

Vavilovia formosa (Stev.) Fed. (Fabeae, Fabaceae) on Meyen's 'panel with a multitude of lamps'

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Summary: The concept of statistical nature of taxon first proposed by S.V. Meyen was applied to system of the Fabeae tribe (Fabaceae) in order to clarify the position of *Vavilovia formosa* (Stev.) Fed. Details of morphology of this rare plant have also been clarified. Molecular markers (RAPD) were used to reveal the infrageneric structure of *Vavilovia*. The discussed form does not show unique features which clearly distinguish it from the related genera *Pisum* and *Lathyrus*, but it may be referred to as genus of its own. The revealed infrageneric differences coincide with the geographical distribution and may evidence the beginning of divergence. However, the subclades within *Vavilovia* are better treated as subspecies or varieties.

Keywords: Fabaceae, Fabeae, *Vavilovia*, *Pisum*, taxonomy

When discussing the nature of taxon, the authoritative palaeobotanist and theorist of evolution S. V. MEYEN (1987: 360–361) compared a space of characters with “panel with a multitude of lamps, each corresponding to a certain character. If the character is present in a taxon the lamp gives a flash. (...) A cloud of switched-on lamps corresponds to the habitual concept of a taxon, with some lamps emitting light continuously (obligate characters), some giving flashes with different frequency. If refrains and all teratic characters are introduced into this model ... the lamps will be organized into a complicated systems of orderly patterns (refrains) ... there are no lamps permanently emitting light at all and the impression of permanent light is produced by very high frequency of flashes. (...) If the taxa are closely related, the shapes of their clouds will coincide and changes will occur only in the frequency of flashes”.

To date, different aspects of systematics of legumes (Fabaceae) remain in scope of intensive researches. The system of tribe Fabeae Rchb. (= Vicieae (Adans.) DC.) is also under discussion with special reference to the position of the rare and endangered highland perennial plant *Vavilovia* Fed.

Detailed information on the history of *Vavilovia* investigation is provided in reviews (MAKASHEVA et al. 1973; MIKIC et al. 2010). It was for the first time described by STEVEN (1812) as *Orobis formosus* Stev. During two subsequent centuries it had been included in the genera *Pisum* (*P. formosum* (Stev.) Alef. = *P. frigidum* Alef.), *Vicia* (*V. aucheri* Boiss. = *V. variegata* var. *aucheri* (Jaub. & Spach) Bornm.) or treated as separate genus, *Vavilovia* Fed. or *Alophotropis* (Jaub. et Spach) Grossh. The latter genus comprised two species, *A. aucheri* (Jaub. et Spach) Grossh. and *A. formosa* (Stev.) Grossh. (GROSSHEIM 1949) growing in different areas and showing diverse leaf morphology. GROSSHEIM (1949) followed the classification of FEDOROV (1939) who also subdivided this genus into two species but later rejected this hypothesis (FEDOROV 1952).

Recent investigations on the tribe system dealing with methods of molecular systematics revealed a certain similarity between *Vavilovia* and *Pisum* (KENICER et al. 2005; SINJUSHIN et al. 2009;

OSKOEIYAN et al. 2010). However, the interpretation of morphological features of this plant remains obscure and ambiguous. The given work represents the effort to apply Meyen's idea of statistical nature of taxon's identity to the similarity between *Vavilovia* and its closest relatives, *Lathyrus* and *Pisum* aiming at a clarification of the taxonomical position. The intrageneric polymorphism of *Vavilovia* is also in scope.

Materials and methods

The herbarium material (MW!; Herbarium of the Institute of Botany of Natl. Acad. Sci., Republic of Armenia) of *Vavilovia* was used for morphological analysis. The features of peas and vetchlings were analyzed using living and herbarium (MW!) material listed in SINJUSHIN et al. (2009). Some descriptions of morphology of *Lathyrus* species were also selected from LEHT (2009). Scanning electron microscopy was performed using CamScan-S2 microscope (Cambridge Instruments, UK). The material was fixed and dissected in 70% ethanol, dehydrated in ethanol series and coated with platinum and palladium in sputter coater Eiko IB-3. Light microscopy was performed by means of an Olympus SZX9 microscope (Olympus Optical Co., Ltd., Japan). DNA extraction, polymerase chain reaction (PCR) conditions, and primer sequences are described in SINJUSHIN et al. (2009).

Genetic distances were calculated according to algorithms of DICE (1945) and simple match, the phylogenetic trees were constructed by use of SplitsTree4 software package (HUSON & BRYANT 2006) applying methods of 'neighbor joining' and 'neighbor-net' (BRYANT & MOULTON 2004). The statistical evaluation of nodes' significance was carried out using bootstrap analysis (ZHARKIKH & LI 1995) for 1000 replicas.

Results

The work was aimed at clarification of some features cited by different authors as obscure or debatable. In our opinion, such traits as 'non/cristate keel of corolla' are more like quantitative: *Vavilovia* and most *Lathyrus* species have a non-cristate keel, while different *Pisum* accessions possess flowers with more or less expressed crest. The 'oroboid' species of *Lathyrus* have their keel more carinated than other vetchlings. Moreover, this feature can be observed exclusively on living material and it is completely lost in herbarium specimens, thus disabling a tribe-wide comparison on available material.

