

## On seedling structure in *Pisum* L., *Lathyrus* L. and *Vavilovia* Fed. (Fabeae: Fabaceae)

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*Summary:* The seedling structure of representatives of three genera in tribe Fabeae (Fabaceae) was studied with special reference to number and morphology of the first scaly leaves (cataphylls), and juvenile leaves as well as to some other features. The correlation between the number of cataphylls and life endurance is discussed. The trait is proposed to be more dependent on life form and environment than on the taxonomical position of species.

*Keywords:* Fabaceae, Fabeae, *Pisum*, *Lathyrus*, *Vavilovia*, seedling, cataphyll, taxonomy, life form

The morphogenesis of plants is characterized by certain peculiarities. Some of them are open growth and slight (compared to animals) extent of integration which enables a high degree of autonomy of morphogenesis in distinct organs and their parts (LODKINA 1983). Shoot development includes repeated formation of elementary modules (internode–node–leaf–axillary bud) but the ontogeny of every component can have some specific features on different stages. Earlier developmental stages are of special interest for investigations on morphogenesis, reconstruction of systematic and phylogenetic relations and uncovering possible evolutionary pathways. The legume family (Fabaceae) represents very interesting objects for studies on early steps of ontogeny due to expressed heterophylly (VASSILCZENKO 1937). The number of works discussing the structure of their seedlings from a phylogenetic point of view is comparatively low. Only the already cited and in some points essential work of VASSILCZENKO (1937) and the reviews of COMPTON (1912) and DUKE & POLHILL (1981) may be listed here.

To date, expressed attention of world scientific community is compelled to the system of the tribe Fabeae Rchb. (= Vicieae (Adans.) DC.). Numerous publications are devoted to a possible solution of the still debatable systematic position of the genus *Vavilovia* Fed. presumably with methods of molecular systematics (SMYKAL et al. 2009; SINJUSHIN et al. 2009; OSKOUHEYAN et al. 2010). The obtained data point at a more proximity of vavilovia to pea than to vetchlings (even with perspectives of treating vavilovia as species within genus *Pisum* L. as *Pisum formosum* (Stev.) Alef.). Morphological and anatomical features of this rare plant were poorly studied due to difficulties to approach this material (MAKASHEVA et al. 1973; PETROVA 1973). The present paper represents the results of comparative studies on the structure of *Vavilovia*, *Pisum* and *Lathyrus* seedlings.

### Materials and methods

The seedlings of *V. formosa* were collected on 17 July 2009 during an expedition in the vicinity of Mt. Ughtasar (Syunik Distr., Armenia) and herbarized. The herbarium material was then macerated by boiling in a mixture of ethanol (96%), water and glycerol (1:1:1). Seedlings of other species were obtained via germination of seeds in laboratory conditions in Petri dishes on humid

filter paper and subsequent growing up in hydroponic conditions. Different *Pisum* accessions were chosen from collections of the Genetics Dept. of Moscow State University and the John Inness Centre (Norwich, Great Britain), as well as from the collection of the Institute of Botany of the National Academy of Sciences of Armenia. We also analyzed the structure of seedlings obtained from 11 *Lathyrus* species representing different sections (genus structure sensu KUPICHA (1983)). The following species were studied: *L. sativus* L., *L. tingitanus* L., *L. sylvestris* L., *L. cicera* L. (sect. *Lathyrus*); *L. pratensis* L. (sect. *Pratensis*); *L. aphaca* L. (sect. *Aphaca*); *L. ochrus* DC., *L. chymenum* L. (sect. *Clymenum*); *L. chloranthus* Boiss. & Balansa (sect. *Cicercula*); *L. nissolia* L. (sect. *Nissolia*); *L. vernus* Bernh. (sect. *Orobus*). Descriptions of the seedling structure of some vetchling species were also taken from published data (COMPTON 1912; VASSILCZENKO 1937; GULENKOVA 1967, 1974, 1977; GULENKOVA & VIKTOROV 1990).

Embryo structure was studied by means of scanning electron microscopy. Seeds were soaked in water for 12 h, then dissected and prepared according to the protocol described by SINJUSHIN & DEMIDENKO (2010).

Seeds were weighted with electronic scales Pioneer PA64 (Ohaus). Statistical treatment of obtained results was carried out applying StatSoft Statistica 8 software.

## Results

### Peculiarities of germination

The cultivation of vavilovia beyond its natural habitat has turned out to be very difficult and almost impossible for a long time (MAKASHEVA et al. 1973; GOLUBEV 1990). Certain results on ex situ conservation of this species were obtained recently (MIKIC et al. 2010). Descriptions of germination of vavilovia seeds in laboratory conditions exist (e.g., COOPER & CADGER 1990) but they don't mention any special approaches to facilitate soaking (scarification, stratification etc.). Field observations demonstrate that juvenile plants of *Vavilovia* are very rare; possibly this plant propagates vegetatively. MAKASHEVA et al. (1973) propose that seed reproduction of *Vavilovia* is suppressed due to daily drops of temperature in highlands (this may cause abscission of flowers and unripe fruits) or represents the feature of certain specialization. Seed and embryo structure of *Vavilovia* are described precisely in the fine monograph of KIRKBRIDE et al. (2003).

