DE GRUYTER OPEN

Polish Botanical Journal 60(2): 147–161, 2015
DOI: 10.1515/pbj-2015-0024

PHYTOGEOGRAPHICAL ANALYSIS OF *EUPHORBIA* SUBGENUS *ESULA* (EUPHORBIACEAE)

Dmitry V. Geltman

Abstract. *Euphorbia* subg. *Esula* is one of four major clades within the genus. A geographical analysis of the 466 species in the subgenus is reported here. Every species was assigned to one of 29 geographical elements clustered in ten groups of elements. This geographical analysis showed that the Tethyan group (comprising nine geographical elements) clearly dominates the subgenus and contains 260 species (55.79% of the total number of species). The most numerous geographical elements are Irano-Turanian (105 species) and Mediterranean (85). Other significant groups of elements are Boreal (91 species, 19.54%), East Asian (40 species, 8.58%), Madrean (26 species, 5.58%), Paleotropical (23 species, 4.94%) and South African (16 species, 3.43%). The area of the Tethyan floristic subkingdom is the center of the modern diversity of *E.* subg. *Esula*. It is likely that such diversity is the result of intensive speciation that took place during the Eocene–Miocene.

Key words: *Euphorbia* subg. *Esula*, geographical elements, Irano-Turanian floristic region, Mediterranean floristic region, phytogeographical analysis, Tethyan floristic subkingdom

Dmitry V. Geltman, Komarov Botanical Institute of the Russian Academy of Sciences, Prof. Popov Street, 2, St. Petersburg, 197376, Russia; e-mail: geltman@binran.ru

Introduction

genus *Euphorbia* and its taxonomy

The giant genus *Euphorbia* L. (Euphorbiaceae) recently became a subject of detailed phylogenetic and taxonomic studies. Four major clades (A–D) were identified in the first phylogenetic investigation of *Euphorbia* by Steinmann and Porter (2002). These clades were later confirmed and formalized by Bruyns *et al.* (2006) as four subgenera: *Euphorbia* subg. *Rhizanthium* (Boiss.) Wheeler (recently an earlier name, *E.* subg. *Athymalus* Neck. *ex* Rchb., was found for this taxon – Peirson *et al.* 2013), *E.* subg. *Esula* Pers., *E.* subg. *Euphorbia*, and *E.* subg. *Chamaesyce* Raf. The concept of four clades/subgenera was supported by further studies (Park & Jansen 2007; Zimmerman *et al.* 2010; Bruyns *et al.* 2011; Horn *et al.* 2012) and is now accepted by the majority of taxonomists dealing with *Euphorbia*.

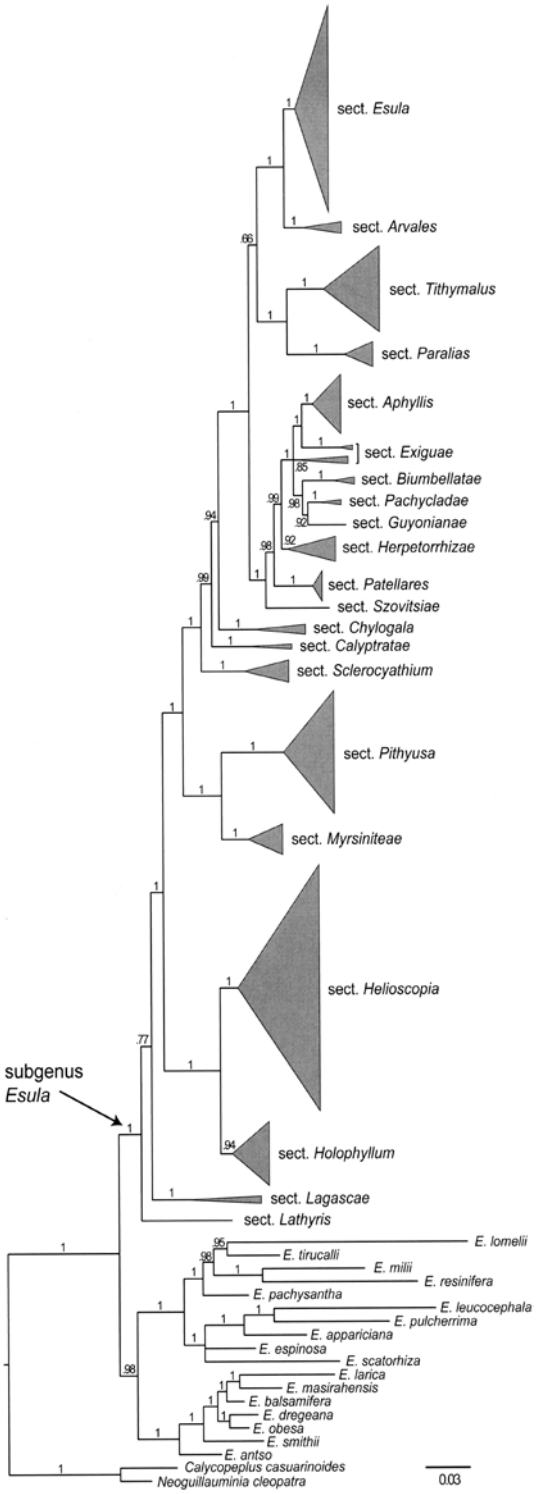
For each clade/subgenus, new taxonomic systems based on robustly sampled molecular phylogenetic analyses have been proposed (Yang *et al.* 2012; Dorsey *et al.* 2013; Peirson *et al.* 2013; Riina *et al.* 2013). In many cases the new systems significantly differ from traditional ones. For subgenus *Esula* (Riina *et al.* 2013), 21 sections were accepted on the basis of analyses of the combined ITS + ndhF dataset (Fig. 1).

The next steps in understanding the evolution and systematics of *Euphorbia* will involve integrating data from traditional fields of botany (morphology, anatomy, karyology, plant geography, etc.) with the new classification systems for the genus and its subgenera – in other words, to fill the new *Euphorbia* system with morphological, geographical and other content.

Riina *et al.* (2013) gave a short biogeographical sketch of the subgenus but their work did not involve a more detailed phytogeographical study. The present paper reports the results of my phytogeographical analysis of the species comprising *E.* subg. *Esula*.

concept of phytogeographical elements

The most important part of any phytogeographical analysis consists in assigning every species (of a flora or taxon) to a particular geographical



element. Such assignments have been made in a number of floras (e.g., Davis 1965–1988); detailed phytogeographical analyses of particular areas, with quantitative assessments, are the subject of special publications (e.g., Ali & Qaiser 1986). Such assignments and analyses can also be found in taxonomic reviews (e.g., Skvortsov 1966; Menitsky 1986, 1992; Budantsev 1998; Kurosawa 2006), and this practice is especially common in the Russian school of plant taxonomy and phytogeography.

Generally, a geographical element is a group of species with a similar distribution pattern. Tolmachev (1974: 134) mentioned that 'species … having more or less similar geographical distributions are regarded as a geographical element of a particular flora, and the element is named according to the details of such a kind of distribution'.

The term 'element' appeared in early works on phytogeography (e.g., Christ 1867; Engler 1879). The modern approach in phytogeographical analysis is connected with works of Braun-Blanquet (1919, 1923) and Eig (1931). Braun-Blanquet (1923: 32) stated that 'l'élément phytogéographique est l'expression floristique et phytosociologique d'un territoire étendu défini; il englobe les 'sippes' et les collectivités phytogéographiques caractéristiques d'une région déterminée'. A similar definition of 'geographical element' was made by Davis (1965): '[a phytogeographical] element … is a taxon confined or centered in one phytogeographical region (or province). A species whose maximum abundance is clearly in one region is treated as an element of this region. Such an element may occur locally in communities of another region, or in association with other elements of its own region, forming enclaves isolated from the main area'. Such an approach is often called a flo-

Fig. 1. Schematic representation of Bayesian phylogram from analysis of the combined ITS + ndhF dataset of *Euphorbia* subg. *Esula* Pers. and outgroups. Sections are represented by filled triangles whose vertical axes are scaled to reflect the number of species in each section. Bayesian posterior probabilities (≥ 0.66) are indicated above the branches (from Riina *et al.* 2013, fig. 4 – reproduced with permission from the International Association for Plant Taxonomy).

ristic one in the classification of geographical elements (Portenier 2000a), but Yurtsev and Kamelin (1991: 43) defined it as 'chorionomic' and also distinguished 'coordinate' and 'relative' types of geographical elements.

