Wulfenia **23** (2016): 162–174

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

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

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Summary: The life form of *Atragene* should be recognized as derivative which had emerged during the transformation of *Clematis* ontomorphogenesis. The main mode of this transformation is retardation (Chubatova 1991). It can be noticed at different stages of development: elongation of seed germination in *Atragene* which is associated with a change in the ratio of parts of the embryo, while maintaining the volume of endosperm; elongation of main shoot and shoot systems morphogenesis. It also acts as an adaptation to the short growing season in most zones with temperate climate, including tundra and high mountains, where *Atragene* may extend.

Keywords: Ranunculaceae, *Atragene*, *Clematis*, ontogeny, morphogenesis, adaptation, retardation

The question about the ways of evolutionary transformation of life forms of flowering plants is far from being resolved. Most botanists have recognized that somatic evolution in different taxonomic groups occurred in different ways, in spite of frequent duplication and convergence. Both woody (Worsdell 1908; Sinnott & Bailey 1914; Golubev 1959) and herbaceous (Scharfetter 1953; Grassl 1967; Hutchinson 1969; Tsvelev 1969, 1970) life forms can be initial. This fact determines the importance of studying the relationships of life forms within concrete taxa of different rank (Serebryakov & Serebryakova 1969).

The genus *Clematis* s.l. is one of the few genera of the family Ranunculaceae Juss., in which woody and herbaceous types of shoot occur. The spectrum of life forms in the genus is very wide. It includes evergreen, semi-evergreen and deciduous woody and herbaceous lianas, upright and prostrate shrubs, subshrubs and perennial grasses. In this regard, the genus is an excellent model for solving questions about the relationship between life forms and the direction of their evolution.

The analysis of life form spectra and their features allows to trace possible ways of transformation from one life form to another. At the same time, not only the mechanism details of these transformations, but also the nature of life forms still remains unclear.

Based on the characteristics cited in literature and their own observations, the authors draw opposite conclusions. For example, Tamura (1963), Takhtadzhan (1964), Golubev & Beskaravaynaya (1980) and Golubev (1982) recognize the woody liana as the original life form in the genus *Clematis* s.l. Disagreements concern only the choice of the concrete ancestor. Tamura (1968, 1970) recognizes the woody liana *Archiclematis alternata* Kitam. with alternate entire-kind leaves, inhabiting the mid-mountain zone of the Himalayas, as the most ancient taxon with a structure close to the ancestral type. Golubev & Beskaravaynaya (1980) prefer evergreen woody lianas and reject the species proposed by Tamura because of its narrow local spread and systematic isolation. The authors believe that shrubby, subshrubby and herbaceous lianas were formed in the course of evolution of evergreen woody lianas. During the ‘secondary biomorphogenesis', associated with the promotion of plants in areas of moderate and cold climate, upright and prostrate shrubs, subshrubs and grasses developed.

Ziman (1981, 1985), on the contrary, finds the primacy of herbaceous polycarpic, upright shoots, with semi-rosette such as *C. ranunculoides* Franch. on the basis of a comparative evaluation of the evolutionary level of some features, among which the features of reproductive sphere predominate.

It is evident that evolutionary appreciation of morphological structure, which is carried out on the basis of some individual features or their complex, is highly subjective.

In 1935 the Russian morphologist and evolutionist Severtsov (1935) convincingly proved that the evolution of animals takes place by changing the entire course of embryonic development. He called evolutionary transformations of ontogeny connected with adaptation of adult organisms 'phylembryogenesis'.

According to Severtsov, evolutionary changes of ontogenesis are the morphological expression of the evolution. A relationship of ontogeny and phylogeny is due to them. Any phylogenetic reconstruction occurs through changes of morphogenetic stages. Deviation of ontomorphogenesis[1] can occur without changing the stage sequence: by slowing down the development (retardation) or by speeding up the development (acceleration) in response to the deterioration of environmental conditions or with a change in stage sequence by loss or addition of new ones.

