



Dwarf subshrub morphological structure variety in species of the genus *Scutellaria* (Lamiaceae) under different growing conditions

Vera CHERYOMUSHKINA, Alexandra GUSEVA*, Evgeniya TALOVSKAYA, Alexey ASTASHENKOV

Central Siberian Botanical Garden, Siberian Branch of Russian Academy of Sciences, Novosibirsk, 630090, Russia. *Corresponding author's e-mail: guseva.sc@list.ru

(Manuscript received 16 July 2021; Accepted 18 January 2022; Online published 22 January 2022)

ABSTRACT: Biomorphological features of the steppe dwarf subshrub *Scutellaria przewalskii* were revealed. In most of the range, in petrophytic variants of temperate steppes, this species develops as a monocentric dwarf subshrub with anisotropic generative shoots. The morphogenesis of *S. przewalskii* individuals under the conditions of temperate steppes (Aridity index (I) = 17) is described in detail. A comparative analysis was performed on morphological functions of five steppe dwarf subshrubs from the genus *Scutellaria* (*S. przewalskii*, *S. supina*, *S. grandiflora*, *S. tuvensis*, *S. sieversii*) was carried out by 14 qualitative and quantitative indicators. As a result of a comparative analysis of individuals growing in different types of steppe communities: meadow steppes (I = 55), temperate steppes (I = 15–17), desert steppes (I = 9), common features of the development of individuals of dwarf subshrub were revealed: the basisympodial growth of the shoot system; the lignification of the shoots' basal parts; the renewal buds location above the substrate surface; short monopodial growth of the primary shoot, the presence of the main root during the entire ontogenesis. Differences between dwarf subshrub are associated with the structural features of shoots and the skeletal axes, their age, the pregenerative period duration decrease.

KEY WORDS: Dwarf subshrubs, *Scutellaria*, morphological structure, ontogenesis, steppe.

INTRODUCTION

The genus *Scutellaria* is one of the largest genera within Lamiaceae family, comprising about 425 taxa (Paton, 1990a). This genus is being studied by researchers from various fields of science, for example, taxonomy (Paton, 1990a; Ranjbar and Mahmoudi, 2017; Zhao *et al.*, 2017), phylogeny (Paton, 1990a, Safikhani *et al.*, 2018; Zhao *et al.*, 2020), natural chemical compounds (Cole *et al.*, 2008; Shang *et al.*, 2010; Dogan *et al.*, 2019). Many species are endemic or rare plants (Kochkareva, 1986; Jackowiak *et al.*, 2007; Paton *et al.*, 2016; Zhao *et al.*, 2017) that may disappear from the natural flora due to climate change and increased anthropogenic pressure. Representatives of the genus *Scutellaria* are distributed in a wide ecological range on all continents except Antarctica (Epling, 1942; Yuzepchuk, 1954; Paton, 1990b; 1992; Li and Hedge, 1994). The species have mastered various ecological niches from swampy plains to highlands in Eurasia, America and tropical Africa. They are the main components and edificators of various ecosystems (vegetation of rocks, talus and steppes) (Yuzepczuk, 1954; Peer *et al.*, 2007; Korolyuk and Makunina, 2009).

The processes of changes in morphological structures under certain environmental conditions have led to a wide variety of life forms of species of the genus: annual and perennial grasses, dwarf subshrubs, dwarf shrubs and shrubs (Epling, 1942; Yuzepchuk, 1954; Paton, 1990a). Some structures in the plant body are plastic and change under the influence of specific ecological-cenotic conditions. Biomorphological analysis of such

morphological structures makes it possible to assess the degree of diversification in the somatic evolution of species, and the most important information can be expected when studying closely related taxa (Serebriakov and Serebriakova, 1969). Similar works have already been done on the example of some multispecies genera (Chomiccki *et al.*, 2017; Bruy *et al.*, 2018; Anest *et al.*, 2021; Astashenkov *et al.*, 2021), which show the transformation of structural units within closely related groups, depending on changes in habitat conditions.

In this respect, the species of the genus *Scutellaria* have not been studied. The spectrum of life forms remains unclear, and there is practically no information on ontogeny and features of the morphological structure of individuals depending on the habitat. Our research focuses on the biomorphological analysis and ontogenesis of *Scutellaria* species growing in meadow, steppe, and desert regions of Siberia and Central Asia (Guseva, 2018; Guseva and Cheryomushkina, 2019a; 2000; Cheryomushkina *et al.*, 2020). Previously, we studied the morphogenesis of 4 species of the dwarf subshrubs life form widespread in different types of steppes (*S. supina*, *S. grandiflora* (Cheryomushkina and Guseva, 2015; 2017), *S. tuvensis*, *S. sieversii* (Guseva and Cheryomushkina, 2017; 2019b)). The life form and features of the morphological development of individuals are described for each species.

In this work, we will consider the morphogenesis of the steppe dwarf subshrub *Scutellaria przewalskii* in habiting the stony variants of the temperate steppes, and we will carry out a comparative analysis of the morphological features of five species of the genus



Scutellaria. We expect to identify common features in the development of steppe dwarf subshrubs and differences associated with the growth of individuals of the species in different types of steppe communities: meadow steppe, temperate steppe, and desert steppe.

MATERIALS AND METHODS

Scutellaria przewalskii is endemic to the Tien Shan (Yuzepchuk, 1951). The northern border of the distribution area runs along the northern macroslope of the Kyrgyz ridge, the southern macroslope of the Kungey Alatau, and the Ketmen ridge; the southern border reaches the northeastern macroslope of the Fergana ridge. In the east, the species' distribution is limited by the eastern extremities of the ridges of Ketmen and Terskey Alatau and, in the west by the central part of the Kyrgyz ridge and its southern spurs, descending into the Susamyr valley (Yuzepchuk, 1954; Lazkov, 2016). The specimens of *S. przewalskii* are mainly confined to petrophytic variants of shallow-grass steppes, widespread on dry clay-stony and sandy open slopes of river terraces, lakes, and river banks. The species is found in the communities of the halophytic (solyankovy *Salsola*) desert of the Western Issyk-Kul region (Shalpykov and Kartanbaev, 2011), in the *Neotrinia splendens* (Trin.) M.Nobis, P.D.Gudkova & A.Nowak formation (Ionov and Lebedeva, 2013), and *Caragana* in the western foothills of the Issyk-Kul Depression (Nikitina, 1962). In the mountains, *S. przewalskii* ranges up to 2600 meters above sea level.

