

ON THE ORIGIN OF EUPHORBIA SUBG. ESULA IN EUROPE (EUPHORBIACEAE)

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A study of the taxonomy and chorology of the Bulgarian species of *Euphorbia* has led me to consider their phytogeography; this entailed a closer view on the main features of florogenesis and distribution of subg. *Esula* in Europe. There are two problems concerned, viz. the origin of the two sections *Tulocarpa* (Raf.) Prokh. and *Murtekias* Prokh. which contain the most primitive and ancient species of the subg. *Esula* and furthermore a consideration of their mutual relationships and the main trends of their evolution within the subgenus.

The data on the distribution of the species examined in the present paper have been taken from the works of Boissier (1862, 1879), Halacsy (1904), Fiori (1925), Hegi (1925), Hayek (1927), Eig (1932), Prokhanov (1933, 1949), Ade & Rechinger (1938), Rechinger (1938, 1943, 1952, 1960), Czecczott (1939), Losa Espagna (1946), Diapoulis (1948), Prodan (1953), Vindt (1953), and Köie & Rechinger (1954/55).

In his examination of the centres of development in *Euphorbia*, Croizat (1958) assumed the Cape region as the main centre of speciation of the arboreous forms of subg. *Euphorbia* (cf. Kuzmanov, 1963) from where a northward migration took place towards West Africa and Macaronesia. Vulf (1944) and Prokhanov (1949) have expressed the opinion that Macaronesia must have been the area where subg. *Esula* evolved; they regard the arboreous representatives of subg. *Esula* which are chiefly concentrated in Macaronesia as the oldest species of the subgenus. A central place in this group is occupied by *Euphorbia regis-jubae* Webb, connected with the remaining representatives: *E. bertheloti* Boiss. (Canary Is), *E. tuckeyana* Steud. (Cape Verde Is), *E. burgeana* J. Gay and *E. atropurpurea* Brouss. (Teneriffe Is), *E. balsamifera* Ait. (Canary Is, West and Central Africa), *E. stygiana* Wats. (Azores), *E. mellifera* Ait. (Madeira), *E. piscatoria* Ait. (Madeira), and *E. dendroides* L. (Mediterranean). Lindberg (1932) regarded *E. pseudodendroides* Lindb. as a species distributed in Morocco and linking *E. regis-jubae* Webb to *E. dendroides* L. Later Vindt (1953) considered the above-mentioned species as a variety of *E. regis-jubae* and made the combination *E. regis-jubae* var. *pseudodendroides* (Lindb.) Vindt.

Vulf (1944) referring to Boissier (1879) links the most primitive species of sect. *Tulocarpa* and sect. *Murtekias* to *E. dendroides* L. The marked morphological resemblance of *E. dendroides* L. and *E. deflexa* Sibth. & Sm. marks their affinity. Boissier (1862), in characterizing subsect. *Pachycladae*, pointed out the close relationship of its representatives with the species of subsect. *Galarrheai* and subsect. *Esulae*. One may assume that the formation of the bush- and tree-like phanerophytes of *Pachycladae*, *Tulocarpa*, and *Murtekias* has proceeded from primitive forms among the Macaronesian species of subg. *Euphorbia*. Their further migration and evolution took place towards the east in the western Mediterranean, in a certain sense parallel, although at a different rate and to a different extent. At present the area of *E. dendroides* L. outlines the eastern boundary of the migration of

subject. *Pachycladae*, whereas sect. *Murtekias*, and particularly sect. *Tulocarpa*, have penetrated far eastward into Asia (Map 3 and Map 6).*

In a general sense sect. *Murtekias* is characteristic for the Mediterranean. Ecologically the species are distinctly thermophilous and xerophilous; they are often found on rocky limestone and other habitats with poor soils. The section is divided in three morphologically, ecologically, and geographically well differentiated subsections. The following two are of interest to the problem discussed:

(i) Subsect. *Murtekioideae* consists of succulent species; it is centered in the mountainous regions of Asia Minor, Iran, and the Caucasus. The species occurring there are *E. biglandulosa* Desf., *E. monostyla* Prokh., *E. myrsinites* L., *E. corsica* Req., *E. anacampseros* Boiss., *E. marschalliana* Boiss., *E. pontica* Prokh., *E. spinidens* Bornm., *E. woronowii* Grosh., *E. armena* Prokh., *E. denticulata* Lamk. and *E. craspedia* Boiss. (Map 1).

(ii) Subsect. *Coniocarpae* has the largest number of representatives. The majority of the perennial species are hemicyptophytes occurring on dry, calcareous, rocky or sandy terrains chiefly in the mountains, reaching up to an altitude of 3000—3500 m.

