Diversity of the genus *Euphorbia* (Euphorbiaceae) in SW Asia

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List of Publications

1. Pahlevani AH, Akhani H, Liede-Schumann S. Diversity, endemism, distribution and conservation status of *Euphorbia* (Euphorbiaceae) in SW Asia. Submitted to the *Botanical Journal of the Linnean Society*. (Revision under review).

2. Pahlevani AH, Liede-Schumann S, Akhani H. 2015. Seed and capsule morphology of Iranian perennial species of *Euphorbia* (Euphorbiaceae) and its phylogenetic application. *Botanical Journal of the Linnean Society* 177: 335–377.

3. Pahlevani AH, Feulner M, Weig A, Liede-Schumann S. 2017. Molecular and morphological studies disentangle species complex in *Euphorbia* sect. *Esula* (Euphorbiaceae) from Iran, including two new species. *Plant Systematics and Evolution*

4. Pahlevani AH, Riina R. 2014. Synopsis of *Euphorbia* subgen. *Esula* sect. *Helioscopia* (Euphorbiaceae) in Iran with the description of *Euphorbia mazandaranica* sp. nov. *Nordic Journal of Botany* 32: 257–278.

Declaration of contribution to publications

The thesis contains four research articles. The major parts of the underlying studies were carried out by myself at the University of Bayreuth and partly in the Department of Botany at Iranian Research Institute of Plant Protection. Most phylogenetic and statistics analyses were carried out with support of Prof. Dr. Sigrid Liede-Schumann. All manuscripts in this thesis have been prepared under consideration of the comments of all coauthors.

1st publication

Pahlevani AH, Akhani H, Liede-Schumann S. Diversity, endemism, distribution and conservation status of *Euphorbia* (Euphorbiaceae) in SW Asia. Submitted to the *Botanical Journal of the Linnean Society*.

Authors' contribution: The idea and concept of the manuscript were developed by the first author with guidance of Prof. Dr. H. Akhani and Prof. Dr. S. Liede-Schumann. About 22,000 specimens in several herbaria (B, BM, E, FUMH, HSBU, IRAN, K, M, MSB, PR, SAV, TARI, TUH, UBT, W, WU) have been studied by the first author. Coordinates of all studied specimens have been extracted and transferred to the dataset by the first author. Several periods of field work have been carried out in Iran by the first author. Drawing The production of 243 maps, analysis of species richness, evaluation of conservation status of the endemic and subendemic species were exclusively performed by A.H. Pahlevani. Four new species, 13 new records, three synonyms were reported and described by A.H. Pahlevani. The manuscript was written by the A.H. Pahlevani taking into account the useful comments of Prof. Dr. S. Liede-Schumann and Prof. Dr. H. Akhani.

2nd publication

Pahlevani AH, Liede-Schumann S, Akhani H. 2015. Seed and capsule morphology of Iranian perennial species of *Euphorbia* (Euphorbiaceae) and its phylogenetic application. *Botanical Journal of the Linnean Society* 177: 335–377.

Authors' contribution: The idea and concept of the manuscript were developed by the first author. Most parts of this manuscript were developed by A.H. Pahlevani, including identification and selection of the specimens used for the work, selection of the characters to be studied, photographing all seeds and capsules, carrying out all measurements, lab work, developing a key based on solely seed and capsule morphology both for the sections and all species, as well as describing two new species. Phylogenetic analysis was completed by the first author under the profound support of Prof. Dr. S. Liede-Schumann. SEM photography was supported by Prof. Dr. H. Akhani. The manuscript was prepared by A.H. Pahlevani taking into account the useful comments of Prof. Dr. S. Liede-Schumann and Prof. Dr. H. Akhani.

3rd publication

Pahlevani AH, Feulner M, Weig A, Liede-Schumann S. 2017. Molecular and morphological studies disentangle species complex in *Euphorbia* sect. *Esula* (Euphorbiaceae) from Iran, including two new species. *Plant Systematics and Evolution*

Authors' contribution: The idea and concept of the manuscript were developed by the A.H. Pahlevani under guidance of Prof. Dr. S. Liede-Schumann. The collection of plant material was conducted by A.H. Pahlevani. ISSR Laboratory work was conducted in Dr. A. Weig laboratory. ISSR data analysis was done by A.H. Pahlevani and Dr. M. Feulner under supervision of Dr. A. Weig and Prof. Dr. Liede-Schumann. Phenetic analysis (PCA) was carried out by A.H. Pahlevani. Preparation of a key to the species, typification and taxonomic evaluation, as well as the description of two new species were carried out by A.H. Pahlevani. The manuscript was prepared by A.H. Pahlevani under recognition of the comments of all coauthors, especially the useful comments of Prof. Dr. S. Liede-Schumann.

4th publication

Pahlevani AH, Riina R. 2014. Synopsis of *Euphorbia* subgen. *Esula* sect. *Helioscopia* (Euphorbiaceae) in Iran with the description of *Euphorbia mazandaranica* sp. nov. *Nordic Journal of Botany* 32: 257–278.

Authors' contribution: The idea and concept of the manuscript were developed by A.H. Pahlevani. Field work, visits to the herbaria housing the studied specimens, all taxonomic treatments, key construction and description of new species, have been undertaken by the first author. Typification was carried out by A.H. Pahlevani and R. Riina. Lastly, the paper was written by A.H. Pahlevani with the useful comments of R. Riina.

Content

Summary

Euphorbia is one of the three most species-rich genera of flowering plants with more than 2000 species occurring in all temperate and tropical regions. They occupy a wide range of habitats and exhibit great diversity in growth forms. In habit, the species vary from small ephemerals to various forms of herbaceous annuals or perennials, cushion-forming subshrubs, large shrubs, small trees and cactus-like succulents. After recent molecular studies, *Euphorbia* has been divided into four monophyletic subgenera including, *Athymalus* (c. 150 species), *Chamaesyce* (c. 600 species), *Esula* (c. 500 species) and *Euphorbia* (c. 800 species). Taxonomy of *Euphorbia* is extremely difficult due to the species richness accompanied by a cosmopolitan distribution, the extreme morphological plasticity among certain species and convergent evolution of certain morphological characters. As a consequence, the circumscription of the *Euphorbia* species especially in SW Asia remained unresolved.

To resolve phylogenetic and taxonomic complex groups and uncertainties among the species of the genus *Euphorbia*, this thesis aims 1) to complete phylogenetic and phylogeographic study of the genus (subgen. *Esula*) in SW Asia, by integrating hitherto unanalyzed species in the existing phylogeny using the markers ITS and *ndhF*, 2) to study seed and capsule morphology of the Iranian species of *Euphorbia* and study their evolution by plotting them on the molecular phylogenetic tree, 3) to evaluate the genotypic diversity of some complex, rare or endemic Iranian *Euphorbia* species (section *Esula*) using ISSR DNA fingerprinting, 4) to trace diversification, endemism, distribution and conservation status of the genus *Euphorbia* in SW Asia, 5) to update the taxonomic treatment of the two largest sections, *Helioscopia* and *Esula* of the subgenus *Esula* in Iran.

The phylogenetic relationships of Iranian species based on internal transcribed spacer (ITS) nuclear and *ndhF* plastid regions are updated and used for the characterization of the synapomorphies of each clade in subgenus *Esula*. It is confirmed that there are 13 sections in subgenus *Esula* in Iran. The presence or absence of granulate elements on seed surfaces represents a phylogenetically important trait for section delimitation. The capsule surface is synapomorphic for several sections, including *Helioscopia* (tuberculate-verrucose), *Myrsiniteae* (vesiculate) and *Esula* (granulate) and seed shape is

synapomorphic for sections *Helioscopia* (ellipsoidal), *Myrsiniteae* (ovoid-quadrangular) and *Herpetorrhizae* (pseudo-hexahedral). However, reversals have also taken place in some features, including capsule surface (*E. mazandaranica*, *E. altissima*) and seed shape (*E. densa*, *E. aleppica*).

Evaluation of diversity, endemism, distribution and conservation status of the genus *Euphorbia* is based on the study of specimens in herbaria rich in SW Asian material and benefits from field excursions in Iran. A total of 22,000 specimens from 20 countries (Afghanistan, Armenia, Azerbaijan, Cyprus, Egypt, Iran, Iraq, Israel/Palestine, Jordan, Kuwait, Lebanon, Oman, Pakistan, Qatar, Saudi Arabia, Syria, Turkey, Turkmenistan, UAE, Yemen) have been studied, including almost all type specimens reported from the studied region. Genus *Euphorbia* in SW Asia (area of study) has 249 taxa of all four existing subgenera comprising, *Athymalus* (13 taxa), *Chamaesyce* (33 taxa), *Esula* (182 taxa) and *Euphorbia* (21 taxa) with three, six, 19 and two sections respectively. Among 20 studied countries in the region, Turkey, Iran and Syria with 103, 90 and 50 species are the richest countries, respectively. The highest number of endemics occurs in Iran, Turkey and Yemen with 19, 13 and eight taxa respectively. Analysis of diversity indicated that the richest places of *Euphorbia* in the extended SW Asia were eastern part of the Mediterranean region (<32 taxa), Alborz, Zagros (Iran) and Anti-Taurus (S Turkey) (<25 taxa) mountains are the second richest areas followed by SW and W Yemen, Lesser Caucasus, N Turkey and west Himalaya (c. 20 taxa). 96 endemic taxa in the region were evaluated against the IUCN Red List categories and criteria and a total of 54 endemic taxa were globally classified as threatened comprising 21 Critically Endangered, 16 Endangered and 17 Vulnerable taxa.

Based on morphological and molecular works, nine species new to science, 15 new records for several countries in the studied region and six synonyms are recognized. Two largest sections *Esula* and *Helioscopia* have been revised in Iran. Description, typification, synonyms, data on distribution and habitat, key to species and pertinent comments are given.

Zusammenfassung

Euphorbia ist eine der drei artenreichsten Blütenpflanzengattungen, deren mehr als 2000 Arten weltweit in allen temperaten und tropischen Gebieten vorkommen. Diese besiedeln verschiedene Habitate und zeigen eine große Vielfalt in ihren Wuchsformen. Die kurzlebigen, annuellen oder ausdauernden Gewächse variieren im Habitus von kissenförmigen Zwergsträuchern, großen Sträuchern und kleinen Bäumen bis hin zu Stammsukkulenten. DNA-Sequenzanalysen unterstützen die Unterteilung in vier monophyletische Subgenera, subgen. *Euphorbia* (ca. 800 species), subgen. *Athymalus* (ca. 150 species), subgen. *Chamaesyce* (ca. 600 species) and subgen. *Esula* (ca. 500 species). Die Taxonomie von *Euphorbia* ist außerordentlich schwierig wegen des Artenreichtums, der kosmopolitischen Verbreitung, der extremen morphologischen Plastizität innerhalb vieler Arten und der konvergenten Evolution verschiedener morphologischer Merkmale. In der Folge blieb die Umschreibung und Abgrenzung vieler *Euphorbia*-Taxa, besonders der südwestasiatischen, unvollständig.

Um die phylogenetischen und komplexen taxonomischen Unsicherheiten auf Artniveau innerhalb von *Euphorbia* aufzuklären, standen die folgenden Aspekte im Fokus dieser Arbeit: 1) Vervollständigung der Phylogenie und Phylogeographie des subgen. *Esula* in SW Asia mit Hilfe von Neuaufsammlungen und unter Einschluß aller bislang nicht analysierter Taxa und molekularer Marker wie ITS und *ndhF*, 2) Untersuchungen zur Samen- und Kapsel-Morphologie der iranischen *Euphorbia*-Arten sowie ihrer Evolution 3) Evaluierung der genotypischen Diversität von schwierigen, seltenen oder endemischen *Euphorbia*-Arten (sect. *Esula*) Irans mit Hilfe des ISSR DNA fingerprinting, 4) Aufklärung von Diversifikation, Endemismus, Verbreitung und Schutzstatus der Gattung *Euphorbia* in SW-Asien, 5) Aktualisierung der taxonomischen Abhandlungen der zwei größten Sektionen im Iran, sectt. *Helioscopia* und *Esula* (subgen. *Esula*).

Die hier präsentierten molekularphylogenetischen Analysen unterstützen die Unterteilung des subgen. *Euphorbia* im Iran in 13 Sektionen. An- bzw. Abwesenheit granulöser Elemente auf den Samenoberflächen erweisen sich als phylogenetisch wichtiges Merkmal, das für die Abgrenzung von Sektionen geeignet erscheint. Merkmale wie Kapseloberflächen besitzen innerhalb mehrerer Sektionen synapomorphe Eigenschaften, so in den sectt. *Helioscopia* (tuberculat-warzig), *Myrsiniteae* (blasig) and *Esula*

(granulöse). Das trifft ebenso auf die Samenform in den sectt. *Helioscopia* (ellipsoid), *Myrsiniteae* (ovoid-quadrangular) and *Herpetorrhizae* (pseudo-hexahedral) zu. Allerdings haben auch Merkmalsumkehrungen stattgefunden, so z.B. bei der Samenform (*E. densa*, *E. aleppica*) oder Samenoberflächen (*E. mazandaranica*, *E. altissima*). Betrachtungen zu Diversität, Endemismus, Verbreitung und Gefährdung innerhalb von *Euphorbia* beruht auf dem Studium von umfangreichem Herbarmaterial und zahlreichen Exkursionen im Iran. Insgesamt wurden 22.000 Belege aus 20 Ländern untersucht: Afghanistan, Armenien, Aserbaidjan, Zypern, Ägypten, Iran, Irak, Israel/Palästina, Jordanien, Kuwait, Libanon, Oman, Pakistan, Katar, Saudi-Arabien, Syrien, Türkei, Turkmenistan, Vereinigte Arabische Emirate und Jemen. Die Gattung *Euphorbia* in SW-Asien umfaßt 249 Taxa aus allen vier Untergattungen mit subgen. *Athymalus* (13 Taxa), subgen. *Chamaesyce* (33 taxa), subgen. *Esula* (182 taxa) und subgen. *Euphorbia* (21 taxa), die zusätzlich in jeweils drei, sechs, 19 und zwei Sektionen untergliedert sind. Innerhalb des Untersuchungsgebietes der 21 Länder sind die Türkei mit 103, der Iran mit 90 und Syrien mit 50 Arten die artenreichsten Länder. Die meisten Endemiten finden sich im Iran (19), in der Türkei (13) und dem Jemen (8). Als Hotspots der *Euphorbia*-Diversität wurden die Ost-Mediterrane Region (ca. 32 Taxa), Alborz, Zagros (Iran) mit dem Anti-Taurus in der Türkei (ca. 25 Taxa), gefolgt von SW-Yemen, Caucasus, N-Türkei, W Himalaya (20 Taxa) identifiziert. 96 endemische Taxa in SW Asien wurden bezügliche der "IUCN Red List categories and criteria" abgeschätzt. Insgesamt 54 Taxa wurden global als bedroht eingestuft, davon 21 als „Critically Endangered", 16 als „Endangered" und 17 als „Vulnerable".

Auf der Grundlage der vorgelegten morphologischen und molekularen Untersuchungen konnten neun neue Arten beschrieben, 15 Erstnachweise für verschiedene Länder getätigt sowie sechs neue Synonyme erkannt werden. Die zwei größten Sektionen im Iran, sectt. *Esula* and *Helioscopia,* wurden taxonomisch revidiert. Umfangreiche Beschreibungen, Typifizierungen, Synonymien, Verbreitung und Standortinformationen sowie ein Bestimmungsschlüssel zu den Arten werden bereitgestellt.

1. General Introduction

Southwest Asia is one of the most important centers of diversity for many groups of flowering plants. Southwest Asia is limited to Asiatic Turkey (Anatolia), Syria, Lebanon, Israel/Palestine, Jordan, the Sinai Peninsula, Iraq, Iran, the southern part of Azerbaijan, Arabian Peninsula (Kuwait, Oman, Qatar, Saudi Arabia, UAE and Yemen) and Afghanistan. The total land area of the SW Asia is *c.* 7,078,670 km^2 (Boulos, *et al.*, 1994). This region is topographically diverse ranging from some very high points (more than 7,000 m) to the lowest one (-392 m) in the Hindu Kush and the Dead Sea respectively. The edaphic conditions also vary from sandy and gravelly deserts, calcareous soils, hammadas, clayey plains, fertile alluvial lowlands, and loess to extremely saline soils. The climate of the region is also extremely diverse, ranging from cool temperate to tropical. There are five main climates in the region including, Irano-Turanian, Mediterranean, Tropical, Temperate and Monsoon (Boulos *et al*., 1994; Djamali *et al*. 2011; Djamali *et al*., 2012). A few of the hottest points and hyper-arid areas of the earth occur (over 70ºC) in S of Iran (Lut desert), Saudi Arabia (Rub Al-Khali) and some very cold and permanent glaciers (below -50ºC) scatter in some high mountains such as Alborz, Zagros (in Iran), Hindu Kush and Himalaya (in Afghanistan and Pakistan), as well as Anti-Taurus (in Turkey) mountains (Ferrigno, 1991). From the geological point of view, SW Asia was covered by the Tethys Sea at the beginning of the Mesozoic (*c* 245 million years BP) which caused the formation of thick layers of sedimentary rocks the region. Since the African plate began to drift northwards toward Eurasia during the Miocene (20-14 million years BP), the sedimentary rocks were lately uplifted to form the existing mountain chains (Boulos *et al*., 1994). Aridity and salinity characteristic for most parts of the lowland areas especially in the south on the one hand, and presence of mountains and steppes in the north and central parts, on the other hand, caused drought-resistant, salt-tolerant and harshness-tolerant species to occupy the region in several different kinds of vegetation. Topographical, bioclimatical, edaphical, geological and ecogeographical complexity and heterogeneity as well as human influence together make the studied region one of the largest and most important centers of speciation both for mountain and desert flora elements, covering several centers of plant diversity, endemism and hot spots in the Old World (Zohary, 1963; Takhtajan, 1986;

Boulos *et al*., 1994; Nieto Feliner, 2014). Among the 34 major hotspots of the world, five partly or completely occur in the study region (Table 1), comprising Irano-Anatolian, a part of Horn of Africa, southern part of the Caucasian region, Mediterranean Basin covering only eastern and southeastern part of the Mediterranean Sea as well as Himalaya (Table 1) (Mittermeier *et al*., 2004). There are more than 24,000 species of the vascular plants in the region of which over 7300 species are endemics distributed mostly in the Irano-Turanian and E Mediterranean regions.

Table 1 The hotspots of SW Asia with their geographical areas, percentage remaining habitat and predominant biome type based on Mittermeier *et al*. (2004).

Hotspot	Remaining habitat (%)	Geographical area in SW Asia	Predominant biome type
Irano-Anatolian	15	Central and eastern Turkey, northeastern Iraq, northern and western Iran, northern Kopet Dagh range in Turkmenistan and Iran	Temperate broadleaf and mixed forests
Caucasus	27	Armenia, Azerbaijan, northeastern Turkey, a part of northwestern Iran	Temperate broadleaf and mixed forests
Horn of Africa	5	The southern coastal parts of the Arabian Peninsula	Tropical and subtropical grasslands, savannas, and shrublands

Himalaya	25	Northern Pakistan, the most northeastern Afghanistan	Tropical and subtropical coniferous forests; montane grasslands and shrublands
Mediterranean Basin	5	Cyprus, Lebanon, western Jordan, western Syria, southern Turkey, Israel/Palestine and northern Egypt	Mediterranean forests, woodlands, and shrubs

The Euphorbiaceae *s.l.* family is composed of about 340 genera and over 8000 species (Webster, 1994; Radcliffe-Smith, 2001; Wurdack *et al*. 2004) which are distributed mainly in the tropics in several types of vegetations and habitats. It is one of the most complex, large and diverse families of angiosperms. Recently it has been divided into four families, according to the most recent classification system based on molecular phylogeny (APG II, 2003; APG IV, 2016), including Euphorbiaceae *s.s.* comprising the subfamilies with uniovulate ovary locules (Euphorbioideae, Crotonoideae and Acalyphoideae) and harbouring c. 6300 species in 247 genera (Wurdack *et al*., 2005), Phyllanthaceae with c. 2000 species in 54 to 60 genera, depending on the author, comprising the former subfamily Phyllanthoideae (biovulate ovary locules), Picrodendraceae, comprising the former Oldfieldioideae (biovulate ovary locules) with 80 species in 24 genera and Putranjivaceae, also with biovulate ovary locules with c. 200 species in two genera, *Drypetes* Vahl and *Putranjiva* Wall. (APG II, 2003; APG IV, 2016). Euphorbiaceae *s.s.* and the other families segregated from Euphorbiaceae *s.l.* are included in order Malpighiales (APG II, 2003; Wurdack *et al.*, 2004; APG III, 2009; Wurdack & Davis, 2009). The tree largest genera of the family Euphorbiaceae *s.s.* are *Euphorbia* L. (Euphorbioideae), *Croton* L. (Crotonoideae) and *Acalypha* L. (Acalyphoideae) with about 2100, 1200 and 600 species respectively (Webster, 1994; Radcliffe-Smith, 2001; Carneiro-Torres *et al.*, 2011). *Euphorbia* is the second largest

genus of flowering plants (Frodin, 2004) with over 2100 species occurring in all temperate and tropical regions (Govaerts *et al*., 2000). Members of this genus are adapted to a wide range of habitats, occurring from the rainforest to very hot and dry deserts or severe environments in alpine regions (Pearcy and Troughton 1975; Riina *et al*., 2013). The morphological diversity in *Euphorbia* varies from ephemeral species to up to 20-meter tall phanerophytes (Horn *et al*. 2012). *Euphorbia* species occur in many biotopes and, in some communities, play a major role as dominant species, in particular in disturbed and severely grazed mountain steppes (Pahlevani & Akhani, 2011). The occurrence of carcinogenic compounds, skin irritants, tumor promoters, anti-cancer agents and recently discovered agents for overcoming multidrug resistance (Hohmann *et al*., 2003; Valente *et al*., 2004; Corea, *et al.*, 2005) is an incentive for detailed studies. Some species are also known as hyper-accumulators of heavy metals and are appropriate candidates in phytoremediation (Chehregani & Malayeri, 2007, Chehregani *et al.,* 2009, Nouri *et al*., 2010). Many species of the genus occur as noxious weeds and invasive plants in different types of cultivated areas such as pastures, rangelands and fields, and are hosts for certain pests and diseases (Tedford & Fortnum, 1988; Tanveer *et al*., 2010; Pahlevani, 2007). Likewise, some endemic species are rare and restricted to few individuals in their habitats and sometimes only known from a single locality (Kilian *et al.*, 2006; Fayed & Al-Zahrani, 2007; Pahlevani *et al*., 2011) (Fig. 1). Remarkably, it is the sole genus with all known photosynthetic pathways, including C_3, C_4, CAM as well as C_2 system that represents an early stage of C_3 to C_4 transition (Webster *et al*., 1975; Batanouny *et al*., 1991; Sage *et al*., 2011; Yang *et al*., 2012). Recent molecular studies have revealed four main evolutionary lineages within *Euphorbia*, corresponding to four monophyletic subgenera: *Euphorbia* (c. 800 species), *Chamaesyce* Raf. (c. 600 species), *Athymalus* Neck. ex Reichb. (c. 150 species) and *Esula* Pers. (c. 500 species) (Steinmann & Porter, 2002; Bruyns *et al*., 2006; Zimmermann *et al*., 2010; Horn *et al*. 2012). Following molecular infrageneric studies, sectional classifications have been developed for all four subgenera (Yang *et al*. 2012; Dorsey *et al*. 2013; Peirson *et al*. 2013; Riina *et al*. 2013; Peirson *et al*. 2014). Among the countries of SW Asia, Turkey and Iran are the most species-rich places with about 8650 and 7500 species respectively. The number of *Euphorbia* species is also highest in Turkey and Iran mostly occurred in subgenus *Esula*

(Pahlevani & Akhani, 2011). Southwest Asia comprises all four subgenera (Yang *et al*. 2012; Dorsey *et al*. 2013; Peirson *et al*. 2013; Riina *et al*. 2013). Based on a review of the published literature in the studied regions (Table 2) as well as herbarium specimens deposited in the SW Asian species-rich herbaria, it was found that there are many misidentification and dislocations in the members of the genus *Euphorbia*. Notably, most floras concerned to the SW Asia have been published 3 to 10 decades ago, and were based on a much fewer number of specimens (Table 2).

As SW Asia harbor several endemic, endangered and localized *Euphorbia* species, especially in subgen. *Esula,* there are many complex group within and among populations and other status levels. The high extinction risk of small or isolated populations is a very severe problem of the current biodiversity crisis. Small populations face increased risks from effects of environmental variation, demographic stochasticity and reduced genetic variation (Menges, 1990, Fischer & Stöcklin, 1997, Fischer & Matthies, 1998, Paschke *et al.*, 2002). On the other hand, correct taxonomic classification is a vital component to implementing conservation management practices and may eliminate erroneous decisions that could otherwise occur (Frankham *et al.*, 2002, Morden & Gregoritza, 2006).

Fig. 1. Four Iranian endemic species of *Euphorbia* (subgenus *Esula*): A. ***E. connata*** (section *Calyptratae*); B. *E. ferdowsiana* (section *Sclerocyathium*), photo by Joharchi; C. *E. erythradenia* (section *Pithyusa*); D. *E. hebecarpa* (section *Esula*)

Table 2 Published flora treatments of the genus *Euphorbia* in the extended SW Asia including, year, authors, number of taxa and countries covered by flora

No.	Title	Country (s)	No. taxa	Year	Author (s)
1	Flora Iranica	Afghanistan, S Azerbaijan, Iran, W Pakistan, S Turkmenistan	98	1964	Rechinger KH, Schiman-Czeika H
2	Vascular plants of Afghanistan	Afghanistan	45	2013	Breckle SW, Hedge IC, Rafiqpoor MD
3	Flora Azerbajdzhana	Azerbaijan	37	1955	Karjagin II
4	Flora of Cyprus	Cyprus	25	1985	Radcliffe-Smith A
5	A manual flora of Egypt	Egypt	19	1912	Müschler R
6	Flora of Egypt	Egypt	41	2000	Boulos L
7	Flore de l' Iran	Iran	74	1949	Parsa A
8	Flora of Iraq	Iraq	44	1980	Radcliffe-Smith A
9	Flora of Lowland Iraq	Iraq	25	1964	Rechinger KH
10	Flora Orientalis	Afghanistan, Armenia, Baluchistan of Pakistan, Egypt, Greece, plateau of Iran, Syria, parts of Iraq and Turkey, a part of Turkmenistan	131	1879	Boissier E
11	Flora of Pakistan	Pakistan & Kashmir	52	1986	Radcliffe-Smith A
12	Flora Palestina	Israel, Palestine	34	1972	Zohary M
13	Flora of the Kingdom	Saudi Arabia	39	2001	Chaudhary SA

	of Saudi Arabia				
14	Nouvelle Flore du Liban et de la Syrie	Lebanon, Syria	52	1986	Mouterde PSJ
15	Flora of Syria, Palestine & Sinai	Syria, Israel, Palestine, a part of Egypt	44	1896	Post GE
16	Flora Turkmenistan	Turkmenistan	27	1950	Nikitin VV
17	Flora of Turkey	Turkey & E Aegean Islands	104	1982	Radcliffe-Smith A
18	Flora of the USSR	Soviet Union	159	1974	Prokhanov YI
19	A handbook of the Yemen flora	Yemen	28	1997	Wood JRI

1. 1. Aims and scope of the study

Using phylogenetic and taxonomic methods, this thesis investigates the SW Asian *Euphorbia* species with focus on the Iranian ones. Molecular and morphological investigations were carried out to infer the relationships among sections and species of the genus *Euphorbia* in SW Asia with emphasis on the largest subgenus *Esula*. So far, there is no comprehensive study on the genus *Euphorbia* in the whole SW Asia, however, some sporadic reports are available. Because SW Asia is one of the most important regions of biodiversity and centers of endemism of the genus, these gaps of knowledge have to be filled.

The aims of my thesis are therefore:

1. To trace diversity, endemism, distribution and conservation status of the genus *Euphorbia* in SW Asia.

2. To complete phylogenetic study of the genus, and especially, of subgenus *Esula*, in Iran, by integrating hitherto unanalyzed species in the existing phylogeny.

3. To study seed and capsule morphology of the species of *Euphorbia* in Iran and study their evolution by plotting the characters on the molecular phylogenetic tree.

4. To perform a revision of the sections *Helioscopia* and *Esula* (subgen. *Esula*) in Iran with informative key, description, typification and nomenclatural treatments.

5. To evaluate the genotypic diversity of some complex, rare or endemic Iranian *Euphorbia* species (section *Esula*) using ISSR DNA fingerprinting.

2. Synopsis

2.1. Material & Methods

2.1.1. Diversity and distribution analyzing of SW Asian *Euphorbia* (Publication 1)

In this part of study, we examined all *Euphorbia* species of 20 countries including, Afghanistan, Arabian Peninsula (Kuwait, Oman, Qatar, Saudi Arabia, UAE and Yemen), Armenia, Azerbaijan, Cyprus, Egypt, Iran, Iraq, Israel/Palestine, Jordan, Lebanon, Pakistan, Syria, Turkey and Turkmenistan as extended SW Asia (Fig. 1; Publication 1). The study area lies between 13° 05′ and 42° 09′ northern latitudes and 24° 40′ and 77° 36′ eastern longitudes bounded in the north by the Black Sea, Caspian Sea, Georgia, Uzbekistan, and Tajikistan (northeast), in the south by the Arabian Sea, in the west by the Mediterranean Sea and in the east by the India as well as Himalaya mountains (Fig.1; Publication 1). The study is mainly based on examination of a total of *c.* 22,000 plant specimens deposited in the herbaria B, BM, E, K, M, MSB, PR, PRC, SAV, UBT, W, WU, which are particularly rich in SW Asian material, and Iranian herbaria FAR, FUMH, IRAN, HSBU, TARI, TUH (abbreviations according to Thiers, 2016) as well as many Iranian local herbaria in Kordestan, Kerman, E. Azerbaijan, W Azerbaijan, Kermanshah, Esfahan, Hormozgan Provinces and Herbarium H. Akhani (Halophytes and C_4 Plants Research Laboratory of the school of Biology, University of Tehran). Notably, many specimens of G and P herbaria also have been studied online. As there are many misidentifications and errors in this group, all herbarium specimens have been studied and identified. All information from the specimen's label was recorded. Among the studied specimens there are some duplicates spread in the above-mentioned herbaria and several imprecise information on sampling location which were discarded. There are also some specimens from the other countries out of the studied region (extended SW Asia) which have been ignored in this work. All GPS coordinates were recorded, or, in the case of absence of coordinate data, were inferred from locality descriptions and geo-referenced using Microsoft Encarta 2008, Google Earth or, in a few cases, maps. In few cases, further localities from pertinent literature are used from standard floras or articles (Radcliffe-Smith, 1982, 1985, 1986; Mouterde, 1986; Lavranos, 1999; Lavranos, 2011;

Hand, 2015; Genc & Kültür, 2016). All geo-referenced records were used to provide individual maps using DMAP software (Morton, 2009). A total of *c.* 11,000 geo-referenced records were used to prepare and analyze species richness using diversity analysis tools in DIVA-GIS 7.3 software (http://WWW.diva-gis.org/; Hijmans *et al*., 2001) comprising alpha diversity (species richness).

2.1.2. Assessment of endemism and conservation status (Publication 1)

Endemic and subendemic taxa were evaluated against the categories and criteria of the International Union for the Conservation of Nature (IUCN) for conservation status. Taxa with adequate and reliable data were classified under three threatened categories, Critically Endangered (CR), Endangered (EN) and Vulnerable (VU), as well as two non-threatened categories, Near Threatened (NT) and Least Concern (LC). The category Data Deficient (DD) was used to taxa with inadequate information. In order to estimate the threat status, 96 endemics and subendemics of the genus *Euphorbia* have been evaluated using GeoCat a browser-based tool that accomplishes rapid geo-spatial analysis to ease the process of Red Listing taxa (http://geocat.kew.org/; Bachman *et al*., 2011). They were applied to categorize the threat status (IUCN, 2011) in the form of the extent of occurrence (EOO) and area of occupancy (AOO) in criterion B. To estimate the AOO, the sliding scale of 1/10th of the maximum distance between any pair of points, calculated by distance tool in Microsoft Encarta 2008, was applied in GeoCat. All endemic and subendemic taxa with threatened status have been mapped in DIVA-GIS environment.

2.1.3. Molecular methods (Publication 2, 3)

2.1.3.1. ITS and *ndhF* (Publication 2, 3)

In order to conduct a molecular phylogenetic study of *Euphorbia* subgenus *Esula*, a total of 273 species (283 taxa) have been sampled within subgenus *Esula*, aiming to cover most of the previously recognized infrasubgeneric taxonomic groups and the geographical distribution of the subgenus with contribution of the expert team of *Euphorbia*. Of the 283 taxa used in this study (Riina *et al*., 2013), A.H. Pahlevani

contributed 48 accessions representing 45 species from Iran. Later 23 more accessions representing 12 species of subgenus *Esula* were added to the molecular analysis.
The DNA samples were obtained either from silica gel collections or from leaf samples taken from herbarium specimens (IRAN, M, MSB, TARI, W, WU). Total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following manufacture's instructions, but adjusted by applying 5 µL of proteinase K at 20 mg mL^{-1} to deactivate the secondary compounds that occur in the genus (Barres *et al*., 2011). Two molecular markers, the Internal Transcribed Spacer of nrDNA (ITS) and chloroplast *ndhF* gene were sequenced. For total DNA isolation and amplification of the ITS region, we followed the protocol described in Kryukov *et al*. (2010), Barres *et al*. (2011), Frajman & Schönswetter (2011), Yang & Berry (2011) and Riina *et al*. (2013).

2.1.3.2. ISSR genomic fingerprinting (Publication 3)

Seven populations of two known species of *Euphorbia* section *Esula* (*E. buhsei* Boiss., three populations; *E. osyridea* Boiss., two populations) and two newly described species (*E. austro-iranica* Pahlevani, one population; *E. khabrica* Pahlevani, one population) as well as a population of *E. mazandaranica* Pahlevani (section *Helioscopia*) as outgroup were sampled from seven Iranian provinces (Table 3; Publication 3). The specimens were sampled either from the field or from herbaria. For each population, ten individuals were collected, five of which were randomly selected. Whole plants and leaf tissues from each individual were collected. Leaves were placed in sealed plastic bags with silica gel for immediate drying and chilled (-30ºC) until DNA was extracted. Total genomic DNA was isolated from dried leaf sections (up to 5 mm in square) using the NucleoMag™ 96 Plant extraction kit (Machery-Nagel, Düren, Germany) and the FastPrep-24™ Instrument (MP Biomedicals, Santa Ana, CA) as described in Feulner *et al*. (2013).

For inter-simple sequence repeat (ISSR) analysis (Gupta *et al*. 1994), an initial set of 31 SSR primers (University of British Columbia primer set #9, Li *et al*. 2006) was analyzed by agarose gel electrophoresis for the appearance of polymorphic fragment patterns using genomic DNA from five selected plant samples. To find clear and reproducible bands all primers were first evaluated based on band quality (clear, rather clear, unclear, negative and smear) and quantity (below 600 bp, between 600-1000 bp

and above 1000 bp) using the GeneTools software (Synoptics Ltd.). Primers producing bands below 600 bp and between 600-1000 bp were considered superior to primers producing bands above 1000 bp. Six primers were selected for subsequent analysis, carrying a fluorescent label at the 5'-end. ISSR fragments were amplified using 1 µl of purified genomic DNA, 10 µM SSR primer and the KAPA3G Plant Kit (Peqlab, Erlangen, Germany) in a 12.5 µl reaction volume (PCR profile: initial activation 95°C/3 min, followed by 35-40 cycles at 95°C /30 s, primer-specific annealing temperature/30 s, extension at 72°C /30 s, followed by a final extension step at 72°C/5 min). A combination of three ISSR reaction products was separated by capillary electrophoresis (CEQ8000 Genetic Analysis System, Beckman-Coulter, Krefeld, Germany; now: ABSciex, Darmstadt, Germany) and scored using GeneMarker 1.95 (SoftGenetics, USA).

2.1.4. Phylogenetic analysis (Publication 2, 3)

2.1.4.1. ITS and *ndhF* analysis (Publication 2, 3)

Sequences were edited and pre-aligned using CodonCode Aligner v.3.7.1 and subsequently adjusted manually. Sequence alignments were performed with Mesquite v.2.75 (Maddison & Maddison, 2011) using the OPAL package (Wheeler & Kececioglu, 2007) with the BlastAlign Web Interface version 1.0 (Belshaw & Katzourakis, 2005). RAxML (Stamatakis *et al*., 2008) was used to conduct maximum likelihood (ML) phylogenetic analyses on the ITS, *ndhF*, and combined ITS and *ndhF* datasets. The nucleotide substitution model was set to GTR + γ as recommended by the RAxML manual; 100 ML bootstrap replicates were performed, followed by a thorough search for the best tree. For Bayesian (BI) analysis of ITS, *ndhF*, and the combined dataset, we used MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), using the nucleotide substitution model GTR + I + γ for ITS and *ndhF* following Riina *et al*. (2013). The process included four runs with four chains each run for 10,000,000 generations, saving one tree every 1000 generations. A relative burnin of 0.5 was set so that only the last 5000 trees of each run were used to estimate the 50% majority rule consensus tree and the Bayesian posterior probabilities.

2.1.4.2. ISSR data analysis (Publication 3)

A neighbor joining (NJ) analysis of the presence-absence (presence = 1 and absence = 0) matrix was conducted (Nei-Li distance), followed by bootstrap (BS) analysis after internode rooting with 1,000 replicates using the program TREECON (Van de Peer & De Wachter, 1994). The tree was rooted with an *E. mazandaranica* individual from section *Helioscopia*. The number and the percentage of polymorphic loci, Nei's gene diversity and Nei's genetic distance were calculated with the program POPGENE (Yeh & Yang, 1999).

2.1.5. Morphometry and phenetic analysis (Publication 3)

Based on the available literature and on our own unpublished results, 23 quantitative (13) and qualitative (10) morphological characters were used for morphometric and phenetic analysis (Table 2; Publication 3). The characters and character states were determined by examination of the materials housed in IRAN and TARI herbaria as well as newly collected specimens. All repetitions (2-9) of each population were measured for selected morphological characters and for quantitative features the mean of all repetitions was taken to represent each population. Both quantitative and qualitative characters were coded as binary-state. The data matrix was scored using binary coding and a dissimilarity matrix of morphological characters was calculated using the Statistical Package for the Social Sciences (SPSS) software package version 18 (George and Mallery, 2010). In order to determine the most variable characters among species, factor analysis based on PCA (Principal Component Analysis) was performed on standardized data and Varimax rotation was carried out to provide minimum number of influencing variables on each factor making results interpretation easier (Manly, 1991). A scatter graph was prepared to show phenetic relationships among the studied taxa.

2.1.6. Morphological analysis in the phylogenetic context (Publication 2)

This part is mainly based on plant material deposited in the Iranian herbaria IRAN, TARI, HSBU, FUMH, FAR. Patterns of character evolution were assessed for six seed and capsule characters that had either been considered taxonomically useful by earlier taxonomic treatments, such as seed and capsule surfaces and caruncle shape, and some

characters of which the taxonomic value is evaluated here, such as presence or absence of granulate elements on seed surfaces, as well as seed and capsule shape. Parsimony mapping of these characters was performed in Mesquite v. 2.75 (Maddison & Maddison, 2011) using the tree derived by Bayesian inference as reference. The following traits were coded in a binary matrix and traced on the tree: (1) presence or absence of granulate elements on seed surface, (2) seed shape (ovoid, hexahedral, pseudo-hexahedral, ovoid-quadrangular, ellipsoidal, ovoid-ellipsoidal, ovoid-subsquare), (3) seed surface (smooth, irregularly pitted, tuberculate-rugulose, shallowly pitted and wrinkled, longitudinally grooved with or without pits, longitudinally sulcate and rugulose-tuberculate, foveolate-reticulate), (4) capsule shape (conical, subglobose, oblong-conical, ovoid-conical, woody globose (*i.e*. strongly lignified and indurated) and hexahedral, rounded-oblong), (5) capsule surface (smooth, vesiculate, tuberculate or verrucose, granulate at least on keel, papillose) and (6) shape of caruncle (conical, reniform, patelliform, petasiform, longitudinally sulcate, absent).

2.1.7. Morphological, Morphometric and SEM studies (Publication 2)

To examine seed coat and sculpturing as well as caruncle morphology using SEM, mature seeds were mounted directly on 12.5-mm-diameter stubs fitted with sticky tape and coated in a sputter coater with a gold-palladium layer. Morphological observations were accomplished under different magnifications (12-500 ×) with a Zeiss SIGMA-VP scanning electron microscope. Morphometric measurements were carried out and all photographs of capsules, seeds and caruncles were taken under a Dino-Lite pro hand digital stereomicroscope. Qualitative seed and capsule morphological characters of all Iranian perennial species of *Euphorbia* were assessed. Quantitative features had to be measured depending on available material, ranging from 4 capsules of one population to a maximum of 92 capsules from 10 populations, and from 5 seeds of one population up to 121 seeds from 12 populations. For species with a wider distribution range, populations from different parts of Iran were selected to cover the geographical and morphological diversity of the species. The characters recorded comprise capsule dimension (length × width), capsule surface, capsule shape and color, pedicel and style length, seed dimension

(length × width), ornamentation of seed surfaces, seed shape and color, and caruncle shape, color as well as size (length × width). Widths of capsules, seeds and caruncles were measured at the widest point. Seed length was considered excluding the caruncle. Range (maximum, minimum) and average of the morphometric measurements, and standard deviations, calculated in Microsoft Excel, are presented.

2.1.8. Taxonomic treatment (Publication 3, 4)

The taxonomic revision of two sections *Esula* and *Helioscopia* is based on a revision of the material from the following herbaria: B, BM, E, FAR, FUMH, HSBU, IRAN, K, M, MSB, PR, SAV, TARI, TUH, W, WU. Almost all species in these revisions were studied in the fields in Iran. Ecological and geographical data were collected from specimen labels and own field observations. Descriptions, synonyms, key to species, typification, vouchers as well as pertinent comments are given for all species.

2.2. Results & Discussion

2.2.1. Diversity, endemism, distribution and conservation status of *Euphorbia* (Euphorbiaceae) in SW Asia (Publication 1)

A total of 249 taxa of the genus *Euphorbia*, belonging to 239 species, five subspecies and five varieties with their infrageneric, sectional and subsectional placement, life form, distribution, habitat, altitude and threat category has been identified from the extended SW Asia (Appendix 1; Publication 1). Of the 249 studied *Euphorbia* taxa occurring in the region, 243 are mapped (Appendix 2; Publication 1).

2.2.1.1. Diversity

In the course of the study of 249 existing *Euphorbia* taxa in the extended SW Asia, all four subgenera, *Athymalus*, *Chamaesyce*, *Esula* and *Euphorbia*, have been representatives in the region. The largest subgenus was *Esula* with 182 taxa (73%) followed by *Chamaesyce*, *Euphorbia*, and *Athymalus* with 33 (13.2%), 21 (8.4%) and 13 (5.2%) ones respectively. Among 21 reported sections in subgenus *Esula* 19 of which occurred in the studied region. The three largest sections were *Pithyusa* (Raf.) Lázaro, *Helioscopia* Dumort., and *Esula* (Pers.) Dumort. with 44 (17.6%), 42 (16.8%) and 21 (8.4%) taxa respectively. The second largest sections were *Myrsiniteae* (Boiss.) Lojac., *Patellares* (Prokh.) Frajman, *Tithymalus* (Gaertn.) Roep., *Herpetorrhizae* (Prokh.) Prokh. and *Sclerocyathium* (Prokh.) Prokh. with 12, 11, 10, 9 and 8 taxa respectively. The third ones were *Arvales* (Geltman) Geltman, *Holophyllum* (Prokh.) Prokh. and *Paralias* Dumort. with four taxa in each section, followed by the smallest ones, *Aphyllis* Webb & Berthel., *Exiguae* (Geltman) Riina & Molero, *Chylogala* (Fourr.) Prokh., *Pachycladae* (Boiss.) Tutin with two and *Calyptratae* Geltman, *Lagascae* Lázaro, *Lathyris* Dumort. and *Szovitsiae* Geltman with only one species. The second largest subgenus in the studied region is *Chamaesyce* with five sections distributed in SW Asia. The largest section was *Anisophyllum* Roep. subsection *Hypericifoliae* Boiss. with 24 species, of which nine are non-native and introduced to the region as weeds and invasive plants. There are 21 species of the subgenus *Euphorbia* in the studied region, of which 19 belong to section *Euphorbia* and the two remaining ones occur in section *Tirucalli* Boiss. The smallest

subgenus is *Athymalus* with three sections in the studied region. Based on Diva GIS analysis and the species richness point of view, the richest places for *Euphorbia* in extended SW Asia were eastern part of Mediterranean region with more than 32 taxa, Alborz, Zagros and Anti-Taurus (S Turkey) with more than 25 taxa are the second richest areas followed by SW and W Yemen, parts of Caucasus (including Armenia, NW Iran, NE Iraq, NE Turkey), N Turkey and W Himalaya (including E and NE Afghanistan, N and NE Pakistan) with about 20 taxa.

2.2.1.2. Life form

Of the 249 taxa in the studied region, the largest groups were hemicryptophytes, therophytes and chamaephytes with 85 (34.1%), 74 (29.7%) and 60 (24%) taxa respectively, followed by nanophanerophytes, phanerophytes and geophytes with 25 (10%), 4 (1.6%) and 3 (1.2%) taxa respectively. In subgenus *Athymalus*, of the six mentioned life forms only four were recognized, chamaephytes, and nanophanerophytes with five species each and phanerophytes and hemicryptophytes with two and one species, respectively. Subgenus *Chamaesyce* comprised solely two life forms, therophytes and chamaephytes with 28 and six taxa, respectively. In subgenus *Esula*, hemicryptophytes (84 taxa, 46.1%), therophytes (46 taxa, 25.2%), and chamaephytes (43 taxa, 23.6%) are the dominant life forms followed by nanophanerophytes (6 taxa, 3.3%) and geophytes (3 taxa, 1.6%). In subgenus *Euphorbia* nanophanerophytes are prevalent (14 species, 73.6%), followed by chamaephytes (5 species, 26.3%) (Appendix 1; Publication 1).

2.2.1.3. Endemism

A total of 96 taxa of *Euphorbia* are listed as narrowly endemic and subendemic to SW Asia. They cover *c.* 38.5% of the whole *Euphorbia* taxa of the studied area belonging to subgenera *Athymalus* (6 species, 6.2%), *Chamaesyce* (5 taxa, 5.2%), *Esula* (70 taxa, 72.9%) and *Euphorbia* (15 species, 15.6%). The countries richest in *Euphorbia* taxa are Turkey (103 taxa), Iran (90 taxa), Syria (50 taxa) and Pakistan (46 taxa), whereas the highest number of *Euphorbia* endemics occur in Iran (19 taxa), Turkey (13 taxa), Yemen (8 taxa) and Afghanistan (5 taxa), respectively. Armenia, Iraq, Israel/Palestine, Jordan,

Kuwait, Lebanon, Qatar and UAE house no endemic *Euphorbia* taxon. All *Euphorbia* endemics of Afghanistan, Azerbaijan, Cyprus, Egypt, Iran, Pakistan, Syria, Turkey and Turkmenistan belong to subgenus *Esula* including, sections *Calyptratae* (one species), *Esula* (seven species), *Helioscopia* (six species), *Holophyllum* (one species), *Myrsiniteae* (two taxa), *Patellares* (three taxa), *Pithyusa* (23 taxa), *Sclerocyathium* (one species) and *Tithymalus* (four species). Other *Euphorbia* endemics occur in Oman, Saudi Arabia and Yemen attributable to subgenera *Athymalus* (five species), *Chamaesyce* (two species) and *Euphorbia* (eight species).

2.2.1.4. Neophyte

Among the listed *Euphorbia* taxa, 17 (6.8%) taxa are neophytes and non-native to the extended SW Asia. Pakistan, Saudi Arabia and Turkey with 11, 10 and 10 species respectively, are richest in introduced species followed by Egypt, Iran, Cyprus and Oman with nine, eight, seven and seven respectively. Among the 17 *Euphorbia* species introduced to the studied region, ten species have originated in the New World.