The same situation, resembling a quantitative trait, is typical for the mode of truncation of androecial tube. It's more or less oblique in vetchlings and straight in peas and *Vavilovia* but the inclination is variable.

One more androecial character which has not been studied before (with reference to the tribal position of *Vavilovia*) is shape of filaments (Fig. 1). They are dilated in *Pisum* and *Vavilovia*; GUNN & KLUVE (1976) describe vetchlings which have only filamentous stamens, but somewhat dilated stamens were also observed in *L. aleuticus* (Greene) Pobed. Hence, this trait cannot be referred to as unique for peas and *Vavilovia* only.

Some features were confirmed in distinguishing *Vavilovia* from all studied *Pisum* accessions. These are: perennial life form (*Pisum* annual) with long creeping rhizomes enabling vegetative propagation; narrow sepals covered with simple trichomes (glabrous and broad sepals with

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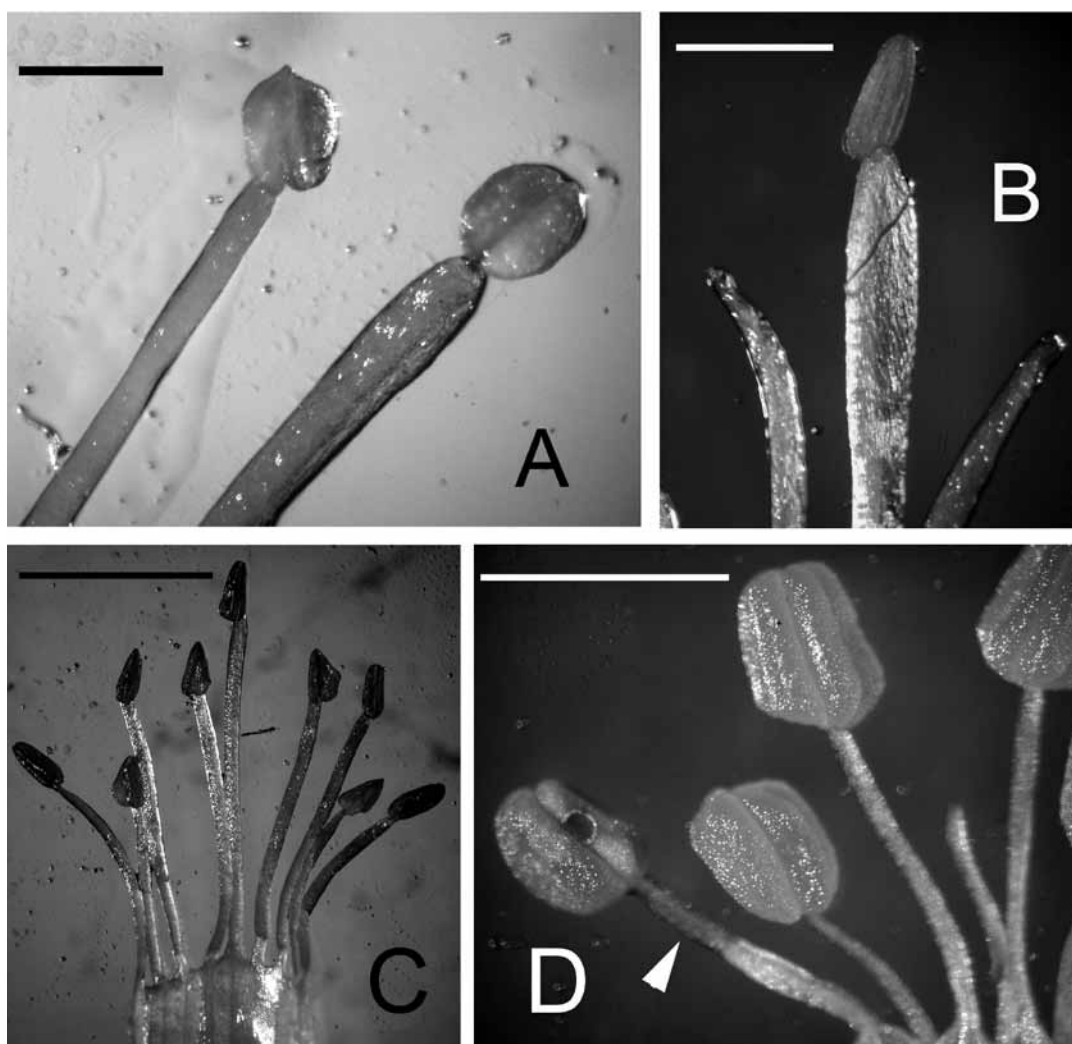


Figure 1. Light microphotograph of stamens of different Fabaceae representatives. A – *Pisum sativum*. B – *Vavilovia formosa* (anthers partially removed). C – *Lathyrus pratensis*. D – *Lathyrus aleuticus* (arrowhead points at slightly dilated filament of outer whorl stamen). Scale bars = 1 mm.

