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Comparative study on the ontomorphogenesis of herbaceous and shrubby *Clematis* species (Ranunculaceae) based on the evo-devo concept

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Summary: The life forms of six species of *Clematis* L. were studied on the basis of an analysis of their ontomorphogenesis. The herbaceous life forms in this genus can be recognized as derivatives. They emerged due to a transformation of woody *Clematis* ontomorphogenesis. The main mode of this transformation in the series from shrubs to herbs is acceleration.

Keywords: Ranunculaceae, *Clematis*, ontomorphogenesis, adaptation, acceleration, retardation, evolution

The question about the ways of evolutionary transformations of life forms of angiosperms is far from being resolved (Serebryakov & Serebryakova 1972). It proofs the importance of studying mutual relations of life forms within concrete taxa of different ranks (Serebryakov & Serebryakova 1969). In this respect, a comparative study of ontomorphogenesis of related taxa with different life forms is rather promising. According to Ejikov (1939), evolutionary changes of adult forms are correlated with evolutionary changes of their individual development. Evolutionary changes of ontogenesis are a morphological expression of evolution. They lead to a connection of ontogenesis with phylogenesis. Beklemiyshev (1964) also considered some phylogenetic reorganizations to have occurred by means of changes of ontomorphogenetic stages. The deviation of ontomorphogenesis may occur without changing the sequence of stages: by means of slowing down of the development (retardation) or by means of accelerating the development (acceleration) in response to the worsening of environmental conditions; or with changing the sequence of stages: by means of excluding or addition of new ones.

Due to comparatively few data on *Clematis* ontomorphogenesis (Winkler 1888; Lubbock 1892; Sterckx 1897; Thomas 1914; Tsinger 1958; Ims 1964; Ivanova 1966; Csapody 1968; Volosenko-Valenis 1971; Satsyperova 1972; Tamura et al. 1977; Barykina & Chubatova 1981; Tonkova 2010), we performed the study of ontogenesis of 6 *Clematis* species in comparative aspect.

The genus *Clematis* s.l. is of tropical origin, where the centre of its biodiversity settles down. According to different authors, the genus includes from 230 to 400 species. Spreading of clematis species to subtropical and temperate zones apparently was connected with the collaboration of different strategies and adaptations to unfavourable environmental conditions.

The goal of the present investigation was studying the regularities of ontomorphogenesis of herbaceous *Clematis* species in comparison with shrubby species with the aim of evolutionary appreciation of some features and revealing of modes of ontogenesis transformation during the formation of herbaceous life forms.

Materials and methods

The materials for investigation were alive and fixed in 70% alcohol. Plants of different age of 6 *Clematis* species from section *Flammula* DC (Tamura 1956): *C. vitalba* L., *C. brevicaudata* Schmalh. ex Lipsky, *C. flammula* L., *C. mandshurica* Rupr., *C. hexapetala* Pall. and *C. recta* L. were chosen as model objects.

Clematis vitalba – shrubby tendril-climber liana (the supporting function is performed by the rachis tendril) up to 15 m high with pinnately compound leaves and white flowers. It is found everywhere in Caucasus and Crimea. Outside Russia it is widespread in Central and South Europe, Minor Asia and Central Africa. It grows in deciduous and temperate rocky forests, on rocky slopes, climbing up trees and shrubs (Krasheninnikov 1937; Tutin 1964).

Clematis brevicaudata – shrubby tendril-climber liana up to 15 m high with pinnately compound leaves and panicled inflorescences of white flowers. It is common in Far East: in the Amur region and Primorsky kray. Outside Russia it is found in the northern part of Mongolia and Manchuria. It grows on the edges of forests, along the banks of rivers and streams, on rocky slopes among shrubs (Krasheninnikov 1937; Komarov 1950; Shipchinsky 1954).

Clematis flammula – shrubby leaf-climber liana with bipinnately compound leaves and loose inflorescences of white flowers. It is found in west Transcaucasia, South Europe, Minor Asia, Iran, on Balkan Mts, in North Africa. It grows in the low forest zone, in thinned out forests, on rocky slopes among shrubs (Krasheninnikov 1937; Tutin 1964).

Clematis mandshurica – perennial herbaceous liana with pinnately compound leaves and loose inflorescences of white flowers. It is widely spread in Russian Far East and in Manchuria. It grows on the edges of forests and forest glades (Krasheninnikov 1937).

