitably to shrink and the limits to dissolve because of supplanting traditional agriculture by its more agrotechnically advanced commercial version oriented to widespread modern cultivars, and also because of availability of diverse seed stock. It seems reasonable, following the system by Maxted and Ambrose (2001) to consider the subspecies *P. sativum* L. subsp. *transcausicum* Makasheva as a later synonym of *P. sativum* L. subsp. *sativum*. At the same time this peculiar taxon deserves recognition as a variety within it. According to the Article 49 of the International Code of Nomenclature of algae, fungi and plants (2012), change of a rank of a taxon creates a new combination:

***Pisum sativum* L. subspecies *sativum* variatio *transcausicum* (Makasheva) Kosterin combinatio nova**
Basionymum: *Pisum sativum* subsp. *transcausicum* Makasheva (Flora of Cultivated Plants. 4(1): 71, 1979).

Asian Pea (*Pisum sativum* L. subsp. *asiaticum* Govorov)

Recognition of the Asian pea as a taxonomical unit fully faces the aforementioned problem of the current rapid ‘dis-

solving' and vanishing of any isolated set of landraces, which are products of long-term traditional agriculture. However, an additional and more serious obstacle for recognition of this subspecies is fuzziness and uncertainty of its diagnostic characters. This is not surprising for a subspecies where primitive cultivated landraces were united, according to L.I. Govorov (1937), the subspecies author, from so vast range as "Anterior, South-Western and Central Asia and mountainous regions of North Africa". Diversity of forms united into this subspecies is reflected in the number of subordinate taxa isolated in it: 19 varieties in the work by L.I. Govorov (1928) where *P. sativum* subsp. *asiaticum* was first described, 34 varieties in his later work (Govorov, 1937) and 39 varieties and subvarieties (monotypical varieties and autonymical subvarieties in polytypic varieties were counted) in R.Kh. Makasheva (1979).

In the subspecies protologue, L.I. Govorov (1928, p. 499) reported the following diagnostic characters: "(1) the presence of a peculiar dirty-pink or cream tint on the flower standard, brought about by the presence, along with the anthocyanin, of a special pigment from the flavonoid group, (2) the predominance of character combinations rarely met together in other subspecies and, lastly, (3) a specific range of distribution, namely South-Western, Central and East Asia, except for the boreal part of the latter". Note that the points (2) and (3) are senseless: the character combinations are not explained, while any biological entity always has some range of occurrence; and in this case it is too broad for a subspecies, approaching that of the entire species. Then a diagnosis of 15 lines follows and a detailed, one and half page long, description of variation of the new subspecies (descriptions of all taxa repeated in Latin). It can be easily seen, that in fact the only diagnostic character is provided – the coloration of the standard.

The subspecies diagnosis in a later work by L.I. Govorov (1937, p. 282) is also very indefinite: "The flowers are small (0.9–1.5 cm), usually with a flavonoid pigment. The standard is narrow, the alae are oblong to ovoid, narrow. The calyx teeth are shorter, or as long as the tube. The leaflets are small to medium-sized, ovoid, serrate or dentate. The stipulae are dentate all over their margins, rarely to 2/3–1/3. The stems are branching at base, medium in height, rarely tall. The peduncles are usually shorter than the stipulae, sometimes exceeding them, with 1, rarely 2 flowers. The pods are small, rarely medium-large, always with a parchment layer. The seeds are small, rarely medium-large, usually pigmented". Govorov did not provide a separate key to the subspecies but this was done by R.Kh. Makasheva (1979); in her key, the Asian subspecies is grouped with the subspecies *transcaucasicum* and *abyssinicum* and is opposed to the subspecies *sativum*, *elatius* and *syriacum* by the following set of characters: stem narrow versus medium-thick or thick, branching at base versus non-branching or weakly branching, branch orientation almost horizontal versus departing at acute (sometimes almost right) angle, and the number of sympodial bundles "in the plant upper part" – 4 versus 6–11 (but sometimes also 4). All these are very unreliable quantitative characters.