The following 6 centres of species formation are distinguished in this subsection (Map 2):

(1) The mountain massifs in the western Mediterranean where the following species are distributed: *E. nicaeensis* All., *E. segetalis* L., *E. terracina* L., *E. megalatlantica* Ball, *E. pithyusa* L., *E. bupleuroides* Desf., *E. malvana* Maire, *E. mazicum* Emb. & Maire, *E. celerieri* Emb. (the last three species are endemic in the mountainous parts of Morocco, reaching an altitude of 3500 m), *E. luteola* Coss., *E. seguieriana* Neck., *E. matritensis* Boiss., *E. baetica* Boiss., *E. pauciflora* Duf. (these three species endemic in Spain), and *E. imbricata* Vahl which is also known from Portugal and the Balearic Is.

(2) The Balkan Peninsula, where thirteen species are distributed: *E. segetalis* L., *E. nicaeensis* All., *E. terracina* L., *E. barrelieri* Savi, *E. glareosa* Pall. ex Bieb., *E. seguieriana* Neck., *E. niciciana* Borb., *E. herniariaefolia* Willd., *E. saxatilis* Jacq., *E. triflora* Schott. & al., *E. orphanidis* Boiss., *E. panci* Beck, and *E. deflexa* Sibth. & Sm.; the last four species are endemic in the region, whilst *E. niciciana* is found in Asia Minor as well.

(3) South Russia, where five species are distributed: *E. seguieriana*, *E. glareosa* Pall. ex Bieb., *E. petrophila* C. A. M., *E. goldei* Prokh., *E. volgensis* Krysh., the last two of which are endemic.

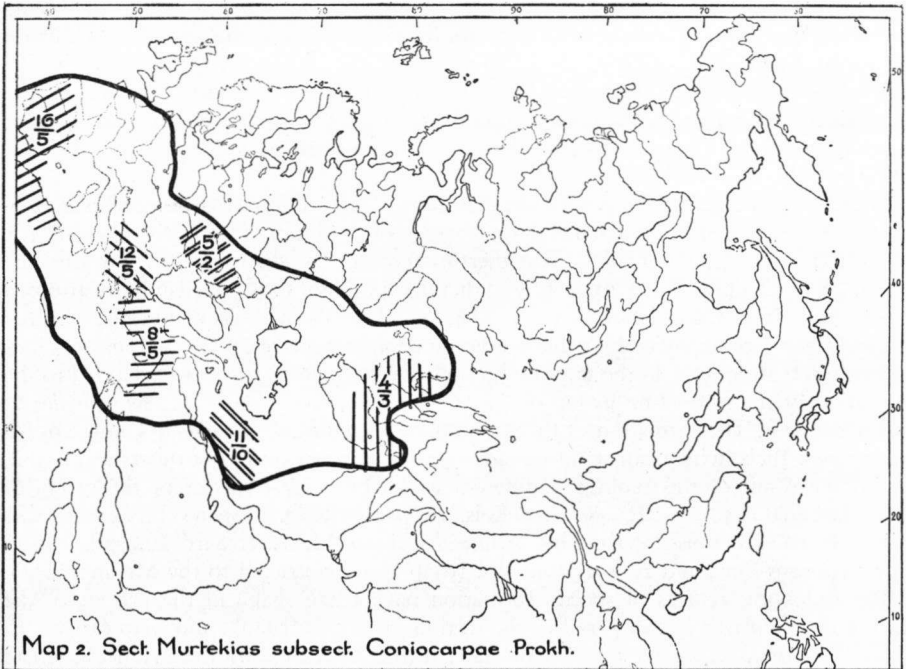
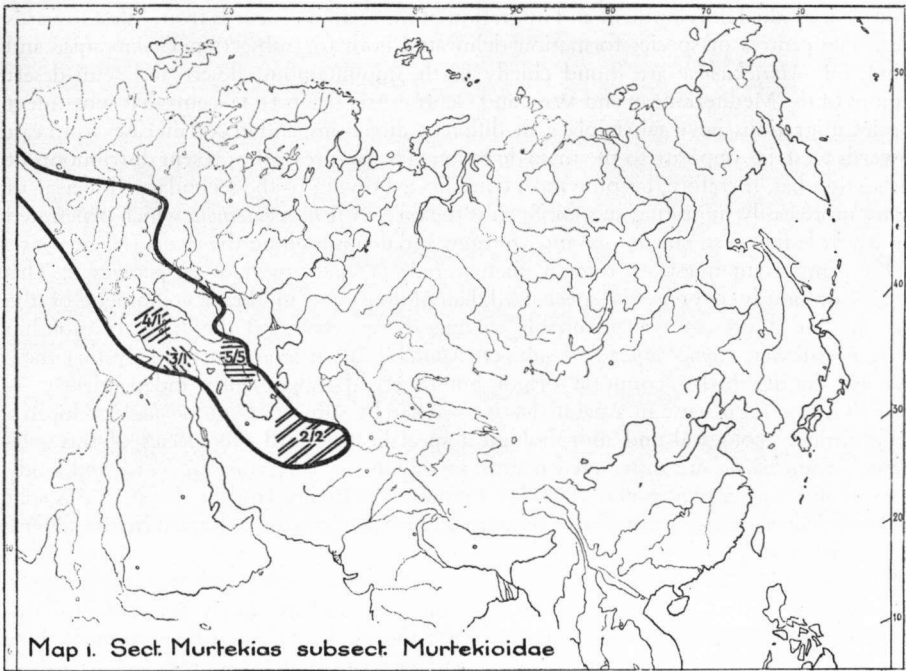
(4) Asia Minor and the Near East, where eight species are distributed: *E. herniariaefolia* Willd., *E. petrophila* C. A. Mey., *E. macroclada* Boiss., *E. chesneyi* (Klotzsch & Garcke) Boiss., *E. bothryosperma* Boiss. & Kotschy, *E. pestalozzae* Boiss., *E. erythron* Boiss. & Heldr., and *E. kurdica* Boiss. & Hausskn.; the last five species are endemic for the region.