overlapping margins in *Pisum*); leaf rachis ending with cusp (always tendrils in *Pisum*); small stipules (in *Pisum* of the same size as leaflets or larger); fluted leaf rachis cross-section (rounded in *Pisum*); supervolute ptyxis (plicate in *Pisum*; this trait is reported to be highly significant by KUPICHA (1981)). All listed characters can be found in *Lathyrus* species too, but their interpretation is ambiguous. The life form (annual or perennial) is not used even to separate sections in *Lathyrus*, e.g., the type section *Lathyrus* includes both, annuals (*L. odoratus* L.) and perennials (*L. latifolius* L., *L. belinensis* N. Maxted & D.J. Goyder). Leaf features are known to be very variable in ontogeny of legumes, and the first pea leaves are always characterized with inversely-ovate leaflets, fluted rachides ending with a short process or even lacking any specialized tip, and even small stipules (*P. fulvum* Sibth. & Smith). Actually, *Vavilovia* leaves combine some features which can be found in juvenile forms of *Pisum* species. The calyx of the latter also possesses ciliate margins before anthesis. The only feature of special significance is the ptyxis.

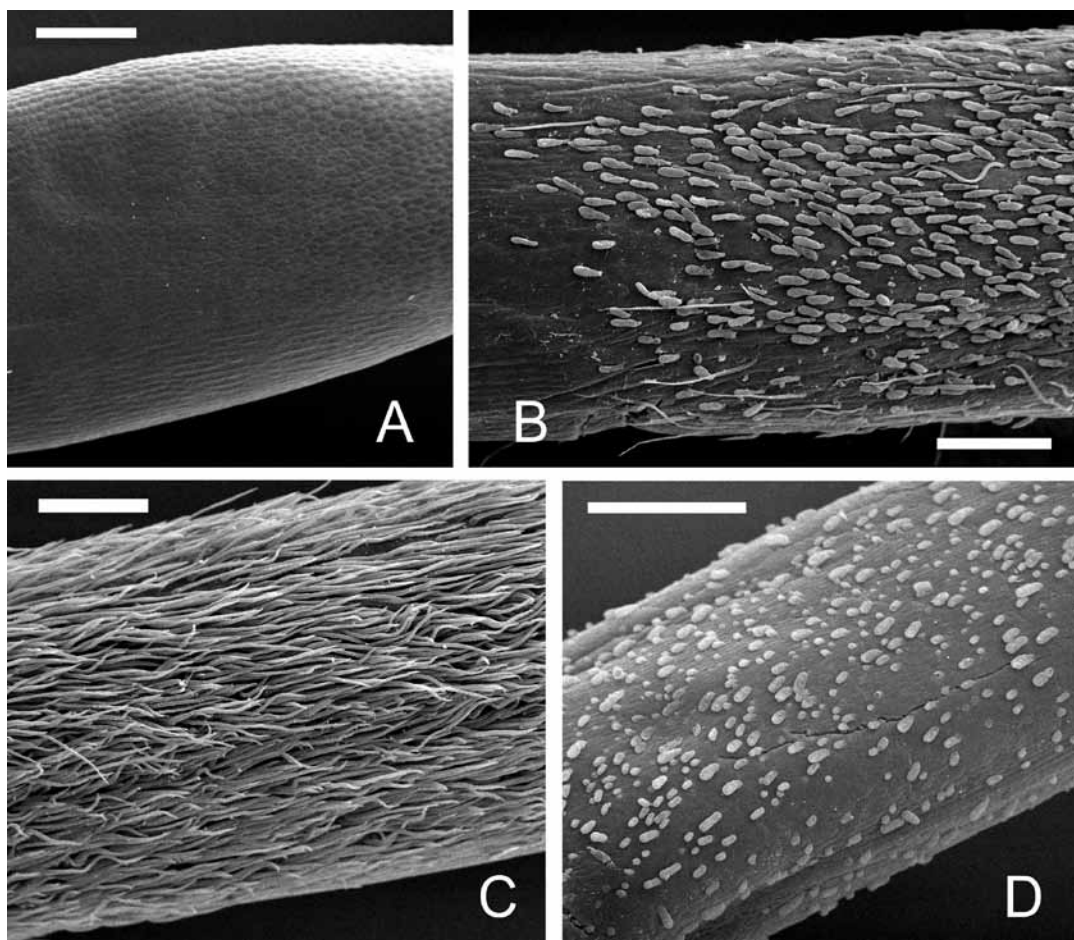


Figure 2. Ovary surfaces (SEM microphotographs). A – *Pisum sativum* (glabrous). B – *Vavilovia formosa* (glands and trichomes). C – *Lathyrus aleuticus* (trichomes). D – *Lathyrus vernus* (few-celled glands). Scale bars = 0.3 mm.

The ovary of the *Pisum* flower is glabrous (GUNN & KLUVE (1976) report a glandular surface for some accessions), while *Lathyrus* species show both, glabrous and pubescent ovaries (simple trichomes, nectariferous glands or combination of two types (GUNN & KLUVE 1976; original observations)). Studied *Vavilovia* samples possess a combination of simple trichomes and few-celled glands on the ovaries' surface (Fig. 2).

Two traits were cited to separate *Vavilovia* from *Pisum*, viz. pistil groove gaping only at the base (at the base and apex in *Pisum*) and a non-cristate keel (cristate in pea). GUNN & KLUVE (1976) reject these differences. Pistils appear to be grooved in the same way in both genera, just like other pistil features such as hair pattern (adaxial). The keel crest is difficult to analyze on herbarium material and needs more detailed investigations.