Clematis hexapetala – perennial herbaceous plant with erect shoots, pinnately compound leaves and terminal inflorescences of white flowers. It is found from Amur River region to south-eastern Transcaucasia. Outside Russia it is found in Mongolia, north-western China and in Japan. It grows on dry rocky and crushed stone slopes, screes and in river valleys (Krasheninnikov 1937; Komarov 1950).

Clematis recta – perennial herbaceous plant with erect shoots, pinnately compound leaves and terminal inflorescences of white flowers. It is widespread in the southern part of European Russia, including Crimea and North Caucasus and in south-eastern Europe. It grows in steppe, river valleys, on forest glades and edges among shrubs (Krasheninnikov 1937).

Individuals of different age of studied species were collected in natural populations: *C. vitalba* – in a mountain deciduous forest near Nikita Botanical Garden (Yalta, Crimea) and in an oak forest near the village Lazorevskoye (North Caucasus), *C. brevicaudata* – on a knoll slope near the village Anisimovka (Primorsky kray), *C. mandshurica* – on a knoll slope near Kuznetsovo station of Partyzansky region (Primorsky kray), *C. hexapetala* – on a knoll slope near the village Chernyatino (Primorsky kray), *C. recta* – on the edge of pine-tree forest in Prioksko-Terrasnyi reserve (Moscow region) and *C. flammula* – in the Botanical Garden of the Academy of Sciences of Uzbekistan.

The morphological structure of plants was drawn. The periodization of ontomorphogenesis was conducted according to classifications of Rabotnov (1950) and Uranov (1975).

Table 1. Morphometric peculiarities of embryo and endosperm in mature seeds of *Clematis* L. species.

Species	Length of embryo in mm	Length of cotyledons in mm	Cotyledons/ embryo length ratio	Length of endosperm in mm	Embryo/ endosperm length ratio	Period of seed germination
C. vitalba	0.79	0.32	0.40	2.73	0.29	20–30
C. brevicaudata	0.68	0.31	0.43	2.20	0.32	17–20
C. flammula	0.70	0.40	0.57	3.40	0.21	40–50
C. mandshurica	0.57	0.32	0.56	3.05	0.19	30–60
C. hexapetala	0.47	0.28	0.55	2.68	0.17	60–70
C. recta	0.55	0.28	0.51	3.45	0.16	80–90

Results

Ontomorphogenesis of *Clematis vitalba* and *C. brevicaudata* (Figs 1, 2)

The embryo in mature seeds is differentiated by a well-developed axis which exceeds the length of the cotyledons (Table 1). Seeds germinate in hypocotylary[1] manner 20–30 days after sowing. The developed seedling has two cotyledons, long hypocotyl (up to 25 mm) and a main root. In the first season, a monocyclic semirosette shoot develops with 2–4 alternate foliage leaves in the rosette and 5–10 metamers with a general length up to 20 cm which form during open growth (Figs 1, 2). Alternate phyllotaxy is replaced by an opposite one, and simple, entire leaves by leaves with dissected and compound leaf blades. Axillary buds form in axils of all leaves. The main shoot grows till late autumn. In connection with this, tissues of the upper part of the shoot stay undifferentiated by the approach of unfavourable season. Buds formed in the axils of cotyledons and rosette leaves become the renewal buds. In winter, the biggest part of the main shoot dies off and only the first metamers with renewal buds remain alive. Next year the plant proceeds to the tillering phase and the formed shoots become renewal shoots. The plant proceeds to sympodial renewal and tillering, marking the beginning of the immature age state. In this state which lasts several years, the plant is an aeroxylic shrub. There are 2–3 weakly branched shoots with the first features of liana structure in its above-ground part. With the development of elongated polymetameric shoots, 4–10 aged individuals proceed into the stage of an adult vegetative plant, the features of liana structure being increased.

Plants proceed to the reproductive phase at the age of 10–15 years, with maximum development at the age of 60–80 years. Annual shoots are up to 3–4 m long and include up to 25 metamers. Compound bracteose inflorescences of dichasial type with white flowers often appear in the axils of leaves. Monocarpic shoots grow during all vegetative seasons, therefore, the upper part of the shoot often doesn't ripen. In the lower part of shoots, the renewal buds form, which provide their branching. Generative individuals are characterized by the formation of compound systems of continuing shoots which include up to 10 orders of branching and achieve 30 mm in diameter. In time, the base of the shrub plungs into the soil and enables shoot formation

1 Seedlings of *Clematis* species undergo two stages: cryptocotylar (cotyledons, which remain inside the seed coat) and phanerocotylar (with visible cotyledons). In epigeous germinated species, seedlings undergo both stages. Cotyledons appear above the soil because of hypocotyl growth (hypocotylary germination) or because of cotyledonary petioles growth (cotyledonary germination). Hypogeous germinated species form cryptocotylar seedlings.