2.2.1.5. Conservation status

With the exception of a few number of endemic *Euphorbia* species, the Red List categories of most endemic and subendemic taxa in SW Asia were evaluated for the first time. A total of 96 endemic taxa were globally classified as Threatened comprising CR, EN and VU. Of the 96 endemics and subendemics of the studied *Euphorbia* taxa in the region, 54 were classified under threatened categories including, CR, EN and VU with 21, 16 and 17 taxa respectively and the remaining ones were considered as NT, LC and DD with eight, 27 and seven taxa, respectively. The highest number of threatened taxa of the genus *Euphorbia* occur in Cyprus with four taxa, S, SE, SW Turkey, the southwestern most part of Saudi Arabia, S, SW, W Yemen and S Oman with three taxa in each area were the second ones, followed by Alborz, Zagros in Iran, N Baluchestan in Pakistan, NE Turkey, W, NW Syria, N Israel/Palestine and Lebanon with two species in each region.

2.2.2. Seed and capsule morphology of Iranian perennial species of *Euphorbia* (Euphorbiaceae) and its phylogenetic application (Publication 2)

This study indicates and confirms that not only macro- and micromorphology of seeds (Pahlevani & Akhani, 2011), but also carpology contribute useful characters to taxonomy and identification of *Euphorbia* taxa from subgeneric to species level. Carpology in this group is at least as important as seed morphology, especially at sectional level. Among the examined parameters, capsule size and shape, seed size and the ornamentation of seed surface are correlated better to phylogeny than the other features. In contrast, variation in life cycle is not always congruent with new molecular phylogenetical classifications (Frajman & Schönswetter, 2011; Horn *et al*., 2012; Riina *et al*., 2013), even though life cycle is a distinctive indicator for certain sections.

2.2.2.1. Character evolution of capsule and seed of Iranian *Euphorbia* subgenus *Esula*

2.2.2.1.1. Carpology

Capsule shape — Although the outgroup *E. larica* Boiss., a member of subgenus *Athymalus*, is characterized by woody globose capsules, fruits of subgenus *Esula* are never woody and can take various shapes. Members of sections *Helioscopia*, *Patellares*, *Esula*, *Szovitsiae*, *Tithymalus* and *Arvales* are characterized by subglobose capsule shape and rounded keel. Subglobose capsule shape has independently evolved three times in clades *Helioscopia*, *Szovitsiae-Patellares* and *Tithymalus-Esula*. Conical capsules occur in sections *Pithyusa*, *Sclerocyathium* and *Calyptratae*. Species of section *Herpetorrhizae* show synapomorphy of oblong-conical capsules and seem to have evolved from subglobose ones. Ovoid-conical capsules are found in the sections *Myrsiniteae* and *Lagascae*, and are most distinctive in section *Myrsiniteae*. Only section *Chylogala*, represented by *E. heteradena* Jaub. & Spach, is distinguished with a unique rounded-oblong capsule (Fig. 135A; Publication 2).

Capsule surface — capsule surface characters are also well correlated with the clades derived from Bayesian analysis. The vesiculate surfaces of section *Myrsiniteae* and the granulate ones of section *Esula* are synapomorphies congruent with the phylogenetic tree. The perennial species and the annual *E. stricta* L., all of section *Helioscopia* and

characterized by tuberculate or verrucose surfaces, are also monophyletic, while most annual species of the section are smooth. Reversals to smooth surfaces have taken place several times, *e.g*., in the perennial species *E. mazandaranica* Pahlevani and *E. altissima* Boiss. *Euphorbia eriophora* Boiss. is unique among all other species in section *Helioscopia* because of its long-pilose capsules. Smooth surfaces seem to constitute the primitive state and have been retained in *Herpetorrhizae*, *Chylogala*, *Calyptratae*, *Pithyusa*, *Tithymalus*, and *Sclerocyathium*. All species with pilose capsules in section *Pithyusa* (*E. gypsicola* Rech.f., Aellen, *E. sahendi* Bornm. and *E. teheranica* Boiss.) are monophyletic. Papillose surfaces, in contrast, have evolved several times in section *Pithyusa* (*e.g*., *E. glareosa* Pall. ex M.Bieb., *E. macroclada* Boiss. and *E. polycaulis* Boiss. & Hohen.) (Fig. 135B; Publication 2).

2.2.2.1.2. Seed morphology

Seed shape — Most of seed shape character states are somewhat homoplasious, but particular states seem to be synapomorphic for specific groups. Among the 13 sections of Iranian leafy spurges, six sections have ovoid seeds as the most common shape. Sections *Helioscopia*, *Myrsiniteae*, and *Esula* are distinguished from the other groups with ellipsoidal, ovoid-quadrangular and ovoid-ellipsoidal seeds shapes, respectively. The case of the annual *E. aleppica* L. with ovoid seeds in *Myrsiniteae* is interesting because it indicates that the change in life form has been paralleled by a change in seed shape. Sections *Herpetorrhizae* and *Tithymalus* possess pseudo-hexahedral and hexahedral seed shapes, respectively. Although these shapes are superficially similar, true hexahedral seeds are only formed in *Tithymalus*, whereas they appear hexahedral because of two ridges on the seeds in *Herpetorrhizae*. Section *Arvales* is unusual because its three annual Iranian members have completely different seed shapes; *E. aulacosperma* Boiss. displays hexahedral, *E. franchetii* B. Fedtsch., pseudo-hexahedral and *E. arvalis* Boiss. & Heldr. ovoid seeds (Fig. 136A; Publication 2). Incongruence between seed shape in this group could indicate reticulate evolution which has already been reported in other groups in *Euphorbia* (Yang & Berry, 2011).

Seed surface — Smooth surfaces are the most common type, which is present in sections *Patellares*, *Esula*, *Chylogala*, *Calyptratae* and *Sclerocyathium*. It is also the most

frequent type in section *Helioscopia*, in which two species, *E. helioscopia* L. and *E. rhabdotosperma* Radcl.-Sm., have evolved a unique ornamentation type, foveolate-reticulate seeds. For section *Pithyusa*, irregularly pitted seeds are characteristic, with the two first-branching species, *E. glareosa* and *E. seguieriana* Neck., still displaying smooth seeds, and several reversals to smooth seeds (*E. acanthodes* Akhani, *E. macroclada*, *E. spartiformis* Mobayen). Reversals to smooth seeds have also taken place in section *Myrsiniteae* (*E. marschalliana* Boiss., *E. monostyla* Prokh.), that is otherwise characterized by tuberculate-rugose seeds. Shallowly to deeply rugulose-wrinkled or irregularly rugose-tuberculate and longitudinally sulcate seeds are synapomorphic in section *Herpetorrhizae*. Section *Tithymalus* is uniform with regards to seed ornamentation, displaying two longitudinal grooves on ventral sides and several pits on dorsal sides ((Fig. 136B; Publication 2). This feature on seed surface occurs only in the Old World species of section *Tithymalus* (Peirson *et al*., 2014). Section *Arvales,* in contrast, is as heterogeneous in seed ornamentation as in seed shape.

Seed granulate elements — Granulate elements are absent from the outgroup, and have evolved in subgenus *Esula* apparently twice, once in the *Myrsiniteae-Pithyusa* clade (Pahlevani & Akhani, 2011: Figs 21C–21D) and once in the *Chylogala-Szovitsiae-Patellares-Herpetorrhizae-Tithymalus-Arvales-Esula* clade (Fig. 136C; Publication 2), with a reversal to absence of granulate elements in section *Patellares*.

Caruncle shape — Caruncle shape shows a strong phylogenetic pattern. In the outgroup, caruncle is absent such as in many members of two other subgenera *Euphorbia* and *Chamaesyce*, so presence of caruncle might constitute a synapomorphy for subgenus *Esula*. The most frequent conical caruncles are found in sections *Lagascae*, *Myrsiniteae-Pithyusa* and *Sclerocyathium, Szovitsiae, Herpetorrhizae*, *Tithymalus*, and *Arvales*. In sections *Esula* and *Patellares* special caruncle shapes have evolved, namely petasiform and patelliform caruncles, respectively. Section *Herpetorrhizae* show synapomorphy of oblique position of the caruncle (Pahlevani & Akhani, 2011: Figs 16A, 18A, 19A–19B, 23A, 26A). Ecarunculate or very small and caducous caruncles (*E. aleppica*) have evolved several times from carunculate seeds (sections *Helioscopia*, *Myrsiniteae* and *Herpetorrhizae* as well as species of subgenera *Chamaesyce* and *Athymalus*). *Euphorbia eriophora* with absent caruncle is retrieved as sister to the remaining species (Pahlevani

& Akhani, 2011: Fig 29A). It seems that ecarunculate seeds are a plesiomorphic feature in section *Helioscopia* occurring in most basal clades (see Riina *et al*. 2013). Generally, absent or very small and unsteady caruncles seem to be a plesiomorphic feature in some sections in subgenus *Esula*.

Thus, although some homoplasy has been observed in most seed and fruit characters studied here, these characters, especially in their combination, have considerable predictive power for the correct placement of a given species, especially when considered together with other morphological characters.

2.2.3. Molecular and morphological studies disentangle species complex in *Euphorbia* sect. *Esula* (Euphorbiaceae) from Iran, including two new species (Publication 3)

The *E. osyridea* alliance in section *Esula* (*E. austro-iranica*, *E. buhsei*, *E. khabrica*, *E. osyridea*) is centered in Iran, but *E. buhsei* ranges from Iran to S of Turkmenistan on the borderline of Iran and *E. osyridea* also occurs in W of Pakistan and Afghanistan. The two new species, *E. austro-iranica* and *E. khabrica* are isolated species, endemic to the Irano-Turanian region of Iran. All these Irano-Turanian species with limited distribution form a monophyletic group. The distribution and phylogenetic pattern along with morphological characters support this monophyly.

2.2.3.1. Principal component analysis

Twenty three vegetative and reproductive characters were identified for numerical analysis and phenetic relationships of existing Iranian populations of four *Euphorbia* species of section *Esula* (Table 2; Publication 3). Factor analysis of morphological data showed that the first three factors are responsible for about 97% of the total variance. The first factor accounts for *c*. 65% of total variance in which characters such as number of rays and ray-leaves, gland shape and color and pedicel length revealed the highest positive correlation (> 0.8). The second factor explains about 22.5% of total variance in which characters like stem indumentum, leaf shape and apex, indumentum of cyathium and capsule surface showed the highest correlation (> 0.9). Finally, the third factor

accounts for almost 10% of total variance including characters with the highest correlation such as leaf indumentum, capsule length and seed size (> 0.9).

2.2.3.2. Phylogenetic studies (ITS, ndhF and ISSR)

The *ndh*F and the combined ITS+*ndh*F trees indicated polytomies and unresolved positions in almost all groups of section *Esula*. In the ITS tree the samples of the four species of the *E. osyridea* alliance formed a monophyletic group, sister to other clades of section *Esula* (Fig. 2; Publication 3). In the neighbour joining tree (Fig. 3; Publication 3), all studied accessions (Table 3; Publication 3) were divided into four main groups, *E. buhsei*, *E. osyridea*, *E. austro-iranica* sp. nov. and *E. khabrica* sp. nov. Individuals of *E. khabrica* and *E. austro-iranica* were more strongly dissimilar than the individuals of *E. buhsei* and *E. osyridea* and were separated with strong supports (BS 100 for *E. khabrica* and 93 for *E. austro-iranica*). Based on Ds analysis, the widest genetic distance was observed between *E. khabrica* and the studied species *E. austro-iranica*, *E. buhsei* and *E. osyridea* with different populations. The closest population to both, *E. austro-iranica* and *E. khabrica* was *E. buhsei* from Semnan province (Table 7, Fig. 3; Publication 3). In comparison, the genetic distances between *E. khabrica* and populations of *E. buhsei* and *E. osyridea* were higher than those between *E. austro-iranica* and the species *E. buhsei* and *E. osyridea*. In other words, *E. austro-iranica* is more closely related to both *E. buhsei* and *E. osyridea* than to *E. khabrica* (Table 7; publication 3). Neither nuclear nor plastid sequences, nor their combination were sufficient to disentangle the diversification patterns within the *E. osyridea* alliance. This could be related to the rapid evolution in section *Esula,* which is one of the youngest groups in the subgenus (Horn *et al*., 2014). The phenomenon of incongruence between chloroplast and nuclear DNA data occurs in other groups of angiosperms with rapid evolution (Fehrer *et al*., 2007). The neighbour joining tree indicated that all studied accessions were divided into four main groups, *E. buhsei*, *E. osyridea*, *E. austro-iranica* and *E. khabrica* (Fig. 3; Publication 3). Individuals of two new species, *E. austro-iranica* and *E. khabrica* were more strongly dissimilar than the individuals of *E. buhsei* and *E. osyridea* and separated with strong support (Fig. 3; Publication 3). All these Irano-Turanian species with limited distribution form a

monophyletic group (Fig. 2; Publication 3). The distribution and phylogenetic pattern along with morphological characters support this monophyly.

2.2.4. Update of the taxonomic treatment of SW Asian species (Publications 1, 2, 3 & 4)

Publication 1. In the course of the morphological and phylogenetic studies of the genus *Euphorbia* in SW Asia, four new species, *E. acanthoclada* Pahlevani from Afghanistan, *E. kavirensis* Pahlevani from Iran, *E. boreo-baluchestanica* Pahlevani and *E. ziaratensis* Pahlevani from Pakistan were discovered. Detailed description, diagnosis, image of herbarium specimens, affinity, habitat, distribution as well as additional specimen examined is provided. According to IUCN threatened categories and our conservation analysis, *E. acanthoclada*, *E. boreo-baluchestanica* and *E. kavirensis* are evaluated their conservation status as 'vulnerable' (VU), whereas *E. ziaratensis* because of its rarity and vulnerability, we suggest the evaluation of this delicate species as 'critically endangered' (CR) (IUCN, 2011). Eight species, *E. heterophylla* L., *E. nutans* Lag., *E. prostrata* Aiton, *E. gedrosiaca* Rech.f., Aell. & Esfand., *E. sororia* Schrenk, *E. thyrsoidea* Boiss., *E. turkestanica* Regel and *E. jaxartica* (Prokh.) Krylov from Afghanistan, two species, *E. coniosperma* Boiss. & Buhse and *E. hirta* L. from Iran, *E. petiolata* var. *petiolata* Banks & Sol. from northernmost part of Oman, *E. petiolata* var. *postii* (Boiss.) Radcl.-Sm. from S Turkey and *E. bungei* Boiss. from Pakistan are reported as new record for the countries. Three synonyms, *E. cashmeriana*, *E. pauciradiata* Blatt. and *E. sanctae-catharinae* Fayed with *E. cornigera* Boiss., *E. prolifera* Buch.-Ham. ex D.Don. and *E. obovata* Decne., respectively, are also reported. Some misidentifications and errors in other species and floras have been indicated in Appendix 1 (Publication 1).

Publication 2. During the course of the phylogenetic and morphological studies in subgenus *Esula*, two new rare and endemic species, *E. ferdowsiana* Pahlevani and *E. sulphurea* Pahlevani, were discovered. A new record for *E. glareosa* in Iran was reported. In addition, *E. gaubae* (Soják) Radcl.-Sm. has fallen within the range of variation of *E. buhsei* and was therefore considered as synonym of this species. *Euphorbia ferdowsiana* was found only on the eastern slopes of the Binaloud Mountains in NE Iran at elevation between 2100-2700 m. It is closely related to *E. bungei* in section *Sclerocyathium*. It has

a conspicuous camouflage with the reddish color of the stones (Fig. 1B). Because of its rarity and restricted occurrence at type location, it is suggested to evaluate its conservation status as 'critically endangered' (CR) according to IUCN threatened categories (IUCN, 2011). *Euphorbia sulphurea* is a geographically isolated and morphologically distinct species known only from the type locality in the alpine zone of the Taftan massif, the isolated mountain system with the highest peak in south-eastern Iran. It was found in the alpine zone of the volcanic peak of Taftan at 3700-3900 m elevation on sulphur bed. Based on the IUCN Red List category it is considered to evaluate its conservation status as 'critically endangered' (CR). It is closely related to *E. spartiformis* in section *Pithyusa* (Fig. 134; Publication 2). These species together with *E. erythradenia* Boiss., *E. gedrosiaca*, *E. plebeia* Boiss., *E. prolifera*, *E. kavirensis*, and *E. boreo-baluchestanica* form a distinct and supported clade in section *Pithyusa*. Their synapomorphy is the presence of only one to three (four) terminal rays.

Publication 3. This publication contains a survey of the morphological characters, and a key to the all species of section *Esula* occurring in Iran. For each species description, typification, synonyms, specimens examined, phenology, and pertinent comments are given. Two new synonyms, *E. khorasanica* Saeidi & Ghayormand and *E. osyridiformis* Parsa are considered with *E. virgata* Waldst & Kit. and *E. hebecarpa* Boiss., respectively. Two morphologically and genetically distinctive new species of *Euphorbia* from southern part of Zagros mountains and south to south-east Iran are described and illustrated which clearly belong to section *Esula* and *E. osyridea* alliance in a monophyletic group (Fig. 2; Publication 3). Detailed morphological examination of herbarium material kept under the name "*E. osyridea*" revealed that the specimens do not belong to the same species, indicating that the concept of Radcliffe-Smith (1986) for *E. osyridea* includes morphologically and genetically heterogeneous populations. The results of the ISSR and morphology studies (Figs 1, 3; Publication 3) indicate that the populations of *E. osyridea* can be divided into two obviously different groups, of which the first one is here considered *E. osyridea sensu* Boissier (Boissier 1846) and the second one is reported here as a new species, *E. austro-iranica*. Although *E. austro-iranica* is morphologically more similar to *E. osyridea*, it is genetically more closely related to *E. buhsei* (Table 7, Fig. 3; Publication 3). The most important morphological difference between the two species is

the tomentose indument of stem, leaf and capsule in *E. osyridea*, which is absent in *E. austro-iranica* (Table 5; Publication 3). Leaf shape and leaf apex can also serve as distinguishing features between *E. austro-iranica* and *E. osyridea*. The overall aspect of their habit and the presence of axillary rays (no terminal rays) make them to appear more similar to each other than to the other species in this group, however, the factor analysis of our phenetic study indicated that position of rays had negative correlation in comparison with other studied characters. On the other hand, a shrub or shrublet life form in these two species can not be considered a synapomorphic character because several more species in other clades of sect. *Esula* are also shrubs or shrublets. The presence of axillary rays alone (without terminal rays) is uncommon in other species of *Euphorbia* subgen. *Esula*, and it has been never reported in other taxa. According to the IUCN Red List category (IUCN, 2011), *E. austro-iranica* and *E. khabrica* are evaluated their conservation status as 'vulnerable' (VU) and 'critically endangered' (CR) respectively.

Publication 4. This publication updates the taxonomy and distribution of existing *Euphorbia* (subgenus *Esula*) section *Helioscopia* in Iran since the publication of Flora Iranica in 1964. A key, species descriptions, illustrations for most species, distribution maps, brief characterization of ecology, voucher specimens examined and relevant notes for the 12 species of this section occurring in Iran is provided. A new species, *E. mazandaranica* Pahlevani is described and illustrated from Hyrcanian forest in Mazandaran Province. It was found in the dense forest of *Fagus Orientalis* Lipsky from sea level to 1450 m elevation. Its conservation status is evaluated as 'vulnerable' (VU) based on the IUCN Red List category (IUCN, 2011) (Publication 1). It is closely related to *E. squamosa* Boiss. in section *Helioscopia* (Fig. 134; Publication 2). *Euphorbia altissima* var. *altissima* is also reported as new from NW Iran.

3. Conclusions & perspectives

In the present work the taxonomic and geographical situation of members of the giant genus *Euphorbia* in extended SW Asia including 20 countries was assessed and resolved. *Euphorbia* shows an exceptional diversity in the study region as one of the most important genus playing a vital role in many communities. So far, there are 249 taxa in the region belonging to all four known subgenera, but most to subgenus *Esula* (182 taxa, 73%). In fact, of the 485 reported species in subgenus *Esula ca*. 38% are concentrated in SW Asia with high degree of endemism (>50%). In spite of antipastoral and invasive behavior of many members of the genus *Euphorbia*, the number of endemic species with threatened status in the study region is rather high (21.6%).

It is also revealed that life form of the genus *Euphorbia* members matches well with available data of the entire flora in the area. The deviation of percentages of hemicryptophytes and chamaephytes from entire flora is probably related to the toxicity of *Euphorbia* species which are avoided by grazers. The spiny trait is also not well developed in *Euphorbia* subgenus *Esula* compared to other steppe groups of the arid regions. Apparently, the toxicity of shoots and leaves defend *Euphorbia* species from herbivores. The field observations also showed that many perennial *Euphorbia* species are highly cold tolerant so that they could well be considered as evergreen plants. Therefore, evolution of woody parts, spiny and cushion forms did not constitute selective advantages.

It is supposed that during interglacial periods many species of the genus *Euphorbia*, together with many other groups of flowering plants in the region, may have been geographically isolated in the high mountainous areas as interglacial refugia (Memariani *et al*., 2016) and the diversity in the region is probably the result of intensive speciation that took place during the Eocene-Miocene (Geltman, 2015). The ability of dispersal via zoochory and ornithochory in some members of the genus to new places followed by rapid speciation, adaptation to new habitats and being not palatable for grazing lead them to be a successful group of angiosperm.

The generally held notion that seed and capsule morphology can contribute useful characters for species delimitation and identification of the Iranian *Euphorbia* taxa from subgeneric to species level has also been tested by methodically collecting such data for

all species in the area and evaluating them in the light of a molecular phylogeny. Several important characters of seed and capsule morphology have been applied in this study for the first time. Although some homoplasy has been observed in some seed and capsule characters studied here, they have considerable predictive power for the correct placement of species, especially when several of these characters are combined or when such characters are considered together with other morphological characters.

In this thesis it was shown that ISSR DNA finger printing could be considered as a reliable marker to resolve complex group of *Euphorbia* which has revealed polytomy and unresolved situation by other nuclear and plastid sequences at species level. So far, DNA finger printing has been carried out only three times in *Euphorbia* and ISSR DNA finger printing has been used for the first time in the genus *Euphorbia*.

So far, comprehensive studies of diversity, endemism, distribution and conservation of the genus *Euphorbia* have been carried out in SW Asia. It would be important and useful to extend these studies further over the Old World to include other hotspots of the genus, such as the Mediterranean region, European countries, Far East and Central Asia. Studying seed and capsule morphology of the remaining taxa of the genus *Euphorbia* subgenus *Esula* distributed to other countries would be necessary to confirm the utility of the selected evolutionary characters. Providing keys based on seed and capsule morphology would allow to delimitate both infrageneric and species over larger geographical areas. Preparation of a taxonomic revision of all taxa of the genus in SW Asia and the adjacent regions will create the base for an intensified study of a wide range of characters. Fine-tuning the available phylogeny using additional markers as well as additional accessions will increase resolution and allow to identify actively radiating species complexes, which, in turn, should be studied with finger printing methods. Such a highly resolved phylogeny will allow to trace the evolution of a wide variety of characters in the genus. Particular emphasis in future work has to be placed on adding observational data on distribution, ecological preferences, cytology, pollination and dispersal biology as well as chemistry and study the evolution of these characters in order to understand the predispositions and events making *Euphorbia* such an extremely successful genus.

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Publication 1

Diversity, endemism, distribution and conservation of the genus *Euphorbia* (Euphorbiaceae) in SW Asia

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Diversity, endemism, distribution and conservation status of *Euphorbia* (Euphorbiaceae) in SW Asia

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Cosmopolitan genus *Euphorbia* with over 2,000 species and four subgenera is largely diversified in the Old World. Southwest Asia is one of the most important centers of its diversity. In order to evaluate the diversity, endemism, distribution and conservation of the genus *Euphorbia* in SW Asian countries we generated an updated and annotated checklist of 249 taxa belonging to four subgenera, 30 sections and five subsections. Subgenus *Esula* with 19 sections and 182 taxa is the largest one followed by subgenera *Chamaesyce* (six sections, 33 species), *Euphorbia* (two sections, 21 species) and *Athymalus* (three sections, 13 species). Among 20 studied countries in the region, Turkey, Iran and Syria with 103, 90 and 50 species, respectively, are the richest countries. Analysis of diversity indicated that the richest places of *Euphorbia* in SW Asia are the eastern part of the Mediterranean region with more than 32 taxa; Alborz, Zagros (Iran) and Anti-Taurus (S Turkey) with more than 25 taxa each are the second richest areas followed by SW and W Yemen, Lesser Caucasus, N Turkey and west Himalaya with about 20 taxa each. The highest number of endemics occurs in Iran, Turkey and Yemen with 19, 13 and eight taxa, respectively. Of the 121 endemic and circumscribed taxa in the studied region 96 are narrow endemics and subendemics. All 96 endemic and subendemic taxa were evaluated against the IUCN Red List categories and criteria and a total of 54 endemic taxa were globally classified as threatened, comprising 21 Critically Endangered, 16 Endangered and 17 Vulnerable taxa. Among whole studied *Euphorbia* taxa in the region, 17 taxa (6.8%) are neophytes. Life form spectrum shows that the majority of species (88%) are hemicryptophytes, therophytes and chamaephytes corresponding the arid nature of the area and the rest of the flora. Four new species, *E. acanthoclada* sp. nov., from Afghanistan, *E. kavirensis* sp. nov. from Iran, *E. boreo-baluchestanica* sp. nov. and *E. ziaratensis* sp. nov. from Pakistan are described. Thirteen new reports and three synonyms are reported for the first time.

ADDITIONAL KEYWORDS: biodiversity – ecology – endemism – hot spot – new species – south-west Asian flora – threatened species

INTRODUCTION

South West Asia or the Middle East is one of the main centers of plant diversity in the Old World with very diverse vegetation and as Fertile Crescent is emerging center of many cultivated plants (Zohary, 1971). Traditionally SW Asia covers Asiatic Turkey (Anatolia), Syria, Lebanon, Israel/Palestine, Jordan, the Sinai Peninsula, Iraq, Iran, the southern part of Azerbaijan, Arabian Peninsula (Kuwait, Oman, Qatar, Saudi Arabia, UAE and Yemen) and Afghanistan with a land area of the SW Asia is *c.* 7,078,670 km^2 (Boulos, Miller & Mill, 1994). In this study, we extend our study area to an "extended SW Asia" by the inclusion of Turkmenistan, European Turkey, Cyprus, Armenia, entire Republic of Azerbaijan, Egypt, and Pakistan and excluded Socotra of Yemen (Fig. 1), covering an area of *c.* 9,431,796 km^2. Aridity and salinity characterizing most parts of the lowland areas especially in the south on the one hand, and presence of mountains and steppes in the north and central parts, on the other hand, caused drought-resistant, salt-tolerant and harshness-tolerant species to occupy the region in several different kinds of vegetation. Topographical, bioclimatical, edaphical, geological and ecogeographical complexity and heterogeneity as well as human influence altogether make the studied region one of the largest and most important centers of speciation both for mountain and desert floras covering several centers of plant diversity, endemism and hot spots in the Old World (Zohary, 1973; Takhtajan, 1986; Boulos *et al*., 1994; Nieto Feliner, 2014). Among the 34 major hotspots of the world, five partly or completely occur in the extended SW Asia, comprising Irano-Anatolian (not to be confused with Irano-Turanian phytogeographic region), part of Horn of Africa, southern part of the Caucasian region, eastern parts of the Mediterranean and western parts of the Himalaya (Mittermeier *et al*., 2004). There are more than 24,000 species of the vascular plants in the region of which over 7,300 species are endemics distributed mostly in the Irano-Turanian and E Mediterranean regions (Boulos *et al*., 1994).

South West Asia is at a phytogeographical crossroads where two huge floristic kingdoms "Holarctic" and "Paleotropics" meet each other (Takhtajan, 1986; Boulos *et al*. 1994). So far, six main phytogeographical regions are recognized, comprising Irano-Turanian, Mediterranean, Somalia-Masai, Saharo-Sindian/Saharo-Arabian, Euro-Siberian, and Sino-Himalayan. However, there are some discrepancies and arguments between

phytogeographers especially in the Irano-Turanian, Saharo-Sindian/Saharo-Arabian and Euro-Siberian regions and their territories in Iran and Pakistan (Zohary, 1973; Kürschner, 1986; Rechinger, 1986; Takhtajan, 1986; Léonard, 1988, 1989; White & Léonard, 1991; Akhani, 2007; Manafzadeh, Staedler & Conti, 2016).

The study on geography and distribution patterns of species is one of the most effective and essential components in conservation and biogeography (Huang *et al*., 2011). Floristic plant geography and evaluation of modern patterns and whole floras is much significant to understand biogeographic processes (McLaughlin, 1994; Manafzadeh, Salvo & Conti, 2013).

Attaining a profound knowledge and data of a huge genus or family with the high percentage of endemism and hotspots in a vast region, provides useful distributional patterns as prerequisite for modern biogeographical, paleobotanical, phytogeographical and paleogeographical disciplines, which, in turn, are vital elements for conservation approaches and programs. These kinds of studies have most often been developed by experienced and professional botanists equipped with a broad knowledge of the groups or floras they are working on. During the last three decades, a number of fundamental phytogeographical treatments of SW Asia have been published, e.g., Meusel *et al*. (1965-1992); Zohary (1973); Breckle (1974); Hedge & Wendelbo (1978); Kürschner (1986); Takhtajan (1986); White & Léonard (1991); Léonard (1993). In addition, several botanical contributions to the diversity, endemism and distributional patterns of flowering plants have been presented (Davis, 1971; Wendelbo, 1971; Ali & Qaiser, 1986; Danin, 1986; Hedge, 1986; Rechinger, 1986; Wagenitz, 1986; Browicz, 1989; Freitag, 1991; Klein, 1991; Miller & Nyberg, 1991; Sales & Hedge, 1996; Akhani, 2004a; Assadi, 2006; Akhani, 2007; Thomas *et al*., 2008; Sarvar & Qaiser, 2012; Geltman, 2015; Memariani, Zarrinpour & Akhani, 2016). However, a few of the studied regions comprehended whole SW Asia or more than one place or country.

In SW Asia, giant genus *Euphorbia* with over 250 out of 2,000 species worldwide distributed in all phytogeographical units of study area and various habitats from coastal to alpine zones and from deserts to forests and therefore is an ideal genus to look for phytochorological patterns (Webster, 1994; Govaerts, Frodin & Radcliffe-Smith, 2000; Pahlevani, Liede-Schumann & Akhani, 2015). *Euphorbia* is either the largest (Egypt,

Saudi Arabia, Yemen) or in some cases, among the five largest genera (Iran, Pakistan, Turkey) in each country of the study region. They are also highly diverse in growth forms, comprising therophytes, geophytes, chamaephytes, hemicryptophytes, nanophanerophytes and phanerophytes (Horn *et al*., 2012). Some members of the genus *Euphorbia* are specialized to occupy very specific ecological niches and they play an important role in halophytic, psammophytic, helophytic, chasmophytic, calcareophytic and xerophytic communities (Frajman & Schönswetter, 2011; Bruyns, Klak & Hanáček, 2011; Pahlevani & Akhani, 2011; Pahlevani *et al*., 2015). Although, some species are often predominant in their respective communities, some endemic ones are rare and restricted to few individuals in their habitats and sometimes only known from a single locality (Kilian, Kürschner & Hein, 2006; Fayed & Al-Zahrani, 2007; Pahlevani *et al*., 2015). Remarkably, *Euphorbia* is the sole genus with all known photosynthetic pathways, including C_3, C_4, CAM as well as C_2 system that represents an early stage of C_3 to C_4 transition (Webster, Brown & Smith, 1975; Batanouny, Stichler & Ziegler, 1991; Sage *et al*., 2011; Yang *et al*., 2012).

Recent molecular studies evidenced division of the *Euphorbia* into four major clades corresponding four subgenera *Athymalus* Neck. ex Rchb., *Chamaesyce* Raf., *Esula* Pers. and *Euphorbia*, 64 sections and 19 subsections (Bruyns, Mapaya & Hedderson, 2006; Steinmann & Porter, 2006; Park & Jansen, 2007; Zimmerman, Ritz & Hellwig, 2010; Bruyns *et al*., 2011; Horn *et al*., 2012; Yang *et al*. 2012; Dorsey *et al*. 2013; Peirson *et al*. 2013; Riina *et al*. 2013). In SW Asia all four subgenera are represented (Yang *et al*. 2012; Dorsey *et al*. 2013; Peirson *et al*. 2013; Riina *et al*. 2013). The genus was reviewed in all countries in standard flora (Table 1). There is no consistency in taxonomic interpretation of individual accounts and check of available herbarium specimens revealed a lot of misidentifications and errors. Notably, most accounts in the Floras are now outdated and many gaps remained because of unavailability of enough material during preparation of older accounts. The accumulation of a huge number of new data and our current knowledge on the morphology, phylogeny and distribution of species of *Euphorbia* facilitate updating of the diversity of this large genus in SW Asia (Carter, 1985; 1992; Ghazanfar, 1993; El-Karemy, 1994; Thulin & Al-Gifri, 1995; Lavranos & Al-Gifri, 1999; Abedin, 2001; Akhani, 2004b; Lavranos, 2011; Pahlevani & Mozaffarian,

2011; Pahlevani, Maroofi & Joharchi, 2011; Pahlevani & Riina, 2014; Hand *et al*., 2016; Genç & Kültür, 2016).

This study aims at: (1) Studying diversity of the genus *Euphorbia* in the extended SW Asia (2) Updating and annotating information on the existing *Euphorbia* species with their life forms and habitats traits across the study area (3) Designing distribution maps of all *Euphorbia* species occurring in SW Asia (4) Prioritizing conservation of the endemics through IUCN Red Listing (5) Prioritizing conservation areas based on endemic *Euphorbia* species and comparing with other vascular plant endemics in the region. In addition, four new species from Afghanistan, Iran, and Pakistan are described and 13 new records from Iran, Afghanistan, Oman, Pakistan and Turkey as well as three synonyms are reported. The phytogeographical analysis and distribution patterns of the genus *Euphorbia* will be discussed in an ongoing publication.

MATERIAL AND METHODS

STUDY AREA

The study area lies between 13° 05′ and 42° 09′ northern latitudes and 24° 40′ and 77° 36′ eastern longitudes bounded in the north by the Black Sea, Caspian Sea, Georgia, Uzbekistan, and Tajikistan (northeast), in the south by the Arabian Sea, in the west by the Mediterranean Sea and in the east by the India as well as Himalaya mountains covering 20 countries (Fig.1).

The topography of the area ranging from some high peaks more than 7,000 m in Hindu Kush and to as low as -392 m at the Dead Sea coasts. The climate of the region is extremely diverse, ranging from temperate to arid and semiarid (Köppen, 1936). There are five main climates in the region including, Irano-Turanian, Mediterranean, Tropical, Temperate and Monsoon (Boulos *et al*., 1994; Djamali *et al*. 2011; Djamali *et al*., 2012). The temperature spectrum ranges from hottest points of the world with records of over 70ºC skin temperature as in Lut desert in Iran to very cold highlands in mountain peaks as low as -50ºC (Ferrigno, 1991). From the geological point of view, SW Asia was covered by the Tethys Sea at the beginning of the Mesozoic (*c* 245 million years BP)

which caused thick layers of sedimentary rocks to form in the region. Since the African plate began to drift northwards toward Eurasia during the Miocene (20-14 million years BP), the sedimentary rocks were lately uplifted to form the existing mountain chains. Afterward the rift of the Red Sea *c.* 15 million years BP separated the Arabian plate from Africa (Boulos *et al*. 1994).

TAXONOMIC STUDIES, SPECIES DATA AND MAPPING OF SPECIES

The data of taxonomic investigations and distribution maps are the result of long-term studies of the genus *Euphorbia* by the first author in Iran and other South-West Asian countries since 2006. This study is mainly based on examination of *c.* 22,000 plant specimens and types deposited in the SW Asian countries species-rich herbaria B, BM, E, K, M, MSB, PR, PRC, SAV, UBT, W, WU and Iranian herbaria FAR, FUMH, IRAN, HSBU, TARI, TUH (abbreviations according to Thiers, 2016) as well as many Iranian local herbaria in Kordestan, Kerman, E. Azerbaijan, W Azerbaijan, Kermanshah, Esfahan, Hormozgan provinces and Herbarium H. Akhani (Halophytes and C_4 Plants Research Laboratory of the school of Biology, University of Tehran). Notably, many specimens of G and P herbaria also have been studied online. Most of the Iranian *Euphorbia* species have been collected and studied in the field by the first author and most type specimens have been examined. The database of the SW Asian *Euphorbia* species is based on data of herbarium labels and geo referencing them using Microsoft Encarta 2008, Google Earth, or, available maps. Sometimes, localities have been retrieved from pertinent literature, such as standard floras or articles (Radcliffe-Smith, 1982, 1985, 1986; Mouterde, 1986; Lavranos, 1999; Lavranos, 2005; Lavranos, 2011; Hand, 2015; Genç & Kültür, 2016). A total of *c.* 11,000 geo-referenced records was used to prepare and analyze species richness using diversity analysis tools in DIVA-GIS 7.3 software (http://WWW.diva-gis.org/; Hijmans *et al*., 2001) comprising alpha diversity (species richness). All geo-referenced records were used to provide individual maps using DMAP software (Morton, 2009). Of the 249 studied *Euphorbia* taxa occurring in the region, 243 are mapped. Six taxa (*E. anisopetala* (Prokh.) Prokh., *E. humilis* Ledeb., *E. irgisensis* Litv., *E. oidorrhiza* Pojark. reported from Turkmenistan and *E. barrelierii*

subsp. *thessala* (Form.) Bornm. and *E. polycnemoides* Hochst. ex Boiss. reported from Turkey and Saudi Arabia respectively), are not mapped because no reliable specimen has been seen in the listed herbaria; but they are included in diversity and endemism analysis. Two species, *E. falcata* L. and *E. szovitsii* Fisch. & C.A. Mey., with high morphological variation and rather wide distribution in the region have been divided into several taxa (*E. falcata* subsp. *macrostegia* (Bornm.) O.Schwarz, *E. falcata* subsp. *falcata* var. *galilaea* (Boiss.) Boiss., *E. szovitsii* var. *kharputensis* Azn. ex M.S. Khan) by some authors (Boiss, 1879; Khan, 1964; Radcliffe-Smith, 1986), but in this paper, we considered a broad view as a single species.

ASSESMENT OF CONSERVATION STATUS

All endemic and subendemic taxa were evaluated according to IUCN threatening categories (IUCN, 2011). Subendemic is considered for taxa occurring in two to three or rarely four countries with very narrow distribution. A taxon occurring in more than one country out of the twenty studied countries was not considered as an endemic. Taxa with adequate and reliable data were classified under three threatened categories, Critically Endangered (CR), Endangered (EN) and Vulnerable (VU), as well as two non-threatened categories, Near Threatened (NT) and Least Concern (LC). The category Data Deficient (DD) was used for taxa with inadequate information. Several local endemics known only from the type locality without or with very limited data, and in few cases doubtful species, were categorized as DD. In order to estimate the threat status, 96 endemics and subendemics of the genus *Euphorbia* have been evaluated using GeoCat, a browser-based tool that accomplishes rapid geo-spatial analysis to ease the process of Red Listing taxa (http://geocat.kew.org/; Bachman *et al*., 2011). For more accuracy in the geographical ranges of taxa and despite the existence of a comprehensive database (more than 22,000 plant specimens), detailed quantitative information on population size and fluctuation is lacking for some taxa. Therefore, they were applied to categorize the threat status (IUCN, 2011) in the form of the extent of occurrence (EOO) and area of occupancy (AOO) in criterion B (Memariani, Akhani & Joharchi, 2016). To estimate the AOO, the sliding scale of 1/10th of the maximum distance between any pair of points, calculated by

distance tool in Microsoft Encarta 2008, was applied in GeoCat. This scale is taxon-specific and not sensitive to collection density (Wills, Moat & Paton, 2003; Rivers *et al*., 2010). Lastly, we mapped all endemic and subendemic taxa with CR, E, VU and NT status in DIVA-GIS environment.

RESULTS

A total of 249 taxa of the genus *Euphorbia*, belonging to 239 species, five subspecies and five varieties with their infrageneric, section and subsection placement, life form, distribution, habitat, altitude and threat category has been identified from the extended SW Asia (Appendix 1). A list of 96 taxa of the studied *Euphorbia* is considered as endemic and subendemic to the area, including their country, the number of record, extent of occurrence (EOO), area of occupancy (AOO) and threatened category (Table 2). The area (km^2) of countries, the number of species and endemics, percent of endemics, number of *Euphorbia* implying the number of taxa of each subgenus, number of endemics and neophytes as well as percent of endemics and neophytes based on the examination of 249 taxa listed in Appendix 1 is summarized in Table 3. The number of total and endemic taxa of each section and subsection of the genus *Euphorbia* in the studied region has also been tabulated (Table 4). Of the 249 studied taxa of *Euphorbia* in the region, the distribution maps of 243 have been presented (Appendix 2, Maps 1-243).

Diversity

In the course of the study of 249 known *Euphorbia* taxa in the extended SW Asia, all four subgenera, *Athymalus*, *Chamaesyce*, *Esula* and *Euphorbia*, have representatives in the region (Appendix 1; Table 3; Table 4). The largest subgenus was *Esula* with 182 taxa (73%) followed by *Chamaesyce*, *Euphorbia*, and *Athymalus* with 33 (13.2%), 21 (8.4%) and 13 (5.2%) taxa, respectively (Table 3). Among 21 reported sections in subgenus *Esula*, 19 occurred in the studied region (Appendix 1; Table 4). The three largest sections were *Pithyusa* (Raf.) Lázaro, *Helioscopia* Dumort., and *Esula* (Pers.) Dumort. with 44 (17.6%), 42 (16.8%) and 21 (8.4%) taxa, respectively. The second largest groups were *Myrsiniteae* (Boiss.) Lojac., *Patellares* (Prokh.) Frajman, *Tithymalus* (Gaertn.) Roep.,

Herpetorrhizae (Prokh.) Prokh. and *Sclerocyathium* (Prokh.) Prokh. with 12, 11, 10, 9 and 8 taxa, respectively. The third largest groups were *Arvales* (Geltman) Geltman, *Holophyllum* (Prokh.) Prokh. and *Paralias* Dumort. with four taxa in each section, followed by the smallest ones, *Aphyllis* Webb & Berthel., *Exiguae* (Geltman) Riina & Molero, *Chylogala* (Fourr.) Prokh., *Pachycladae* (Boiss.) Tutin with two and *Calyptratae* Geltman, *Lagascae* Lázaro, *Lathyris* Dumort. and *Szovitsiae* Geltman with only one species (Appendix 1). The second largest subgenus in the studied region is *Chamaesyce*, including 15 sections, of which only five are distributed in SW Asia (Appendix 1; Table 4). The largest section was *Anisophyllum* Roep. subsection *Hypericifoliae* Boiss. with 24 species, of which 9 are non-native and introduced to the region as weeds and invasive plants (Appendix 1; Table 3). Other sections, *Cheirolepidium* Boiss. with three, and *Frondosae* Bruyns, *Scatorhizae* Yang & Berry and *Poinsettia* (Graham) Baill. with two taxa each are the smaller sections, of which the last is of New World origin and non-indigenous in the Old World (Appendix 1; Table 4). Of the 21 sections of subgenus *Euphorbia* only two, *Euphorbia* and *Tirucalli* Boiss., have been reported from SW Asia region. There are 21 species of the subgenus in the studied region, of which 19 belong to section *Euphorbia* and the two remaining ones occur in section *Tirucalli* (Appendix 1; Table 4). The smallest subgenus is *Athymalus* with seven sections, of which three are present in the studied region (Appendix 1; Table 4). Sections *Balsamis* Webb & Berthelot and *Pseudacalypha* Boiss. with six and five species, respectively, are the largest groups in the region, whereas, *Lyciopsis* Boiss. with only two species is the smallest one (Table 4). Based on Diva GIS analysis and the species richness point of view, the richest places for *Euphorbia* in study area are the eastern part of the Mediterranean region with more than 32 taxa; Alborz, Zagros and Anti-Taurus (S Turkey) with more than 25 taxa are the second richest areas, followed by SW and W Yemen, parts of Caucasus (including Armenia, NW Iran, NE Iraq, NE Turkey), N Turkey and west Himalaya (including E and NE Afghanistan, N and NE Pakistan) with about 20 taxa (Fig. 2).

Life form

Among the studied *Euphorbia* species which are distributed and spread in SW Asia, all different kinds of life forms including chamaephytes, geophytes, hemicryptophytes,

nanophanerophytes, phanerophytes, and therophytes have been found. Of the 249 taxa in the study region, the largest groups were hemicryptophytes, therophytes and chamaephytes with 85 (34.1%), 74 (29.7%) and 60 (24%) taxa, respectively, followed by nanophanerophytes, phanerophytes and geophytes with 25 (10%), 4 (1.6%) and 3 (1.2%) taxa, respectively (Appendix 1). In subgenus *Athymalus*, of the six mentioned life forms only four, chamaephytes, and nanophanerophyte with five species each and phanerophyte and hemicryptophytes with two and one species, respectively, were recognized (Appendix 1). Subgenus *Chamaesyce* comprised solely two life forms, therophytes and chamaephytes, with 28 and six taxa, respectively (Appendix 1). In subgenus *Esula*, hemicryptophytes (84 taxa, 46.1%), therophytes (46 taxa, 25.2%), and chamaephytes (43 taxa, 23.6%) are the dominant life forms followed by nanophanerophytes (6 taxa, 3.3%) and geophytes (3 taxa, 1.6%). Subgenus *Euphorbia* is prevalent by nanophanerophytes (14 species, 73.6%) followed by chamaephytes (5 species, 26.3%) (Appendix 1).

Endemism

A total of 96 taxa of *Euphorbia* are listed as narrow endemic and subendemic to the SW Asia (Table 2). They cover *c.* 38.5% of the whole *Euphorbia* taxa of the study area belonging to subgenera *Athymalus* (6 species, 6.2%), *Chamaesyce* (5 taxa, 5.2%), *Esula* (70 taxa, 72.9%) and *Euphorbia* (15 species, 15.6%). Among the listed endemic and subendemic taxa of *Euphorbia* in the study region, 62 (64.6%) and 34 (35.4%) taxa, respectively, are endemic to only one country or shared between more than one country (subendemic) (Table 2). Notably, the subendemic species to the studied region with widespread distribution have not been calculated for evaluation of their threat status.

The five countries richest in vascular plants species in the studied region are Turkey (8,650 taxa), Iran (7,500 taxa), Pakistan (5,700 taxa), Azerbaijan (4,300 taxa) and Afghanistan (4,000 taxa), respectively (Table 3). The highest percentages of endemics were observed in Turkey, Iran and Afghanistan with 30.9, 20 and 20 percent, respectively (Table 3). The most *Euphorbia* taxon-rich countries are Turkey (103 taxa), Iran (90 taxa), Syria (50 taxa) and Pakistan (46 taxa), whereas the highest number of endemics of *Euphorbia* occur in Iran (19 taxa), Turkey (13 taxa), Yemen (8 taxa) and Afghanistan (5 taxa) (Table 3). The highest percentage of *Euphorbia* endemics is also encountered in

Iran (21.1%), Yemen (15.5%), Oman (13.7%), Turkey (12.6%) and Afghanistan (12.5%) (Table 3). There was no *Euphorbia* endemic in Armenia, Iraq, Israel/Palestine, Jordan, Kuwait, Lebanon, Qatar and UAE (Tables 3, 4). All *Euphorbia* endemics of Afghanistan, Azerbaijan, Cyprus, Egypt, Iran, Pakistan, Syria, Turkey and Turkmenistan belong to subgenus *Esula* including, sections *Calyptratae* (one species), *Esula* (seven species), *Helioscopia* (six species), *Holophyllum* (one species), *Myrsiniteae* (two taxa), *Patellares* (three taxa), *Pithyusa* (23 taxa), *Sclerocyathium* (one species) and *Tithymalus* (four species). Other *Euphorbia* endemics occur in Oman, Saudi Arabia and Yemen comprising, five species of subgenus *Athymalus*, two species of *Chamaesyce* and eight species of *Euphorbia* (Tables 3, 4).

Neophytes

Among the listed *Euphorbia* taxa, 17 (6.8%) taxa are neophytes and non-native to the SW Asia (Table 3). Pakistan, Saudi Arabia and Turkey with 11, 10 and 10 species, respectively, are richest in introduced species followed by Egypt, Iran, Cyprus and Oman with nine, eight, seven, and seven, respectively (Table 3). The highest percentage of neophytes occurred in the three countries with the fewest numbers of *Euphorbia* species, the UAE (13), Qatar (13) and Kuwait (11), with 46.1%, 38.4% and 36.3%, respectively (Table 3). Among the 17 *Euphorbia* species introduced to the studied region, ten species have originated from the New World (Appendix 1; Table 3). The fewest non-native species were found in Syria and Turkmenistan with only one species, followed by Armenia, Azerbaijan, Jordan and Lebanon with two species in each country (Table 3).