(5) Iran, where eleven species are distributed: *E. striatella* Boiss., *E. erythradenia* Boiss., *E. macroclada* Boiss., *E. obovata* Decne, *E. teheranica* Boiss., *E. plebeia* Boiss., *E. bounophila* Boiss., *E. decipiens* Boiss. & Buhse, *E. polycaula* Boiss. & Hohen., *E. cheiradenia* Boiss. & Hohen., and *E. malleata* Boiss. All these species, *E. malleata* excepted, are endemic to the region.

(6) Central Asia and the western Himalayas, where four species are distributed: *E. seguieriana* Neck., *E. humilis* C. A. Mey., *E. sogdiana* M. Pop., and *E. kopetdagi* Prokh. The last three are endemic to the region.

Accepting the view that sect. *Murtekias* originated in the Macaronesian region, the

*) In all maps the shaded parts are the main centres of speciation. The numerals of the fractions mean: numerator indicates the total number of species in a region, the denominator the number of endemic species in the same region.



process of gradual development and migration of the section proceeds from West towards East. The centres of species formation delineated both for subsection *Coniocarpae* and subsection *Murtekioideae* are found chiefly in the mountainous, desert and semi-desert regions of the Mediterranean and West and Central Asia (Map 3). It seems that subsequent species migrations have taken place in different directions, and in certain cases from east towards west, i.e. opposite to the main direction. The picture of the present distribution of the section has, therefore, become most complicated owing to the secondary dispersal of many more easily migrating species. Such is the case with *E. seguieriana* which penetrated far towards the west, chiefly on sandy terrains and deposits along the rivers (Hegi, 1925).

Two important questions remain unanswered: (1) the origin of *E. paralias* L. This species obviously expresses a specialized halophilous line in the development of the section, but at present we are unable to trace its ancestry. (2) the exact relationship between subsect. *Coniocarpae* and subsect. *Murtekioideae*. It seems most likely that these two subsections had a common origin but diverged subsequently independently — though in a certain sense in a parallel way — whereby subsect. *Murtekioideae* developed a very distinct ecological and morphological specialization. All the species of this subsection *Murtekioideae* are distributed mainly in mountainous regions on rocky and sandy terrains and have a winter period of development. At higher latitude this period is split into two halves: late-autumn and early-spring (Prokhanov, 1949), divided by the adverse dry summer and cold winter periods.

The difficulties in elucidating the historical phytogeography and evolution of sect. *Tulocarpa*, as well as of sect. *Murtekias*, are considerable and are chiefly due to the following factors: the genetic relationships between the species have not been studied; there is a lack of phylogenetical, karyological, and experimental-taxonomic study on these groups; the taxonomic elaboration of a large number of species distributed in the Mediterranean, Asia Minor, and the Near East and Iran is incomplete; the groups of vicarious species are frequently not clear; the arrangement of the species with smooth seeds into two subsections (Prokhanov, 1949) does not throw light on their genesis owing to the approximate boundaries of the groups and the presence of numerous intermediate species; as yet I am not well acquainted with the phyletically oldest species of the section which link it to subs. *Pachycladae*.