Here I follow the above mentioned floristic (chorionomic) approach to the classification of geographical elements. Recently this approach was developed by Portenier (2000a, b) in connection with work on the flora of the Caucasus. According to his concept, the term 'geographical element' is connected with phytochoria of various ranks (kingdoms, subkingdoms, regions, provinces, etc.). A geographical element is a set of species comprising the nucleus of a flora of a concrete phytochorion, and such species also are members of plant communities determining the specificity of the vegetation of the phytochorion.

As the basic phytochorion for the current analysis I selected the floristic region, although in other cases (depending on the aim and scope of the analysis) other levels of floristic division could be selected (e.g., province or even district).

It is not problematic to assign a species to a geographical element if it occurs within the limits of a single floristic region only. In this case the name of the element usually repeats the name of the phytochorion. The situation is more complicated if a species occurs in two or more floristic regions without evident preferences for one or the other. In this case one can consider 'plantes de liaison' (Eig 1931: 13), binding species (or elements) (Portenier 2000a), or bi- and pluriregional elements (Ali & Qaiser 1986).

I follow Portenier (2000b) in treating geographical elements as clustered into groups of elements which mainly correspond with the scheme of floristic subkingdoms or kingdoms.

Material and methods

The distribution of every species of *E.* subg. *Esula* was analyzed and compared with the accepted scheme of floristic zoning (see below). For data on the geographical distribution of species, standard floras, the *World Checklist of Euphorbiaceae* (Govaerts *et al.* 2015) and especially the 'Euphorbia Planetary Biodiversity Inventory database' (Riina & Berry 2015) were used. However, in several cases, especially for species occurring in areas of my special interest (Eastern and Central Europe, the Caucasus, Asia Minor, Central Asia, Siberia), original data from herbarium holdings (first of all LE, but also AA, BAK, BM, E, ERE, FRU, K, KW, MHA, MW, P, TASH, TBI, TGM) were very important.

Accepted scheme of floristic zoning

The most developed and generally accepted system of floristic regions, proposed by Takhtajan (1986), was selected as the basis for this work, modified as described below.

1. The East Asian region is separated into Sino-Japanese and Sino-Himalayan regions; their limits generally match those of the Sino-Japanese and Sino-Himalayan subkingdoms proposed by Wu and Wu (1998), but the Sino-Himalayan region is extended to cover all of the Western Himalayas, as recently proposed by Kamelin (2010).

2. The Crimean-Novorossiysk province is moved from the Mediterranean to the Circumboreal region, as proposed by Portenier (2000a).

3. The Hyrcanian province is moved from the Irano-Turanian to the Circumboreal province. Although its flora contains several Irano-Turanian elements, it has more links with Caucasian and Euxine provinces, which are traditionally placed in the Circumboreal province.

4. The limit between the Circumboreal and Irano-Turanian regions is changed such that the Altay-Dhungarian and Tuva-Mongolian provinces recently proposed by Kamelin (2010) are placed in the Circumboreal region.

As mentioned above, geographical elements are clustered into groups of elements according to the scheme of floristic subkingdoms (sometimes kingdoms). Takhtajan's (1986) scheme was accepted as the basis for such clustering, but with some important additions recently proposed by Kamelin (2012):

1. The East Asian subkingdom covering the Sino-Japanese and Sino-Himalayan regions is added.

2. A new South African kingdom is added, covering not only the Cape region but also much more extensive areas of South Africa: the Karoo-Namib region, the south part of the Tongoland-Pondolan

province of the Uzumbara-Zululand region, and the montane part of the Zambesian province of the Sudano-Zambesian region in Takhtajan's system.

SPECIES COMPOSITION

The species composition and sectional delimitation of *Euphorbia* subg. *Esula* are generally accepted according to Riina *et al.* (2013), with the following amendments.

Euphorbia lathyris L. (the only species of section *Lathyris* Dumort.) is excluded from the analysis because it is impossible to determine its native area: it is found in the wild in the Mediterranean area, Central Europe and East Asia, but it is unclear which area is primary. It is likely that this species was developed in cultivation.

Euphorbia section *Holophyllum* (Prokh.) Prokh.: *E. fischeriana* Steudel is regarded as the priority name for *E. pallasii* Turcz.

Euphorbia section *Helioscopia* Dumort.: *E. polychroma* A. Kern. and *E. cybirensis* Boiss. are excluded and treated as synonyms of *E. epithymoides* L. and *E. valerianifolia* Lam. respectively. *E. donii* Oudejans and *E. schilingii* Radcl.-Sm. according to Kurosawa (2006) are treated as synonyms of *E. pseudosikkimensis* (Hurus. & Yu. Tanaka) Radcl.-Sm., and *E. hakutosanensis* Hurus. as a synonym of *E. fauriei* H. Lév., following Chang *et al.* (2014). *E. insularis* Boiss. and *E. canuiti* Parl. (commonly treated as subspecies of *E. hyberna* L.), as well as the recently described *E. mazandaranica* Pahlevani (Pahlevani & Riina 2014) and *E. maoershanensis* F. N. Wei & J. S. Ma[1] (Ma *et al.* 2013), are added. The enigmatic *E. peltata* Roxb., described in 1832 from the Coromandel coast in India and never collected later, is likely a synonym of the weedy *E. stricta* L. which has occasionally been introduced from Europe. *E. sendaica* Makino, after closer examination, was moved to section *Esula* (Pers.) Dumort.

Euphorbia normannii Schmalh. *ex* Lipsky was moved from section *Arvales* (Geltman) Geltman to section *Myrsiniteae* (Boiss.) Lojac., according to newly obtained molecular data (A. Kryukov, D. Geltman, unpubl. data).

Euphorbia section *Pithyusa* (Raf.) Lázaro: the recently described *E. khorasanica* Saeidi & Ghayormand (Saeidi Mehrvarz & Ghayormand 2015) as well as the previously known *E. antilibanotica* Mouterde, *E. cuspidata* Bertol. and *E. sanctae-catarinae* Fayed, suggested by Riina *et al*. (2013) as possible members of this section, are added; however, *E. sanctae-catarinae* could also belong to section *Paralias*[2].

Euphorbia section *Patellares* (Prokh.) Frajman: *E. meuselii* Geltman (= *E. amygdaloides* L. subsp. *arbuscula* Meusel) and *E. wulfenii* Hoppe *ex* W. D. J. Koch (= *E. characias* L. subsp. *wulfenii* (Hoppe *ex* W. D. J. Koch) Radcl.-Sm. are added.

The New World species of section *Tithymalus* (Gaertn.) Roep. are accepted according to a recent revision (Peirson *et al.* 2014).

Euphorbia section *Esula* (Pers.) Dumort.: *E. discolor* Ledeb. is excluded from the analysis, because this name is a later homonym; the information connected with this name should be attributed to *E. borealis* Baikov (Baikov 2007). *Euphorbia lioui* C. Y. Wu & J. A. Ma and *E. gulestanica* Podlech are added.

Euphorbia ensifolia Baker from Madagascar, close to section *Esula* according to Riina *et al.* (2013), is not included in the analysis because I have doubts as to its belonging to *E.* subg. *Esula*.

RESULTS

In total, 466 species were included in the analysis. Following the above proposed concept I have separated 29 geographical elements clustered in ten groups of elements. The results of the analysis are summarized in Tables 1 and 2.

Below are brief descriptions of all elements, with lists of the species assigned to them. Uniregional elements have the same names as those of the floristic regions; it is assumed that the distribu-

[1] The authors of *E. maoershanensis* Wei & Ma (Ma *et al*. 2013) included their species in section *Holophyllum*. In my opinion, this species more likely belongs to section *Helioscopia*.