Material for the study of individuals' development was collected in 2017 and 2019 in the Kegen Depression (Kazakhstan), the Issyk-Kul Depression (Kyrgyzstan), and in the Kochkor and Susamyr valleys (Kyrgyzstan) (Fig. 1A, B).

Kegen Depression: The second terrace of the Karkara river. N 42°52'21.5", E 079°14'42.1", 1933 meters above sea level. Dry petrophytic shallow-grass steppe, fescue-vermouth community (*Artemisia frigida* Willd., *Festuca valesiaca* Schlecht. ex Gaudin, *Koeleria cristata* Pers., *Thymus seravschanicus* Klokov). Species richness - 9 species. The total projective grass cover (TPGC) amounts to 30%, stony content is up to 40%.

Issyk-Kul Depression: Koi-Sary area. Sandy lake terrace. N 42°34'30.2", E 078°10'38.1", 1577 meters above sea level. Sandy dry steppe with *Calamagrostis epigejos* (L.) Roth, *Leymus racemosus* (Lam.) Tzvelev, *Neotrinia splendens* (Trin.) M.Nobis, P.D.Gudkova & A.Nowak, закустаренная *Berberis heteropoda* Schrenk, *Caragana pleiophylla* (Regel) Pojark. Species richness - 12 species. TPGC 15–20%.

Coordinates are set using a Garmin eTrex Vista GPS.

The life form and the shoot system

The life-form characteristics of *S. przewalskii* are

given using the eco-morphological classification of the life-forms developed by I. G. Serebryakov (1962) for individuals in a middle-aged generative state. The biomorph type (monocentric and sparse polycentric) was established in accordance with the phytocenotic classification based on the spatial distribution features of shoots, innovation buds, and plant roots (Smirnova, *et al.*, 2002). When describing the shoots system, we used the concepts of shrub and dwarf shrub shoots (Serebryakov, 1962; Mazurenko and Khokhryakov, 1977). The following concepts were used to describe the structure of individual:

1. *Primary shoot* - the basis of the plant's perennial shoot system, which is formed in the seed.

2. *Branch shoot* - lateral shoot developing on the primary or any other shoot. It serves to increase the vegetative mass of assimilation organs and seed productivity. They develop from hibernating buds.

3. *Formation (renewal) shoot* - a perennial shoot performing the function of rejuvenating the shoot system of the bush. Morphologically, these are large shoots with enhanced growth, especially in the first year of life, and are the basis for the skeletal axis construction. They develop from a dormant or hibernating bud.

4. *Enrichment shoot* - a sylleptic annual shoot that completely dies off at the end of the growing season. It can be both vegetative and generative.

5. *Compound skeletal axis (skeletal axis, axis)* - a perennial formation consisting of a set of basal parts of formation shoots of different orders.

Ontogenesis

While studying *S. przewalskii*, the concept of a discrete ontogenesis description was adopted, which is based on the identification of stages characterized by qualitative characteristics in the process of individual development (Rabotnov, 1950; Uranov, 1975). The following ontogenetic states have been identified: a seedling (p), juvenile (j), immature (im), virginal (v), young generative (g1), mature generative (g2), old generative (g3) and subsenile (ss); with the stages of ontogenesis being determined based on structural indicators: the presence or absence of embryonic, juvenile or mature morphological characters; the ratio of living and dead parts of the plant; and the ability of vegetative reproduction among individuals (Gatzuk *et al.*, 1980; White, 1985). 25 individuals were taken for the quantitative characterization of ontogenetic states. The obtained data were processed statistically, calculated: arithmetic mean \pm standard errors, minimum and maximum values of the features using the computer program Microsoft Excel.

The ontogenesis state duration of the individual and the age of the compound skeletal axes were determined from the annual rings on the anatomical section in the basal part of the root and the axis using a stereomicroscope Carl Zeiss

