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Morpho-Evolutionary Relations of Spurges (Genus *Euphorbia*) of *Esula* Section from the Urals Region

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ABSTRACT

A morpho-evolutionary analysis of interspecific relationships in the *Esula* section of *Euphorbia* genus from the Urals Region revealed 22 elementary evolutionary vectors (vector-traits), describing evolutionary trends in the morphology of the group. For the first time the scheme of morpho-evolutionary relations for the spurges of the Urals region is constructed using the SYNAP method, with priority given to the new trait origin. The method allowed a more accurate determination of the evolutionary and morphological distinction within the *Esula* section series and justifies the reattribution of *E. pseudagraria* from the *Caesia* series into the *Latifoliae* series.

Keywords

evolutionary analysis, morphological traits, *Euphorbia*, the Urals region, SYNAP method, spurge, *Esula* section

РЕЗЮМЕ

Байков К.С., Соловьев С.В. Морфолого-эволюционные отношения молочаев (род *Euphorbia*) секции *Esula* Уральского региона

Для выявления межвидовых отношений молочаев из секции *Esula* во флоре Уральского региона были выделены и описаны 22 элементарных эволюционных вектора (вектор-признака), характеризующие основные эволюционные преобразования в морфологии исследованных видов. С помощью метода SYNAP впервые получена схема морфолого-эволюционных связей, в которой предпочтение отдано возникновению новых признаков. Данный метод позволил более точно установить морфологические и эволюционные границы между рядами в секции *Esula* и подтвердить необходимость перемещения вида *Euphorbia pseudagraria* из ряда *Caesia* в ряд *Latifoliae*.

Ключевые слова

эволюционный анализ, морфологические признаки, *Euphorbia*, Уральский регион, метод SYNAP method, молочай

INTRODUCTION

The Ural mountains (within the borders of the Russian Federation) lie with the adjacent plain territories of the Cis- and Trans-Urals and are referred hereafter as the Urals region. Administratively the region embraces the Orenburg, Chelyabinsk and Sverdlovsk Regions, Bashkortostan Republic and Perm Krai, as well as the western part of the Kurgan and Tyumen Territories, Khanty-Mansy and Yamal-Nenets Autonomous Districts and the eastern part of Komi Republic.

In the flora of the Urals region, the genus *Euphorbia* L. is represented by 24 species from two subgenera and six sections. The section *Esula* Dumort. has 17 species, or 71 % of the total number of *Euphorbia* species in the region. All the species belong to the type *Esula* subsection and to eight series: *Latifoliae* Baikov, *Lucidae* Prokh., *Esulae* Prokh., *Virgatae* Prokh., *Leptocaula* Geltman, *Subcordatae* Baikov, *Caesia* Geltman and *Andrahnoides* Prokh.

The aim of the study was to reveal the evolutionary-morphological relationships within the group of closely-related species from the *Esula* section in order to obtain a better understanding of its phylogeny.

The study arose from the working hypothesis that the most primitive species from *Esula* section in the flora of Urals region are *E. lucida* Waldst. et Kit. and *E. agraria* M. Bieb. (ser. *Lucidae*). These species exhibit the maximum primitive morphological states which allows us to regard them as a hypothetical ancestor. In the Urals region the European species *E. lucida* can be found in the local area in the south of the Tyumen territory. The *E. agraria* grows mainly in the East and Central Europe and the Mediterranean, its closest to the Urals populations being found in the Crimea, Caucasus, and Asia Minor (Geltman 1996, 2002). In the Urals region *E. agraria* can be found in Bashkortostan. The height of mature plants of these species exceeds 40 cm. Their middle leaves are often broader at the base. *E. lucida* tends to grow mostly in mires and meadow wetlands, while *E. agraria* grows mostly in steppe habitats (Baikov & Solovyev 2012).

Other species belonging to *Esula* section manifest significant polymorphism in their traits and high ecological plasticity, which may be due to their relatively young evolutionary age (Geltman 1996, Baikov 2007).

MATERIALS AND METHODS

We studied plant specimens from the herbaria of the Komarov's Botanical Institute of the Russian Academy of Sciences (LE, Saint-Petersburg, Russia), the Institute of Plant and Animal Ecology of the Urals Branch of Russian Academy of Sciences (SVER, Ekaterinburg, Russia), the Institute of North Development Problems (Tyumen, Russia), the Central Siberian Botanical Garden of the Siberian Branch of the Russian Academy of Sciences (NSK, Novosibirsk, Russia), as well as from the herbaria of the State Universities in Saint-Petersburg (LECB), Moscow (MW), Perm (PERM), Tomsk (TK), Kurgan and Tyumen. We also studied plant specimens collected by S.V. Solov'yev in different habitats of the Urals region during 2007–2012, including some serial sets (population sampling).

To assess the directions of morpho-evolutionary transformation in this group of plant species we used the SYNAP method of phylogenetic analysis (Baikov 1996, 1999, 2001) with its computer software (Baikov & Zverev 2000).

The SYNAP initial step requires identifying and describing the elementary evolutionary vectors, characterizing directions of morpho-evolutionary transformation in spurges of the Urals region, representing the *Esula* section, as it was performed previously for the spurges of the Northern Asia (Baikov 2006, 2008).

Each elementary evolutionary vector (named also vector-trait) represents a pair of adjacent states, related to each other as initial and new states. Hence such vector-traits can be used to describe directions of the evolutionary and morphological transformation in the studied group (Baikov 2004). Such transformation is triggered by a phylogenetic signal (Pavlinov 2005), in many cases the latter being shifts in environmental conditions. It is important to understand that a set of vector-traits reflects the most essential events in the phylogenetic history of a given group (Baikov 2008).

RESULTS

For spurges of *Esula* section in the Urals region we composed 22 vector-traits. The directions of the evolutionary vectors, adopted in our study, we regard as null-hypotheses (Pavlinov 1990, Baikov 2008). These null hypotheses were tested for conformity using a logical procedure, implemented in the SYNAP algorithm (Baikov 1996, 1999). Below we present the list of elementary evolutionary vectors, with directions of the morphological transformation being explained.

1. Plants of 40 cm high and more → plants not exceeding 40 cm in height. This vector determines the general trend of plant size decreasing as evolutionary young species expand into new habitats with more open space, less soil humus and shorter vegetative period. Such species as *E. lucida*, *E. agraria*, *E. borodini* Sambuk, *E. virgata* Waldst. et Kit., *E. esula* L. and *E. uralensis* Link, generally are more than 40 cm high, but often their height does not exceed 40 cm, so these species are polymorphic in respect to this vector-trait.