[2] *Euphorbia elymaitica* Bornm., which was not placed in any particular section by Riina *et al.* (2013), most probably is a synonym of *E. microsciadia* Boiss.

tion areas of species belonging to those elements are within the particular region.

I. Boreal group (91 species)

1. *West-Palearctic element* (pluriregional). Portenier (2000b) assigned to this element species with distributions in Europe, West Siberia and the western part of Tethyan subkingdom, and I follow this definition. Species (2): *E. seguieriana* Neck., *E. virgata* Waldst. & Kit.

2. *Euro-Siberian element* (uniregional). Species occurring in the Eurasian part of the Circumboreal floristic region, which is often separated as the Euro-Siberian region (Hayek 1926; Good 1964; Davis 1965). Species (81): *E. agraria* M. Bieb., *E. alpina* Ledeb., *E. altaica* Ledeb., *E. amygdaloides* L., *E. angulata* Jacq., *E. ardonensis* Galushko, *E. aristata* Schmalh., *E. austriaca* A. Kern., *E. borealis* Baikov, *E. borodinii* Sambuk, *E. buchtormensis* Ledeb., *E. buschiana* Grossh., *E. caesia* Kar. & Kir., *E. carniolica* Jacq., *E. carpatica* Wol., *E. cyparissias* L., *E. czerepanovii* Geltman, *E. daghestanica* Geltman, *E. djimilensis* Boiss., *E. dubovikiae* Oudejans, *E. dulcis* L., *E. epithymoides* L., *E. eugeniae* Prokh., *E. esula* L., *E. fischeriana* Steudel, *E. glaberrima* K. Koch, *E. gmelinii* Steud., *E. gregersenii* K. Malý *ex* Beck, *E. hyberna* L., *E. iberica* Boiss., *E. illirica* Lam., *E. jenisseiensis* Baikov, *E. kaleniczenkoi* Czern., *E. kerneri* Huter *ex* A. Kern., *E. kirimzjulica* Stepanov, *E. korshinskyi* Geltman, *E. latifolia* Ledeb., *E. lenensis* Baikov, *E. leptocaula* Boiss., *E. lucida* Waldst. & Kit., *E. macroceras* Fisch. & C. A. Mey., *E. macrorhiza* Ledeb., *E. mazandaranica* Pahlevani, *E. microcarpa* (Prokh.) Krylov, *E. mongolica* (Prokh.) Prokh., *E. normannii* Schmalh. *ex* Lipsky, *E. oblongifolia* (K. Koch) K. Koch, *E. palustris* L., *E. pancicii* Beck, *E. pannonica* Host, *E. pilosa* L., *E. platyphyllos* L., *E. polygalifolia* Boiss. & Reut., *E. potaninii* Prokh., *E. procera* M. Bieb., *E. pseudagraria* P. A. Smirn., *E. pyrenaica* Jord., *E. rossica* P. A. Smirn., *E. rupestris* Ledeb., *E. salicifolia* Host, *E. sareptana* Becker, *E. saurica* Baikov, *E. saxatilis* Jacq., *E. scripta* Sommier & Levier, *E. semivillosa* (Prokh.) Krylov, *E. sojakii* (Chrtek & Křísa) Dubovik, *E. squamosa* Willd., *E. stepposa* Zoz, *E. subamplexicaulis* Kar. & Kir., *E. subcordata* Ledeb., *E. subtilis* (Prokh.) Prokh., *E. tauricola* Prokh., *E. tristis* Besser, *E. tshuiensis* (Prokh.) Serg. *ex* Krylov, *E. undulata* M. Bieb., *E. uralensis* Fisch. *ex* Link, *E. valdevillosocarpa* Arvat & Nyár., *E. valliniana* Belli, *E. variabilis* Ces., *E. verrucosa* L., *E. wittmannii* Boiss.

3. *North American Atlantic element* (uniregional). Species (5): *E. georgiana* M. H. Mayfield, *E. longicruris* Scheele, *E. ouachitana* M. H. Mayfield, *E. purpurea* (Raf.) Fernald, *E. texana* Boiss.

4. *North American element* (pluriregional). Species found in at least in two of the following regions: Circumboreal (American part), North American Atlantic, Rocky Mountain and Madrean. Species (3): *E. brachycera* Engelm., *E. commutata* Engelm. *ex* A. Gray, *E. spathulata* Lam.

II. East Asian group (40 species)

5. *Sino-Japanese element* (uniregional). The Sino-Japanese floristic region is accepted here within the limits of the following provinces according to Takhtajan (1986): Manchurian, Sakhalin-Hokkaido, Japanese-Korean, Volcano-Bonin, Ryukyu (Tokara-Okinawa), Taiwanian, Northern Chinese and Central Chinese (Wu & Wu 1998). Species (20): *E. adenochlora* C. Morren & Decne., *E. dahurica* Peschkova, *E. ebracteolata* Hayata, *E. fauriei* H. Lév. & Vaniot, *E. jolkinii* Boiss., *E. kansuensis* Prokh., *E. kansui* S. L. Liou, *E. komaroviana* Prokh., *E. lucorum* Rupr., *E. lunulata* Bunge, *E. mandshurica* Maxim., *E. maoershanensis* F. N. Wei & J. S. Ma, *E. nakaii* Hurus., *E. octoradiata* H. Lév. & Vaniot, *E. pekinensis* Rupr., *E. sendaica* Makino, *E. sieboldiana* C. Morren & Decne., *E. togakusensis* Hayata, *E. tongchuanensis* C. Y. Wu & J. S. Ma, *E. yanjinensis* W. T. Wang.

6. *Sino-Himalayan element* (uniregional). The Sino-Himalayan floristic region is accepted here within the limits of the following provinces according to Takhtajan (1986): Southeastern Chinese, Sikang-Yunnan, Northern Burmese, Eastern Himalayan, Khasi-Manipur (Wu & Wu 1998), plus the Western Himalayan province (following Kamelin 2010) which Takhtajan placed in the

Table 1. Distribution of species of *Euphorbia* subg. *Esula* among geographical elements and groups of elements.

Group of elements	Number of species in the group	% of total species number	Element	Number of species	% of total number	% of number of species in group of elements
Boreal	91	19.54	*West-Palearctic*	2	0.43	2.20
			Euro-Siberian	81	17.38	89.01
			North American Atlantic	5	1.07	5.49
			North American	3	0.64	3.30
East Asian	40	8.58	*Sino-Japanese*	20	4.29	50
			Sino-Himalayan	20	4.29	50
Tethyan (Ancient Mediterranean)	260	55.79	*Pantethyan*	2	0.43	0.77
			European-Pantethyan	8	1.72	3.08
			Macaronesian	14	3.00	5.39
			Mediterranean	85	18.24	32.69
			Macaronesian-Mediterranean	7	1.50	2.69
			Submediterranean	32	6.87	12.31
			Saharo-Arabian	4	0.86	1.54
			Irano-Turanian	105	22.53	40.38
			Irano-Turanian-Sino-Himalayan	3	0.64	1.15
Madrean	26	5.58	*Madrean*	18	3.86	69.23
			Submadrean	8	1.72	30.77
Paleotropical	23	4.94	*Panpaleotropical*	1	0.21	4.35
			Sudano-Zambesian	22	4.72	95.65
Madagascan	3	0.64	*Madagascan*	3	0.64	100
Indomalesian	2	0.43	*Indomalesian*	1	0.22	50
			Fijian	1	0.22	50
Neotropical	3	0.64	*Carribean*	3	0.64	100
South African	16	3.43	*Karoo-Namib*	1	0.22	6.25
			Uzambara-Zululand	4	0.86	25.00
			Cape	4	0.86	25.00
			South African	7	1.50	43.75
Golantarctic	2	0.43	*Chile-Patagonian*	1	0.22	50
			Neozeylandic	1	0.22	50

Irano-Turanian region. The Sino-Himalayan species can also be found in exclaves in Tibet. Species (20): *E. cashmeriana* Royle, *E. cornigera* Boiss., *E. griffithii* Hook. f., *E. heishuiensis* W. T. Wang, *E. himalayensis* (Klotzsch) Boiss., *E. hylonoma* Hand.-Mazz., *E. jacquemontii* Boiss., *E. khasyana* Boiss., *E. kingdonwardii* Binojkumar & N. P. Balakr., *E. luteoviridis* D. G. Long, *E. maddenii* Boiss., *E. micractina* Boiss., *E. prolifera* Buch.-Ham. *ex* D. Don, *E. pseudosikkimensis* (Hurus. & Yu. Tanaka) Radcl.-Sm., *E. saxicola* Radcl.-Sm., *E. sharmae* Battacharyya, *E. sikkimensis* Boiss., *E. stracheyi* Boiss., *E. thyrsoidea* Boiss., *E. wallichii* Hook. f.