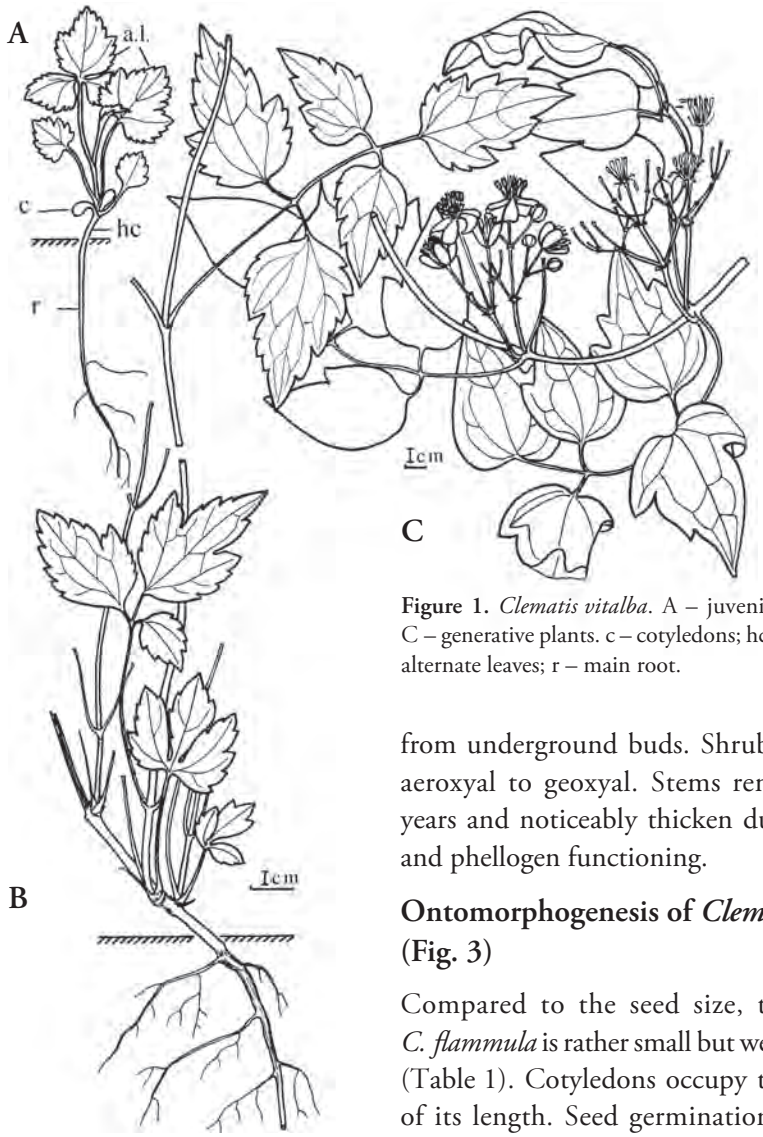

Figure 1. *Clematis vitalba*. A – juvenile; B – immature; C – generative plants. c – cotyledons; hc – hypocotyl; a.l. – alternate leaves; r – main root.

from underground buds. Shrub changes from aeroxyal to geoxyal. Stems remain for many years and noticeably thicken due to cambium and phellogen functioning.

Ontomorphogenesis of *Clematis flammula* (Fig. 3)

Compared to the seed size, the embryo of *C. flammula* is rather small but well differentiated (Table 1). Cotyledons occupy the greater part of its length. Seed germination in laboratory begins 40–50 days after sowing. The type of germination is cotyledonary, blades of cotyledons appear on the surface because of the elongation of the petioles up to 20 mm. Plumule stays in the soil inspite of an elongation of the hypocotyl up to 10 mm. Seedling phase lasts only a few days. The developed seedling has two long-petaled cotyledons with oblong-elliptical blades up to 12 mm long, 5–6 mm wide, a short hypocotyl and the main root with numerous absorbing trichomes. 1.5 months later, the main shoot begins to form and the plant proceeds to juvenile age state. If seedlings appear late, the development of the main shoot delays until spring. The elongated shoot is erect, with two pairs of scale leaves at its base and two pairs of short-petioled foliage leaves. In winter, the main shoot stays alive along the most part, even in the conditions of Moscow the leaves stay green until spring.

