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REVIEW ARTICLE

The bicentenary of the research on 'beautiful' vavilovia (*Vavilovia formosa*), a legume crop wild relative with taxonomic and agronomic potential

ALEKSANDAR MIKIĆ[1]*, PETR SMÝKAL[2], GREGORY KENICER[3], MARGARITA VISHNYAKOVA[4], NUNE SARUKHANYAN[5], JANNA AKOPIAN[6], ARMEN VANYAN[5], IVAN GABRIELYAN[6], IVA SMÝKALOVÁ[7], EKATERINA SHERBAKOVA[6], LANA ZORIĆ[8], JOVANKA ATLAGIĆ[1], TIJANA ZEREMSKI-ŠKORIĆ[1], BRANKO ĆUPINA[9], ĐORĐE KRSTIĆ[9], IGOR JAJIĆ[9], SVETLANA ANTANASOVIĆ[9], VUK ĐORĐEVIĆ[1], VOJISLAV MIHAILOVIĆ[1], ALEXANDR IVANOV[10], SERGIO OCHATT[11] and MIKE AMBROSE[12]

[1]*Institute of Field and Vegetable Crops, Novi Sad, Serbia*
[2]*Palacký University at Olomouc, Olomouc, Czech Republic*
[3]*Royal Botanical Garden, Edinburgh, UK*
[4]*State Scientific Centre N.I. Vavilov All-Russian Research Institute of Plant Industry of Russian Academy of Agricultural Science, St Petersburg, Russia*
[5]*Green Lane Agricultural Assistance NGO, Yerevan, Armenia*
[6]*National Academy of Sciences, Institute of Botany, Yerevan, Armenia*
[7]*Agritec Plant Research Ltd., Šumperk, Czech Republic*
[8]*Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Serbia*
[9]*Department of Field and Vegetable Crops, Faculty of Agriculture, University of Novi Sad, Novi Sad, Serbia*
[10]*Botany Department Herbarium, Stavropol State University, Stavropol, Russia*
[11]*INRA, UMR1347, PCMV, Dijon, France*
[12]*Department of Crop Genetics, John Innes Centre, Norwich, UK*

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Vavilovia formosa is a relict, endangered species from the highlands of the Caucasus and the Near East. Described in 1812, it has had an uncertain status and was finally recognized as a separate genus of tribe Fabeae (Fabaceae). Our informal international group was established in 2007 to revive the interest in this species as it had been seriously neglected for decades. Here, we provide an overview of the accumulated knowledge on *V. formosa* and present the results of the most recent multidisciplinary research. Three expeditions were made to two locations in Armenia in 2009, providing the material for anatomical, morphological, chemical and molecular analysis. Unlike previous attempts, *ex situ* conservation in Yerevan and *in vitro* propagation, important for potential interspecific hybridization, were successful. Molecular tools were used to clarify the taxonomic position of *V. formosa*, often considered the closest to the extinct ancestor of the whole tribe. The analysis of four informative regions of plastid and nuclear DNA showed that *V. formosa* belongs to the same clade as *Lathyrus* and *Pisum*, with a distinct status. Preservation and maintenance of *V. formosa* remains the only basis for further development of all other scientific aspects, especially breeding and uses in agronomy.

ADDITIONAL KEYWORDS: biodiversity – characterization – ecogeography – evaluation – *ex situ* conservation – Fabeae – *in situ* preservation – legume evolution – molecular taxonomy.

*Corresponding author. E-mail: aleksandar.mikic@nsseme.com; aleksandar.mikich@gmail.com

HISTORY AND ECOGEOGRAPHY

The species referred to as *Vavilovia formosa* (Stev.) Fed. was first described by Steven in 1812 as *Orobus formosus* Stev. (Steven, 1812). Afterwards, it was classified with its closest relatives, *Lathyrus* L., *Pisum* L and *Vicia* L., and was mostly referred to as *Pisum formosum* (Stev.) Alef. (Alefeld, 1861). More than a century after its discovery, it gained the status of a separate genus in tribe Fabeae Rchb. as the monospecific *Vavilovia* Fed. (Fedorov, 1952), in honour of N. I. Vavilov for his promotion of the importance of crop wild relatives. The paucity of material *Vavilovia* has resulted in there being almost no data on intraspecific or intrageneric variability for this plant (Sinjushin & Belyakova, 2010), although the differences between the specimens of diverse geographic origin can be interpreted as corresponding to subspecies rather than to distinct species or varieties (Sinjushin *et al.,* 2009).