III. Tethyan (Ancient Mediterranean) group (260 species)

7. *Pantethyan element* (pluriregional). Plants found in at least three regions of the Tethyan (Ancient Mediterranean) floristic subkingdom; sometimes they have a wider secondary distribution. Species (2): *E. chamaepeplus* Boiss. & Gaill., *E. dracunculoides* Lam.

8. *European-Pantethyan element* (pluriregional). Usually widely distributed species occurring in at least two regions of the Tethyan floristic subkingdom and also in the European part of the Circumboreal region, at least in the Atlantic and

Table 2. Distribution of species of *Euphorbia* subg. *Esula* by section, geographical element, and group of elements. Mad. – Madagascan, I-Mal. – Indomalesian, NT – Neotropical, S. African – South African, GA – Golantarctic group of elements.

Group of elements	Boreal				E. Asian		Tethyan									Madrean		Paleotropical		Mad.	I-Mal.		NT	S. African				GA		Total in the section
Section \ Geographical element	West-Palearctic	Euro-Siberian	North American Atlantic	North American	Sino-Japanese	Sino-Himalayan	Pantethyan	European-Pantethyan	Macaronesian	Mediterranean	Macaronesian-Mediterranean	Submediterranean	Saharo-Arabian	Irano-Turanian	Sino-Himalayan- Irano-Turanian	Madrean	Submadrean	Panpaleotropical	Sudano-Zambesian	Madagascan	Indo-Malesian	Fijian	Caribbean	Karoo-Namib	Uzambara-Zululand	Cape	South African	Chile-Patagonian	Neozeylandic	
Lagascae											1	1		1																3
Holophyllum		3			3	9				1				11																27
Helioscopia		35	2	1	7	7		2	2	37	2	11		18	1	1			5									1		132
Myrsiniteae		1								6		2		7																16
Pithyusa	1	4				2		1		11		10	1	24																54
Sclerocyathium														8	1															9
Calyptratae													1	1																2
Chylogala										1			1	2																4
Szovitsiae														1																1
Patellares		4								9		3																		16
Herpetorrhizae														11	1															12
Guyonianae													1																	1
Pachycladae											2																			2
Biumbellatae										3																				3
Exiguae							1	1		3																				5
Aphyllis									11										8	1				1		1	1			23
Paralias								3	1	5	1	1											1							12
Tithymalus			3	2			1	1		6						17	8						2							40
Arvales						1					1	1		3																6
Esula	1	34			10	1				3		3		18				1	9	2	1	1			4	3	6		1	98

Central European provinces. Most of the species of this group are weeds, and it is impossible to separate their primary and secondary distribution areas. Species (8): *E. exigua* L., *E. falcata* L., *E. helioscopia* L., *E. paralias* L., *E. peplus* L., *E. portlandica* L., *E. stricta* L., *E. taurinensis* All.

9. *Macaronesian element* (uniregional). Species (14): *E. anachoreta* Svent., *E. aphylla* Brouss. *ex* Willd., *E. atropurpurea* Brouss., *E. azorica* Hochst., *E. berthelotii* Bolle *ex* Boiss., *E. bourgaeana* J. Gay *ex* Boiss., *E. bravoana* Svent., *E. lamarckii* Sweet, *E. mellifera* Aiton, *E. pedroi* Molero & Rovira, *E. piscatoria* Aiton, *E. regis-jubae* Webb & Berthel., *E. stygiana* H. C. Watson, *E. tuckeyana* Steud. *ex* Webb.

10. *Mediterranean element* (uniregional). Species (85): *E. acanthothamnos* Heldr. & Sart. *ex* Boiss., *E. akenocarpa* Guss., *E. aleppica* L., *E. antilibanotica* Mouterde, *E. anthula* Lavrent. & Papan., *E. apios* L., *E. arguta* Banks & Sol., *E. austroanatolica* Hub.-Mor. & M. S. Khan, *E. barrelieri* Savi, *E. berythea* Boiss. & Blanche, *E. biumbellata* Poir., *E. bivonae* Steud., *E. boetica* Boiss., *E. briquetii* Emb. & Maire, *E. bupleuroides* Desf., *E. canuti* Parl., *E. capitulata* Rchb., *E. caudiculosa* Boiss., *E. celerieri* (Emb.) Emb. *ex* Vindt, *E. ceratocarpa* Ten., *E. characias* L., *E. clementei* Boiss., *E. corallioides* L., *E. corsica* Req., *E. cossoniana* Boiss., *E. cuneifolia* Guss., *E. davisii* M. S. Khan, *E. deflexa* Sibth. & Sm., *E. dimorphocaulon* P. H. Davis, *E. durandoi* Chabert, *E. erinacea* Boiss. & Kotschy, *E. fontqueriana* Greuter, *E. gaditana* Coss., *E. gasparrinii* Boiss., *E. gayi* Salis, *E. gebelica* Brullo, *E. graminifolia* Vill., *E. haussknechtii* Boiss., *E. herniariifolia* Willd., *E. hieroglyphica* Coss. & Durieu *ex* Boiss., *E. hierosolymitana* Boiss., *E. insularis* Boiss., *E. isatidifolia* Lam., *E. isaurica* M. S. Khan, *E. kotschyana* Fenzl, *E. lagascae* Spreng., *E. maresii* Knoche, *E. margalidiana* Kuhbier & Lewej., *E. matritensis* Boiss., *E. mazicum* Emb. & Maire, *E. medicaginea* Boiss., *E. megalatlantica* Ball, *E. melapetala* Gasp. *ex* Guss., *E. melitensis* Parl., *E. meuselii* Geltman, *E. minuta* Loscos & Pardo, *E. nereidum* Jahand. & Maire, *E. nevadensis* Boiss. & Reut., *E. nicaeensis* All., *E. nurae* P. Fraga & Rossello, *E. oblongata* Griseb., *E. oxyphylla* Boiss., *E. paniculata* Desf., *E. papillaris* (Boiss.) Raffaelli & Ricceri, *E. pestalozzae* Boiss., *E. pisidica* Hub.-Mor. & M. S. Khan, *E. pithyusa* L., *E. promecocarpa* Davis, *E. pseudoapios* Maire & Weiller, *E. punctata* Delile, *E. rechingeri* Greuter, *E. reuteriana* Boiss., *E. rhytidosperma* Boiss. & Balansa, *E. rimarum* Coss. & Balansa, *E. schottiana* Boiss., *E. semiperfoliata* Viv., *E. serrata* L., *E. sintenisii* Boiss. *ex* Freyn, *E. spinosa* L., *E. squamigera* Loisel., *E. sultan-hassei* Strid *et al.*, *E. thompsonii* Holmboe, *E. transtagana* Boiss., *E. valerianifolia* Lam., *E. veneris* M. L. S. Khan., *E. wulfenii* Hoppe *ex* W. D. J. Koch.

11. *Macaronesian-Mediterranean element* (biregional). Plants occurring in both the Mediterranean (usually western) and Macaronesian regions. It is quite possible that at least some of these species originally occurred in the Mediterranean only and then were introduced to Macaronesia, but it is now impossible to present indisputable evidence of this. Species (7): *E. dendroides* L., *E. hirsuta* L., *E. lagascae* Spreng., *E. pterococca* Brot., *E. segetalis* L., *E. sulcata* Lens *ex* Loisel, *E. terracina* L.