From the above presented information it is evident that no objective reasons for isolation of the Asian subspecies ever existed. The reasons why L.I. Govorov isolated it concerned solely his theoretical notion on pea evolution, including under

cultivation, which he formulated as follows: "It is difficult to suppose that any single species could include in its genotypical basis all the subsequently appeared diversity of cultivated forms, from the West European hygrophilous forms to the Asian drought-prove ones, from thermophilous to withstanding temperatures of –10 °C (or sometimes lower), from day-neutral to demanding long illumination..." (Govorov, 1937, p. 240). Nowadays we know that the original genetic diversity of wild forms of the species *P. sativum* is much more than Govorov supposed (but he would hardly agree to consider them within one species). Govorov supposed that "Mutation and repeated crosses of the species *P. fulvum* and *P. elatius* with their derivative species – *P. humile* and *P. abyssinicum*, or the initial cross of only the two former species, resulted in segregation and mutation of a hybrid complex, picked up in different ancient cradles of human culture and giving rise to appearance of new diversity of cultivated forms..." (Govorov, 1937, p. 240). So, Govorov, without sufficient objective reasons, supposed, first, multiple interspecies hybridisation to take place in the natural history of the cultivated pea, and, second, multiple independent domestication.

L.I. Govorov formulated the arguments in favour of isolation of the Asian subspecies as follows: "In South-East Asia, in one of the primary cradles... of formation of a number of crops, a diversity was concentrated of the pea cultivated forms described by us... and attributed to ssp. *asiaticum* of the species *P. sativum* s. a. A more detailed study of forms of this subspecies with the complex use of the methods of physiology, anatomy and genetics, managed to reveal their hybrid origin from the cross of the species *P. elatius* and *P. fulvum*" (Govorov, 1937, p. 240). It should be noted that the results mentioned in the last phrase have never been published, while the very inference of participation of the gene pool of *P. fulvum* in the origin of forms attributed to subsp. *asiaticum* was not supported by modern studies.

L.I. Govorov (1937, p. 242) supposed that the subspecies including the Mediterranean and European forms, which he called *P. sativum* subsp. *commune* (*P. sativum* subsp. *sativum* in the modern sense) originated "while departing from the two... ancient centres of cultivated pea, the Asian and Transcaucasian, westwards to the Mediterranean [Средиземье]" by means of gradual missing the complex of "such dominant pea characters as small flower size, its flavonic coloration, brown marbled pattern of seeds, often combined with violet specks and a black hilum, strong serration of leaflet margins". Thus Govorov actually combined all, without exception, 'primitive' cultivated pea forms into the subspecies *asiaticum*, and the 'advanced' forms, in fact having undergone systematic selection, to the subspecies "*commune*". This point of view corresponds to his (Govorov, 1928) erroneous supposition that the pea culture originated in Afghanistan, in view of revealing the greatest diversity of cultivated peas in this region. In fact, the pea, one of the founder crops, was domesticated in 'Fertile Crescent' (Zohary, Hopf, 2000; Weiss, Zohary, 2011), that is in the Mediterranean in the sense of Govorov. The greater genetic diversity of cultivated peas in Afghanistan as compared to Anterior Asia is partly associated with their persistence under conditions of primitive agriculture in Afghanistan, while the diversity in Anterior Asia could be partly lost during longer and more 'advanced' agriculture, and

partly could arise *de novo* already under cultivation (Kosterin, 2015). Note that the mountainous relief of Afghanistan favours isolation of local populations (including those of crops) and hence genetic diversification.

Enough is said above to refrain from recognition of the subspecies *P. sativum* subsp. *asiaticum*, which has neither reliable diagnostic characters nor a distinct geographical range and was isolated solely as a widest set of ‘primitive’ (that is not undergone directional selection) cultivated forms, up to its authors’ notions what ‘primitive’ is. So, *P. sativum* L. subsp. *asiaticum* Govorov should be considered a later synonym of *P. sativum* L. subsp. *sativum*,

***Pisum sativum* L. subsp. *sativum* = *Pisum sativum* L. subsp. *asiaticum* Govorov,**

while a diverse set of accessions attributed to it by L.I. Govorov (1928, 1937) and R.Kh. Makasheva (1979) hardly deserves a taxonomical fixation at any rank.