There is no doubt that the general development of the section has proceeded in accordance with the well-known general regularities of evolution manifested also in sect. *Murtekias*; from the bush-like, megatherm, xerophilous chamaephytes towards the perennial, mesophytic and hygrophytic hemicryptophytes of grasslands, distributed chiefly in the forest association of the moderate and northern zones of Eurasia. This has probably been accompanied by a differentiation of annual species, on numerous occasions and in different periods, in the separate lines of development. This process has led to the formation of the interesting group of *E. helioscopia* L., and also of *E. plathyphyllos* L. and *E. stricta* L. The formation of the geophytes *E. apios* L., *E. isatidifolia* Lamk. and *E. condylocarpa* Bieb. which can stand the adverse dry summer period as tubers in the soil, is also the result of this biological differentiation. The oldest species of the group of shrub-like chamaephytes: *E. squamigera* Lois., *E. bivonae* Steud., *E. spinosa* L., *E. thamnoides* Boiss., *E. erinacea* Boiss. & Kotschy, *E. acanthothamnus* Heldr. & Sart., *E. cypria* Boiss., *E. cartaginensis* Por., and *E. glabriflora* Vis. (Map 4) are restricted to the Mediterranean.

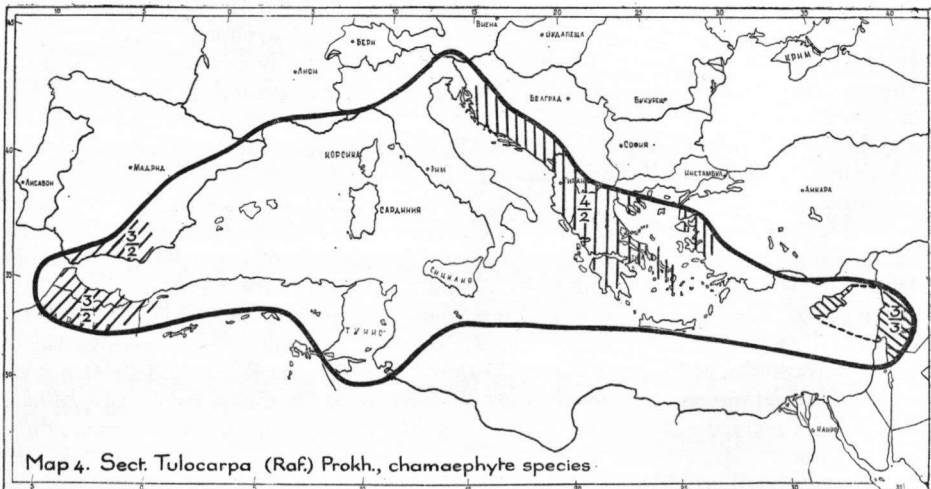
The following centres of species formation have taken shape in the process of the further development and dispersal of the section eastwards (Map 5 and Map 6):

(1) The massifs in the western Mediterranean (the Atlas Mts and the Pyrenees), where 15 species are found: *E. pubescens* Vahl, *E. dulcis* L., *E. verrucosa* L. em. Jacq., *E. hyberna*

L., *E. angulata* Jacq., *E. flavicoma* DC., *E. atlantis* Maire, *E. paniculata* Desf., *E. clementei* Boiss., *E. polygalaeifolia* Boiss. & Reut., *E. isatidifolia* Lamk, *E. duvalii* Lecoq & Lamtte, *E. ruscionensis* Boiss., *E. chamaebuxus* Bernd., *E. uliginosa* Urev., and *E. nereidum* Jahand. & Maire. The last ten species are endemic to the region.

(2) South Italy, where seven species occur of which three, viz. *E. coralloides* L., *E. gasparinii* Boiss., and *E. ceratocarpa* Ten. are endemic, and *E. insularis* Boiss. is endemic in the islands of Corsica and Sardinia.

(3) The Carpathians and the Balkan, where seventeen species are found: *E. palustris* L., *E. dulcis* L., *E. verrucosa* Lamk, *E. angulata* Jacq., *E. villosa* Waldst. & Kit. ex Willd., *E. polychroma* Kern., *E. epithymoides* L. em. Jacq., *E. apios* L., *E. carniolica* Jacq., *E. gregers-*



henii K. Maly, *E. lingulata* Heuff., *E. capitulata* Rchb., *E. carpatica* Woloczcz., *E. valdevillosocarpa* Arv. & Nyar., *E. montenegrina* (Bald.) Rohl., *E. velenovskyi* Bornm., and *E. oblongata* Griseb., of which the last nine species are endemic.