2. Plants of 20–40 cm high and more → plants generally not exceeding 20 cm in height. This vector describes the second step in plant size decreasing due to the same factor, as described above (see explanation for vector 1).

3. Plants always glabrous → plants both glabrous and pubescent. Most of the studied species are plants without hairs. Development of hairs arose through the need to protect plants from increased solar radiation and transpiration in the more open habitats. It occurred both in meadow and steppe communities, including those on rocky denudation sites. Species having pubescent plants are polymorphic in respect to this trait as there can be both pubescent and glabrous specimen in the same population.

4. Plants glabrous or pubescent → plants always pubescent. Among all the studied *Esula* section species of the Urals region, only one species, namely *E. cyparissias* L. is always thickly covered by very short trichomes.

5. Medial leaves are relatively wide (more than 6 mm) → medial leaves narrower (not exceeding 6 mm in width). The lamina width decrease is a universal trend in *Euphorbia* evolution in the North Eurasia, correlating with the decrease in plant size. The *Euphorbia* plants of the Urals region display very clearly the transition from relatively wide and dense leaves (*E. lucida*, *E. agraria*, *E. pseudagraria* P.A. Smirn., *E. borodini*) to narrower leaves with relatively less density (*E. esula*, *E. borealis* Baikov, *E. korshinskyi* Geltman, and others).

6. Medial leaves 4–6 mm wide → medial leaves 2–4 mm wide. This vector describes the hypothesis that narrower (2–4 mm wide) medial leaves, that are common for many studied species (*E. cyparissias*, *E. uralensis*, *E. leptocaula* Boiss. and others), originated from the denser leaves of moderate width. Narrower leaf blades could enhance plant adaptability under sharply continental cryoaridic climate.

7. The base of the medial leaves significantly broadened and subcordate → the base of the medial leaves sharply narrowed or rounded. This transformation of the medial leaves' base of *Esula* section species appeared to be more likely in the direction described by vectors 7, 8 and 9. We believe this to be the result of species expanding into colder and drier habitats, which inevitably should have affected the leaf base, the latter decreasing in total area, including the base. Among the *Esula* section members the broadened or subcordate leaf base was found to be common for *E. agraria*, with *E. lucida* being polymorphic in respect to this trait as well.

8. The base of the medial leaves sharply narrowed or rounded → the base of the medial leaves gradually narrowed or late cuneate. Three species have narrowed or rounded leaf bases, i.e. possess the original trait of this vector-trait, namely *E. pseudagraria*, *E. rossica* P.A. Smirn. and *E. cyparissias*, whereas *E. gmelinii* Steud. and *E. undulata* M. Bieb. are polymorphic in respect to this vector-trait. The new state is characteristic for *E. virgata*, *E. borszczowii* Prokh., *E. uralensis* and *E. caesia* Kar. et Kir.

9. The base of the medial leaves gradually narrowed or late cuneate → the base of the medial leaves narrow cuneate, attenuate. This vector-trait depicts the final step (for a given moment) of leaf base transformation. In respect to this trait such species as *E. borealis*, *E. microcarpa* (Prokh.) Krylov and *E. leptocaula* are evolutionary more advanced, while *E. borodini*, *E. esula* and *E. korshinskyi* are polymorphic.

10. The pedicels of the apical umbel doubly or triply bifid → the pedicels of the apical umbel simple or once bifid. Most of the studied species were shown to have simple or once bifid pedicels of the apical umbel, while the rest are polymorphic in respect to this vector-trait. No *Esula* section member growing in the Urals region was found to have only this initial state.

11. The apical umbel of many rays (usually 8–13) → the apical umbel of fewer rays (usually 4–6). The reduction in

number of pedicels (rays) in the apical umbel-like pleiochasium and the bifid nature of the pedicels is an universal trend among spurges of the North Eurasia, being characteristic of the evolutionarily advanced species. We assert that the trend was caused by plant expansion into the more severe habitats, resulting in a shorter vegetative period and accelerated plant growth (Baikov 2008). The same trend was also observed in the *Esula* section in the Urals region.

12. The outer bracts narrower or equal in width to medial leaves → the outer bracts wider than medial leaves. We believe the increased width of the outer bracts (the lower leaves of the pedicels of the apical umbel-like inflorescence) as compared to the medial leaves to be an advanced evolutionary state. This vector-trait corresponds directly with decreased general size of plants, most likely due to xerophytisation. This regularity can be observed not only among the spurges from the Urals region, but in the North Asia as well (Baikov 2008). The initial state of this vector-trait can be found in *E. lucida*, *E. agraria* and *E. borodinii*, while polymorphism is common for *E. pseudagraria*. Other studied species have outer bracts wider than medial leaves.

13. Glands transverse elliptic, without horns → glands transverse elliptic, with two long subulate horns, growing from the gland base. Hereafter the elongated terminal parts of the semilunar glands – the so called horn-shaped appendages are referred to as horns. The evolution of the studied species diverged. Transverse elliptic glands without horns were the initial state. This vector-trait depicts one of the possible two-horned nectary transformations, namely development of nectary horns protruding from the bottom, rather than nectary edge. Among the *Esula* section species of the Urals region such a trait is common only for *E. lucida*.

14. Transverse elliptical glands without horns → two-horned glands with short and dense horns at the nectary margin. The emergence of nectary horns protruding from the nectary edge is believed to be an advanced evolutionary trait. This vector reflects the evolutionary advance of *Esula* section and its possible relatedness to other sections of subgenus *Esula*, such as *Tulocarpa*, *Paralias*, *Helioscopia* and some other sections (Khan 2006).

15. Glands with two short and dense horns on the margin → glands with two long and dense horns on the margin. This vector describes a new step in gland horns transformation, caused by xero- and cryophytisation. In the Urals region the *Esula* section is dominated by species with short and dense horns, whereas *E. virgata* and *E. uralensis* have long horns, and *E. pseudagraria* and *E. caesia* being polymorphic in respect to this vector-trait.

16. Glands with two long and dense horns on the margin, the horn tops being sharp or dull → glands with two long and dense horns on the margin, horns being flattened or broadened at the end, or divided into 2–3 small lobes. This vector appears to reflect the next step in horn transformation via increasing their shape complexity; thus this vector-trait can be regarded as evolutionarily advanced. Flattening, end broadening and 2–3 lobes formation are characteristic for *E. virgate* and *E. uralensis*, and often such complex horn formations can be observed in *E. pseudagraria* and *E. caesia*. These species are polymorphic in respect to this trait.

17. Styles longer than 3 mm → styles 1.5–3 mm long. This vector denotes decreased styles length, most likely due to xero- and cryophytisation. Among the studied *Esula* section *E. lucida* has the longest styles.