At least two features distinguish *Vavilovia* from all other studied species. These are leathery leaflets and a specific leaflet shape. In all studied plants except *Vavilovia*, the proximal leaflet half (i.e., the one directed to the leaf base) is wider than the distal one (directed to leaf rachis tip; so-called basiscopic leaflet) or has almost the same width. In all *Vavilovia* plants, the distal half is notably wider than the proximal one (acrosopic).

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The *Vavilovia* specimens are not completely morphologically uniform in the sample studied. All Armenian plants differed from the rest in having leaflets with keel-like bases (rounded base in other specimens). This feature was used by GROSSHEIM (1949) to separate two different species within *Alphotropis* (= *Vavilovia*), namely *A. formosa* and *A. aucheri*, but in our opinion, the whole genus should be treated as monotypic (at least basing on available material), probably with the different forms interpreted as subspecies. The morphologically distinct forms of *Pisum formosum* (= *V. formosa*) were treated as separate varieties by GOVOROV (1937), viz. var. *typicum* Gov. and var. *microphyllum* Ser.

Based on RAPD analysis, three clades were revealed corresponding to *Pisum*, *Vavilovia* and *Lathyrus* genera (Fig. 3). Different methods were applied and the position of certain accessions alters depending on the algorithm chosen. The whole topology of consensus tree remains unchanged which is an evidence for the reliability of the obtained data. Bootstrap values in basic nodes exceed 50 also confirming the trees' significance.

Analysis of phylogenetic nets ('neighbor-net' algorithm) also confirms data obtained via neighbor joining. All differences are unessential for results of analysis. In all cases the monophyletic *Vavilovia* clade is subdivided into two groups corresponding to areas of the samples' collection. These data may evidence for a transitional stage of allopatric speciation with Caucasian mountains serving as isolating factor.

Discussion

The situation is complicated enough. We compare morphological variations in genus *Lathyrus* (ca. 150 species (KUPICHA 1981)) and two species-poor genera, *Pisum* (two species) and *Vavilovia* (one or two species; our results give evidence for the monotypic character of this genus). The range of morphological variation within *Lathyrus* is wide as it can be seen in numerous species growing in different areas throughout the world. Peas represent a small group with a comparatively low degree of natural variability, but the garden pea (*P. sativum* ssp. *sativum*) is an ancient crop having its artificial populations saturated with plenty of morphological traits never recorded in nature (dwarfism, non-shattering seeds, tendrilled leaf, colorless corolla, etc.). On the other hand, pea is a traditional model object for genetics and plant physiology, actually the oldest model plant species serving as material for G. Mendel's classical experiments (MENDEL 1866). Numerous inherited developmental variations were recorded and isolated as isogenic lines for more than one and a half centuries (the most complete list of known pea genes is available at <http://data.jic.bbsrc.ac.uk/cgi-bin/pgene/default.asp>). The range of mutational (or, more generally, teratological) variation in pea is obviously wider than normal variability within a tribe (or even subfamily). According to Meyen's concept, anomalous features need to be taken into consideration regardless of their frequency when discussing polymorphism of structures within a certain taxon (MEYEN 1973, 1987).

Compared with peas and vetchlings, *Vavilovia* is a small monotypic taxon with poorly studied morphology and natural variation and nothing is known on teratological mutability of this plant. Such phenomenon possibly results from paucity of material for studies.

To understand statistical differences in the occurrence of certain traits distinguishing (or, oppositely, bringing together) genera under discussion, the obtained matrix of morphological variation (Tab. 1) needs to be analyzed.