In spring, the renewal shoots develop from axillary buds of the main shoot. During immature age state, which lasts 2–3 years, the plant looks like a low-axilled aeroxyle subshrub with elongated shoots, a shortened underground rhizome zone and fibrils on adventitious roots. In the leaf series, leaves of annual shoots are replaced in mature vegetative individuals by dissected leaves

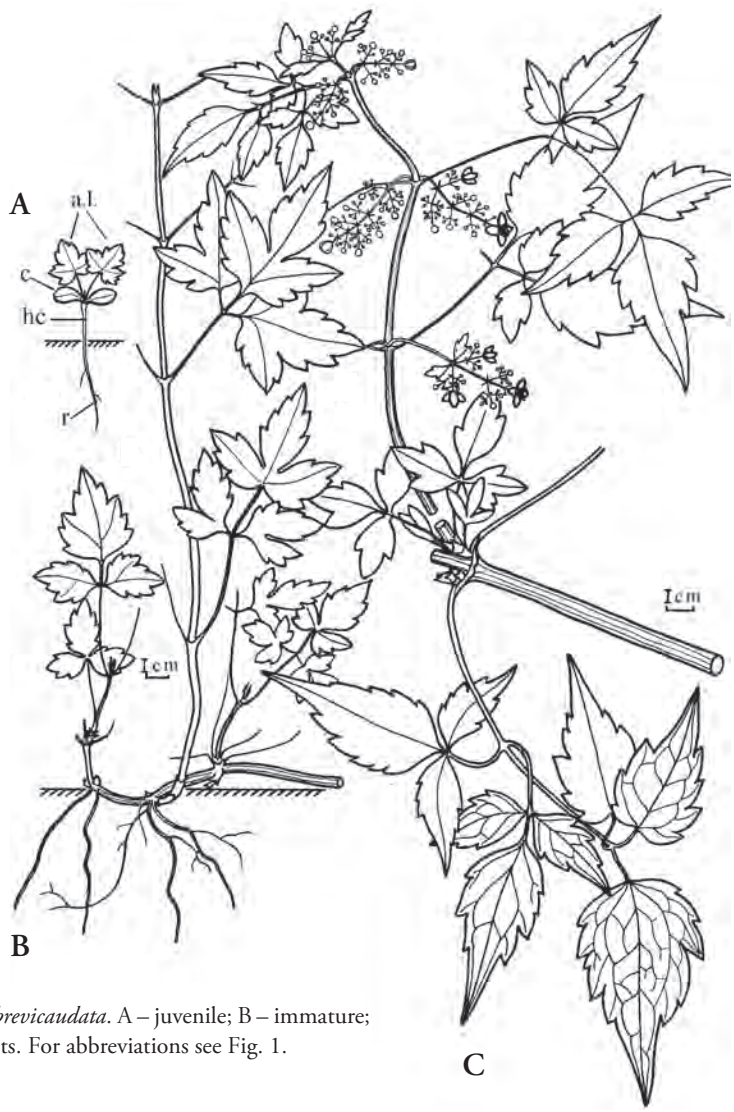

Figure 2. *Clematis brevicaudata*. A – juvenile; B – immature; C – generative plants. For abbreviations see Fig. 1.

and afterwards by compound leaf blades. Annually, polymetameric shoots up to 2 m develop from buds. They have simple, entire leaves at the base, simple lobed leaves in different degree and bipinnate compound leaves. Annual shoots of mature vegetative individuals are branched. Branching shoots don't have scale leaves unlike the maternal one.

In some cases, new shoots develop from buds which are in the soil, what leads up to a transition of the plant to the geoxylic shrub phase. Plant blossom out sometimes already at the age of four. Non-specialized floral shoots have a long polymetameric vegetative zone below the terminal, frondose, polyanthous inflorescence. As a rule, they appear on the vegetative shoots of the previous year. More specialized shoots with a little number of leaves develop as branches of third and fourth order on the vegetative shoots of the current year. They form in their turn during open growth and reach a considerable length (up to 3 m). In Moscow region, most of the shoot dies off and the plant is like a semi-shrubby liana.

In adulthood, *C. flammula* is a geoxylic, subshrubby, tendril-climbing liana with semi-rosette, strongly branching shoots and a fibrillose root system.