18. Styles 1.5–3 mm long → styles shorter than 1.5 mm. Average style length of 1.5–3 mm was shown to be charac-

teristic for most of the studied spurges from *Esula* section. Styles shorter than 1.5 mm were found in *E. uralensis*, *E. cyparissias*, *E. leptocaula*, *E. microcarpa*, *E. undulata* and *E. gmelinii*, while *E. esula* was found to be polymorphic in respect to this vector-trait.

19. Bracts broadly elliptic or almost circular, with length exceeding their width (maximal width in the upper section) → bracts semicircular or subcordate, with their length less than their width (maximal width in the bottom section). This direction of bracts' transformation was determined according to the comparative analysis of leaf morphology, performed earlier on the assumption that the *Esula* section species originated from the ancestor common with *Holophyllum* and *Tulocarpa* sections, in which more primitive species have bracts of the length exceeding the width (Baikov 1992, 2008). The majority of spurges from *Esula* section, represented on the studied territory, have semicircular or subcordate bracts, with their width exceeding their length.

20. Bracts broadly elliptic or almost circular, with length exceeding their width (maximal width is in the upper section) → bracts irregularly rhomboid or deltoid with the length approximately equal to the width (maximal width is in the middle or up). Only three species (*E. microcarpa*, *E. leptocaula* and *E. cyparissias*) have bracts of irregularly rhomboid shape, with their length nearly equaling the width. Such species as *E. caesia* and *E. uralensis* are polymorphic in respect to this vector-trait.

21. Fruits along the mericarp backs are distinctly raised-dotted or ridged and folded → fruits along the mericarp backs are scabrous. Scabrous fruits with numerous small ridges along the mericarp backs should be regarded as an ancestor type for the *Esula* section. Between the fruit lobes in the hollows the surface remains smooth (Baikov 1993, 2008). The vector-traits 21 and 22 reflect successive steps in the evolution of almost glabrous fruits in *Esula* section. Most of the studied species have fruits with distinctly raised dots or with ridges and folds along the mericarp backs.

22. Fruits scabrous along the mericarp backs → fruits sub-smooth along the mericarp backs. *E. uralensis* and *E. undulata* were found to be more evolutionarily advanced with respect to the state of their fruit surface, while *E. gmelinii*, *E. microcarpa* and *E. leptocaula* were found to be polymorphic in respect to this vector-trait.

Unique combinations of morphologic states for each species are listed as the coded form in Table 1.

The obtained matrix of the initial data (see Table 1) was analyzed by SYNAP algorithm (Baikov 1996, 1999). Taking into consideration active speciation and relatively young age of many *Euphorbia* species in the Urals region, where most of them belong to the *Esula* section, in order to construct the evolutionary tree using SYNAP algorithm we chose an evolutionary scenario with priority given to the emergence of new traits. We used the following settings to construct the scheme: optimization of the initial data turned off, the reverse negative (–1), the weighing of the vector-traits turned on. By default the weight of each vector-trait was set as equal to 1. Some vector-traits due to their evolutionary significance were attributed with additional weight: the weight of vector-traits 1 and 17 was doubled, while that of the vector-trait 12 was tripled.

The first step of constructing the evolutionary scheme is to compare two the most primitive species with respect to the set of vector-traits (Table 2): *E. lucida* with the potential relationship index (PRI) is equal 2 and *E. agraria* (PRI =

Table 1. Optimized data matrix for spurges from the *Esula* section in Urals region

Vector	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	PRI	
Weight	2	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	
LUC	P	P	P	P	P	P	B	P	P	B	P	P	A	P	M	M	P	P	A	M	P	P		2
AGR	B	P	P	P	P	P	P	P	P	B	P	P	P	A	P	P	A	P	A	M	P	P		4
BRD	B	P	P	P	B	P	A	A	B	A	P	P	P	A	P	P	A	P	A	M	P	P		7
PSE	A	P	P	P	B	P	A	P	P	A	B	B	P	A	B	B	A	P	A	M	P	P		8
VIR	B	P	P	P	B	P	A	A	P	B	P	A	P	A	A	B	A	P	A	M	P	P		10
ESU	B	P	A	P	B	P	A	A	B	B	P	A	P	A	P	P	A	B	A	M	P	P		10
BRS	A	P	P	P	B	P	A	A	P	B	P	A	P	A	P	P	A	P	A	M	U	U		11
KOR	A	B	A	P	B	P	A	A	B	A	B	A	P	A	P	P	A	P	A	M	P	P		13
BOR	A	B	P	P	B	P	A	A	A	A	B	A	P	A	P	P	A	P	A	M	A	P		14
GME	A	B	P	P	B	P	A	B	P	A	A	A	P	A	P	P	A	A	A	M	A	B		14
URA	B	P	P	P	A	B	A	A	P	B	P	A	P	A	B	A	A	A	A	B	A	A		14
ROS	A	A	A	P	A	B	A	P	P	A	A	A	P	A	P	P	A	P	A	M	P	P		15
CYP	A	B	A	A	A	A	P	P	A	P	A	P	A	P	P	A	A	M	A	P	P		16	
CAE	A	B	A	P	A	A	A	P	P	A	A	A	P	A	B	B	A	P	A	B	P		16	
UND	A	A	P	P	A	P	A	B	P	A	A	A	P	A	P	P	A	A	M	A	A		17	
MIC	A	B	A	P	A	A	A	A	A	A	A	A	P	A	P	P	A	A	M	A	A	B		19
LEP	A	A	A	P	A	A	A	A	A	A	A	A	P	A	P	P	A	A	M	A	A	B		20

Note. Vector-traits are numbered in accordance to their numbers given in the text. Rows (species) are marked by the first letters of their species names: BRD – *E. borodinii*; LUC – *E. lucida*; AGR – *E. agraria*; ESU – *E. esula*; BOR – *E. borealis*; KOR – *E. korschinskyi*; VIR – *E. virgata*; URA – *E. uralensis*; CYP – *E. cyparissias*; LEP – *E. leptocaula*; MIC – *E. microcarpa*; ROS – *E. rossica*; PSE – *E. pseudagraria*; CAE – *E. caesia*; UND – *E. undulata*; GME – *E. gmelinii*; BRS – *E. borszczowii*. The letter-codes are: P – an initial trait (state), A – a new trait, B – polymorphism, when a species display both initial and new traits (states); M – the absence of vector-trait, when there are neither initial, nor new traits; U – an unknown trait. PRI – stands for the potential relationship index, calculated as the sum of new traits (A-codes)

4). Their nearest common ancestor is a median m01 with the mean of real relationship index (RRI) of 1 that is characterized by origin of a new trait (coded as N) 19 with semicircular or subcordate bracts with their length less than their width (maximal width in the bottom section), as well as by one polymorphic trait 10 (the pedicels of the apical umbel doubly or triply bifid → the pedicels of the apical umbel simple or once bifid).