Jomard’s Pea (*Pisum jomardii* Schrank)

The exact translation of the name *Pisum jomardii* into English would be ‘Jomardius’ Pea’, since the Latin singular, genitive case ending *-ii* corresponds to the ending *-ius* in the nominative case, that is the name was derived from a previously latinised surname, *Jomardius*. For simplicity we, however, will speak on Jomard’s Pea.

Under the name *P. jomardii* local cultivated forms from Egypt were described (Schrank, 1818) differing by a rather characteristic complex of external characters: small flowers with a narrow, apically truncated, dirty-violet (pale-greenish pink at withering) standard and narrow dirty-purple (dirty-pink at withering) alae, whole-margined leaflets, an anthocyanin semiring at the stipulae (Makasheva, 1979).

Of this taxon, we have at our disposal accessions VIR3424, VIR3429 (Egypt) and VIR3439 (Egypt, Asuan) received from VIR, where R.Kh. Makasheva worked. The plants grown up in the greenhouse of the Institute of Cytology & Genetics SB RAS, Novosibirsk, had unbranched stems, narrow, pointed leaflets and stipulae, one pair of leaflets in the plant lower part, two pairs since node 7 to 12, singular anthocyanin ring at the stipula base (phenotype A, D^{co}), clear-cut, rather numerous aerial cameras on blade organs (phenotype Fl), flowering since node 20, totally 29–32 nodes in the stem, the first peduncle 2.5 cm in length, further shortening, small pale-pinkish flowers with somewhat elongate petals (especially the alae), the standard with rather conspicuous violet veins, pods without a spongy inner layer and outer neoplastic pustules (phenotype np), non-dehiscing (phenotype dpo, the key character of a cultivated pea), small seeds with smooth (phenotype gty) testa of an evenly olivaceous colour without pattern (phenotype m, u, fs). I also incline to attribute to the taxon considered the accession VIR3171, originating from “Madrid Botanical Garden” (the actual origin unclear), with the same characters except for well expressed lateral branches. The evenly olivaceous seeds are the most conspicuous external character of this taxon (unfortunately, the seeds are not mentioned in the original description by Schrank (1818)).

Later authors recognised the taxon in question retaining its name but at lower ranks: variety (Govorov, 1937; Makasheva, 1979) or subspecies (Alefeld, 1866; Hedrick et al., 1928; Kosterin, Bogdanova, 2008). Govorov (1937, p. 283–284) attrib-

uted it to his Asiatic subspecies as “*P. sativum* subsp. *asiaticum* var. *Jomardi* (Schrank pr. sp.) Gov.” (note an erroneous spelling with single ‘i’), while Makasheva (1979) – to the Persian group of varieties of the same subspecies, as *P. sativum* subsp. *asiaticum* convar *persicum* Govorov var. *jomardii* (Schrank) Alefeld. However H. Lamprecht (1956) claimed synonymy of *P. jomardii* with ‘*P. arvense*’ basing on fertility of reciprocal hybrids suggesting identical karyotypes and absence of deviations in segregation of markers. Taking into account that the latter ‘species’ is a synonym of *P. sativum* (Makasheva, 1979; Maxted, Ambrose, 2001), this implies synonymy of *P. jomardii* and *P. sativum*.