Vavilovia formosa grows in rocky areas at altitudes from 1500 m up to 3500 m, with the central and eastern Caucasus as the main area of distribution (Grossheim, 1952). It occurs in Armenia, Azerbaijan, Georgia, Iran, Iraq, Lebanon, Russia, Syria and Turkey (Fig. 1) (Maxted & Ambrose, 2001) and in most of these countries it is recognized as an endangered and protected plant (Gabrielyan, 1990). It is perennial, herbaceous, with long roots, strong rhizomes, creeping stems, leaves with only one pair of leaflets and a mucro-like rachis tip (Fig. 2A), pink flowers (Fig. 2B) and linearly oblong pods (Fig. 2C) containing round, smooth, dark-coloured seeds (Davis, 1970).

An international group on *V. formosa* research, comprising scientists from Armenia, the Czech Republic, Serbia, Russia and the UK, was developed in late 2007 in an attempt to revive interest in this species (Vishnyakova *et al*., 2007). The primary goal was to conduct new expeditions in the search for *V. formosa* after the last (by a Soviet–British team two decades earlier; Mikić *et al*., 2009), since when only a few minor botanical reports have been made about its existence, mainly from Turkey (Deniz & Sümbül, 2004; Eren, Gökçeoğlu & Parolly, 2004).

This brief review gives the current status of the knowledge on *V. formosa* on the bicentenary of its inclusion in the botanical records, presenting both the seminal milestones in the pioneering research and the most recent achievements in its complex characterization, preservation and use in taxonomy and agronomy.

IN SITU PRESERVATION

During the summer 2009, three expeditions were carried out at two locations in Armenia (Sarukhanyan *et al*., 2009; Mikić *et al*., 2011). On 17 July and 27 August 2009, visits were made to Mount Ughtasar in southern Armenia, already recognized as a potential habitat of *V. formosa* (Akopian & Gabrielyan, 2008), and on 20 August to the Geghama Mountains in the central region of the country.