All chosen forms of *Pisum sativum* subsp. *sativum* germinated without special treatment. Seeds of *P. fulvum* and partially *P. sativum* subsp. *elatius* did not soak without preliminary scarification. Seeds of some vetchlings (*L. sylvestris*, *L. pratensis*) soaked in laboratory conditions with difficulties and were scarified. Due to small amounts of seeds of some species detailed statistical analysis of the efficiency of soaking (like NOZZOLILLO (1977)) was not conducted.

All analyzed species exhibit a similar type of germination. Fleshy cotyledons remain in the seed coat during the whole ontogeny and do not emerge above ground level ('cryptohypogaeal seedling' sensu DUKE & POLHILL (1981)).

### Number and morphology of the first scaly leaves

The expressed heterophylly is characteristic for the whole legume family and studies on seedlings are important for uncovering evolutionary relations of certain groups. Many authors agree that seedlings of Fabaeae are strongly specialized. The existence of two basal scale-like leaves ('cataphylls' sensu DUKE (1965) and DUKE & POLHILL (1981)) is interpreted as one of the most

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characteristic features of vicioid legumes. For example, VASSILCZENKO (1937: 418) notes that “presence of two alternate scaly leaves in tribe Viciae is constant”.

The presence of two alternate cataphylls in pea was mentioned many times (see MAKASHEVA et al. 1973; MAKASHEVA 1979). Garden pea represents a traditional model object in genetics and developmental biology and numerous mutants with altered morphology have been described (BLIXT 1972). BLIXT (1972) describes pea seedlings and lists mutations which modify seedlings' structure but even mutational variability does not distort the number of cataphylls. The only known mutation which strongly reduces the third leaf making it scale-like is *stamina pistilloida* (*stp*) (TAYLOR et al. 2001). These data allow to indicate this feature as strongly stable.

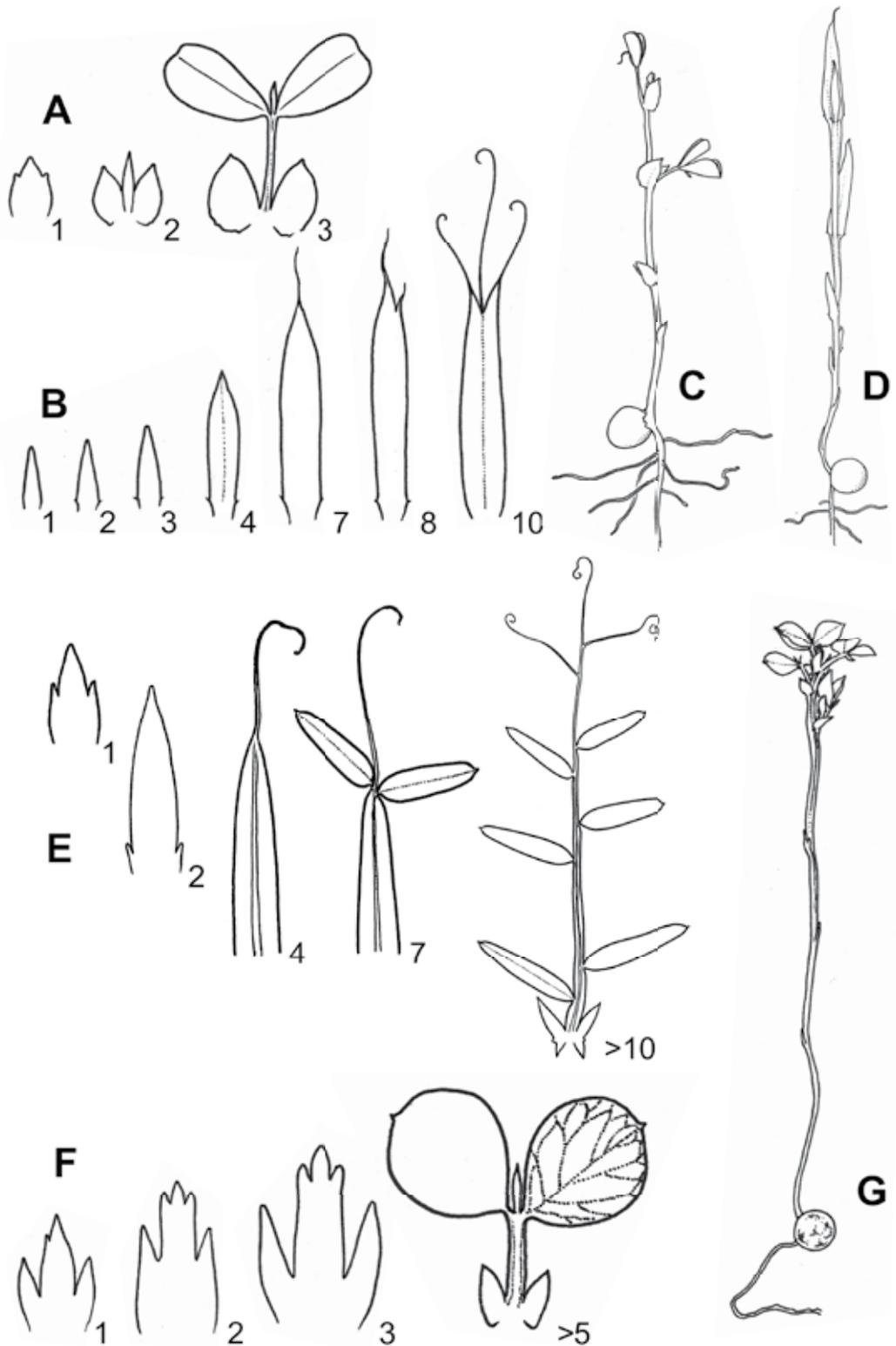
All observed forms of pea developed two green cataphylls which were additionally pigmented by anthocyanin in *P. fulvum* in the same way as epicotyl and first internodes. Similar habit was observed in *L. aphaca*.