Conservation status

With the exception of a few number of endemic *Euphorbia* species, the Red List categories of most endemic and subendemic taxa in SW Asia were evaluated for the first time (Table 2). A total of 96 endemic taxa were globally classified as Threatened comprising CR, EN and VU. Of the 96 endemics and subendemics of the studied *Euphorbia* taxa in the region, 54 were classified under threatened categories including, CR, EN and VU with 21, 16 and 17 taxa respectively and the rest ones were considered as NT, LC and DD with eight, 27 and seven taxa, respectively (Table 2). Mapping the

density of endemics and subendemics with CR, EN, VU and NT status demonstrated some areas with the highest importance (Fig. 3). The highest number of threatened taxa of the genus *Euphorbia* occurred in Cyprus with four taxa, followed by S, SE, SW Turkey, the southwestern most part of Saudi Arabia, S, SW, W Yemen and S Oman with three taxa in each area, followed by Alborz, Zagros in Iran, N Baluchestan in Pakistan, NE Turkey, W, NW Syria, N Israel/Palestine and Lebanon with two species in each region (Fig. 3).

Taxonomic enumeration

In the course of the morphological and phylogenetic studies of the genus *Euphorbia* in SW Asia, four new species, from Afghanistan, Iran, and Pakistan were discovered.

Euphorbia acanthoclada *Pahlevani* ***sp. nov.***

(*Fig. 4*; Breckle & Rafiqpoor, 2010: *Fig. Eu-03*)
Type: AFGHANISTAN. SW Afghanistan, Herat, between Shindand and Farah Rud, 1150 m, 23.iv.1967, *Rechinger 33383* (Holotype: B100846959; Isotypes: M0224496, WU).
Diagnosis: Most closely related to *E. acanthodes* Akhani, but differing by bark and stem pilose (not smooth), less intricate branching system, abaxial leaf face, especially margins, sparsely pilose; leaves without any conspicuous veins or only obscure midrib (instead of 1–3 prominent palmate veins), glands with two long horns (instead of two short ones or no horns), glands reddish-brown.

Description: Perennial, caespitose, spinescent and pubescent subshrubs, 15–20 cm high, woody last year branches becoming whitish. Cauline leaves lanceolate, oblong to oblanceolate, glaucous, without prominent veins or only with obscure midrib, occasionally sparsely pilose beneath, especially at margin, glabrous above, 10–15 × 3–5 mm, sessile, truncate to rounded at the base, acute to subacute at apex, entire to subentire and cartilaginous at margin. Terminal rays 2–3, once dichotomously branched; with 0–3 axillary rays; rays and axillary rays later becoming rigid spinescent. Ray leaves similar to cauline leaves in shape and size; raylet leaves mostly ovate to rather rhombic, rounded at

base, acute and mucronulate at apex, entire to subentire and cartilaginous at margin. Cyathial involucre campanulate, 3–3.5 mm in diameter, internally pilose and externally glabrous; lobes lanceolate and acute, glands lunate, two long horns, reddish-brown. Capsules immature, trilobate, 5.5–7 mm in diameter, glabrous. Seeds unknown.

Affinity and plant geography: Morphological characters of the newly discovered species indicate that it belongs to section *Pithyusa*. Despite our attempts for phylogenetic studies, no DNA could be extracted from the rather old herbarium specimens. This species, like many other members of section *Pithyusa*, is an Irano-Turanian element. *Euphorbia acanthoclada* has been collected only from type locality in SW Afghanistan, Herat province and once from an uncertain place [Gijam] in SW Afghanistan by Köie (4227 W) (Appendix 2, Map 45). This species was misidentified and reported as *E. acanthodes*, an endemic and rare species from SW Iran, by Breckle *et al*. (2013). There is no ecological information of its habitat, it is found at elevations between 900 and 1150 m. Based on conservation analysis and IUCN threatened categories, it is suggested to evaluate its conservation status as 'vulnerable' (VU) (IUCN, 2011).

Additional specimens examined: AFGHANISTAN: Gija [Gijam], 900 m, 10.iv.1949, *Köie* (4227 W).

Etymology: The epithet '*acanthoclada*' refers to its spiny shoots.

Euphorbia boreo-baluchestanica *Pahlevani* ***sp. nov.***

(*Fig. 5*)

Type: PAKISTAN. W Pakistan, Baluchistan, Kalat, between Basima and Surab, 1600-1700 m, 28º 29′ N 66º 19′ E, 21.iv.1965, *Rechinger 28318* (Holotype: W; Isotypes: B100846955, M0224484).

Diagnosis: *Euphorbia boreo-baluchestanica* is closely related to *E. prolifera* Buch.-Ham. ex D.Don. It differs from the latter by orbicular to obovate cauline leaves (instead of linear, lanceolate or oblanceolate ones), 7–18 × 5–11 mm (instead of 20–50 × 2–5 mm),

cuneate to rounded at the base (not attenuate or truncate), mostly with 3–5 conspicuous palmate nerves (instead of inconspicuous ones or only midrib), mostly mucronulate or rounded apex (instead of obtuse, acute to subacute), absence of densely-leafy sterile shoots (instead of presence of densely-leafy sterile shoots), cyathial glands with two long and mostly lobate horns (instead of very short and simple or rather denticulate ones), narrowly conical (instead of chubby conical), smaller (3.5–4 × 3–3.5 mm instead of 4.5 × 6 mm) capsules; narrowly conical, irregularly pitted (instead of ovoid-subglobose, shallowly rugulose-ridged), smaller seeds (2.2–2.5 × 1.7–2 mm instead of 3.5 × 3 mm), larger and permanent caruncles (instead of minute and caducous ones).

Description: Perennial herbs, erect, 25–35 cm high, several shoots arising from rather woody stock, glabrous, glaucous. Stem base 2.5–3 mm diameter. Cauline leaves orbicular to obovate, 7–18 × 5–11 mm, glabrous, glaucous, apex mucronulate or rounded, rounded to cuneate at the base, margin entire to subentire, cartilaginous, sessile, with 3–5 palmate nerves. Terminal rays (3) 4 (5), two to three times dichotomous, usually elongated (up to 12 cm), axillary rays 3–8, more elongated than the terminal ones (up to 20 cm), once or mostly twice dichotomously. Ray-leaves similar to cauline leaves, 3–4; raylet-leaves similar to the cauline and ray leaves but remarkably smaller (6–10 × 6–12 mm). Cyathial involucre campanulate, 2.5–2.8 mm in diameter, lobes lanceolate, lacerate; glands lunate, brown, with 2 long, yellowish horns, mostly 2-lobate. Capsules conical, superficially trilobate, 3.5–4 × 3–3.5 mm, glabrous, occasionally whitish punctate, pedicels, 3.5–4 mm long, styles 2 mm long. Seeds conical, irregularly pitted, 2.2–2.5 × 1.7–2 mm, yellowish to light brown, caruncle conical, 0.7–1 × 0.5 mm, brownish.

Affinity and plant geography: The newly discovered species belongs to section *Pithyusa* and is sister to *E. prolifera* (Pahlevani, unpubl. data). *Euphorbia boreo-baluchestanica* is limited to the N part of Baluchistan, Pakistan near the frontier of Afghanistan (Appendix 2, Map 68). In addition to obvious morphological differences which have been mentioned in diagnosis, its chorotype is also different from *E. prolifera*. *Euphorbia boreo-baluchestanica* is an Irano-Turanian element (Appendix 2, Map 68), whereas, *E. prolifera* is a Sino-Himalayan element (Appendix 2, Map 177) (Geltman, 2015). It occurs

from SW China, Thailand, Burma, Nepal and N India to NW Pakistan as the most western part of its distribution. Our unpublished molecular data indicate that these two species and *E. erythradenia* Boiss., *E. gedrosiaca* Rech.f., Aell. & Esfand., *E. plebeia* Boiss., *E. spartiformis* Mobayen and *E. sulphurea* Pahlevani form a distinct and supported clade in section *Pithyusa*. Of the seven species of this group, two occur in Pakistan and the five remaining ones are endemic to Iran (Pahlevani *et al*., 2015). With the exception of *E. prolifera*, other members of this clade are Irano-Turanian elements, distributed from south-eastern parts of the Zagros Mountains toward Baluchistan of Iran and Pakistan (Appendix 2, Maps 99, 107, 175, 200, 204). The specimens deposited in the mentioned herbaria have been mistakenly identified and reported as *E. microsciadia* Boiss. by Radcliffe-Smith (1986).

Ecology and conservation status: *Euphorbia boreo-baluchestanica* has been collected by several botanists from the semi-desert zone of lower mountane regions at elevation between 1600–2130 m on gravelly and stony beds. According to IUCN threatened categories and our conservation analysis, it is suggested to evaluate its conservation status as 'vulnerable' (VU) (IUCN, 2011).

Additional specimens examined: PAKISTAN: W. Pakistan, Baluchistan, Kalat, 24 km S Surab, 28º 29′ N 66º 19′ E, 1.iv.1965, *Rechinger* (27380 M, W, WU); W. Pakistan, Kalat, Surab, 69 km from Kalat towards Khuzdar, 1700 m, 28º 29′ N 69º 19′ E, 1.iv.1965, *Rechinger* (27371 M); Baluchistan, Kalat, 9.v.1963, *Siddigi* (2009 K); Skalku [Iskalku], Kalat, 2134 m, 19.vi.1957, *Akbar* (1882 K); Kalat, Gandava pass, *Stocks* (401 K); 30 km S of Quetta in Pass, 2000 m, 19.vii.1969, *Andersen & Petersen* (464 K).

Etymology: The epithet '*boreo-baluchestanica*' refers to place N of Baluchistan, Pakistan where the species occur.

Euphorbia kavirensis *Pahlevani* **sp. nov.**
(*Fig. 6*)

Type: IRAN. Esfahan, Kashan, Deh-abad, near Abuzeyd-abad, 1000 m, 3.vi.1975, *Moussavi & Tehrani* 30689 E (Holotype: W; Isotype: IRAN55498).

Diagnosis: *Euphorbia kavirensis* is closely related to *E. gedrosiaca* but differing by obovate to cuneate cauline leaves (instead of linear-lanceolate to oblong ones), 3 conspicous to rather inconspicuous palmate nerves (instead of midrib only), terminal rays 1–2 (3) (instead of 3–4), branching once dichotomous (instead of twice dichotomous), raylet-leaves sparsely pilose at the base (instead of glabrous), seeds smaller (2.5–2.8 × 1–1.5 mm instead of 3–3.3 × 1.5–2.2 mm).

Description: Perennial erect, glabrous herbs, 18–50 cm high, with several branches from base. Cauline leaves rather sparse, obovate to cuneate, 3-conspicuous to rather inconspicuous palmate nerves, 6–11 × 3–5 mm, glabrous, glaucous, apex acute, mucronulate or obtuse, cuneate to rounded at the base, margin entire, sessile. Terminal rays 1–2 (3), up to once dichotomous, axillary rays 0-2, mostly longer than terminal ones. Ray-leaves similar to the cauline leaves but smaller, 2–3; raylet-leaves ovate to suborbicular, sparsely pilose at the base, 3–4 × 3–3.5 mm. Cyathial involucre campanulate, 2.5–3 mm in diameter; lobes lanceolate, lacerate; glands trapeziform, hornless or with two short horns. Capsules conical, shallowly trilobate, glabrous, immature or opened. Seeds conical, irregularly pitted, 2.5–2.8 × 1–1.5 mm, dark brown, caruncle conical, 1 × 0.5 mm.

Affinity and plant geography: *Euphorbia kavirensis* belongs to section *Pithyusa* and is sister to *E. gedrosiaca* (Pahlevani, unpubl. data). It is misidentified as *E. gedrosiaca* or *E. erythradenia* on the herbarium sheets. All three mentioned species comprise (1) 2–3 (4) terminal rays, but with the exception of morphological and phylogenetical differences, their distributional pattern is also different. *Euphorbia erythradenia* is limited to the south-eastern part of Zagros Mountains, *E. gedrosiaca* is distributed to SE and E Iran to W Afghanistan, whereas, *E. kavirensis* occurs in C Iran in desert of central Iran (Appendix 2, Map 131).

Ecology and conservation: *Euphorbia kavirensis* was found in the large Iranian interior desert "Dashte Kavir" in steppes of *Artemisia* L. and on gypsum hillsides at 950–1400 m elevation. So far this species in known from six localities, however, because of homogenous conditions in interior steppes we expect further locations in the future. For more precise assessment of conservation status of the species, some more excursions in its habitat will be needed. Based on IUCN threatened categories and existing data of *E. kavirensis*, it is suggested to evaluate its conservation status as 'vulnerable' (VU) (IUCN, 2011).

Additional specimens examined: IRAN: Esfahan, Kavir Protected region, In desert 50-54 km from Chashmeh-ye Safid Ab [Cheshme Sefid Ab] towards Haji Ali Abbas, 950 m, 26.v.1974, *Rechinger* (46480 IRAN, M, W); Esfahan, Nain, Anarak, 14 km on the road to Chopanan, 1400 m, 13.x.1974, *Foroughi & Assadi* (15140 W); Between Tehran and Tabas, south of Dasht-e Kavir, 950 m, 33º 32´ N 54º 59´ E, 6.iv.1972, *J. Léonard* (5413 IRAN, K); Yazd, on the desert margin between Nain and Aghda, 1000 m, 21.iv.1948, *Rechinger et al*. (2695 K); Between Tehran and Tabas, east of Dasht-e Kavir, 34º 05´ N 52º 27´ E, 900 m, 3.iv.1972, *J. Léonard* (5332 IRAN, K).

Etymology: The epithet '*kavirensis*' refers to Dasht-e Kavir, Persian name for the temperate desert of the interior Iran.

Euphorbia ziaratensis *Pahlevani* **sp. nov.**

(*Fig. 7*)

Type: PAKISTAN. Ziarat, ±2440 m, 28.v.1968, *Zaffar Ali 4827* (Holotype: K)

Diagnosis: *Euphorbia ziaratensis* is closely related to *E. sulphurea*, but differing by glabrous, purplish plants, smaller (3–5 × 1–2 mm instead of 5–13 × 3–7 mm) ovate-lanceolate cauline leaves with mostly irregularly minutely denticulate margins, cyathial glands with two long stramineous horns, larger (4–4.5 × 3–3.2 mm instead of 3.1–3.5 × 2.7–3 mm) capsules, seeds rather longer with obscure pits, compressed and flattened.

Description: Glabrous, procumbent-ascending perennial herbs, 4–8 cm high. Many stems arising from caudiculi borne upon the rootstock. Cauline leaves ovate-lanceolate, 3–5 × 1–2 mm, apex subacute, obtuse to rounded, tapering at the base, margins subentire to irregularly minutely denticulate, sessile. Terminal rays 3–4, one to two times dichotomous, with no axillary ray. Ray-leaves 3–4, rhombic-ovate, 4–5 × 3–5 mm, subacute or obtuse, cuneate at the base; raylet-leaves similar to ray-leaves but smaller, truncate at the base. Cyathial involucre campanulate, 1.5–2 mm in diameter, lobes lanceolate, lacerate; glands transversely ovate, reddish, with two long, stramineous and subulate horns. Capsules conical, 4–4.5 × 3–3.2 mm, shallowly trilobate, glabrous; styles 1 mm long. Seeds compressed-conical, 2.5–2.8 × 1.5–1.8 mm, shallowly pitted, dark brown, caruncle conical, 0.7–1 × 0.8–1 mm.

Affinity and plant geography: Based on the morphological characteristics of *E. ziaratensis*, it belongs to section *Pithyusa*. The type specimen has been mistakenly considered as *E. aucheri* Boiss. from Pakistan by Radcliffe-Smith (1986). But after close examination of the specimens, it was found that it not only doesn't belong to section *Herpetorrhizae* but it is a member of section *Pithyusa*. The most distinguishable features to separate the new species from *E. aucheri* are its capsules and seeds (Pahlevani *et al*., 2015). It is remarkable that sole specimen of *E. aucheri* reported from Pakistan (Radcliffe-Smith, 1986) in fact belongs to this new species. *Euphorbia ziaratensis* was found from highlands of northern Baluchistan of Pakistan (Appendix 2, Map 222) which is the hotspot of medicinal and endemic plants in Pakistan (Ali & Qaisar, 1986; Bibi *et al*., 2015).

Ecology and conservation: Based on information from herbarium specimens *E. ziaratensis* was found in the alpine zone of the highlands of northern Baluchistan on stony ground at 2400–2600 m elevation. So far, only two specimens of the species have been found in the studied herbaria both of which from type locality in Ziarat or nearby. It seems *E. ziaratensis* is very rare. Because of its rarity and vulnerability, we suggest the evaluation of this delicate species as 'critically endangered' (CR) according to the

International Union for Conservation of Nature (IUCN) threatened categories (IUCN, 2011).

Additional specimens examined: PAKISTAN: Quetta, In jugo E Ziarat, 30º 20´ N 67º 30´ E, 2500–2600 m, 13.v.1965, *Rechinger* (29395 W).

Etymology: The epithet '*ziaratensis*' refers to the type locality of the new species in Ziarat, a place in northern Baluchistan of Pakistan.

DISCUSSION

Among 249 *Euphorbia* taxa reported in the updated checklist of the region, 121 (48.6%) taxa are endemic and occur only from the extended SW Asia (Appendices 1, 2). Of the 121 endemic species to the studied region, 94 (77.7%) belong to subgenus *Esula* and the remaining ones have been attributed to subgenera *Euphorbia*, *Athymalus* and *Chamaesyce* with 14 (11.5%), seven (5.7%) and six (4.9%) taxa respectively (Appendix 1).

Subgenus *Chamaesyce* is the only subgenus with a New World origin and diversification in the genus *Euphorbia* (Yang *et al*., 2012), so that the number of endemics in SW Asia is smaller than in the other subgenera. They are mostly weeds and invasive plants, especially the members of the section *Anisophyllum* subsection *Hypericifoliae* with C_4 photosynthetic pathway (Pahlevani & Riina, 2011; Yang & Berry, 2011). Among 32 taxa reported from subgenus *Chamaesyce* in SW Asia, 24 belong to section *Anisophyllum* subsection *Hypericifoliae* (Appendix 1). Of these 24 species, eight are pervasive weedy species of New World origin and the 16 remaining ones are Old World native species. Some species of the section are probably well-known for their globally weedy character in mainly temperate regions such as *E. maculata* L. and *E. humifusa* Willd. (Appendix 2, Maps 27, 33) and some others are species widespread in warm temperate and tropical regions like *E. hirta* L. and *E. hyssopifolia* L. (Appendix 2, Maps 25, 29) (Yang & Berry, 2011). However, some species in this section such as *E. peplis* L. are specialized on either coastal sandy beaches around Black Sea and Mediterranean Sea or inland shores

and salt lakes (Appendix 2, Map 35). With the exception of the doubtful species, *E. abdulghafooriana* Abedin from Saudi Arabia (so far known only from type collection), there was no endemic species from section *Anisophyllum* in SW Asia. Therefore, SW Asia is not an autochthonous developing centre of C_4 species of *Chamaesyce* clade *sensu* Yang & Berry (2011) and most species in this group indicate a New World distribution which has occurred in other angiosperms such as *Heliotropium* L. (Akhani, 2007). In contrast to many other groups of *Euphorbia*, none of the species of subsection *Hypericifoliae* has a caruncle. Thus, in subsection *Hypericifoliae*, the common ant dispersal of carunculate seeds is replaced by bird dispersal (ornithochory). In fact, long-distance seed dispersal in this group is most likely related to this strategy (Pahlevani & Akhani, 2011; Yang & Berry, 2011). All these features pre-adapt some species of this group, *E. granulata* Forssk. and *E. forskaolii* J.Gay (Appendix 2, Maps 23, 22), to successfully pioneer hot and dry deserts with saline soils and to conquer new areas via long-distance dispersal.

Among four other sections of subgenus *Chamaesyce* occurring in the study area, section *Poinsettia* with two weedy introduced species, *E. cyathophora* Murray and *E. heterophylla* L. (Appendix 2, Maps 21, 24; Table 7), is another New World group, while the remaining three are distributed in the Old World. Section *Frondosae* is of African origin, including a total of seven species, of which two delicate and tuberous species, *E. pirottae* N.Terrac. and *E. quaitensis* S.Carter, occur in Oman, Saudi Arabia and Yemen (Appendix 2, Maps 38, 40; Table 4). Section *Scatorhizae*, also with seven species, is mostly distributed in and restricted to E and NE Africa and, rarely, India with two species, *E. agowensis* Hochst. ex Boiss. and *E. applanata* Thulin & Al-Gifri penetrating to S of Arabian Peninsula and one endemic species in S Yemen (Appendix 2, Maps 15, 16). Lastly, three annual C_3 taxa, *E. cheirolepis* Fisch. & C.A. Mey, *E. petiolata* var. *petiolata* Banks & Sol. and *E. petiolata* var. *postii* (Boiss.) Radcl.-Sm., with a limited geographical distribution from E Mediterranean region to C Asia (Appendix 2, Maps 19, 36, 37; Table 7) belong to the small Old World section *Cheirolepidium* with only the above three mentioned taxa. Of these, *E. cheirolepis* is specialized to sandy dunes in Irano-Turanian inlands (Pahlevani & Akhani, 2011), *E. petiolata* var. *petiolata* has been collected up to the most northern part of Oman as the lowest latitude of this species, and

E. petiolata var. *postii* is a rare subendemic taxon occurring in calcareous lowlands of N Syria and S Turkey.

In the studied region, *Athymalus* is the smallest subgenus with 13 species of which seven are endemic, mostly distributed and limited to the southern part of the SW Asia in the lowlands near the Red Sea and Arabian Sea (S Oman, SW Saudi Arabia and Yemen) and two species *E. larica* Boiss. and *E. cuneata* Vahl. (Appendix 2, Maps 3, 6) penetrating to the countries around the Persian Gulf (Bahrain, S to SE Iran, Qatar and UAE) and SE Egypt respectively. In spite of the highly succulent lifeform of the species in subgenus *Athymalus* in Southern Africa, the Iranian, Arabian and Socotran members are not too succulent having mostly pencil-like assimilating stems (Bruyns *et al*., 2011; Peirson *et al*., 2013). The aridity in these lowlands favors nanophanerophytes and chamaephytes, and rarely phanerophytes (Peirson *et al*., 2013).

Of the subgenera with Old World origin, subgenus *Euphorbia* is the second largest one as concerns the number of endemics in the studied region. Almost all its species are restricted to the Arabian Peninsula, however, two species, *E. caducifolia* Haines and *E. royleana* Boiss. (Appendix 2, Maps 225, 237) are distributed in Pakistan toward Indian subcontinent (Appendix 1). The members of the subgenus are almost completely succulent without any annual species (Bruyns *et al*., 2011). Although *Euphorbia* is the largest genus in Saudi Arabia and Yemen with 44 and 45 taxa respectively, these countries have been too arid for *Euphorbia* to have speciated there significantly (Bruyns *et al*., 2011). This theme is similar in some other groups of angiosperms, in other words, Saudi Arabia as the largest country (about 2,000,000 km^2) in the studied region comprises only roughly 2,000 species which is much less than a small country like Azerbaijan (86,600 km^2) with *c.* 4300 species (Table 3). It is most likely related to very harsh and arid situation in the area (Table 3). It is considerable that most species are distributed in SW part of Saudi Arabia near the Red Sea (Appendix 2, Maps 1, 2, 3, 15, 17, 30, 38, 42, 223, 224, 226, 227, 229, 231, 232, 234, 238, 240, 242).

The largest and the most diversified subgenus is *Esula* with the largest number of species and endemics in SW Asia (Tables 2, 3). As can be derived from figure 1, the larger part of the studied region is situated in the temperate area where also most species of *Euphorbia* subgenus *Esula* are concentrated and distributed. With the exception of

several New World species (38 species), mostly (25 species) retrieved in section *Tithymalus* and the 13 remaining ones in sections *Helioscopia* and *Paralias*, the other 442 taxa inhabit the Old World and there mainly the northern hemisphere (Riina *et al*, 2013; Geltman, 2015). Of the 19 sections of the subgenus occurring in the region nine have endemic species (Appendix 1; Table 4). The three largest sections of the subgenus *Esula* are *Helioscopia* (128 taxa), *Esula* (101 taxa) and *Pithyusa* (60 taxa) are also the largest ones in the area, with 42, 21, and 44 taxa, respectively.

Thus, more than 73% taxa of section *Pithyusa* occur in SW Asia and 28 taxa (63.6%) are endemic to one or two countries in the studied region (Table 2). Iran and Turkey with 21 (47.7%) and 16 (36.3%) species and 13 (29.5%) and four (9.1%) endemics, respectively, are the most species-rich countries both in the number of species and endemics in section *Pithyusa* (Appendix 2, Maps 46, 99, 100, 113, 126, 131, 143, 150, 168, 173, 175, 176, 186, 197, 200, 204, 208; Table 4). Afghanistan and Pakistan with two endemic species each are the second richest countries in the section followed by Cyprus and Egypt with only one endemic taxon (Appendix 2, Maps 45, 68, 73, 144, 157, 222; Table 4). The members of this section are mostly hemicryptophytes (70.4%) and the remaining ones are chamaephytes (25%) and therophytes (4.5%). The dominance of hemicryptophytes underlines that the members of the section are well adapted to the cold semi-arid climate of the mountainous regions during their speciation (Kamakhina, 1994). The two therophytes, *E. falcata* and *E. gaillardotii* Boiss. & Blanche, are distributed to almost all part of SW Asia and eastern Mediterranean to western Irano-Turanian regions respectively (Appendix 2, Maps 102, 106). These two therophyte species are mostly spread in the disturbed and areas under human influence, such as fields, gardens, roadsides *etc*. It is remarkable that their seeds are either ecarunculate (*E. gaillardotii*) or readily caducous (*E. falcata*), both possible adaptations to long-distance dispersal (Pahlevani & Akhani, 2011). *Euphorbia falcata* is either the sole or one of two species in the countries just harbouring one or two members of this section, Egypt, Kuwait, Oman, Qatar, Saudi Arabia, UAE and Yemen (Table 4). Apparently, small seed size, ballistic mechanism as a primary seed dispersal, myrmecochory and ornithochory as the secondary seed dispersal mechanisms in *E. falcata* have been the main reason for wide distribution pattern. The two sole endemic species of this section in Egypt and Arabian

Peninsula are *E. obovata* Decne. and *E. petitiana* A. Rich., respectively, of which the former one is reported from the south Sinai mountains at the elevation between 1700–2300 m, and the latter one from elevations between 1800–3000 m in the W to SW Yemen and Ethiopia (Appendix 2, Maps 157, 169). *Euphorbia petitiana* has been wrongly considered in section *Helioscopia* (Riina *et* al., 2013; Geltman, 2015) but both its morphology and phylogeny proved that it is a member of section *Pithyusa* (Pahlevani, unpubl. data).

Members of section *Helioscopia*, the second largest group of subgenus *Esula* in the studied region, are mostly distributed in the mesic areas (Riina *et al*., 2013; Pahlevani & Riina, 2014; Hand *et al*., 2015). Of all 128 taxa in section *Helioscopia*, 32.8% occur in SW Asia. Turkey, Syria, Iran, as well as Lebanon are the most species-rich countries with 34 (81%), 18 (42.8%), 13 (31%) and 13 (31%) taxa, respectively (Table 4). The number of species in the section decreases from west to east and north to south together with decreasing humidity and rainfall. Geobotanical and bioclimatic situation make the Mediterranean and C European regions one of the most species-rich areas for section *Helioscopia*. Its members are mostly found in mesic habitats such as forests, woods, seashores, riverbanks, steppe forests and irrigated and cultivated areas (Appendix 1). Although the cosmopolitan weedy species *E. helioscopia* L. is found everywhere, even in Arabian Peninsula, it is restricted to irrigated and arable lands with sufficient amounts of accessible water. The members of the section in Iran are limited to Alborz, Zagros and northwest mountains where the rainfall is higher than in other parts of Iran. In the western part of the SW Asia they mostly occur around the Black and Mediterranean Sea with rather high humidity. In the eastern part of SW Asia (E Afghanistan and NE Pakistan) only two sino-Himalayan elements, *E. cornigera* Boiss. and *E. maddenii* Boiss. as well as the cosmopolitan weedy species *E. helioscopia* are found (Appendix 2, Maps 82, 116, 142). Members of the section are mostly hemicryptophytes and therophytes with 18 (42.8%) and 16 (38.1%) taxa, respectively, followed by geophytes, nanophanerophytes and chamaephytes with 3 (7.1%), 3 (7.1%) and 2 (4.7%) taxa, respectively (Appendix 1). The dominance of hemicryptophytes and therophytes in the region manifest the harsh mountainous conditions for the hemicryptophytes as well as the availability of disturbed areas such as arable lands for therophytes. With the exception of a nanophanerophyte

endemic of Cyprus, *E. lemesiana* Hadjik, Hand & Frajman (Appendix 2, Map 137), all other endemics of the section in the studied region are hemicryptophytes of the mountainous regions (Appendix 1).

The third largest group of subgenus *Esula* in SW Asia is section *Esula* which includes 20.8% of whole species (101 taxa) of the section. The members of the section are found in many parts of the Old World from Madagascar to Asia and Europe and they are also introduced in the New World (Riina *et al*., 2013). They are mostly phylogenetically poorly understood taxa with complicated and complex patterns of morphological variation (Frajman & Schönswetter, 2011; Pahlevani *et al*., 2016). They have also occupied a wide range of habitats including, meadows, steppes, semi-deserts, littoral vegetation, arable lands and other disturbed areas (Riina *et al*., 2013). The members of the section are mostly hemicryptophytes (85.7%) and rarely chamaephytes (14.2%) and there are no therophytes in this group. In the extended SW Asia, Afghanistan, Iran, Pakistan and Turkmenistan with eight (38.1%), seven (33.3%), six (28.5%) and six (28.5%) species, respectively, are the richest countries in section *Esula* (Table 4). The number of endemics is proportional the number of species, with the three and two species in Iran and Afghanistan, respectively, followed by Pakistan and Turkmenistan with only one species in each country (Appendix 2, Maps 65, 95, 112, 115, 132, 206; Table 4). There is no representative of the section in eastern part of Mediterranean region as well as Arabian Peninsula with the exception of rather widespread weedy species, *E. schimperiana* Scheele, a tropical African species which penetrates to some highland parts of Oman, Saudi Arabia and Yemen (Appendix 2, Map 189). The members of the section are distributed mostly in the Irano-Turanian region, especially C Asia, and from east to west the number of species has been decreased. It seems they are adapted to a wider range of habitats and for this reason many members of this section are found in disturbed areas such as roadsides, arable lands, eroded soils, and fallow lands. Although there are some problematic invasive species like *E. cyparissias* L., *E. schimperiana* and *E. virgata* Waldst. & Kit. (Appendix 2, Maps 85, 218, 189) in this section, several endemic and isolated species such as *E. ecorniculata* Kitam., *E. khabrica* Pahlevani and *E. gulestanica* Podlech (Appendix 2, Maps 95, 112, 132) with limited populations have also been reported (Pahlevani *et al*., 2016).

Sections *Tithymalus* and *Patellares* with three endemics for each section in the region are the second largest groups of the subgenus *Esula* (Appendix 1; Table 4). Of the 40 taxa in section *Tithymalus*, 32 occur in the New World and the eight remaining ones in the Old World (Peirson *et al*., 2014). In addition to the eight species of the section in the Old World which two species (*E. herniariifolia* Willd. and *E. peplus* L.) falling in two varieties are also added. With the exception of Algerian endemic *E. hieroglyphica* Coss. & Durieu ex Boiss. the remaining nine Old World taxa of the section *Tithymalus* occur in the extended SW Asia (Appendix 1; Table 4), mostly in the Mediterranean region. Syria, Turkey and Lebanon with five, five and four taxa are the richest countries (Table 4). The widespread, weedy species *E. peplus* has been introduced not only to the New World but also to many other countries in the Old World and *E. chamaepeplus* Boiss. & Gaill. has penetrated to Iraq, S Iran and NW and W Saudi Arabia (Peirson *et al*., 2014). Three rare endemic species of this section are *E. isaurica* M.S. Khan, *E. promecocarpa* Davis and *E. punctata* Delile which are distributed to Turkey, Syria, and Egypt, respectively (Appendix 2, Maps 127, 178, 180). The perennial taxa of section *Tithymalus* in the Old World such as *E. caudiculosa* Boiss., *E. herniariifolia*, *E. isaurica* and *E. promecocarpa* are very delicate and fragile species which occur in crevices of limestone and cliffs. Other taxa of the section are therophytes which are found in disturbed areas, even the endemic species *E. punctata* (Boulos, 2000).

Section *Patellares* is well-known and recognizable among the other sections of the subgenus *Esula* because of its connate raylet-leaves (Geltman, 2002). There are 18 taxa in the section, 11 (61%) of which occur in the studied region (Appendix 1; Table 4). Turkey with 10 (90.1%) taxa was the richest country followed by Armenia, Azerbaijan and Iran with four (36.3%), three (27.2%) and three (27.2%) species respectively (Table 4). There is no representative of the section in Afghanistan, Egypt, Israel/Palestine, Jordan, Pakistan, Turkmenistan and Arabian Peninsula (Table 4). Among the 11 taxa in the region, there are three endemics, *E. akmanii* I.Genç & Kültür, *E. amygdaloides* subsp. *robbiae* (Turrill) Stace and *E. davisii* M.S. Khan, all occurring in Turkey (Appendix 2, Maps 49, 54, 87). The members of the section are chamaephytes with a rather robust habit which are mostly distributed to the Mediterranean region, Caucasus, Hyrcanian region and highlands of W Iran. They are adapted growing in mesic habitats such as

dense forests (Hyrcanian forests), sparse and open forests (Zagros forests), mountane meadows (Taurus Mts.) and seldom in rocky places (Riina *et al*., 2013). This group of *Euphorbia* decreases dramatically from west to east and north to south in the studied region, both in the number of species and endemics. The eastern and southern distribution limits of this section are both in Iran, namely the eastern part of the Hyrcanian forests and southwestern of Zagros, respectively (Appendix 2, Maps 53, 98).

The remaining sections with endemic species in subgenus *Esula* in SW Asia are *Calyptratae*, *Holophyllum*, *Paralias*, *Sclerocyathium* and *Myrsiniteae* with one species for each section but two in the last one (Table 4). There are 17 taxa in section *Myrsiniteae* mostly distributed in the Mediterranean region followed by Iranian highlands and Caucasus, 12 of which are found in the studied region (Appendix 1). Turkey and Iran are the richest countries with nine (75%) and eight (66.6%) taxa respectively (Table 4). No representative of the section was observed from Egypt and the Arabian Peninsula. Two endemic taxa *E. anacampseros* var. *tmolae* M.S. Khan and *E. veneris* M.S. Khan have been reported from Turkey and Cyprus respectively (Appendix 2, Maps 56, 217). With the exception of *E. aleppica* L. and the recently transferred *E. normannii* Schmalh. ex Lipsky from section *Arvales* (Geltman, 2015) as therophytes (11.7%), the other taxa in the section are chamaephytes (88.3%). The members in this group constitute mostly semi-shrubs with fleshy or almost succulent leaves, which are kept in winter, adapted to harsh and unfavorable environmental conditions including mostly stony limestone slopes (Pahlevani, Geltman & Riina, 2011). There are in total two perennial species in section *Calyptratae*, *E. connata* Boiss. and *E. calyptrata* Coss. & Durieu which are endemic to C to S Iran and widespread in N Africa respectively (Appendix 2, Map 80), where they are found only in the deserts (Pahlevani *et al*., 2015). Apparently, one reason for their rather limited distribution is related to their very large seed and caruncle size. Generally, perennial leafy spurges distributed to the open deserts possess rather gross seeds and caruncles, but seed projection in such a large and heavy seed as primary seed dispersal seems inefficient and the transfer of such a large seed as secondary seed dispersal needs larger ants in comparison with smaller ones in different habitats (Pahlevani *et al*., 2015).

Members of section *Holophyllum* are mostly distributed outside of the studied region in the Far East, C Asia, S Siberia and the Himalayas (Riina *et al.*, 2013; Geltman, 2015). Of

the 27 species in this section, there are only four species (14.8%), *E. jacquemontii* Boiss., *E. megalocarpa* Rech.f., *E. thomsoniana* Boiss. and *E. wallichii* Hook.f. in the extended SW Asia, whose distribution is limited to Afghanistan and Pakistan in the western part of Himalaya (Appendix 2, Maps 128, 148, 211, 219). The sole and remote endemic species in the section is *E. megalocarpa* with a rather high morphological similarity to *E. wallichii* but with different distributional pattern. *Euphorbia wallichii* is a Sino-Himalayan element whereas *E. megalocarpa* is an Irano-Turanian element in west Afghanistan (Geltman, 2015).

There are ten species in the section *Sclerocyathium*, seven of which (70%) occur in the studied region (Appendix 1; Table 4). With the exception of the annual species, *E. grossheimii* (Prokh.) Prokh., distributed and penetrated sparsely to western part of SW Asia (Azerbaijan, Iraq, Israel/Palestine, Saudi Arabia, some parts of Iran and Pakistan), the other species mostly occur in N, E Iran, Turkmenistan, Afghanistan and Pakistan (Appendix 2, Maps 70, 71, 103, 111, 191, 192, 213, 215). The members of the section with large capsules and seeds are mostly found in the semidesert areas (Pahlevani *et al.*, 2015). The most species-rich countries in the section *Sclerocyathium* are Iran, Pakistan, Afghanistan, and Turkmenistan with 5 (50%), 4 (40%), 3 (30%) and 3 (30%) species, respectively (Table 4). The single endemic species in this section is *E. ferdowsiana* Pahlevani from NE Iran with very limited distribution in Binalood mountain of Khorasan province (Pahlevani *et al*., 2015). The most dominant life form in the section are hemicryptophytes with four (57.1%) species followed by therophytes and chamaephytes with two (28.5%) and one (14.2%) species, respectively (Appendix 1).

Section *Paralias* with 13 species distributed in the Mediterranean region, Balkans, Caucasus, Macaronesia and Caribbean (Riina *et al*., 2013) has five species in the extended SW Asia (Appendix 1; Table 4). Among these five species, there is only one endemic species, *E. hyrcana* Grossh. in Caucasus (Azerbaijan) area. This species, of which ecology, distributional range and habitat are still poorly known, has been considered in section *Lagascae* by Riina *et al.* (2013) but after closer examination of its seed morphology with foveolate ornaments and also its distribution pattern, we transfer it to section *Paralias*. The members of this section are mostly found in coastal sandy habitats, seldom farther inland and upland (Riina *et al*., 2013). *Euphorbia paralias* L. is a

chamaephyte of sandy beaches (Appendix 2, Map 164), while the other four species, *E. hyrcana*, *E. ledebourii* Boiss., *E. reuteriana* Boiss., and *E. taurinensis* All. are therophytes on steppes, rocky grounds and disturbed areas (Appendix 2, Maps 122, 136, 182, 207).

The life form pattern matches well with available data of the entire flora in the area. The steppic flora of the southern Alborz Mountains represented by 28% therophytes, 43% hemicryptophytes, 19% chamaephytes, 9% geophytes and less than 1% phanerophytes (Mahdavi, Akhani & Van der Maarel, 2013). In Golestan National Park, located in easternmost extension of Alborz and western highlands of Khorasan and Kopetdagh with large area of forests has a rather different pattern: therophytes (30.2%), hemicryptophytes (35.9%), chamaephytes (10.2%), geophytes (15.1%), phanerophytes (7.8%) and hydrophytes (0.8%) (Akhani, 1998). The deviation of percentages of hemicryptophytes and chamaephytes from entire flora is probably related to the toxicity of *Euphorbia* species which are avoided by grazers. The spiny trait is also not well developed in *Euphorbia* subgenus *Esula* comparing to other steppic groups of the arid regions. The toxicity of shoots and leaves defend *Euphorbia* species from herbivores (Kingsburg, 1964). Our field observations also showed that many perennial *Euphorbia* species are highly cold tolerant which could well be considered as evergreen plants such as the members of the section *Myrsiniteae* (Pahlevani *et al*., 2011a). Therefore, evolving of woody parts, spiny and cushion forms did not take advantages.

Conservation

In this study, 96 endemic and subendemic taxa of the genus *Euphorbia* in the SW Asia have been globally evaluated and red-listed for the first time (Table 2). Although, Jalili & Jamzad (1999) evaluated 15 species of the Iranian *Euphorbia* species, but four of them constituted synonyms and three of them were categorized as Data Deficient (DD), while the eight remaining ones were evaluated as LR/LC (Least Concern). In this study, all valid names were re-evaluated based on updated data of their distribution and exact identification. The three species, *E. erythradenia*, *E. gypsicola* Rech.f., Aellen and *E. sahendi* Bornm. listed as Data Deficient by Jalili & Jamzad (1999), are considered Endangered (EN), Endangered (EN), and Critically Endangered (CR) respectively (Table

2). Of the eight species considered Least Concern (LR/LC) by Jalili & Jamzad (1999), two, *E. plebeia* and *E. teheranica* Boiss., are re-evaluated as Vulnerable (VU) and Near Threatened (NT), respectively (Table 2). The remaining six species are kept under the Least Concern category. The present study attempts to resolved misidentifications and dislocations accumulated since the publication of all floras in the studied region. Of the endemic taxa, a small number (7.2%) in the studied area have been categorized as DD because of their inadequate data for Red Listing (Table 2). To judge the status of these species, their taxonomic reality and other information about their distribution, population and ecology is needed.

Identifying the endemic taxa under extremely high (CR), very high (EN) and high (VU) risk of extinction, and localizing centers of endemism and hotspots are prerequisite to evaluate conservation management. In this case, giant genera like *Euphorbia* with a huge number of species and endemics and biodiversity centers in the studied regions play an important role as complementary and comprehensive data for conservation actions. The richest region of *Euphorbia* species in the SW Asia were eastern part of Mediterranean region followed by C Alborz, C, N Zagros, Kopetdagh, S Turkey (Anti-Taurus Mts.), Lesser Caucasus (SW Armenia, W Azerbaijan, NW Iran, NE Turkey), W Himalaya and the southwestern most part of Arabian Peninsula (Fig. 2). Based on analysis of endemic species of the genus *Euphorbia* with CR, EN and VU status in the SW Asia, most of them have been collected from protected areas (Fig. 3). In Iran they mostly occur in C Alborz Protected Area, that also harbours many endemic species of other groups of flowering plants (Wendelbo, 1971; Hedge & Wendelbo, 1978), S to C Zagros with several protected areas (like Khabr, Oshtorankuh, Zardkuh Protected Area) comprising the richest area of endemism of flowering plants in Iran (Hedge & Wendelbo, 1978; Wagenitz, 1986; Akhani, 2007) followed by few species in Khorasan Kopetdagh (Binalood Mt.) in NE, Sahand Mt. in NW, Taftan Protected Area in SE, Touran and Kavir Protected Areas (Rechinger & Wendelbo, 1976; Rechinger, 1977), and Hyrcanian forests (both in Azerbaijan and Iran) (Zohary, 1973; Browicz, 1989) of which the two primary ones, some parts of Kopetdagh and Sahand Mt., with rather high endemism in other groups of plants are not protected (Wagenitz, 1986; Memariani *et al*., 2016). Some protected areas in Afghanistan with high percentage of endemism including endemic

species of *Euphorbia* are Bamiyan National Heritage Park, Band-e Amir National Park and Dashte Nawar. In Saudi Arabia the endemics occur mostly in SW parts whereas, only one region, Asir National Park, is considered as protected area (Boulos *et al*., 1994). Although there is no legal protected area in Yemen and Oman, almost all endemics not only in *Euphorbia* but in other group of angiosperms have been reported from Dhofar Fog Oasis, Hadramaut and Jebal Areys near Arabian and Red Sea as centers of plant diversity in the region and they need special attention by their governments (Boulos *et al*., 1994). The Sinai Mts. in Egypt with rather high endemism of flowering plants is another protected area in which the endemic species *E. obovata* has been reported. Most endemic species of Turkey are mainly restricted to the so-called Fertile Crescent and the mountains bordering it, with a maximum concentration of species in the Amanus and Anti-Taurus mountains, a pattern also found in some other flowering plants (Davis, 1971; Hedge, 1986; Wagenitz, 1986; Akhani, 2007). This area comprises several protected areas such as Akdag, Aladaglar, and Altinbesik Cave National Parks and the remaining ones are limited to NE Turkey with some protected areas like Altindere Valley and Hatila Valley National Parks as well as NW Turkey including protected areas like Ilgaz Mts. In Pakistan three regions with high percentage of endemism are Kashmir, N Baluchistan (including Kalat, Quetta, Ziarat *etc.*) and Chitral (Ali & Qaisar, 1986) where all endemic species of *Euphorbia* and many other endemic groups of vascular plants in Pakistan are distributed (Sarwar & Qaisar, 2012; Bibi *et al*., 2015).

It is remarkable that some annual species of the genus *Euphorbia* with Least Concern (LC) conservation status are rare in the studied herbarium materials. The number of individuals in their habitats is also scarce and many times only one specimen has been found. Apparently, these plants are restricted to very special niches; some examples are *E. arvalis* Boiss. & Heldr., *E. coniosperma* Boiss. & Buhse (clay mud), *E. consanguinea* Schrenk (sand dunes), *E. grossheimii* (dried ravine) and *E. sororia* Schrenk (sand and solonchak) (Appendix 2, Maps 60, 79, 81, 111, 199).

However, while some areas have been considered as protected areas, the selected ranges of many parts of them have not enough extended they mainly serve to protected several endangered mammals. In other words, the protected areas, in general, are not primarily

selected based on plant diversity and richness, and therefore, some regions with high potential of endemism and diversity are still unprotected.

CONCLUSION

Genus *Euphorbia* plays a very vital role in many different kinds of biotopes around the World (Horn *et al*., 2012). It is highly diversified in SW Asia and Mediterranean region as the modern biodiversity centers and hotspots in many groups of the genus. Species of the genus *Euphorbia* subgenus *Esula* are clearly dominant in the Tethyan group (*ca*. 56% of whole) in which the Irano-Turanian (111 species) and the Mediterranean (85 species) elements are the most numerous ones (Geltman, 2015). It is supposed that during interglacial periods many species of the genus *Euphorbia*, together with many other groups of flowering plants in the region, may have been geographically isolated in the high mountainous areas as interglacial refugia (Memariani *et al*., 2016a) and the diversity in the region is probably the result of intensive speciation that took place during the Eocene-Miocene (Geltman, 2015). This speciation probably passed on the influence of two processes, including diminution of Paratethys causing the formation of desert areas and Alpine orogenesis (Geltman, 2015). According to the existing of more species in the mountainous regions in the genus *Euphorbia*, it seems orogeny was more effective as motor of speciation than desertification at least in subgenus *Esula*. The lineages within the clades had the ability for dispersal via several different kinds of manners to new areas, followed by rapid speciation and adaptation to new habitats like some cosmopolitan genera (Emadzade *et al*., 2011). One of the most prominent examples in the studied region was Cyprus Island which was the most taxa-rich country in threatened status point of view (Fig. 3), although the number of species of the genus *Euphorbia* in Cyprus is 33 and less than in many countries in SW Asia (Table 3). However, geographical isolation by existing barriers and decreased or interrupted gene flow during the Neogene which made up allopatric speciation, is another important reason that might have increased the number of species and endemics in the studied region (Djamali *et al*., 2012).