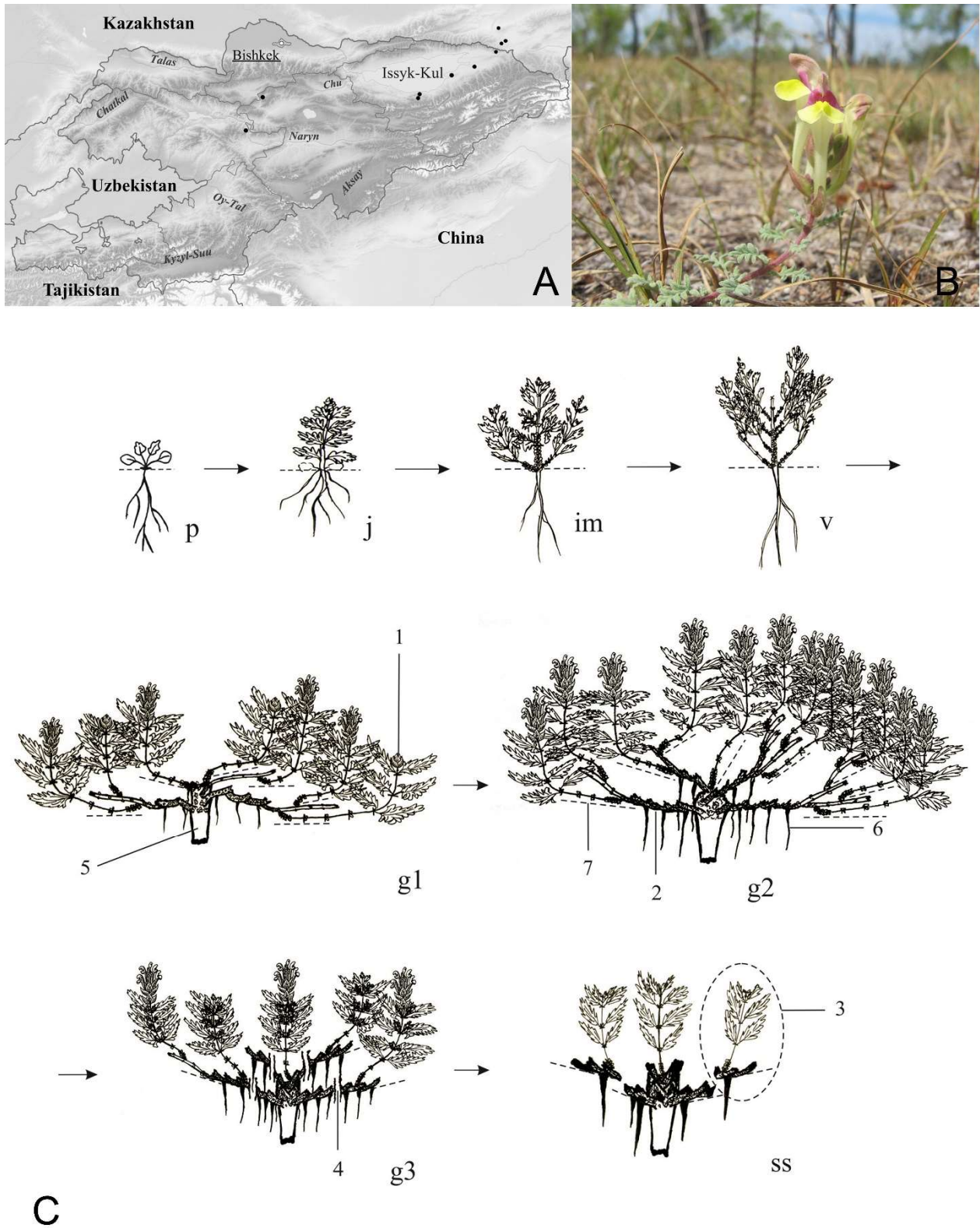


Fig. 1. A schematic development of *Scutellaria przewalskii*. **A.** Collecting sites, **B.** Habitat in the steppes of the Kyrgyzstan. **C.** A schematic development. 1, formation shoot; 2, skeletal axis; 3, particular; 4, decayed site; 5, main root; 6, adventitious root; 7, soil level; p, j, im, v, g1, g2, g3, ss, ontogenetic states.

**Table 1.** Climate data of research sites

Species	Average annual temperature, °C	Average annual Rainfall, mm/y	Aridity index (I)
<i>S. supina</i>	1.3	656	55
<i>S. grandiflora</i>	0.5	160	15
<i>S. przewalskii</i>	-5.4	78	17
<i>S. sieversii</i>	13.1	222	9
<i>S. tuvensis</i>	12.2	202	9

SteREO Discovery.V12 with AxioCam HRc (Germany). Annual rings are visualized under a microscope very well. The age of 25 individuals of each ontogenetic state was calculated.

For a comparative characteristic of morphogenesis and shrub structure of five steppe dwarf subshrubs, 14 quantitative and qualitative features were selected. They are: the monopodial growth duration of the primary shoot, pregenerative period duration, growth duration of the formation shoot, maximum branching order of the branch shoot, formation shoot length, skeletal axes number, skeletal axis length, number of formation shoots (which are part of the axis), axis life span, bush diameter, root diameter, presence of vegetative reproduction, ontogenesis duration. All traits were taken from 25 individuals of all studied species. About 250 individuals of each species (1250 individuals in total) were analyzed. The results of the morphological analysis were reported as mean \pm standard errors. Statistical analysis was performed using the Statistica 10 software package.

The aridity index was used for comparing the habitats of the studied species. Climatic data were taken from the site <https://rp5.ru>. Climate aridity was characterized by the de Morton aridity index (I): $I = P/(T+10)$. P - average annual rainfall, T - the average annual temperature (Oliver and Fairbridge, 1987). The minimum absolute value of the index corresponds to the maximum climate aridity (Table 1).

RESULTS

In most of the area, in petrophytic variants of shallow-grass temperate steppes, *S. przewalskii* develops as a monocentric dwarf subshrub with anisotropic generative shoots.

Seed germination is aboveground. *Seedlings* - single-shoot plants with a pair of oval cotyledonous leaves and a pair of true green leaves. The main root reaches 2–3 cm, and many thin lateral roots develop on it. Individuals stay in the seedling stage from several days to 2 weeks.

Individuals enter the *juvenile state* in the same year. The monopodial shoot is orthotropic, its height is 0.7–1 cm. The cotyledonous leaves die off, and the number of true green leaves increases to 6–14. The main root elongates to 7 cm and branches out to form lateral roots of the II – IV orders (Fig. 1C).

In the second year of life, the individual passes into

an *immature state*. The primary shoot continues to grow monopodially. The second annual growth consists of short (2–8) and long (2–5) metameres bearing green leaves. In this state, the individual branches out. At the first annual growth, from the buds of the cotyledonous node, 1–2 orthotropic elongated branch shoots of the II order, with short metameres in the basal part, develop. Their length is 2.5–4 cm. 2–4 short branch shoots of the II order, 0.5–1 cm long, grow from the buds of the second annual growth, all unrealized buds become dormant, and a primary bush is formed. At the end of the second growing season, the apical bud and several long metameres of the primary and lateral shoots die off in the first annual growth. The shoots of the second annual growth remain and overwinter, while the remaining part of the bush is lignified. The main root grows up to 10 cm, and 1–2 of the most powerful lateral roots are preserved on it.

In the third year, individuals pass into a *virginal state*. The bush is formed by lateral shoots of two types: 1) biennial with the first short annual growth formed in the immature state, and the second one long; 2) long annual with short metameres in the basal part; they develop from hibernating buds on the second annual growth of the primary shoot.

In the apical part of the branch shoots of the II order, short enrichment shoots develop. At the end of the growing season, they die off together with part of the branch shoot (2/3 of the length remains). In subsequent years, branch shoots of the II – III order develop in the bush. Shoots of the II order (1–2) grow from dormant buds preserved on the primary shoot. Shoots of the III order develop from hibernating buds on the shoots of the II order. They are long and monocyclic. On shoots of the III order, 1.5–4 cm long enrichment shoots grow from lateral buds. During the virginal state, the primary shoot dies off to the basal part, which is 0.9–1.5 cm long and consists of the first annual growth and short metameres of the second annual growth. Lateral shoots die off to short metameres of the basal part. The bases of the primary and lateral shoots thicken, unrealized buds intensively branch, and a reserve of buds is formed. These buds will be realized in subsequent age states. The root system consists of a main root 9–12 cm long and 1–2 lateral ones. The diameter of the main root's base is 0.3–0.4 cm. The virginal state lasts 3–4 years.