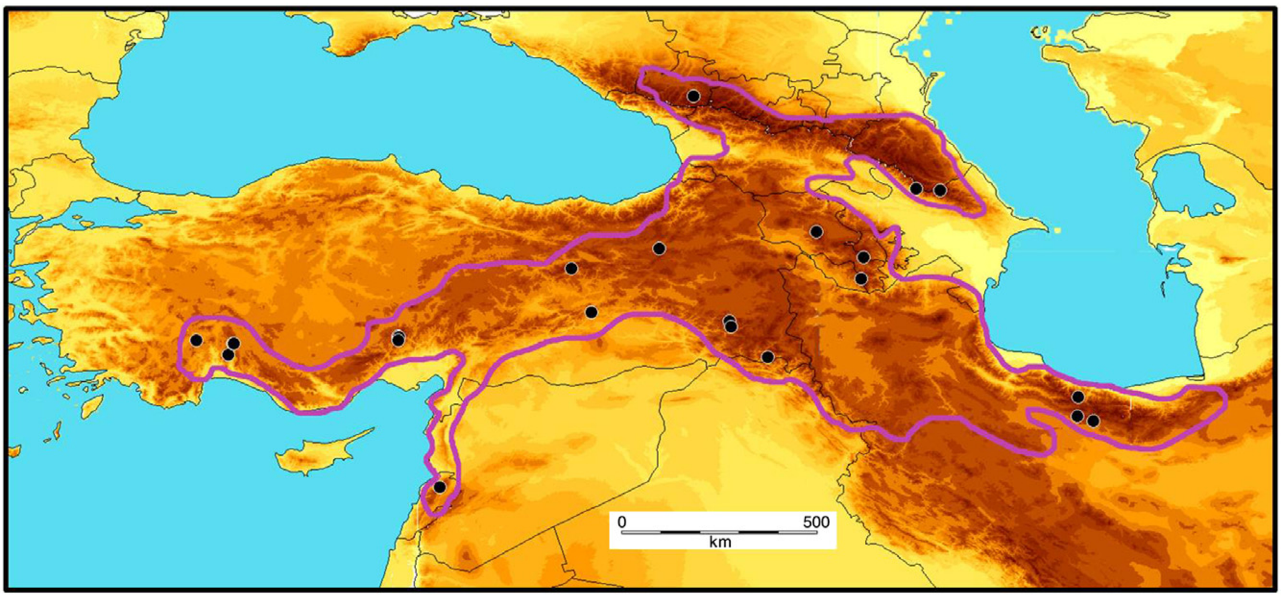

Figure 1. Distribution map of *Vavilovia formosa*: black dots are georeferenced from herbarium specimens in Edinburgh and Kew, bounding line shows estimated distribution based on additional specimens without accurate georeferences; *V. formosa* is only found at relatively high altitudes, so bounding line does not imply continuous distribution.

Figure 2. Distinct morphological features of *Vavilovia formosa*. A, leaf, with one pair of broad, thick and glabrous leaflets and a mucro-like rachis tip. B, flower, axillary, pedunculate and usually solitary. C, pod, 20 to 35 mm in length and prone to dehiscence at full maturity.

During the first expedition to Ughtasar, a vast population of *V. formosa*, some 7.5 hectares in size, was located and was in full bloom (Fig. 3A). Samples of all plant organs were taken for herbarium and chemical and molecular analysis, fresh parts of stems, leaves and flowers were fixed in Carnoy I, a 3:1 solution of ethanol and glacial acetic acid for anatomical, morphological and cytogenetic tests, and whole plants were collected for *ex situ* conservation. The expedition to the Geghama Mountains located further populations, but also discovered that one had been completely destroyed by grazing domestic and wild animals (Fig. 3B).

The second expedition to Ughtasar took place when early frost had begun to destroy most of the flowers (Fig. 3C). A small number of pods with immature and mature seeds were collected for further chemical analysis and potential *in vitro* propagation. It was not possible to collect the already shattered seeds because they had apparently been collected by mice (Fig. 3D).

MORPHOLOGICAL AND CHEMICAL CHARACTERIZATION

The stems of the Armenian population of *V. formosa* were found to have two non-prominent wings, whereas its leaves have helio-xeromorphic adaptations as a consequence of growing on sunlit mountain slopes. Leaflets of *V. formosa* are covered with a thick cuticle and have slightly sunken stomata and strongly developed palisade tissue (Fig. 4A). The leaflet palisade tissue cells are elongated, narrow and arranged in three rows, developed in order to survive in its natural habitat (Petrova, 1973). The anatomy of the stipules is similar to that of leaves, whereas the cross section of the petioles is triangular. The cross section of the rachis tip is elliptical with one layer of palisade cells on the adaxial side. The calyx has an oval cross section with thick cuticle covering the outer epidermis (Zorić *et al*., 2010).

The androecium in *V. formosa* is diadelphous, with fused filaments and spherical, two-parted anthers. The pollen grains of *V. formosa* are ellipsoid, with a thin exine and one pore. The fertile pollen grains are easily coloured by staining, with some beginning to germinate (Fig. 4B). A high average vitality of pollen grains (93.3%) shows good potential for *in situ* seed production, whereas sterile pollen grains are smaller and often deformed (Atlagić *et al*., 2010). The youngest leaves are usually used for determining the chromosome number by the acetocarmine method. Most of the *V. formosa* cells in the preparations of the material collected in Armenia were in interphase, but some were in metaphase and anaphase (Fig. 4C), confirm-