(4) Asia Minor and the Near East, where 13 species are distributed of which seven: *E. cypria* Boiss., *E. erinacea* Boiss. & Kotschy, *E. berythea* Boiss. & Blanch., *E. cardiophylla* Boiss. & Heldr., *E. shottiana* Boiss., *E. djimilensis* Boiss., and *E. squamosa* Willd. are endemic to the area.

(5) Caucasus to Iran, where eight species are distributed of which five: *E. condylocarpa* Bieb., *E. macrocarpa* Boiss. & Buhse, *E. coniosperma* Boiss. & Buhse, *E. wittmanni* Boiss., and *E. eugeniae* Prokh. are endemic, and *E. microsphaera* Boiss. is spread in Iraq as well.

(6) Altai — Tyanshan, where the species *E. songarica* Boiss., *E. lamprocarpa* Prokh., *E. mucronulata* Prokh., *E. kudrjashevii* (Pazj.) Prokh., *E. transoxana* Prokh., *E. alata* Boiss., *E. pachyrriza* Kar. & Kir., *E. talastavika* Prokh., *E. pilosa* L., *E. macrozrhiza* Led., *E. buchtormensis* Led., *E. altaica* Led., and *E. alpina* C. A. M. are distributed. All the species except *E. songarica* are endemics of the region.

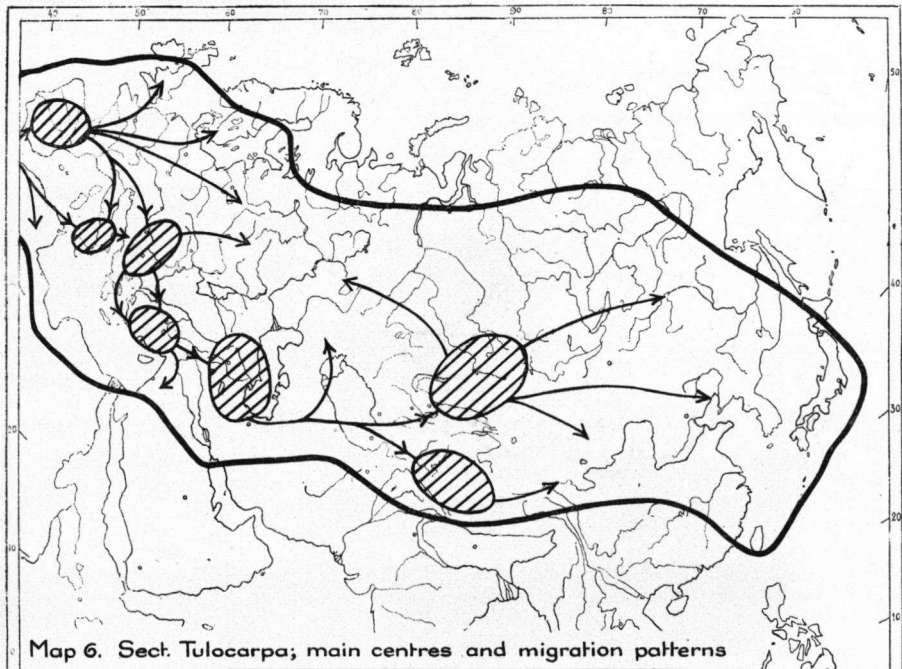
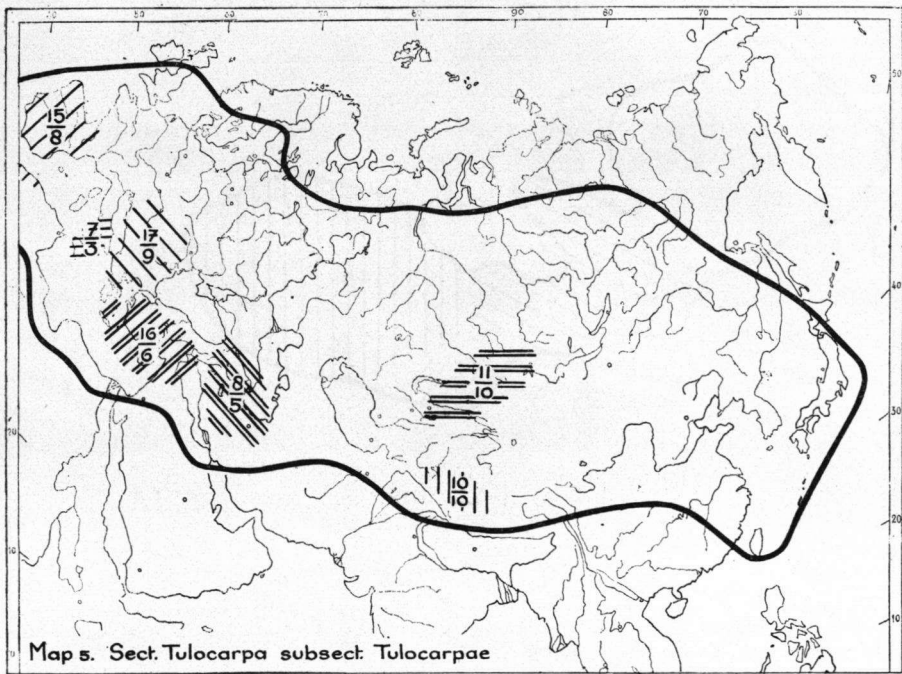
(7) The Himalayas (the mountain systems of Kashmir, Nepal, and northwestern India). Ten species occur in this area, some of which reach an altitude up to 4000 to 4500 m; all are endemic.