De Beer (1930), Ezhikov (1939), Beklemishev (1964) and others also considered evolutionary changes in adult forms to be associated with evolutionary changes in their individual development (morphogenesis). At present, theory of phylembryogenesis by Severtsov (1935) is getting deeper into the evolutionary morphology of animals. In botany, it has not been applied for a long time.

Takhtadzhan (1943) attempted to prove the applicability of Severtsov's theory to explain the morphological evolution of plant organisms. Many common ideas which were formulated in zoology subsequently turned out to be applicable to plants and so they acquired general biological significance (Takhtadzhan 1950).

Among the first works on evolution of life forms, which were carried out on the basis of ontomorphogenesis, were the investigations of Eichwald (1959), Sokolova (1964, 1971, 1973), Serebryakova & Kagarlitskaya (1972) and others. Such approach permitted to reveal the main directions of evolutionary transformations in concrete taxa.

Moreover, Gould (1977) proposed an approach to the relationship between ontogeny and phylogeny as to the process of converting a sequence of stages of ontogeny and on the other hand – as to a result of the phylogenetic transformation. These ideas have increased the interest to many aspects of ontogenesis: the analysis of evolutionary processes and rhythms, the study of adaptive and ecological significance of developmental transformations, establishing of relationship

At the time, the idea has been further developed in the evo-devo concept, but mainly for unitary organisms. In modular organisms (including plants) cyclic morphogenesis is both the condition and the way of normal functioning of the system (Notov 1999). At the same time,

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[1] Ontomorphogenesis (Notov 2005): development of morphological structures of plants during their ontogenesis. This term includes structural and dynamical aspects as well.

the development, operation and regulation of a living system are carried out by changing its macrostructure (Notov 2005). That is why studies of plant structure should always include its dynamical and functional aspect (Bologova 1989).

Very promising in this regard is a comparative study of ontomorphogenesis of some members of the genus *Clematis*, which have similar life forms, but are adapted to different environmental conditions. This determines the importance not only of a detailed study of life forms in the genus *Clematis* s.l. and its transformations, but also the dynamics of the development.

According to different authors, *Clematis* includes from 230 (Rehder 1949; Shipchinsky 1954) to 400 (Scharfetter 1953) species. This genus is most often associated with areas of tropical and subtropical climate (Grossheim 1950), despite the differing views on the place of its primary differentiation. Most species of *Clematis* extend to subtropical and tropical regions of the northern hemisphere with their maximum concentration in China (Fisk 1962). Extending of *Clematis* species to subtropical and temperate regions was associated with the development of different strategies and adaptations to unfavourable environmental conditions. However, only the members of *Atragene* (= *Clematis* sect. *Atragene*; Tamura 1987, 1991), maintaining the shape of shrubby liana, could spread far to the north and climb high in the mountains.

The aim of this study is to establish the mode of evolutionary transformations of the ontogenesis of ancestral forms of *Atragene*. So, it was necessary to conduct a study of ontomorphogenesis of *Atragene* and shrubby lianas of lowlands or plains from the genus *Clematis*, to give the evolutionary appreciation of some features and to outline the ways of ontogenetical transformation of ancestral forms of *Atragene* during adaptation to life in severe environmental conditions.

As model objects we chose two species of *Atragene*: *A. speciosa* and *A. ochotensis* and two species of *Clematis*: *C. serratifolia* and *C. orientalis,* which represent the section *Meclatis* and are very close to the section *Atragene*. Formerly, both sections were united in a single subgenus *Campanella* (Tamura 1987, 1991).

There are comparatively few data on *Clematis* and *Atragene* ontomorphogenesis in literature. The first results of the study of morphological and anatomical seedling structure in a small number of species, some of them growing outside of Russia, are found in the works of foreign authors (Winkler 1888; Lubbock 1892; Sterckx 1897, 1900). Later, more studies were conducted: Vasilchenko (1960), Csapody (1968), Tamura et al. (1977), Schnettker (1978), Barykina & Chubatova (1981), Essig (1991), Tonkova (2010), etc.