In a *young generative state*, plagiotropic sympodial skeletal axes begin to form, consisting of the basal parts of 2–4 formation shoots. The first formation shoots develop from the reserve of dormant buds in the basal part of the primary bush, and then the formation shoots unfold from the hibernating buds on the first/second long metamere of the formation shoot of the previous order. In a young generative state, the bush is formed by 3–4 skeletal axes extending from the center, they consist of 2–3 component parts, up to 2 cm long and 0.25–0.3 cm in

**Table 2.** Comparative characteristics of ontogenesis and bush structure of steppe dwarf subshrubs of the genus *Scutellaria*.

Feature	Meadow steppe	Temperate steppe		Desert steppe	
	<i>S. supina</i>	<i>S. grandiflora</i>	<i>S. przewalskii</i>	<i>S. sieversii</i>	<i>S. tuvensis</i>
Monopodial growth duration of the primary shoot, years	1	2	2	2	3
Pregenerative period duration, years	7–9	6–7	6–7	4	3–4
Growth duration of the formation shoot, years	1	2	2	1	2
Max branching order of the formation shoot	IV	IV	III	III	III
Length of formation shoot, cm	25.8 ± 1.2	10.8 ± 0.6	6 ± 0.8	8.4 ± 0.6	8.3 ± 0.7
Number of skeletal axes in mature generative state, pcs	8–20	4–8 (10)	3–4	4–6 (8)	6–7(10)
Position of the axes in space	orthotropic	plagiotropic	plagiotropic	plagiotropic	plagiotropic
Length of skeletal axis, cm	6.8 ± 0.5	6.2 ± 0.7	3.7 ± 0.4	3.6 ± 0.4	6.1 ± 0.7
Number of formation shoots included in the axis, pcs	2–4	3–4	2–8	4–7	5–7
Life span of skeletal axis, years	8.9 ± 0.5	8.6 ± 0.7	8.8 ± 0.6	5.7 ± 0.2	4.4 ± 0.3
Diameter of bush, cm	64.1 ± 2.9	16.4 ± 1.3	15.8 ± 1.3	13 ± 1.2	20.3 ± 1.4
Diameter of root, cm	0.8–1	2.5–4	0.6–0.9	0.5–0.7	0.8–1
Presence of vegetative reproduction	–	–	+	–	–
Ontogenesis duration, years	30	23–28	22–35	17–23	14–24

diameter. Formation shoots in a young generative state are monocyclic orthotropic elongated generative, 4–6 cm long with short metameris in the basal part (0.2–0.4 cm). The shoot branches out. In the first year of the shoot life, in its apical part, vegetative enrichment shoots 1–4 cm long develop. At the end of the growing season, they die off together with a part of the formation shoot. Most of the formation shoot, consisting of short metameris and 4–5 long ones, remains, lodges, lignifies and hibernates. In the second year, an $n+1$ formation shoot and $n+1$ branch shoots develop from the hibernated buds. They are monocyclic, generative and elongated, with short metameris in the basal part. As the buds are realized on the formation shoot, it dies off at the formation shoot junction of the next order. The main root is up to 18 cm long. Individuals stay in a young generative state for up to 4 years.

In the *mature generative state*, the skeletal axes continue to build higher on the lignified basal parts of the formation shoots. New skeletal axes develop from dormant buds in the basal part of the bush. Formation shoots in a mature generative state can be annual and biennial. Individuals in a mature generative state represent a bush formed by 3–4 skeletal axes. Their length is 1.5–4 cm, and they include 2–7 basal parts of the formation shoots with a supply of dormant buds. The axes are 0.2–0.6 cm thick. Their lifespan ranges up to 13 years. In places where the axes touch the soil, a large number of adventitious roots are formed, 0.1–0.2 cm thick. The bushes' diameter of 8–18 cm is achieved due to the plagiotropic position of the skeletal axes. The base of the main root continues to grow, with its diameter ranging up to 1 cm. The duration of the state is 12–18 years.

In the *old generative state*, the primary bush particulates. The axes sections rot through. The primary bush splits into separate bushy particulates, which are not rejuvenated. In the old generative state, old dormant buds on the axes are realized. The monocyclic vegetative branch shoots develop from them, which consist of 8–13

metameris with scaly leaves. On these shoots, short vegetative enrichment shoots can develop. Skeletal axes gradually dry out and break off. The duration of the old generative state is 2–4 years.

In the *subsenile state*, from the preserved dormant buds, annual elongated branch shoots, that are 3–4 cm high, develop. The subsenile state lasts 2–4 years. The ontogenesis duration of individuals lasts from 22 to 35 years.

Under conditions of a mobile substrate, covering of individuals with sand leads to a change in the course of development. The axes begin to form already in a virginal state in the second or third year of an individual's life. The covered basal parts of branch shoots of the II order become the first link of the sympodially growing skeletal axis. Reproduction on shoots immersed in the substrate is shifted higher along the axis. One monocyclic elongated shoot develops. It is an $n+1$ order formation shoot. The formation shoots of the following orders, as in the typical development, are monocyclic generative anisotropic elongated with short metameris in the basal part. The development of the axes also does not differ from that described above. The length of skeletal axes on sands grows due to an increase in the length of internodes. The number of formation shoots included in their composition does not differ. New skeletal axes develop from dormant buds on axes located on the surface of the substrate. Individuals in a mature generative state on a mobile substrate are represented by a clump consisting of a primary bush and 3–5 partial bushes (ramets), connected by a skeletal axis. The axes are 3–8 cm length, and 0.3–0.8 cm thick. The axes lifespan increases to 21 years. Adventitious roots form at the points of contact of the axes with the soil. On a mobile substrate, the number of adventitious roots is less (3–5), they are strongly thickened up to 0.3–0.5 cm, and are the place of ramets fixation. The clump diameter in a mobile substrate is 9–29 cm, achieved by increasing the axes length and the anisotropic position of the shoots. In the old generative