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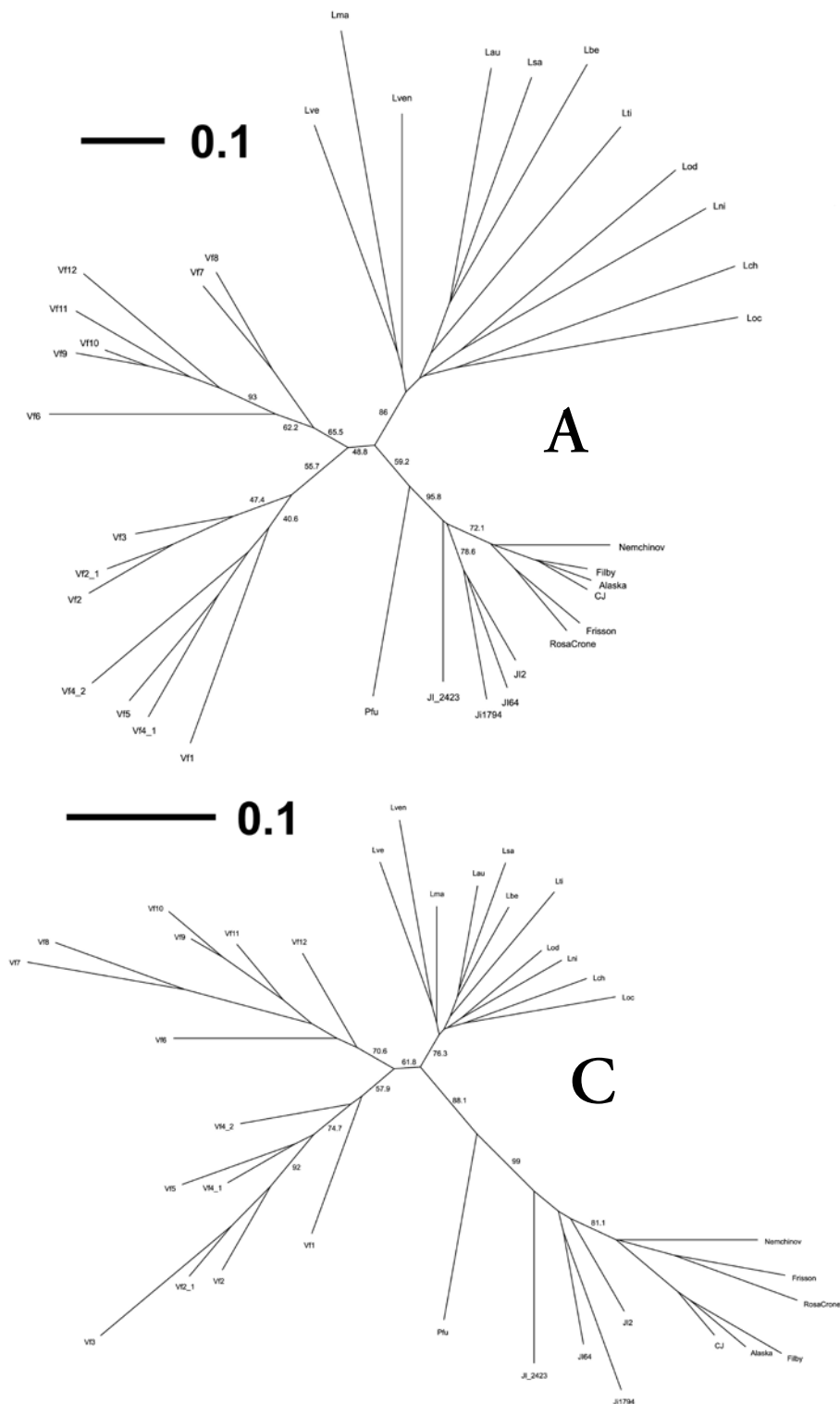
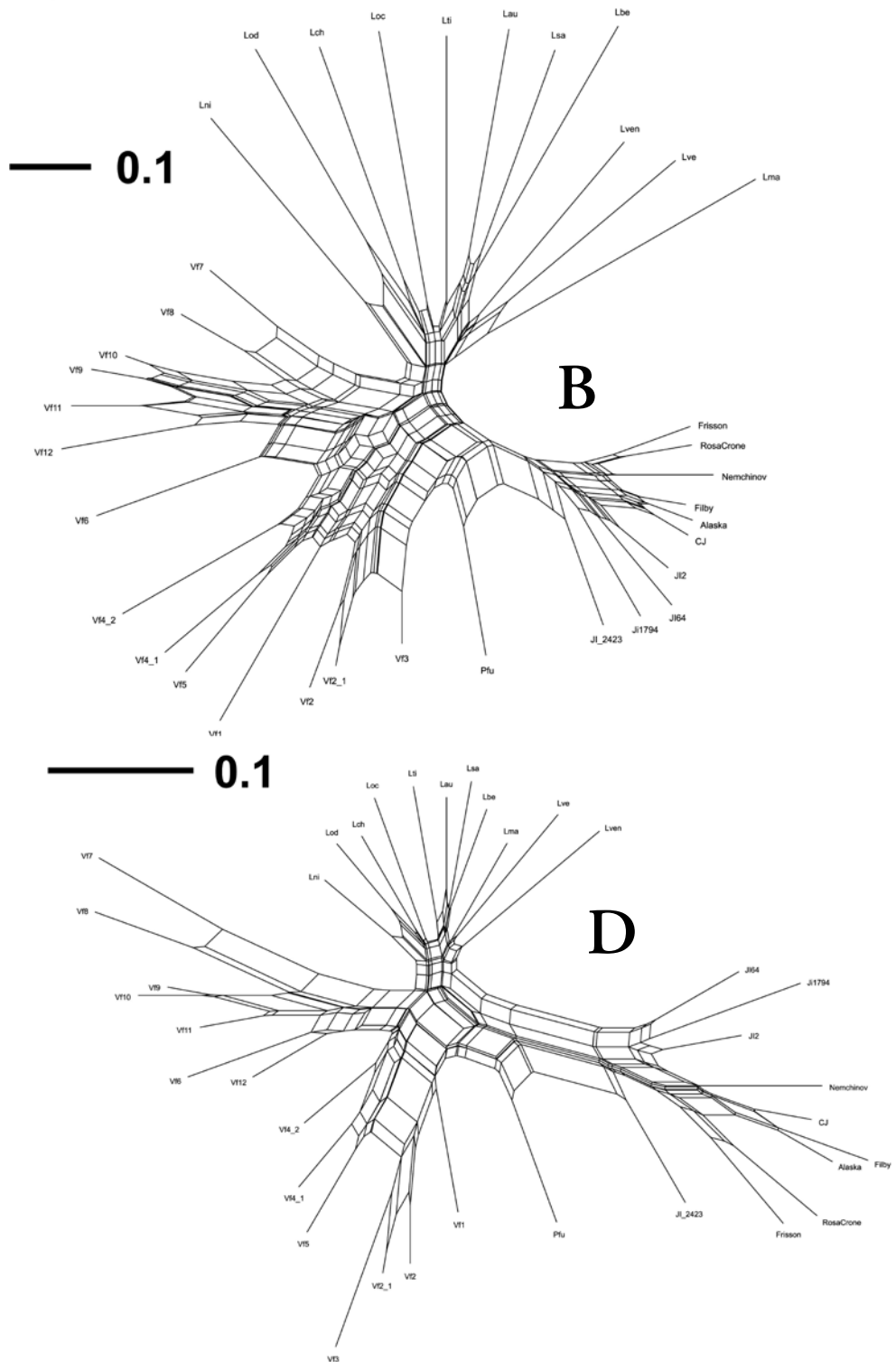