Ontomorphogenesis of *Clematis mandshurica* and *C. hexapetala* (Figs 4, 5)

Cotyledonary germinated leatherflowers includes, besides *C. flammula, C. mandshurica* and *C. hexapetala.*

Their embryo is bigger than in *C. vitalba* and *C. brevicaudata*, but compared to the endosperm size it is rather small. Its greater part are cotyledons. Seeds germinate after 25–60 days in cotyledonary type (Table 1). Cotyledons change their function from haustorial to photosynthetic, when they appear on the surface like in hypocotylary-germinated leatherflowers. As some individuals proceed to juvenile stage only in spring of the next year, cotyledons may stay the only assimilative organs during the first growing season. When the cotyledons unfold and the main shoot begins to develop, roots start to branch intensively. Morphogenesis at early stages of development is similar to *C. flammula*, which was described earlier. Seedlings have two long-petioled cotyledons (up to 11 mm) with elliptical or wide-elliptical blades approximately 9 mm long and 6.5 mm wide, a short hypocotyl and is slightly branching in the middle part of the main root (up to 70 mm) with root hairs. Petioles of cotyledons grow together at the base into a short tube and thereby provide the plumule with protection. Plant may stay in such state until the end of the vegetative season or may form leafy extending main shoots.

The main shoot is erect, elongated, up to 13 cm high. The epicotyl is 2–3 mm long. Foliage leaves are sessile, elliptical (5 mm long, 3 mm wide). Main root branches up to the roots of third order. The first adventitious roots are simple or lightly branched. They develop on the hypocotyl. Unlike *C. flammula*, most of the shoot dies off in winter. Only the basal part, which isn't always hidden in the soil, may stay alive and becomes the place, where renewal buds initiate. The juvenile phase is short and lasts less than one year. Immature plants form several (2–4) erect elongated shoots up to 30 cm high, which have 3–4 pairs of scale-like and 6–8 pairs of sessile entire foliage leaves. The bases of annual shoots with scale leaves and buds, which are hidden in the soil, form a compact epigeogenic rhizome. It grows in sympodial manner. As a result of development of numerous long adventitious roots, the root system becomes fibrillose. The main root is not distinguishable.

Transition of the plant to the mature vegetative state marks the appearance of definitive leaves which are pinnately compound in the majority of species.

After 4–6 years the plants transit to the generative age state. Generative individuals are short-rhizome plants with 1–3 non-specialized elongated (up to 20 metamers) lianoid (*C. mandshurica*) or erect (*C. hexapetala*) shoots with 4 pairs of scale-like and 5–6 pairs of assimilative leaves with the white-flowered inflorescence on its top.

Ontomorphogenesis of *Clematis recta* (Fig. 6)

Clematis recta belongs to the group of hypogeously germinating species. The embryo is small but with well-developed cotyledons (Table 1). Morphogenesis of *C. recta* is similar in many respects to cotyledonary germinating species. But the cotyledons remain inside the seed coat during the whole life. Therefore, the phase of phanerocotylar seedling is absent. Plants usually lead an underground way of life during the first year because of the prolonged period of germination. In laboratory, seeds germinate after 90 days (Table 1).

In juvenile individuals, the elongated main shoot including up to 5 metamers has scale leaves at its base, and in the upper part it has simple, entire, short-petioled leaves differing in their form. The