The next step is to compare each of these two early connected species and the median m01 with *E. borodinii*, in which the potential relationship index was found to be minimal among the remaining species (PRI = 7). Judging by the maximal value of the RRI, the best connection is by the median m02 (see Table 2). The SYNAP performs links sorting by decreasing RRI means at each step of a construction.

In our case, among the calculated variants of relationship, the maximal mean of RRI = 4 is revealed for the median m02 which connects *E. borodinii* and *E. agraria*. Besides trait 19, which originated earlier (coded N in the 19th vector can be changed into code S), the median m02 is characterized by two new traits: 14 (two-horned glands with short and dense horns at the nectary margin) and 17 (styles 1.5–3 mm long). The median m02 is also polymorphic in two other vectors: 1 (plants of 40 cm high and more as well as plants not exceeding 40 cm in height) and 10 (the pedicels of the apical umbel doubly or triply bifid as well as the pedicels of the apical umbel simple or once bifid).

On the 4th step *E. pseudagraria* (PRI = 8) connects to *E. borodinii* by median m03 (RRI = 6), that has two new traits: in vectors 7 (the base of the medial leaves sharply narrowed or rounded) and 10 (the pedicels of the apical umbel simple or once bifid). In two vector-traits the median is polymorphic: 1 (plants of 40 cm high and more as well as plants not exceeding 40 cm in height) and 5 (medial leaves are relatively wide, more than 6 mm, as well as medial leaves

narrower, not exceeding 6 mm in width).

On the following step *E. virgata* (PRI = 10) is compared with all early connected species and numbered medians; maximal RRI = 5 has its combinations with *E. borodinii* and median m03. The connection of *E. virgata* with *E. borodinii* indicates reversion in vector-trait 10, while the relationship with median m03 is not required, so that this variant is preferable and numbered as median m04. Median m04 supports the earlier origin of the new trait 7 (the base of the medial leaves sharply narrowed or rounded), as compared with median m03.

Euphorbia esula (PRI = 10) with a very high mean of real relationship index (RRI = 9) is joined to *E. virgata* via a new median m05. Compared with median m04, median m05 has two new traits: in vector 8 (the base of the medial leaves gradually narrowed or late cuneate) and vector 12 (the outer bracts wider than medial leaves). The latter trait is common for the majority of evolutionarily advanced species from the *Esula* section.

The median m06 (RRI = 9) connects *E. borszczowii* (PRI = 11) to the last group. Median m06 does not differ significantly from median m05, having the same set of new traits. *E. borszczowii* differs from such species as *E. esula*, *E. virgata*, *E. uralensis* with less height, having a new trait with respect to the vector-trait 1 (plants up to 40 cm high), whereas the aforementioned species were found to be polymorphic with respect to this vector-trait.

Euphorbia korschinskyi (PRI = 13) is joined with *E. borszczowii* via median m07 (RRI = 11), that has an additional new trait in vector-trait 1 (plants up to 40 cm high). The emergence of this trait separates the high spurge species (as discussed above) from the relatively low ones, less than 40 cm high.

On the next step *E. borealis* (PRI = 14) is fixed near *E. korschinskyi* via median m08 with RRI = 12. Their nearest common ancestor is characterized with one new trait 10 (the

Table 2. Stepwise protocol of morphologic-evolutionary scheme construction for the *Esula* section species. The combinations with maximal or near maximal values of real relationship index (RRI) are included