Figure 3. Dendrograms representing infrageneric structure of *Vavilovia* with *Lathyrus* and *Pisum* taken as outgroups. A – Dice's coefficient (neighbor joining). B – Dice's coefficient (split decomposition net). C – Simple match coefficient (neighbor joining). D – Simple match coefficient (split decomposition net). Vf = *V. formosa* accessions (Vf1 from Kabardino-Balkaria, Vf2–4_2 from Dagestan, Vf6–12 from Armenia). L = *Lathyrus* accessions (Lsa = *L. sativus*,

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Lve = *L. vernus*, Lven = *L. venetus*, Loc = *L. ochrus*, Lau = *L. aureus*, Lod = *L. odoratus*, Lti = *L. tingitanus*, Lch = *L. chloranthus*, Lbe = *L. belinensis*, Lma = *L. aleuticus*, Lni = *L. nissolia*). Pfu = *Pisum fulvum*. Other designations stand for names of pea cultivars and lines.

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Table 1. Morphological features of genera *Pisum*, *Vavilovia* and *Lathyrus*. Dot stands for presence of feature in normal (including ontogenetic) variation, circle for its presence as teratological phenomenon (including mutations). No symbol = feature not described.

			<i>Lathyrus</i>	<i>Vavilovia</i>	<i>Pisum</i>
Leaf	No. of pairs of leaflets	1	•	•	•
		>1	•		•
		None	•		◦
	Rachis end	Leaflet	•		◦
		Tendrill	•		•
		Cusp	•	•	•
	Leaflet margin	Entire	•	•	•
		Dentate or dissected	•		•
	Ptyxis	Plicate			•
		Supervolute	•	•	
	Leaflet pubescence	Pubescent	•		•
		Glabrous	•	?	
	Stipules size	Same as or > than leaflets	•		•
		< than leaflets	•	•	•
	Leaflet symmetry	Acroscopic		•	
		Symmetric	•		•
		Basiscopical	•		•
	Phyllodia	Present	•		
		Absent	•	•	•
	Rachis shape (cross section)	Rounded	•		•
		Costate	•	•	
		Winged	•		◦
	No. of cataphylls on seedling	2	•		•
		>2	•	•	
	Stomatal index ratio	Hypostomatic	•		
		Amphistomatic	•	•	•
		Epistomatic	•		
Axillary inflorescence	No. of flowers	Single	•	•	•
		2	•	•	•
		>2	•		•
	Bracts	Present	•		◦
		Absent	•	•	•
	Length of sterile part, i.e., hypotagma	Strongly > than pedicel	•	•	•
		Same as or < than pedicel	•		•

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			<i>Lathyrus</i>	<i>Vavilovia</i>	<i>Pisum</i>
Flower	Corolla color	Yellow	•		
		Anthocyanine specter	•	•	•
		White	o		o
	Style shape	Filamentous	•		
		Lateral compression	•		
		Dorsal-ventral compression	•		
		Twisted	•		
		Grooved		•	•
	Carpel pubescence	Glabrous	•		•
		Simple trichomes	•		
		Trichomes and glands	•	•	
		Glandular pubescence	•		•
	Calyx pubescence	Glabrous	•		
		Sepals pubescent	•	•	
		Sepals glabrous with ciliate margins	•		•
	Shape of filaments of outer whorl stamens	Linear	•		
		Dilated	•	•	•
	Anther tube truncation	Straight	•	•	•
		Oblique	•		
Other features	Stem shape (cross section)	Rounded or tetrahedral	•		•
		Costate	•	•	•
		Winged	•		
	Hilum shape	Linear	•		
		Elliptic	•	•	•
		Rounded	•		
	Life form	Annual	•		•
		Perennial	•	•	
Fruit	Pod dehiscence	Dehiscent	•	•	•
		Indehiscent	•		•
	Pod surface	Smooth	•	•	•
		Moniliform (seed chambers visible)	•		o

It is clearly seen that almost all listed features can be observed in *Lathyrus* as normal variation. Some of them can also be found in pea accessions but only in a range of mutational variability. Cases when manifestation of certain trait coincides both, in *Vavilovia* and *Lathyrus*, are rare, viz. life form, leaflet ptyxis, rachis shape, number of seedling's cataphylls and carpel and sepal pubescence (Fig. 4). Only the ptyxis type was reported as variable in some *Vicia* accessions by KUPICHA (1981). The others seem to be strongly constant.