Maybe the Jomard’s pea would not worth mentioning here if ‘the problem of Jomard’s pea’ was not created earlier by ourselves, by assuming it at the subspecific rank again (Kosterin, Bogdanova, 2008), as “*Pisum sativum* L. subsp. *jomardii* (Schrank) Kosterin stat. n.” That (erroneous) authorship of the combination occurred because of our fallacy that this name had not earlier been used at the subspecific rank, while it was used so before, as ‘*Pisum sativum jomardii*’, by Alefeld (1866) and Hedrick et al. (1928). The reason why we ascribed one of so many and diverse traditional local pea landraces such a high rank consisted in its having a plesiomorphic, electrophoretically more mobile allelic variant of seed albumin SCA^f. This variant occurs in about a half of representatives of the wild subspecies *P. sativum* subsp. *elatius* and in all representatives in two other pea species – wild *P. fulvum* Sibth. et Smith and cultivated *P. abyssinicum* A. Br. (Kosterin, Bogdanova, 2008; Zaytseva et al., 2017), but not found in *P. sativum* subsp. *sativum* (with two exceptions probably resulting from germplasm contamination) (Kosterin, Bogdanova, 2008). With this allele, the Jomard’s pea has combination D of three diagnostic molecular markers (Kosterin et al., 2010). We (Kosterin, Bogdanova, 2008) supposed this taxon to be an independently domesticated in Egypt ‘missing link’ between our conventional evolutionary lineages A and B, both represented in *P. sativum* subsp. *elatius*, in contrast to *P. sativum* subsp. *sativum* entirely belonging to the lineage B (Kosterin, Bogdanova, 2008; Kosterin et al., 2010). Consistently assuming the character ‘wild/cultivated’ as taxonomical and a principle to accept paraphyletic taxa in pea, followed in the system by Maxted and Ambrose (2001), we granted the subspecific rank also to the Jomard’s pea (Kosterin, Bogdanova, 2008).

Later in a hybridological analysis we found out that accession VIR3439, representing the Jomard’s pea, was fully reproductively compatible with the common cultivate pea in both reciprocal directions (Bogdanova et al., 2014) while its plastidic genome had a deletion in the *psbA-trnH* spacer characteristic for *P. sativum* subsp. *sativum* (Zaytseva et al., 2012, 2017). This circumstance practically excludes domestication of the Jomard’s pea in Egypt independently from the Near Eastern (Kurdic) domestication centre, which would imply a broad distribution of this deletion among wild peas over East Mediterranean, which is not the case (Zaytseva et al., 2017).

More plausible looks secondary introgression of the plesiomorphic allele SCA^f into the local cultivated pea because of a spontaneous cross with *P. sativum* subsp. *elatius*, *P. abyssinicum*, or even *P. fulvum* (surely a very rare but still possible event). Hedrick et al. (1928) considered the Jomard’s pea

as close to *P. abyssinicum* – a cultivated plant endemic for Yemen and Ethiopia, which is presently considered a product of hybridisation between *P. sativum* and *P. fulvum* (Vershinin et al., 2003; Jing et al., 2010; Kosterin, 2017). Of external characters, they share small habitus, small pale flowers, absence of any pattern on the seed testa (so in most representatives of *P. abyssinicum*) and of the pod neoplasia. Taking into account the territorial proximity of Ethiopia and Egypt, one can suppose that the history of the Jomard's pea included introgression from *P. abyssinicum*, or even that the Jomard's pea is yet another descendant from the same hybridisation event which gave rise to *P. abyssinicum* itself. In this respect it is interesting that in Sudan (which is situated just between Ethiopia and Egypt), cultivated pea landraces occur (e. g. accession JI281) belonging to the evolutionary lineage B, as normally in *P. sativum* subsp. *sativum*, but with gritty seed testa (phenotype Gty). This character is common in the wild *P. sativum* subsp. *elatius* but extremely rare in the cultivated peas, known only from Sudan and Canary Islands (Michael Ambrose, pers. comm.; Zaytseva et al., 2017). This may be another sign of introgression of 'wild' alleles into cultivated peas in North Africa.

Hence, presently I, following Govorov (1937), Lamprecht (1956) and Makasheva (1979), do not consider the Jomard's pea deserving a subspecific rank. It is reasonable to return to its treatment as a variety (although considering taxonomical ranks below subspecies is not so useful). It was considered for the first time at this rank by L.I. Govorov (1937, p. 283–284, see above). As a cultivated representatives of *P. sativum*, and taking into account that I, following Maxted and Ambrose (2001) do not recognise the subspecies *P. sativum* subsp. *asiaticum*, this variety should be attributed to the subspecies *P. sativum* subsp. *sativum*. According to Article 49 of the International Code of Nomenclature of algae, fungi and plants (2012), the authorship of a variety does not change when it is transferred to another subspecies, so the correct name for this taxon is as follows:

***Pisum sativum* L. subspecies *sativum* variatio *jomardii* (Schrank) Govorov.**

Our previous paper (Zaytseva et al., 2017, p. 1419) mentioned (as "broadly accepted") the combination "*Pisum sativum* subsp. *sativum* var. *jomardii* (Schrank) Alefeld)", again with an erroneous authorship ascribed to Alefeld, who did not consider this taxon in the rank of variety.