Step	Objects		00000000111111111222 1234567890123456789012	RRI	Step	Objects		00000000111111111222 1234567890123456789012	RRI
1	LUC		PPPPPPBPPFPAPMPPAMPP	(2.0)		URA/m06		BPPBPSNBPNSPSPSPSMUU	9.0
2	AGR		BPPPPPPBPPFPAPAPAMPP	(4.0)		URA/GME		XPPBPSXPSPSPSPSPSMSP	8.0
	AGR/LUC	<i>m01</i>	PPPPPPBPPFPAPAPAMPP	1.0		URA/BOR		XPPBPSXPSPSPSPSPSMSP	7.0
3	BRD		BPPBPAABAPFPAPAPAMPP	(7.0)		URA/m09		XPPBPSXPSPSPSPSPSMNP	7.0
	BRD/AGR	<i>m02</i>	BPPPPPPBPPFPNPNPNSMPP	4.0		URA/m08		XPPBPSXPSPSPSPSPSMPP	7.0
	BRD/m01		PPPPPPBPPFPMPMPPNMP	1.0		URA/BR		XPPBPSXPSPSPSPSPSMUU	7.0
	BRD/LUC		PPPPPPBPPFPMPMPPSMP	1.0	12	ROS		AAAPABAPAAAPAPAPAMPP	(15.0)
4	PSE		APFPBAPFABBPABAPAMPP	(8.0)		ROS/KOR	<i>m11</i>	SBNPBPSXPSPSPSPSPSMPP	11.0 x
	PSE/BRD	<i>m03</i>	BPPBPNPNPNSPSPSMPP	6.0		ROS/GME		SBPPBPSXPSPSPSPSPSMXP	10.0
	PSE/m02		BPPPPPPBPPFPNPNPNSMPP	4.0		ROS/m08		SBPPBPSXPSPSPSPSPSMPP	10.0
	PSE/AGR		BPPPPPPBPPFPSPSPSMPP	4.0		ROS/m09		SBPPBPSXPSPSPSPSPSMPP	10.0
	PSE/LUC		PPPPPPBPPFPMPMPPSMP	1.0		ROS/BR		SPPBPSXPSPSPSPSPSMUU	9.0
	PSE/m01		PPPPPPBPPFPMPMPPNMP	1.0		ROS/BOR		SBPPBPSXPSPSPSPSPSMXP	9.0
5	VIR		BPPBPAABPAPAPABAPAMPP	(10.0)		ROS/m07		NPPBPSXPSPSPSPSPSMUU	9.0
	VIR/m03	<i>m04</i>	BPPBPNPNPNSPSPSMPP	5.0		ROS/m06		BPPBPSXPSPSPSPSPSMUU	8.0
	VIR/BRD		BPPBPSNFXPPSPSPSMPP	5.0		ROS/ESU		BNPBPSPSPSPSPSPSMPP	8.0
	VIR/PSE		BPPBPSXPSPSPSPSMPP	4.0		ROS/PSE		NPPBPSXPSPSPSPSPSMPP	8.0
	VIR/m02		BPPPPPPBPPFPNPNPNSMPP	4.0	13	CYP		ABAAAAAPAPAPAPAMPP	(16.0)
	VIR/AGR		BPPPPPPBPPFPSPSPSMPP	4.0		CYP/ROS	<i>m12</i>	SBSBPSXPSPSPSPSPSMPP	11.0 x
	VIR/LUC		PPPPPPBPPFPMPMPPSMP	1.0		CYP/KOR		SBSPBPSXPSPSPSPSPSMPP	10.0
	VIR/m01		PPPPPPBPPFPMPMPPNMP	1.0		CYP/m11		SBNPBPSXPSPSPSPSPSMPP	10.0
6	ESU		BPAPBPAABBPAPAPABAMPP	(10.0)		CYP/GME		SBPPBPSXPSPSPSPSPSMXP	9.0
	ESU/VIR	<i>m05</i>	BPPBPSNBPNSPSPSMPP	9.0		CYP/m09		SBPPBPSXPSPSPSPSPSMPP	9.0
	ESU/m04		BPPBPNPNPNSPSPSMPP	5.0		CYP/m08		SBPPBPSXPSPSPSPSPSMPP	9.0
	ESU/m03		BPPBPSXPSPSPSPSMPP	5.0		CYP/m07		NPPBPSXPSPSPSPSPSMUU	8.0
	ESU/BRD		BPPBPSNFXPPSPSPSMPP	5.0		CYP/BR		SPPBPSXPSPSPSPSPSMUU	8.0
	ESU/m02		BPPPPPPBPPFPNPNPNSMPP	4.0		CYP/BOR		SBPPBPSXPSPSPSPSPSMXP	8.0
	ESU/PSE		BPPBPSXPSPSPSPSMPP	4.0	14	CAE		ABAAAAAPABBPABAPBPP	(16.0)
	ESU/AGR		BPPPPPPBPPFPSPSPSMPP	4.0		CAE/ROS	<i>m13</i>	SBSBPSXPSPSPSPSPSMPP	14.0
	ESU/LUC		PPPPPPBPPFPMPMPPSMP	1.0		CAE/CYP		SBSPBPSXPSPSPSPSPSMPP	13.0
	ESU/m01		PPPPPPBPPFPMPMPPNMP	1.0		CAE/KOR		SBSPBPSXPSPSPSPSPSMPP	13.0
7	BRS		APFPBAPFABBPAPAPAMPP	(11.0)		CAE/m12		SBSBPSXPSPSPSPSPSMPP	13.0
	BRS/m05	<i>m06</i>	BPPBPSNBPNSPSPSMUU	9.0		CAE/m11		SBNPBPSXPSPSPSPSPSMPP	13.0
	BRS/ESU		BPPBPSXPSPSPSPSMUU	9.0		CAE/m09		SBPPBPSXPSPSPSPSPSMPP	12.0
	BRS/VIR		BPPBPSXPSPSPSPSMUU	9.0		CAE/GME		SBPPBPSXPSPSPSPSPSMXP	12.0
	BRS/PSE		NPPBPSXPSPSPSPSMUU	6.0		CAE/m08		SBPPBPSXPSPSPSPSMPP	12.0
	BRS/m03		BPPBPSXPSPSPSPSMUU	5.0		CAE/m07		NPPBPSXPSPSPSPSMUU	11.0
	BRS/m04		BPPBPNPNPNSPSPSMUU	5.0		CAE/BR		SPPBPSXPSPSPSPSMUU	11.0
	BRS/BRD		BPPBPSNFXPPSPSPSMUU	5.0		CAE/BOR		SBPPBPSXPSPSPSPSMXP	11.0
	BRS/AGR		BPPPPPPBPPFPSPSPSMUU	4.0		CAE/ESU		BNPBPSPSPSPSPSMPP	10.0
	BRS/m02		BPPPPPPBPPFPNPNPNSMPP	4.0	15	UND		AAFPBAPBAPAPAPAMAA	(17.0)
8	KOR		ABAPBPAABAPAPAPAMPP	(13.0)		UND/GME	<i>m14</i>	SBPPBPSXPSPSPSPSPSMSP	14.0
	KOR/BR	<i>m07</i>	NPPBPSXPSPSPSPSMPP	11.0		UND/ROS		SNPSPSPSPSPSPSPSMPP	13.0
	KOR/ESU		BNPBPSPSPSPSPSMPP	10.0		UND/m13		SBXPSXPSPSPSPSPSMPP	12.0
	KOR/VIR		BPPBPSXPSPSPSPSMPP	9.0		UND/CAE		SBXPSXPSPSPSPSPSMPP	12.0
	KOR/m06		BPPBPSNBPNSPSPSMUU	9.0		UND/CYP		SBXPSXPSPSPSPSPSMPP	11.0
	KOR/m05		BPPBPSXPSPSPSPSMPP	9.0		UND/m09		SBPPBPSXPSPSPSPSMNP	11.0
	KOR/PSE		NPPBPSXPSPSPSPSMPP	8.0		UND/BOR		SBPPBPSXPSPSPSPSMXP	11.0
	KOR/BRD		BPPBPSNBPNSPSPSMUU	7.0		UND/URA		BPPBPSXPSPSPSPSMNN	10.0
	KOR/m03		BPPBPSXPSPSPSPSMPP	6.0		UND/m11		SBPPBPSXPSPSPSPSMPP	10.0
	KOR/m04		BPPBPNPNPNSPSPSMPP	5.0		UND/m08		SBPPBPSXPSPSPSPSMPP	10.0
9	BOR		ABFPBPAABAPAPAPAMPP	(14.0)		UND/m12		SBXPNPSPSPSPSPSMPP	10.0
	BOR/KOR	<i>m08</i>	SBPPBPSXPSPSPSPSMPP	12.0	16	MIC		ABAAAAAPAPAPAMAA	(19.0)
	BOR/m07		NPPBPSXPSPSPSPSMUU	11.0		MIC/CYP	<i>m15</i>	SBSBPSXPSPSPSPSMPP	15.0
	BOR/BR		SPPBPSXPSPSPSPSMUU	11.0		MIC/CAE		SBSPBPSXPSPSPSPSMPP	15.0
	BOR/ESU		BPPBPSXPSPSPSPSMPP	9.0		MIC/UND		SBPPBPSXPSPSPSPSMSP	14.0
	BOR/m05		BPPBPSXPSPSPSPSMPP	9.0		MIC/GME		SBPPBPSXPSPSPSPSMPP	14.0
	BOR/m06		BPPBPSNBPNSPSPSMUU	9.0		MIC/ROS		SBSPBPSXPSPSPSPSMPP	13.0
	BOR/VIR		BPPBPSXPSPSPSPSMPP	9.0		MIC/m14		SBPPBPSXPSPSPSPSMNP	13.0
	BOR/PSE		NPPBPSXPSPSPSPSMPP	8.0		MIC/m12		SBPNBPSXPSPSPSPSMPP	13.0
	BOR/BRD		BPPBPSNBPNSPSPSMPP	7.0		MIC/m13		SBSPBPSXPSPSPSPSMPP	13.0
	BOR/m03		BPPBPSXPSPSPSPSMPP	6.0		MIC/BOR		SBPPBPSXPSPSPSPSMPP	13.0
10	GME		ABFPBPAABAPAPAMAA	(14.0)		MIC/m11		SBNPBPSXPSPSPSPSMPP	12.0
	GME/BOR	<i>m09</i>	SBPPBPSXPSPSPSPSMNP	11.0 x		MIC/m09		SBPPBPSXPSPSPSPSMNP	12.0
	GME/KOR		SBPPBPSXPSPSPSPSMPP	10.0		MIC/KOR		SBPPBPSXPSPSPSPSMPP	12.0
	GME/m08		SBPPBPSXPSPSPSPSMPP	10.0		MIC/m08		SBPPBPSXPSPSPSPSMPP	11.0
	GME/BR		SPPBPSXPSPSPSPSMUU	9.0	17	LEP		AAAAAPAPAPAMAA	(20.0)
	GME/m07		NPPBPSXPSPSPSPSMUU	9.0		LEP/MIC	<i>m16</i>	SBSBPSXPSPSPSPSMNP	19.0
	GME/m06		BPPBPSXPSPSPSPSMUU	8.0		LEP/m15		SBSPBPSXPSPSPSPSMNP	15.0
	GME/PSE		NPPBPSXPSPSPSPSMPP	8.0		LEP/UND		SNPBPSPSPSPSPSMNP	15.0
	GME/m05		BPPBPSXPSPSPSPSMPP	7.0		LEP/CAE		SBSPBPSXPSPSPSPSMNP	15.0
	GME/ESU		BPPBPSXPSPSPSPSMPP	7.0		LEP/CYP		SBSPBPSXPSPSPSPSMNP	15.0
	GME/VIR		BPPBPSXPSPSPSPSMPP	7.0		LEP/GME		SBPPBPSXPSPSPSPSMNP	14.0
11	URA		BPPBPAABPAPAPABAA	(14.0)		LEP/ROS		SNSBPSXPSPSPSPSMPP	14.0
	URA/VIR	<i>m10</i>	BPPBPSXPSPSPSPSMPP	10.0		LEP/m13		SBSPBPSXPSPSPSPSMNP	13.0
	URA/m05		BPPBPSXPSPSPSPSMPP	9.0		LEP/m12		SBPNBPSXPSPSPSPSMNP	13.0
	URA/ESU		BPPBPSXPSPSPSPSMPP	9.0		LEP/m14		SBPPBPSXPSPSPSPSMNP	13.0
	URA/m07		BPPBPSXPSPSPSPSMUU	9.0		LEP/BOR		SBPPBPSXPSPSPSPSMNP	13.0