12. *Submediterranean element* (uni- or pluriregional). This element incorporates species having different distribution patterns but in some way connected with the Mediterranean region. Within this element at least three principal groups can be separated: (a) species occurring in the Mediterranean region itself (usually at higher elevations) and also in neighboring areas like the Balkans, Caucasus, Crimea or Anatolia (*E. myrsinites*, *E. flavicoma*, *E. rigida*, etc.); (b) species found in the Mediterranean and/or at the western edge of the Irano-Turanian region and at the same time in southern parts of the Circumboreal region, where such plants are usually restricted to 'Mediterranean-like' habitats such as exposed rocks or limestone outcrops (*E. condylocarpa*, *E. glareosa*, *E. petrophila*); (c) species endemic to mountain systems located at the northern border of the Mediterranean, or local endemics to areas adjoining the Mediterranean (Crimean-Novorossiysk, Euxine, Illirian provinces) and occupying 'Mediterranean-like' habitats (*E. heldreichii*, *E. orphanidis*, *E. panjutinii*). Species (32): *E. androsaemifolia* Willd.

ex Schlecht., *E. aulacosperma* Boiss., *E. condylocarpa* M. Bieb., *E. duvalii* Lecoq & Lamotte, *E. erubescens* Boiss., *E. erythrodon* Boiss. & Heldr., *E. filicina* Port., *E. flavicoma* DC., *E. fragifera* Jan, *E. glabriflora* Vis., *E. glareosa* Pall. *ex* M. Bieb., *E. heldreichii* Orph. *ex* Boiss., *E. hercegovina* Beck, *E. imperfoliata* Vis., *E. ledebourii* Boiss., *E. microsphaera* Boiss., *E. montenegrina* (Bald.) K. Malý, *E. myrsinites* L., *E. niciciana* Borbás *ex* Novák, *E. obovata* Decne., *E. orjeni* Beck, *E. orphanidis* Boiss., *E. panjutinii* Grossh., *E. petrophila* C. A. Mey., *E. phymatosperma* Boiss. & Gaill., *E. rhabdotosperma* Radcl.-Sm., *E. rigida* M. Bieb., *E. serpentini* Novák, *E. thessala* (Formánek) Degen & Dörfl., *E. triflora* Schott *et al.*, *E. uliginosa* Welw. *ex* Boiss., *E. velenovskyi* Bornm.

13. *Saharo-Arabian element* (uniregional). Species (4): *E. calyptrata* Coss. & Durieu, *E. guyoniana* Boiss. & Reut., *E. retusa* Forssk., *E. sanctae-catarinae* Fayed.

14. *Irano-Turanian element* (uniregional). As mentioned above, in the current analysis the Western Himalayan province is excluded here from the Irano-Turanian region. Species (105): *E. acanthodes* Akhani, *E. alaica* (Prokh.) Prokh., *E. alatavica* Boiss., *E. altissima* Boiss., *E. altotibetica* Paulsen, *E. anacampseros* Boiss., *E. andrachnoides* Schrenk, *E. armena* Prokh., *E. arvalis* Boiss. & Heldr., *E. aserbajdzhanica* Bordz., *E. astrachanica* C. A. Mey. *ex* Trautv., *E. aucheri* Boiss., *E. blatteri* Oudejans, *E. blepharophylla* Ledeb., *E. buhsei* Boiss., *E. bungei* Boiss., *E. caeladenia* Boiss., *E. cassia* Boiss., *E. chaborasia* Gomb., *E. cheiradenia* Boiss. & Hohen., *E. coniosperma* Boiss. & Buhse, *E. connata* Boiss., *E. consanguinea* Schrenk, *E. craspedia* Boiss., *E. cuspidata* Bertol., *E. cyrtophylla* (Prokh.) Prokh., *E. deltobracteata* (Prokh.) Prokh., *E. densa* Schrenk, *E. densiuscula* M. Pop., *E. densiusculiformis* (Pazij) Botsch., *E. denticulata* Lam., *E. eriophora* Boiss., *E. erythradenia* Boiss., *E. ferganensis* B. Fedtsch, *E. fistulosa* M. S. Khan, *E. franchetii* B. Fedtsch., *E. gaillardotii* Boiss. & Blanche, *E. gedrosiaca* Rech. f. *et al.*, *E. glomerulans* (Prokh.) Prokh., *E. grisophylla* M. S. Khan, *E. grossheimii* (Prokh.) Prokh., *E. guntensis* (Prokh.) Prokh., *E. gypsicola* Rech. f. & Aellen, *E. gulestanica* Podlech, *E. hebecarpa* Boiss., *E. heptapotamica* Golosk., *E. heteradena* Jaub. & Spach, *E. humilis* Ledeb., *E. hyrcana* Grossh., *E. inderiensis* Less. *ex* Kar. & Kir., *E. iranshahri* Pahlevani, *E. irgisensis* Litv., *E. jaxartica* (Prokh.) Krylov, *E. khorasanica* Saeidi & Ghayormand, *E. kopetdaghi* (Prokh.) Prokh., *E. kozlovii* Prokh., *E. kudrjaschevii* (Pazij) Prokh., *E. lamprocarpa* (Prokh.) Prokh., *E. lioui* C. Y. Wu & J. S. Ma, *E. lipskyi* (Prokh.) Prokh., *E. macrocarpa* Boiss. & Buhse, *E. macroclada* Boiss., *E. malleata* Boiss., *E. malurensis* Rech. f., *E. marschalliana* Boiss., *E. megalocarpa* Rech. f., *E. microsciadia* Boiss., *E. monocyathium* (Prokh.) Prokh., *E. monostyla* Prokh., *E. mucronulata* (Prokh.) Pavlov, *E. oidorrhiza* Pojark., *E. orientalis* L., *E. osyridea* Boiss., *E. oxyodonta* Boiss., *E. pachyrrhiza* Kar. & Kir., *E. pamirica* (Prokh.) Prokh., *E. pauciradiata* Blatt., *E. physocaulos* Mouterde, *E. plebeia* Boiss., *E. poecilophylla* (Prokh.) Prokh., *E. polycaula* Boiss. & Hohen., *E. rapulum* Kar. & Kir., *E. rosularis* Fed., *E. sahendii* Bornm., *E. sarawschanica* Regel, *E. schugnanica* B. Fedtsch., *E. sclerocyathium* Korovin & Popov, *E. sewerzowii* (Prokh.) Pavlov, *E. smirnovii* Geltman, *E. sogdiana* Popov, *E. soongarica* Boiss., *E. sororia* Schrenk, *E. spartiformis* Mobayen, *E. spinidens* Bornm. *ex* Prokh., *E. szovitsii* Fisch. & C. A. Mey., *E. talaina* Radcl.-Sm., *E. talastavica* (Prokh.) Prokh., *E. teheranica* Boiss., *E. thomsoniana* Boiss., *E. tianshanica* (Prokh.) Popov, *E. transoxana* (Prokh.) Prokh., *E. triodonta* (Prokh.) Prokh., *E. turczaninowii* Kar. & Kir., *E. turkestanica* Regel, *E. yaroslavii* Poljakov.

15. *Sino-Himalayan–Irano-Turanian element* (biregional). Species occurring in montane areas of the Irano-Turanian region (Pamir, Tien-Shan, Tibet) and also in the Sino-Himalayan region (mainly in the Himalayas). Species (3): *E. edgeworthii* Boiss., *E. kanaorica* Boiss., *E. tibetica* Boiss.

IV. Madrean group (26 species)

16. *Madrean element* (uniregional). Species (18): *E. alta* Norton, *E. beamanii* M. C. Johnst., *E. chamaesula* Boiss., *E. chiribensis* V. W. Steinm. & Felger, *E. correllii* M. C. Johnst., *E. creberrima*

McVaugh, *E. crenulata* Engelm., *E. cressoides* M. C. Johnst., *E. greggii* Engelm. *ex* Boiss., *E. ivanjohnstonii* M. C. Johnst., *E. longicornuta* S. Watson, *E. lurida* Engelm., *E. mcvaughiana* M. C. Johnst., *E. neilmuelleri* M. C. Johnst., *E. nesomii* M. H. Mayfield, *E. pinkavana* M. C. Johnst., *E. schizoloba* Engelm., *E. yaquiana* (Cockerell) Tidestr.