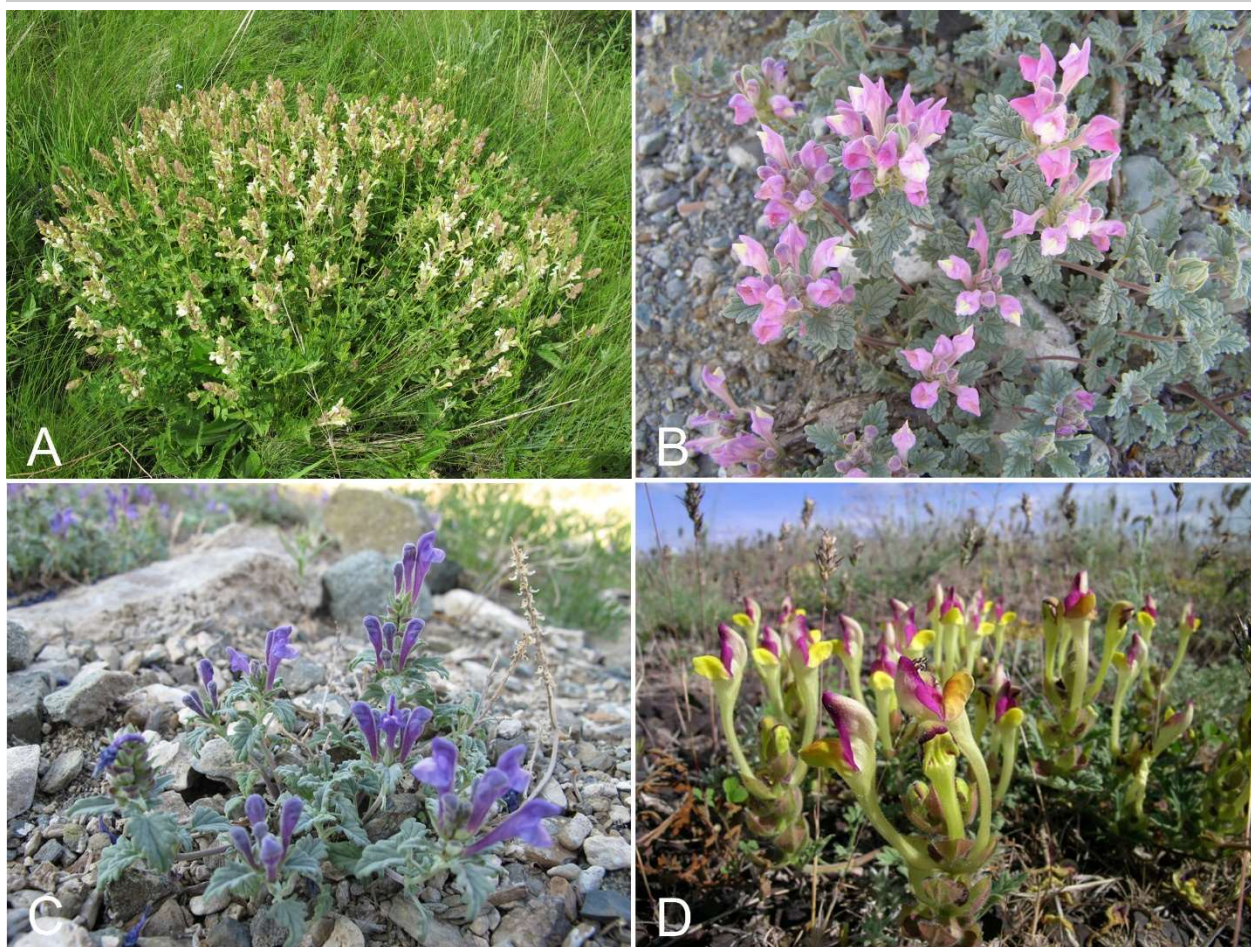


Fig. 2. Comparison morphogenesis of the previous studied steppe dwarf subshrubs **A.** *Scutellaria supina*, **B.** *S. grandiflora*, **C.** *S. tuvensis*, **D.** *S. sieversii*.

state, vegetative reproduction takes place, the clump splits into separate ramets.

Comparison of *S. przewalskii* morphogenesis and the previous studied steppe dwarf subshrubs *S. supina*, *S. grandiflora*, *S. tuvensis*, and *S. sieversii* (Fig. 2) was carried out according to 14 quantitative and qualitative characters indicated in Table 2. Differences were observed between individuals in different steppe communities and were observed as the climate aridized: meadow steppes ($I = 55$) – stony temperate steppes ($I = 15–17$) – desert steppes ($I = 9$).

DISCUSSION

A comparative morphogenesis analysis of 5 species of steppe dwarf subshrubs of the genus *Scutellaria* showed that a common feature being the early termination of the monopodial growth of the primary (main) shoot (Table 2). Aside from that, in different types of steppe communities, it increases with climate aridization. Thus, in meadow steppes ($I = 55$, Table 2), the growth of the primary shoot of *S. supina* lasts one year

while, in desert steppes ($I = 9$), the primary shoot of *S. tuvensis* individuals grows for 3 years. On the contrary, under conditions of climate aridization, the pregenerative period duration is reduced. The longest pregenerative period duration was noted in the meadow steppes ($I = 55$) in *S. supina*, it amounts to 7–9 years. In stony temperate steppes ($I = 15–17$), individuals of *S. grandiflora* and *S. przewalskii* come into bloom for 5–6 years, while individuals of *S. tuvensis* and *S. sieversii* in desert steppes ($I = 9$) for 3–4 years. By the beginning of flowering, all species have a fully formed primary bush, the basal areas of the primary and lateral shoots thicken, dormant buds branch, their number increases. In the future, the perennial structure of the bush will be formed from the reserve of dormant buds formed in the pregenerative period.

The perennial structure of adult individuals of all the studied dwarf subshrubs is formed by a multiply repeating branched basisympodially growing compound skeletal axis (Fig. 3). The same repetitive skeletal axis is characteristic of dwarf subshrubs of the *Thymus* L. (Talovskaya, *et al.*, 2019; Talovskaya, 2020; Cheryomushkina and Talovskaya, 2019) and *Ziziphora* L.