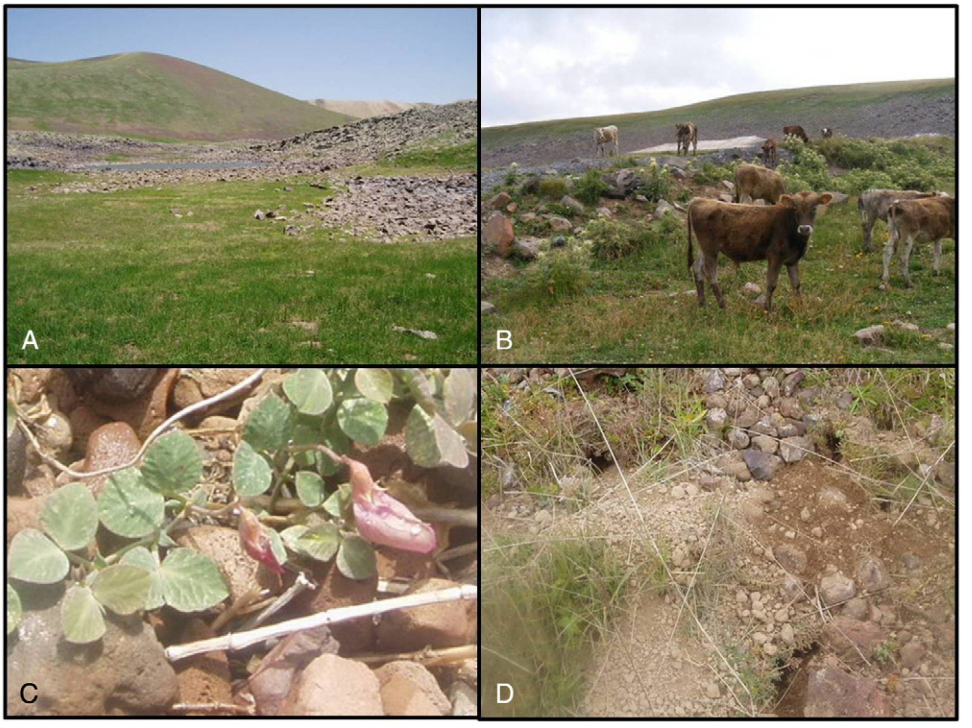

Figure 3. Details from *Vavilovia formosa in situ* research in 2009. A, the distant slope of the Ughtasar Mountain with a *V. formosa* population; the greatest biotic and abiotic threats to a successful *in situ V. formosa* preservation. B, grazing domestic and wild animals. C, early frost. D, mice.