However, only one case of coincidence between *Vavilovia* and pea was found out, viz. style shape. This trait was discussed to be of strong significance by numerous authors (e.g., GUNN & KLUVE 1976). More precise investigations of style structure in pea and *Vavilovia* had revealed that they are somewhat different. The style is conjoined with the ovary via a contraflexure in pea. This is lacking in *Vavilovia*. The style is grooved in gynoecea of both species (Fig. 5). Hence, this similarity is not as strong as it was proposed earlier.

Actually, certain convergence (or similarity in broader sense) is observed between distantly related taxa growing in same environments. *Vicia janeae* Mard. (= *L. woronowii* Bornm., = *Ervum woronowii* (Bornm.) Stankev.) was characterized as a highland plant *sui generis* strongly resembling *Vavilovia* (REPJEV et al. 1999). Possibly the whole complex of traits can arise repeatedly in evolution in tribe. As a result, strongly habitually cognate forms arise (*L. dominianus* Litv., *L. mulkak* Lipsky, etc.). Some of them also have obscure taxonomical position clearly evident from numerous synonyms.

Some cases of mutational variations which lead to appearance of features of another genus were described by NILSSON-LEISSNER (1924) as '*Pisum aphacoides*' and by LAMPRECHT (1962). The spontaneous mutation in *LATHYROIDES* (*LATH*) gene leads to the acquirement of some *Lathyrus* characters: unijugate leaves with narrow and pointed leaflets, reduced stipules, and altered inflorescence morphology. *LATH* together with some other genes was interpreted as

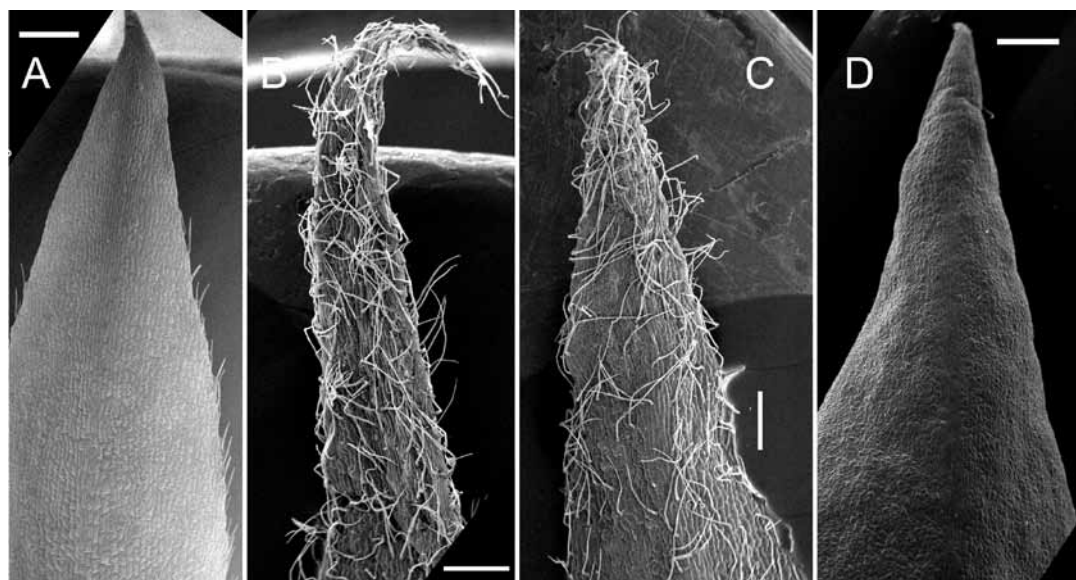


Figure 4. Calyx pubescence in studied species, abaxial sepal (SEM microphotographs). A – *Lathyrus vernus* (ciliate margin). B – *Vavilovia formosa* (trichomes). C – *Lathyrus aleuticus* (trichomes). D – *Pisum sativum* (glabrous). Scale bars = 0.3 mm.