Note. P – initial trait (state), A – new trait (state), N – the appearance of a new state in ancestor, S – result of passing a new trait in linkage, B – polymorphism (simultaneous presence of initial and new states), M – the absence of vector-trait, i.e. when there are no initial, or new traits, U – an unknown trait, X – a reversion. The names of species are reduced to the first three letters of their species epithets. Symbols m01, m02 and so on stand for the chosen medians, i.e. hypothetical ancestral forms. New evolutionary events, characteristic for the chosen medians, are underlined. Means of potential relationship indices (PRI) for species are given in brackets

pedicels of the apical umbel simple or once bifid). These two species are located at the base of the evolutionary tree bifurcation (Fig. 1): *E. borealis* belongs to the branch with species always glabrous, while *E. korshinskyi* belongs to the branch with species always pubescent or glabrous and pubescent as well.

Then *E. gmelinii* (PRI = 14) is connected with *E. borealis* via median m09 (RRI = 11). This median has one new trait 21 (fruits are scabrous along the mericarpal backs), as well as a reversion in vector-trait 8 (the base of the medial leaves gradually narrowed or late cuneate).

As a result of its comparison with all the previously joined species and medians, *E. uralensis* (PRI = 14) is fixed near *E. virgata* by means of the median m10 with RRI = 10. Median m10 has one new trait in vector-trait 15 (glands with two long and dense horns on the margin).

On the next step of tree construction, *E. rossica* (PRI = 15) and *E. korshinskyi* are connected via median m11 (RRI = 11). This median has origin of a new trait 3 (plants glabrous or pubescent) and a reversion in vector-trait 8 (the base of the medial leaves gradually narrowed or late cuneate).

Next *E. cyparissias* (PRI = 16) via median m12 (RRI = 11) is related to *E. rossica*. Median m12 is characterized by one new trait 5 (medial leaves 4–6 mm wide) and a reversion in vector 8 (the base of the medial leaves gradually narrowed or late cuneate), like median m11.

The nearest common ancestor of these species denotes the qualitative transition from *Esulae* series (plants with moderate leaf width, preferring forest and forest-steppe zones) to the members of *Subcordatae*, *Caesiae* and *Leptocaula* series (plants with narrower leaves preferring steppe).

On the next step, *E. caesia* (PRI = 16) is joined with *E. rossica* via median m13 (RRI = 14). This median has

one new state in vector-trait 11 (the apical umbel usually consists of 4–6 rays).

Comparison of *E. undulata* (PRI = 17) with all other connected species and medians revealed its maximal similarity in new traits with *E. gmelinii*. Their nearest common ancestor – median m14 with RRI = 14 – has two new states: 11 (the apical umbel usually consists of 4–6 rays) and 18 (styles shorter than 1.5 mm). The new traits, fixed by this median, clearly discriminate between *E. undulata*, the sole species of *Andrachnoides* series in the Urals region, and species of *Esulae* series.

On the next step *E. microcarpa* (PRI = 19) is connected by median m15 to *E. cyparissias* (RRI = 15). Median m15 has three new traits, namely 6 (medial leaves 2–4 mm wide), 18 (styles shorter than 1.5 mm) and 20 (bracts irregularly rhomboid or deltoid with the length approximately equal to the width and maximal width in the middle or top). These traits distinctly separate *Leptocaula* series in the Urals region from other series of *Esula* section.

On the last step *E. leptocaula* (PRI = 20) is fixed near *E. microcarpa* by median m16 (RRI = 19). This median m16 is characterized with three new traits, namely 9 (the base of the medial leaves anguste cuneate, attenuate), 11 (the apical umbel usually consists of 4–6 rays) and 21 (fruits scabrous along the mericarpal backs).