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TABLES

Table 1 Published flora treatments of the genus *Euphorbia* in the extended SW Asia including, year, authors, number of taxa and countries covered by flora

No.	Title	Country (s)	No. taxa	Year	Author (s)
1	Flora Iranica	Afghanistan, S Azerbaijan, Iran, W Pakistan, S Turkmenistan	98	1964	Rechinger KH, Schiman-Czeika H
2	Vascular plants of Afghanistan	Afghanistan	45	2013	Breckle SW, Hedge IC, Rafiqpoor MD
3	Flora Azerbajdzhana	Azerbaijan	37	1955	Karjagin II
4	Flora of Cyprus	Cyprus	25	1985	Radcliffe-Smith A
5	A manual flora of Egypt	Egypt	19	1912	Müschler R
6	Flora of Egypt	Egypt	41	2000	Boulos L
7	Flore de l' Iran	Iran	74	1949	Parsa A
8	Flora of Iraq	Iraq	44	1980	Radcliffe-Smith A
9	Flora of Lowland Iraq	Iraq	25	1964	Rechinger KH
10	Flora Orientalis	Afghanistan, Armenia, Baluchistan of Pakistan, Egypt, Greece, plateau of Iran, Syria, parts of Iraq and	131	1879	Boissier E

		Turkey, a part of Turkmenistan			
11	Flora of Pakistan	Pakistan & Kashmir	52	1986	Radcliffe-Smith A
12	Flora Palestina	Israel, Palestine	34	1972	Zohary M
13	Flora of the kingdom of Saudi Arabia	Saudi Arabia	39	2001	Chaudhary SA
14	Nouvelle Flore Du Liban Et De La Syrie	Lebanon, Syria	52	1986	Mouterde PSJ
15	Flora of Syria, Palestine & Sinai	Syria, Israel, Palestine, a part of Egypt	44	1896	Post GE
16	Flora Turkmenistan	Turkmenistan	27	1950	Nikitin VV
17	Flora of Turkey	Turkey & E Aegean Islands	104	1982	Radcliffe-Smith A
18	Flora of the USSR	Soviet Union	159	1974	Prokhanov YI
19	A handbook of the Yemen flora	Yemen	28	1997	Wood JRI

Table 2 Checklist of endemic and sub-endemic *Euphorbia* of SW Asia, countries, number of records of studied herbaria specimens (material & methods) and/or rarely recorded ones in the literature, extent of occurrence (EOO), area of occupancy (AOO), 10% of maximum distance, Red List categories and criteria. Abbreviations: Red list categories: CR = critically endangered, EN = endangered, VU = vulnerable, NT= near threatened, LC = least concern, and DD = data deficient. (IUCN 2011).

No.	Endemic taxa	Country (s)	No. of records	EOO (km^2)	AOO (km^2)	10% of maximum distance (km)	Redlist categories & criteria
1	*E. abdulghafooriana* Abedin	Saudi Arabia	1	0	1	1	DD
2	*E. acanthoclada* Pahlevani	Afghanistan	3	7430	867	17	VU
3	*E. acanthodes* Akhani	Iran	2	< 5	392	14	CR
4	*E. acanthothamnos* Heldr. & Sart.	Greece, W Turkey	22	182287	36864	58	LC
5	*E. akmanii* İ.Genç & Kültür	S Turkey	3	1.05	108	6	CR
6	*E. altissima* var. glabrescens Boiss. ex. M.S.Khan	Syria, Turkey	7	62056	11045	77.8	LC
7	*E. ammak* Schweinf.	W Saudi Arabia, Yemen	12	205177	27500	120	LC
8	*E. amygdaloides* subsp. *robbiae* (Turrill) Stace	NE Turkey	2	0	200	10	CR
9	*E. anacampseros* var. *tmolae* M.S.Khan	Turkey	5	81755	7500	95	LC
10	*E. applanata* Thulin & Gifri	Yemen	1	0	1	1	DD
11	*E. austroanatolica* Hub.-Mor. & M.S.Khan	SW Turkey	8	3185	5046	29	EN
12	*E. austro-iranica* Pahlevani	S, SE Iran	6	60746	12150	45	LC
13	*E. berythea* Boiss. & Blanche	Cyprus, Israel/Palestine, Lebanon, Syria	10	29796	10368	36	NT

14	*E. boreo-baluchestanica* Pahlevani	Pakistan	6	12813	7605	39	VU
15	*E. caducifolia* Haines	India, Pakistan	8	30140	17500	55	LC
16	*E. caeladenia* Boiss.	SE Iran, Pakistan	52	331921	60000	100	LC
17	*E. cassia* subsp. *cassia* Boiss.	Cyprus, Lebanon, W, NW Syria, S Turkey	14	63433	19166	40	LC
18	*E. cassia* subsp. rigoi (Boiss. ex Freyn) Holmboe	Cyprus	12	6517	2250	15	VU
19	*E. caudiculosa* Boiss.	Lebanon, W Syria	6	2558	980	14	EN
20	*E. chaborasia* Gomb.	Iraq, Syria	16	144104	25000	50	LC
21	*E. connata* Boiss.	Iran	57	77126	45630	39	LC
22	*E. cuspidata* Bertol.	Iraq, Jordan, Syria	25	76889	42500	60	LC
23	*E. davisii* M.S.Khan	S Turkey	4	10156	2704	26	VU
24	*E. deltobracteata* (Prokh.) Prokh.	NE Iran, S Turkmenistan	26	73272	25600	26	LC
25	*E. dhofarensis* S. Carter	Oman	8	3713	1800	15	EN
26	*E. djimilensis* Boiss.	NE, S Turkey	6	27375	15000	50	NT
27	*E. ecorniculata* Kitam.	Afghanistan	5	6426	2000	20	VU
28	*E. erythradenia* Boiss.	Iran	5	4129	500	20	EN
29	*E. erythrodon* Boiss. & Heldr.	Turkey	6	100358	15000	60	LC
30	*E. ferdowsiana* Pahlevani	NE Iran	3	8	12	2	CR
31	*E. fistulosa* M.S. Khan	N Syria, Turkey	6	7984	5400	30	VU
32	*E. fractiflexa* S. Carter & J.R.I.Wood	Saudi Arabia, Yemen	5	23368	10000	50	NT
33	*E. frankii* Lavranos	Yemen	1	0	1	1	DD
34	*E. fruticulosa* Forssk.	Saudi Arabia, Yemen	8	40346	17500	57	NT

35	*E. gedrosiaca* Rech.f., Aellen & Esfand.	Afghanistan, E, SE Iran	33	186080	47500	65	LC
36	*E. greuteri* N. Kilian, Kürschner & P. Hein	S Yemen	1	0	1	1	CR
37	*E. grisophylla* M.S.Khan	W Iran, E Turkey	18	71378	30000	70	LC
38	*E. gulestanica* Podlech	Afghanistan	1	0	1	1	CR
39	*E. gypsicola* Rech.f., Aellen	Iran	10	205	36	2	EN
40	*E. haussknechtii* Boiss.	N Syria, SE Turkey	3	3161	768	16	EN
41	*E. hebecarpa* Boiss.	Iran	94	239473	72500	90	LC
42	*E. hyrcana* Grossh.	Azerbaijan	1	0	1	1	DD
43	*E. inarticulata* Schweinf.	Saudi Arabia, Yemen	19	118771	35000	80	LC
44	*E. iranshahri* Pahlevani	Iran	18	9139	4096	16	VU
45	*E. isaurica* M.S.Khan	Turkey	2	0	8	2	CR
46	*E. kanaorica* Boiss.	NE Afghanistan, N Pakistan, NW India	10	46385	15000	50	LC
47	*E. kavirensis* Pahlevani	C Iran	6	18721	3750	25	VU
48	*E. khabrica* Pahlevani	Iran	4	3854	7500	55	EN
49	*E. kopetdaghii* (Prokh.) Prokh.	NE Iran, S Turkmenistan	104	37718	31500	30	NT
50	*E. lemesiana* Hadjik., Hand, Christodoulou & Frajman	Cyprus	8	206	112	4	EN
51	*E. maddenii* Boiss.	NW India, NE Pakistan	14	48347	10890	33	LC
52	*E. madinahensis* Fayed & Al-Zahrani	Saudi Arabia	4	640	144	6	EN
53	*E. malleata* Boiss.	Iran	20	36209	19200	40	LC
54	*E. malurensis* Rech.f.	Afghanistan	36	186449	62500	70	LC

55	*E. masirahensis* Ghaz.	Oman	2	0	200	10	CR
56	*E. mazandaranica* Pahlevani	N Iran	10	5294	5184	24	VU
57	*E. megalocarpa* Rech.f.	Afghanistan	1	0	1	1	CR
58	*E. meuleniana* O. Schwartz	S Yemen	11	30948	14400	40	NT
59	*E. microsciadia* Boiss.	Iran	207	729902	162500	50	LC
60	*E. momccoyae* Lavranos	Oman (Dhofar)	1	0	1	1	DD
61	*E. monostyla* Prokh.	NE Iran, S, W Turkmenistan	39	80543	42500	70	LC
62	*E. obovata* Decne.	Egypt (Sinai)	2	0	0.18	0.3	CR
63	*E. orbiculifolia* S. Carter	Oman, Yemen	6	721	180	6	EN
64	*E. parciramulosa* Schweinf.	Saudi Arabia, Yemen	3	11832	7500	65	VU
65	*E. pestalozzae* Boiss.	Turkey	11	51296	9600	40	LC
66	*E. petiolata* var. *postii* (Boiss.) Radcl.-Sm.	Syria, Turkey	2	0	1352	26	CR
67	*E. physocaulos* Mouterde	Syria, Turkey	3	1789	5000	60	EN
68	*E. pisidica* Hub.-Mor. & M.S. Khan	SW Turkey	3	70	27	3	CR
69	*E. plebeia* Boiss.	Iran	7	17561	9600	40	VU
70	*E. polycaulis* Boiss.	Iran	107	139839	96148	43	LC
71	*E. promecocarpa* Davis	Syria	2	0	2	1	CR
72	*E. punctata* Delile	Egypt	6	53	20	2	CR
73	*E. qarad* Deflers	S Yemen	3	7614	1323	21	VU
74	*E. quaitensis* S. Carter	Oman, Yemen	2	-	-	-	DD
75	*E. reuteriana* Boiss.	Israel/Palestine, Jordan, Lebanon, Syria	9	7035	4732	26	VU
76	*E. rhytidosperma* Boiss. &	S Turkey	2	0	392	14	CR

	Balansa						
77	*E. riebeckii* Pax	Oman, Yemen	11	211662	22500	120	LC
78	*E. rubriseminalis* S. Carter	S Yemen	5	6295	3645	27	VU
79	*E. sahendi* Bornm.	NW Iran	1	0	1	1	CR
80	*E. saudiarabica* Fayed & Al-Zahrani	Saudi Arabia	3	2262	768	16	EN
81	*E. schottiana* Boiss.	Turkey	2	0	2592	36	CR
82	*E. schugnanica* B. Fedtsch.	Afghanistan, Tajikistan	5	23333	3920	28	NT
83	*E. seibanica* Lavranos & Gifri	Yemen	1	0	1	1	DD
84	*E. smirnovii* Geltman	E Turkey	2	0	128	8	CR
85	*E. smithii* S. Carter	S Oman	9	4225	2023	17	EN
86	*E. sogdiana* Popov	Afghanistan, Tajikistan, Uzbekistan	14	100396	16807	48	LC
87	*E. spartiformis* Mobayen	S Iran	5	1188	1323	21	EN
88	*E. sulphurea* Pahlevani	SE Iran	3	16	12	2	CR
89	*E. taifensis* Fayed & Al-Zahrani	Saudi Arabia	1	0	1	1	CR
90	*E. talaina* Radcl.-Sm	Pakistan	3	18014	7500	50	VU
91	*E. teheranica* Boiss.	Iran	69	33024	16464	28	NT
92	*E. thompsonii* Holmboe	Cyprus, S Turkey	3	5482	2523	29	VU
93	*E. uzmuk* S. Carter & J.R.I.Wood	Oman, Yemen	3	399	4232	46	EN
94	*E. veneris* M.S.Khan	Cyprus	5	100	45	3	EN
95	*E. wittmannii* Boiss.	Georgia, Turkey	3	5522	768	16	VU
96	*E. ziaratensis* Pahlevani	Pakistan	2	0	8	2	CR

Table 3 Area (km^2) of the countries, number of species, number and percent of endemics, number of *Euphorbia* taxa (species, subspecies, variety) and subgenus with respective numbers and percent of endemics and neophyte species in South-West Asian countries

Country	**Area (km^2)**	**No. species**	**No. endemic**	**% endemic**	**No. *Euphorbia* taxa**	**Subgen. *Athymalus***	**Subgen. *Chamaesyce***	**Subgen. *Esula***	**Subgen. *Euphorbia***	**No. *Euphorbia* endemics**	**% *Euphorbia* endemics**	**No. *Euphorbia* neophyte**	**% *Euphorbia* neophyte**
Afghanistan	652230	4000	800	20	40	-	9	31	-	5	12.5	4	10
Armenia	29743	3800	144	3.7	36	-	3	33	-	0	0	2	5.5
Azerbaijan	86600	4300	200	4.6	33	-	4	29	-	1	3	2	6
Cyprus	9251	1628	141	8.6	33	-	10	23	-	3	9	7	21.2
Egypt	1002450	2075	62	2.9	44	2	17	24	1	2	4.6	9	20.4
Iran	1648195	7500	1500	20	90	1	12	75	1	19	21.1	8	8.8
Iraq	438317	3000	190	6.3	37	-	7	30	-	0	0	4	10.8
Israel/Palestine	26990	2225	165	7.4	37	-	10	27	-	0	0	5	13.5
Jordan	89342	2100	145	6.9	22	-	6	16	-	0	0	2	9
Kuwait	17818	282	0	0	11	-	5	6	-	0	0	4	36.3
Lebanon	10452	2600	311	11.9	41	-	6	35	-	0	0	2	4.8
Oman	309500	1200	73	6	29	8	12	6	3	4	13.7	7	24.1
Pakistan	881912	5700	203	3.5	46	-	14	29	3	3	6.5	11	23.9
Qatar	11586	306	0	0	13	1	7	5	-	0	0	5	38.4
Saudi Arabia	2149000	2028	34	1.7	44	4	18	11	11	4	9	10	22.7
Syria	185,180	3100	395	12.7	50	-	6	44	-	1	2	1	2
Turkey	783562	8650	2675	30.9	103	-	11	92	-	13	12.6	10	9.7
Turkmenistan	488100	2900	332	11.4	31	-	5	26	-	1	3.2	1	3.2
UAE	83600	340	0	0	13	1	7	4	1	0	0	6	46.1
Yemen	527968	2810	287	10.2	45	9	16	8	12	7	15.5	6	13.3
Total	9431796	±25000	7657	30.6	249	13	33	182	21	63	25.3	17	6.8

Table 4 The number of total and endemic taxa of each section and subsection of the genus *Euphorbia* in the extended SW Asian countries; the first, second and third numbers are the whole taxa, the number of taxa occur in the country and the number of endemic taxa in section or subsection respectively; Total No. (number of section or subsection in the extended SW Asia), N (Non represent); § (subsection); Country: Afg. (Afghanistan), Arm. (Armenia), Azr. (Azerbaijan), Cyp. (Cyprus), Egy. (Egypt), Irn. (Iran), Irq. (Iraq), Isr./Pal. (Israel/Palestine), Jor. (Jordan), Kuw. (Kuwait), Leb. (Lebanon), Oma. (Oman), Pak. (Pakistan), Qat. (Qatar), Sar. (Saudi Arabia), Syr. (Syria), Tur. (Turkey), Tum. (Turkmenistan), Yem. (Yemen). The names of the taxa are in the appendix 1.

Taxa/Total No.	Afg.	Arm.	Azr.	Cyp.	Egy.	Irn.	Irq.	Isr./Pal.	Jor.	Kuw.	Leb.	Oma.	Pak.	Qat.	Sar.	Syr.	Tur.	Tum.	UAE	Yem.
Subgen.	N	N	N	N	N	10/1/0	N	N	N	N	N	10/4/2	N	10/1/0	10/1/0	N	N	N	10/1/0	10/4/2
Athymalus																				
Sect. *Balsamis*/6																				
Lyciopsis/2	N	N	N	N	19/1/0	N	N	N	N	N	N	19/2/1	N	N	19/1/0	N	N	N	N	19/1/0
Pseudacalypha/5	N	N	N	N	11/1/0	N	N	N	N	N	N	11/2/0	N	N	11/2/0	N	N	N	N	11/4/0
Subgen.	N	N	N	N	N	N	N	N	N	N	N	N	115/1/0	N	N	N	N	N	N	N
Chamaesyce																				
Sect.																				
Alectoroctonum/1																				
Anisophyllum §	365/7/0	365/3/0	365/5/0	365/8/0	365/14/0	365/9/0	365/6/0	365/8/0	365/4/0	365/5/0	365/4/0	365/8/0	365/10/0	365/6/0	365/15/1	365/4/0	365/8/0	365/3/0	365/6/0	365/11/0
Hypericifoliae/24																				
Cheirolepidium/3	3/1/0	N	N	3/1/0	3/1/0	3/2/0	3/1/0	3/1/0	3/1/0	N	3/1/0	3/1/0	3/1/0	N	N	3/2/0	3/2/0	3/2/0	N	N
Frondosae/2	N	N	N	N	N	N	N	N	N	N	N	7/2/0	N	N	7/1/0	N	N	N	N	7/2/0
Poinsettia §	21/1/0	N	N	21/1/0	21/2/0	21/2/0	N	21/1/0	21/1/0	N	21/1/0	21/1/0	21/2/0	21/1/0	21/1/0	N	21/1/0	N	21/1/0	21/1/0
Stormieae/2																				
Scatorhizae/2	N	N	N	N	N	N	N	N	N	N	N	N	N	N	7/1/0	N	N	N	N	7/2/1
Subgen. *Esula*	N	N	N	N	12/3/0	N	N	N	N	N	N	12/1/0	N	N	12/2/0	N	N	N	N	12/2/0
Sect. *Aphyllis* §																				

africanae /2																				
Arvales/4	6/1/0	6/1/0	6/1/0	N	N	6/3/0	6/1/0	6/1/0	6/1/0	N	6/1/0	N	6/1/0	N	N	6/1/0	6/2/0	6/1/0	N	N
Calyptratae/1	N	N	N	N	N	2/1/1	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Chylogala/2	N	4/1/0	4/1/0	N	4/1/0	4/1/0	4/2/0	4/1/0	4/1/0	4/1/0	N	4/1/0	N	4/1/0	4/1/0	N	4/1/0	N	4/1/0	N
Esula/21	101/8/2	101/3/0	101/2/0	N	N	101/7/3	101/2/0	N	N	N	N	101/1/0	101/6/1	N	101/1/0	N	101/6/0	101/5/1	N	101/1/0
Exiguae/2	N	N	N	5/1/0	5/3/0	N	5/1/0	5/1/0	N	N	5/1/0	N	5/1/0	N	5/1/0	5/1/0	5/1/0	N	N	5/1/0
Helioscopia/42	128/2/0	128/10/0	128/10/0	128/9/1	128/8/0	128/13/1	128/7/0	128/10/0	128/6/0	128/1/0	128/13/0	128/1/0	128/3/0	128/1/0	128/1/0	128/18/0	128/34/4	128/1/0	128/1/0	128/1/0
Herpetorrhizae	N	N	N	N	N	2/2/0	2/1/0	N	N	N	N	N	N	N	N	N	N	2/2/0	N	N
§ *Aucheriae*/2																				
Herpetorrhizae	10/6/0	10/1/0	10/1/0	N	N	10/6/0	10/1/0	10/1/0	N	10/1/0	N	N	10/4/0	10/1/0	10/1/0	10/1/0	N	10/5/0	N	N
§ *Oppositifoliae*/7																				
Holophyllum/4	27/3/1	N	N	N	N	N	N	N	N	N	N	N	27/3/0	N	N	N	N	N	N	N
Lagascae/1	N	N	N	N	N	2/1/0	2/1/0	2/1/0	2/1/0	N	2/1/0	N	N	N	N	2/1/0	2/1/0	N	N	N
Lathyris/1	N	1/1/0	N	N	N	N	N	N	N	N	N	N	1/1/0	N	N	N	1/1/0	1/1/0	N	N
Myrsiniteae/12	17/1/0	17/3/0	17/2/0	17/3/1	N	17/8/0	17/3/0	17/1/0	17/1/0	N	17/2/0	N	N	N	N	17/3/0	17/9/1	17/2/0	N	N
Pachycladae/2	N	N	N	2/1/0	2/2/0	N	N	2/2/0	N	N	2/2/0	N	N	N	N	2/1/0	2/2/0	N	N	N
Paralias/5	N	13/1/0	13/2/1	13/2/0	13/1/0	N	N	13/2/0	13/1/0	N	13/2/0	N	N	N	N	13/2/0	13/3/0	N	N	N
Patellares/11	N	18/4/0	18/3/0	18/1/0	N	18/3/0	18/1/0	N	N	N	18/2/0	N	N	N	N	18/1/0	18/10/3	N	N	N
Pithyusa/44	60/5/2	60/6/0	60/4/0	60/3/1	60/2/1	60/21/13	60/6/0	60/4/0	60/3/0	60/1/0	60/6/0	60/1/0	60/5/2	60/1/0	60/1/0	60/7/0	60/16/4	60/4/0	60/1/0	60/2/0
Sclerocyathium/7	10/3/0	N	10/1/0	N	10/1/0	10/5/1	10/1/0	10/1/0	N	10/1/0	N	N	10/4/0	N	10/1/0	10/1/0	N	10/3/0	N	N
Szovitziae/1	1/1/0	1/1/0	1/1/0	N	N	1/1/0	1/1/0	N	N	N	1/1/0	N	1/1/0	N	N	1/1/0	1/1/0	1/1/0	N	N
Tithymalus/9	N	40/1/0	40/1/0	40/3/0	40/3/1	40/3/0	40/2/0	40/2/0	40/2/0	40/1/0	40/4/0	40/1/0	40/1/0	40/1/0	40/2/0	40/5/1	40/5/1	40/1/0	40/1/0	40/1/0
Subgen.	N	N	N	N	343/1/0	N	N	N	N	N	N	343/2/1	343/2/0	N	343/11/3	N	N	N	N	343/11/4
Euphorbia																				
Sect.																				
Euphorbia/19																				
Tirucalli/2	N	N	N	N	N	24/1/0	N	N	N	N	N	24/1/0	24/1/0	N	N	N	N	N	24/1/0	24/1/0

CAPTIONS FOR FIGURES

Figure 1. Map of South-West Asia showing countries and seas

Figure 2. Map of alpha diversity of *Euphorbia* taxa in South-West Asia

Figure 3. Map of endemic and subendemic richness of the threatened (CR, E, VU) and near threatened (NT) *Euphorbia* taxa in South-West Asia

Figure 4. Photograph of holotype specimen of *Euphorbia acanthoclada*

Figure 5. Photograph of holotype specimen of *Euphorbia boreo-baluchestanica*

Figure 6. Photograph of holotype specimen of *Euphorbia kavirensis*

Figure 7. Photograph of holotype specimen of *Euphorbia ziaratensis*

APPENDICES

Appendix 1 List of the SW Asian species of *Euphorbia* studied in this article with their infrageneric, section and subsection position (Yang *et al*. 2012; Dorsey *et al*. 2013; Peirson *et al*. 2013; Riina *et al*. 2013), life form, distribution, habitat, altitude and threat category. Life form: Ch., Chamaeophyte; Ph., Phanerophyte; Th., therophyte; G., Geophyte; Hem., Hemicryptophyte; NPh., Nanophanerophyte.

Taxa	Section & subsection	Life form	Distribution/Map No. in appendix 2	Habitat	Altitude	Threat category
Subgenus *Athymalus* Neck. ex Rchb.	*Pseudacalypha* Boiss.	Ch.	Asia: Saudi Arabia, Yemen; E & NE tropical Africa/1	Drifted sands, near sea shores	0-400	LC
E. acalyphoides Hochst.						
E. balsamifera subsp. *adenensis* (Deflers) P.R.O. Bally	*Balsamis* Webb & Berthelot	NPh.	Asia: Oman, Saudi Arabia, Yemen; Africa: Somalia, Sudan/2	Stony hillsides, limestone rocky slopes, screes, grasslands	700-2430 m	LC
E. cuneata Vahl	*Lyciopsis* Boiss.	Ph.	Asia: Oman, Saudi Arabia, Yemen; Africa: Egypt, Ethiopia, Kenya, Somalia, Sudan/3	Gravelly and sandy plains, rocky foothills, on volcanic soils, *Acacia* woodlands	0-1600 m	LC
E. dhofarensis S. Carter	*Balsamis* Webb & Berthelot	NPh.	Asia: Oman/4	Stony grounds around the lower slopes of the mountains, rocky hillsides	0-870 m	EN
E. hadramautica Baker	*Pseudacalypha* Boiss.	Ch.	Asia: Oman, Yemen; NE tropical Africa: Ethiopia, Somalia/5	Rock crevices, sea cliffs, calcareous soils, under small shrubs, open stony hills	0-2300 m	LC
E. larica Boiss.	*Balsamis* Webb & Berthelot	NPh.	Asia: Bahrain, S to SE Iran, Oman, Qatar, UAE, Yemen/6	Dry rocky hillsides, sandy wadi beds, sub-desert shrublands, coastal rocks	20-1700 m	LC
E. longetuberculosa Hochst. ex Boiss.	*Pseudacalypha* Boiss.	Ch.	Asia: Saudi Arabia, Yemen; Africa: Ethiopia, Kenya, Somalia/7	Sandy soils, hill slope of volcanic rocks	50-900 m	DD
E. masirahensis Ghaz.	*Balsamis* Webb & Berthelot	NPh.	Asia: Oman/8	Stony slopes	0-250 m	CR
E. meuleniana O. Schwartz	*Balsamis* Webb & Berthelot	NPh.	Asia: S Yemen/9	Calcareous slopes, rocky hillsides	350-1450 m	NT
E. orbiculifolia S. Carter	*Pseudacalypha* Boiss.	Ch.	Asia: Oman, Yemen?/10	Escarpment woodlands, low rocky hills, sea cliffs	5-1400 m	EN
E. rubriseminalis S. Carter	*Balsamis* Webb & Berthelot	Ch.	Asia: S Yemen/11	Rocky slopes, coastal dunes, calcareous slopes	1200-1650 m	VU
E. smithii S. Carter	*Lyciopsis* Boiss.	Ph.	Asia: S Oman/12	Wooded escarpment slopes, coastal plains	90-540 m	EN
E. systyla Edgew	*Pseudacalypha* Boiss.	Hem.	Asia: S Yemen; Africa: Somalia/13	On volcanic rocks in the middle of desert	0-300 m	DD

Subgenus *Chamaesyce* Raf.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Saudi Arabia/14	Unknown	Unknown	DD
E. abdulghafooriana Abedin						
E. agowensis Hochst. ex Boiss.	*Scatorhizae* Yang & Berry	Ch.	Asia: SW Saudi Arabia, Yemen, India; Africa: Angola, Eritera, Ethiopia, Kenya, Somalia/15	In grass and small thickets, cultivated land, open woodland usually with *Acacia*	70– 1700 m	DD
E. anisopetala (Prokh.) Prokh.[i]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Kazakhstan, Kyrgyzstan, Turkmenistan, Uzbekistan	Saline soils, weed in cultivated fields	Unknown	LC
E. applanata Thulin & Al-Gifri	*Scatorhizae* Yang & Berry	Ch.	Asia: S Yemen/16	Crevices of limestone rocks	1850 m	DD
E. arabica Hochst. & Steud. ex. Anderson	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Oman, Saudi Arabia, UAE, Yemen; NE Africa: Djibouti, Egypt, Eritrea, Ethiopia, Kenya, Somalia, Sudan/17	Stony sheltered cliffs, calcareous rocks, sandy soils, disturbed areas	0–1400 m	LC
E. chamaesyce L.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Afghanistan, Iran, Iraq, Israel/Palestine, Jordan, Lebanon, Saudi Arabia, Syria, Turkey, Turkmenistan; N Africa: Algeria, Egypt, Libya, Morocco, Tunisia; S & SW Europe; Caucasus/18	Cultivated & disturbed areas, gravely and sandy plains, saline and calcareous soils, hillsides, cracks in pavements	0–1600 (2300) m	LC
E. cheirolepis Fisch. & C.A. Mey.	*Cheirolepidium* Boiss.	Th.	Asia: Afghanistan, Iran, Pakistan, Tajikistan, Turkmenistan, Uzbekistan/19	Desert dune	200–1200 m	LC
E. clarkeana Hook. f.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Afghanistan, NW India, Pakistan/20	On waste places, sandy, clay and pebbly ground	0-2400 m	LC
E. cyathophora Murray	*Poinsettia* (Graham) Baill. subsect. *Stormieae* Croizat	Th.	New World native, naturalized in tropical and subtropical regions (Egypt, SE Iran, Pakistan)/21	Disturbed areas, fields, hedges	0-1200 m	LC
E. forskaolii J. Gay[ii]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Ch.	Asia: S Israel/Palestine (rare), Oman, Saudi Arabia, Yemen; N & NE Africa/22	Sandy soil, cultivated land	0-1200 m	LC
E. granulata Forssk.	*Anisophyllum* Roep. subsect. *Hypericifoliae*	Th.	SW & Central Asia; N, NE & E Africa/23	In hot deserts, bare hillside, sandy dunes and gravelly plains, stony banks of canal, gypsum and saline soils,	0-2000 m	LC

	Boiss.			ruderal places		
E. heterophylla L.[iii]	*Poinsettia* (Graham) Baill. subsect. *Stormieae* Croizat	Th.	New World native, naturalized in tropical and subtropical regions in the Old World/24	Ruderal species in orchards, fields, roadsides and other disturbed areas	0-2800 m	LC
E. hirta L.[iv]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	New World native, naturalized in tropical and subtropical regions/25	Pantropical weed in disturbed areas, irrigated grounds near cultivation, sandy soils, hillside, sea shore	0-1700 m	LC
E. hispida Boiss.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: NE & E Afghanistan, N Pakistan, NW India/26	Dry stony ground, silty loam, granite, irrigation channel-banks, grassy slopes, fields and gardens	670-2800 m	LC
E. humifusa Willd.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: China, Iran, Japan, Kazakhstan, Kirgizstan, Korea, Mongolia, Tajikistan, Turkey, Uzbekistan, Caucasus, Mediterranean area, Central & E Europe/27	Sea shores, cultivated areas, in gravel of riverbanks	0-3000 m	LC
E. hypericifolia L.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Tropical & subtropical New World native, introduced into some parts of the Old World (China, Cyprus, India, Iraq, Israel/Palestine, Oman, Pakistan, Turkey)/28	Humus rich soils, fields, roadsides, scrubs, waste irrigated grounds, pavements	0-1600 m	LC
E. hyssopifolia L.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Tropical & subtropical New World native, introduced into some parts of the Old World tropics & subtropics/29	Disturbed areas, roadsides, near channels, ditches, garden weed	0-1500 m	LC
E. inaequilatera Sond.[v]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Saudi Arabia, Yemen; Africa/30	Garden weed, stony grounds, sandy and silty plains, slope of escarpments	400-2300 m	LC
E. indica Lam.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: E Afghanistan, China, S, SE Iran, SE Iraq, India, Kuwait, Oman, Pakistan, Qatar, Saudi Arabia, Sri Lanka, UAE, Yemen; Africa: E, SE Egypt, Somalia/31	Weed in fields and orchards, disturbed areas, sand dunes, dry and waterlogged, irrigation canals, slightly saline soils	0-2200 m	LC
E. lasiocarpa Klotzsch	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	New World native, introduced to some places of tropical and subtropical regions in the Old World (Israel/Palestine, Egypt)/32	Disturbed places, along roadsides and railroad tracks	0-40 m	LC
E. maculata L.	*Anisophyllum* Roep. subsect. *Hypericifoliae*	Th.	New World native, introduced to many places of temperate to subtropical regions in the Old	Weed in lawns, ornamental gardens, forests, roadsides, cracks in sidewalks, coastal sands	0-1800 m	LC

	Boiss.		World/33			
E. nutans Lag.[vi]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	New World native, introduced to many places in the Old World (Azerbaijan, Cyprus, Iran, Israel/Palestine, Jordan, Lebanon, Saudi Arabia, Syria)/34	Cultivated areas, ruderal places in forests, roadsides, sea shores	0-1400 m	LC
E. peplis L.[vii]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Israel/ Palestine, Jordan, Lebanon, Syria, Turkey; Africa: Algeria, Egypt, Libya, Morocco, Tunesia; Mediterranean parts of Europe, Georgia, Ukraine/35	Coasts of Mediterranean and Black seas; coastal dune, shingle, shores of inland salt lakes	0-900 m	LC
E. petiolata var. *petiolata* Banks & Sol.[viii]	*Cheirolepidium* Boiss.	Th.	Asia: Iran, Iraq, Israel/Palestine, Jordan, Lebanon, N Oman, Syria, Turkey, Turkmenistan; Africa: Egypt; Europe: Cyprus/36	Rocky mountain slopes, hillsides, roadsides, waste and disturbed places, on clay and sandy deserts, gypsum and saline soils	40-2400 m	LC
E. petiolata var. *postii* (Boiss.) Radcl.-Sm.[ix]	*Cheirolepidium* Boiss.	Th.	Asia: N Syria, S Turkey/37	Field margins, riversides	450-650 m	CR
E. pirottae N. Terrac.	*Frondosae* Bruyns	Th.-Ch.	Asia: Oman, Saudi Arabia, Yemen; NE & E tropical Africa: Ethiopia, Kenya, Somalia, Tanzenia/38	Fixed sand, open to dense bushlands, stony slopes	0-1600 m	LC
E. polycnemoides Hochst. ex Boiss.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Saudi Arabia, Yemen; Africa: arid tropical Africa	Open woodlands, among rocks	400-1000 m	LC
E. prostrata Aiton[x]	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	New World native, introduced to many places in the Old World/39	Weed in cultivated areas and sea shores	0-2000 m	LC
E. quaitensis S. Carter	*Frondosae* Bruyns	Ch.	Asia: Oman, Yemen/40	Rocky limestone slopes	1100-1300 m	DD
E. riebeckii Pax	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Ch.	Asia: Oman, Yemen/41	Sandy soils, along the coasts, upper slopes of sand dunes, rocky ground below crater	10-350 m	LC
E. scordiifolia Jacq.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Saudi Arabia, Yemen; Africa: SE Egypt, Ethiopia, Somalia to Cape Verde/42	Coastal sandy plains, reddish sand dunes, low rocky hills	0-330 m	LC
E. serpens Kunth	*Anisophyllum* Roep.	Th.	New World native, introduced to many places	Naturalized weed in many disturbed habitats like lawns,	0-1600 m	LC

	subsect. *Hypericifoliae* Boiss.		in the Old World/43	ornamental garden, orchard, roadside, sea shore, sandy desert ground		
E. thymifolia L.	*Anisophyllum* Roep. subsect. *Hypericifoliae* Boiss.	Th.	Asia: Assam, Bangladesh, Bhutan, Ceylon, China, India, Maldives, Nepal, Pakistan, Seri Lanka; Introduced to tropical Africa and America/44	Plains & lower hills, cultivated areas	400-1700 m	LC
Subgenus *Esula* Pers.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Afghanistan/45	Unknown	900-1150 m	VU
E. acanthoclada Pahlevani						
E. acanthodes Akhani[xi]	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Iran/46	Gypsum hills	300-400 m	CR
E. acanthothamnos Heldr. & Sart.	*Helioscopia* Dumort.	Ch.	Asia: W Turkey, Europe: Greece/47	Rocky limestone slopes	30-300 m	LC
E. agraria M. Bieb.	*Esula* (Pers.) Dumort.	Hem.	Asia: NW Turkey; E & SE Europe, Caucasus/48	Rocky mountains, fields, roadsides	10-1700 m	LC
E. akmanii İ.Genç & Kültür	*Patellares* (Prokh.) Frajman	Ch.	Asia: S Turkey/49	Open deciduous forest of *Pinus brutia* and *Quercus coccifera*, serpentine	700-980 m	CR
E. aleppica L.	*Myrsiniteae* (Boiss.) Lojac.	Th.	Asia: W Iran, N Iraq, Israel/Palestine, Jordan, Lebanon, Syria, Turkey; Europe: Mediterranean parts, Armenia, Azerbaijan, Georgia; Africa: Algeria, Tunisia/50	Stony slopes, hillsides and valleys, cultivated and waste lands, roadsides	-10-1600 m	LC
E. altissima var. *altissima* Boiss.	*Helioscopia* Dumort.	Hem.	Asia: NW Iran, N, NE Iraq, Lebanon, Syria, Turkey; Europe: Cyprus/51	Riverbanks, springs, irrigation ditches, oak woods, clay soils	500-1500 m	LC
E. altissima var. *glabrescens* Boiss. ex M.S. Khan	*Helioscopia* Dumort.	Hem.	Asia: Syria, Turkey/52	Railways, riverbanks, hillsides	800-1100 m	LC
E. amygdaloides subsp. *amygdaloides* L.	*Patellares* (Prokh.) Frajman	Ch.	Asia: N Iran, Turkey; W & C Europe, Caucasus, S Russia/53	*Fagus* & *Carpinus* Forests, scrubs, *Abies* woods	50-2000 m	LC
E. amygdaloides subsp. *robbiae* (Turrill) Stace	*Patellares* (Prokh.) Frajman	Ch.	Asia: NW Turkey/54	*Fagus* & *Quercus* forests	900 m	CR
E. anacampseros var. *anacampseros* Boiss.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: Turkey; Europe: Bulgaria, Greece/55	Rocky slopes, mountain steppes, stream sides, meadows, *Pinus brutia* forest	600-2200 m	LC
E. anacampseros var. *tmolae* M.S. Khan	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: Turkey/56	Rocky slopes	1200-1850 m	LC
E. antilibanotica Mouterde	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Israel/Palestine, Lebanon, Syria/57	Rocky limestone slopes	Unknown	LC

E. apios L.	*Helioscopia* Dumort.	G.	Asia: Lebanon, Syria, Turkey; Europe: Bulgaria, Greece, SE Italy/58	Rocky limestone slopes, oak and juniper forests, screes	50-1700 m	LC
E. arguta Banks & Sol.	*Helioscopia* Dumort.	Th.	Asia: Israel/Palestine, Jordan, Lebanon, Syria, Turkey; Europe: Cyprus, Greece; Africa: Egypt/59	Weed of cultivated fields (corn, cotton and broad bean fields), waste lands	0-350 m	LC
E. arvalis subsp. *arvalis* Boiss. & Heldr.[xii]	*Arvales* (Geltman) Geltman	Th.	Asia: NW Iran, Turkey; Europe: Armenia, Azerbaijan/60	Steppes, fields, hillsides	950-1600 m	LC
E. aserbajdzhanica Bordz.[xiii]	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: Iran, Turkmenistan; Europe: Armenia, Azerbaijan/61	Dry stony slopes, saline and calcareous soils	950-2000 m	LC
E. aucheri Boiss.[xiv]	*Herpetorrhizae* subsect. *aucheriae*	Hem.	Asia: Iran, N Iraq, Turkmenistan/62	Steep dry alpine and subalpine slopes, screes, metamorphic rocks, calcareous stones	1600-4100 m	LC
E. aulacosperma Boiss.	*Arvales* (Geltman) Geltman	Th.	Asia: Iran, Iraq, Israel/Palestine, Jordan, Lebanon, Syria, Turkey/63	Mountain slopes, pastures, fields	250-1700 m	LC
E. austroanatolica Hub.-Mor. & M.S. Khan	*Helioscopia* Dumort.	Hem.	Asia: SW Turkey/64	Limestone cliffs, *Pinus brutia* forests, serpentine grounds	50-1600 m	EN
E. austro-iranica Pahlevani	*Esula* (Pers.) Dumort.	Ch.	Asia: S, SE Iran/65	Rocky hills, in limestone gorges, gravelly sand and clay soils	450-2400 m	LC
E. barrelieri subsp. *thessala* (Form.) Bornm.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: NW Turkey; SE Europe: Albania, Bulgaria, Greece, Macedonia, Serbia	Rocky slopes	Unknown	LC
E. berythea Boiss. & Blanche	*Helioscopia* Dumort.	Th.	Asia: Israel/Palestine, Lebanon, Syria; Europe: Cyprus/66	Cultivated and waste lands, rocky places	50-500 m	NT
E. bivonae Steud.	*Helioscopia* Dumort.	NPh.	Africa: Algeria, Egypt, Libya, Tunisia; Europe: Crete, Malta, W Sicilia/67	Rocky ridges of the Mediterranean coastal lands, calcareous rocks	0-700 m	LC
E. boreo-baluchestanica Pahlevani	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Pakistan/68	Semi deserts, sandy and stony places	1600-2130 m	VU
E. buhsei Boiss.[xv]	*Esula* (Pers.) Dumort.	Hem.	Asia: Iran, Turkmenistan, Uzbekistan?/69	Rocky mountain slopes, sandy semi-deserts, calcareous and saline soils, disturbed areas	1200-2800 m	LC
E. bungei Boiss.[xvi]	*Sclerocyathium* (Prokh.) Prokh.	Hem.	Asia: Afghanistan, Iran, Pakistan, Turkmenistan/70	Foothills, arable lands, grazed areas, semi-desert regions, calcareous mountain slopes	500-3000 m	LC

E. caeladenia Boiss.[xvii]	*Sclerocyathium* (Prokh.) Prokh.	Hem.	Asia: S Afghanistan?, SE Iran, W Pakistan/71	Deserts, foothills, *Artemisia* and *Zygophyllum* steppes	1200-2400 m	LC
E. cassia Boiss. subsp. *cassia*	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Lebanon, W, NW Syria, S Turkey; Europe: Cyprus/72	Eroding slopes, clay hillsides, shady ridges, open pine forests	0-1200 m	LC
E. cassia subsp. *rigoi* (Boiss. ex Freyn) Holmboe	*Pithyusa* (Raf.) Lázaro	Hem.	Europe: Cyprus/73	Stony ground at edge of pine forest	300-1950 m	VU
E. caudiculosa Boiss.	*Tithymalus* (Gaertn.) Roep.	Hem.	Asia: Lebanon, W Syria/74	Rocky slopes and screes	2400-2850 m	EN
E. chaborasia Gomb.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iraq, Syria/75	Clay soils, gravelly soils, steppic and sub-desert plains, fields	150-400 m	LC
E. chamaepeplus Boiss. & Gaill.	*Tithymalus* (Gaertn.) Roep.	Th.	Asia: Iran, Iraq, Israel/Palestine, Jordan, Lebanon, Saudi Arabia, Syria; Africa: Egypt/76	Limestone cliffs, near rivers, steppes, deserts	150-2000 m	LC
E. cheiradenia Boiss. & Hohen.[xviii]	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran, N Iraq, E to C Turkey; Europe: Armenia/77	Stony mountains, igneous hillsides, *Artemisia* and *Astragalus* steppes, pastures, steppe- forest, grassy slopes, rocky limestone	1000-3350 m	LC
E. condylocarpa M. Bieb.	*Helioscopia* Dumort.	G.	Asia: Iran, Iraq, NW Syria, Turkey; Europe: Armenia, Azerbaijan, Georgia/78	Oak scrubs, rocky slopes, steppe-forest, open conifer forests, shale rocks and rock chips	450-2400 m	LC
E. coniosperma Boiss. & Buhse[xix]	*Helioscopia* Dumort.	Th.	Asia: NW Iran, Turkey; Europe: Armenia, Azerbaijan, Georgia/79	In cracked clay mud, exposed hillsides, steppes	950-1400 m	LC
E. connata Boiss.	*Calyptratae* Geltman	Hem.	Asia: Iran/80	Open gravel deserts, open *Artemisia* steppes	1100-1950 m	LC
E. consanguinea Schrenk	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: N Afghanistan, NE Iran, Kazakhstan, Turkmenistan, Tajikistan/81	Sand dunes	150-400 m	LC
E. cornigera Boiss.[xx]	*Helioscopia* Dumort.	Hem.	Asia: E Afghanistan, NW India, NE Pakistan/82	Steep grassy hillsides, on old avalanche tracks, sandy soils	1000-3800 m	LC
E. craspedia Boiss.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: W, NW Iran, E, NE Iraq, SE Turkey/83	Open oak scrubs, stony limestone steppes	600-1600 m	LC
E. cuspidata Bertol.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iraq, Jordan, Syria/84	Deserts, near hot springs, coarse gravelly and sandy deserts	65-600 m	LC
E. cyparissias L.	*Esula* (Pers.) Dumort.	Hem.	Asia: NW Turkey; W, S, C Europe, S, C Russia/85	Pine forests, sandy soils, fallow lands	0-2600 m	LC

E. cyrtophylla (Prokh.) Prokh.	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan, N Pakistan, Tajikistan, Uzbekistan/86	Sub-alpine regions, river banks, along springs, roadsides	1900-3000 m	LC
E. davisii M.S. Khan	*Patellares* (Prokh.) Frajman	Ch.	Asia: S Turkey/87	Rocky calcareous slopes	1900-2300 m	VU
E. deltobracteata (Prokh.) Prokh.	*Herpetorrhizae* subsect. *aucheriae*	Hem.	Asia: NE, N Iran, S Turkmenistan/88	Steppe grassy slopes	1200-2500 m	LC
E. dendroides L.	*Pachycladae* (Boiss.) Tutin	NPh.	Asia: Israel/Palestine, Lebanon, Turkey; N Africa: Algeria, Egypt, Libya, Morocco, Tunisia; Europe: Canary Islands, Macaronesia, Mediterranean region/89	Rocky limestone slopes, mostly near the sea	10-400 m	LC
E. densa Schrenk	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: Afghanistan, Bahrain, Iran, Iraq, Israel/Palestine (rare), Kazakhstan, Kuwait, Pakistan, E Saudi Arabia, NE Syria (rare), Tajikistan, Turkmenistan, Uzbekistan/90	Gypsum hills, gravelly deserts, loam to sandy-clay plains, saline soils	10-2000 m	LC
E. denticulata Lam.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: NW, W Iran, N, NE, E Iraq, N Syria, C to E Turkey/91	Rocky limestone and igneous slopes, steppe-forest, oak woods and scrubs	740-2800 m	LC
E. dimorphocaulon P.H. Davis	*Helioscopia* Dumort.	G.	Asia: S Turkey; Europe: Cyprus, Greece/92	*Quercus coccifera* macchie on metamorphic slopes	10-750 m	LC
E. djimilensis Boiss.	*Helioscopia* Dumort.	Hem.	Asia: NE, S Turkey/93	Alpine pastures, subalpine meadows	2000-2400 m	NT
E. dracunculoides Lam. subsp. *dracunculoides*	*Exiguae* (Geltman) Riina & Molero	Th.	Asia: Afghanistan? China, India, Iraq (rare), Kuwait?, Nepal, Pakistan, Saudi Arabia, Yemen; N, NE, NW, C Africa/94	Cultivated lands, roadsides, riverbanks, valleys	400-2000 m	LC
E. ecorniculata Kitam.	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan/95	Dry, semi plains, eroded, bare hills, crevices of rocks	2000-2550 m	VU
E. erinacea Boiss. & Kotschy	*Helioscopia* Dumort.	Ch.	Asia: Israel/Palestine, Lebanon, SW Syria; Africa: NE Egypt/96	Deserts, stony slopes	1500-2100 m	LC
E. eriophora Boiss.	*Helioscopia* Dumort.	Th.	Asia: Iran, N, NE Iraq, Lebanon, N, NW Syria, Turkey; Europe: Armenia, Azerbaijan/97	Fallow fields, calcareous and clay steppes, vineyards	600-1900 m	LC
E. erubescens Boiss.	*Patellares* (Prokh.) Frajman	Ch.	Asia: Iran, NE Iraq, Lebanon, Turkey/98	Open oak forests, scrubs, *Pinus nigra* forests, rocky slopes, serpentine soils	650-2740 m	LC
E. erythradenia Boiss.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran/99	Rocky mountain slopes	1900-2500 m	EN
E. erythrodon Boiss. & Heldr.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Turkey/100	Rocky limestone slopes, screes	1670-2300 m	LC
E. exigua L.[xxi]	*Exiguae* (Geltman) Riina & Molero	Th.	Asia: Israel/Palestine, Lebanon, W, SW Syria, Turkey; Africa: Egypt, Libya, Morocco, Tunisia; Europe: most parts of Europe/101	Arable lands, rocky limestone places, fallow fields, open *Pinus brutia* woods, pastures	0-450 m	LC