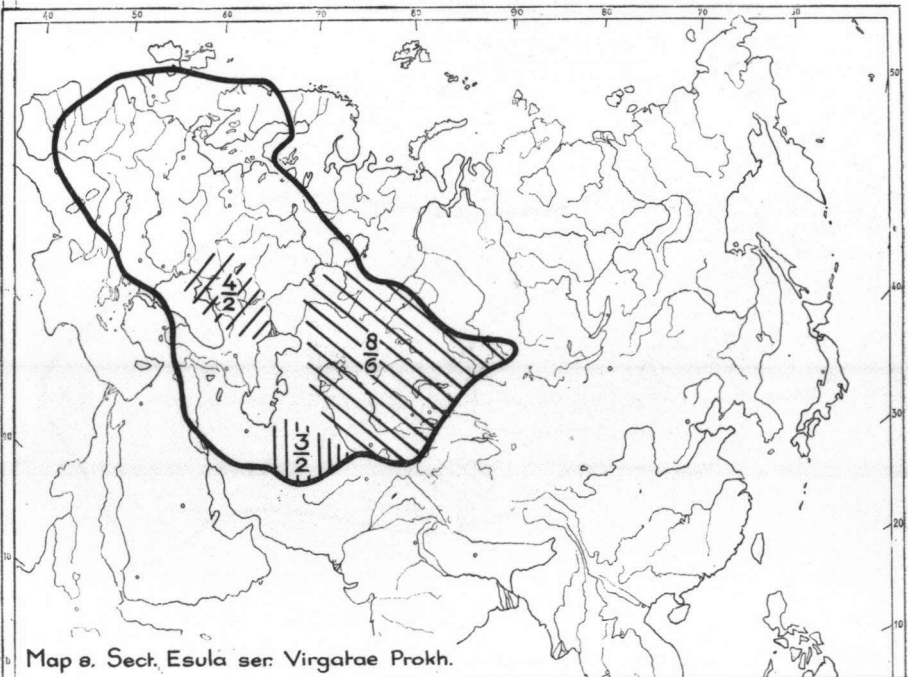
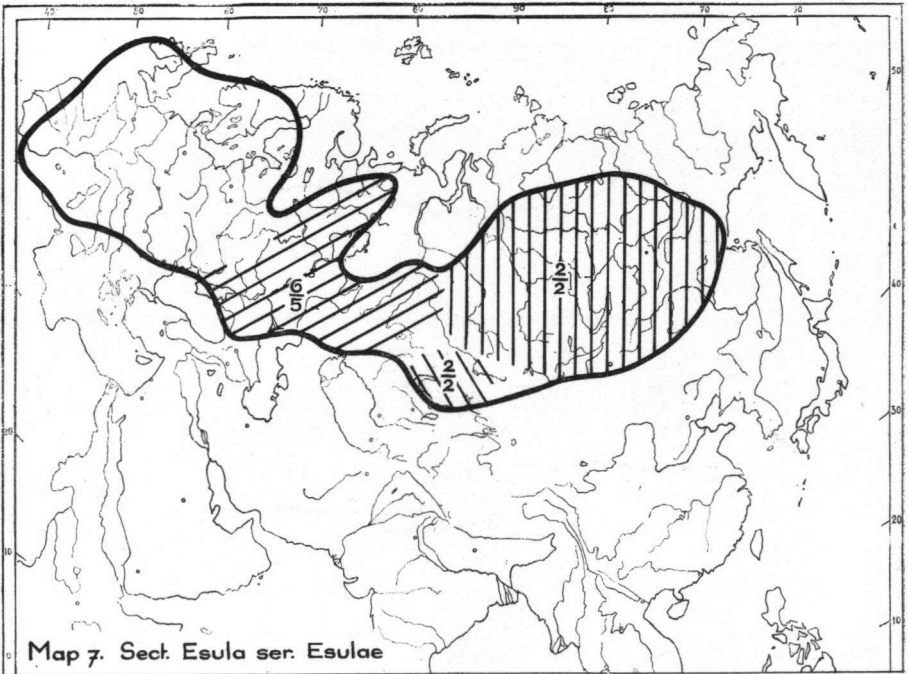
The origin of sect. *Esula* Prokh. should be traced in sect. *Murtekias*. Central Asia emerges as the initial centre of development with subsequent migration in two main directions: eastwards and westwards. Several groups of closely related species have developed in both directions, with marked vicariation (Prokhanov, 1949) (Maps 7, 8, and 9) and parallel evolution, from xerophytic thermophytes towards mesophytic and hygrophytic mesotherms and microtherms. Ser. *Esulae* Prokh. is an expression of eastward migration (Map 7). Eight species of this series are distributed in the zone southern Russia — Central Asia — western Siberia. Only one species, *E. esula* L., has penetrated westwards. To a certain extent a similar regularity is observed in ser. *Virgatae* Prokh. (Map 8), the study of which we owe chiefly to Prokhanov (1933, 1949). Seven species, viz. *E. uralensis* Tisch., *E. pamirica* Prokh., *E. tsuiensis* (Prokh.) Serg., *E. cyrtophylla* Prokh., *E. guntensis* Prokh., *E. jaxartica* Prokh., *E. subcordata* C. A. M. out of the 13 species known are endemic in central Asia and western Siberia (Map 8).