17. *Submadrean element* (biregional). Species found in the Madrean region and also in neighboring areas or in the transitional zone between Madrean and other floristic regions. Species (8): *E. austrotexana* M. H. Mayfield, *E. esuliformis* S. Schauer *ex* Nees & S. Schauer, *E. furcillata* Kunth, *E. helleri* Millsp., *E. orizabae* Boiss., *E. peplidion* Engelm., *E. roemeriana* Scheele, *E. tetrapora* Engelm.

V. Paleotropical group (23 species)

18. *Panpaleotropical element* (pluriregional). Plants with a wide distribution at least in the Guineo-Congolian and Sudano-Zambesian regions. Species (1): *E. schimperiana* Scheele.

19. *Sudano-Zambesian element* (uniregional). Species (22): *E. brevicornu* Pax, *E. calamiformis* P. R. O. Bally & S. Carter, *E. citrina* S. Carter, *E. crebrifolia* S. Carter, *E. cyparissioides* Pax, *E. daviesii* E. A. Bruce, *E. depauperata* Hochst. *ex* A. Rich., *E. dumalis* S. Carter, *E. furcatifolia* M. G. Gilbert, *E. gossypina* Pax, *E. lateriflora* Schumach., *E. nubica* N. E. Br., *E. pachyclada* S. Carter, *E. papilionum* S. Carter, *E. petitiana* A. Rich., *E. repetita* Hochst. *ex* A. Rich., *E. sareciana* M. G. Gilbert, *E. schimperi* C. Presl, *E. ugandensis* Pax & K. Hoffm., *E. usambarica* Pax, *E. wellbyi* N. E. Br., *E. whyteana* Baker f.

VI. Madagascan group (3 species)

20. *Madagascan element* (uniregional). Species (3): *E. borbonica* Boiss., *E. emirnensis* Baker, *E. orthoclada* Baker.

VII. Indo-Malesian group (2 species)

21. *Indo-Malesian element* (pluriregional). Plants occurring in the Indian and Malesian regions and penetrating to the Indo-China region. Species (1): *E. rothiana* Spreng.

22. *Fijian element* (uniregional). Species (1): *E. reineckei* Pax.

VIII. Neotropical group (3 species)

23. *Caribbean element* (uniregional). Species (3): *E. eggersii* Urb., *E. trichotoma* Kunth, *E. tuerckheimii* Urb.

IX. South African group (16 species)

24. *Karoo-Namib element* (uniregional). Species (1): *E. berotica* N. E. Br.

25. *Uzambara-Zululand element* (uniregional). Species (4): *E. albanica* N. E. Br., *E. muraltioides* N. E. Br., *E. ruscifolia* (Boiss.) N. E. Br., *E. sclerophylla* Boiss.

26. *Cape element* (uniregional). Species (4): *E. erythrina* Link, *E. foliosa* N. E. Br., *E. ovata* (E. Mey. *ex* Klotzsch & Garcke) Boiss., *E. stolonifera* Marloth.

27. *South African element* (pluriregional). Plants occurring in at least two of the following regions: Cape, Karoo-Namib, Uzambara-Zululand, and sometimes in neighboring parts of the Sudano-Zambesian region. Species (7): *E. epicyparissias* (E. Mey. *ex* Klotzsch & Garcke) Boiss., *E. ericoides* Lam., *E. genistoides* P. J. Bergius, *E. kraussiana* Bernh. *ex* Krauss, *E. mauritanica* L., *E. natalensis* Bernh. *ex* Krauss, *E. striata* Thunb.

X. Golantarctic group (2 species)

28. *Chile-Patagonian element* (uniregional). Species (1): *E. philippiana* (Klotzsch & Garcke) Boiss.

29. *Neozeylandic element* (uniregional). Species (1): *E. glauca* G. Forst.

Discussion

distribution of *Euphorbia* subg. *Esula* among geographical elements and groups of elements

Our data show that species belonging to the Tethyan group of elements clearly dominate

Euphorbia subg. *Esula* (260 species, 55.79% of the total number). Irano-Turanian (105) and Mediterranean (85) elements are the most numerous, together comprising 73.07% of the total number of species in the Tethyan group and 40.77% of the number of species analyzed here.

Species of the Tethyan group are found in all 20 analyzed sections of the subgenus. Members of ten sections [*Lagascae* Lázaro, *Sclerocyatium* (Prokh.) Prokh., *Calyptratae* Geltman, *Chylogala* (Fourr.) Prokh., *Szovitsiae* Geltman, *Herpetorrhizae* (Prokh.) Prokh., *Guyonianae* Molero & Riina, *Pachycladae* (Boiss.) Tutin, *Biumbellatae* Molero & Riina, *Exiguae* (Geltman) Riina & Molero] belong entirely to the Tethyan group, and three other sections (*Patellares*, *Paralias* Dumort., *Arvales*) have only single or a few species outside that group. Only sections *Holophyllum*, *Aphyllis* Webb & Berthel., *Tithymalus* and *Esula* have less than 50% Tethyan species. Irano-Turanian species are present in 12 sections, and Mediterranean species in 11 sections.

The Boreal group of elements is represented by 91 species (19.54%) and is second in terms of species number. Species of the Euro-Siberian element clearly dominate this group (89.01% of total number of species in the group). It needs to be pointed out that most species of the Euro-Siberian element are restricted to western or southern parts of temperate Eurasia (Atlantic-European, Central European, Illyrian, Euxine, Caucasian provinces) and also to the Altay-Sayan and Altay-Dzhungar provinces. If we were to use another scheme of floristic subkingdoms for the analysis, such as that of Kamelin (2010) who included the Caucasus and Balkans into the Tethyan floristic subkingdom, about a quarter of the Euro-Siberian species (first of all endemics and subendemics to the Caucasus and Balkans) could be assigned to the Tethyan group. Species of the Boreal group belong to only seven sections and do not dominate any of them.

Species of the Boreal group occur in both the Old World (Euro-Siberian and West-Palearctic elements, 83 species) and the New World (North American Atlantic and North American elements, 8 species). The latter belong to two sections only (*Helioscopia* and *Tithymalus*).

The East Asian group of elements is third in terms of number of species (40, 8.58%). Those species are equally divided between two elements, but there are no species with a wide distribution in the whole East Asian subkingdom. East Asian species are found in five sections, but mostly in sections *Holophyllum*, *Helioscopia* and *Esula*. Two species of section *Pithyusa* and one of section *Arvales* classified here as belonging to the Sino-Himalayan element could in fact occur in exclaves of the Tethyan flora in the Himalayas; this remains to be clarified.

Tethyan, East Asian and Eurasian representatives of the Boreal groups belong to 13 elements and comprise 383 species or 82.19% of the total number of species in the subgenus. It is clear that the territory of the Tethyan, Boreal (Old World part) and East Asian floristic subkingdoms (in fact, the whole of temperate Eurasia and North Africa) is the main area of the modern diversity of subgenus *Esula*.

Other groups of elements contain many fewer species but should be thoroughly analyzed because these data can provide very important phylogenetic and phytogeographic information.

There are 38 species of *E.* subg. *Esula* native to the New World. Species belonging to the Madrean group of elements (26 species, 5.58% of the total number) clearly dominate them, so the Madrean floristic region could be regarded as the center of the modern diversity of *E.* subg. *Esula* in the Americas. Eighteen species occur strictly within the limits of the Madrean region, and the other 8 (Submadrean element) extend into neighboring areas. Species of the Madrean group are represented mainly by section *Tithymalus* (25 species); the only exception is *E. alta* from section *Helioscopia*.

Besides species of the Madrean group and the above-mentioned 8 species of the Boreal group in the New World, there are also 3 species of the Caribbean group (with a single Caribbean element) and the enigmatic *E. philippiana* – a single species of the subgenus native to South America (described from central Chile). Two Caribbean species belong to section *Tithymalus* and one (*E. trichotoma*) to section *Paralias*.