Hedrick et al. (1928) indicated a controversy between the original description of *P. jomardii* by Schrank (1818) (flowers white with pinkish alae, one pair of leaflets) and the later description of "*Pisum sativum jomardii*" by Alefeld (1866) mentioning a coloured flower and two leaflet pairs. Having no possibility to evaluate differences between plants described in the second last century other than by concise descriptions, I would nevertheless note that both characters are rather quantitative – pea plants with one pair of leaflets often have leaves with two pairs in the upper part of their stem (so in most wild peas and in the representatives of the Jomard's pea studied by us), and the pinkish alae in the flowers of Schrank's plants evidenced that the anthocyanin synthesis was not suppressed in them (phenotype A), while the pigmentation intensity may vary even in related forms (in our Jomard's pea plants it was quite pale).

Conclusion

As recently as in 2011, Coyne et al. (2011, p. 243) wrote on the genus *Pisum*: "There is general agreement over the number of taxa and less agreement in their rank". Recognition of taxa at the rank of species and subspecies in *P. sativum* (the only species of *Pisum* in which subspecies were described) and is especially discrepant. For this reason, the online resource Integrated Taxonomic Information System (2017) does not recognise subspecies in *P. sativum*, although it does recognise varieties. (It should be noted, however, that (i) such comprehensive systems are compiled by those who are not experts in taxonomy of any particular genus and species and cannot be free of errors, and (ii) solutions as to any botanical names made in such systems are not validly published and cannot be considered as taxonomical novelties). The widely accepted system by Maxted and Ambrose (2001) recognises only two subspecies in *P. sativum* based on an artificial but very practical character: being wild (*P. sativum* subsp. *elatius*) versus cultivated (*P. sativum* subsp. *sativum*). It could be supposed that these authors may have insufficiently taken into account the taxonomical contributions by Russian authors (Govorov, 1937; Makasheva, 1979). However, the above consideration of three presumed cultivated subspecies of pea lead us to their downgrading to varieties or pure synonymisation, and hence to the conclusion coinciding with that by Maxted and Ambrose (2001) that only one cultivated subspecies of the common pea is worth recognition: *P. sativum* subsp. *sativum*. The same conclusion was recently made from the AFLP analysis by Dyachenko et al. (2017) who showed, both in dendrograms and by principle component analysis, a continuous variation of cultivated pea accessions from the collection of Vavilov All-Russian Institute of Plant Genetic Resources (VIR), which earlier served as a basis for the work by Govorov (1937) and Makasheva (1979).

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Conflict of interest

The author declares no conflict of interest.

References

- Alefeld F. Landwirthschaftliche Flora. VIII. Berlin. 1866.
- Berdnikov V.A., Bogdanova V.S., Rozov S.M., Kosterin O.E. Formation of diversity of histone H1 genes in the course of cultural evolution of pea. In: Vavilovskoe Nasledie v Sovremennoy Biologii. Moscow: Nauka Publ., 1989;72-89. (in Russian)
- Berdnikov V.A., Bogdanova V.S., Rozov S.M., Kosterin O.E. Geographic patterns of histone H1 allelic frequencies formed in the course of *Pisum sativum* L. (pea) cultivation. Heredity. 1993;71:199-209. DOI 10.1038/hdy.1993.125.
- Blixt S. Mutation genetics in *Pisum*. Agri Hort. Genet. 1972;30:1-293.
- Bogdanova V.S., Kosterin O.E., Yadrikhinskiy A.K. Wild peas vary in their cross-compatibility with cultivated pea (*Pisum sativum* subsp. *sativum* L.) depending on alleles of a nuclear-cytoplasmic incompatibility locus. Theor. Appl. Genet. 2014;127:1163-1172. DOI 10.1007/s00122-014-2288-9.