All four species are shrubby lianas. Species of the genus *Atragene* have twice ternate leaves and solitary terminal flowers, which have double perianth. Species of the genus *Clematis* have twice ternate or pinnate leaves and axillary dichasial inflorescences and their flowers have simple perianth (Shipchinsky 1954).

Atragene speciosa Weinm. (= *A. sibirica* L., nom. ambig. (Serov & Jarvis 1988)) is distinguished by the largest Eurasian distribution area, including northern Europe, Siberia and the Far East. It grows in the mountains of Central Asia, up to the northern ranges of the Tian-Shan, in Mongolia and in Scandinavia as well (Wille 1917; Marklund 1947; Hjelmstad 1978), in coniferous and deciduous forests, in forest edges, coastal bushes, in mountainous areas on rocky slopes, rocky outcrops, sometimes rising beyond the forest zone (Krasheninnikov 1937a).

Atragene ochotensis Pall. grows in sparse forests and in their edges, in bushes and on rocky slopes in Eastern Siberia, the Far East, north-east China, the north of the Korean Peninsula and in north-east Mongolia (Krasheninnikov 1937a).

Clematis serratifolia Rehder grows among shrubs along river banks, in the Far East, Korea and Manchuria (Krasheninnikov 1937b).

Clematis orientalis L. grows in the southern regions of the European part of Russia, including Crimea and Caucasus, Central Asia, Mediterranean, Asia Minor, Iran, Mongolia and China (Krasheninnikov 1937b).

Materials and methods

Studied specimens of different ages of *A. speciosa* were collected in the mixed forest at the lake Shchuchye (Buryatia) and grown in the botanical garden of the Moscow State University as well. Specimens of *A. ochotensis* were gathered on the banks of the creek in Bolshekhekhtsirsky nature reserve (Primorsky Region).

Uneven-aged specimens of *C. serratifolia* were sampled in the edge of mixed forests near village Anisimovka of Shkotovsky District (Primorsky Region), specimens of *C. orientalis* were collected in sparse bushes on the south shore of Lake Issyk-Kul (Kyrgyzstan) and on the right bank of the river Aksai (Dagestan).

Living plants were fixed with 70% alcohol. Morphological structure of plants was sketched. The periodization of the ontogenesis was carried out in accordance with the classification of Rabotnov (1950), partially modified by Uranov (1975). Later classification of Day et al. (1997) quitely corresponds with them.

Results

Morphogenesis of *C. serratifolia* and *C. orientalis*

The embr+years. Annual shoots of *C. serratifolia* and *C. orientalis* reach 3–4 m in length and include up to 25 metamers with axillary vegetative buds and dichasial cymes in the axils of the upper leaves. The simple dichasium of *C. serratifolia* includes a pair of entire-like small leaves, one terminal and two axillary flowers with long stalks. In *C. orientalis* a compound dichasium with small hypsophylls (Figs 1 C; 2 C) is formed.

Annual shoots grow during the whole growing season. So, the upper parts of shoots often don't mature and die off in winter. Renewal buds develop in the basal part of shoots and provide their branching. The lower part of stem is stored for many years and thickens significantly. Cambium is active, providing an annual xylem growth of 20–25 cell-layers.

Morphogenesis of *A. speciosa* and *A. ochotensis*

The mature seeds of *Atragene* include differentiated embryos with two well-developed cotyledons, exceeding the length of the axis (0.34–0.4 mm) and the endosperm. Seedlings emerge 2–3 months after sowing (Barykina & Chubatova 1981).

Germination is epigeal hypocotyledonary, but the hypocotyl is short and cotyledons raise above the ground not more than 3–5 mm. The well-developed seedling has two cotyledons, a short (7–