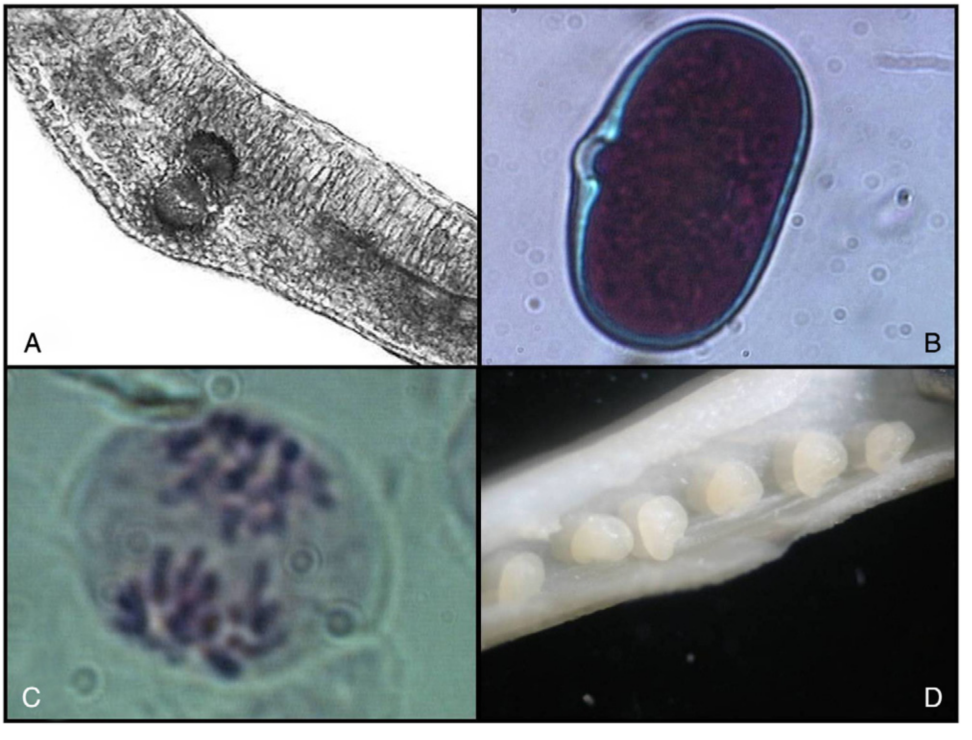

Figure 4. Details of anatomical, morphological and cytogenetic analysis of *Vavilovia formosa*. A, cross section of the leaflet with evident palisade tissue. B, fertile and germinating pollen grain. C, anaphase in a dividing leaf cell. D, lateral section of an ovary showing several developing ovules (Atlagić *et al*., 2010; Zorić *et al*., 2010).

Table 1. Basic chemical composition and some quality parameters (g kg^{-1}) in dry matter of organs of *Vavilovia formosa* (Zeremski-Škorić *et al.*, 2010)

	Root	Stem	Leaf	Seed
Nitrogen	19.21	22.52	35.31	57.25
Sulphur	1.61	1.39	2.71	3.38
Calcium	5.72	8.26	27.64	–
Potassium	5.82	7.42	14.36	–
Magnesium	1.39	1.56	2.85	–
Crude protein	120.06	140.75	220.69	357.81
Neutral detergent fibre	467.74	452.74	364.05	–
Acid detergent fibre	320.12	344.64	246.67	–
Lignin	90.48	58.10	42.50	–

ing reports of 14 chromosomes in somatic cells of *V. formosa* (Abramova, 1971). The majority of the fertilized ovaries contain seven or eight spherical ovules (Fig. 4D). It appears that there is a significant level of ovule abortion as *V. formosa* pods usually only contain three to five mature seeds (Mikić *et al.*, 2010).

The extent of variation for the determined parameters of the chemical composition in *V. formosa* (Table 1) is not known, not allowing any error estimates or indication of variability between individuals. Of the vegetative organs of the population of *V. formosa* from Ughtasar, leaves were richest in nitrogen and other important macroelements such as sulphur, calcium, potassium and magnesium (Zeremski-Škorić *et al.*, 2010). The average crude protein content in *V. formosa* leaf dry matter (220.69 g kg^{-1}) is similar to the values in its closest relatives, such as pea (*Pisum sativum* L.) and vetch (*Vicia* spp.) (Krstić *et al.*, 2007). The nutritional value of *V. formosa* forage may also be considered high because of its apparently high digestibility. Values of neutral detergent fibre (NDF) and acid detergent fibre (ADF) content in stem and leaf dry matter are similar to those of the most significant perennial forage legumes, such as lucerne (*Medicago sativa* L.) and red clover (*Trifoilum pratense* L.) (Vasiljević, Milić & Mikić, 2009). The lignin content in stems and leaves are far lower than in lucerne and red clover and in the model legume *Medicago truncatula* (Mihailović *et al.*, 2011). The crude protein content in seed dry matter of *V. formosa* (357.81 g kg^{-1}) is rather high in comparison with many economically important grain legumes (Mikić *et al.*, 2006). Because of a limited number of available *V. formosa* seeds collected in Ughtasar, it was not possible to determine the content of anti-nutritional factors.

Ex situ Conservation and *in vitro* Propagation

So far, only short-term success at *ex situ* conservation has been achieved for *V. formosa*, notably in the former USSR (Makasheva *et al.*, 1973) and the UK (Cooper & Cadger, 1990). Today, the only place where *ex situ* conservation is carried out is in the plot *Flora and Vegetation of Armenia* in the Botanical Garden in Yerevan (Akhverdov & Mirzoeva, 1964). The specimens of *V. formosa* collected in the Ughtasar and Geghama Mountains in 2009 were transplanted into the alpine hill with artificial scree in Yerevan, to mimic that which had been observed of the growth habit *in situ*, with the rhizomes oriented almost horizontally to the ground or at a small decline, but never directed vertically downwards. The plants in the plot require only moderate watering. About 12 plants were successfully established, with the first signs of rooting and new leaves appearing after 10 days (Akopian *et al.*, 2010). At the present time, the plants are in a vegetative stage, with no fully developed flowers so far (Fig. 5A).