E. falcata L.	*Pithyusa* (Raf.) Lázaro	Th.	Asia: All SW & C Asian countries; Mediterranean region, some European countries, N Africa/102	Cultivated lands, roadsides, waste fallows, fields, dry stony soils, dry grasslands, foothills	0-2600 m	LC
E. ferdowsiana Pahlevani	*Sclerocyathium* (Prokh.) Prokh.	Hem.	Asia: NE Iran/103	Rocky slopes, screes	2100-2800 m	CR
E. fistulosa M.S. Khan	*Helioscopia* Dumort.	Th.	Asia: N Syria, Turkey/104	Cultivated fields	750-900 m	VU
E. franchetii B. Fedtsch.	*Arvales* (Geltman) Geltman	Th.	Asia: Afghanistan, China (N Xinjiang), NE Iran, Kazakhstan, Kirgizstan, Tajikistan, Turkmenistan, Uzbekistan/105	Stony and pebbly mountain slopes	750-1500 m	LC
E. gaillardotii Boiss. & Blanche[xxii]	*Pithyusa* (Raf.) Lázaro	Th.	Asia: N Iraq, Israel/Palestine, Lebanon, Syria, Turkey/106	Fallow fields, roadsides, steppes	300-1400 m	LC
E. gedrosiaca Rech.f., Aellen & Esfand.[xxiii]	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: W Afghanistan, E, SE Iran/107	Steppes, rocky hillsides, deserts	1550-1950 m	LC
E. glaberrima K. Koch	*Patellares* (Prokh.) Frajman	Ch.	Caucasus: Armenia, Georgia, S Russia/108	Subalpine meadows, mountain forests	800-2800 m	LC
E. glareosa Pall. ex M. Bieb.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: NW Iran, Turkey; Europe: Armenia, Azerbaijan, Bulgaria, Georgia, S Russia, Ukraine (Krym)/109	Stony places, steppes, stream sides, scrubs	500-1500 m	LC
E. grisophylla M.S. Khan	*Helioscopia* Dumort.	Hem.	Asia: W Iran, E Turkey/110	Dry rocky igneous and limestone slopes, screes	2100-3100 m	LC
E. grossheimii (Prokh.) Prokh.[xxiv]	*Sclerocyathium* (Prokh.) Prokh.	Th.	Asia: Iran, Iraq, Israel/ Palestine, Kuwait, SW Pakistan, Saudi Arabia, Syria; Africa: Egypt; Europe: Azerbaijan/111	Deserts, sandy gravely banks, dry river-beds, dry salt steppes	0-600 m	LC
E. gulestanica Podlech	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan/112	Mountain slopes	1600 m	CR
E. gypsicola Rech.f., Aellen	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran/113	Gypsum hills	1170-1500 m	EN
E. haussknechtii Boiss.	*Helioscopia* Dumort.	Th.	Asia: N Syria, SE Turkey/114	Basalt plains	Unknown	EN
E. hebecarpa Boiss.[xxv]	*Esula* (Pers.) Dumort.	Hem.	Asia: Iran/115	Sub alpine to alpine regions, rocky limestone slopes, *Artemisia* steppes	2100-4000 m	LC
E. helioscopia L.	*Helioscopia* Dumort.	Th.	Cosmopolitan/116	Ruderal weed in disturbed and cultivated areas, city gardens	0-2100 m	LC
E. herniariifolia Halácsy var. *glaberrima*	*Tithymalus* (Gaertn.) Roep.	Ch.	Asia: Lebanon, SW Syria, Turkey; Europe: Greece/117	Limestone cliffs, rocky igneous slopes, screes, subalpine meadows, *Abies* forests, poor pastures	50-3050 m	LC
E. herniariifolia var.	*Tithymalus* (Gaertn.)	Ch.	Asia: Syria, Turkey; Europe: Albania, Cyprus,	Rocky limestone slopes, crevices of limestone &	300-2900 m	LC

herniariifolia Willd.	Roep.		Greece/118	igneous cliffs, *Juniperus* forests		
E. heteradena Jaub. & Spach[xxvi]	*Chylogala* (Fourr.) Prokh.	Hem.	Asia: Iran, N, NE, E Iraq, E Turkey; Europe: Armenia, Azerbaijan/119	Steppes, rocky slopes, deserts, sandy hills, fallow fields, arable lands, roadsides	1100-2300 m	LC
E. hierosolymitana Boiss.	*Helioscopia* Dumort.	NPh.	Asia: Israel/ Palestine, Jordan, Lebanon, Syria, SE Turkey; Africa: Egypt/120	Roadsides, limestone rocks and cliffs, open forests	5-1570 m	LC
E. hirsuta L.[xxvii]	*Helioscopia* Dumort.	Hem.	Asia: Israel/ Palestine, Lebanon, W Syria, Turkey; Europe: Mediterranean region, Georgia, Canary Island; Africa: Algeria, Morocco, Tunisia/121	Salt marshes, marshy fields, riverbanks, sandy beaches	0-1300 m	LC
E. humilis Ledeb.[xxviii]	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: China, Kazakhstan, Kyrgyzstan, Turkmenistan, Uzbekistan	Rocky and stony slopes, foothills, steppes, scrubs	Unknown	LC
E. hyrcana Grossh.[xxix]	*Paralias* Dumort.	Th.	Europe: Azerbaijan/122	Unknown	Unknown	DD
E. iberica Boiss.	*Esula* (Pers.) Dumort.	Hem.	Asia: NW Iran, NE Iraq, E Turkey; Europe: Armenia, Azerbaijan, Georgia, S Russia/123	Alpine to sub alpine stony slopes, *Astragalus* and *Artemisia* steppes	1700-3550 m	LC
E. illirica Lam.	*Helioscopia* Dumort.	Hem.	Asia: NW Turkey; Europe: Mediterranean region, C Europe/124	Open woods, riverbanks, damp meadows, lowlands	0-700 m	LC
E. inderiensis Less. ex Kar. & Kir.	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: Afghanistan, NW China (N Xinjiang), Iran, Kazakhstan, Kyrgyzstan, NW Pakistan (rare), Tajikistan, Turkmenistan, Uzbekistan/125	*Artemisia* steppes, dry stony hillsides	500-2530 m	LC
E. iranshahri Pahlevani	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran/126	Mountain rocky slopes	2100-3000 m	VU
E. irgisensis Litv.	*Esula* (Pers.) Dumort.	Hem.	Asia: Kazakhstan, Turkmenistan	Clay steppes	Unknown	DD
E. isaurica M.S. Khan	*Tithymalus* (Gaertn.) Roep.	Ch.	Asia: S Turkey/127	Mouths of limestone caverns	1400-1550 m	CR
E. jacquemontii Boiss.	*Holophyllum* (Prokh.) Prokh.	Hem.	Asia: NW India, NE Pakistan/128	Unknown	Unknown	DD
E. jaxartica (Prokh.) Krylov[xxx]	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan, Kazakhstan, Uzbekistan/129	Irrigation ditches, riparian woodlands, fallow fields	2000 m	DD
E. kanaorica Boiss.	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Hem.	Asia: NE Afghanistan, N Pakistan, NW India/130	Stony slopes, screes, gravel slides	3000-4350 m	LC
E. kavirensis Pahlevani	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: C Iran/131	Gravelly desert in *Artemisia* steppes	900-1400 m	VU

E. khabrica Pahlevani	*Esula* (Pers.) Dumort.	Hem.	Asia: Iran/132	Screes, calcareous rocky slopes	2200-2800 m	EN
E. kopetdaghii (Prokh.) Prokh.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: NE Iran, S Turkmenistan/133	Steppe-forests, scrubs, foothills, *Juniperus* open woodlands, stony slopes, field margins	1250-2300 m	NT
E. kotschyana Fenzl	*Patellares* (Prokh.) Frajman	Ch.	Asia: Lebanon, Syria, Turkey/134	Limestone screes, rocky grounds, *Quercus* scrubs, *Abies*, *Cedrus* and *Juniperus* forests, stony meadows	500-2650 m	LC
E. lathyris L.	*Lathyris* Dumort.	Th.	C Asia, Turkey, Far East, Pakistan, Caucasus, Europe/135	Gravelly and sandy shores, cultivated as ornamental in many places	0-500 m	LC
E. ledebourii Boiss.	*Paralias* Dumort.	Th.	Asia: N Turkey, Europe: Armenia, Azerbaijan, Georgia, Romania, Ukraine/136	Steppes, gypsum hills, rocky grounds	300-900 m	LC
E. lemesiana Hadjik., Hand, Christodoulou & Frajman	*Helioscopia* Dumort.	NPh.	Europe: Cyprus/137	Igneous rocks, forests, streamside	200-600 m	EN
E. lucida Waldst. & Kit.	*Esula* (Pers.) Dumort.	Hem.	Asia: NW Turkey; Europe: C Europe, Siberia & Balkans to C Asia?/138	Granite stones and boulders, riverbanks	1800-2000 m	LC
E. macrocarpa Boiss. & Buhse	*Helioscopia* Dumort.	Hem.	Asia: N, W Iran, N Iraq, Turkey; Europe: Armenia, Azerbaijan/139	Oak forests, stony volcanic slopes, rocky limestone pass	1100-3000 m	LC
E. macroceras Fisch. & C.A. Mey.	*Patellares* (Prokh.) Frajman	Ch.	Asia: N Iran, N Turkey; Europe: Armenia, Azerbaijan, Georgia, SW Russia/140	Hyrcanian and Caucasian forests	1300-2600 m	LC
E. macroclada Boiss.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran, Iraq, Israel/ Palestine, Jordan, Lebanon, Syria, Turkey; Europe: Armenia/141	Disturbed areas, arable lands, dry meadows, road sides, *Artemisia* and *Astragalus* steppes, open oak forests	700-2300 m	LC
E. maddenii Boiss.	*Arvales* (Geltman) Geltman	Th.	Asia: NW India, NE Pakistan/142	Dry hillsides, earthy cliffs, forest paths	2100-3000 m	LC
E. malleata Boiss.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: C Iran/143	*Artemisia* and *Astragalus* steppes, overgrazed and dry mountain slopes	1700-3450 m	LC
E. malurensis Rech.f.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Afghanistan/144	Rocky dry and steep slopes, granite beds, fields	2000-3850 m	LC
E. marschalliana subsp. *armena* (Prokh.) Oudejans	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: NW Iran, NE Turkey; Europe: S Armenia/145	River banks, sandy plains and gravelly steppes	800-1650 m	LC
E. marschalliana subsp. *marschalliana* Boiss.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: NW Iran, NE Turkey; Europe: Armenia, Azerbaijan/146	Roadsides, dry stony and pebbly slopes, river banks, igneous slopes	1000-2100 m	LC
E. mazandaranica Pahlevani	*Helioscopia* Dumort.	Hem.	Asia: N Iran/147	Hyrcanian forests	50-1200 m	VU
E. megalocarpa Rech.f.[xxxi]	*Holophyllum* (Prokh.) Prokh.	Hem.	Asia: Afghanistan/148	Rocky limestone slopes	2600-2800 m	CR
E. micractina Boiss.	*Helioscopia* Dumort.	Hem.	Asia: China, India, N Pakistan/149	Grasslands, birch woods, meadows, sparse forest margins	1600-4250 m	LC

E. microsciadia Boiss.[xxxii]	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran/150	Steppes, roadsides, foothills, mountain slopes, arable lands	1200-3000 m	LC
E. microsphaera Boiss.	*Helioscopia* Dumort.	Th.	Asia: Iran, Iraq, Israel/ Palestine, Jordan, Lebanon, Syria, Tajikistan? Turkey, Uzbekistan; Europe: Armenia, Azerbaijan/151	Fields, roadsides, marshlands, stream sides, lakesides	0-2800 m	LC
E. monostyla Prokh.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: NE Iran, S, SW Turkmenistan/152	Dry stony and pebbly slopes, schistose soil	600-1400 m	LC
E. myrsinites L.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: Iran, Turkey; Europe: Mediterranean region/153	Mountain pastures, rocky dry slopes, calcareous slopes	400-3400 m	LC
E. nubica N.E. Br.	*Aphyllis* Webb & Berthel. subsect. *africanae* Molero & Barres	NPh.	Asia: Saudi Arabia, Yemen; Africa: Djibouti, Egypt, Ethiopia, Kenya, Somalia, Sudan, Uganda/154	Open *Acacia* bushlands, rocky slopes, margin of *Juniperus* forests, overgrazed areas	400-1900 m	LC
E. oblongata Griseb.	*Helioscopia* Dumort.	Hem.	Asia: W Turkey; Europe: Greece, S Balkans, introduced to several parts of C European countries & the New World/155	Damp meadows, mica-schist hillsides in maquis, disturbed areas	0-1200 m	LC
E. oblongifolia (K. Koch) K. Koch[xxxiii]	*Patellares* (Prokh.) Frajman	Ch.	Asia: Turkey; Europe: Armenia, Azerbaijan, Georgia/156	Mountain forests, subalpine meadows, *Fagus* forests by stream	1000-2800 m	LC
E. obovata Decne.[xxxiv]	*Pithyusa* (Raf.) Lázaro	Hem.	Africa: NE Egypt (Sinai)/157	Rocky slopes, red granite boulders	1700-2300 m	CR
E. oidorrhiza Pojark.	*Esula* (Pers.) Dumort.	Hem.	Asia: Turkmenistan	Unknown	Unknown	DD
E. orientalis L.	*Helioscopia* Dumort.	Hem.	Asia: Iran, Iraq, E Turkey; Europe: Armenia, Azerbaijan/158	Rocky slopes, screes, scrubs, metamorphic rocks, eroded clay hills, dry river banks	650-2400 m	LC
E. osyridea Boiss.	*Esula* (Pers.) Dumort.	Ch.	Asia: Afghanistan, Iran, Pakistan/159	Rocky foothills, in limestone gorges, gravelly and sandy beds, siliceous rocks	350-2200 m	LC
E. oxyodonta Boiss.	*Helioscopia* Dumort.	Th.	Asia: Israel/ Palestine, Jordan, Lebanon, Syria, Turkey; Africa: Egypt, Libya/160	Grassy patches, limestone plains, arable lands	100-600 m	LC
E. palustris L.	*Helioscopia* Dumort.	Hem.	Asia: Turkey; Europe: almost all parts of Europe/161	Riversides, lakesides, swamps, coastal marshes	5-1160 m	LC
E. pamirica (Prokh.) Prokh.	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan, N Pakistan, Tajikistan/162	Rocky slopes	2900-3700 m	DD
E. pannonica Host	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: N, NW Turkey; Europe: C & E Europe to Caucasus/163	*Pinus nigra* forests, scrubs, steppes, streamsides	600-1600 m	LC
E. paralias L.	*Paralias* Dumort.	Ch.	Asia: Israel/ Palestine, Lebanon, Syria, Turkey;	Sandy coasts, shingle beaches	0-15 m	LC

			Africa: Egypt, Libya, Morocco, Tunicia; Europe: Macaronesia, W Europe, Black sea & Mediterannean coasts/164			
E. parvula Delile	*Exiguae* (Geltman) Riina & Molero	Th.	Africa: Egypt, Libya/165	Stony roadsides	0-150 m	DD
E. peplus DC. var. *minima*	*Tithymalus* (Gaertn.) Roep.	Th.	Asia: N Iran, Lebanon, Turkey; Africa: Egypt, Morocco; Europe: Mediterranean regions/166	Sea shores, margin of forests, fallow fields, roadsides	0-1400 m	LC
E. peplus L.	*Tithymalus* (Gaertn.) Roep.	Th.	Asia: Bahrain, India, Iran, Iraq, Israel/Palestine, Jordan, Kuwait, Lebanon, Oman, Pakistan, Qatar, Saudi Arabia, Syria, Turkey, UAE, Yemen, Far East; Africa: Algeria, Egypt, Libya, Morocco, Tunisia; Most parts of European countries; Introduced to the New World/167	Weed in arable lands, waste grounds, disturbed forests, ornamental gardens, rocky and grassy places	0-2500 m	LC
E. pestalozzae Boiss.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Turkey/168	Rocky summit ridges, screes	2000-2500 m	LC
E. petitiana A. Rich.[xxxv]	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Yemen; Africa: Ethiopia/169	Rocky silty scree slopes, field edges, stony summits, open grasslands, evergreen bushlands	1800-3000 m	LC
E. petrophila C.A. Mey.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Turkey; Europe: S Russia, Ukraine/170	Open rocky places, stony steppes, pine groves, sandstone hills, meadows	750-2000 m	LC
E. phymatosperma subsp. *phymatosperma* Boiss. & Gaill.	*Lagascae* Lázaro	Th.	Asia: Iran, Iraq, Israel/Palestine, Jordan, Lebanon, Syria, Turkey/171	Steppes, limestone hills, *Quercus* scrubs, valleys	550-2000 m	LC
E. physocaulos Mouterde	*Helioscopia* Dumort.	Th.	Asia: Syria, Turkey/172	Fallow fields	600-850 m	EN
E. pisidica Hub.-Mor. & M.S. Khan	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: SW Turkey/173	Pastures, on volcanic rocks, serpentine soils, scree slopes	1490-1700 m	CR
E. platyphyllos L.	*Helioscopia* Dumort.	Th.	Asia: Turkey; Europe: C Europe to Mediterranean parts, Transcaucasus; Africa: N Africa/174	Fields, forests, roadsides, sandy shores, ditches	50-1300 m	LC
E. plebeia Boiss.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: S Iran/175	Mountain slopes	1350-1700 m	VU
E. polycaulis Boiss. & Hohen.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Iran/176	Dry stony slopes, overgrazed pastures and rangelands, clay and limestone slopes	1300-3500 m	LC
E. prolifera Buch.-Ham. ex D.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: NE Afghanistan, N Burma, SW China, N India, Nepal, Pakistan, Thailand/177	Open grassy slopes, pine forests, valleys	450-2300 m	LC

Don[xxxvi]						
E. promecocarpa Davis	*Tithymalus* (Gaertn.) Roep.	Hem.	Asia: Syria/178	Among rocks, cliffs	1400-1700 m	CR
E. pterococca Brot.	*Helioscopia* Dumort.	Th.	Asia: W Turkey?; Africa: Algeria, Egypt, Libya, Morocco, Tunisia; Europe: Mediterranean parts/179	Cultivated areas, calcareous regions	50-500 m	LC
E. punctata Delile	*Tithymalus* (Gaertn.) Roep.	Th.	Africa: Egypt/180	Cultivated grounds	0-100 m	CR
E. retusa Forssk.	*Chylogala* (Fourr.) Prokh.	Hem.	Asia: Iraq, Israel/Palestine, Jordan, Kuwait, Oman, Qatar, Saudi Arabia, UAE; Africa: Algeria, Egypt, Libya, Morocco, Mauritania, Tunisia/181	Deserts, sandy hills, red sandstones, roadsides, clay soils, stony deserts, abandoned fields	300-900 m	LC
E. reuteriana Boiss.	*Paralias* Dumort.	Th.	Asia: Israel/Palestine, Jordan, Lebanon, Syria/182	Fields, plains and valleys, mountain slopes	40-300 m	VU
E. rhabdotosperma Radcl.-Sm.	*Helioscopia* Dumort.	Th.	Asia: Iran, Turkey; Europe: Armenia, Azerbaijan, Georgia/183	River banks, foothills, edge of irrigated fields, limestone rocks, steppes	1100-1400 m	LC
E. rhytidosperma Boiss. & Balansa	*Helioscopia* Dumort.	Hem.	Asia: S Turkey/184	Rocky gorges	1500 m	CR
E. rigida M. Bieb.[xxxvii]	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: NW, W Syria, Turkey; Europe: E Mediterranean & Balkans; Africa: Algeria, Morocco/185	Road embankments, open oak and pine forests, Islands, bare rocky limestone slopes, dry river beds, fallow fields	50-2000 m	LC
E. sahendi Bornm.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: NW Iran/186	Alpine steppe, igneous mountain slopes	3100-3600 m	CR
E. salicifolia Host	*Esula* (Pers.) Dumort.	Hem.	Asia: NW Turkey (rare); Europe: Balkan peninsula to C Europe/187	Lowland meadows, under forests	30-350 m	LC
E. schimperi C. presl	*Aphyllis* Webb & Berthel. subsect. *Africanae* Molero & Barres	NPh.	Asia: S Oman, Saudi Arabia, Yemen; Africa: SE Egypt, Eritrea, Ethiopia, Sudan?/188	Steep hillsides, granite boulders, rocky and pebbly slopes	150-2500 m	LC
E. schimperiana Scheele var. *schimperiana*	*Esula* (Pers.) Dumort.	Th. to Ch.	Asia: Oman, Saudi Arabia, Yemen; Africa: many parts of E, SE, C, W Africa/189	Grasslands, mountain forests, cultivation weeds, evergreen bushlands, swampy grounds, rocky slopes, fine vesicular basalt screes	250-3100 m	LC
E. schottiana Boiss.	*Helioscopia* Dumort.	Hem.	Asia: Turkey/190	Mountain valleys	2800-3100 m	CR

E. schugnanica B. Fedtsch.	*Sclerocyathium* (Prokh.) Prokh.	Hem.	Asia: Afghanistan, Tajikistan/191	Rock debris on slopes, subalpine zones, granite beds	2600-3300 m	NT
E. sclerocyathium Korovin & Popov	*Sclerocyathium* (Prokh.) Prokh.	Ch.	Asia: Kazakhstan, Turkmenistan/192	Stony deserts and sands	0-600 m	DD
E. seguieriana subsp. *hohenackeri* (Boiss.) Rech. f.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Turkey; Europe: Armenia, Azerbaijan/193	Rocky slopes, Steppes	1500-1700 m	LC
E. seguieriana Neck.subsp. *seguieriana*[xxxviii]	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Afghanistan? Iran, Kazakhstan, Turkey, Turkmenistan, Uzbekistan; Europe: Armenia, Azerbaijan, Georgia, C Europe, Balkan peninsula, Mediterranean region/194	Calcareous and stony slopes, fallow fields, pastures, shrubby steppes, foothills, roadsides, lakesides, river banks, dry *Astragalus* steppes	700-3100 m	LC
E. seguieriana subsp. *niciciana* (Borbás ex Novák) Rech. f.	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: Iran, Turkey; Europe: Balkan peninsula/195	Limestone slopes, beech forests, igneous rocky slopes, riversides	50-2600 m	LC
E. sintenisii Boiss. ex Freyn	*Helioscopia* Dumort.	Th.	Asia: Israel/Palestine, Jordan, Lebanon, Syria, Turkey; Africa: Egypt; Europe: Cyprus/196	Fields, roadsides, irrigated chanels	50-800 m	LC
E. smirnovii Geltman	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: E Turkey/197	Open rocky places, stony steppes	1400-2000 m	CR
E. sogdiana Popov	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Afghanistan, Tajikistan, Uzbekistan/198	Crevices of limestone rocks, gorges	1000-2200 m	LC
E. sororia Schrenk[xxxix]	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: Afghanistan, NW China?, Iran, Kazakhstan, Kirghizstan, Pakistan, Tajikistan/199	Sands and solonchak meadows, deserts, *Artemisia* steppes	600-1300 m	LC
E. spartiformis Mobayen	*Pithyusa* (Raf.) Lázaro	Ch.	Asia: S Iran/200	Chasmophyte, calcareous slopes	600-1350 m	EN
E. spinidens Bornm. ex Prokh.	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: Afghanistan, NE Iran, Tajikistan, Turkmenistan, Uzbekistan/201	Gypsum hills, *Juniperus* forests, dry mountain slopes, rock fissures	490-2100 m	LC
E. squamosa Willd.	*Helioscopia* Dumort.	Hem.	Asia: NW Iran, NE Turkey; Europe: Armenia, Azerbaijan, Georgia, SW Russia/202	Caucasian forests, ecotone between alpine meadows and forests, calcareous rocky slopes, woodlands, cliffs near sea shores	20-2050 m	LC
E. stricta L.	*Helioscopia* Dumort.	Th.	Asia: N, NW Iran, Turkey; Europe: Armenia, Azerbaijan, Georgia, C Europe, Balkan peninsula, UK/203	Forests, edge of woods, roadsides, grassy slopes, streamsides, salt marshes, fallow fields, irrigated ditches, sandstone and limestone rocks	5-2400 m	LC
E. sulphurea Pahlevani	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: SE Iran/204	Alpine stony ground in volcanic mountain on the sulphur bed	3700-3900 m	CR
E. szovitsii Fisch. & C.A. Mey.	*Szovitsiae* Geltman	Th.	Asia: Afghanistan, Iran, Iraq, Lebanon, Pakistan, Syria, Tajikistan, Turkey, Turkmenistan, Uzbekistan; Europe: Armenia,	Dry stony slopes, valleys by streams, hillsides and fields, steppes, open oak forests, vineyards, fallow fields	300-2800 m	LC

			Azerbaijan, Georgia/205			
E. talaina Radcl.-Sm.	*Esula* (Pers.) Dumort.	Hem.	Asia: Pakistan/206	Moist and damp areas, by freshwater springs, shady gardens	2200-2750 m	VU
E. taurinensis All.	*Paralias* Dumort.	Th.	Asia: Turkey; Europe: Cyprus, C, S, E Europe/207	Limestone screes, pine forests, oak scrubs, roadsides, fallow fields, vineyards, grassy places	50-1600 m	LC
E. teheranica Boiss.	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Iran/208	Gypsum hills, *Artemisia, Stipa* and *Astragalus* steppes, dry mountain slopes	950-2000 m	NT
E. terracina L.	*Pachycladae* (Boiss.) Tutin	Ch.	Asia: Israel/Palestine, Lebanon, Syria, Turkey; Africa: Algeria, Egypt, Libya?, Morocco, Tunisia; Europe: Macaronesia, Mediterranean region, Georgia/209	Coastal dunes, rocky limestone slopes, roadsides	0-200 m	LC
E. thompsonii Holmboe	*Patellares* (Prokh.) Frajman	Ch.	Asia: S Turkey; Europe: Cyprus/210	Igneous slopes, *Quercus coccifera* macchie	350-1200 m	VU
E. thomsoniana Boiss.	*Holophyllum* (Prokh.) Prokh.	Hem.	Asia: Afghanistan, NW, W China, NW India, Kyrgyzstan, Pakistan, Tajikistan/211	Alpine to subalpine meadows, scrubs	2000-4300 m	LC
E. thyrsoidea Boiss.[xl]	*Esula* (Pers.) Dumort.	Hem.	Asia: NE Afghanistan, NW India, N Pakistan, Tajikistan, Turkmenistan, Uzbekistan/212	Limestone slopes	1100-2100 m	LC
E. tibetica Boiss.	*Sclerocyathium* (Prokh.) Prokh.	Hem.	Asia: NW China, NW India, Kyrgyzstan?, N Pakistan/213	High altitude deserts, sandy, stony soils on stream banks, dry and semidry fields, screes and rocky slopes	3000-4900 m	LC
E. turczaninowii Kar. & Kir.	*Herpetorrhizae* subsect. *Oppositifoliae* Boiss.	Th.	Asia: Afghanistan, China, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Tajikistan, Turkmenistan, Uzbekistan/214	Mobile to semi-mobile sandy hills	800-2400 m	LC
E. turkestanica Regel[xli]	*Sclerocyathium* (Prokh.) Prokh.	Th.	Asia: Afghanistan, NW China, NE Iran, Kazakhstan, Kyrgyzstan, Tajikistan?, Turkmenistan, Uzbekistan/215	Lowlands on foothills, semi-deserts area	350-1600 m	LC
E. valerianifolia Lam.[xlii]	*Helioscopia* Dumort.	Th.	Asia: Israel/Palestine, Lebanon, Syria, Turkey; Europe: Cyprus, Greece/216	Rocky limestone slopes, oak scrubs, roadsides, fallow fields, macchie, edge of fields	0-1530 m	LC
E. veneris M.S. Khan	*Myrsiniteae* (Boiss.) Lojac.	Ch.	Asia: Cyprus/217	*Pinus nigra* forests, stony serpentine slopes	700-1700 m	EN
E. virgata Waldst. & Kit.	*Esula* (Pers.) Dumort.	Hem.	Asia: Afghanistan, Iran, Iraq, Kazakhstan, Kyrgyzstan, Pakistan, Tajikistan, Turkey, Turkmenistan; Europe: Armenia, Azerbaijan, Georgia to C Europe; introduced to the N	Steppes, grasslands, rocky slopes, limestone slopes, marshes, streamside, damp places, roadsides, fields, edge of irrigation ditches, scrubs	90-3000 m	LC

			America/218			
E. wallichii Hook. f.	*Holophyllum* (Prokh.) Prokh.	Hem.	Asia: Afghanistan, China, India, Nepal, Pakistan/219	Alpine to subalpine meadows and shrublands, timberlines, juniper scrubs	2000-4500 m	LC
E. wittmannii Boiss.	*Helioscopia* Dumort.	Hem.	Asia: NE Turkey; Europe: SW Georgia/220	Steppes, rocky slopes	1000-1500 m	VU
E. wulfenii Hoppe ex W.D.J. Koch	*Patellares* (Prokh.) Frajman	Ch.	Asia: W, SW Turkey; Europe: Balkans, S France/221	Rocky limestone slopes, screes, roadsides	0-1000 m	LC
E. ziaratensis Pahlevani	*Pithyusa* (Raf.) Lázaro	Hem.	Asia: Pakistan/222	Stony and rocky ground in mountains	2400-2600 m	CR
Subgenus *Euphorbia* L.	*Euphorbia* L.	Phan.	Asia: W Saudi Arabia, Yemen/223	Rocky hillsides, valleys, granite hills	1000-2300 m	LC
E. ammak Schweinf.						
E. cactus Ehrenb. ex Boiss.	*Euphorbia* L.	NPh.	Asia: Oman, Saudi Arabia, Yemen; Africa: Eritrea, Ethiopia, Sudan/224	Rocky open grounds, escarpments, sandy coastal plains, *Acacia oerfota* bushlands	10-2150 m	LC
E. caducifolia Haines	*Euphorbia* L.	NPh.	Asia: India, Pakistan/225	Stony grounds, coastal plains and hills, sandy coasts	0-800 m	LC
E. collenetteae D. Al-Zahrani & El-Karemy	*Euphorbia* L.	NPh.	Asia: Saudi Arabia; Africa: Eritrea, Sudan/226	Sandy grounds, fossil coral substratum	5-20 m	LC
E. fractiflexa S. Carter & J.R.I. Wood	*Euphorbia* L.	NPh.	Asia: Saudi Arabia, Yemen/227	Coastal areas, flat sandy plains, line drifted dunes, among *Salvadora persica* shrubs	100-350 m	NT
E. frankii Lavranos	*Euphorbia* L.	Ch.	Asia: N Yemen/228	Steep rocky slopes	2800 m	DD
E. fruticosa Forssk.	*Euphorbia* L.	Ch.	Asia: SW Saudi Arabia, Yemen/229	Gorges, rocky sandstone slopes and cliffs	1050-2700 m	NT
E. greuteri N. Kilian, Kürschner & P. Hein	*Euphorbia* L.	Ch.	Asia: S Yemen/230	Rocky to gravelly volcanic substrate, lava gravels	100-550 m	CR
E. inarticulata Schweinf.	*Euphorbia* L.	NPh.	Asia: Saudi Arabia, Yemen/231	Rocky hillsides, escarpments, roadsides, stony slopes	400-1700 m	LC
E. madinahensis Fayed & Al-Zahrani	*Euphorbia* L.	NPh.	Asia: Saudi Arabia/232	Barren rocky hillsides, granite mountains	1050-2350 m	EN
E. momccoyae Lavranos	*Euphorbia* L.	NPh.	Asia: Oman/233	Limestone terrains, low hillsides to level grounds, cliffs	700-1000 m	DD
E. parciramulosa Schweinf.	*Euphorbia* L.	NPh.	Asia: Saudi Arabia, Yemen/234	Granite sands, valleys, rocky hillsides	280-2800 m	VU
E. polyacantha Boiss.	*Euphorbia* L.	NPh.	Asia: S Yemen; Africa: NE tropical Africa: SE Egypt, Eritrea, Ethiopia, Somalia, Sudan/235	Stony slopes, dry hilly savanna of the hills near Red Sea	800-2250 m	LC
E. qarad Deflers	*Euphorbia* L.	Ph.	Asia: S Yemen/236	Gravelly plains, dry slopes, foothills of escarpment on limestone	150-200 m	VU
E. royleana Boiss.	*Euphorbia* L.	NPh.	Asia: S China, N India, Myanmar, Nepal, NE Pakistan/237	Hot and dry rocky hills and slopes	450-1830 m	LC
E. saudiarabica Fayed & Al-Zahrani	*Euphorbia* L.	NPh.	Asia: Saudi Arabia/238	Sea shores, black basalt blocks, fine drifting clay-sand	0-30 m	EN

E. seibanica Lavranos & Gifri	*Euphorbia* L.	Ch.	Asia: Yemen/239	Rocky slopes	1750-2000 m	DD
E. taifensis Fayed & Al-Zahrani	*Euphorbia* L.	NPh.	Asia: Saudi Arabia/240	Stony and rocky slopes	1700-2100 m	CR
E. tirucalli L.	*Tirucalli* Boiss.	NPh.	Tropical Africa to India, cultivated elsewhere/241	Semi-arid tropical regions, bushland thickets, open woodlands and grasslands	0-2000 m	LC
E. triaculeata Forssk.	*Euphorbia* L.	Ch.	Asia: SW Saudi Arabia, Yemen; Africa: Djibouti, Eritrea, Ethiopia, Somalia, Sudan/242	Foot of escarpments, rocky hillsides, foothills, sandy plain with reddish marking	45-800 m	LC
E. uzmuk S. Carter & J.R.I. Wood	*Tirucalli* Boiss.	NPh.	Asia: Oman?, Yemen/243	On low knolls and rocky hills	800-1300 m	EN

[i] Based on Govaerts *et al*. (2000) this species occurs in Iran, whereas no individual has been seen and recorded till now.

[ii] This species has been reported from Turkey by Parolly & Eren (2007). Both morphological features described in the paper and distributional pattern reject correct identification. However, it is necessary to check the specimen for final judgment.

[iii] A new record from Afghanistan (Afghanistan: Jalalabad, weed in parks, in shadow of trees, 650 m, 18.x.1969, *Freitag* 7426 MSB).

[iv] A new record from Iran.

[v] The species have been reported from Afghanistan, Iran and Pakistan (Rechinger & Schiman-Czeika, 1964; Govaerts *et al*., 2000), but after examination of the specimens, it was clarified that specimens from Afghanistan and Pakistan belong to *E. clarkeana* and that of Iran likely belongs to *E. humifusa*.

[vi] The species has been introduced to some places of the Old World as a weed and is here reported for the first time from Afghanistan (Afghanistan: Nuristan, Gusalak, 1000 m, 4.viii.1948, *L. Edelberg* 1189 W).

[vii] This species has been reported from Flora Iranica area from Caspian Sea shore and Persian Gulf coast (Rechinger & Schiman-Czeika, 1964; Radcliffe-Smith, 1980; 1982). It is more likely that it was either misidentified or simply the records are misspelling of *E. peplus*.

[viii] A new record from northernmost parts of Oman (Oman: Rowdah Bowl, Musandam Peninsula, on sandy alluvial plain with *Tephrosia* and *Hammada*, 23.viii.1982, *Maconochie* 3693 E).

[ix] This newly report from S Turkey was already known from Syria. Its status as a separate species should be checked in the future (Turkey: Gaziantep, ca 5 km N Halfeti, 450 m, 23.v.1983, *Sorger* 83-4-9 W).

[x] This weedy species has been introduced to many parts of the Old World and here is reported from Afghanistan for the first time (Afghanistan: Jalalabad, parks, 650 m, 18.x.1969, common weed, *Freitag* 7425 MSB; Kunar, Dewagal Darrah, near Chambel, 1000 m, 34º 43´ N 70º 53´ E, 29.viii.1973, *O. Anders* 11011 MSB; Kunar, Nuristan, Kunar-valley, Jalalah, ca. 46 km above Chigha Serai, 1020 m, 21.viii.1969, *Podlech* 16132 MSB).

[xi] A local endemic of southwestern parts of Iran. The doubtful presence of this species in Afghanistan by Breckle, Hedge & Rafiqpoor (2013) is corrected by describing the new species *E. acanthoclada* in this paper.

[xii] The previous records of this species from Iraq are misidentification of *E. densa* (Radcliffe-Smith, 1980).

[xiii] Previous report of this species from Afghanistan and Pakistan (Radcliffe-Smith, 1986; Govaerts *et al*., 2000; Breckle *et al*., 2013) are misidentification of *E. szovitsii*.

[xiv] This is misidentified from Afghanistan and Pakistan (Radcliffe-Smith, 1986; Govaerts *et al*., 2000; Breckle *et al*., 2013). The reported specimens from Afghanistan belong to *E. kanaorica* and those of Pakistan are described in this paper as *E. ziaratensis*.

[xv] Reports of *E. buhsei* from Afghanistan (Govaerts *et al*., 2000; Breckle *et al*., 2013) are misidentified of *E. ecorniculata*.

[xvi] A new record from Pakistan occurring in N Baluchistan near the border of Afghanistan (Pakistan: Quetta, between Bostan and Khanozai, 1600 m, 30º 23´ N 67º 00´ E, 10.v.1965, *Rechinger* 29143 K, W; Quetta, Spin Karez, near Quetta, 1800 m, 31.iii.1965, *Rechinger* 27345 W).

[xvii] All the studied herbarium specimens of the species reporting from Afghanistan belong to *E. bungei* and despite its occurrence near the border of Afghanistan, no specimen has been seen from this country.

[xviii] Reports from Afghanistan and eastern part of Mediterranean region (Zohary, 1972; Govaerts *et al*., 2000; Breckle *et al*., 2013) are misidentifications. Those from Afghanistan belong to *E. sogdiana* and those of E Mediterranean countries (Israel/Palestine, Lebanon) are more likely an affinity of *E. antilibanotica*.

[xix] A new record for Iran (Iran: Ardebil, 10 km from Givi to Ardebil, 37º 44´ N 48º 17´ E, 1383 m, 28.iv.2010, *Akhani et al.* 21138 Hb. Akhani); the type specimen has been collected from Gamarlu occurring in Armenia near Iranian border.

[xx]*E. cornigera* is a complex taxon with high morphological plasticity in the western Himalaya. Checking of *E. cashmeriana*, reported from the same area showed its synonymy with *E. cornigera*.

[xxi] A Mediterranean element erroneously reported from Iran (Rechinger & Schiman-Czeika, 1964; Govaerts *et al*., 2000). Iranian reports belong to *E. szovitsii*.

[xxii] This species has been reported from Iran by Parsa (1949) and Govaerts *et al*. (2000), but so far, no specimen has been seen yet. Apparently, subsequent authors have followed Parsa.

[xxiii] The species has been known hitherto from SE Iran. It is reported here for the first time from W Afghanistan (Afghanistan: Farah, 55.6 miles S of Heart, road to Khandahar, Rocky scree, 18.iv.1971, *C. Grey-Wilson & Hewer* 535 E, K, W).

[xxiv] No herbarium specimen from Yemen has been found despite its report in flora of Yemen (Wood, 1997; Govaerts *et al*. 2000).

[xxv] An endemic species from Iran. Its presence in Iraq as mentioned in Flora Iranica (Rechinger & Schiman-Czeika, 1964) is misidentification of *E. orientalis* (Pahlevani *et al*., 2016).

[xxvi] Record of this species from E Afghanistan (Breckle *et al*., 2013) is probably *E. bungei*.

[xxvii] It is recorded only once from Iraq (Radcliffe-Smith, 1980). Checking the specimen (Nabelek 1220 SAV) revealed its misidentification of *E. altissima.*

[xxviii] This species has been recorded by Akhani (1998) from NE Iran, after examination of the collected and reported specimens, it was found that they are misidentification of *E. deltobracteata*.

[xxix] This species has been considered in the section *Lagascae* (Riina *et al.*, 2013), but after study of type specimen its position is corrected within section *Paralias*.

[xxx] Reports of *E. esula* subsp. *tommasiniana* from Afghanistan (Govaerts *et al*., 2000; Breckle *et al*., 2013), cannot be accepted. Studied herbarium specimens showed presence of a pilose plant of the section *Esula* which might be either *E. jaxartica* or belong to a new species.

[xxxi] An endemic species from Afghanistan with similarity to *E. wallichii*. Both are not only morphologically but also their range is different.

[xxxii] It is reported from Afghanistan, Iran, Jordan and Pakistan (Rechinger & Schiman-Czeika, 1964; Govaerts *et al*., 2000). After examination of the herbarium specimens, it was found that materials from Afghanistan belong to

E. malurensis, those of Pakistan belong to a new species (*E. boreo-baluchestanica*) and those from Jordan are *E. cuspidata* and therefore *E. microsciadia* is endemic to Iran.

[xxxiii] It is reported from Moldova, Caucasus, Turkey to Iran (Govaerts *et al*., 2000), but those specimens occurred in Iran are *E. macroceras*. However, these two species are very similar to each other, no representative of *E. oblongifolia* was seen from Iran based on available herbarium specimens.

[xxxiv] Based on Govaerts *et al*. (2000), it is known from Israel and Syria, whereas, it is only limited and endemic to the southern mountains of the Sinai Peninsula in Egypt. *E. sanctae-catharinae* is a synonym of *E. obovata*.

[xxxv] This species has been considered as a member of section *Helioscopia* (Riina *et al*., 2013), but after morphological and newly obtained molecular data (Pahlevani, unpubl. data), it is moved to section *Pithyusa*.

[xxxvi] *E. pauciradiata* Blatt. described as endemic to Afghanistan and Pakistan (Govaerts *et al*., 2000) is considered here as a new synonym of *E. prolifera*.

[xxxvii] Rechinger & Schiman-Czeika (1964) and Govaerts *et al*. (2000) reported this species from Iran but after revision of the section *Myrsiniteae* in Iran (Pahlevani, Geltman & Riina, 2011) it was revealed that Iranian plants belong to *E. monostyla*. Therefore, presence of *E. rigida* as a Mediterranean element is rejected to occur in Iran.

[xxxviii] This species has been reported from Afghanistan and Pakistan by some authors (Rechinger & Schiman-Czeika, 1964; Govaerts *et al*., 2000; Breckle *et al*., 2013), but after close examination of all specimens deposited in the studied herbaria, no material of *E. seguieriana* from Afghanistan and Pakistan was found. They are misidentification by either *E. jaxartica* or *E. prolifera*. It is considerable that distribution of *E. seguieriana* from west is limited to eastern part of Alborz and it has never reached to Kopetdagh region in NE Iran.

[xxxix] This rather rare species is here reported for the first time from Afghanistan (Afghanistan: Bamian, 6 km W, semi-desertic plains, 2550 m, 28.vi.1967, *Freitag* 1244 MSB; Bamian, Ajar valley (Kamard valley), near Roysang, 1700 m, 35º 19´ N 67º 38´ E, 14.v.1971, *O. Anders* 6298 MSB).

[xl] It is a new record for Afghanistan (Afghanistan: Kalifghan, Kataghan, 1981 m, 26.vi.1966, *Furse* 8110 K; Hills above Kasem, 1829 m, 7.vi.1971, *R.B. & L. Gibbons* 784 K; below Farkhar-valley, W slope of Farkhar, 1500 m, 10.v.1965, *Podlech* 10552 MSB; Takhar, 12 km SE of Eshkamesh, 1300-2100 m, 24.v.1971, *Podlech* 21575 MSB; Takhar, Farkhar, SW slopes, 1400-1650 m, 14.v.1977, *Podlech & Jarmal* 30164 MSB; Badakhshan, Keshem valley, E of Kangurchi, 1200-1500 m, 22.v.1971, *Podlech* 21465 MSB). Apparently, reports of *E. lucida* from C Asia should belong to *E. thyrsoidea* and the range of *E. lucida* restricted from C Europe to European part of Turkey.

[xli] This species is here reported for the first time from Afghanistan (Afghanistan: Faryab, near Gorzad, 30 km S Dawlatabad toward Maymana, 580 m, 36º 11´ N 64º 52´ E, 23.iv.1971, *Podlech* 20638 MSB; Faryab, 2 km N of Sara-i-Qala, 33 km N of Maymana toward Dawlatabad, 655 m, 25.iv.1971, *Podlech* 20825 MSB; Takhar, Badam-Darrah, S of Taluqan, 900 m, 4.v.1965, *Podlech* 10380 MSB, M, W; Samangan, 11 km W of Tashqurghan toward Mazar-i Sharif, 370 m, 22.iv.1971, *Podlech* 20510 K, M, MSB; Baghlan, 54.4 km N of Pol-i-Khumri, road to Samangan, 1310 m, 20.v.1971, *C. Grey-Wilson & T.F. Hewer* 873 E, K, W; Balkh, 2 km W of Shadyan (S Mazar-i-Sharif), 1400 m, 36º 31´ N 67º 11´ E, 13.vii.1978, *Podlech* 32050 MSB; Baghlan, Dasht-e-Layeqa, 20 km NE of Surkh-Kotal toward Narin, 1150 m, 25.v.1971, *Podlech* 21656 MSB; Baghlan, among Andarab-valley, between Banu and Deh-Salah, 1580 m, 1.vi.1965, *Podlech* 10991 MSB, M; Baghlan, 2 km N of

Nahrin toward Eshkamesh, 1300 m, 36º 05´ N 69º 07´ E, 25.v.1971, *O. Anders* 6845 MSB; Mazar-i-Sharif, 23-35 km E Mazar-i-Sharif toward Tashkurghan, 400 m, 10.v.1967, *Rechinger* 34221 B, E, W).

[xlii] The species has been reported from Iran and Iraq by some authors (Parsa, 1949; Radcliffe-Smith, 1980; Govaerts *et al*., 2000), but based on both existing specimens in the studied herbaria as well as distributional pattern of the species, it was found that it is absent from Iran and Iraq.

Additional changes:

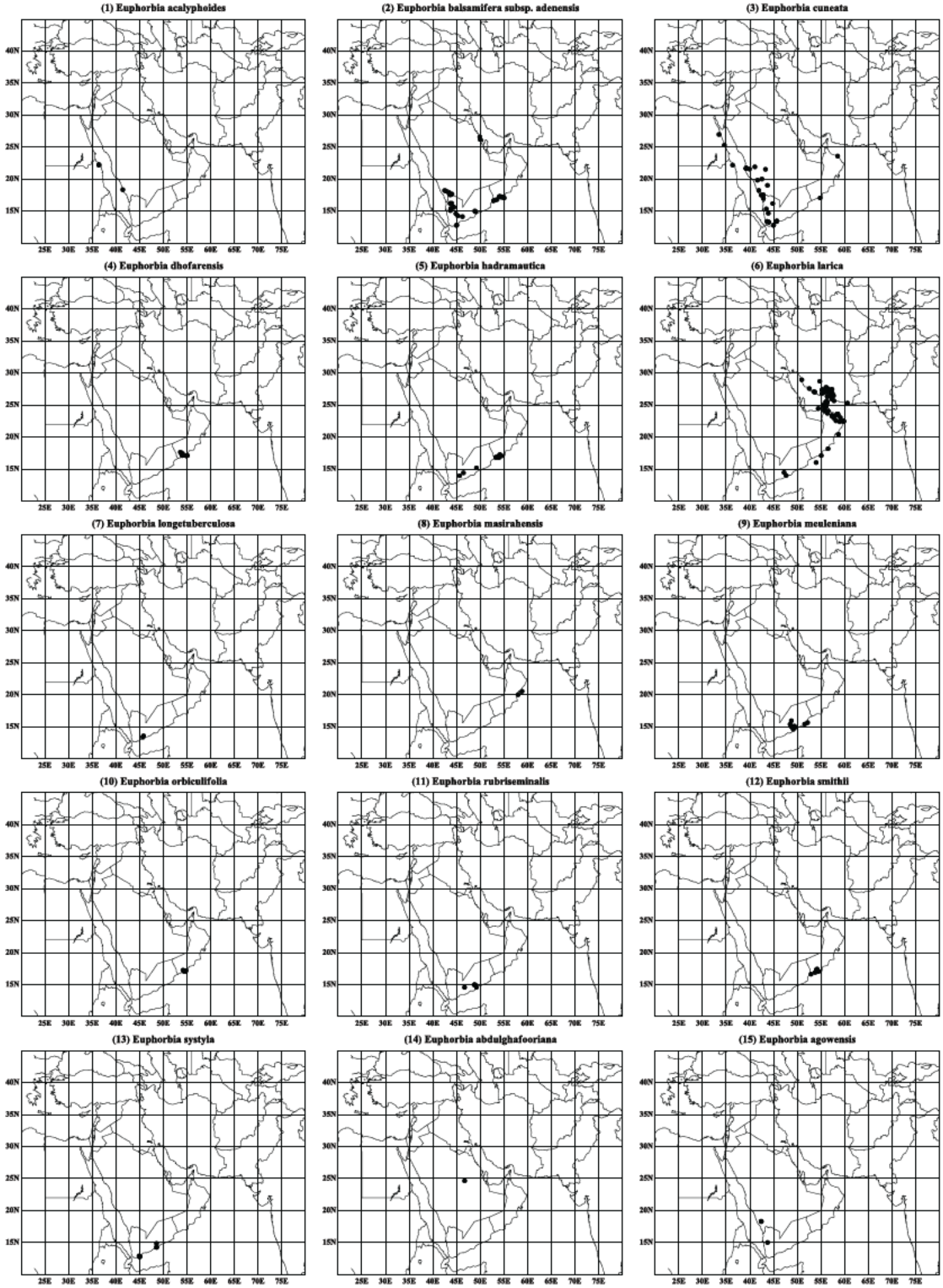
Euphorbia epithymoides L.: In flora of Turkey (Radcliffe-Smith, 1982) it has been doubtfully reported based on a very old specimen collected by Noë (1845). The Turkish origin of Noë's material is doubtful (Radcliffe-Smith, 1982).