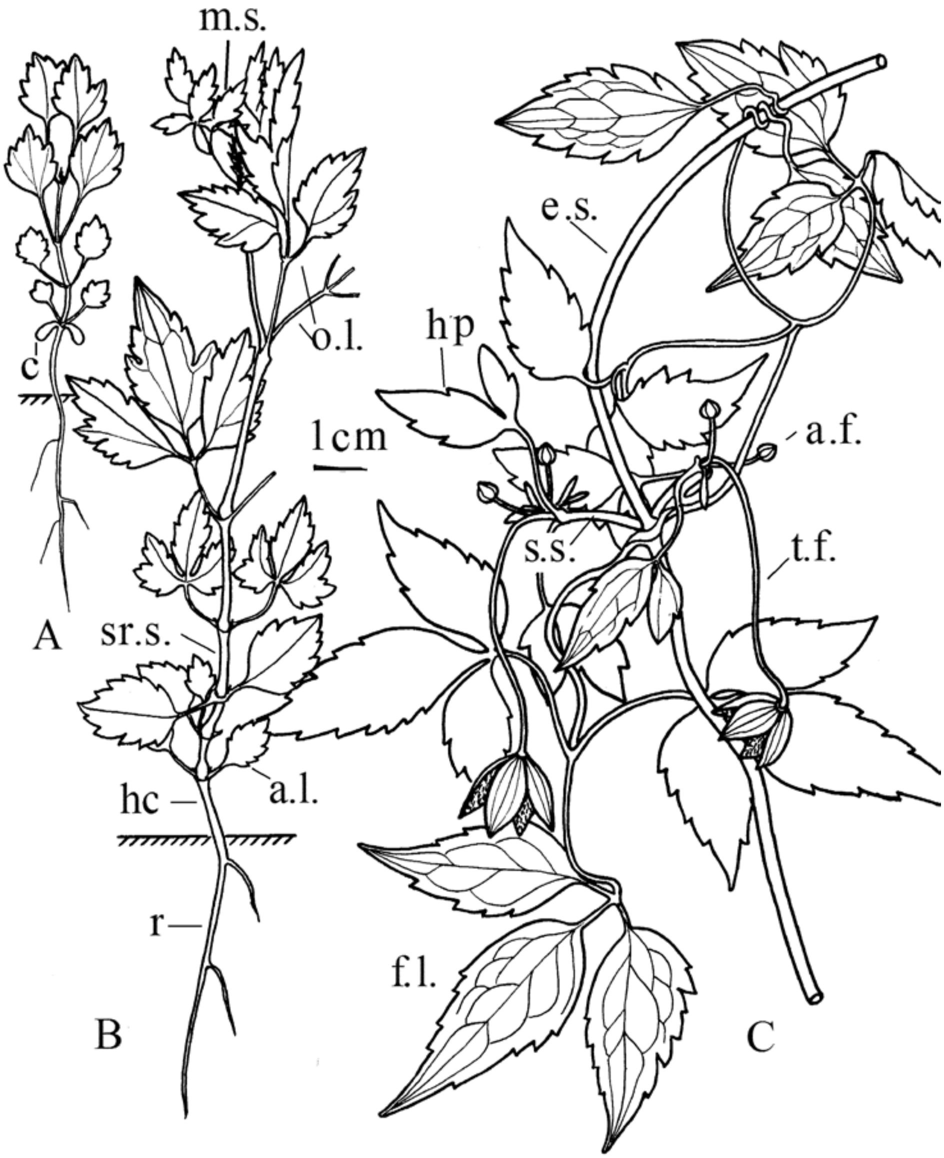

Figure 1. *Clematis serratifolia*: A, B – juvenile individuals; C – annual branch of generative individual. c – cotyledons; hc – hypocotyle; r – main root; a.l. – alternate leaves; o.l.– opposite leaves; e.s. – elongated shoot; s.s. – short shoot; sr.s. – semi-rosette shoot; t.f. – terminal flower; a.f. – axillary flower; f.l. – foliage leaf; h.p. – hypsophyll; m.s. – main shoot.

10 mm) hypocotyl, a terminal plumule and root. The juvenile stage of the plant is characterized by the development of the main shoot. It lasts 2–3 years (Fig. 3 A–D).