Cataphylls of all studied species are characterized by a more or less oblong shape and they are clearly tripartite (Fig. 1). Median part corresponds to the lamina (possibly the rachis) while the lateral ones correspond to stipules. In *cochleata* mutants of pea, which lack stipules in basal nodes, the cataphylls consist of the median part only (SINJUSHIN et al. 2011).

Three basal scaly leaves were observed in *Vavilovia* seedlings. The first two lacked pigmentation, the third one was green. Cataphylls of *Vavilovia* are characterized by a median part bearing three lobes. This feature was not recorded in other species studied for this paper (Fig. 1F). This peculiarity points at a homology between the median part of the *Vavilovia* cataphyll and a whole lamina rather than a rachis. Other species with compound leaves have an entire median part of cataphyll. The observed phenomenon is possibly connected with the fact that cessation of proliferation of leaf primordium occurs on different stages in different species. When proliferation ceases after leaf initiation, an entire scale develops. If it occurs after differentiation of upper leaf and lower leaf (first ternation), the cataphyll becomes trifid. Primordia of lateral leaflets seem to initiate in *Vavilovia* cataphylls.

The number of basal scaly leaves is different in the studied vetchling species. Two cataphylls develop in *L. odoratus*, *L. sativus*, *L. cicera*, *L. nissolia*, *L. aphaca* and *L. chloranthus*. VASSILCZENKO (1937, 1965) described also two cataphylls in seedlings of *L. tuberosus* L., *L. annuus* L., *L. mulkaka* Lipsky, *L. pallescens* K. Koch and *L. inconspicuus* L. *Lathyrus vernus*, *L. pratensis* and *L. tingitanus* bear three cataphylls, *L. sylvestris* has four (Fig. 1).

Hence, the infrageneric polymorphism of cataphylls' number within *Lathyrus* does not coincide with section structure of this genus. The type section *Lathyrus* includes species with two or three (*L. tingitanus*) scaly leaves. ASMUSSEN & LISTON (1998) together with KENICER et al. (2005) point at the somewhat isolated position of *L. tingitanus* in type section revealed in studies on different types of molecular markers. Except this, section *Lathyrus* is heterogenous in life forms (annuals *L. odoratus*, *L. sativus*; perennials *L. latifolius*, *L. sylvestris* etc.). *Vavilovia* exhibits more similarity with vetchlings than with peas in this feature, and this circumstance obscures its taxonomical relations even more. On the other hand, three studied genera follow in general the tendency revealed by NOZZOLILLO (1985) for chickpeas: annual forms (*Pisum*, *Lathyrus* p.p.) bear two cataphylls, while perennials (*Vavilovia*, *Lathyrus* p.p.) have more than two cataphylls. A significant variability of cataphyll number (2–5) was reported earlier for *Vicia* (NOZZOLILLO



**Figure 1** A–G. Seedling morphology of the studied species. Numbers indicate the sequential number of the leaf on the main axis. A, C - *Pisum sativum* 'Kapital'. B, D - *Lathyrus ochrus*. E - *L. clymenum*. F, G - *Vavilovia formosa*. Scaling not maintained. Drawings: A. A. Sinjushin.