- Coulot P., Rabaute P. Monographie de Leguminosae de France. 4. Tribus des Fabeae, des Cicereae et des Genisteeae. Bulletin de la Société Botanique du Centre-Ouest. 2016;46:1-902.
- Coyne C.J., McGee R.J., Redden R.J., Ambrose M.J., Furman B.J., Miles C.A., Genetic adjustment to changing climate: pea. In: S.S. Yadav, J.H. Redden, H. Lotze-Campen, A.J. Hall (Eds.) Crop Adaptation to Climate Change. N. Y.: John Wiley & Sons, 2011;238-250.
- Dyachenko E.A., Ryzhova N.N., Kochieva E.Z., Vishnyakova M.A. Molecular genetic diversity of the pea (*Pisum sativum* L.) from the Vavilov Research Institute collection by the AFLP analysis. Russ. J. Genet. 2017;50:916-924. DOI 10.7868/S0026898415040023.
- Ellis T.H.N., Poyser S.J., Knox M.R., Vershinin A.V., Ambrose M.J. Polymorphism of insertion sites of *Ty1-copia* class retrotransposons and its use for linkage and diversity analysis in pea. Mol. General Genet. 1998;260:9-19. DOI 10.1007/PL00008630.
- Govorov L.I. Pea of Afghanistan (on the problem of the origin of the cultivated pea). Trudy po prikladnoy botanike, genetike i selektsii = Bulletin of Applied Botany, Genetics and Plant Breeding. 1928;19:497-522. (in Russian)
- Govorov L.I. Pea. Kulturnaya flora SSSR. Vol. IV. Grain legumes. Moscow: Gosudarstvennoe izdatelstvo sovkhoznnoi i kolkhoznnoi literatury, 1937;229-336. (in Russian)
- Hedrick U.P., Hall F.R., Hawthorn L.V., Berger A. The Vegetables of New York: Report of the New York State Agricultural Experiment Station for the Year Ending June 30, 1928. Vol. 1. Pt. 1. Peas of New York. Albany: J.B. Lyon Company, Printers, 1928.
- Integrated Taxonomic Information System, online resource, 2017. www.itis.gov. Accessed 05.08.2017.
- International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Oberreifenberg: Koeltz Scientific Books, 2012.
- Jing R., Vershinin A., Grzebota J., Shaw P., Smýkal P., Marshall D., Ambrose M.J., Ellis T.H.N., Flavell A.J. The genetic diversity and evolution of field pea (*Pisum*) studied by high throughput retrotransposon based insertion polymorphism (RBIP) marker analysis. BMC Evol. Biol. 2010;10:44. DOI 10.1186/1471-2148-10-44.
- Kosterin O.E. Pea (*Pisum sativum* L.): the uneasy fate of the first genetical object. Vavilovskii Zhurnal Genetiki i Selektzii = Vavilov Journal of Genetics and Breeding. 2015;19(1):13-26. DOI 10.18699/VJ15.002. (in Russian)
- Kosterin O.E. Abyssinian pea (*Lathyrus schaeferi* Kosterin nom. nov. pro *Pisum abyssinicum* A. Br.) is a problematic taxon. Vavilovskii Zhurnal Genetiki i Selektzii = Vavilov Journal of Genetics and Breeding. 2017;21(2):158-169. DOI 10.18699/VJ17.234. (in Russian)
- Kosterin O.E., Bogdanova V.S. Relationship of wild and cultivated forms of *Pisum* L. as inferred from an analysis of three markers, of the plastid, mitochondrial and nuclear genomes. Genet. Res. Crop Evol. 2008;55:735-755. DOI 10.1007/s10722-007-9281-y.
- Kosterin O.E., Bogdanova V.S., Gorel F.L., Rozov S.M., Trusov Yu.A., Berdnikov V.A. Histone H1 of the garden pea (*Pisum sativum* L.): composition, developmental changes, allelic polymorphism and inheritance. Plant Sci. 1994;101:189-202. https://doi.org/10.1016/0168-9452(94)90255-0.