The main shoot of *Atragene* is semi-rosette, monopodially increasing and its annual growth ends in terminal buds. In the first year, a rosette shoot with alternate leaves is formed. In the next year, a rosette or an elongated shoot with opposite leaves develops. Terminal and axillary buds are well protected by 5–6 leathery, pubescent scales. In the second year the rosette growth form retains in its juvenile form even in the case of development of sympodial renewal shoots. Only in the third year several (2–5) elongated internodes appear after the short ones. Thus, the main shoot in *Atragene* is di- to tricyclic, semi-rosette (Fig. 3 E). So, alternate phyllotaxis is replaced

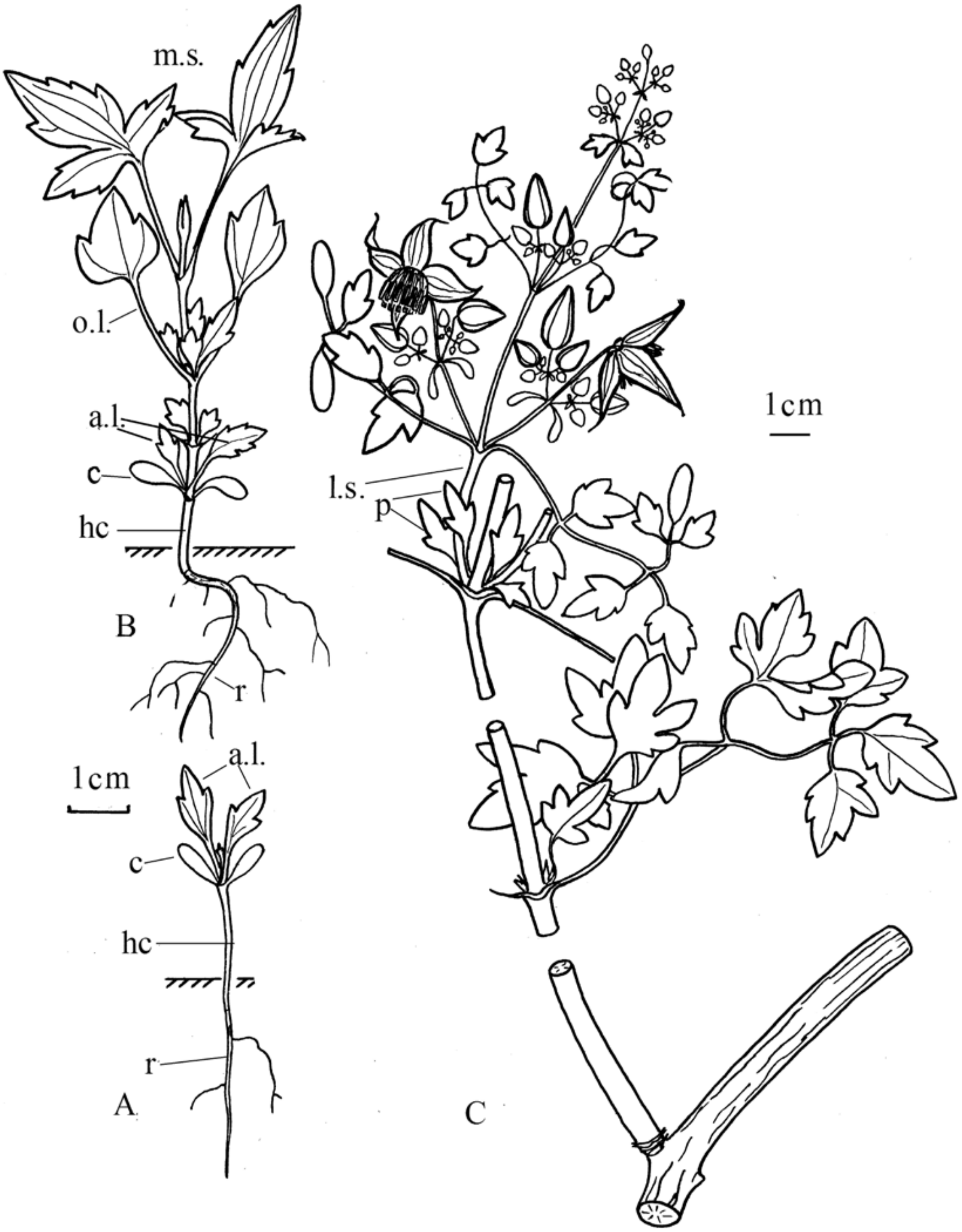

Figure 2. *Clematis orientalis*: A, B – juvenile individuals; C – annual shoot of generative individual, which branches up to third order. p – prophyll; l.s. – lateral shoot; m.s. – main shoot. For further explanations, see legend of Fig. 1.

by opposite phyllotaxis. In the axils of the cotyledons and rosette leaves numerous buds arise. Sometimes, they become resting buds. The further tillering zone differentiates (Fig. 3 E).