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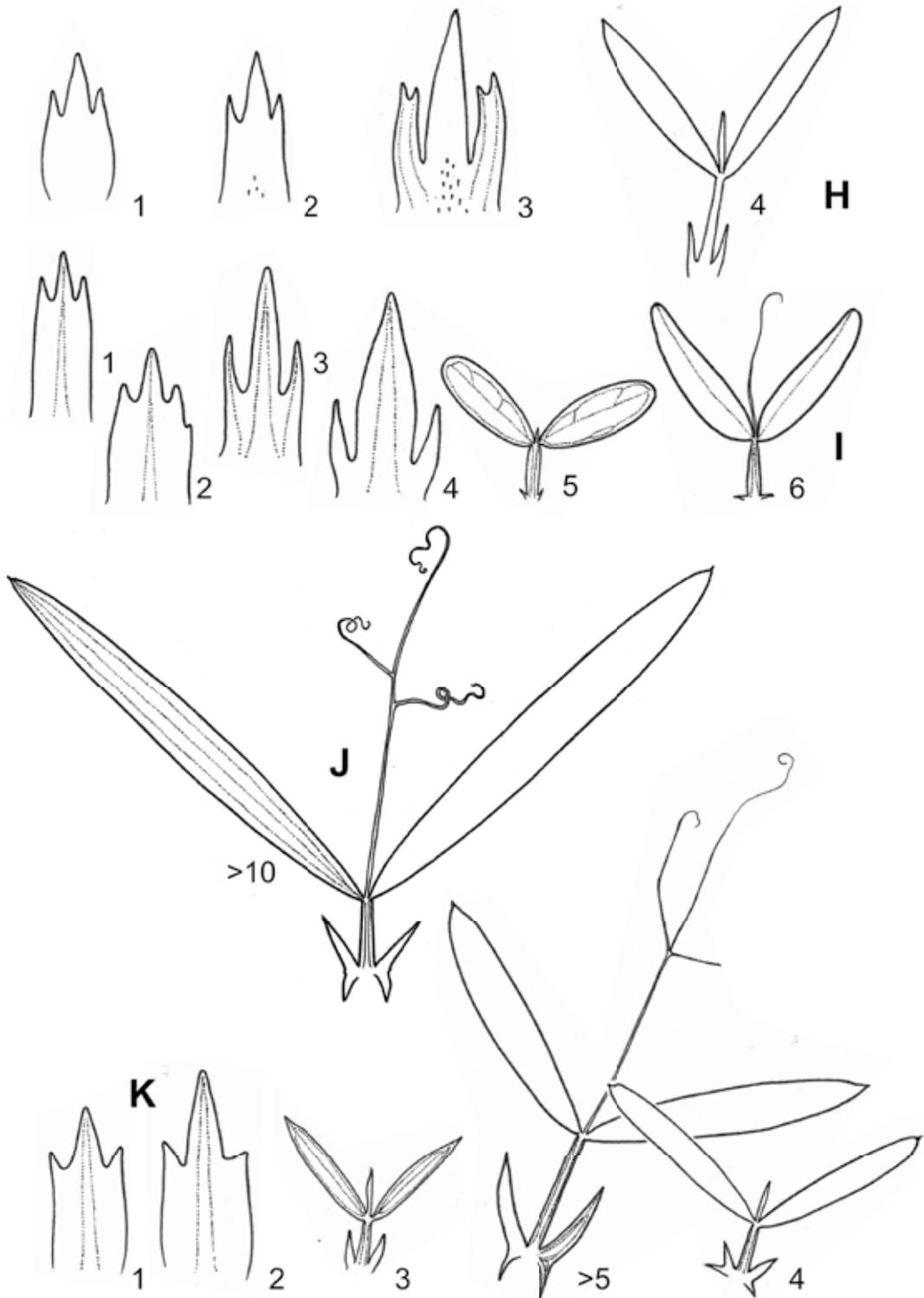


Figure 1 H–K. Seedling morphology of the studied species. Numbers indicate the sequential number of the leaf on the main axis. H - *L. tingitanus*. I, J - *L. sylvestris*. K - *L. sativus*. Scaling not maintained. Drawings: A. A. Sinjushin.