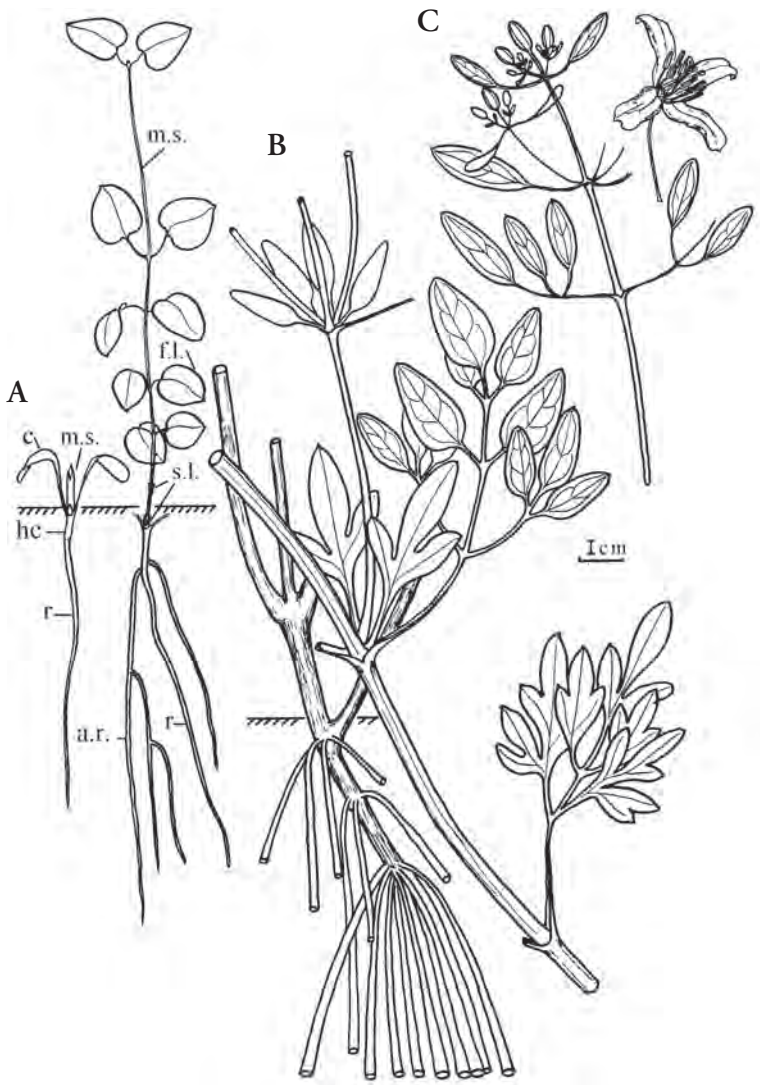

Figure 3. *Clematis flammula*. A – phanerocotylar seedling; B – juvenile; C – generative plants. m.s. – main shoot; f.l. – foliage leaf; s.l. – scale leaf; a.r. – adventitious root. For other abbreviations see Fig. 1.

development of scale leaves is connected with the underground initiation of the first metamers. The epicotyl is underdeveloped in cotyledonary germinated species. In hypogeously-germinated species, the epicotyl grows lengthwise up to 10 mm. Groups of cotyledonary germinated and hypogeously-germinated leatherflowers are similar in the underground position of the plumule already during the early stages of development.

Based on the results of our investigations, we revealed two main directions of adaptive evolution of life forms in the genus *Clematis* as the result of early deviation (archallaxis) which is connected with a distinct change in the ratio of the embryo parts as well as in the ratio of embryo and endosperm length. The reduction of the axil part of the embryo and the increase of the endosperm length, which lead up to the transition from epigeous to hypogeous mode of germination, demonstrate the tendency to geophilia already at the early stage of ontogenesis. Hypogeous germination, according to the peculiarities of cotyledon structure, is of derivative nature.

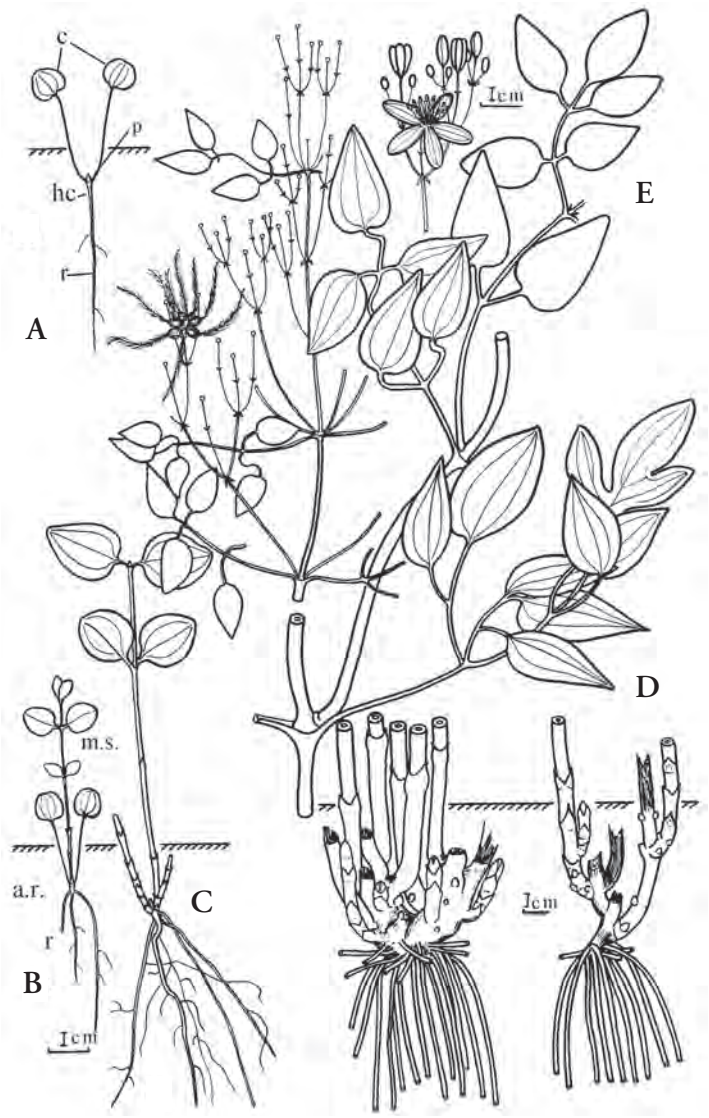

Figure 4. *Clematis mandshurica*. A – phanerocotylar seedling; B – juvenile; C – immature; D – mature vegetative; E – generative plants. p – plumule. For further abbreviations see Figs 1 and 3.