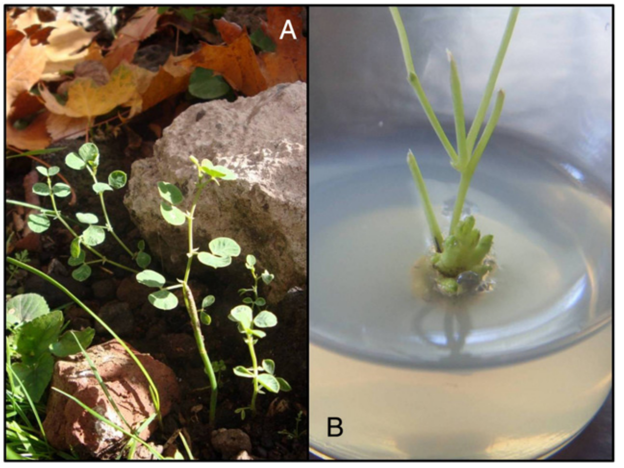

Figure 5. Achievements in Yerevan. A, successfully transplanted *Vavilovia formosa* specimens from the Ughtasar Mountain in *ex situ* conservation. B, shoots developing of *V. formosa in vitro* culture.

From the few mature seeds collected on Ughtasar Mountain, a successful *in vitro* culture of *V. formosa*

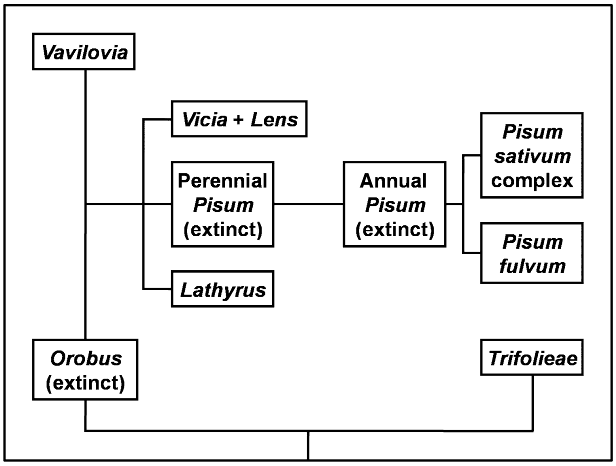

Figure 6. Evolution of tribe Fabeae based upon comparative morphology and classical genetics.

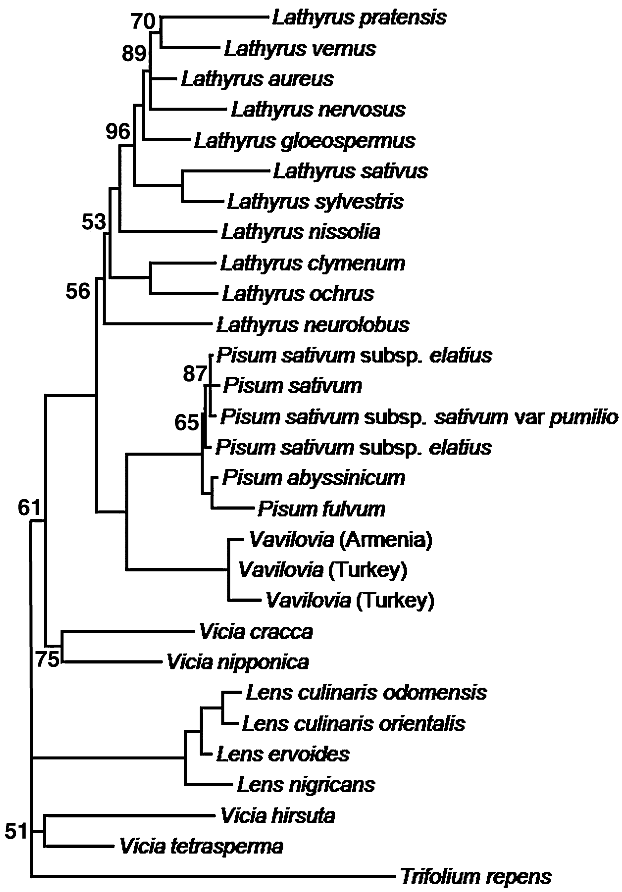

Figure 7. A phylogenetic tree of tribe Fabeae based upon molecular tools.