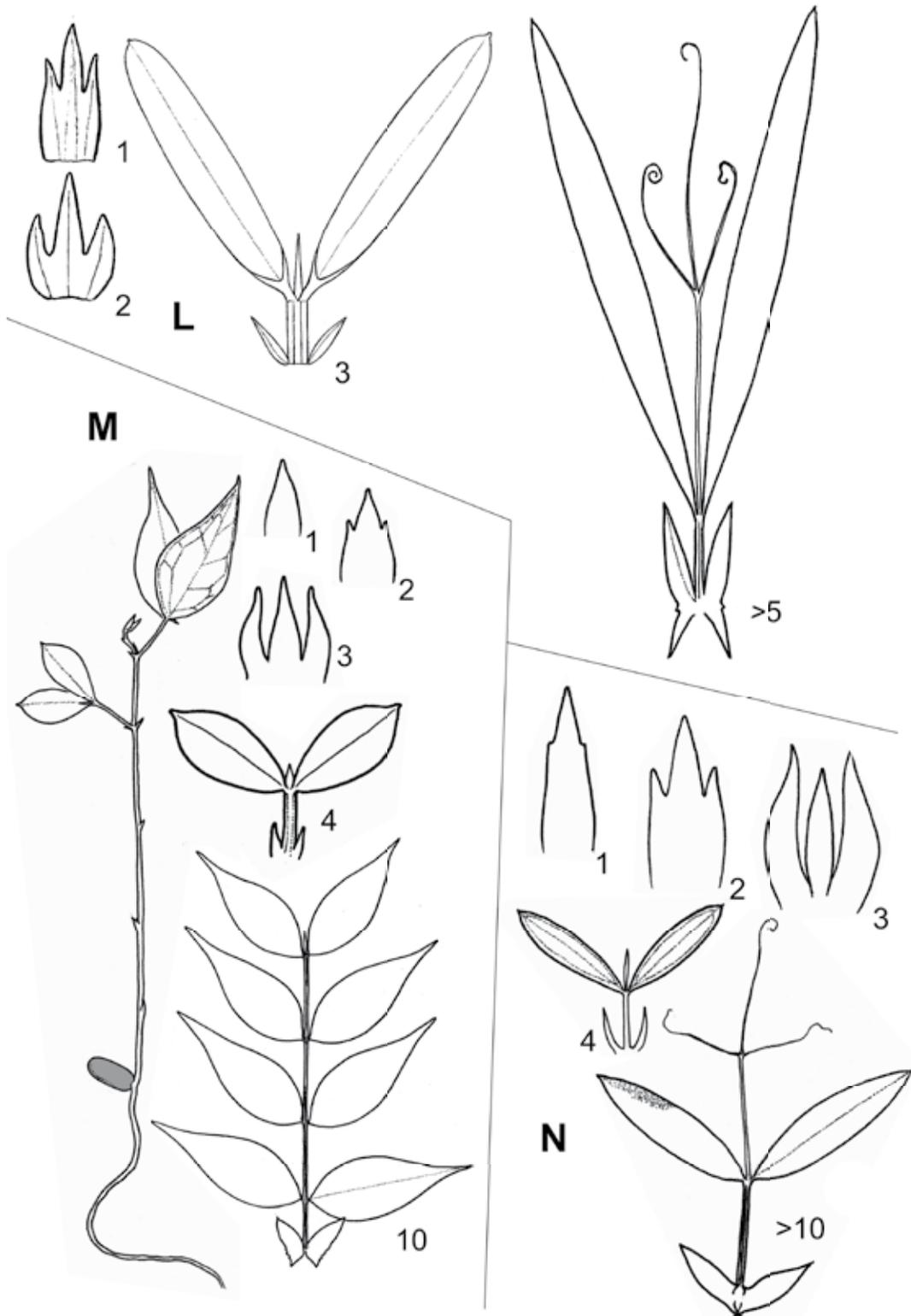
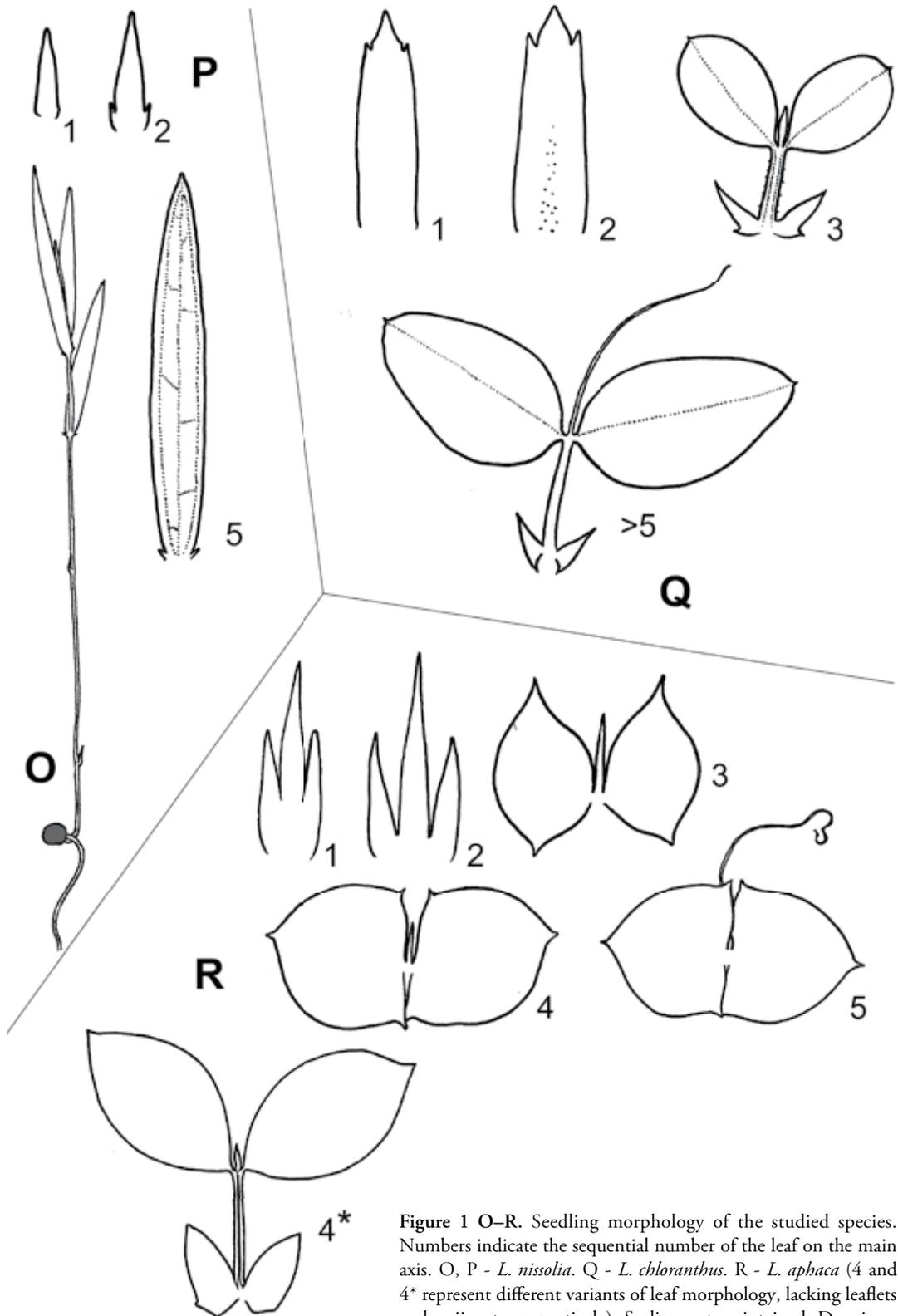