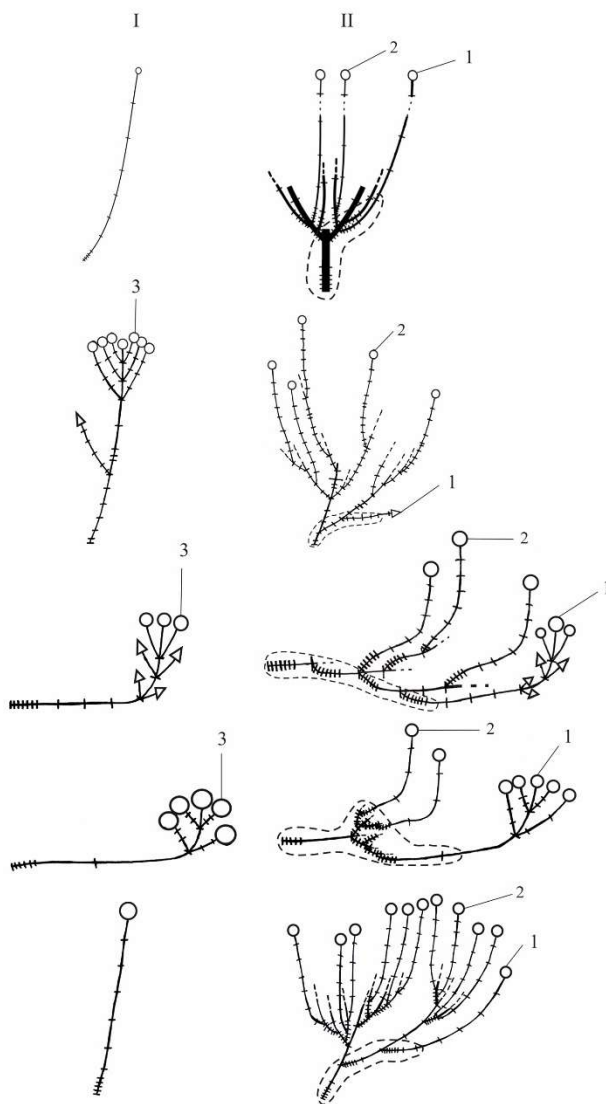


Fig. 3. Schematic structure: I, shoot formation; II, skeleton axis; 1, shoot formation; 2, branch shoot; 3, enrichment shoot; ---, compound skeletal axis.

(Cheryomushkina and Bobokalonov, 2020) genera.

Skeletal axes of different species of the genus *Scutellaria* differ in several parameters: space position, length, lifespan; the number and structure of the formation shoots included in the axis; monopodial growth duration of formation shoots.

According to the space position, the studied dwarf subshrubs have orthotropic and plagiotropic skeletal axes. Orthotropic axes are found only in meadow steppes in individuals of *S. supina*. Plagiotropic axes are found in species of temperate and desert steppes. The lifespan of skeletal axes varies considerably - from 3 to 19 years. There is a tendency to its reduction with an increase in climate aridization: meadow steppes 8.9 years → temperate steppes – 8.6–8.8 years → desert steppes 4.3–

5.7 years (Table 2). The table shows that the number of formation shoots in the skeletal axis is different. It is the smallest species growing in meadow steppes (*S. supina*), and the highest species under xerophytic conditions (*S. tuvensis*, *S. sieversii*).

The species also differ in the monopodial growth duration of the formation shoot. It can be annual (*S. supina*, *S. sieversii*), biennial (*S. grandiflora*, *S. tuvensis*, *S. przewalskii*) and, less often, triennial (*S. tuvensis*). The formation shoot structure is of the same type in all studied species - it is elongated, with short metamerer in the basal part (Fig. 3). The formation shoot is monocarpic (in the understanding by Serebryakov (1952), Barthélémey and Caraglio (2007)). With a biennial development, as in other subshrubs and dwarf subshrubs in arid habitats (Rachkovskaya, 1957; Bessalova, 1960; Orshan, 1982; Montserrat-Martí *et al.*, 2011), a shoot with short and long metamerer develops in the first year. In the second years – a shoot with only long metamerer. The formation shoot branches up to the II – IV orders. From the axillary buds in the basal part of the shoot, annual or biennial orthotropic elongated branch shoots are formed, increasing the vegetative perennial mass of assimilation organs and the crown of the bush. In the apical part of the shoot, enrichment shoots develop from sylleptic buds, completely dying off after fruiting. The formation shoot dying-off occurs until the last short or first long metamerer bearing renewal buds from which a new formation shoot of the next order develops.

Most of the studied steppe dwarf subshrubs are not capable of vegetative reproduction (*S. grandiflora*, *S. tuvensis*, *S. supina* and *S. sieversii*). However, in *S. przewalskii*, at the end of ontogenesis, a complete particulation of the bush and the formation of bushing particles (ramets) with an adventitious root system occurs. One of the adventitious roots thickens and becomes a secondary taproot. At the same time, the monocentricity of the dwarf subshrub is preserved. The formation of a sparse polycentric dwarf subshrub in individuals of *S. przewalskii* occurs on sandy or sandy-loam substrates. In such ecotopes, new centers of fixation (partial bushes) with an adventitious root system are formed. Vegetative reproduction occurs due to the axes destruction. The presence of vegetative reproduction can also be found in dwarf subshrubs (*Artemisia taurica* Willd., *A. pauciflora* Weber ex Stechmann and *A. lercheana* Weber ex Stechm.) growing in the desert steppes of Kazakhstan (Bessalova, 1960).

CONCLUSION

Comparative analysis of the structure and morphogenesis of steppe dwarf subshrubs of the genus *Scutellaria* revealed common features in their development. They are characterized by: the basisympodial growth of the shoot system; the



lignification of the shoots' basal parts; the renewal buds location above the substrate surface; short monopodial growth of the primary shoot; the primary bush formation before the first flowering; the basal parts thickening (often accretion) of the primary and lateral shoots, and the preservation of a large number of dormant viable buds on them; the presence of the main root during the entire ontogenesis. The adult individuals' bush structure of the studied species consists of branched basisympodially growing perennial orthotropic and plagiotropic skeletal axes formed by biennial, less often – annual formation shoots. At the same time, the studied dwarf subshrubs differ by the formation shoot structure and shoot types developing on it, by the number, size, and lifespan of the axes that form a perennial bush of an adult plant. On lighter sandy substrates, individuals of some species shows the polyvariety of ontogenesis, which manifests itself in the formation of new morphological structures (clump, partial bush) and the emergence of a new mixed reproduction modus (seed in combination with vegetative). With an increase in climate aridization in a row “meadow steppes - temperate steppes - desert steppes”, the pregenerative period duration and the skeletal axes age in dwarf subshrubs decrease, which leads to frequent changes of the skeletal axes in the structure of the dwarf subshrub due to the large number of dormant buds in the basal part of the bush.