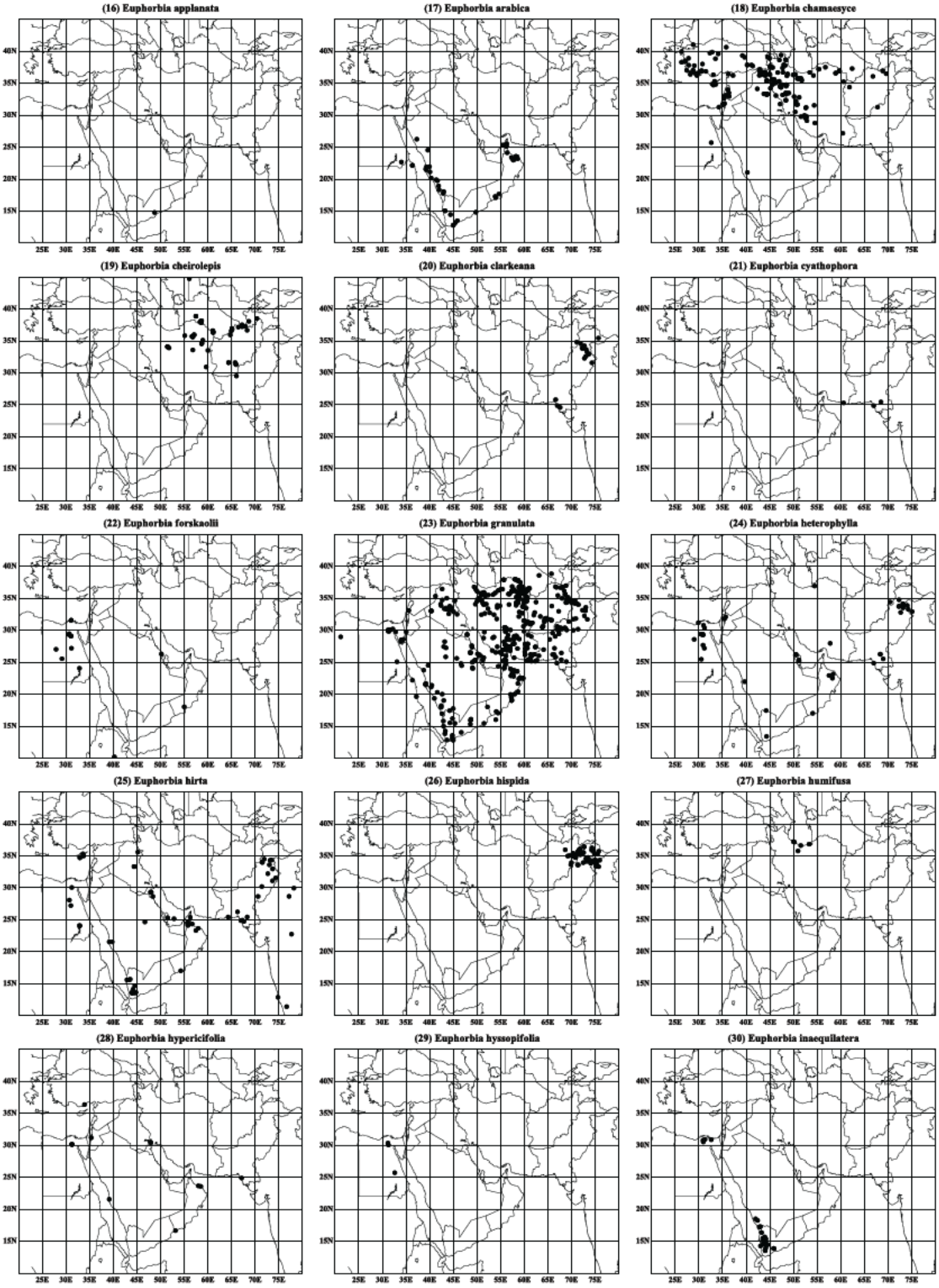
Euphorbia lagascae Spreng.: It has been reported from Istanbul, Turkey (Radcliffe-Smith, 1982) once by Noë (226) but its correctness of this locality is doubtful. No representative of this species was found in the studied herbarium specimens.

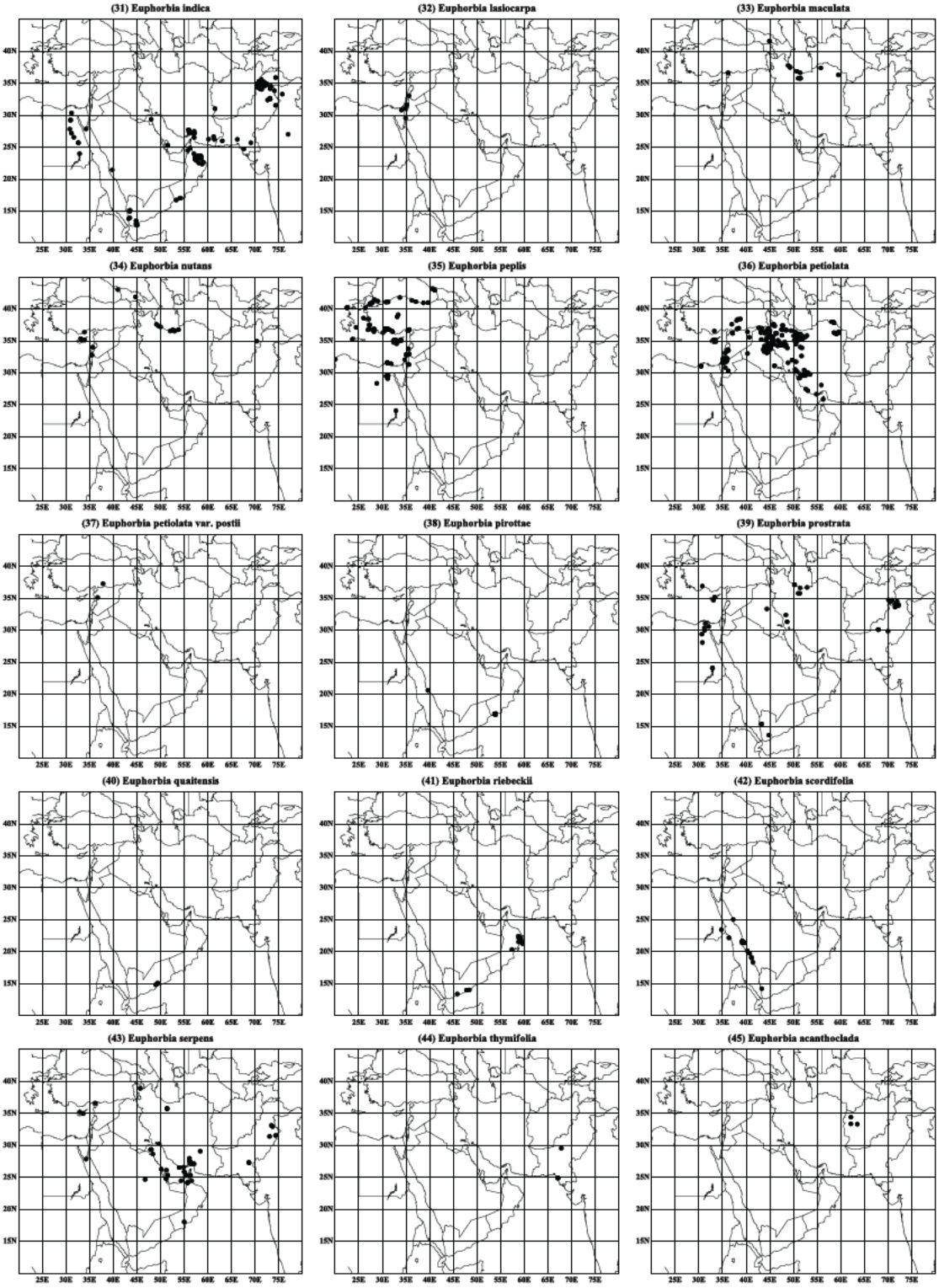
Euphorbia neriifolia L.: This species has been reported by some authors (Parsa. 1949; Radcliffe-Smith, 1986; Govaerts *et al*., 2000) from Iran and Pakistan. In Iran is wrongly reported by Parsa (1949) and in Pakistan it is just cultivated as ornamental plant (Radcliffe-Smith, 1986).

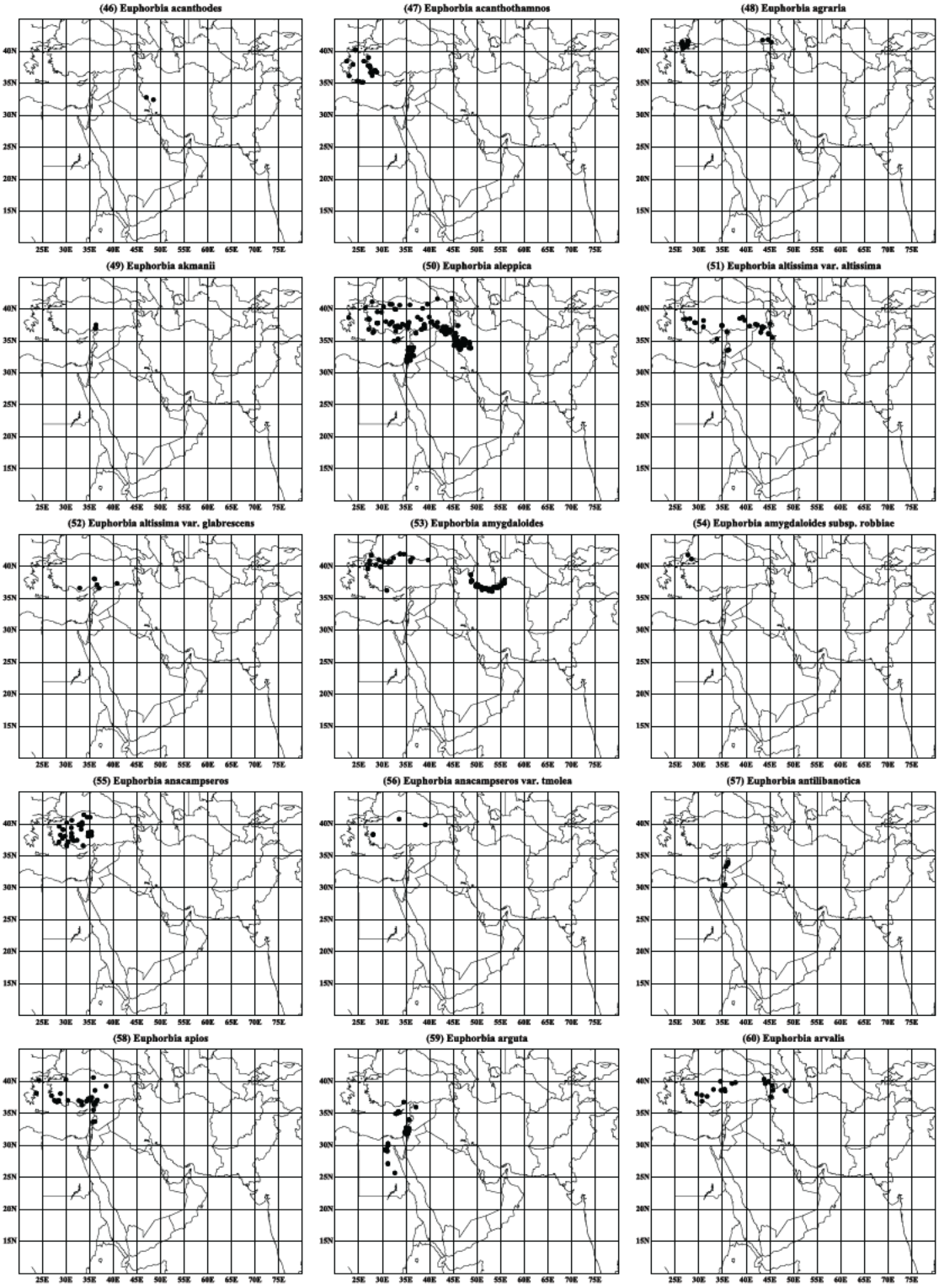
Euphorbia rosea Retz.: It is reported from Afghanistan, Iran and Pakistan (Rechinger & Schiman-Czeika, 1964; Govaerts *et al*., 2000) whereas, the specimens from Afghanistan and Pakistan are *E. hispida* and in Iran is mistakenly reported.

Appendix 2 Distribution maps of *Euphorbia* taxa in South-West Asia

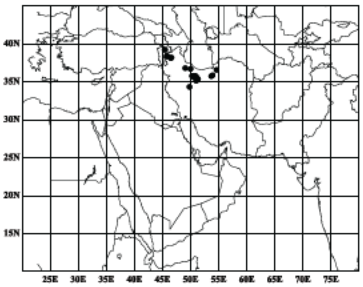



(16) Euphorbia applanata
(17) Euphorbia arabica
(18) Euphorbia chamaesyce
(19) Euphorbia cheirolepis
(20) Euphorbia clarkeana
(21) Euphorbia cyathophora
(22) Euphorbia forskaolii
(23) Euphorbia granulata
(24) Euphorbia heterophylla
(25) Euphorbia hirta
(26) Euphorbia hispida
(27) Euphorbia humifusa
(28) Euphorbia hypericifolia
(29) Euphorbia hyssopifolia
(30) Euphorbia inaequilatera

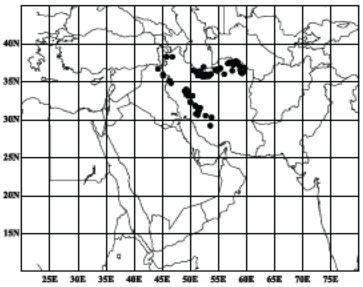

(31) Euphorbia indica
(32) Euphorbia lasiocarpa
(33) Euphorbia maculata
(34) Euphorbia nutans
(35) Euphorbia peplis
(36) Euphorbia petiolata
(37) Euphorbia petiolata var. postii
(38) Euphorbia pirottae
(39) Euphorbia prostrata
(40) Euphorbia quaitensis
(41) Euphorbia riebeckii
(42) Euphorbia scordifolia
(43) Euphorbia serpens
(44) Euphorbia thymifolia
(45) Euphorbia acanthoclada


(46) Euphorbia acanthodes
(47) Euphorbia acanthothamnos
(48) Euphorbia agraria
(49) Euphorbia akmanii
(50) Euphorbia aleppica
(51) Euphorbia altissima var. altissima
(52) Euphorbia altissima var. glabrescens
(53) Euphorbia amygdaloides
(54) Euphorbia amygdaloides subsp. robbiae
(55) Euphorbia anacampseros
(56) Euphorbia anacampseros var. tmolea
(57) Euphorbia antilibanotica
(58) Euphorbia apios
(59) Euphorbia arguta
(60) Euphorbia arvalis

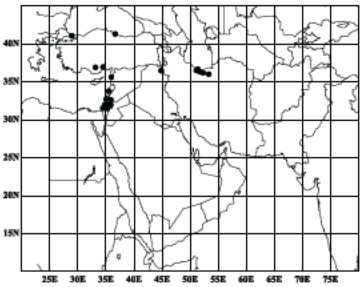
(61) Euphorbia aserbajdzhanica



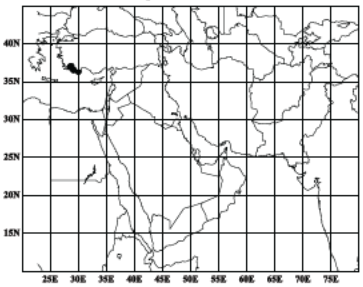
(62) Euphorbia aucheri



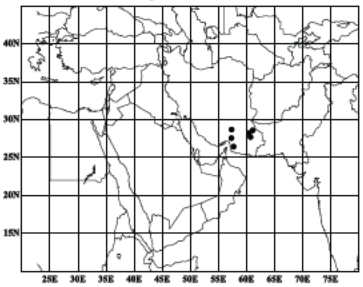
(63) Euphorbia aulacosperma



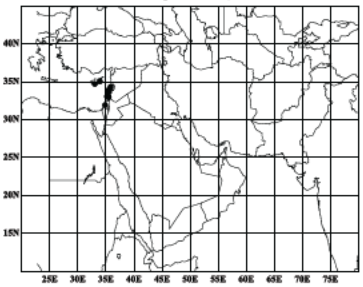
(64) Euphorbia austroanatolica



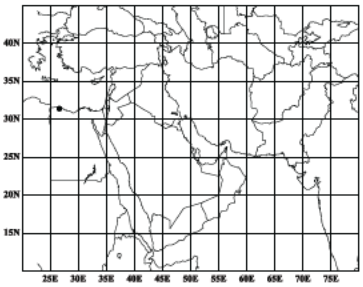
(65) Euphorbia austro-iranica



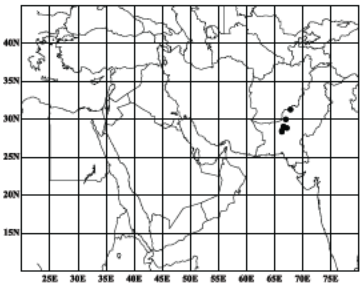
(66) Euphorbia berythea



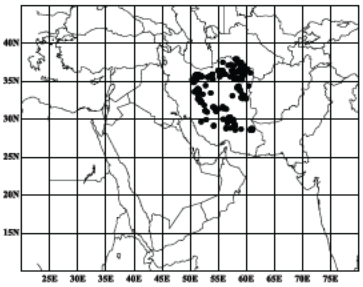
(67) Euphorbia bivonae



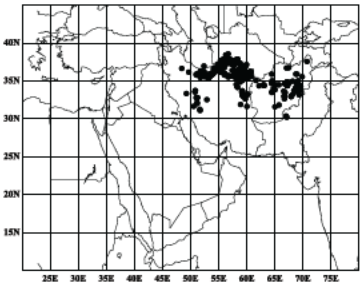
(68) Euphorbia boreo-baluchestanica



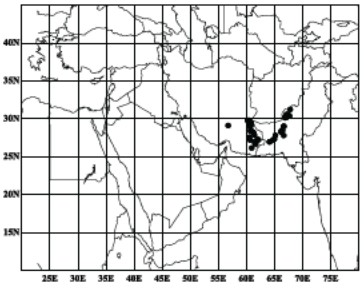
(69) Euphorbia buhsei



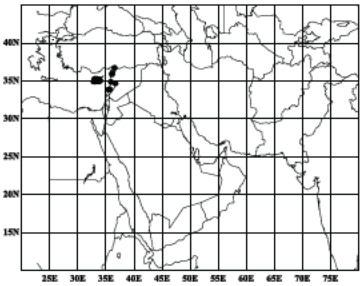
(70) Euphorbia bungei



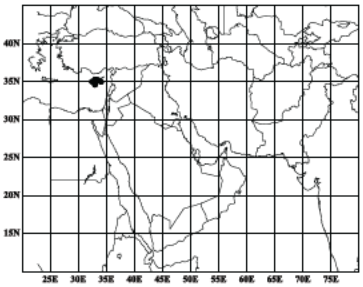
(71) Euphorbia caeladenia



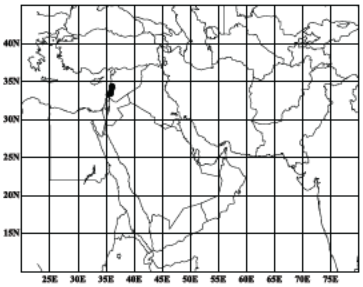
(72) Euphorbia cassia



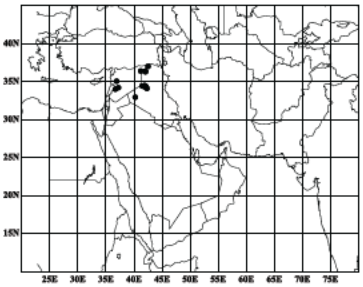
(73) Euphorbia cassia subsp. rigoi

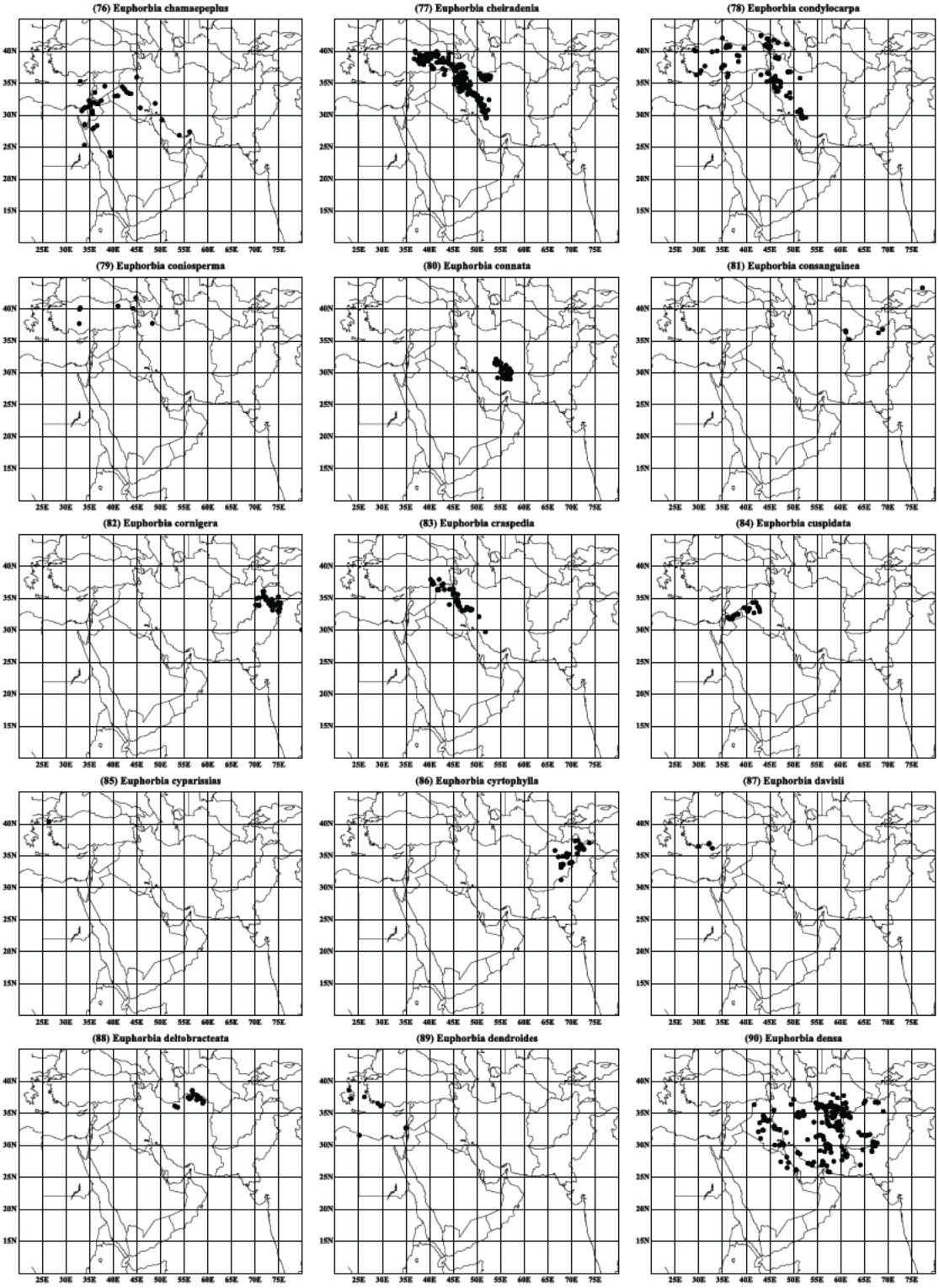


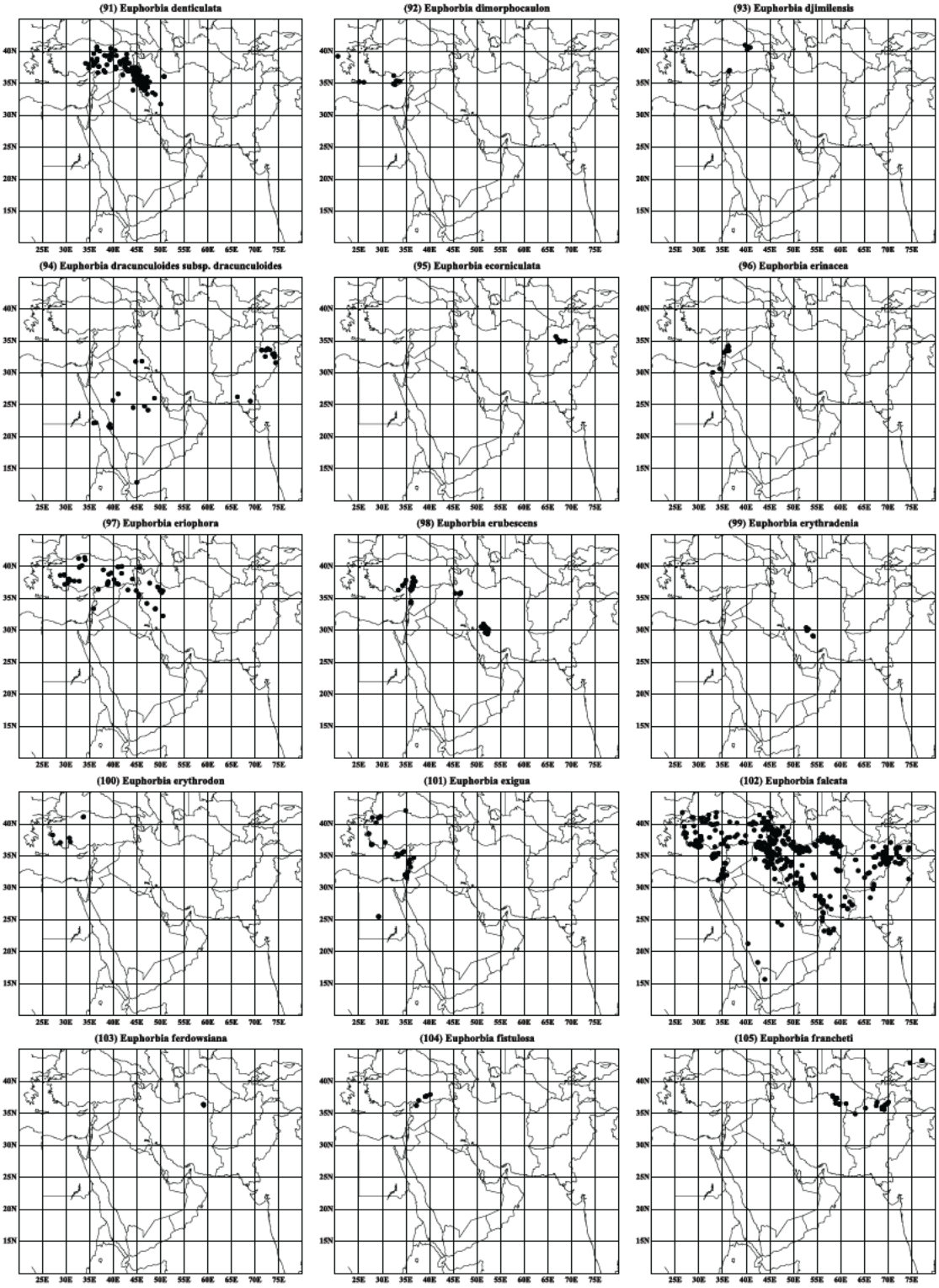
(74) Euphorbia caudiculosa



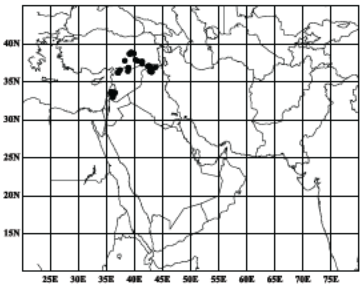
(75) Euphorbia chaborasia



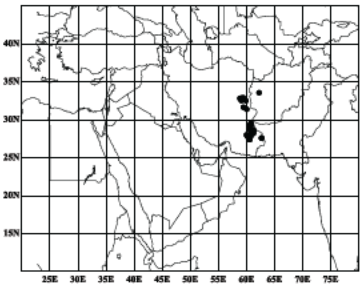

(76) Euphorbia chamaepeplus
(77) Euphorbia cheiradenia
(78) Euphorbia condylocarpa
(79) Euphorbia coniosperma
(80) Euphorbia connata
(81) Euphorbia consanguinea
(82) Euphorbia cornigera
(83) Euphorbia craspedia
(84) Euphorbia cuspidata
(85) Euphorbia cyparissias
(86) Euphorbia cyrtophylla
(87) Euphorbia davisii
(88) Euphorbia deltobracteata
(89) Euphorbia dendroides
(90) Euphorbia densa


(91) Euphorbia denticulata
(92) Euphorbia dimorphocaulon
(93) Euphorbia djimilensis
(94) Euphorbia dracunculoides subsp. dracunculoides
(95) Euphorbia ecorniculata
(96) Euphorbia erinacea
(97) Euphorbia eriophora
(98) Euphorbia erubescens
(99) Euphorbia erythradenia
(100) Euphorbia erythrodon
(101) Euphorbia exigua
(102) Euphorbia falcata
(103) Euphorbia ferdowsiana
(104) Euphorbia fistulosa
(105) Euphorbia francheti

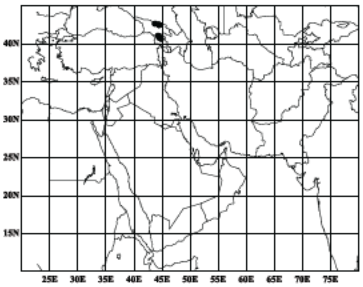
(106) Euphorbia gaillardotii



(107) Euphorbia gedrosiaca



(108) Euphorbia glaberrima



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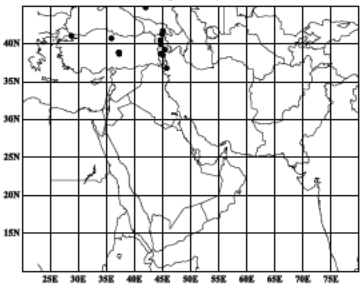

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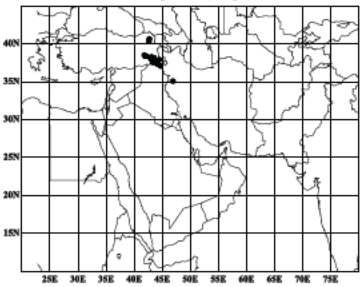
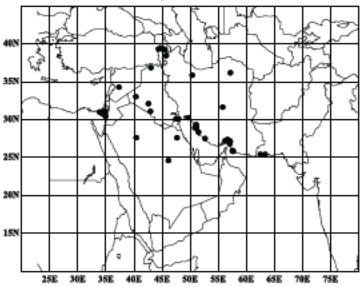
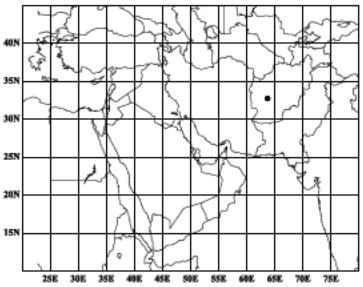


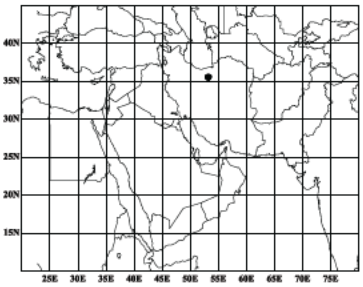
(111) Euphorbia grossheimii



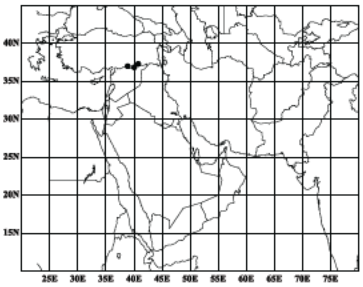
(112) Euphorbia gulestanica



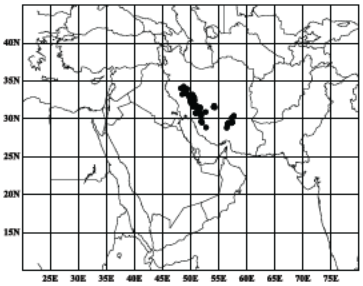
(113) Euphorbia gypsicola



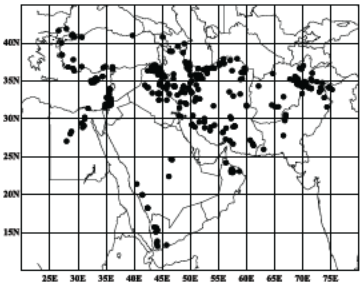
(114) Euphorbia haussknechtii



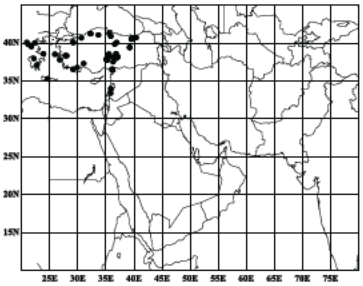
(115) Euphorbia hebecarpa



(116) Euphorbia helioscopia



(117) Euphorbia herniarifolia var. glabrima



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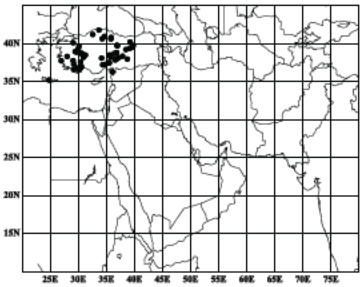
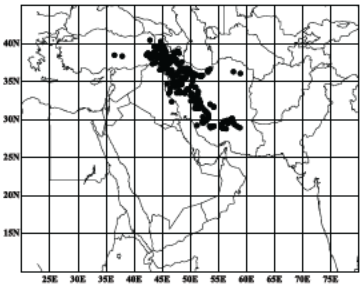
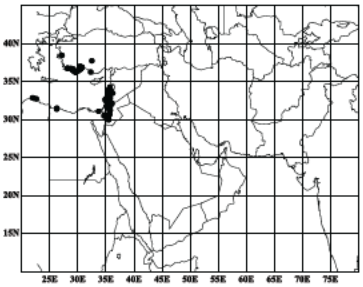
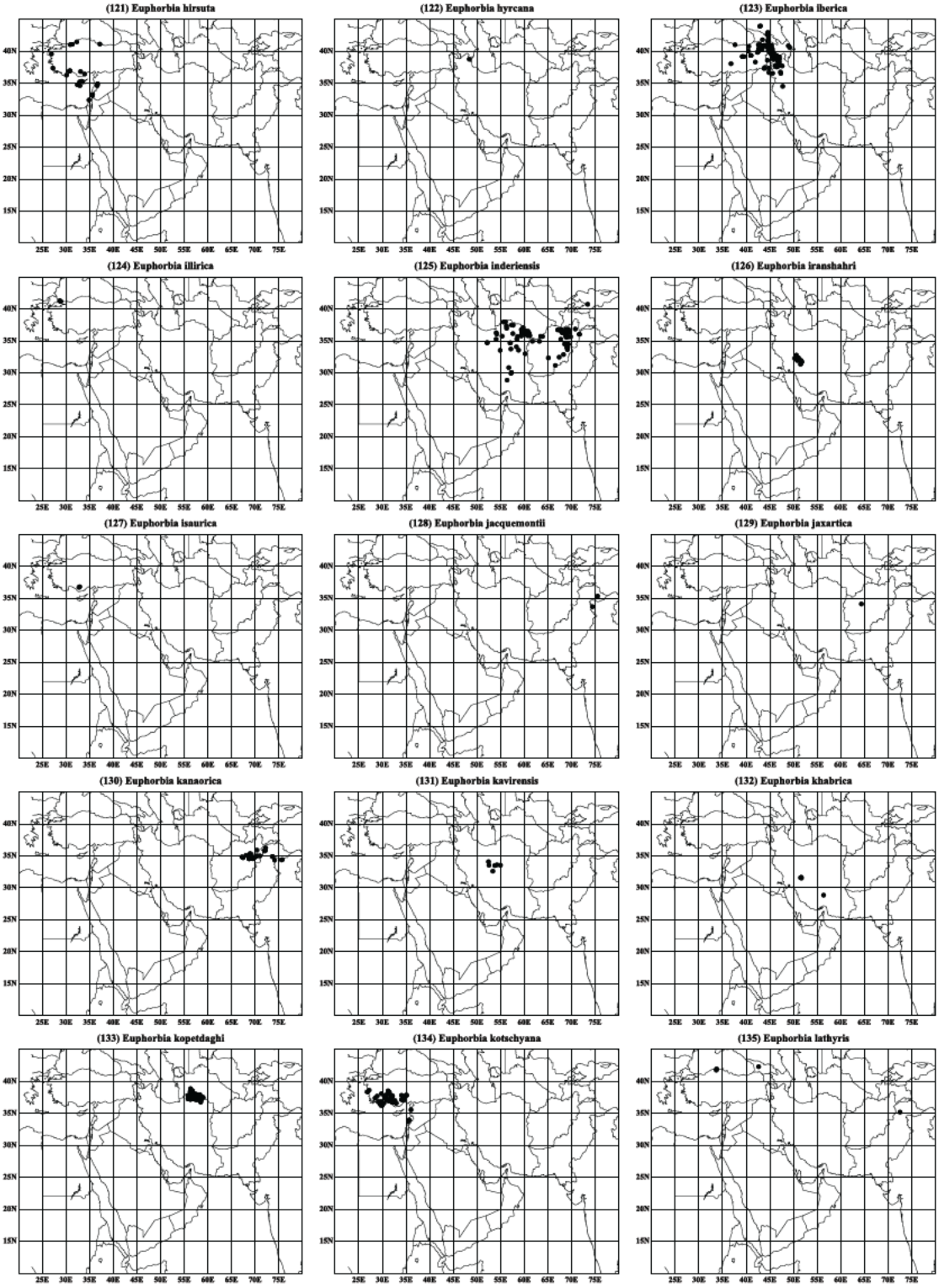


(119) Euphorbia heteradena



(120) Euphorbia hierosolymitana

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(126) Euphorbia iranshahri
(127) Euphorbia isaurica
(128) Euphorbia jacquemontii
(129) Euphorbia jaxartica
(130) Euphorbia kanaorica
(131) Euphorbia kavirensis
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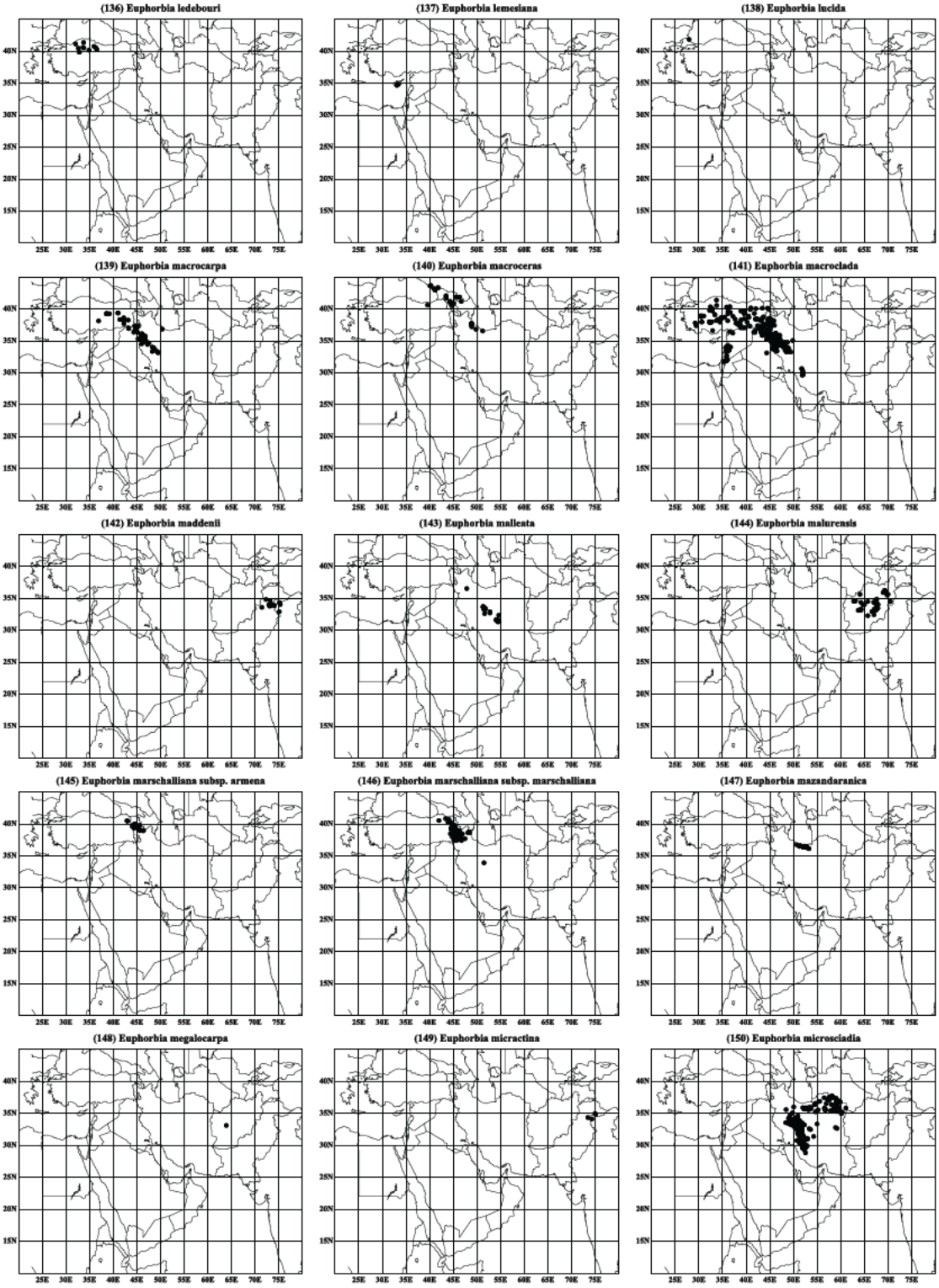
(134) Euphorbia kotschyana
(135) Euphorbia lathyris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(141) Euphorbia macroclada
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(143) Euphorbia malleata
(144) Euphorbia malurensis
(145) Euphorbia marschalliana subsp. armena
(146) Euphorbia marschalliana subsp. marschalliana
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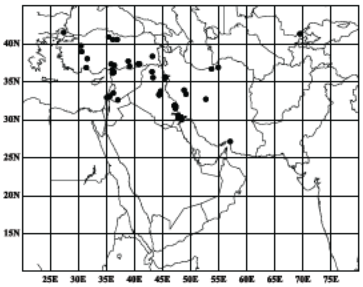
(150) Euphorbia microsciadia

(151) Euphorbia microsphaera



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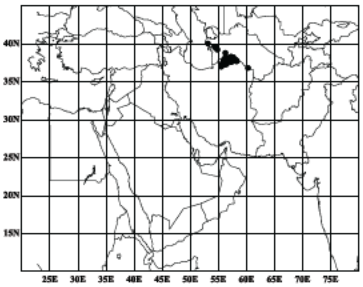

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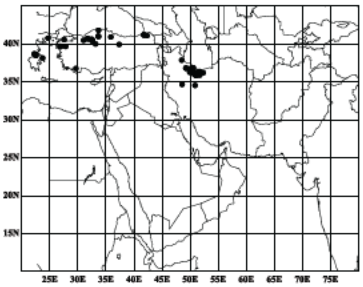

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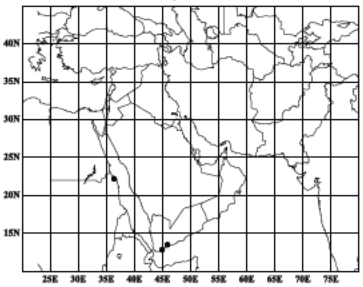

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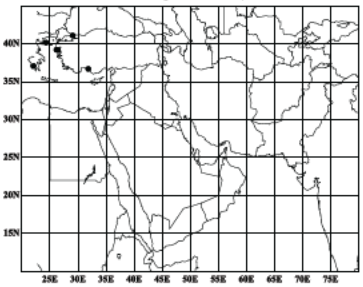
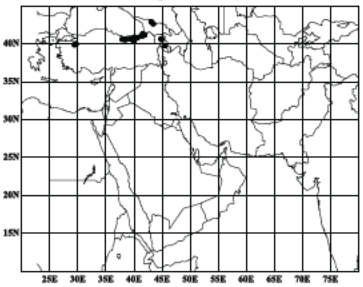


(156) Euphorbia oblongifolia



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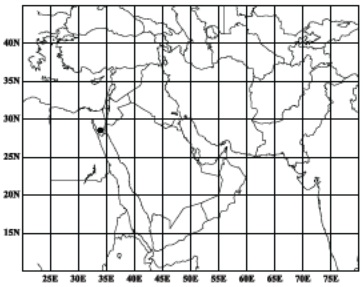

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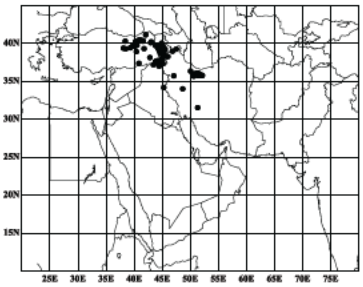

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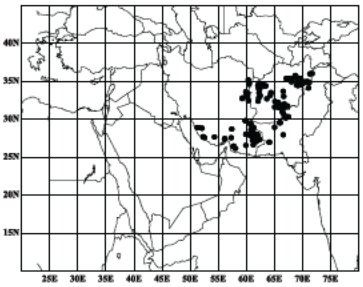

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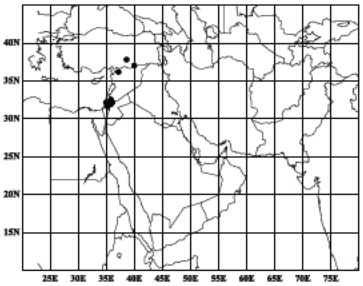

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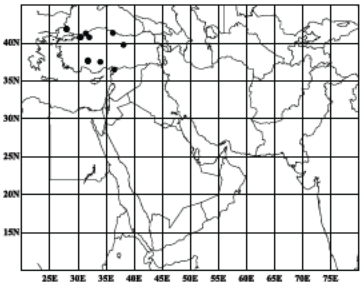

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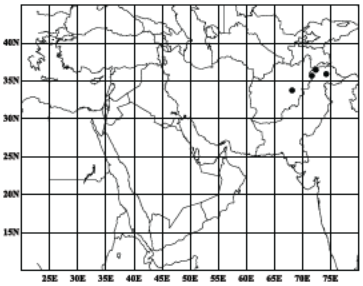

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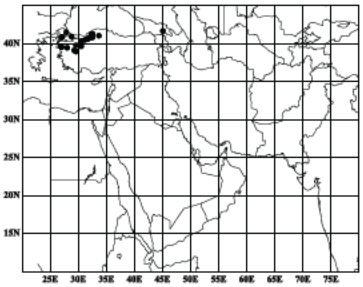

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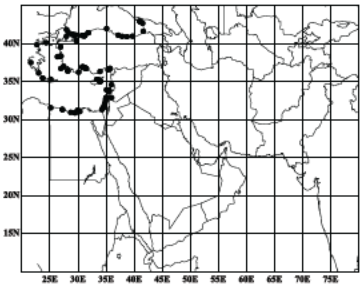

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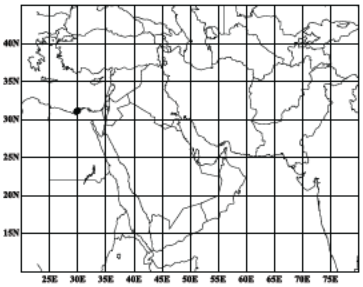