Figure 1 L–N. Seedling morphology of the studied species. Numbers indicate the sequential number of the leaf on the main axis. L - *L. cicera*. M - *L. vernus*. N - *L. pratensis*. Scaling not maintained. Drawings: A. A. Sinjushin, J. A. Akopian (L 1–3).

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**Figure 1** O–R. Seedling morphology of the studied species. Numbers indicate the sequential number of the leaf on the main axis. O, P - *L. nissolia*. Q - *L. chloranthus*. R - *L. aphaca* (4 and 4\* represent different variants of leaf morphology, lacking leaflets and unijugate, respectively). Scaling not maintained. Drawings: A. A. Sinjushin.

1977). The number of first scaly leaves is also variable in different *Cicer* species (tribe Cicereae Alef.) (NOZZOLILLO 1985). The following regularity was observed: number of cataphylls always exceeds two in perennials and is rarely higher than two in annual species.

It is notable that scaly or modified leaves also develop on annual aerial shoots of perennial species outgrowing from rhizomes in different Viciae. In some vetchlings the number of cataphylls on axillary sprouts sometimes exceeds their number in seedling (GULENKOVA 1974). This phenomenon is weakly studied in *Vavilovia* but certain differences were found between first ones and all subsequent leaves on axillary shoots when examining herbarium material (MW) of *Vavilovia*. For example, plants from Krasnodar region bear metaphylls with ovate leaflets but first leaves on axillary shoots are characterized by obovate leaflets.

It is unclear whether the number of cataphylls correlates with the taxonomical position of species or not. For example, some authors provide data on the proximity of the small sections *Aphaca* and *Pratensis* (ASMUSSEN & LISTON 1998; KENICER et al. 2005) or even unity between them (LEHT 2009). *L. aphaca* is an annual plant with two cataphylls while *L. pratensis* is perennial with three cataphylls. So at least at these features the mentioned species are distinct. However, some data on molecular phylogeny exist which evidence a significant distinctness of these species (RYZHOVA et al. 2007).