CONCLUSIONS

1. The SYNAP analysis provided the first evolutionary scheme of morphological transformation of spurge of the *Esula* section. The species of *Lucidae* series, namely *E. lucida* and *E. agraria*, i.e. species with the maximal sum of primitive traits, form the initial basis of the scheme. Closely related to this series, but still distinctly separate, *E. pseudagraria* and

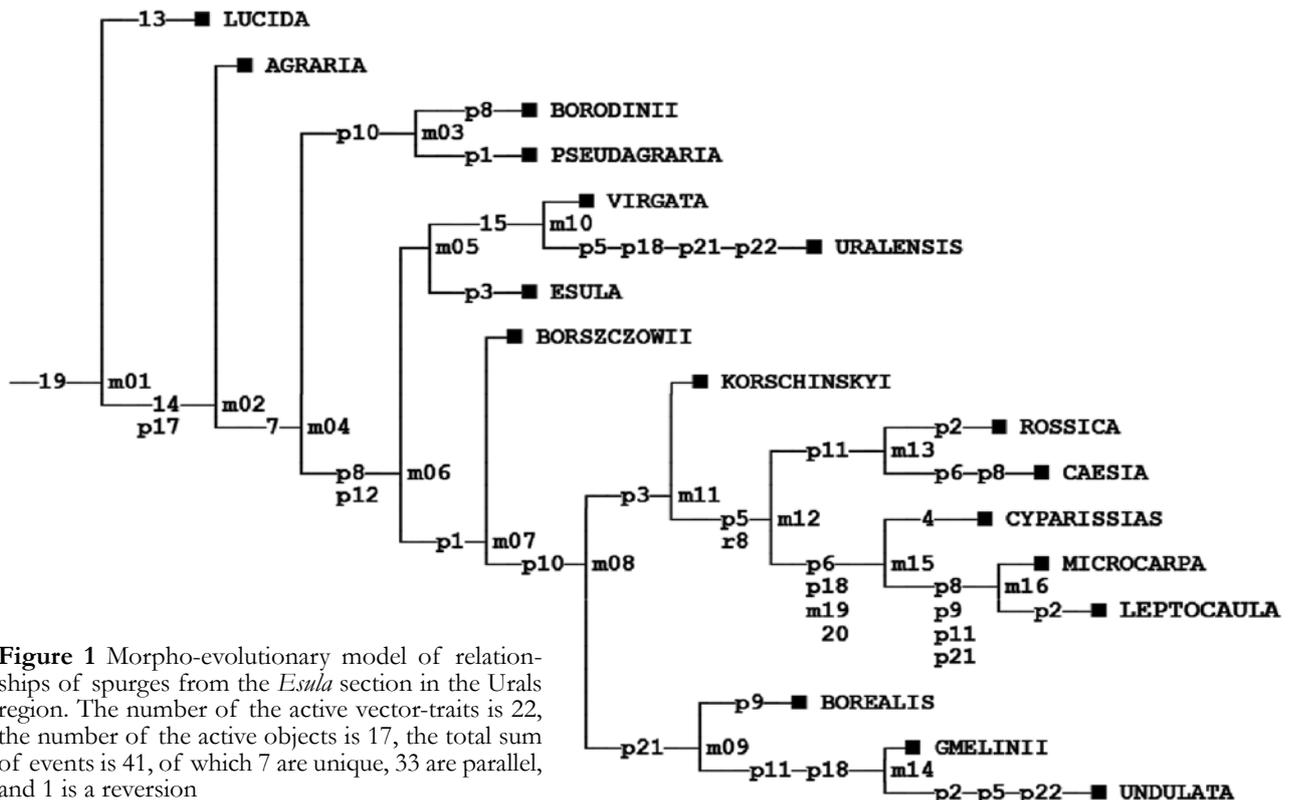


Figure 1 Morpho-evolutionary model of relationships of spurge from the *Esula* section in the Urals region. The number of the active vector-traits is 22, the number of the active objects is 17, the total sum of events is 41, of which 7 are unique, 33 are parallel, and 1 is a reversion

E. borodinii are fixed (both from *Latifoliae* series). The results from this analysis required the placement of *E. pseudagraria*, earlier placed in *Caesia* series (Geltman 2001), to the *Latifoliae* series, to which *E. borodinii* also belongs (Baikov 2007).

2. Such series as *Virgatae* and *Esulae* are in the central part of the evolutionary scheme: they are closely interrelated, providing the gradual transition from the more primitive series *Lucidae* and *Latifoliae* towards the more advanced series of *Leptocaula*, *Subcordatae*, *Caesia* and *Andrabnoides*.

3. The species of the *Virgatae* series were found to be less evolutionarily advanced compared to the *Esulae* series. The most advanced species of the latter series, such as *E. borealis* and *E. korshinskyi*, form a dichotomy with respect to hairiness. It should be noted that after this branching point all the species have plants no higher than 40 cm. *E. borealis*, joined later with *E. undulata* from the *Andrabnoides* series, continues the evolutionary direction without hairs, while *E. korshinskyi* lies at the beginning of a group of species with hairs.

4. Narrow leaves, 2–4 mm wide, indicate a group of species belonging to *Subcordatae*, *Caesia* and *Leptocaula* series. The members of the *Subcordatae* (*E. rossica*) and *Caesia* (*E. caesia*) series are the most closely related. Somewhat separately from them is located a group of the more evolutionarily advanced species from *Leptocaula* series (*E. cyparissias*, *E. microcarpa* and *E. leptocaula*).

5. The morpho-evolutionary analysis of relationships within the group of closely related spurges of the *Esula* section allowed us to show and confirm distinct species lineages within the studied section, with the exception of the proposed moving of *E. pseudagraria* from *Caesia* into *Latifoliae* series.

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LITERATURE CITED

Baikov, K.S. 1992. Defining Siberian species of *Euphorbia* L. genus (Euphorbiaceae) by the morphological traits of their leaves. *Bulleten' Moskovskogo Obshchestva Ispytatelei Pripody. Otd. Biol.* 97(5): 52–59 (in Russian). [Байков К.С. 1992. Определение сибирских видов рода *Euphorbia* L. (Euphorbiaceae) по морфологическим признакам листьев // Бюл. Моск. о-ва испытат. прир. Отд. биол. Т. 97. Вып. 5. С. 52–59].

Baikov, K.S. 1993. On systematics of Siberian spurges: comparative morphological analysis of fruits. *Bulleten' Moskovskogo Obshchestva Ispytatelei Pripody. Otd. Biol.* 98(4): 106–111 (in Russian). [Байков К.С. 1993. К систематике сибирских молочаев: сравнительно-морфологический анализ плодов // Бюл. Моск. о-ва испыт. прир. Отд. биол. Т. 98, вып. 4. С. 106–111].