Subsect *Patellares* Prokh. occupies a special place in the elucidation of the genesis of sect. *Esula* (Map 10). Fifteen species are known; all are chamaephytes with \pm laethery, evergreen leaves; they occur in rocky or forest habitats chiefly in the eastern Mediterranean, often reaching altitudes of 2000 to 3000 m. All are rather close morphologically and their discrimination is frequently difficult. The coalescence of the bracteal leaves and the fact that there are two types of stem leaves, rosette leaves at the base and the leaves sustaining the flower stalks, are characteristic.

Two groups of vicarious species may be distinguished in subsect. *Patellares*: (1) a south Mediterranean group, composed of more thermophilous, more xerophilous and heliophilous species: *E. characias* L., *E. melapetala* Gasp., *E. sibthorpii* Bois., *E. wulfenii* Hoppe, *E. heldreichii* Orph., and *E. lycia* Boiss., and (2) a north Mediterranean group, composed of relatively more microtherm, more mesophilous and sciophilous species: *E. amygdaloides* L., *E. semiperfoliata* Viv., *E. semiverticillata* Hall., *E. glaberrima* C. Koch, *E. macroceras* Fisch. & Mey., *E. rumicifolia* Boiss., *E. kotschyana* Fenzl., and *E. macrostegia* Boiss. The chief species in the first group is *E. characias*, and in the second *E. amygdaloides*. It should be pointed out that out of the six species found in the Balkan Peninsula, three are endemic.

Rather essential problems remain unsolved, viz. the origin of and relationship between