A definite correlation between the type of germination and the mature plant has been revealed. Hypocotylary germination of leatherflowers takes place in shrubby and subshrubby forms, which are characterized by main root system, cotyledonary and hypogeal one – with subshrubby and herbal biomorphs, roots in clusters are characteristic of them.

As initial life form in the genus *Clematis* s.l., we suppose an aeroxyle, mainrooted, lianoid shrub with alternate leaves.

Acceleration is the dominant modus of leatherflowers morphogenesis transformation in the morphological row shrub – subshrub – herbal polycarpic. In this case, the acceleration reveals itself in basal abbreviations of ontogenesis:

as the result of removing the phanerocotylar seedling phase and rosette phase of the main shoot development;

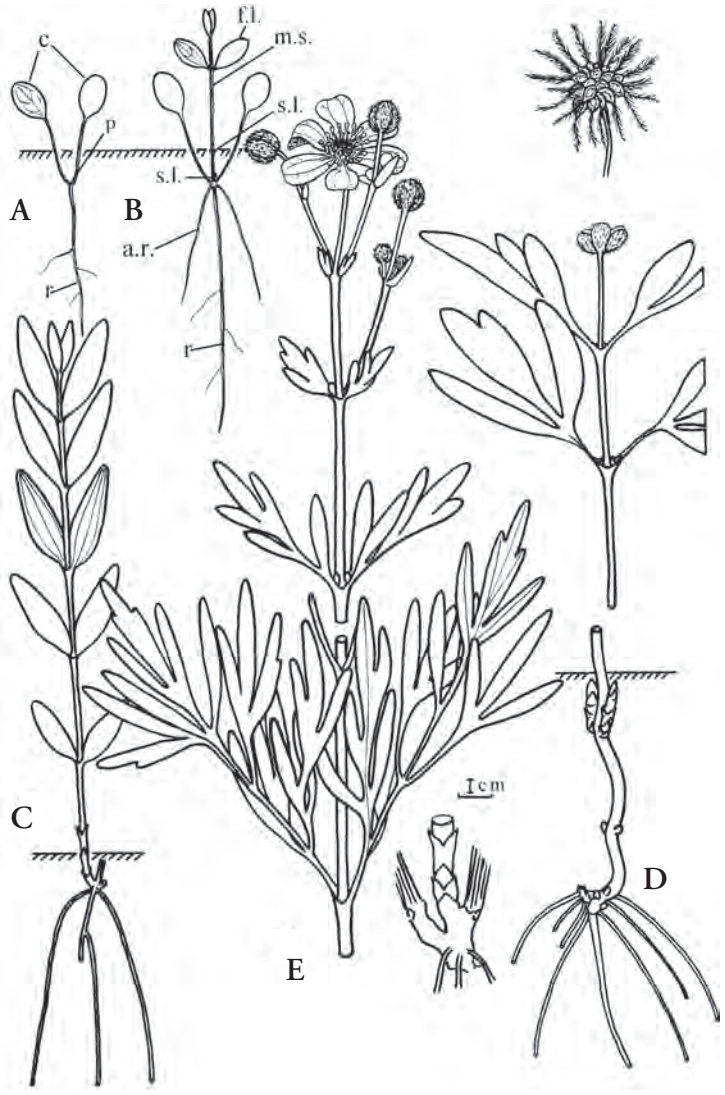

Figure 5. *Clematis hexapetala*. A – phanerocotylar seedling; B – juvenile; C – immature; D – mature vegetative; E – generative plants. For further abbreviations see Figs 1, 3 and 4.

in the gradual reduction of the pregenerative period in their development, the duration of aeroxyle phase in subshrubs and its loss in herbs;
in the decrease of branching intensity and dimensions of annual shoots as well;
in the decrease of dimensions of skeletal axis, strengthening of underground sphere;
in the development of xylorhizomes;
in the transition of renewal buds below the ground;
in the increase of development of the renewal axis up to one year;
in the decrease of the duration of their minor life cycle (much earlier flowering).