Monopodial renewal is replaced by a sympodial one and the juvenile phase of plant development is followed by the immature one in the third or fourth year, when buds sprout in the tillering zone. They form elongated tillers with several pairs of foliage leaves.

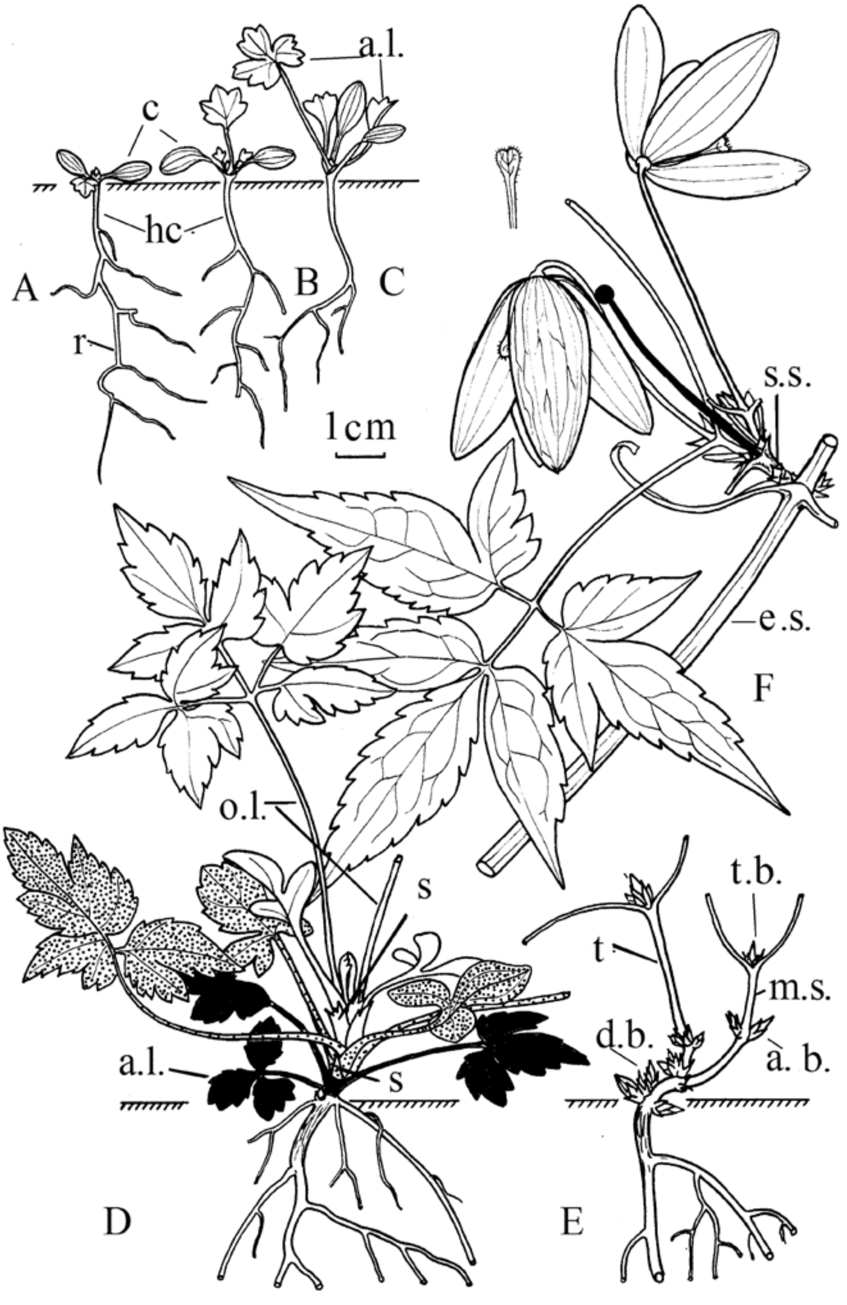

Figure 3. *Atragene speciosa*: A–C – one year old, and D – three-years old juvenile individuals; E – immature individual; F – branch of generative plant. e.s. – elongated shoot; s.s. – short shoot; t.b. – terminal and a.b – axillary bud; s. – scale; t – tiller; d.b. – dormant bud. For further explanations, see legend of Fig. 1.

The reproductive phase of development begins at the age of 5–10 years. Generative individuals are characterized by distinct morphological and functional differentiation of the shoots: elongated vegetative shoots and short generative shoots which develop on accretions of the last year. The number of leaf primordia in vegetative buds is small. They have numerous scales and rudiments of 4–5 pairs of foliage leaves. Subsequent shoot metamers develop during its open growth that lasts until the middle of the growing season and ends with the formation of terminal and axillary buds.

Stems of vegetative shoots persist more than 10 years, but they remain fairly thin because the cell division of the active cambium usually lasts only until the middle of the growing season and the annual xylem growth produces not more than 16 layers of conductive, mechanical and parenchymal cells (Chubatova 2015; Chubatova & Timonin 2015).

Generative shoots have a large number (12–14) of leathery protective scales, 1–2 pairs of foliage leaves with axillary buds and a large terminal flower (Barykina & Chubatova 1983). After fruiting the generative shoots die off, but in some species (*A. speciosa*, *A. ochotensis*) the vegetative part of floriferous shoots remains viable for 2–3 years and its axillary buds produce new lateral floriferous shoots, which in turn can also branch (Fig. 3 F). As a result, a perennial system of generative shoots is formed on the vegetative shoot. Projection of this system into one time level demonstrates a system which is homologous to the dichasial inflorescence of some *Clematis* species, for example *C. serratifolia* and *C. orientalis* (Figs 1 C; 2 D).