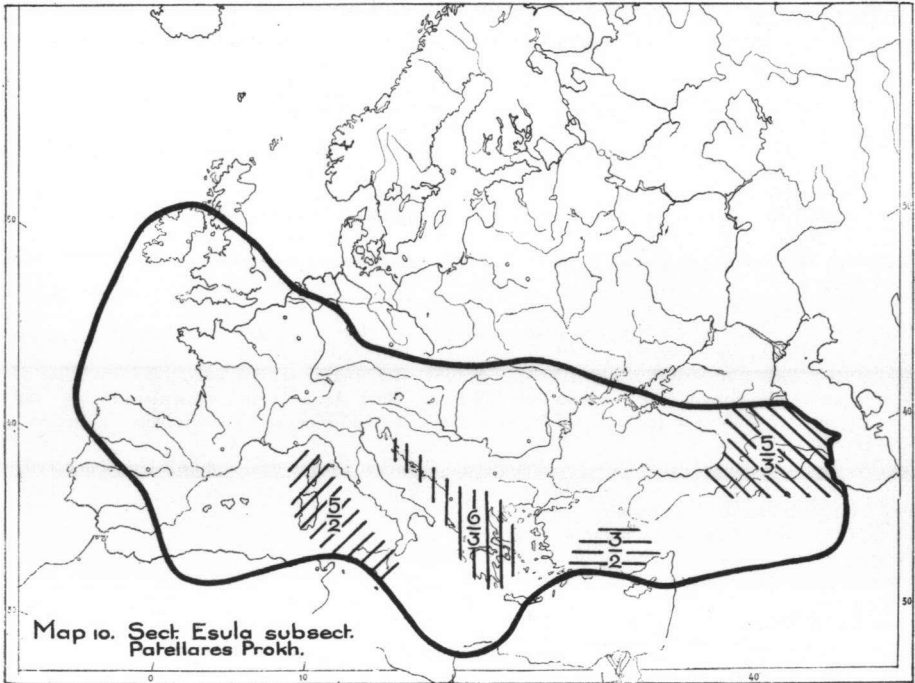
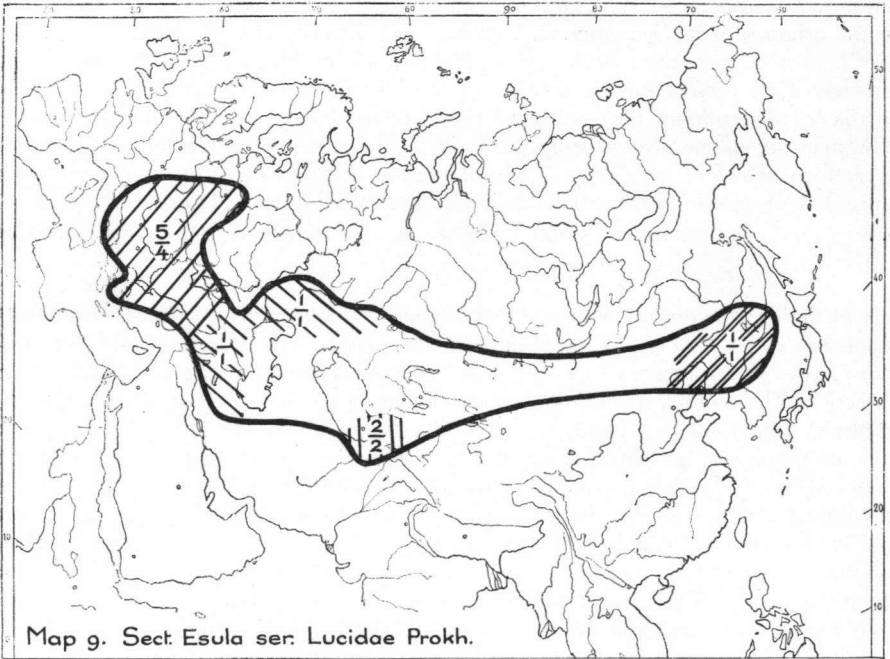


subsect. *Sieboldianae*, subsect. *Patellares*, and subsect. *Esulae* within sect. *Esula*, as well as the origin of sect. *Cymatospermum* Prokh., sect. *Dematra* (Raf.) Prokh., sect. *Lathyris* Godr., sect. *Herpetorrhiza* Prokh., sect. *Holophyllum* Prokh., etc. Also the problem of the age of the present Eurasian species of the subgenus remains rather obscure, as well as that of determining the geological epoch of its development in Europe and Asia. The majority of the now existing perennial Mediterranean and Central Asiatic species were formed before the *Oligocene*; the migration of subg. *Esula* in the Mediterranean must have begun still earlier (Kirchheimer, 1957; Nikitin, 1957; Dorofeev, 1955, 1956a, 1956b, 1959; Szafer, 1954; C. and E. M. Reid, 1908; C. Reid, 1882, 1899; Reid and Chandler, 1923).

Concluding, the origins of subg. *Esula* should be sought in the tree-like forms of subg. *Euphorbia* which have given rise to subsect. *Pachycladae*, sect. *Murtekias*, and sect. *Tulocarpa* in the Macaronesian region. The migration of the latter two sections had an eastern direction. The ecological evolution of the subgenus proceeded from xerophytes, phanerophytes, chamaephytes, heliophytes, and thermophytes to mesophytes, hygrophytes, hemicyptophytes, geophytes, therophytes, sciophytes, mesotherms, and microtherms. This evolution developed parallel in the individual sections and taxa of lower rank, reaching different degrees of hygrophytism and microthermism. The perennial representatives of the subg. *Esula* differentiated into five biological types best meeting the varied ecological conditions of Eurasia: phanerophytes, chamaephytes, hemicyptophytes, geophytes, and therophytes. Historically, the group of phanerophytes is the oldest. Only two sections, *Tulocarpa* and *Murtekias*, comprise species of this type, which contain also the most numerous hemicyptophytes. The following chief centres of species formation of the subgenus were: the western Mediterranean, Carpathians to Balkan, Asia Minor, Caucasia, Iran, the Eurasian steppe, Central Asia, the Altai-Tyanshan, and the Himalayas.

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