Baikov, K.S. 1996. SYNAP as a new algorithm for phylogenetic constructions. *Zhurnal obshchei biologii* 57(2): 165–176 (in Russian). [Байков К.С. 1996. SYNAP – новый алгоритм филогенетических построений // Журнал общей биологии. Т. 57, № 2. С. 165–176].

Baikov, K.S. 1999. *The basics of phylogenetic modeling using SYNAP method*. Novosibirsk, 95 pp. (in Russian). [Байков К.С. 1999. Основы моделирования филогенеза по методу SYNAP. Новосибирск. 95 с.].

Baikov, K.S. 2001. Advancing a new method of phylogenetic analysis and employing it to study interspecies and intergenera relations, variability and hybridization. *Proc. SB RAS (young scientists) Biol. Sci.* Novosibirsk. P. 45–49 (in Russian). [Байков К.С. 2001. Развитие нового метода филогенетического анализа и изучение на его основе межвидовых и межродовых связей, изменчивости и гибридизации // Сб. тр. мол. уч. СО РАН. Биол. науки. Новосибирск. С. 45–49].

Baikov, K.S. 2002. On systematics of spurges from *Euphorbia esula* L. (Euphorbiaceae) section in the Northern Asia. *Turczaninovia* 5(4): 102–106 (in Russian). [Байков К.С. 2002. К систематике молочаев из рода *Euphorbia esula* L. (Euphorbiaceae) в Северной Азии // Turczaninovia. Т. 5, вып. 4. С. 102–106].

Baikov, K.S. 2004. Development of the divergent-parallel model of polymorphic taxon phylogenesis based on the studies of novel traits. *Sibirskii ekologicheskii zhurnal* 5: 653–664 (in Russian). [Байков К.С. 2004. Разработка дивергентно-параллельной модели филогенеза полиморфного таксона, основанной на исследовании новых признаков // Сибирский экологический журнал. № 5. С. 653–664].

Baikov, K.S. 2006. Simulating the phylogenetic relations of the closely related species using *Esula* section spurges (*Euphorbia* L.) of the Northern Asia as an example // *Biodiversity and ecosystems dynamics: computer technologies and simulation*. Novosibirsk. P. 97–104 (in Russian). [Байков К.С. 2006. Моделирование филогенетических связей близкородственных видов на примере молочаев (*Euphorbia* L.) Северной Азии из секции *Esula* // Биоразнообразие и динамика экосистем: компьютерные технологии и моделирование. Новосибирск. С. 97–104].

Baikov, K.S. 2007. *Spurges of the Northern Asia*. Nauka, Novosibirsk. 362 pp. (in Russian). [Байков К.С. 2007. Молочай Северной Азии. Новосибирск: Наука. 362 с.].

Baikov, K.S. 2008. Plant evolutionary morphology: a circuit of argumentation (using *Esula* section spurges of the Northern Asia as an example). In: *Contemporary problems of spermatophytes morphology and reproductive biology*. Ulyanovsk. P. 15–21 (in Russian). [Байков К.С. 2008. Эволюционная морфология растений: замкнутый круг аргументации (на примере молочаев Северной Азии из секции *Esula*) // Современные проблемы морфологии и репродуктивной биологии семенных растений. Ульяновск. С. 15–21].

Baikov, K.S. & S.V. Solov'yev 2012. Expert estimation of phylogenetic scheme of plants (on the example of spurges from section *Esula* distributed in Ural region). In: *Problems of Botany of South Siberia and Mongolia* (Proceedings of the 11th International Scientific and Practical Conference) Barnaul. P. 22–25. [Байков К.С., Соловьев С.В. 2012. Экспертная оценка филогенетических схем растений (на примере молочаев из секции *Esula* Уральского региона) // Проблемы ботаники Южной Сибири и Монголии. Сбор. науч. стат. по матер. XI Междунар. науч.-практич. конф. Барнаул. С. 22–25].

Baikov, K.S. & A.A. Zverev. 2000. A new version of SYNAP computer program for logical modeling of phylogeny. In: *Proceedings of the Second Int. conf. on Bioinformatics of Genome Regulation and Structure*. Novosibirsk. Vol. 2. P. 115–117. (in Russian and English).

Geltman, D.V. 1996. Euphorbiaceae Juss. In: *Flora of the Eastern Europe. Mir i sem'ya*–95, Saint-Petersburg. Vol. 9, pp. 256–287 (in Russian). [Гельтман Д.В. 1996. Сем. Euphorbiaceae Juss. // Флора Восточной Европы. Т. 9. С. 256–287. СПб.: Мир и семья–95.]

Geltman, D.V. 2001. About the size of the *Esula* Dumort. section of *Euphorbia* L. genus (Euphorbiaceae) and its subsections. *Novosti sistematiki vysshib rastenii* 33: 151–163 (in Russian). [Гельтман Д.В. Об объеме секции *Esula* Dumort. рода *Euphorbia* L. (Euphorbiaceae) и ее подсекциях // Новости систематики высших растений. Т. 33. С. 151–163].

Geltman, D.V. 2002. The genus *Euphorbia* L. (Euphorbiaceae) in the floras of the Crimea, the Caucasus and the Middle Asia. II. Section *Esula* Dumort. *Novosti sistematiki vysshib rastenii* 34:

- 102–124 (in Russian). [Гельтман Д.В. 2002. Род *Euphorbia* L. (Euphorbiaceae) во флоре Крыма, Кавказа и Малой Азии. II. Секция *Esula* Dumort. // Новости систематики высших растений. Т. 34. С. 102–124].
- Khan, I.V. 2006. Simulating major directions of the morphological transformations of spurge (*Euphorbia* L.) inflorescences of the nontropical Asia using SYNAP method. *Sibirskii botanicheskii vestnik: electronic journal* 1(1): 87–91 (in Russian). [Хан И.В. 2006. Моделирование основных направлений морфологических преобразований соцветий молочаев (*Euphorbia* L.) внетропической Азии с помощью метода SYNAP // Сибирский ботанический вестник: электр. журнал. Т. 1, вып. 1. С. 87–91].
- Pavlinov, I.Y. 1990. *Cladistic analysis (methodological problems)*. Moscow State University Press, Moscow. 160 pp. (in Russian). [Павлинов И.Я. 1990. Кладистический анализ (методологические проблемы). М.: Изд-во МГУ. 160 с.].
- Pavlinov, I.Y. 2005. *Introduction into modern phylogenetics*. Moscow. 391 pp. (in Russian). [Павлинов И.Я. 2005. Введение в современную филогенетику. М. 391 с.]