Perhaps the appearance of additional secondary bundles in the medullary rays of short shoot stems is due to this branching (Chubatova 2015; Chubatova & Timonin 2015).

Discussion

Seeds of *C. serratifolia* and *C. orientalis* have embryos, which are well-equipped for germination (embryo axis is longer than the cotyledons). The volume of endosperm is smaller compared to seeds of *Atragene*. They germinate 30 days after sowing.

In *Atragene*, the higher volume of endosperm allows embryos with a short axis to elongate the germination period up to 2–3 months. Germination is epigeal but hypocotyl in *Atragene* is shorter than in *C. serratifolia*. So, all buds are located on the ground level and are better protected from unfavourable environmental factors than in *C. serratifolia*.

The semi-rosette main shoot grows throughout the whole year and increases until the onset of the unfavourable season. Most of it dies off in winter. The axillary buds in its basal part become renewal buds, from which the semi-rosette monocyclic tillers develop in spring. In *Atragene* species, the rosette phase of the main shoot development lasts 2–3 years. It causes the appearance of a monopodial type of shoot growth which is uncommon for *Clematis*. The extended portion of the primary shoot of *Atragene* includes a small number of metamers and often ends in a terminal innovation bud, which is not the case in *Clematis*. The elongated part of the main shoot of *Atragene* includes a small number of metamers and usually ends with the resumption of the terminal renewal bud, which is not characteristic of *Clematis*. Thus, the main semi-rosette primary shoot of *Clematis* is monocyclic, developing during one year. In *Atragene* it is di- to tricyclic, growing for 2–3 years. Terminal and axillary buds are well protected by 6–8 leathery scales in *Atragene* unlike *Clematis*. Metamorphosis of green rosette leaves into the scales is an adaptive feature of plants from unfavourable habitats.