The Sudano-Zambesian element (22 species) clearly dominates the Paleotropical group (23 species). Species of this group belong to sections *Helioscopia*, *Aphyllis* and *Esula*. The Madagascan group, with a single element, contains only 3 species: 2 of them (*E. emirnensis*, *E. orthoclada*) occur in Madagascar itself, and one is endemic to the island of Réunion, belonging to the Madagascar floristic region. The South African group contains 16 species, and the pluriregional South African element (species with a comparatively wide distribution) is the largest in this group. Only 4 species belong to the Cape element; they are restricted to the Cape province/region, known for its high endemism. Species assigned to the South African and Madagascan groups belong to sections *Aphyllis* and *Esula*.

The Indo-Malesian group is represented by *E. rothiana*, with a comparatively wide distribution (Indo-Malesian element), and *E. reineckei*, endemic to Samoa (Fijian element); both are members of section *Esula*.

The Golantarctic group is represented by 2 species: *E. philippiana* (Chile-Patagonian element), mentioned above, and *E. glauca* (Neozeylandic element).

geographical analysis of largest sections

The members of section *Helioscopia*, the largest section in the subgenus (132 species), belong to 15 elements clustered in seven groups. As in the whole subgenus, the Tethyan group (73 species, 56.06%) predominates. However, Mediterranean species (37) are more than twice as numerous as Irano-Turanian species (18); this may reflect the more mesic character of habitats preferred by species of this section (Riina *et al*., 2013). A significant number of species (35, or 26.52% of the total number) belong to the Euro-Siberian element. Like the majority of Euro-Siberian species of the whole subgenus, members of section *Helioscopia* inhabit the Atlantic-European, Central European, Illyrian, Euxine and Caucasian provinces, but 7 species are restricted to the Altay-Sayan and Altay-Dzhungar provinces. Two species of this section are also found in the New World, and 5 are found in tropical Africa. The section is absent from South Africa and Madagascar, however.

Ninety-eight species of section *Esula*, the second highest number of species in the subgenus, belong to 16 elements clustered into eight groups. More than a third of its species (34 species, 34.69%) belong to the Euro-Siberian element. Species belonging to this section (e.g., *E. borodinii*, *E. gmelinii*, *E. korshynskyi*, *E. lenensis*) have the northernmost distribution (reaching to the Arctic Circle) of all species of the genus *Euphorbia*. Ten species of this section belong to the East Asian group, mostly to the Sino-Japanese element. Several Euro-Siberian taxa of section *Esula* probably are in the process of intensive modern speciation, so species delimitation is uncertain and disputable in several taxonomic groups, for example the *E. esula* L. s.l. complex (Geltman 1996, 1998) or *E. illirica* Lam. and closely related species (Geltman 2009).

In section *Esula* there are 24 species in the Tethyan group (24.49%). Most of them belong to the Irano-Turanian element and there are only 3 Mediterranean species. Twenty-five species of section *Esula* occur in tropical Africa, South Africa and Madagascar (Paleotropical, South African and Madagascan groups of elements). There are also 2 species of the Indo-Malesian group (one of them endemic to Samoa) and one endemic to New Zealand. All these species form two well-supported clades which lie outside the temperate Eurasian species (Riina *et al.* 2013).

Section *Pithyusa* contains 54 species that belong mainly to the Tethyan group of elements (47 species, 87.04%), and the number of Irano-Turanian species is more than twice that of the Mediterranean species. This section is well known for having the highest proportion of Submediterranean species (10 species, 18.52%).

Members of the mostly New World section *Tithymalus* (40 species) are shared between Madrean (25 species, 62.5%), Tethyan (8, 20%) and Boreal (5, all native in the New World, 12.5%) groups.

Section *Holophyllum*, with 27 species, has a good representation in the East Asian subkingdom (66.97%) and there are also 3 Euro-

Siberian species restricted to southern Siberia and northern Mongolia. Other representatives of this section belong to the Tethyan group, mainly to the Irano-Turanian element, but one species (*E. isatidifolia*) occurs in the Iberian Peninsula and shows a considerable disjunction from the rest of the section.

Twenty-three species of section *Aphyllis* are separated into two subsections (Riina *et al.* 2013); this separation is based on several molecular trees, morphological differentiation, and geographical distribution patterns (Riina *et al.* 2013; Barres *et al.* 2011). Subsection *Macaronesicae* (11 species) has an exclusively Macaronesian distribution. Species of *E.* subsect. *Africanae* (12 species) occur in Africa and Madagascar and belong mainly to the Sudano-Zambesian element (7 species).

Other sections are comparatively small (less than 15 species, sometimes 1–3) and, as mentioned above, have mainly a Tethyan distribution.

Geographical analysis and phylogeny of the subgenus

Data presented here clearly show that the Tethyan floristic subkingdom and adjacent areas are the center of the modern diversity of *E.* subg. *Esula*. Very likely, such diversity is the result of intensive speciation that took place here during the Eocene–Miocene. Horn *et al.* (2014) estimated the age of the crown clade of *Euphorbia* at *ca* 47.8 Ma and also showed that the divergence of the main lineages within *E.* subg. *Esula* took place between *ca* 38 and 10 Ma. This speciation probably proceeded under the influence of two processes: shrinkage of Paratethys (with the formation of desert areas) and Alpine orogenesis. There are some grounds for speculating that orogeny was more important in this, because there are few true desert species of the subgenus.

Only after the formation of the main clades (taxonomically separated as sections) did some species representing such groups migrate to areas outside the original center of diversity. Riina *et al.* (2013) suggested that there were four independent migrations of the subgenus to the New World, and at least three into tropical and South Africa. The New World species of section *Tithymalus* are likely the result of intensive speciation after a single introduction from the Mediterranean area.

It is likely that the colonization of boreal areas of Eurasia took place comparatively recently (although a special phylogeographical study in this area would be desirable) and that it involved representatives of only a few sections, mostly *Esula*, *Helioscopia*, and *Holophyllum*. It seems strange that there are no native species of section *Esula* in temperate areas of the New World and that they did not use the Beringian land bridge although some of them (e.g., *E. lenensis*) are found in Siberia near the Arctic circle.

Long-distance dispersal seems the best explanation for the isolated occurrence of some species. The presence of *E. glauca* in New Zealand and *E. reineckii* on Fiji, at least, is impossible to explain by any schemes of land bridges and continental movements.

Acknowledgements. I am grateful to Rudolf Kamelin for numerous valuable consultations, Paul Berry for linguistic corrections of the submitted text and for other comments, and Hans-Joachim (Hajo) Esser and the anonymous reviewer for important suggestions which improved the manuscript. The work was supported by the Russian Foundation for Basic Research (project 13-04-00541). I am grateful to the International Association for Plant Taxonomy for permission to reproduce Figure 1.

References

Ali S. I. & Qaiser M. 1986. A phytogeographical analysis of the phanerogams of Pakistan and Kashmir. *Proc. Roy. Soc. Edinburgh, B* **89**: 89–101.

Baikov K. S. 2007. *Euphorbia Asiae Borealis*. Nauka, Novosobirsk (in Russian).

Barres L., Vilatersana R., Molero J., Susanna A. & Galbany-Casals M. 2011. Molecular phylogeny of *Euphorbia* subg. *Esula* sect. *Aphyllis* (Euphorbiaceae) inferred from nrDNA and cpDNA markers with biogeographic insights. *Taxon* **60**(3): 705–720.

Braun-Blanquet J. 1919. Essai sur les notions «d'element» et de «territoire» phytogeographiques. *Arch. Sci. Phys. Nat.* **1**: 497–512.

Braun-Blanquet J. 1923. *L'origine et le developpement des flores dans le massif central de France*. L. Lhomme, Paris – Zürich.

Bruyns P. V., Klak C. & Hanáček P. 2011. Age and diversity in Old World succulent species of *Euphorbia* (Euphorbiaceae). *Taxon* **60**(6): 1717–1733.

Bruyns P. V., Mapaya R. J. & Hedderson T. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and psbA-trnH sequence data. *Taxon* **55**(2): 397–420.

Budantsev A. L. 1998. Conspectus of the genus *Verbascum* (Scrophulariaceae) of the Caucasian flora. *Bot. Zhurn.* **83**(7): 128–139 (in Russian).