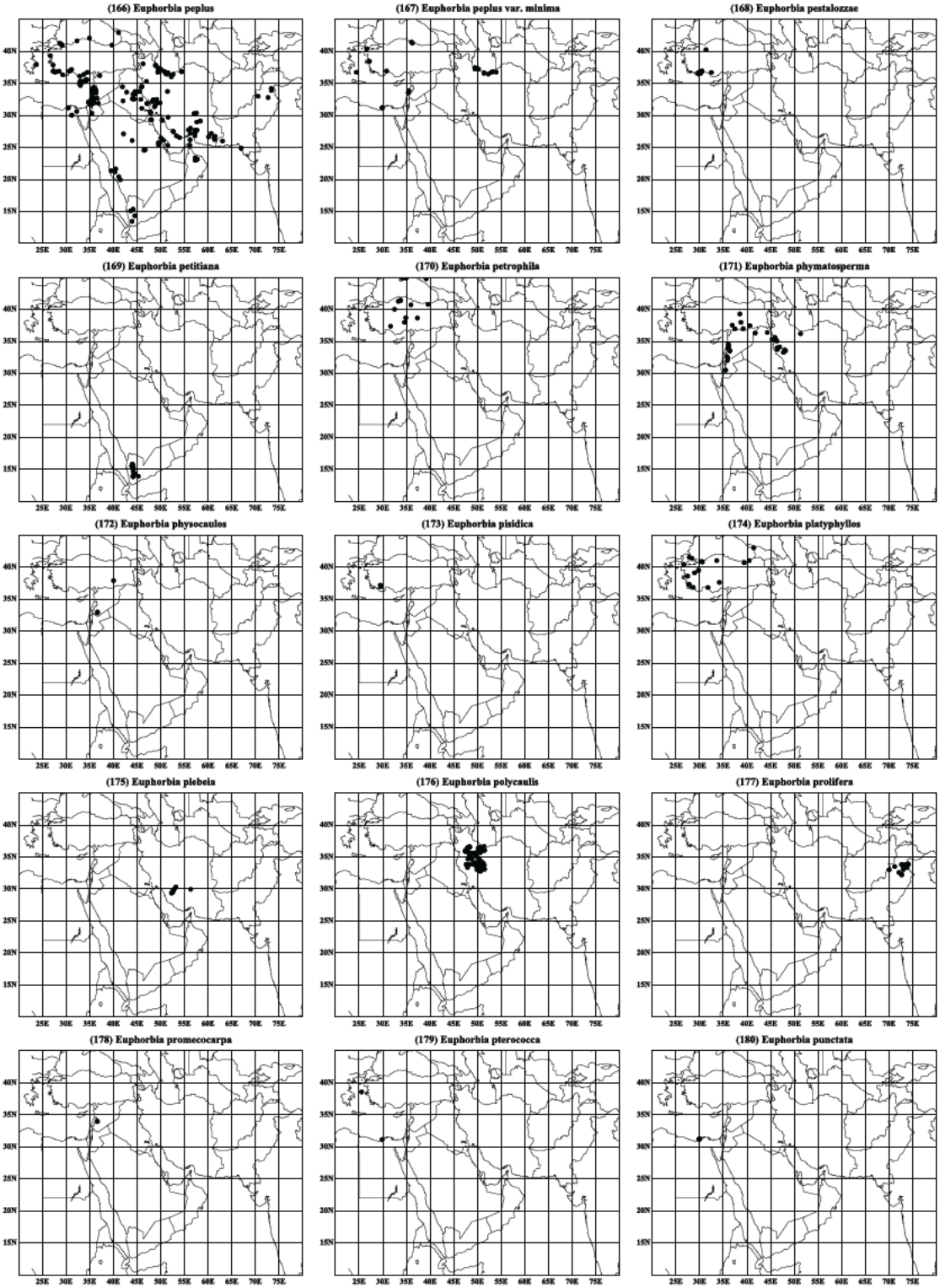
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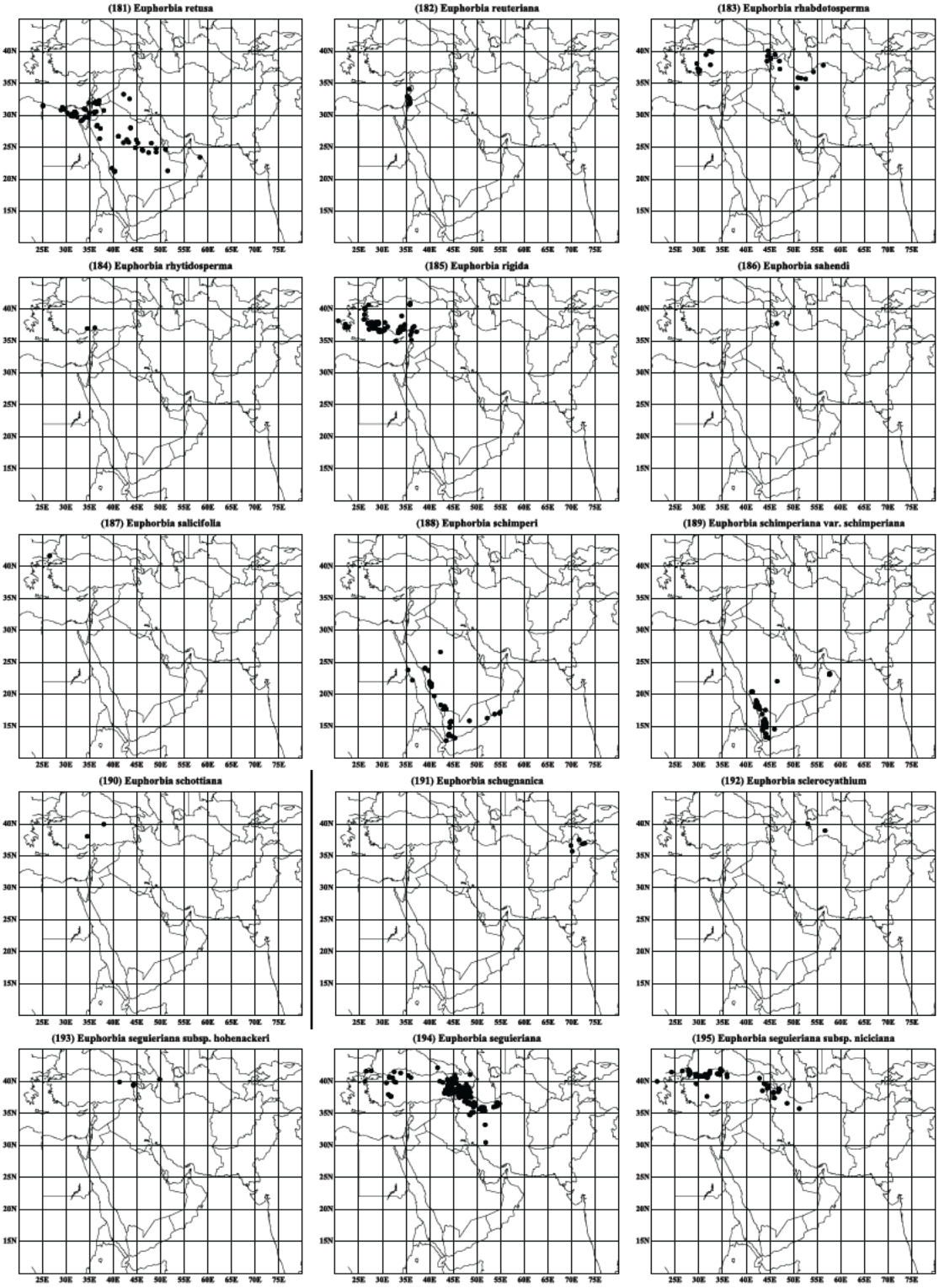
(170) Euphorbia petrophila
(171) Euphorbia phymatosperma
(172) Euphorbia physocaulos
(173) Euphorbia pisidica
(174) Euphorbia platyphyllos
(175) Euphorbia plebeia
(176) Euphorbia polycaulis
(177) Euphorbia prolifera
(178) Euphorbia promecocarpa
(179) Euphorbia pterococca
(180) Euphorbia punctata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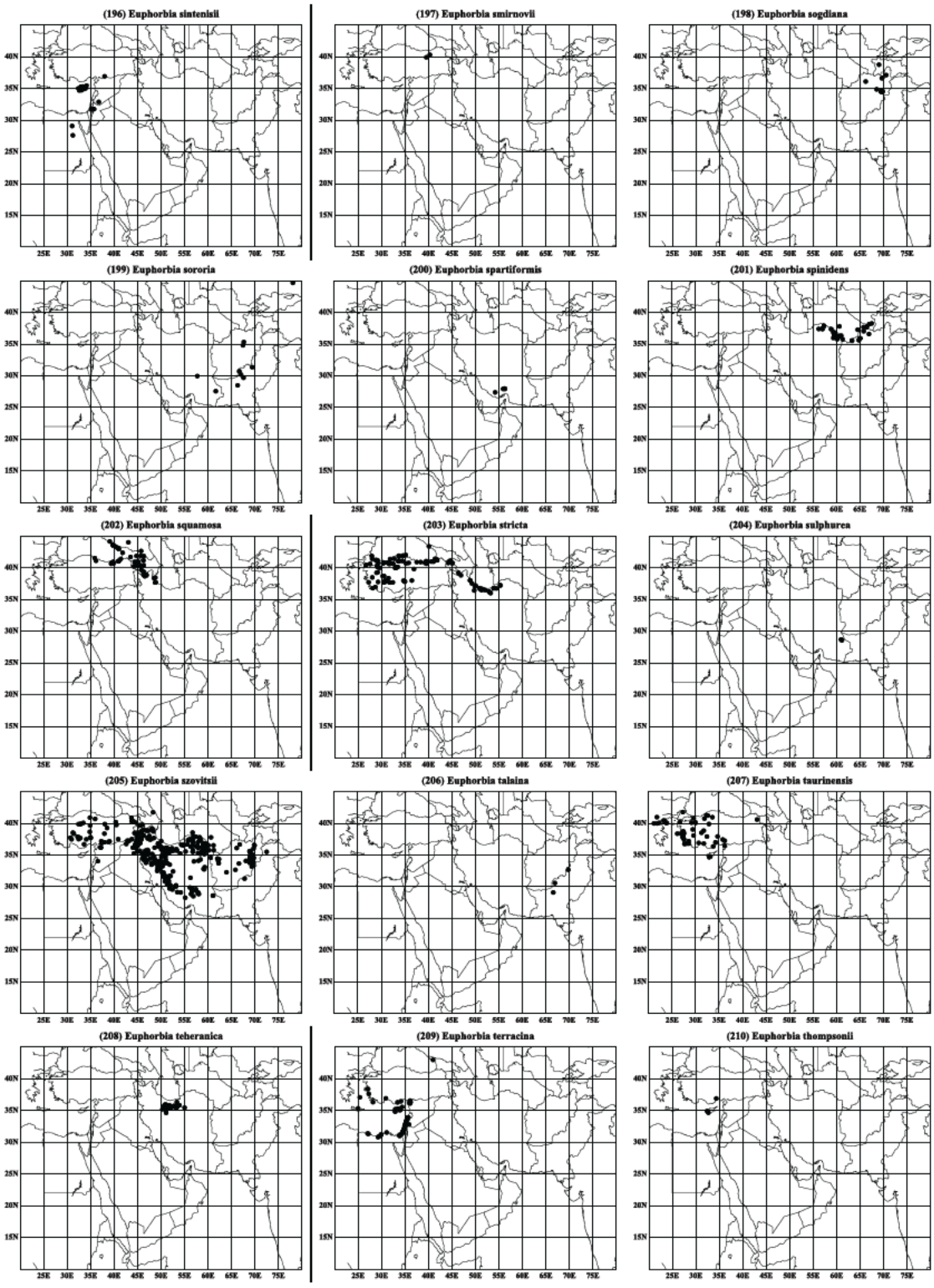
(186) Euphorbia sahendi
(187) Euphorbia salicifolia
(188) Euphorbia schimperi
(189) Euphorbia schimperiana var. schimperiana
(190) Euphorbia schottiana
(191) Euphorbia schugnanica
(192) Euphorbia sclerocyathium
(193) Euphorbia seguieriana subsp. hohenackeri
(194) Euphorbia seguieriana
(195) Euphorbia seguieriana subsp. niciciana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(199) Euphorbia sororia
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(201) Euphorbia spinidens
(202) Euphorbia squamosa
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(204) Euphorbia sulphurea
(205) Euphorbia szovitsii
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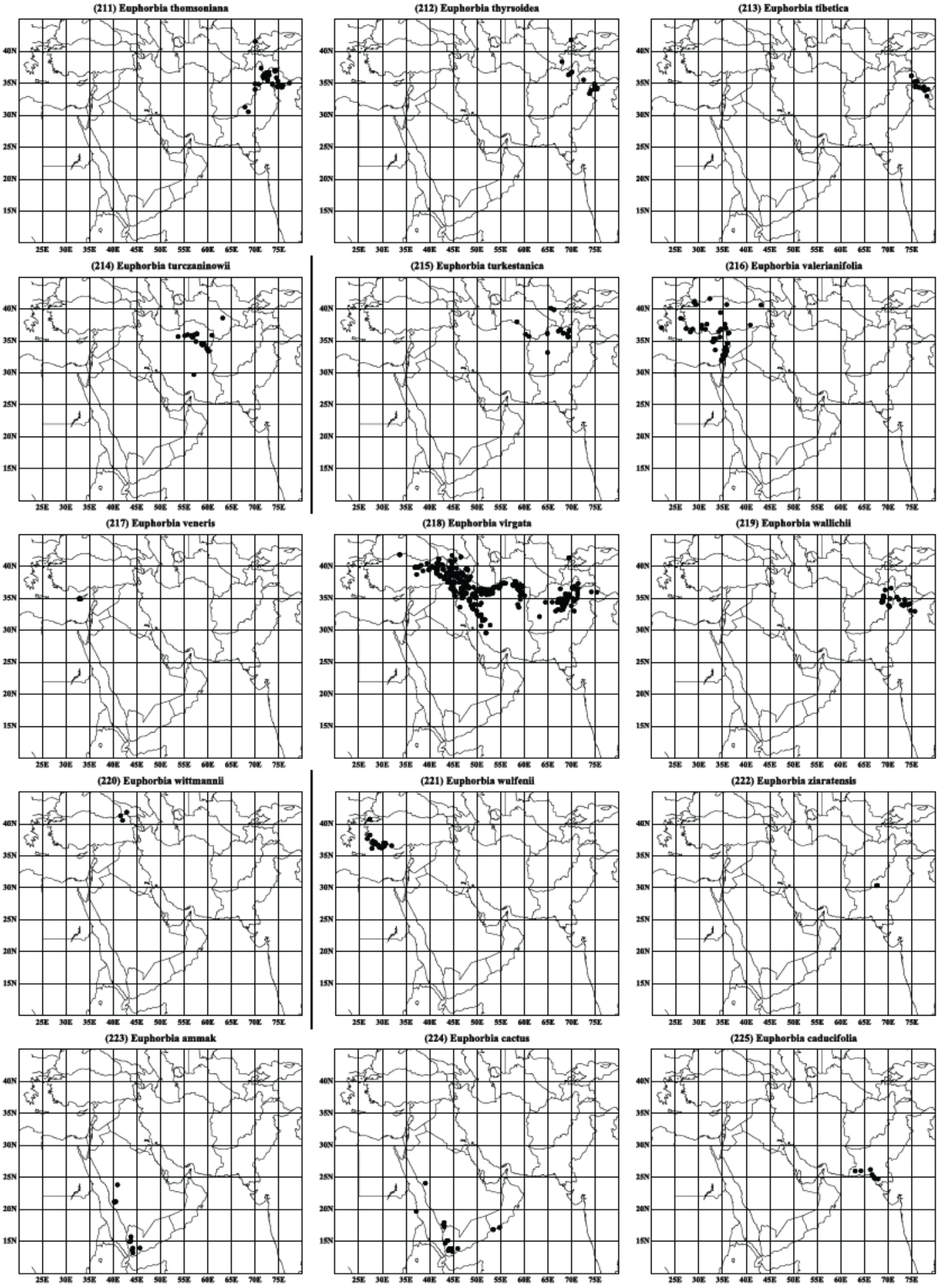
(208) Euphorbia teheranica
(209) Euphorbia terracina
(210) Euphorbia thompsonii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(216) Euphorbia valerianifolia
(217) Euphorbia veneris
(218) Euphorbia virgata
(219) Euphorbia wallichii
(220) Euphorbia wittmannii
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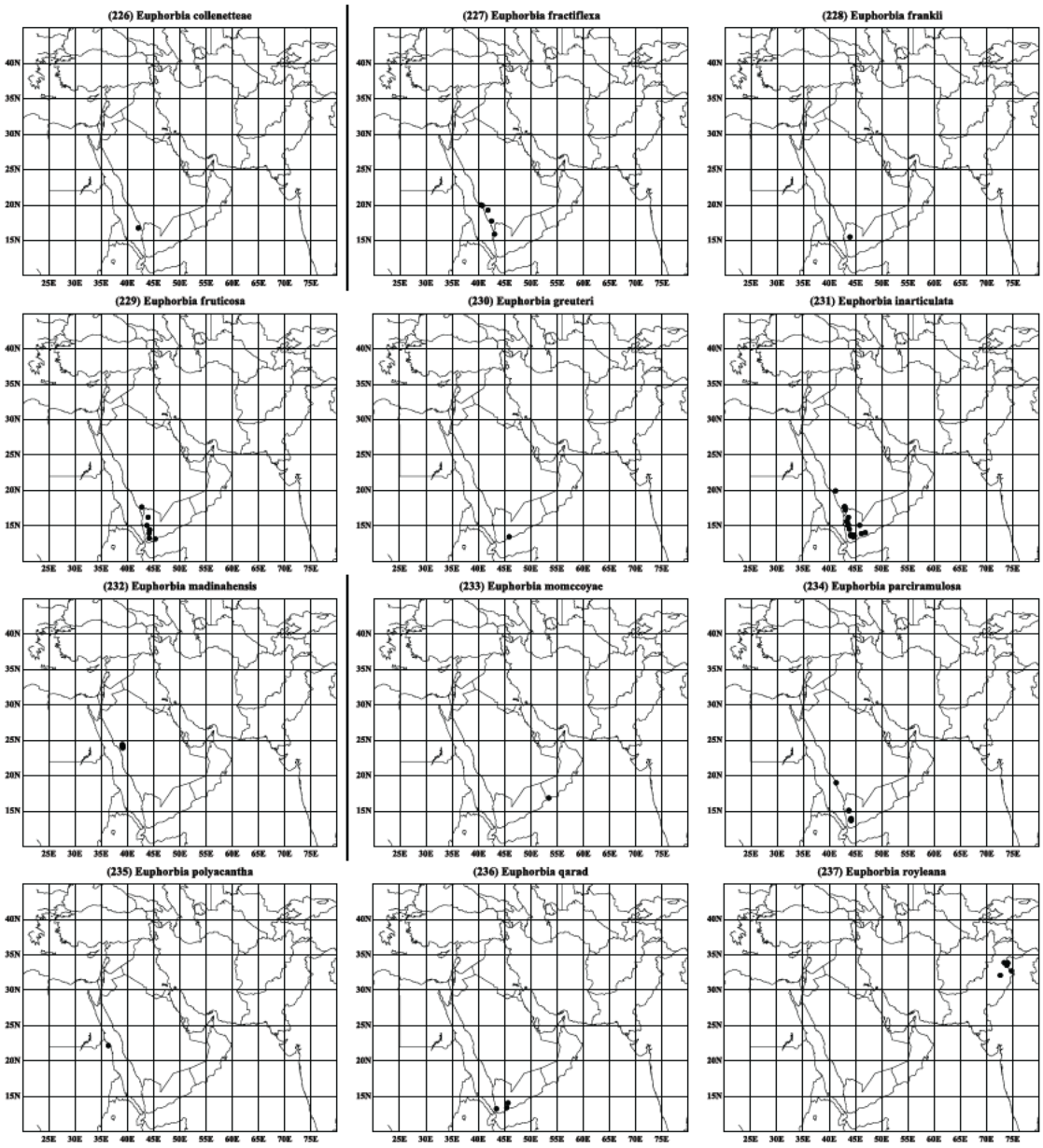
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(231) Euphorbia inarticulata
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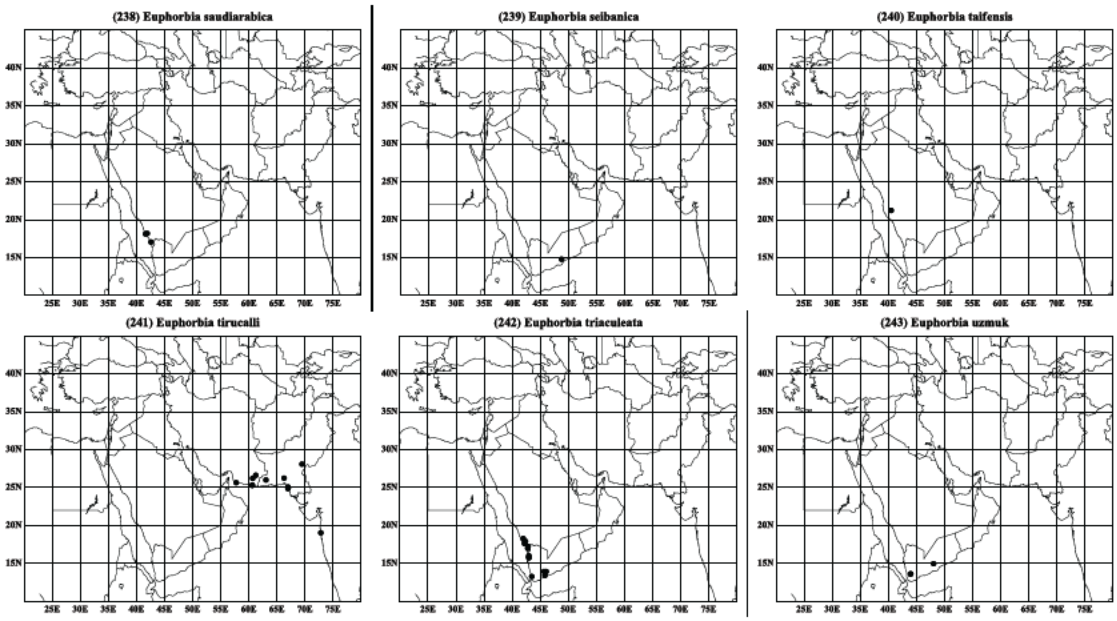
(236) Euphorbia qarad
(237) Euphorbia royleana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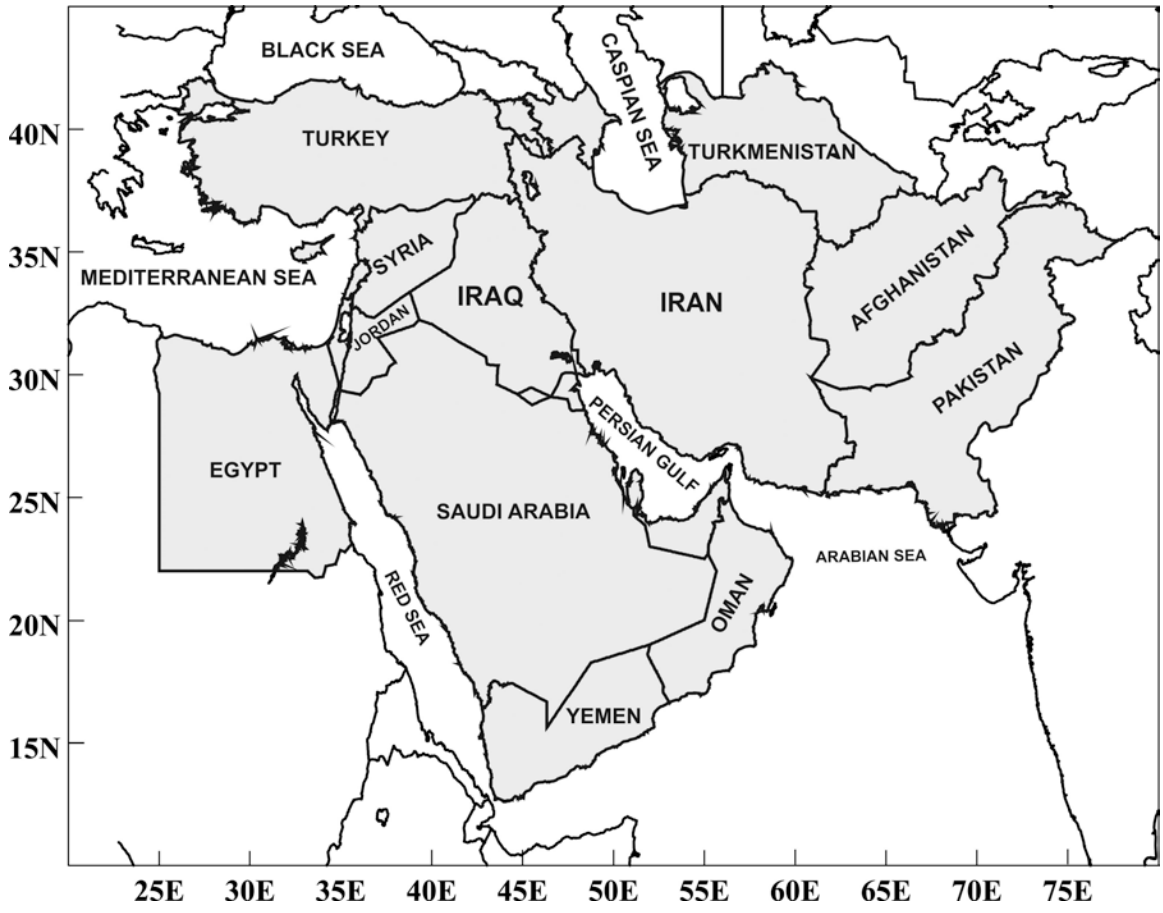
(243) Euphorbia uzmuk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CASPIAN SEA
TURKEY
TURKMENISTAN
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15N
MEDITERRANEAN SEA
SYRIA
IRAQ
IRAN
AFGHANISTAN
JORDAN
PAKISTAN
PERSIAN GULF
EGYPT
SAUDI ARABIA
ARABIAN SEA
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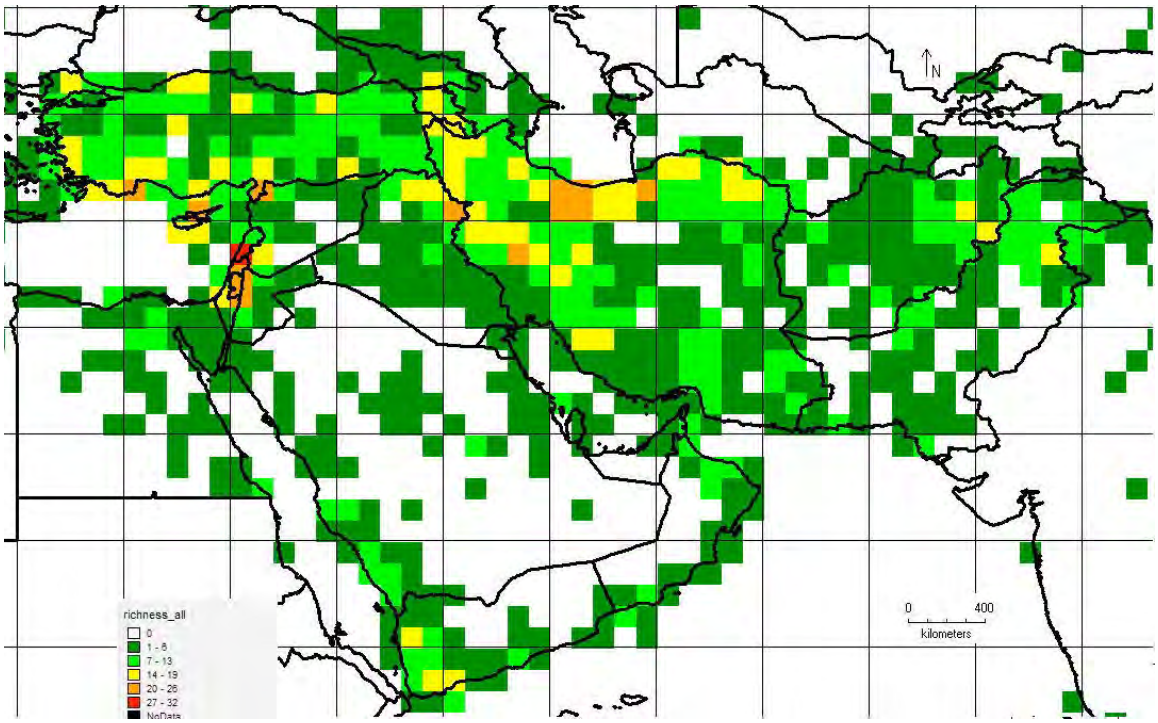
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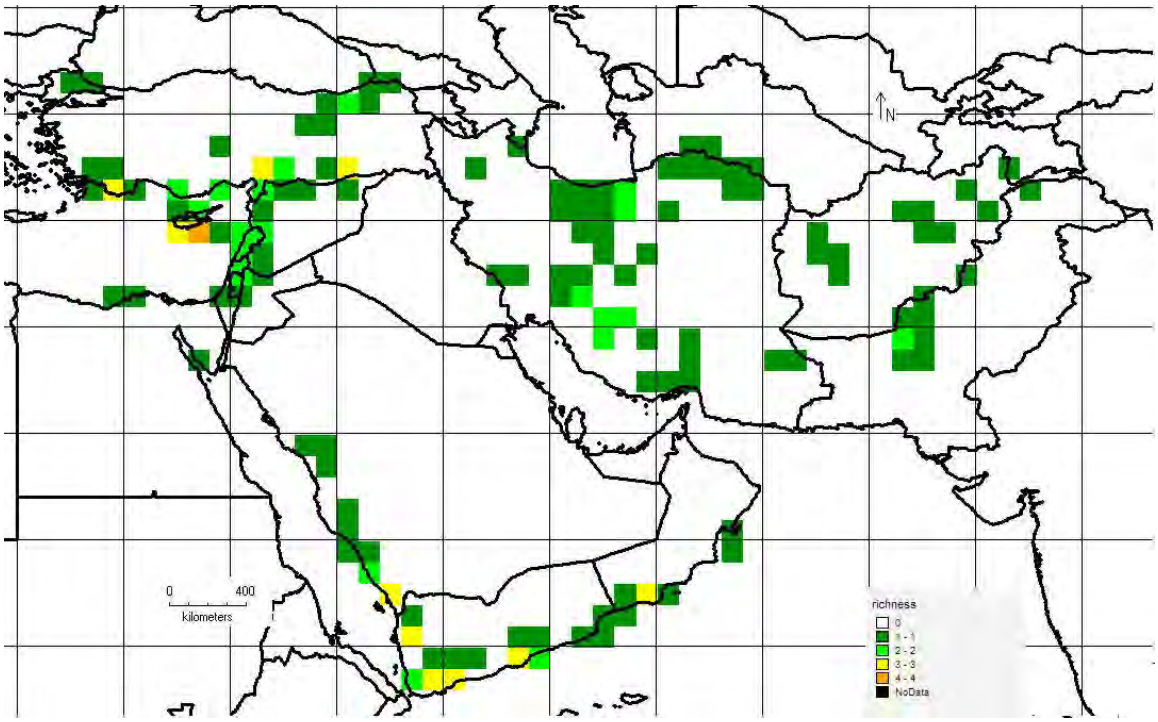
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Herbarium Ministerii Iranici Agriculturae (IRAN)

Euphorbia *acanthoclada* Pahlevani Holotype

sp. nov.

2016 Rev./Det.: A. H. Pahlevani

K. H. RECHINGER, ITER ORIENTALE 1967

33383

Euphorbia

SW-AFGHANISTAN, HERAT:

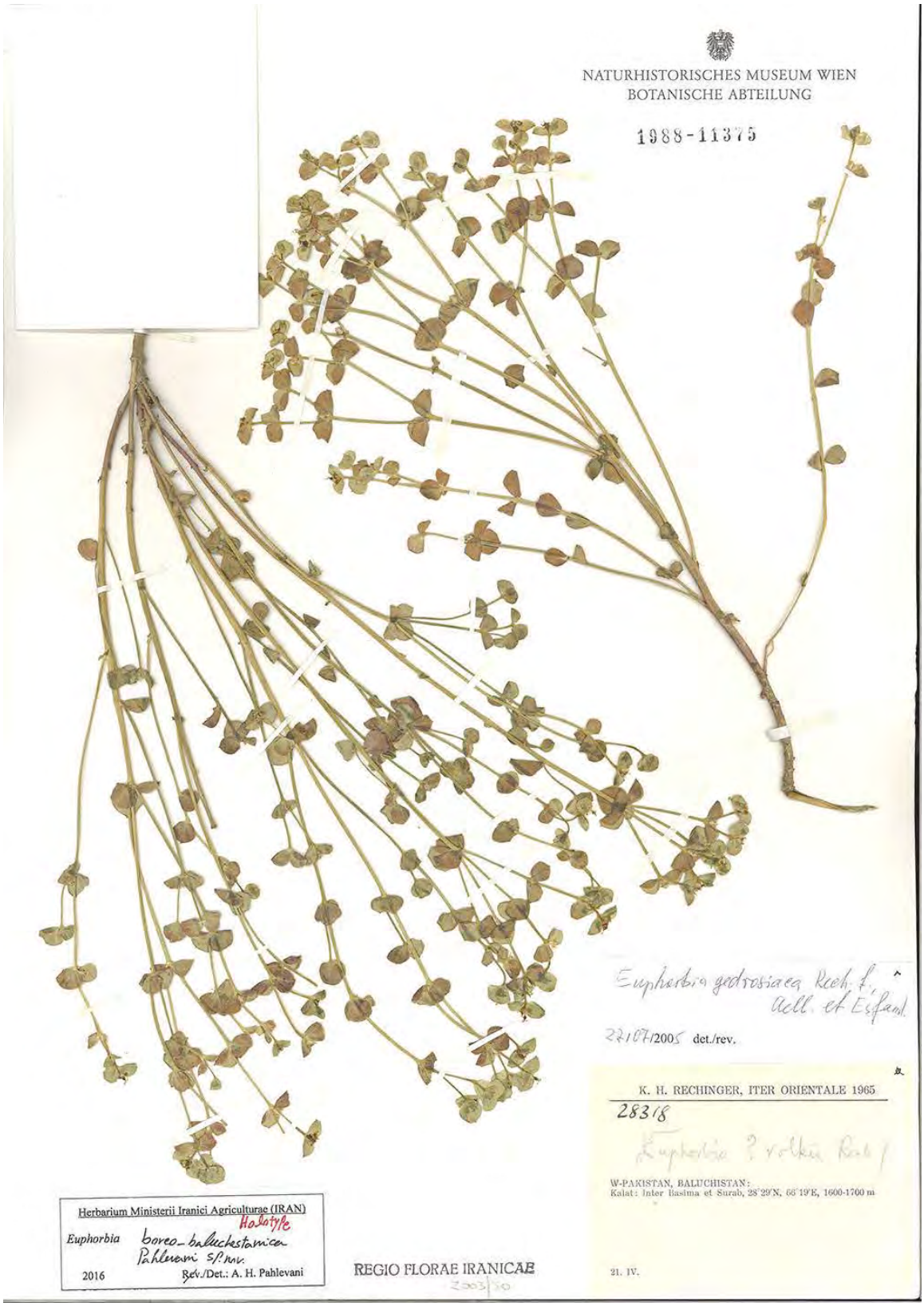
Inter Shindand et Farah Rud, 1150 m

acc.

23. IV

98/612-7

Mus. Bot. Berol.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BOTANISCHE ABTEILUNG
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K. H. RECHINGER, ITER ORIENTALE 1965
28318
Euphorbia ? volkii Rech. f.
W-PAKISTAN, BALUCHISTAN:
Kalat: Inter Basima et Surab, 28°29'N, 66°19'E, 1600-1700 m
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Herbarium Ministerii Iranici Agriculturae (IRAN)
Holotype
Euphorbia boreo-baluchestanica Pahlevani sp. nov.
2016
Rev./Det.: A. H. Pahlevani
REGIO FLORAE IRANICAE
25031/50


HERB. MUS. HIST. NATUR. VINDOB.
Acqu. 1979 No. 0735
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مجموعه گیاهان وزارت کشاورزی (اوین)
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Euphorbia
Prov
Datum
Leg
Det
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Euphorbia Kavirensis Pahlevani
Holotype
sp. nov.
2016
Rev./Det.: A. H. Pahlevani

Herbarium Ministerii Iranici Agriculturae (IRAN)

Euphorbia *ziaratensis* Pahlevani Holotype
sp. nov.
2016 Rev./Det.: A. H. Pahlevani

GORDON COLLEGE HERBARIUM
PLANTS OF PAKISTAN

No. 4827 Date 29.V.68
Name Euphorbia
Ver. Name
Locality Ziarat: ± 8,000 ft
Remarks in stones

Collected by Zaffar Ali

Publication 2

Seed and capsule morphology of Iranian perennial species of *Euphorbia* (Euphorbiaceae) and its phylogenetic application.

Botanical Journal of the Linnean Society 177: 335–377 (2015).

LINNEAN SOCIETY BOTANICAL Journal of the Linnean Society

Botanical Journal of the Linnean Society, 2015, **177**, 335–377. With 13 figures

Seed and capsule morphology of Iranian perennial species of *Euphorbia* (Euphorbiaceae) and its phylogenetic application

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Of the 480 species of *Euphorbia* subgenus *Esula*, *c.* 290 occur in the Mediterranean and Irano-Turanian regions. Turkey and Iran are the most species-rich countries in Asia with 83 and 74 species, respectively. Following our previous paper on annual species of Iranian *Euphorbia*, we studied the quantitative and qualitative macro- and micromorphological traits of seeds and capsules of 47 perennial species, including ***E. ferdowsiana* sp. nov.**, ***E. sulphurea* sp. nov.** and *E. glareosa*, as a first report from Iran. A key for all Iranian perennial *Euphorbia* spp. based on seed and capsule morphology is provided. The phylogenetic relationships of Iranian species based on internal transcribed spacer (ITS) nuclear and *ndhF* plastid regions are updated and used for the characterization of the synapomorphies of each clade. Capsule shape, seed shape, seed surface and shape of the caruncle have been found to be homoplastic, whereas the presence or absence of granulate elements on seed surfaces represents a phylogenetically important trait for section delimitation. The capsule surface is synapomorphic for several sections, including *Helioscopia* (tuberculate-verrucose), *Myrsiniteae* (vesiculate) and *Esula* (granulate), and seed shape is synapomorphic for sections *Helioscopia* (ellipsoidal), *Myrsiniteae* (ovoid-quadrangular) and *Herpetorrhizae* (pseudo-hexahedral). Reversals have also taken place in some features, including capsule surface (*E. mazandaranica*, *E. altissima*) and seed shape (*E. densa*, *E. aleppica*). It seems that ecarunculate seeds are plesiomorphic in sections *Helioscopia* (*E. eriophora*) and *Herpetorrhizae* (*E. consanguinea* and *E. turczaninowii*). © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **177**, 335–377.

ADDITIONAL KEYWORDS: dispersal mechanism – ecology – Iranian flora – leafy spurges – micromorphology – new species – phylogeny – SEM – south-west Asian flora.

INTRODUCTION

Micromorphological and ultrastructural data have provided useful information for the evolution, classification and phylogenetic inference of seed plants, and have contributed to our understanding and to modern synthetic systems of angiosperms (Dahlgren, 1980; Moïse *et al.*, 2005). It has been shown that macro- and microstructural characters of fruits and seeds are useful and significant for the delimitation of species, sections and genera in many groups of flowering plants (Tokuoka & Tobe, 1995, 2002; Buss, Lammers & Wise, 2001; Zhang *et al.*, 2005; Abdel Khalik & Osman, 2007; Kaya *et al.*, 2011; Çeter *et al.*, 2012). Scanning electron microscopy (SEM) has been used for more than five decades to study seed and fruit surfaces for diagnostic features, and these patterns have found widespread use in systematics, in particular at specific and subspecific levels (Heywood, 1971; Hassan, Meve & Liede-Schumann, 2005; Gontcharova *et al.*, 2009; Zorić *et al.*, 2010; Kasem, Ghareeb &

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Marwa, 2011). The taxonomic usefulness of seed and fruit morphology is variable between plant groups, however; compared with many vegetative and floral structures, seed coat and fruit morphology show very low phenotypic plasticity and are little affected by environmental conditions (Zorić *et al*., 2010).

Euphorbia L. is well known as a genus of angiosperms with a great diversity of seed characters (Ehler, 1976; Simon, Molero & Blanche, 1992; Heubl & Wanner, 1996; Park, 2000; Pahlevani & Akhani, 2011; Salmaki *et al*., 2011). As a result of the existence of several different kinds of seed ornaments and caruncles in the genus, these characters are widely used to delimit species and sections in the genus. Although some papers on the functional role of seed and capsule morphology of *Euphorbia* have been written, previous studies have been limited in their taxonomic sampling, and have not provided a useful key, a fact probably a result of the large number of species and nomenclatural complexity in this group (Rössler, 1943; Khan, 1964; Ehler, 1976; Mangaly, Swarupanandan & Madhusoodan, 1979; Heubl & Wanner, 1996; Hügin, 1998; Park, 2000; Salmaki *et al*., 2011). Although both seed and fruit characters are useful for distinguishing taxa in *Euphorbia*, there are considerably fewer studies of capsule morphology than of seed morphology. After a worldwide molecular phylogenetic study of *Euphorbia* subgenus *Esula* Pers. (Riina *et al*., 2013) and a study of seed morphology of annual Iranian *Euphorbia* spp. (Pahlevani & Akhani, 2011) have recently been published, a comprehensive treatment of the fruit and seed morphology of perennial species is needed to complete our understanding of the evolutionary patterns found in the subgenus.

Euphorbia has a worldwide distribution and comprises *c*. 2000 species harbouring an astonishing diversity in life forms; this lactiferous genus is considered as a giant genus (Frodin, 2004). According to molecular phylogenetic studies (Steinmann & Porter, 2002; Bruyns, Mapaya & Hedderson, 2006; Horn *et al*., 2012), *Euphorbia* falls into four main clades (A–D) that are recognized as subgenera: *E.* subgenus *Esula* with *c.* 480 species, *E.* subgenus *Athymalus* Neck. ex. Rchb. with *c*. 150 species, *E.* subgenus *Chamaesyce* Raf. with *c*. 600 species and *E.* subgenus *Euphorbia* with *c.* 750 species. Horn *et al*. (2012) produced a well-supported backbone topology which indicated that subgenus *Esula* is sister to the other three subgenera. Systems of sectional divisions have been developed for all four subgenera: *Athymalus* (Peirson *et al*., 2013); *Chamaesyce* (Yang *et al*., 2012); *Esula* (Riina *et al*., 2013); and *Euphorbia* (Bruyns, Klak & Hanáček, 2011; Dorsey *et al*., 2013).

Of the *c.* 480 species in subgenus *Esula*, most are annual and perennial herbs and only a few constitute dendroid, leafless or succulent shrubs. Subgenus *Esula* is considered as 'leafy spurges' in a broad context. Leafy spurges are distributed mostly in the temperate regions of the Northern Hemisphere, where they are most diverse in central and southwest Asia and the Mediterranean region; however, some species occur in Africa, the Indo-Pacific region and the New World (Riina *et al*., 2013; Peirson *et al*., 2014). From the phytochorological point of view, the subgenus is most diverse in the Mediterranean and the Irano-Turanian regions, in particular in Anatolia and the Iranian plateau.

The recent molecular study by Riina *et al*. (2013) using internal transcribed spacer (ITS) and plastid *ndhF* sequences showed that the species of subgenus *Esula* belong to 21 sections, 13 of which are represented in Iran. Of these, four comprise only perennials [*Chylogala* (Fourr.) Prokh., *Calyptratae* Geltman, *Patellares* (Prokh.) Frajman and *Esula* (Pers.) Dumort.], four only annuals [*Lagascae* Lázaro, *Szovitsiae*, *Arvales* (Geltman, 2013) Geltman and *Tithymalus* (Gaertn.) Roep.] and five perennials and annuals [*Helioscopia* Dumort., *Sclerocyathium* (Prokh.) Prokh., *Herpetorrhizae* (Prokh.) Prokh., *Pithyusa* (Raf.) Lázaro and *Myrsiniteae* (Boiss.) Lojac.].

Following Turkey with 91 known species, Iran is the second richest country for *Euphorbia* in Asia, with *c.* 87 species, 74 of which belong to subgenus *Esula* (Pahlevani, Maroofi & Joharchi, 2011b), 11 to subgenus *Chamaesyce* (Pahlevani & Riina, 2011; Yang *et al*., 2012) and only one species (*E. larica* Boiss.) to subgenus *Athymalus. Euphorbia tirucalli* L. from southeastern Iran is the sole Iranian representative of subgenus *Euphorbia,* but its native occurrence in Iran is doubtful. It is expected that, after completion of revision and molecular phylogenetic studies in *Euphorbia*, the species number in Iran will rise to *c*. 90 species. There are 18 endemic species in Iran, all members of subgenus *Esula*. The leafy spurges occupy a wide range of habitats, including deserts, inland and coastal sand dunes, roadsides, arable lands, foot hills, river banks, forests, steppes, rocky slopes, saline soils and gypsum hills, from below sea level along the coasts of the Caspian Sea to more than 4000 m on some peaks. Although some leafy spurges are frequent and may occur as invasive plants, some species have restricted areas and are rare local endemics. Leafy spurges have attracted pharmacologists, toxicologists and phytochemistry experts (Ahmad, Jassbi & Parvez, 1998; Nawito *et al*., 1998; Hohmann *et al*., 2003; Valente *et al*., 2004; Jassbi, 2006; Mwine & Van Damme, 2011; Jørgensen *et al*., 2013), because they contain carcinogenic compounds, anti-cancer agents, medicinal drugs, skin irritants and latex poisonous to both humans and livestock.

The study of carpology and seed morphology provides an easy way to identify species not only for

botanists, but also for agronomists, gardeners, weed scientists, food experts, archaeologists, archaeobotanists, pharmacologists, ecologists and conservation authorities. This article follows our previous contribution on the seed morphology of the annual *Euphorbia* spp. from Iran (Pahlevani & Akhani, 2011), describing and illustrating the perennial species. In our previous research, we could not evaluate the use of seed characters as phylogenetic markers, because no detailed phylogenetic analysis of the south-west Asian species existed. Indeed, the available studies covered only parts of the region and few Iranian species (Steinmann & Porter, 2002; Bruyns *et al*., 2006; Kryukov *et al*., 2010; Zimmermann, Ritz & Hellwig, 2010). With the molecular data now available, we provide such an evaluation for subgenus *Esula*.

In a recent paper, Salmaki *et al*. (2011) provided information on the seed and carpel morphology of selected Iranian *Euphorbia* spp. belonging to various subgenera and sections. They included 18 stereomicroscopic images and 25 scanning electron micrographs and presented data on shape, size, ornamentation and periclinal wall form of seeds and on the indumentum and surface of the capsule. The description of the caruncle in their paper is simply a categorization as large, medium and small without any further shape description. In addition, they inferred the phylogenetic relationships of selected species using ITS sequences, and mapped data for life form, gland appendage, caruncle size (in relation to seed size) and the presence or absence of seed surface ornamentation on an ITS tree. However, the study of Salmaki *et al*. (2011) suffered from incomplete sampling, a lack of statistical analysis for quantitative characters, small number of measured seeds (up to 20), absence of voucher citations and incorrect measurements in some species, improper selection of seed shape characters and absence of an identification key to species. Furthermore, several species were incorrectly identified; for example, *E. aserbajdzhanica* Bordz. (figs 17, 65), *E. myrsinites* L. (fig. 15) and *E. grossheimii* (Prokh.) Prokh. (fig. 48) should be corrected as *E. szovitsii* Fisch. & C.A.Mey., *E. marschalliana* Boiss. and *E. cheirolepis* Fisch. & C.A.Mey., respectively. In their fig. 77 (page 969), we found nine mistakes in the assignment of characters of individual species; e.g. *E. stricta* L. is an annual species (not perennial), *E. larica* is ecarunculate (not carunculate), *E. connata* Boiss. has smooth seeds (not ornamented) and the glands of *E. craspedia* Boiss. are denticulate (not two-horned). Therefore, a critical and comprehensive study of seed morphology and carpology of the Iranian *Euphorbia* spp. in the light of their phylogenetic relationships is needed.

This article aims to provide the following information: (1) quantitative and qualitative morphological seed and capsule descriptions of the Iranian perennial *Euphorbia* spp. with complete voucher citations for all studied specimens; (2) full illustrations with light and scanning electron micrographs of all species; (3) an identification key to all sections and species of Iranian perennial *Euphorbia*; and (4) correlation between seed and capsule morphological characters and the phylogenetic tree of Iranian *Euphorbia* spp.

Based on these data, the following questions are answered. (1) How useful are seed and carpological characters for taxonomic identification at specific and intraspecific levels? (2) Are seed and capsule morphological traits congruent with phylogenetic patterns? In addition, two new species are described and one new record from Iran and a new synonym are reported.

MATERIAL AND METHODS

SAMPLING

This study is mainly based on plant material deposited in the Iranian herbaria IRAN, TARI, HSBU, FUMH and FAR, one and two specimens in W (*E. plebeia* Boiss.) and M [*E. glareosa* Pall. ex M.Bieb. and one specimen of *E. deltobracteata* (Prokh.) Prokh.], respectively (abbreviations according to Thiers, 2014), and Herbarium Akhani (Halophytes and C_4 Plants Research Laboratory of the School of Biology, University of Tehran).