- Kosterin O.E., Bogdanova V.S., Kechin A.A., Zaytseva O.O., Yadrinkhinskiy A.K. Polymorphism in a histone H1 subtype with a short N-terminal domain in three legume species (Fabaceae, Fabaceae). Mol. Biol. Rep. 2012;39:10681-10695. DOI 10.1007/s11033-012-1959-3.
- Kosterin O.E., Zaytseva O.O., Bogdanova V.S., Ambrose M. New data on three molecular markers from different cellular genomes in Mediterranean accessions reveal new insights into phylogeography of *Pisum sativum* L. subsp. *elatius* (Beib.) Schmahl. Genet. Res. Crop Evol. 2010;57:733-739. DOI 10.1007/s10722-009-9511-6.
- Lamprecht H. Zur Artberechtigung *Pisum elatius* Stev. und *Jomardi* Schrank. Agri Hort. Genet. 1956;14:5-18.
- Lehmann C. Das morphologische system der Saarerbsen. Der Züchter. 1954;24:316-337.
- Lehmann C., Blixt S. Artificial infraspecific classification in relation to phenotypic manifestation of certain genes in *Pisum*. Agri Hort. Genet. 1984;42:48-74.
- Makasheva R.Kh. Flora of Cultivated Plants. Vol. IV. Grain legumes. Pt. I. Pea. Leningrad: Kolos Publ., 1979. (in Russian)
- Maxted N., Ambrose M. Peas (*Pisum* L.). In: Plant Genetic Resources of Legumes in the Mediterranean. Current Plant Science and Biotechnology in Agriculture 39. N. Maxted, S.J. Bennett (Eds.). Dordrecht: Kluw. Acad. Publ., 2001;181-190.
- Mendel G. Versuche über Pflanzenhybriden. Verhandlungen des naturforschenden Vereines in Brünn. Bd. IV für das Jahr 1865 (Abhandlungen). 1866:3-47.
- Schaefer H., Hechenleitner P., Santos-Guerra A., Menezes de Sequeira M., Pennington R.T., Kenicer G., Carine M.A. Systematics, biogeography, and character evolution of the legume tribe Fabeae with special focus on the middle-Atlantic island lineages. BMC Evol. Biol. 2012;12:250. DOI 10.1186/1471-2148-12-250.
- Schrank F. Flora Monacensis. T. 4. Monachii, 1818.
- Singh R.J. Plant Cytogenetics. 2nd ed. Boca Raton: CRC Press, 2003.
- Vershinin A.V., Allnutt T.R., Knox M.R., Ambrose M.J., Ellis T.H.N. Transposable elements reveal the impact of introgression, rather than transposition, in *Pisum* diversity, evolution, and domestication. Mol. Biol. Evol. 2003;20(12):2067-2075. DOI 10.1093/molbev/msg220.
- Weiss E., Zohary D. The Neolithic Southwest Asian founder crops, their biology and archaeobotany. Curr. Anthropol. 2011;52:S237-S254. DOI 10.1086/658367.
- Zaytseva O.O., Bogdanova V.S., Kosterin O.E. Phylogenetic reconstruction at the species and intraspecies levels in the genus *Pisum* (L.) (peas) using a histone H1 gene. Gene. 2012;504:192-202. http://dx.doi.org/10.1016/j.gene.2012.05.026.
- Zaytseva O.O., Bogdanova V.S., Mglinets A.V., Kosterin O.E. Refinement of the collection of wild peas (*Pisum* L.) and search for the area of pea domestication with a deletion in the plastidic *psbA-trnH* spacer. Genet. Resour. Crop Evol. 2017;64:1417-1430. DOI 10.1007/s10722-016-0446-4.
- Zaytseva O.O., Gunbin K.V., Mglinets A.V., Kosterin O.E. Divergence and population traits in evolution of the genus *Pisum* L. as reconstructed using genes of two histone H1 subtypes showing different phylogenetic resolution. Gene. 2015;556:235-244. http://dx.doi.org/10.1016/j.gene.2014.11.062.
- Zhukovskiy P.M. Cultivated plants and their relatives (systematics, geography, ecology, origin, use). 2nd ed. Moscow: Kolos Publ., 1964. (in Russian)
- Zohary D., Hopf M. Domestication of Plants in the Old World. 3rd ed. Oxford: Clarendon Press, 2000.