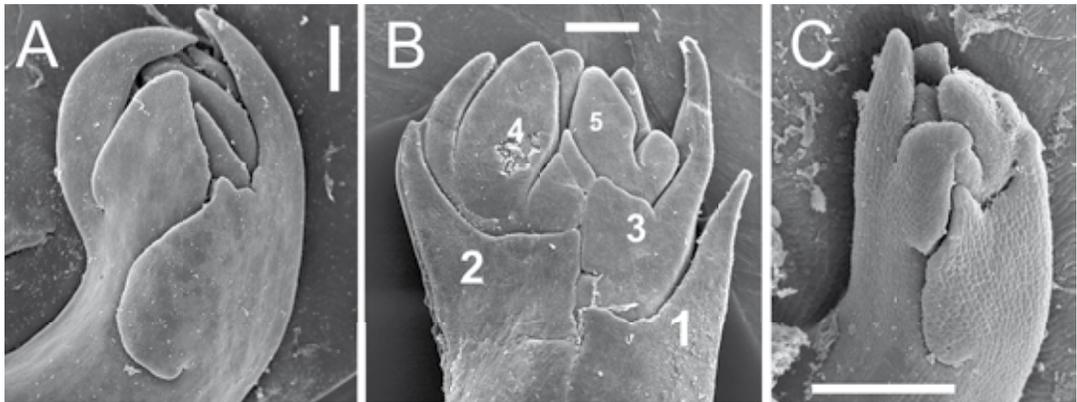
The number of cataphylls may vary even within species as demonstrated by illustrations and determination keys by NOZZOLILLO (1977). The first compound leaf can be the third or fourth in different subspecies of *Vicia sativa* L. A wide range of variation of this species was also reported by REPJEV et al. (1999). This feature is very stable in pea and we never observed any variability during long-term observations. Some vetchlings exhibit a variable manifestation of this trait (GULENKOVA 1977). Obviously, the stability of ontogeny is unequal within tribe.

The position of the first cataphyll is the same in all studied species, viz. on the outer (convex) side of the crooked embryo and, as a consequence, the seedling. Some data on the instability of this characteristic exist for *Cicer* species (NOZZOLILLO 1985).

Regardless of morphology, all leaves have alternate (distichous) phyllotaxis in all studied species.

A certain correlation between the number of scaly leaves and the longevity can possibly deal with peculiarities of germination. Numerous Fabae species are characterized by hard seeds. The adaptive aim of this feature is the possibility to accumulate seeds stored in soil which germinate in different time rather than simultaneously. Seeds which have been hibernating in ground for few years can be found in the layer of shed leaves and other organic remains. Growing through this layer requires protection for the apical meristem. In related tribes (Trifolieae, Galegeae), such protection is provided by cotyledons which emerge above ground level. In Fabae, cotyledons remain in the ground and the first leaves represent the only protection for the apex. Moreover, formation of large compound leaves is inappropriate because the first leaves often remain in soil. This fact may explain the strongly reduced habit of the first few leaves in Fabae. Some recent observations, however, contradict these proposals: the first cataphylls do not envelope the apex before germination in *L. tingitanus* (Fig. 2B).

It can be proposed that seed germination is more prolonged in perennial plants than in annuals. Germination of the latter ones should happen in the same or subsequent season. Oppositely, perennials sprout during a long period after dissemination when a thicker and denser layer of

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**Figure 2.** SEM images of seedling apices before germination. A - *P. sativum* 'Kapital'. B - *L. tingitanus* (sequential numbers of leaves are indicated). C - *V. formosa*. Scale bar 300  $\mu$ m.

soil is accumulated. On the other hand, some perennials grow in habitats where accumulation of soil is very slow. More analysis is needed and certain results could be obtained by studying the correlations between the number of cataphylls and the duration of seeds' hibernation period.

### Morphology of the first compound leaves

The third leaf of *Pisum sativum* is unijugate, with a grooved leafstalk and an axis ending with a very short tendril-like organ. Leaflets are obovate (more or less ovate on subsequent leaves). In *P. fulvum* leaflets of the third leaf have an entire margin while margins of subsequent leaves are dentate. Leaves of the median part of pea stem ('metaphylls' sensu DUKE (1965)) are paripinnate, with two or three pairs of leaflets (unijugate in *P. fulvum*), with a rachis rounded in cross-section.

The possibility of formation of untypical trifoliolate leaves (as the first compound leaves) in *Vicia faba* L., *V. cracca* and *P. sativum* was recorded by SEFEROVA (2001).

Leaves of *Vavilovia* plants from the Armenian part of the natural habitat possess obovate leaflets (Fig. 1F) and a grooved rachis. Leaflets of Daghestan plants are ovate. These differences were sufficient for some authors to describe two species (*Alphotropis aucheri* (Jaub. & Spach) Grossh. and *A. formosa* (Stev.) Grossh. (GROSSHEIM 1949)) or two intraspecific taxa (*Pisum formosum* var. *typicum* Gov. and var. *microphyllum* Ser. (GOVOROV 1937)). In earlier works it was demonstrated that leaf features are insufficient for a clear distinction of different species (SINJUSHIN & BELYAKOVA 2010). No qualitative differences between basal and apical leaves were found in Armenian plants. It can be concluded that leaves of *Vavilovia* have features which manifest as juvenile in pea (number and shape of leaflets, rachis cross-section shape and apex).