Chang C.-S., Kim H. & Chang K. S. 2014. *Provisional checklist of vascular plants for the Korean Peninsula Flora* (KPF) (Version 1.0). Desingpost, Seoul. http://hosting03.snu.ac.kr/~quercus1/Checklist_version%20revision%20may.pdf.

Christ H. 1867. Ueber die Verbreitung der Pflanzen in der alpinen Region der europaeischen Alpenkette. *Neue Denkschr. Schw. Nat. Ges.* **22**: 1–84.

Davis P. H. (ed.) 1965. *Flora of Turkey and East Aegean Islands*. **1**. University Press, Edinburgh.

Davis P. H. (ed.) 1965–1988. *Flora of Turkey and East Aegean Islands*. **1–10**. University Press, Edinburgh.

Dorsey B. L., Haevermans T., Aubriot X., Morawetz J. J., Riina R., Steinmann V. W. & Berry P. E. 2013. Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*. *Taxon* **62**(2): 291–315.

Eig A. 1931. Les éléments et les groupes phytogéographiques auxiliaires dans la flore palestinienne 1. Texte. *Feddes Repert. Beih.* **63**: 1–201.

Engler A. 1879. *Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der nördlichen Hemisphäre. Teil 1. Die extratropischen Florengebiete der nördlichen Hemisphäre*. Verlag von Wilhelm Engelmann, Leipzig.

Geltman D. V. 1996. Taxonomic notes on species of subsection Esulae of the genus *Euphorbia* (Euphorbiaceae) from Eastern Europe. *Bot. Zhurn.* **81**(9): 73–89 (in Russian with English summary).

Geltman D. V. 1998. Taxonomic notes on *Euphorbia esula* (Euphorbiaceae) with special reference to its occurrence in the east part of the Baltic region. *Ann. Bot. Fennici* **35**(2): 113–117.

Geltman D. V. 2009. On the taxonomy of the *Euphorbia illirica* (Euphorbiaceae) affinity complex. *Bot. Zhurn.* **94**(7): 921–937 (in Russian with English summary).

Good R. 1964. *The geography of the flowering plants*. 3 ed. Longmans, London & Colchester.

Govaerts R., Fernández Casas F. J., Barker C., Carter S., Davies S., Esser H.-J., Gilbert M., Hoffmann P., Radcliffe-Smith A., Steinmann V. W., van Welzen P. C. & Whitmore T. 2015. World Checklist of Euphorbiaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. [July 2015]. http://apps.kew.org/wcsp/.

Hayek A. 1926. *Allgemeine Pflanzengeographie*. Gebrüder Borntraeger, Berlin.

Horn J. W., van Ee B. W., Morawetz J. J., Riina R., Steinmann V. W., Berry P. E. & Wurdack K. J. 2012. Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). *Molec. Phylogenet. Evol.* **63**(2): 305–326.

Horn W. H., Zhenxiang X., Riina R., Peirson J. A., Yang Y., Dorsey B. L., Berry P. E., Davis C. C. & Wurdack K. J. 2014. Evolutionary bursts in *Euphorbia* (Euphorbiaceae) are linked with photosynthetic pathway. *Evolution* **68**(12): 3485–3504.

Kamelin R. V. 2010. Oreocryophytic elements of the montane Middle Asian flora. *Bot. Zhurn.* **95**(6): 730–757 (in Russian with English summary).

Kamelin R. V. 2012. Floristic division of the world land: new solutions. *Bot. Zhurn.* **97**(12): 1481–1488 (in Russian with English summary).

Kurosawa T. 2006. The family Euphorbiaceae s.l. in Nepal. A checklist and taxonomic notes. In: H. Ohba (ed.), *Himalayan Plants.* 4. *Bull. Univ. Mus. Univ. Tokyo* **42**: 155–346.

Ma J. S., Liu Y. & Wei F. N. 2013. A new species of *Euphorbia* (Euphorbiaceae) from Guangxi, China. *Phytotaxa* **87**(3): 45–49.

Menitsky Y. L. 1986. Conspectus specierum generis *Thymus* L. (Lamiaceae) in flora Caucasi. *Novosti Sist. Vyssh. Rast.* **23**: 117–142 (in Russian).

Menitsky Y. L. 1992. Conspectus of Lamiaceae (Labiatae) of the Caucasian flora. *Bot. Zhurn.* **77**(6): 63–78 (in Russian).

Pahlevani A. H. & Riina R. 2014. Synopsis of *Euphorbia* subgen. *Esula* sect. *Helioscopia* (Euphorbiaceae) in Iran with the description of *Euphorbia mazandaranica* sp. nov. *Nordic J. Bot.* **32**: 257–278.

Park K.-R. & Jansen R. K. 2007. A phylogeny of Euphorbieae subtribe Euphorbiinae (Euphorbiaceae) based on molecular data. *J. Pl. Biol.* **50**(6): 644–649.

Peirson J. A., Bruyns P. V., Riina R., Morawetz J. J. & Berry P. E. 2013. A molecular phylogeny and classification of the largely succulent and mainly African *Euphorbia* subg. *Athymalus* (Euphorbiaceae). *Taxon* **62**(6): 1178–1199.

Peirson J. A., Riina R., Mayfield M. H., Ferguson C. J., Urbatsch L. E., Berry P. E. 2014. Phylogenetics and taxonomy of the New World leafy spurges, *Euphorbia* section *Tithymalus* (Euphorbiaceae). *Bot. J. Linn. Soc.* **175**: 191–228.

Pornetier N. N. 2000a. Methodical aspects of the elaboration of geographical elements in Caucasian flora. *Bot. Zhurn.* **85**(6): 76–84 (in Russian with English summary).

Portenier N. N. 2000b. System of geographical elements of the Caucasian flora. *Bot. Zhurn.* **85**(9): 26–33 (in Russian with English summary).

Riina R. & Berry P. E. (coord.) 2015. Euphorbia Planetary

Biodiversity Inventory database. [2015]. http://www.tolkin.org/projects/72.

Riina R., Peirson J. A., Geltman D. V., Molero J., Frajman B., Pahlevani A., Barres L., Morawetz J. J., Salmaki Y., Zarre S., Kryukov A., Bruyns P. V. & Berry P. E. 2013. A worldwide molecular phylogeny and classification of the leafy spurges, *Euphorbia* subgenus *Esula* (Euphorbiaceae). *Taxon* **62**(2): 316–342.

Saeidi Mehrvarz S. & Ghayormand M. 2015. *Euphorbia khorasanica* (Euphorbiaceae), a new species from Iran. *Ann. Bot. Fennici* **52**(1–2): 38–40.

Skvortsov A. K. 1966. Obzor iv Kavkaza i Maloy Azii. *Trudy Bot. Inst. Akad. Nauk Armyansk. S.S.R.* **15**: 91–141.

Steinmann V. W. & Porter J. M. 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and *ndh*F sequence data. *Ann. Missouri Bot. Gard.* **89**(4): 453–490.

Takhtajan A. 1986. *Floristic regions of the world*. University of California Press, Berkeley & Los Angeles.

Tolmachev A. I. 1974. *Vvedenie v geografiyu rasteniy*. Izdatel'stvo Leningradskogo Universiteta, Leningrad.

Wu Z. & Wu S. 1998. A proposal for a new floristic kingdom (realm) – the E. Asiatic Kingdom, its delimitation and characteristics. In: A. L. Zhang & S. G. Wu (eds), *Floristic characteristics and diversity of East Asian plants*, pp. 3–42. China Higher Education Press, Beijing & Springer-Verlag, Berlin.

Yang Y., Riina R., Morawetz J. J., Haevermans T., Aubriot X. & Berry P. E. 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Taxon* **61**(4): 764–789.

Yurtsev B. A. & Kamelin R. V. 1991. *Osnovnye ponyatiya i terminy floristiki: Uchebnoe posobie po spetskursu*. Izdatel'stvo Permskogo Universiteta, Perm.

Zimmermann N. F. A., Ritz C. M. & Hellwig F. H. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and trnL-trnF IGS sequence data. *Pl. Syst. Evol*. **286**: 39–58.

Received 8 April 2015