AUTHOR CONTRIBUTIONS

All authors contributed to the study concept and design. All authors collected data, prepared the material, and analyzed it. Vera Cheryomushkina and Alexandra Guseva wrote the manuscript. The description of the community was conducted by Vera Cheryomushkina. The photos were taken by Vera Cheryomushkina. The drawings are made by Alexandra Guseva. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

This work was supported by the framework of the state task of the Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, № AAAA-A21-121011290026-9.

LITERATURE CITED

- Anest, A, T. Charles-Dominique, O. Maurin, M. Millan, C. Edelin and K. W. Tomlinson 2021 Evolving the structure: climatic and developmental constraints on the evolution of plant architecture. A case study in Euphorbia. *New Phytol.* **231(3)**: 1278–1295.
- Astashenkov, A.Y., E.A. Karpova and V.A. Cheryomushkina 2021 Diversity patterns of life forms and phenolic profiles of endemic *Nepeta* plants along an aridity gradient of a high-mountain zone in Central Asia. *Taiwania* **66(4)**: 541–556.
- Barthélémy, D. and Y. Caraglio 2007 Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Ann. Bot.* **99(3)**: 375–407.
- Bespalova, Z.G. 1960 On the biology of edificator dwarf subshrubs of phytocenoses of the Nogai desert steppes and dry steppes of Central Kazakhstan. *Botanicheskii Zhurnal* **45(10)**: 1463–1475 [in Russian]
- Bruy, D., T. Hattermann, L. Barrabé, A. Mouly, D. Barthélémy and S. Isnard 2018 Evolution of Plant Architecture, Functional Diversification and Divergent Evolution in the Genus *Atractocarpus* (Rubiaceae) for New Caledonia. *Front. Plant Sci.* **9**: 1775.
- Cheryomushkina, V.A. and A.A. Guseva 2015. Life forms of *Scutellaria supina* L. (Lamiaceae). *Contemporary Problems of Ecology* **8(5)**: 624–635.
- Cheryomushkina, V.A. and A.A. Guseva 2017 Morphogenesis of *Scutellaria grandiflora* (Lamiaceae) and ontogenetic structure of its cenopopulations. *Rastitelnye Resursy* **53(3)**: 380–393. [in Russian]
- Cheryomushkina, V.A. and E.B. Talovskaya 2019 Life forms of some *Thymus* (Lamiaceae) species: an architectural approach. *Botanicheskii Zhurnal* **104(3)**: 377–390. [in Russian]
- Cheryomushkina, V.A. and K.A. Bobokalonov 2020 Life form, ontogenesis and ontogenetic structure of *Ziziphora suffruticosa* in Tajikistan. *Plant Life of Asian Russia* **2(38)**: 25–33. [in Russian]
- Cheryomushkina, V.A., A.A. Guseva, N.I. Makunina, A. Yu. Astashenkov and G.R. Denisova 2020 Phytocenotic Characteristics, Ontogenetic Structure and Assessment of the State of *Scutellaria scordiifolia* (Lamiaceae) Coenopopulations in Siberia. *Rastitelnye Resursy* **56(2)**: 138–150.
- Chomicki, G., M. Coiro and S.S. Renner 2017 Evolution and ecology of plant architecture: integrating insights from the fossil record, extant morphology, developmental genetics and phylogenies. *Ann. Bot.* **120(6)**: 855–891.
- Cole, I.B., J. Cao, A.R. Alan, P.K. Saxena and S.J. Murch 2008 Comparisons of *Scutellaria baicalensis*, *Scutellaria lateriflora* and *Scutellaria racemosa*: genome size, antioxidant potential and phytochemistry. *Planta Med.* **74(4)**: 474–481.
- Dogan, Z., K. Ishiuchi, M. Toshiaki and I. Saracoglu 2019 New acylated iridoid glucosides from *Scutellaria glaphyrostachys* Rech.f. and chemotaxonomic importance for the genus *Scutellaria*. *Phytochem. Lett.* **32**: 157–161.
- Epling, C. 1942 The American species of *Scutellaria*. University of California Publications in Botany **20**: 1–137.
- Gatzuk, L. E., O. V. Smirnova, L. I. Vorontsova, L. B. Zaugol'nova and L. A. Zhukova 1980 Age state of plants of various growth forms: a review. *J. Ecol.* **68(2)**: 675–696.
- Guseva, A.A. 2018. Features of development of the clonal plant *Scutellaria scordiifolia* Fischer ex Schrank (Lamiaceae) in Siberia. *BIO Web Conf.* **11**: 00019.
- Guseva, A.A. and V.A. Cheryomushkina 2017 Morphogenesis and state of cenopopulations of endemic species *Scutellaria tuvensis* (Lamiaceae). *Byull. MOIP. Otd. Biol.* **122(2)**: 68–77. [in Russian]
- Guseva, A.A. and V.A. Cheryomushkina 2019a Polyvariation of the development *Scutellaria* L. species and the structure of their populations in Siberia. *BIO Web Conf.* **16**: 00010.
- Guseva, A.A. and V.A. Cheryomushkina 2019b The development of individuals and the state of the population of *Scutellaria sieversii* (Lamiaceae) in the Chu-Ili mountains. *Plant Life of Asian Russia*. **3**: 47–52. [in Russian]