All *Vavilovia* leaves beginning from the third one are unijugate with grooved rachis. Rachis terminates with a cusp. The anatomy of this structure was analyzed by PETROVA (1973). The cusp is clearly bifacial. Interestingly, hybrids of crosses between *V. formosa* and *P. sativum* bear rather pinnate trifoliolate leaves; unfortunately, there are no data on number of cataphylls (GOLUBEV 1990). A terminal leaflet (not tendril) is normally present in some vicioid legumes (*Vicia argentea* Lapeyr., *V. semiglabra* Rupr. ex Boiss., etc.) but it's relatively rare. Some representatives of section Orobis (*Lathyrus vernus* Bernh., *L. aureus* (Stev.) Bornm., *L. venetus* Rouy, *L. niger* (L.) Bernh., etc.) comprise a kind of exclusion: the rachis end terminates with a soft flattened cusp which can be interpreted as reduced terminal leaflet.

The unusual characteristic feature of *Vavilovia* is the symmetry of leaflets on the upper leaves. Leaf half directed to leaf base is somewhat larger than one directed to leaf tip in all examined specimens of pea and vetchlings (basiscopic leaflet). Opposite situation is observed in *Vavilovia* (acrosopic leaflet). Leaflets of this plant are tough and leathery but this phenomenon is not unique for the whole tribe.

Leaflets of *V. formosa* are supervolute in bud like in *Lathyrus* but not plicate (folded along the midvein in most *Vicia* species except *V. biennis* L. and *V. faba* p.p., *Lens* and *Pisum*; furthermore, leaflets are plicate in members of the related tribes Trifolieae and Cicereae). This peculiarity was classified by KUPICHA (1981) as important for distinguishing genera in tribe, although she presents data on the presence of both types in *V. faba*. No supervolute leaflets are known in pea even in mutational variations.

Plants of *L. nissolia* develop no leaflets but linear phyllodia. Similar phyllodia can be observed in *L. ochrus* and *L. chymenum*, but on later developmental stages they are substituted by true compound leaves (Fig. 1B, D, E).

Normally, leaflets are also absent in *L. aphaca*, but VASSILCZENKO (1937) presented data on unijugate habit of third and fourth leaves of this species' seedling. These observations could be confirmed by new material (Fig. 1R): either third and fourth leaves were unijugate or all leaves lacked leaflets.

### Other characteristics

Seedling size: COMPTON (1912) and later VASSILCZENKO (1937) point at the significance of seedling size in phylogenetic reconstructions. Sizes of seedlings are obviously correlated with seed sizes; cited authors propose that large seeds and seedlings are typical for primitive taxa. Weights of all studied seeds formed more or less a gradual range from  $0.011 \pm 0.001$  g (*L. nissolia*) to  $0.209 \pm 0.047$  g (*L. sativus*), average weight  $\pm$  standard deviation is presented. According to data generously provided by E. Sherbakova, seeds of Armenian *Vavilovia* obtained at the plot 'Flora and Vegetation of Armenia' (Institute of Botany, National Academy of Sciences, Armenia) were of different weight (0.048–0.285 g) but only the largest ones germinated in experimental conditions. If their weight is considered to be normal for mature seeds, *Vavilovia* exceeds all other studied species in this parameter.

However, it is obvious that large pea seeds result from artificial selection and their weight strongly depends on cultivation conditions. In our opinion, this feature is not significant enough for specification of *Vavilovia's* position within Fabaeae.

Seedling pubescence: Seedlings bear scant pubescence in a form of pigment-containing glands in some species (*L. chloranthus*, *L. tingitanus*, *L. sylvestris*, *L. pratensis*). Such pubescence is observed from the beginning of the epicotyl in *L. pratensis* or from the first internode (*L. tingitanus*). In *L. tingitanus* this pubescence also spreads on cataphylls, the first being glabrous and second and third partially covered with glands. The adaxial surface of upper leaves is covered by short simple trichomes in *L. pratensis* while cataphylls and first metaphylls have glandular pubescence.

Epicotyl length: The epicotyl is elongated and has a length comparable with subsequent internodes in all species except for *L. sativus* and *L. sylvestris* which possess very short epicotyls.

## Conclusion

The observations conducted on seedling structure in representatives of *Vavilovia*, *Pisum* and *Lathyrus* show a common structural plan. Seedling features can be used to identify any of the analyzed species but efforts to compare them to their position within the tribe uncover certain difficulties. The manifestation of the most variable characteristic, the number of cataphylls, is presumably connected to life form (annual or perennial) rather than to the position in the tribe but usually stable within the section. The most problematic genus, *Vavilovia*, exhibits more similarity with vetchlings than with pea which, in general, corresponds to existing data on morphological features and contradicts to results of molecular taxonomy.

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