This quite corresponds with the results on a study of evolution of life forms in the genus *Potentilla* L. (Shafranova 1968).

It is possible that leatherflowers were widely spread in Eurasia during Cretaceous period, later they were the members of warmly-temperate Arcto-Tertiary flora as finds of *Clematis uralensis*

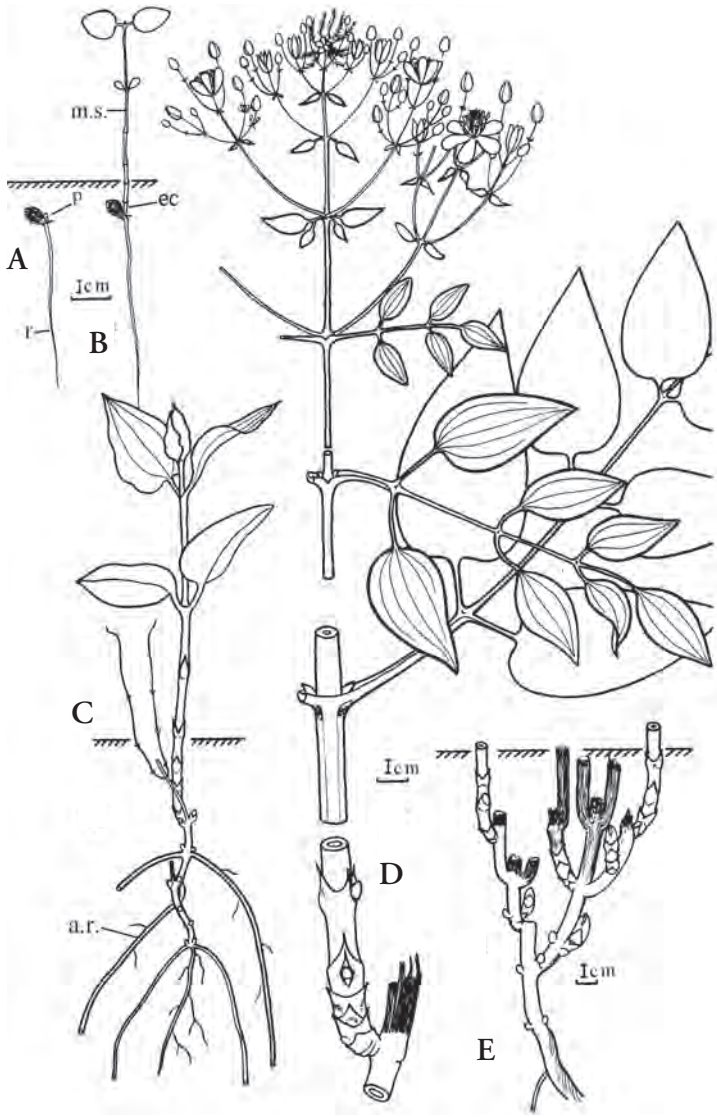

Figure 6. *Clematis recta*. A – cryptocotylar seedling; B – juvenile; C – immature; D – mature vegetative; E – generative plants. ec – epicotyl. For further abbreviations see Figs 1, 3 and 4.

Dorof. fruits show (Dorofeev 1974). They are similar to fruits of subshrubby and herbaceous leatherflowers (*C. viorna* L., *C. ovata,* etc.). In connection with the sudden fall of temperature in the north of Eurasia in the second half of Tertiary period (Krishtofovich 1957), the territory of leatherflowers distribution was suddenly reduced: the heat-loving species moved back to the southeast of Asia. Psychrophile species of boreal section *Atragene* (Tamura 1987, 1991), which had formed earlier in the conditions of middle and upper mountain zones, began to settle down in colder zones. For all that, they kept the ancestral form of a shrubby liana. The main modus of transformation of ontogenesis of the ancestral form in this line is retardation, which represents the adaptation to a short vegetative season of the majority of temperate zones, including tundra (Chubatova 1991; Chubatova & Churikova 2016). Overwhelming majority of leatherflower species were forced to move to more southern regions. The transition of renewal buds below the soil (strengthening geophilia), which appeared already in thermophilic species, should be

considered as a result of preadaptation. At the same time, during the developing of herbaceous forms it didn't turn out without grave reconstructions (for example, reducing of small life cycle of shoots, etc.) which were of obviously adaptive nature. This way turned out to be the less effective of the two directions of morphological evolution because the border of herbaceous species extending runs rather southerly and in mountains lower than the border of *Atragene* extending.

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