Many scaly buds in *Atragene* are accumulated in the axils of cotyledons and rosette leaves of the main shoot or the shoot which is replaced. Some buds form elongated tillers, the remaining buds change into dormant buds.

If reproductive shoots of *Clematis* (elongated shoots with axillary inflorescences in its upper half) are formed during one growing season and if they are transferred into unfavourable conditions, the seeds do not have enough time to ripen. The formation of reproductive shoots in *Atragene* requires two seasons. In the first year, vegetative shoot develop. Their development is completed by formation of generative buds in the middle of the season. In spring of next year, generative shoots rise from them. At the end of the season, which is short in the north and in the highlands, the buds have enough time to form and fruits can ripen. This dynamics appears to be associated with a less intense and shorter cambium functioning than in *Clematis*. Perennial systems of generative shoots in *Atragene* are the result of a prolonged formation of dichasial inflorescences. The species of section *Atragene*, which Linnaeus (1753) refers to an independent genus, form an independent basal nineth clade in the cladogram, which Miikeda et al. (2006) created on the basis of analysis of nuclear and chloroplast DNA of 32 species of *Clematis* s.l. (Tamura 1956, 1987, 1991).

It is evident that *Clematis* species from the sections *Meclatis* and *Atragene*, which retain the life form of shrubby liana, adapted in different ways to the habitat conditions.

Shoots of most shrubby *Clematis* species grow continuously until the tops of their non-lignified shoots are killed by frost. Their buds are weakly protected by green scales. The shoots of *Atragene* are more specialized with well-formed buds. Terminal and axillary buds are protected by leathery pubescent scales. The short period of shoot growth in *Atragene* often does not correspond with the duration of growing season. So, we have a reason to suppose that *Atragene* could arise in areas with a short growing season. Nowadays, the most of *Atragene* species are confined to mountain forests and only one species, *A. speciosa*, grows also in the lowland area of forests and tundra in the north. Thus, we can suppose that the center of origin and differentiation of *Atragene* was located in the mountains of the subtropical or temperate zone.

Woody lianas are completely absent and grassy ones are mostly absent in polar and alpine regions, i.e. where unfavourable climatic conditions exclude the possibility of rapid and prolonged growth of shoots (Golovach 1973). So, it would be a mistake to assume that *Atragene* spread from the polar to the southern regions. The reverse direction assumes the development of such adaptive features which correspond with the reduction of the plant growing season.

In this case, the adaptation has not only morphological but also other aspects, in particular, rhythmic ones. Alpine plants are characterized by early initiation of flowers in the buds, the complete formation of the leaves during the most favourable time of the growing season and the completion of all phases during the short period of vegetation (Serebryakov 1964; Nakutshrishvili 1981).

In *Atragene*, such adaptive features are: prolongation of the period of seed germination; prolonged rosette-stage of main shoot development; appearance of monopodial main shoot development; formation of well-protected buds with scales; prolonged period of generative shoot formation (throughout two seasons) and, thus, the related dimorphism of shoots; formation of a perennial system of generative shoots, homologous to a dichasial inflorescence, which allows to provide flowering during the most favourable time of the year and maturing of seeds as well.

Thus, inspite of great morphological similarity of studied species, the life form of *Atragene* should be recognized as derivative, which emerged during the transformation of *Clematis* ontomorphogenesis. The main mode of transformation of ontomorphogenesis is retardation (Chubatova 1991). It can be noticed at different stages of development (prolongation of seed germination in *Atragene* which is associated with a change in the ratio of parts of the embryo, while maintaining the volume of endosperm; prolongation of main shoot and shoot system morphogenesis), and acts as an adaptation to the short growing season of most zones with temperate climate, including tundra and high mountains, where *Atragene* may extend.

Acknowledgements

The present contribution is supported by the Russian Science Foundation (RNF, grant # 14-50-00029).

The authors are extremely grateful to Professor Alexander C. Timonin for help and assistance.

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Zeitschrift/Journal: Wulfenia

Jahr/Year: 2016

Band/Volume: 23

Autor(en)/Author(s): Chubatova Nina V., Churikova Olga A.

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