has been developed at both Agritec Plant Research Ltd (Šumperk, Czech Republic) and the Institute of Botany (Yerevan, Armenia). These plants are developing vegetatively (Fig. 5B), but the rooting is progressing slowly.

A WINDOW ON THE LEGUME PAST: MOLECULAR TAXONOMY

The exact position of *V. formosa* in the tribe has been frequently discussed since its description (Kenicer *et al.*, 2009). Once defined as the only species of a separate genus, it has been commonly regarded as closest to the common, extinct ancestor of the whole tribe (Fig. 6), sometimes referred to by the reintroduced Linnean name of *Orobus* (Fedorov, 1939; Makasheva, 1975), particularly because of its scattered habitats high in mountain refugia, where it has been regarded as being a kind of living fossil.

One of the first attempts to apply molecular tools to resolve the issue of the position of *V. formosa* and the taxonomy of Fabeae used herbarium specimens of this and approximately 30 other species of all other genera of Fabeae. This research targeted four phylogenetically informative regions, namely plastid maturase K (*matK*), *trnL-trnF* and *trnS-trnG* fragments and the internal transcribed spacer (ITS) region of nuclear DNA. The results of both maximum parsimony and Bayesian analysis of combined sequence data show that *V. formosa* belongs to the same clade as *Lathyrus* and *Pisum*, but with a distinct status (Smýkal, Kenicer & Mikić, 2009). The outcomes of this preliminary molecular research (Smýkal, Kenicer & Mikić, 2010) also include that Fabeae are a monophyletic relative to Trifolieae and that *Lathyrus*, *Lens* L., *Pisum* and *Vavilovia* are all monophyletic, that *Vicia* is paraphyletic, with all other genera nested inside it, and that *Vavilovia* is a sister to *Pisum*; together these two are sister to *Lathyrus* (Fig. 7). However, it is necessary to mention that some other recent research using molecular tools, nrDNA ITS and plastid DNA sequences, have led to *V. formosa* being treated not as a species in its own genus, but as *P. formosum* (Oskoueiyan *et al.*, 2010). It may be concluded that these contrasting viewpoints simply confirm that numerous additional and combined molecular and morphological approaches are needed to achieve a true and lasting consensus on the status of this iconic species.

THE FUTURE OF *VAVILOVIA*

The last 5 years have witnessed a considerable resurgence in interest and progress in understanding more of this hitherto enigmatic legume. Further research on *V. formosa* will surely split into narrowly specialized approaches to individual issues, with numerous positive consequences expected. The primary task in the future must be to develop and implement a coherent strategy to improve the *V. formosa in situ* preservation, which should include a special focus on populations in Armenia and Turkey as the most accessible. Efforts for *ex situ* conservation are encouraging, but there is clearly much room for improvement. The recent progress in *in vitro* propagation also shows promise. If and when the flowers develop fully, it will be possible to perform several interspecific hybridization combinations of *V. formosa* with pea, common vetch (*Vicia sativa* L.) or grass pea (*Lathyrus sativus* L.). This would check the reports on achievements at State Scientific Centre N. I. Vavilov All-Russian Research Institute of Plant Industry of Russian Academy of Agricultural Science (VIR) (Golubev, 1990), where F_1 plants were obtained from crosses between pea and *V. formosa*, but without developed F_2 seeds or plant material being saved. This, with the use of molecular tools, should help shed more light on the evolution of tribe Fabeae. From a wider perspective, *V. formosa* could be used as a potential source of adaptive traits, especially in the area of mechanisms of perenniality and as a source of resistance to various biotic and abiotic stress.

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