- Guseva, A.A. and V.A. Cheryomushkina 2020 Features of the development of xylorhizomes in a dwarf subshrub *Scutellaria mongolica* K. Sobol. BIO Web Conf. **24**: 00026.
- Ionov, R.N. and L.P. Lebedeva 2013 Formation *Achnatherum splendens* (Ttin.) Nevski (*Lasiagrostis splendens* (Ttin.) Kunth.) in the Tien Shan and Alai of Kyrgyzstan. Izvestiya NAN KR **2**: 53–59. [in Russian]
- Jackowiak, B., Z. Celka, J. Chmiel, K. Latowski and W. Żukowski 2007 Red list of vascular flora of Wielkopolska (Poland). Biodiv. Res. Conserv. **5-8**: 95–127.
- Kochkareva, T.F. 1986 Family Lamiaceae In: Flora of the Tajik SSR. **8**: 63–92. Nauka, Leningrad. [in Russian]
- Korolyuk, A.Y. and N. I. Makunina 2009 Steppes of the Altai-Sayan mountain area (Order Stipetalia krylovii Kononov, Gogoleva et Mironova 1985). Plant Life of Asian Russia **2(4)**: 43–53. [in Russian]
- Lazkov, G.A. 2016 Labiatae (Family Labiatae Juss.) in Flora of Kyrgyzstan. In: Lazkov, G.A. (eds.). KH Botanical Monograph et Revision Series. **1**: 384. Republic of Korea.
- Li, X.W. and I.C. Hedge 1994 Lamiaceae. In: Wu, Z. Y. and P. H. Raven (eds.) Flora of China. **17**: 50–299. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.
- Mazurenko, M.T. and A.P. Khokhryakov. 1977. The structure and morphogenesis of shrubs, Nauka, Moscow. 160 pp. [in Russian]
- Montserrat-Martí, G., S. Palacio, R. Milla and L. Giménez-Benavides. 2011. Meristem Growth, Phenology, and Architecture in Chamaephytes of the Iberian Peninsula: Insights into a Largely Neglected Life Form. Folia geobot. **46(2-3)**: 117–136.
- Nikitina, E.V. 1962 Flora and vegetation of pastures and hayfields of the Kyrgyz Ala-Too ridge, Izd-vo AN Kirg. SSR, Frunze. 286 pp. [in Russian]
- Oliver, J.E. and R.W. Fairbridge (eds.) 1987 The Encyclopedia of Climatology. Van Nostrand Reinold, New York.
- Orshan, G. 1982 Monocharacter growth form types as a tool in an analytic-synthetic study of growth forms in Mediterranean type ecosystems. A proposal for an inter-regional program. Ecol Medit. **8(1)**: 159–171.
- Paton, A.J., S. Suddee and B. Bongcheewin 2016 Two new species of *Scutellaria* (Lamiaceae) from Thailand and Burma. Kew Bull. **71(1)**: 3.
- Paton, A.J. 1990a A Global Taxonomic Investigation of *Scutellaria* (Labiatae). Kew Bull. **45(3)**: 399–450.
- Paton, A. J. 1990b The phylogeography of *Scutellaria* L. Notes of the Royal Botanic Gardens **46**: 345–359.
- Paton, A.J. 1992 The adaptive significance of calyx and nutlet morphology in *Scutellaria*. In: Harley R. M. and T.Reynolds (eds). Advances in Labiate Science. 203–210. Royal Botanic Gardens, Kew.
- Peer, T., J.P. Gruber, A. Millinger, and F. Hussain 2007. Phytosociology, structure and diversity of the steppe vegetation in the mountains of Northern Pakistan. Phytocoenologia **37(1)**: 1–65.
- Rabotnov, T.A. 1950 The life cycle of perennial herbaceous plants in meadow coenoses. Tr. Bot. inst. AN SSSR, ser. III. **6**: 7–204. [in Russian]
- Rachkovskaya, E.I. 1957 Towards the biology of desert dwarf subshrubs. Tr. Bot. inst. AN SSSR, ser. III. **11**: 69–87. [in Russian]
- Ranjbar, M. and C. Mahmoudi 2017 A taxonomic revision of *Scutellaria* sect. *Lupulinaria* subsect. *Lupulinaria* (Lamiaceae) in Iran. Feddes Rept. **128(3-4)**: 63–101
- Safikhani, K., Z. Jamzad and H. Saeidi 2018 Phylogenetic relationships in Iranian *Scutellaria* (Lamiaceae) based on nuclear ribosomal ITS and chloroplast trnL-F DNA data. Plant Syst. Evol. **304(9)**: 1077–1089.
- Serebryakov, I. G. 1952 Morphology of vegetative organs of higher plants, Sovetskaya nauka, Moscow. 391 pp. [in Russian]
- Serebryakov, I.G. 1962 Ecological plant morphology, Vyssh.shk., Moskva. 378 pp. [in Russian]
- Serebriakov, I.G. and T.I. Serebriakova 1969. Live forms of Angiosperms and their evolution within separate systematic groups. Botanicheskii Zhurnal **54**: 1321–1326. [in Russian]
- Shalpykov, K.T. and J.K. Kartanbaev. 2011. Ontogenetic spectra of the main life forms of cenopopulations of the deserts of the Western Issyk-Kul region. Izv. NAN Kyrg. Resp. **3**: 41–45. [in Russian]
- Shang, X., X. He, M. Li, R. Zhang, P. Fan, Q. Zhang and Z. Jia 2010 The genus *Scutellaria*: an ethnopharmacological and phytochemical review. J Ethnopharmacol. **128(2)**: 279–313.
- Smirnova, O.V., M.M. Palenova and A.S. Komarov 2002 Ontogeny of different life forms of plants and specific features of age and spatial structure of their populations. Russ. J. Dev. Biol. **33(1)**: 1–10.
- Talovskaya, E.B. 2020. Modification of architecture of dwarf subshrub *Thymus seravschanicus* (Lamiaceae) in the Republic of Tajikistan. Contemp. Probl. Ecol. **13(3)**: 266–273.
- Talovskaya, E.B., V.A. Cheryomushkina, A. Yu Astashenkov, A.A. Guseva and E. Naizabekova 2019 Biology of *Thymus karatavicus* Dm., an endemic plant of the West Tien Shan. J Asia Pac. Biodivers. **12(4)**: 668–673.
- Uranov, A.A. 1975. Age spectrum of the phytocoenopopulations as a function of time and energetic wave processes. Nauchnye doklady vysshei shkoly, Biologicheskie nauki **2**: 7–34. [in Russian]
- White, J. (eds.) 1985 The Population Structure of Vegetation. Handbook of Vegetation Science **3**: 369. Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster.
- Yuzepchuk, S.V. 1951 Sixty new *Scutellaria*. Botanical materials of the herbarium of the V.L. Komarov Academy of Sciences of the USSR. **XIV**: 356–453. [in Russian]
- Yuzepchuk, S.V. 1954 Genus *Scutellaria* L. In: Komarov, V. L. (eds.). Flora SSSR. **20**: 183–184. Izd. AN SSSR, Moskva, Leningrad. [in Russian]
- Zhao, F., B. Li, B.T. Drew, Y.P. Chen, Q. Wang, W. Yu, E. Liu, Y. Salmaki, H. Peng and C. Xiang 2020 Leveraging plastomes for comparative analysis and phylogenomic inference within Scutellarioideae (Lamiaceae). PLOS ONE **15(5)**: e0232602.
- Zhao, F., E. Liu, H. Peng and C. Xiang. 2017. A new species of *Scutellaria* (Scutellarioideae, Lamiaceae) from Sichuan Province in southwest China. PeerJ. **5**: e3624.