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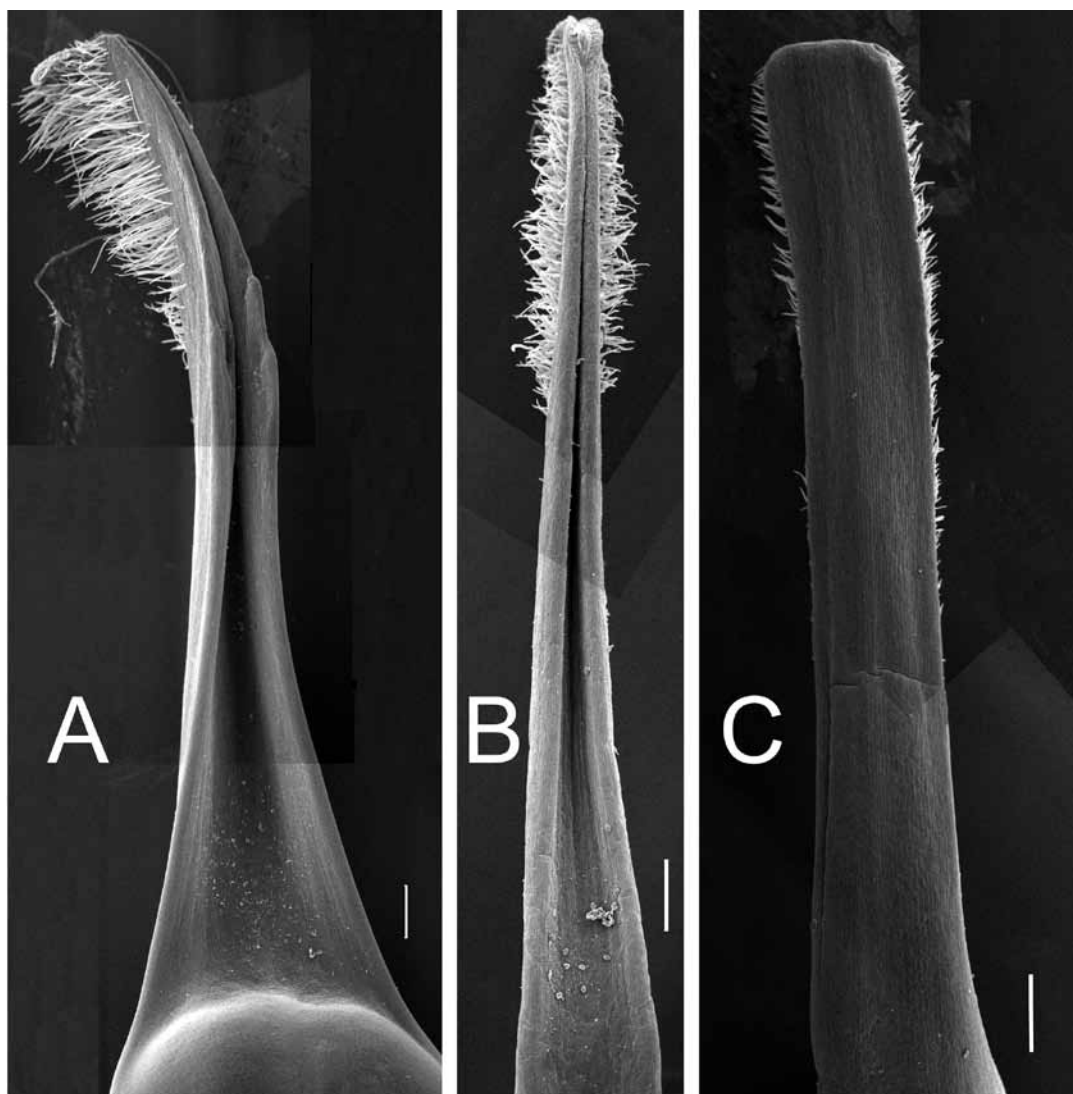


Figure 5. Stylar features. A – *Pisum sativum*. B – *Vavilovia formosa*. C – *Lathyrus vernus*. SEM microphotographs. Scale bars = 0.3 mm.

‘interspecific gene’ by H. Lamprecht; mutations in such genes are responsible for differences between species but always lead to sterility (LAMPRECHT 1945).

The listed examples ensure that specific and even generic features can appear in different taxa abruptly and repeatedly. These cases can be interpreted as saltations. In terms of S. Meyen’s concept, they represent phenomena of transitive polymorphism when the whole spectrum of variation persists through evolution of taxon and is inherited from the precursor to the filial group (MEYEN 1973). Obviously, only a part of this range can manifest as natural variability in certain taxons (especially in species-poor ones). The rest part of the range can be observed as teratological or ontogenetic variation.

The phenomenon of transitive polymorphism strongly obscures the solution of question on distinguishing ancestral forms from advanced ones. One can hardly conclude unambiguously,

whether *Vavilovia* is close to the common precursor of the whole tribe (as it was proposed by MAKASHEVA (1979)) or it is a strongly specialized genus. The latter hypothesis seems more trustworthy both, in light of repeated origin of *Vavilovia*-like habitus in different lineages (see above) and according to molecular data.

In this connection, *Vavilovia* can be evaluated as a form combining features of related genera, *Pisum* and *Lathyrus*. We could not find any unique features during our analysis. When searching for coincidence between genera, more cases of similarity between *Vavilovia* and *Lathyrus* were found. The molecular data provide evidences for a relation between *Vavilovia* and *Pisum* (KENICER et al. 2009; SINJUSHIN et al. 2009; OSKOEIYAN et al. 2010). Hence, applying the Meyen's concept of nature of differences between taxa may serve as reason for considering *Vavilovia* as a genus of its own. The results of both, molecular and morphological analyses ensure that this genus needs to be treated as monotypic, because differences between specimens from different parts of habitat area (Armenia and Dagestan) can hardly be interpreted as interspecific. The proposals to consider distinct groups as different varieties (GOVOROV 1937) or subspecies seem to be more valid. The disruption of the initial habitat area into few isolated parts lacking genetic flows between them nevertheless can serve as basis of the divergence of an uniform genus into few ones. The initial stages of such divergence can be already seen in both, morphology and in DNA polymorphism.

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