All species, their authors, habitats, flowering and fruiting time, general distribution, chorotype and voucher specimens are listed in Table 1, and Appendices 1 and 2. We use the classification according to the most recent molecular phylogenetic study (Riina *et al*., 2013), with some additional molecular results from the present article.

MORPHOLOGICAL, MORPHOMETRIC AND SEM STUDIES

To examine seed coat and sculpturing and caruncle morphology using SEM, mature seeds were mounted directly on 12.5-mm-diameter stubs fitted with sticky tape and coated in a sputter coater with a gold–palladium layer. Morphological observations were accomplished under different magnifications (12–500×) with a Zeiss SIGMA-VP scanning electron microscope at the Scanning Electron Microscopy Unit in the Applied Geological Research Center of Iran, Karaj. Morphometric measurements were carried out and all photographs of capsules, seeds and caruncles were taken under a Dino-Lite pro hand digital stereomicroscope. Qualitative seed and capsule morphological characters of all Iranian perennial *Euphorbia* spp. were assessed (Tables 2 and 4). Quantitative features had to be measured depending on the available material, ranging from four capsules of one

Table 1. List of all Iranian perennial species of *Euphorbia* studied in this article with their infrageneric and section position (Riina *et al*., 2013), habitat, growing season (Gr. Sea.), flowering and fruiting time (Fl. and Fr. time), monocarpic or polycarpic (M, P) and general distribution. Growing season: Sp, spring perennial; Su, summer perennial; W, winter perennial. Chorotypes: H, Hyrcanian; ES, Euro-Siberian; IT, Irano-Turanian; M, Mediterranean; SS, Saharo-Sindian

Taxon	Section and subsection	Habitat	Gr. Sea.	Fl. and Fr. time	General distribution and chorotype
Subgenus *Athymalus* Neck. ex. Rchb.					
E. larica Boiss.	*Balsamis* Webb & Berthelot	Lowlands, hot desert, sea shores, river banks, foothills, scrubs	Sp	April–June	S to SE Iran, the Arabian peninsula (Oman, Yemen, United Arab Emirates), Qatar, Bahrain SS
Subgenus *Esula* Pers.					
E. acanthodes Akhani	*Pithyusa* (Raf.) Lázaro	Lowlands on gypsum hills, eremophilous	W-Sp	March–April, M	Endemic to SW Iran. IT
E. altissima ssp. *altissima* Boiss.	*Helioscopia* Dumort.	On clay soil by river banks, streams, springs, irrigation ditches, field margin, oak forest slopes	Su	June–August, M	N Iraq, NW Iran, Turkey, Syria, Lebanon, Cyprus? IT-M
E. amygdaloides L.	*Patellares* (Prokh.) Frajman	*Fagus* and *Carpinus* forests, woods	Sp-Su	April–July, P	W and C Europe, S Russia, Caucasus, N Iran, Turkey. ES
E. aucheri Boiss.	*Herpetorrhizae* (Prokh.) Prokh. subsection *Aucheriae* Geltman & Pahlevani	Metamorphic rocks, calcareous stones, steep dry alpine and subalpine slopes	Su	June–August, M	Iran, Iraq, Afghanistan, W Pakistan, Turkmenistan. IT
E. buhsei Boiss.	*Esula* (Pers.) Dumort.	Disturbed areas, saline and calcareous soils, rocky mountain slopes, deserts	Sp	April–June, P	Iran, W Afghanistan, S Turkmenistan. IT
E. bungei Boiss.	*Sclerocyathium* (Prokh.) Prokh.	Foothills, arable lands, calcareous mountain slopes	Sp-Su	May–July, P	Iran, Afghanistan, Turkmenistan, Tajikistan. IT
E. caeladenia Boiss.	*Sclerocyathium* (Prokh.) Prokh.	Deserts, foothills	Sp	April–May, M	SE Iran, Afghanistan, W Pakistan. IT
E. cheiradenia Boiss. & Hohen.	*Pithyusa* (Raf.) Lázaro	Rocky mountain slopes, *Artemisia* steppes, pastures	Sp	April–July, M	N, NW to SW Iran, E Turkey, Iraq, Syria, Palestine, Lebanon. IT-M
E. condylocarpa M.Bieb.	*Helioscopia* Dumort.	Rocky slopes, oak scrubs, screes, steppe forests on limestone	Sp	April–June, M	NW, W and SW Iran, N Iraq, Turkey, Caucasus (Armenia, Azerbaijan, Georgia and Russia). IT
E. connata Boiss.	*Calyptratae* Geltman	Deserts	Sp	April–June, M	Endemic to S Iran. IT
E. craspedia Boiss.	*Myrsiniteae* (Boiss.) Lojac.	Open oak scrubs, stony limestone steppes	Sp	April–June, P	W Iran, N Iraq, E Turkey. IT
E. deltobracteata (Prokh.) Prokh.	*Herpetorrhizae* (Prokh.) Prokh. subsect. *aucheriae* Geltman & Pahlevani	Rocky slopes, steppe grassy slopes	Sp	April–June, M	NE Iran, Turkmenistan. IT
E. denticulata Lam.	*Myrsiniteae* (Boiss.) Lojac.	Rocky limestone and igneous slopes, steppes, oak woods and scrubs	Sp	March–June, P	NW and W Iran, N Iraq, Turkey. IT
E. erubescens Boiss.	*Patellares* (Prokh.) Frajman	Open oak forests, scrubs, rocky slopes	Sp-Su	April–July, P	W and SW Iran, Syria, Lebanon, S Turkey. IT-M
E. erythradenia Boiss.	*Pithyusa* (Raf.) Lázaro	Rocky mountain slopes	Sp	May–June, M	Endemic to S Iran. IT
E. ferdowsiana Pahlevani	*Sclerocyathium* (Prokh.) Prokh.	Rocky slopes	Su	June–August	Endemic to NE Iran. IT
E. gedrosiaca Rech.f., Aell. & Esfand.	*Pithyusa* (Raf.) Lázaro	Deserts, foot and rock hills	Sp	May–June, M	Endemic to C and SE Iran. IT
E. glareosa Pall. ex M.Bieb.	*Pithyusa* (Raf.) Lázaro	Steppes, mountain slopes	Sp-Su	May–August, M	E Mediterranean (Bulgaria, Turkey), S Caucasus (Armenia), NW Iran. IT
E. grisophylla M.S.Khan	*Helioscopia* Dumort.	Dry rocky igneous and limestone slopes, screes	Sp-Su	June–July, M	W Iran and E Turkey. IT
E. gypsicola Rech.f. & Aellen	*Pithyusa* (Raf.) Lázaro	Gypsum lowlands	Sp	April–June, M	Endemic to NC Iran. IT
E. hebecarpa Boiss.	*Esula* (Pers.) Dumort.	Rather higher mountains, steppes	Sp	May–June	Iran, N Iraq. IT
E. heteradena Jaub. & Spach	*Chylogala* (Fourr.) Prokh.	Arable lands, deserts, foothills, steppes, abandoned fields, roadsides, stony slopes	Sp-Su	May–August, P	Iran, N Iraq, E Turkey, Armenia, Azerbaijan? IT
E. iberica Boiss.	*Esula* (Pers.) Dumort.	Higher mountain stony slopes (more than 2000 m), valleys, screes, *Astragalus* and *Artemisia* steppes	Sp-Su	June–August, M	NW and W Iran, NE and E Turkey, N Iraq, Caucasus (Armenia, Azerbaijan). IT

Table 1. *Continued*

Taxon	Section and subsection	Habitat	Gr. Sea.	Fl. and Fr. time	General distribution and chorotype
E. iranshahri Pahlevani	*Pithyusa* (Raf.) Lázaro	Rocky mountain slopes	Sp	May–June, M	Endemic to C Zagros Mt. in Iran. IT
E. kopetdaghi (Prokh.) Prokh.	*Pithyusa* (Raf.) Lázaro	Steppes, pastures	Sp	May–July, M	NE Iran, S Turkmenistan. IT
E. macrocarpa Boiss. & Buhse	*Helioscopia* Dumort.	Open ground in oak scrubs, igneous slopes, on limestone and serpentine	Sp	May–June, M	N, NW and W Iran, N Iraq, Turkey, Azerbaijan. IT
E. macroceras Fisch. & C.A.Mey.	*Patellares* (Prokh.) Frajman	Hyrcanian and Caucasian forests	Sp-Su	June–August	N Iran, N Turkey, Caucasus (Armenia, Azerbaijan, Georgia and Russia). ES
E. macroclada Boiss.	*Pithyusa* (Raf.) Lázaro	Disturbed areas, arable lands, road sides, *Artemisia* and *Astragalus* steppes	Su	June–August	NW, W and SW Iran, N Iraq, Turkey, Syria, Jordan. IT-M
E. malleata Boiss.	*Pithyusa* (Raf.) Lázaro	*Artemisia* and *Astragalus* steppes, overgrazed and dry mountain slopes	Su	July–August, P	Endemic to C Iran. IT
E. marschalliana Boiss.	*Myrsiniteae* (Boiss.) Lojac.	Roadsides, rocky slopes, river banks, igneous slopes	Sp	April–June, P	NW Iran, NE Turkey, Armenia. IT
E. mazandaranica Pahlevani	*Helioscopia* Dumort.	Hyrcanian forest	Sp	April–May	Endemic to N Iran. H
E. microsciadia Boiss.	*Pithyusa* (Raf.) Lázaro	Steppes, roadsides, foothills, mountain slopes, arable lands	Sp-Su	May–August, P	Iran, W Pakistan? IT
E. monostyla Prokh.	*Myrsiniteae* (Boiss.) Lojac.	Stony and rocky slopes, schistose soil	Sp	March–May, M	NE Iran, S Turkmenistan. IT
E. myrsinites L.	*Myrsiniteae* (Boiss.) Lojac.	Mountain pastures, rocky slopes, calcareous slopes	Sp	April–June, P	S Europe, N and NW Turkey, N Iran, Caucasus (Georgia, Russian Black Sea coast). M
E. orientalis L.	*Helioscopia* Dumort.	Rocky slopes, screes, scrubs, on metamorphic rocks, dry river banks	Su	June–August, M	N, NW and W Iran, N Iraq, E Turkey, Azerbaijan (Nakhichevan), Armenia. IT
E. osyridea Boiss.	*Esula* (Pers.) Dumort.	Rocky hills, in limestone gorges and gravelly sands	Sp	March–June, P	SW to SE Iran, Afghanistan, Pakistan, W Himalaya. IT
E. plebeia Boiss.	*Pithyusa* (Raf.) Lázaro	Mountain slopes	Sp	May–July, M	Endemic to S Iran. IT
E. polycaulis Boiss.	*Pithyusa* (Raf.) Lázaro	Mountain slopes, overgrazed pastures and rangelands, limestone	Sp-Su	May–July, P	Endemic to W and WC Iran. IT
E. sahendii Bornm.	*Pithyusa* (Raf.) Lázaro	Oreophilous, igneous mountain slopes, steppes	Su	August–September, M	Endemic to NW Iran. IT
E. seguieriana Neck.	*Pithyusa* (Raf.) Lázaro	Disturbed areas, road sides, fields margin, scrubs, steppes, fallow fields	Sp-Su	May–September, P	C and W Europe, SW Asia, Caucasus. ES
E. spartiformis Mobayen	*Pithyusa* (Raf.) Lázaro	Chasmophyte, calcareous slopes	W-Sp	March–April, M	Endemic to S Iran. IT
E. spinidens Bornm. ex Prokh.	*Myrsiniteae* (Boiss.) Lojac.	Mountain slopes and rocky fissures	Sp	April–June, M	NE Iran, E Turkmenistan, N Afghanistan, Uzbekistan. IT
E. squamosa Willd.	*Helioscopia* Dumort.	Caucasian forests, ecotone between meadow and forest on calcareous rocky slopes	Su	June–July, M	NW Iran, N Turkey, Caucasus. ES
E. sulphurea Pahlevani	*Pithyusa* (Raf.) Lázaro	Oreophilous, volcanic mountain on the sulphur bed	Sp	May–June, M	Endemic to SE Iran. IT
E. teheranica Boiss.	*Pithyusa* (Raf.) Lázaro	Foothills, mountain steppes	Sp	April–July, P	Endemic to NC Iran. IT
E. virgata Waldst. & Kit.	*Esula* (Pers.) Dumort.	Arable lands, roadsides, river banks, grasslands, marshes and ditches	Sp-Su	May–September, P	SW and C Asia, Europe, Far East, Caucasus. IT-M-ES

Table 2. Qualitative capsule morphological characters of Iranian perennial species of *Euphorbia*

Species	Capsule shape	Capsule surface	Capsule and style colour
E. acanthodes	Conical, shallowly trilobate	Smooth, glabrous	Yellowish-green
E. altissima ssp. *altissima*	Subglobose, rather deeply to shallowly trilobate	Smooth, glabrous or rarely sparingly pilose	Green
E. amygdaloides	Subglobose, deeply trilobate	Smooth, glabrous	Green
E. aucheri	Oblong-conical	Smooth, glaucous, mostly reticulate	Bluish-green
E. buhsei	Subglobose, deeply trilobate	Smooth, glabrous, glaucous or rarely pilose, granulate	Bluish-green
E. bungei	Rounded-conical, shallowly trilobate	Smooth, glabrous, glaucous	Bluish-green
E. caeladenia	Conical, shallowly trilobate	Smooth, glabrous, glaucous	Yellowish-green with brownish style
E. cheiradenia	Conical, shallowly trilobate	Smooth, glabrous, usually with outstanding sharp keels	Yellowish-green, style ochreous to yellowish-green
E. condylocarpa	Subglobose, shallowly trilobate	Covered with shortly cylindrical, often purplish warts, glabrous	Green to purple, style brown to purplish
E. connata	Conical, rather shallowly trilobate, pedicel pilose	Smooth, glabrous with prominent reticulate veins	Yellowish-green, style ochreous
E. craspedia	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels	Blue to purple, style reddish
E. deltobracteata	Oblong-conical	Smooth, glaucous	Bluish-green
E. denticulata	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels	Blue to purple, style reddish
E. erubescens	Subglobose	Smooth, pilose to subglabrous	Yellow to straw-coloured
E. erythradenia	Narrowly conical, shallowly trilobate	Smooth, glabrous, glaucous	Bluish-green, style brown
E. ferdowsiana	Rounded-conical, shallowly trilobate	Smooth, glabrous, glaucous	Reddish to purplish
E. gedrosiaca	Narrowly conical, shallowly trilobate	Smooth, glabrous, glaucous	Grey to bluish-green, style brown
E. glareosa	Conical, shallowly trilobate	Pruinose-papillose	Yellowish
E. grisophylla	Subglobose, shallowly trilobate	Sparingly covered with conic-cylindrical warts, glabrous	Green
E. gypsicola	Conical, shallowly trilobate	Smooth, pilose, glaucous	Grey to bluish-green, style brown to ochreous
E. hebecarpa	Subglobose, deeply trilobate	Smooth, pilose to rarely subglabrous, granulate	Greyish-green to yellow, style green to ochreous
E. heteradena	Rounded-oblong trilobate	Smooth, glabrous, to some extent glaucous	Greenish-yellow, style light brown
E. iberica	Subglobose, deeply trilobate	Smooth, glabrous, to some extent glaucous, granulate	Yellowish-green, style brown
E. iranshahri	Conical, shallowly trilobate	Smooth, glabrous, glaucous, sharp keeled	Greyish-green to purplish, style light brown
E. kopetdaghi	Conical, shallowly trilobate	Smooth, glabrous	Greyish-green, style brownish-ochreous to rarely mixed purple and green
E. larica	Globose, obscurely hexalobate, woody	Smooth, glabrous, glaucous	Light green to yellow with purplish keels, style mixed green and brown

Table 2. *Continued*

Species	Capsule shape	Capsule surface	Capsule and style colour
E. macrocarpa	Subglobose, deeply trilobate and thick	Covered with short filiform warts, glabrous	Greenish-yellow to ochreous, warts sometimes purplish
E. macroceras	Subglobose, deeply trilobate	Smooth, glabrous	Green, style green to brown or mixed
E. macroclada	Conical, shallowly trilobate	Pruinose-papillose, villose to sparingly villose, glaucous	Greenish-yellow, style brown
E. malleata	Conical, shallowly trilobate	Smooth, glabrous, sharp keeled	Light yellow, style yellow to ochreous
E. marschalliana	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels	Blue to purple, style reddish
E. mazandaranica	Subglobose, deeply trilobate	Smooth or rarely with a few short warts, glabrous-subglabrous	Green to some extent yellowish, style brown
E. microsciadia	Conical, shallowly trilobate	Smooth, glabrous	Olive green, style ochreous to brown
E. monostyla	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels	Blue to purple, style reddish
E. myrsinites	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels	Blue to purple, style reddish
E. orientalis	Subglobose, rather deeply to shallowly trilobate	Covered with two rows of tubercles on each lobe, sparingly pilose to subglabrous	Light green, style green to brown
E. osyridea	Subglobose, deeply trilobate	Smooth, pilose or rarely subglabrous, glaucous, granulate	Greyish-green, style ochreous to light brown
E. plebeia	Conical, shallowly trilobate	Smooth, glabrous, glaucous, sharp keeled	Grey to olive green, style ochreous to brown
E. polycaulis	Conical, shallowly trilobate	Pruinose-papillose, glabrous, glaucous	Greyish-green to purplish, style as same as capsule
E. sahendii	Conical, shallowly trilobate	Smooth, completely pilose, glaucous	Greyish-green sometimes with purplish spots, style ochreous
E. seguieriana	Conical, shallowly trilobate	Smooth, glabrous	Yellowish-green, style ochreous to green
E. spartiformis	Conical, shallowly trilobate	Smooth, glabrous, glaucous	Greyish-green, style ochreous to brown
E. spinidens	Ovoid-conical, trigonous	Vesiculate, glaucous, with thick keels, usually granulate	Blue to purple, style reddish
E. squamosa	Subglobose, deeply trilobate	Covered with long cylindrical-filiform warts, glabrous	Green to straw-coloured, style green to ochreous
E. sulphurea	Conical, shallowly trilobate	Smooth, glabrous to subglabrous, glaucous	Greyish-blue, style purplish
E. teheranica	Narrowly conical, shallowly trilobate	Smooth, pilose to subglabrous, glaucous	Greyish-green, style ochreous
E. virgata	Subglobose, deeply trilobate	Smooth, glabrous, granulate (mainly cocci)	Yellowish-green, style ochreous to brown

Table 3. Morphometric measurements of capsules of the perennial species of Iranian *Euphorbia* showing maximum (Max.), minimum (Min.), average (Ave.) and standard deviation (Std.) of capsule length (*l*), capsule width (*w*), pedicel length (*l*), style length (*l*) and capsule index (average of length to average of width of capsule)

	Capsule size								Pedicel size				Style size				
Species	Max. *l* (mm)	Min. *l* (mm)	Ave. (mm)	Std.	Max. *w* (mm)	Min. *w* (mm)	Ave. (mm)	Std.	Max. *l* (mm)	Min. *l* (mm)	Ave. (mm)	Std.	Max. *l* (mm)	Min. *l* (mm)	Ave. (mm)	Std.	Capsule index
E. acanthodes (1/4)	4.3	4.1	4.2	–	3.1	2.9	3	–	2.7	2.45	2.57	–	–	–	–	–	1.4
E. altissima ssp. *altissima* (1/4)	4.9	4.5	4.7	0.29	4.62	4.6	4.61	0.01	3	2	2.5	0.7	1.2	0.94	1	0.1	1.02
E. amygdaloides (4/22)	4.4	3.3	3.86	0.3	5.5	3.25	4.57	0.57	2.3	1.33	1.84	0.41	1.93	1.3	1.57	0.16	0.84
E. aucheri (7/43)	4.9	3.33	3.77	0.34	4.4	2.76	3.58	0.38	3.4	0.96	1.71	0.63	1.51	0.8	1.14	0.21	1.05
E. buhsei (8/56)	5.7	4.6	5.07	0.36	6.6	4.5	5.17	0.47	5.8	1.9	3.83	0.95	2.8	1.4	2.05	0.37	0.98
E. bungei (9/72)	7.5	5.5	6.1	0.49	8.7	5	6.14	0.81	5.9	2	3.24	0.8	1.2	0.65	0.9	0.16	0.99
E. caeladenia (6/38)	5.7	4.6	5.01	0.26	5.1	4	4.45	0.27	3.5	2.1	2.64	0.38	1	0.65	0.82	0.09	1.12
E. cheiradenia (8/76)	6.8	4.48	5.38	0.72	5.2	3.5	4.2	0.39	6	1.8	2.8	1.18	2.4	1.5	1.75	0.25	1.28
E. condylocarpa (3/21)	5.6	4.35	4.98	0.34	6.2	4.28	5.36	0.5	3.98	1.95	2.77	0.66	1.4	0.8	1.04	0.15	0.93
E. connata (5/37)	8.2	5.9	6.81	0.48	7.7	5	6.56	0.62	7.5	2.33	3.73	1.35	2.5	1.4	1.95	0.31	1.03
E. craspedia (1/10)	11.5	10	10	0.5	9.5	7.5	8.61	0.65	5.5	3	3.83	0.93	3.5	2.5	3.01	0.28	1.16
E. deltobracteata (2/5)	3.2	3	3.13	0.11	3.8	3.7	3.73	0.05	1.5	1	1.23	0.25	1.2	1	1.1	0.1	0.83
E. denticulata (5/37)	11.5	8.59	9.91	0.72	10	6.8	8.01	0.78	7.2	2.2	3.93	1.19	3.3	1.86	2.48	0.41	1.23
E. erubescens (4/17)	8.26	6.3	7.29	0.56	8.3	6.7	7.39	0.14	6.4	1.9	3.51	1.85	2.7	1.95	2.3	0.24	0.98
E. erythradenia (2/18)	5	4.2	4.6	0.27	3.8	2.9	3.34	0.23	3.6	1.8	2.37	0.52	1.8	1.3	1.46	0.15	1.37
E. ferdowsiana (3/10)	6.1	4.8	5.18	0.45	6.5	4	5.13	0.88	2.2	1.1	1.68	0.4	0.7	0.38	0.45	0.1	1.49
E. gedrosiaca (6/45)	5.7	4.3	4.99	0.33	4.6	2.85	3.78	0.4	5	1.34	2.68	0.82	1.4	0.8	1.28	0.16	1.32
E. glareosa (2/10)	4	3.2	3.59	0.23	3	2.5	2.76	0.14	2.1	1	1.75	0.32	2.3	1.79	2	0.16	1.29
E. grisophylla (1/10)	6.4	4.95	5.6	0.5	7.4	6.1	6.86	0.47	3	2	2.49	0.41	2.1	1.65	1.88	0.14	0.81
E. gypsicola (2/15)	5.9	4.6	5.22	0.32	4.8	3.5	4.18	0.41	3.7	1.8	2.65	0.49	1.7	1	1.34	0.23	1.24
E. hebecarpa (8/59)	6.05	4.07	5.04	0.4	6.4	4.35	5.29	0.51	3.5	1.62	2.6	0.6	2.7	0.98	1.8	0.34	0.95
E. heteradena (10/82)	9.5	5.8	6.94	0.64	8.4	5	6.26	0.58	7.5	1.85	3.99	1.4	2.5	1.2	1.87	0.25	1.1
E. iberica (3/26)	3.9	3	3.43	0.27	5.2	3.46	4.53	0.45	3.6	1.4	2.23	0.7	1.5	1	1.27	0.15	0.75
E. iranshahri (6/27)	8	4.4	5.26	0.72	6.5	3.8	4.42	0.5	3.9	1.7	2.4	0.65	1.8	0.86	1.14	0.23	1.19
E. kopetdaghi (5/36)	5.69	3.87	4.62	0.64	4.74	3.5	4.02	0.56	3.7	1.38	1.97	0.6	1.6	1.1	1.36	0.11	0.87
E. larica (4/24)	8	6	6.69	0.7	8.9	6	7.68	1.03	4.9	1.59	2.46	0.8	2.1	1.24	1.55	0.25	0.8
E. macrocarpa (7/41)	8.4	6	7.28	0.56	10	8	9.01	0.51	5.2	1.56	3.07	1.25	2.85	1.6	2.15	0.42	0.74
E. macroceras (2/15)	4.4	3.2	3.98	0.35	6.7	4.22	5.35	0.78	2.8	1.3	1.9	0.86	1.65	0.99	1.41	0.18	1.07
E. macroclada (5/45)	7.97	5	6.27	0.6	6.67	4.95	5.85	0.42	5.2	1.45	2.76	0.85	3	1.4	2.12	0.35	1.2
E. malleata (7/49)	5.5	3.68	4.65	0.57	4.57	3.2	3.87	0.49	3.2	1.48	2.21	0.46	2.58	1.23	1.9	0.34	1.19
E. marschalliana (7/54)	7.3	4.73	6.32	0.69	6.42	4.23	5.31	0.47	5.5	1.56	2.8	0.83	2.6	1.2	1.88	0.3	0.76
E. mazandaranica (3/19)	3.4	2.45	2.92	0.28	4.3	3	3.83	0.36	1.2	0.68	0.98	0.15	1.4	0.9	1.08	0.16	1.23
E. microsciadia (9/78)	5.68	3.98	4.92	0.29	4.5	3.5	3.98	0.23	4.5	1.79	2.44	0.6	1.55	0.79	1.13	0.17	1.17
E. monostyla (3/30)	7.64	5	6.42	0.74	6.78	4.31	5.48	0.66	3.8	1.64	2.56	0.53	2.1	1.28	1.62	0.21	1.09
E. myrsinites (3/25)	7.5	5.2	6.53	0.54	6.6	5	5.98	0.45	4.5	2.2	2.97	0.7	3.4	1.9	2.53	0.4	0.84
E. orientalis (2/18)	5.28	3.6	4.85	0.4	6.76	4.8	5.73	0.59	2.5	1.8	2.2	0.24	2.36	1.81	1.99	0.17	0.82
E. osyridea (7/54)	6.4	4	5	0.51	7.7	4.55	6.04	0.78	9.5	3.5	5.29	1.47	3.4	1.5	2.19	0.47	1.27
E. plebeia (1/4)	4.9	4.55	4.72	0.24	3.9	3.5	3.7	0.28	1.3	1	1.15	0.21	1.38	1.35	1.36	0.02	1.23
E. polycaulis (6/50)	5.2	4	4.64	0.31	4.5	3.25	3.75	0.29	4	1.4	2.18	0.63	2.5	1.35	1.83	0.26	1.1
E. sahendii (1/10)	5.3	4.5	4.97	0.27	5	4.2	4.49	0.34	4.8	2.2	3.05	0.88	1.5	1.2	1.32	0.1	0.92
E. seguieriana (10/92)	3.7	2.55	3.07	0.28	3.7	2.5	3.32	0.25	4.2	1.1	1.77	0.71	1.59	0.85	1.17	0.2	1.17
E. spartiformis (2/18)	4.5	3.53	3.94	0.34	3.94	2.6	3.36	0.3	3.4	1.85	2.49	0.49	1.3	0.82	1.01	0.15	1.12
E. spinidens (6/42)	7.08	5.3	6.21	0.39	6.69	3.97	5.52	0.7	3.45	1.57	2.49	0.48	2.7	1.64	2.08	0.27	0.94
E. squamosa (2/18)	5.8	4.3	5.02	0.44	6.2	4.95	5.34	0.31	2.67	2	2.41	0.19	3	1.9	2.39	0.38	1.3
E. sulphurea (2/5)	3.9	3.1	3.5	0.45	3.5	2.7	3.15	0.35	2	0.88	1.44	0.19	1	0.8	0.9	0.2	1.15
E. teheranica (6/39)	6.55	4.24	4.95	0.55	4.6	2.91	3.81	0.49	3.2	1.7	2.25	0.41	1.5	0.8	1.13	0.19	0.79
E. virgata (10/78)	4.4	3	3.63	0.25	5.3	3.8	4.57	0.39	3.9	1.55	2.24	0.53	2.9	1.1	1.62	0.35	1.3

Numbers after the species names indicate the number of populations and number of measured capsules, separated by a slash.

population to a maximum of 92 capsules from ten populations, and from five seeds of one population up to 121 seeds from 12 populations (Tables 3 and 5). For species with wider distribution ranges, populations from different parts of Iran were selected to cover the geographical and morphological diversity of the species. The characters recorded comprised the capsule dimension (length × width), capsule surface, capsule shape and colour, pedicel and style length, seed dimension (length × width), ornamentation of seed surfaces, seed shape and colour and caruncle shape, colour and size (length × width). The seed index and capsule index were measured by the division of the average length by the average width for each species. Widths of capsules, seeds and caruncles were measured at the widest point. Seed length was considered excluding the caruncle. The range (maximum, minimum) and average of the morphometric measurements and standard deviations, calculated in Microsoft Excel, are presented.

Scanning electron micrographs of seeds which have already been published in other publications are not repeated in this article. They include *E. acanthodes* Akhani (Akhani, 2004), *E. iranshahri* Pahlevani and *E. microsciadia* Boiss. (Pahlevani & Mozaffarian, 2011), and *E. larica* and *E. osyridea* Boiss. (Salmaki *et al*., 2011), except for a few cases in which our improved magnification provides additional information discussed in this article.

Phylogenetic studies

Sampling strategy

This study includes the phylogenetic analysis of Iranian species of subgenus *Esula* already sequenced by Riina *et al*. (2013) (57 ITS and 46 *ndhF* sequences), in addition to nine accessions representing eight species (*E. monostyla* Prokh., *E. glareosa*, *E. aulacosperma* Boiss., *E. chamaepeplus* Boiss. & Gaill., *E. ferdowsiana* sp. nov., *E. sulphurea* sp. nov., *E. grisophylla* M.L.S.Khan and *E. eriophora* Boiss.). In total, ITS sequences of 66 accessions and *ndhF* sequences of 55 accessions comprising 62 species have been analysed. Unfortunately, in several cases, ITS and *ndhF* sequences were obtained from different individuals of the same species in Riina *et al*. (2013); nevertheless, we followed Riina *et al*. (2013) in combining these sequences. *Euphorbia larica* was considered as the outgroup, and sections without representatives in the area were omitted. The specimens studied were collected during field work by the first author or obtained from herbarium specimens.

DNA analysis

Total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions, but adjusted by applying 5 μL of proteinase K at 20 mg mL^{-1} to deactivate the secondary compounds that occur in the genus (Barres *et al*., 2011). For total DNA isolation and amplification of the ITS region, we followed the protocol described in Kryukov *et al*. (2010), Barres *et al*. (2011), Frajman & Schönswetter (2011), Yang & Berry (2011) and Riina *et al*. (2013). We tried to amplify the chloroplast *ndhF* gene as two overlapping fragments using primers 536f and 1318r (Olmstead & Sweere, 1994) for the 5′ region, and primers 1000f (Riina *et al*., 2013) and 2110ri (Steinmann & Porter, 2002) for the 3′ region. However, the second part of *ndhF* could not be amplified from our material, so that only ITS and the first part of *ndhF* are included for the specimens newly sequenced for the present article.

Data assembly and phylogenetic analyses

Sequences were edited and pre-aligned using CodonCode Aligner v.3.7.1 and subsequently adjusted manually. Sequence alignments were performed with Mesquite v.2.75 (Maddison & Maddison, 2011) using the OPAL package (Wheeler & Kececioglu, 2007) with the BlastAlign Web Interface version 1.0 (Belshaw & Katzourakis, 2005). PAUP (Swofford, 2000) and RAxML (Stamatakis, Hoover & Rougemont, 2008) were used to conduct maximum likelihood (ML) phylogenetic analyses on the ITS, *ndhF* and combined ITS + *ndhF* datasets. The nucleotide substitution model was set to GTR + γ as recommended by the RAxML manual; 100 ML bootstrap replicates were performed, followed by a thorough search for the best tree. For Bayesian inference (BI) analysis of ITS, *ndhF* and the combined dataset, we used MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Analysis was conducted using the nucleotide substitution model GTR + I + γ for ITS and *ndhF* following Riina *et al*. (2013). The process included four runs with four chains each run for 10 000 000 generations.

Analysis of morphological data

Patterns of character evolution were assessed for six seed and capsule characters that had been considered to be taxonomically useful in earlier taxonomic treatments, such as seed and capsule surfaces and caruncle shape, and some characters for which the taxonomic value is evaluated here, such as the presence or absence of granulate elements on seed surfaces and seed and capsule shape. Parsimony mapping of these characters was performed in Mesquite v. 2.75 (Maddison & Maddison, 2011) using the tree derived by BI as the reference. The following traits were coded in a binary matrix and traced on the tree: (1) presence or absence of granulate elements on the seed surface; (2) seed shape (ovoid, hexahedral,

Table 4. Qualitative seed morphological characters of Iranian perennial species of *Euphorbia* (GE, granulate elements present)

Species	Seed shape	Seed surface	Seed colour	Caruncle shape and colour
E. acanthodes	Ovoid	Smooth (GE)	Light brown	Conical, yellow
E. altissima ssp. *altissima*	Ellipsoidal	Smooth	Shiny dark brown	Reniform, yellowish-ochreous
E. amygdaloides	Ovoid	Smooth	Dark grey	Patelliform, light yellow to ochreous
E. aucheri	Pseudo-hexahedral, protruding at the end	Shallowly pitted and wrinkled with longitudinal furrow (GE)	Pale grey	Conical, oblique, light yellow to white
E. buhsei	Ovoid-ellipsoidal	Smooth (GE)	Dark grey to brown	Petasiform, ochreous
E. bungei	Compressed-ovoid, flat at the end	Smooth	Dark grey to brown	Conical, sulcate, yellow to white
E. caeladenia	Ovoid	Smooth	Pale grey to brown, sometimes with green mottled	Shovel shaped, yellowish-orange
E. cheiradenia	Compressed ovoid	Irregularly deeply pitted and wrinkled (GE)	Pale grey	Conical, mixed yellow and white to ochreous
E. condylocarpa	Ellipsoidal	Smooth	Shiny dark brown	Reniform, ochreous
E. connata	Ovoid-subglobose, flat at the end	Smooth	Dark grey to brown	Longitudinally sulcate, brownish-yellow
E. craspedia	Ovoid-quadrangular, flat at the end	Tuberculate (GE)	Pale grey	Fluted-conical, stipitate, white to yellow
E. deltobracteata	Pseudo-hexahedral, depressed at the end	Concave faces, faintly and sparingly tuberculate (GE)	Pale grey	Flattened-conical, oblique, white to light yellow
E. denticulata	Ovoid-quadrangular	Tuberculate-rugulose (GE)	Pale grey to pale brown	Conical, white to yellow
E. erubescens	Compressed-ovoid	Smooth	Pale grey to brown	Lunate to patelliform, brownish-ochreous
E. erythradenia	Ovoid, protruding at the end	Irregularly pitted (GE)	Pale grey	Conical, brownish-yellow
E. ferdowsiana	Compressed-ovoid	Smooth	Dark grey to brown	Conical with two ligulate arms at the base, pale yellow
E. gedrosiaca	Ovoid	Irregularly pitted (GE)	Pale grey to sometimes pale brown	Prominent narrowly conical, ochreous or mixed white and yellow
E. glareosa	Ovoid	More or less smooth to obscurely pitted (GE)	Brown	Conical, yellow
E. grisophylla	Broadly ellipsoidal	Smooth	Pale brown to pale grey	Reniform, yellow
E. gypsicola	Ovoid	Irregularly pitted (GE)	Pale grey to brown	Conical, brownish-yellow
E. hebecarpa	Ovoid-ellipsoidal	Smooth (GE)	Pale grey to brown	Petasiform, brown to yellow
E. heteradena	Ovoid-subsquare	Smooth (GE)	Pale grey	Strongly fluted, ochreous to brown
E. iberica	Ovoid-ellipsoidal	Smooth (GE)	Grey to sometimes brown or mottled	Petasiform, light yellow to white

Table 4. *Continued*

Species	Seed shape	Seed surface	Seed colour	Caruncle shape and colour
E. iranshahri	Ovoid	Smooth (GE)	Grey to brown or mottled	Conical, mixed white and yellow or yellow and brown
E. kopetdaghi	Ovoid	Irregularly pitted (GE)	Grey to light brown	Conical, ochreous
E. larica	Ovoid-subsquare	Superficially tuberculate to subsmooth	Dark grey to brown	Absent
E. macrocarpa	Ellipsoidal-subglobose	Smooth	Pale grey–brown or mottled	Minutely reniform, readily deciduous, ochreous
E. macroceras	Ovoid	Smooth	Dark grey	Patelliform, ochreous
E. macroclada	Ovoid	Smooth (GE)	Pale grey	Conical, yellow
E. malleata	Narrowly ovoid	Irregularly pitted (GE)	Pale grey	Conical, yellow
E. marschalliana	Ovoid-quadrangular to oblong	Smooth to shallowly rugulose (GE)	Pale grey to pale brown	Swollen conical, brown to yellow or mixed
E. mazandaranica	Ellipsoidal	Smooth	Dark brown	Reniform, ochreous to light yellow
E. microsciadia	Ovoid	Irregularly pitted (GE)	Grey to light brown	Conical, ochreous
E. monostyla	Ovoid-quadrangular to oblong	Smooth (GE)	Pale grey to pale brown	Truncate-notched conical, ochreous
E. myrsinites	Ovoid-quadrangular to oblong	Vermiculate-rugulose (GE)	Grey to light brown	Notched-conical, brown
E. orientalis	Ellipsoidal	Smooth	Shiny brown	Reniform, ochreous
E. osyridea	Broadly ovoid-ellipsoidal	Smooth (GE)	Dark grey to brown, mostly papillose	Petasiform, ochreous
E. plebeia	Ovoid	Irregularly pitted (GE)	Grey to light brown	Conical, brown
E. polycaulis	Ovoid	Irregularly pitted (GE)	Grey to brown	Conical, with a depression at the base, ochreous
E. sahendii	Ovoid	Irregularly elongated-pitted (GE)	Light brown to grey	Conical, ochreous
E. seguieriana	Ovoid	Smooth to subsmooth (GE)	Pale grey	Hemispherical, ochreous
E. spartiformis	Ovoid	Smooth to rarely slightly pitted (GE)	Grey	Conical, ochreous to light yellow
E. spinidens	Ovoid-quadrangular	Vermiculate-rugulose and tuberculate (GE)	Grey to light brown	Small conical, brown to ochreous
E. squamosa	Ellipsoidal	Smooth	Dark brown	Reniform, ochreous
E. sulphurea	Ovoid, depression at the end	Irregularly pitted (GE)	Grey to brown	Conical, brown to ochreous
E. teheranica	Ovoid	Irregularly pitted (GE)	Grey to brown	Elongated-conical, mostly stipitate, ochreous to white
E. virgata	Ovoid-ellipsoidal	Smooth (GE)	Grey to brown	Petasiform, yellow to brown

Table 5. Morphometric measurements of seeds of the perennial species of Iranian *Euphorbia* showing maximum (Max.), minimum (Min.), average (Ave.) and standard deviation (Std.) of seed length (*l*), seed width (*w*), caruncle length (*l*), caruncle width (*w*) and seed index (average of length to average of width of seed)

	Seed size								Caruncle size								
Species	Max. *l* (mm)	Min. *l* (mm)	Ave. (mm)	Std.	Max. *w* (mm)	Min. *w* (mm)	Ave. (mm)	Std.	Max. *l* (mm)	Min. *l* (mm)	Ave. (mm)	Std.	Max. *w* (mm)	Min. *w* (mm)	Ave. (mm)	Std.	Seed index
E. acanthodes (1/10)	3	2.78	2.88	0.08	2.03	1.7	1.87	0.1	1.2	1.05	1.12	–	1.3	1.1	1.2	–	1.54
E. altissima ssp. *altissima* (1/5)	2.9	2.7	2.78	0.05	2.45	2.36	2.39	0.04	0.58	0.5	0.52	0.04	1.17	0.8	1.03	0.2	1.15
E. amygdaloides (6/57)	3.2	2.34	2.7	0.2	2.55	1.96	2.13	0.16	0.7	0.35	0.51	0.07	0.88	0.39	0.6	0.11	1.26
E. aucheri (10/91)	3.2	2.25	2.66	0.19	2.03	1.21	1.57	0.18	1	0.53	0.77	0.09	1.14	0.66	0.9	0.09	1.69
E. buhsei (11/93)	3.74	2.64	3.06	0.23	2.78	1.93	2.36	0.16	1.42	0.5	0.92	0.19	1.95	0.84	1.5	0.95	1.29
E. bungei (10/99)	4.5	2.98	3.76	0.38	3.8	2.3	2.93	0.33	1.5	0.65	1.05	0.19	2	0.7	1.43	0.32	1.28
E. caeladenia (7/71)	3.4	2.65	2.96	0.13	2.5	1.8	2.1	0.15	1.87	1.25	1.50	0.15	1.54	0.9	1.21	0.16	1.41
E. cheiradenia (10/97)	3.9	2.75	3.27	0.27	2.5	1.68	2.13	0.18	1.19	0.7	0.91	0.1	1.23	0.78	0.98	0.1	1.53
E. condylocarpa (3/28)	3.95	3.3	3.54	0.16	3.3	2.14	2.66	0.31	1.25	0.5	0.8	0.19	2.08	0.62	1.09	0.35	1.33
E. connata (6/54)	4.2	3.3	3.72	0.21	3.9	2.55	3.06	0.26	4.2	2.56	3.44	0.46	3.5	2	2.82	0.27	1.21
E. craspedia (1/10)	5.6	5.13	5.41	0.18	4	3.44	3.77	0.18	1.7	1.4	1.51	0.11	2.05	1.4	1.78	0.19	1.43
E. deltobracteata (2/9)	2	1.8	1.95	0.05	1.3	1.05	0.95	0.08	0.65	0.48	0.52	0.04	0.7	0.66	0.6	0.04	1.89
E. denticulata (6/60)	5.47	4.5	4.98	0.27	3.85	2.9	3.36	0.22	2.38	1.25	1.55	0.21	2.44	1.45	1.93	0.23	1.48
E. erubescens (5/51)	5	3.93	4.42	0.22	3.9	2.9	3.45	0.2	1.39	0.7	1.01	0.13	2.14	1.19	1.68	0.22	1.28
E. erythradenia (2/21)	3	2.5	2.83	0.17	2.14	1.59	1.9	0.13	1.1	0.61	0.89	0.11	1.1	0.79	0.94	0.06	1.49
E. ferdowsiana (2/8)	4	3.93	3.97	0.02	3.66	2.96	3.33	0.29	1.14	1	1.08	0.04	1.53	1.47	1.5	0.02	1.44
E. gedrosiaca (6/53)	3.3	2.5	2.88	0.21	2.2	1.45	1.94	0.16	2.05	1.1	1.53	0.22	1.4	0.75	1.11	0.16	1.48
E. glareosa (3/15)	2.3	1.8	2.03	0.18	1.25	0.9	1.09	0.11	1.1	0.89	0.99	0.05	1	0.87	0.95	0.05	1.86
E. grisophylla (1/15)	3.9	3.6	3.73	0.1	3.4	3	3.18	0.11	0.79	0.58	0.66	0.05	1.3	1	1.13	0.1	1.17
E. gypsicola (2/16)	3.1	2.65	2.85	0.11	2.3	1.8	2.08	0.17	1.4	1	1.21	0.11	1.15	0.64	0.94	0.14	1.37
E. hebecarpa (9/90)	3.71	2.69	3.12	0.27	2.89	1.8	2.32	0.24	0.97	0.48	0.64	0.11	1.3	0.5	0.89	0.2	1.34
E. heteradena (12/121)	4.66	3.04	3.87	0.3	3.84	2.43	3.05	0.28	2.67	1.47	1.88	0.28	2.71	1.18	1.95	0.36	1.26
E. iberica (3/32)	2.7	1.78	2.27	0.22	2.2	1.8	2	0.11	0.7	0.44	0.56	0.07	1.42	0.9	1.06	0.11	1.13
E. iranshahri (7/59)	3.4	2.5	2.92	0.25	2.11	1.5	1.82	0.11	1.05	0.64	0.78	0.12	1.3	0.61	1.02	0.16	1.6
E. kopetdaghi (8/84)	3.49	2.48	2.91	0.27	2.34	1.69	2.01	0.16	0.99	0.5	0.68	0.1	1	0.57	0.74	0.1	1.23
E. larica (7/51)	4.3	2.89	3.6	0.37	3.46	2.34	2.91	0.24	1.21	0.55	0.76	0.15	1.9	0.78	1.19	0.26	1.1
E. macrocarpa (8/76)	5.1	3.7	4.48	0.29	4.88	3.6	4.07	0.26	0.44	0.18	0.3	0.05	0.7	0.28	0.43	0.08	1.23
E. macroceras (2/22)	3.11	2.68	2.91	0.12	2.6	2.11	2.36	0.12	0.7	0.35	0.53	0.11	1	0.49	0.76	0.17	1.34
E. macroclada (6/59)	4.4	2.65	3.41	0.34	3.32	2	2.53	0.19	1.37	0.8	1.04	0.12	1.8	0.98	1.42	0.17	1.57
E. malleata (6/58)	3.49	2.8	3.11	0.17	2.17	1.7	1.97	0.11	1.06	0.68	0.89	0.09	1.25	0.8	1	0.11	1.48
E. marschalliana (10/104)	3.7	2.98	3.27	0.15	2.7	1.83	2.21	0.17	2.55	1.34	1.87	0.28	2.35	1.32	1.77	0.21	1.1
E. mazandaranica (3/35)	2.55	2.03	2.34	0.14	2.34	1.9	2.14	0.12	0.4	0.3	0.35	0.03	0.57	0.33	0.43	0.07	1.55
E. microsciadia (10/106)	3.6	2.52	3.04	0.21	2.31	1.67	1.96	0.14	1.17	0.69	0.91	0.09	1.12	0.65	0.91	0.1	1.63
E. monostyla (3/34)	3.71	3.11	3.34	0.15	2.28	1.76	2.04	0.11	0.95	0.57	0.8	0.1	1.14	0.7	0.89	0.1	1.52
E. myrsinites (5/54)	4.2	3.1	3.59	0.22	2.65	2	2.35	0.2	1.5	1	1.23	0.13	1.9	1.2	1.58	0.24	1.17
E. orientalis (4/36)	3.2	2.7	2.95	0.12	2.71	2.2	2.51	0.13	0.86	0.4	0.64	0.09	1.4	0.88	1.1	0.13	1.18
E. osyridea (10/91)	3.66	2.55	3.07	0.25	3	2	2.59	0.24	0.9	0.25	0.55	0.12	1.5	0.6	1.11	0.2	1.58
E. plebeia (1/9)	3.1	2.86	2.96	0.08	2	1.76	1.87	0.09	0.95	0.61	0.86	0.11	1	0.7	0.85	0.13	1.55
E. polycaulis (12/117)	3.3	2.49	2.86	0.17	2.2	1.5	1.84	0.14	1.06	0.63	0.84	0.11	1.25	0.67	0.97	0.13	1.39
E. sahendii (1/12)	3.2	2.7	3	0.15	2.3	2.04	2.15	0.09	0.9	0.75	0.81	0.05	1	0.79	0.9	0.07	1.35
E. seguieriana (11/106)	2.5	1.67	2.07	0.19	1.78	1.26	1.53	0.11	0.8	0.43	0.6	0.16	1.14	0.5	0.81	0.14	1.39
E. spartiformis (2/20)	2.69	2.1	2.46	0.18	1.98	1.39	1.77	0.16	1.29	0.81	1.01	0.15	1.2	0.7	0.97	0.12	1.66
E. spinidens (7/75)	4.02	2.78	3.43	0.26	2.41	1.64	2.06	0.17	1	0.55	0.77	0.11	1.1	0.54	0.83	0.12	1.22
E. squamosa (3/30)	3.5	2.6	3.02	0.22	2.75	2.16	2.46	0.13	0.48	0.28	0.39	0.05	0.85	0.39	0.57	0.11	1.41
E. sulphurea (2/7)	2.8	2.5	2.65	0.05	1.8	1.6	1.7	0.1	0.75	0.4	0.55	0.12	0.7	0.4	0.5	0.1	1.22
E. teheranica (7/70)	3.3	2.23	2.85	0.24	2.5	1.5	2.02	0.22	1.65	0.9	1.29	0.21	1.4	0.57	1.08	0.22	1.28
E. virgata (10/103)	2.8	2.06	2.48	0.16	2.33	1.7	2.02	0.14	0.7	0.28	0.5	0.09	1.21	0.36	0.84	0.17	1.52

Numbers after the species names indicate the number of populations and number of measured seeds, separated by a slash.

pseudo-hexahedral, ovoid-quadrangular, ellipsoidal, ovoid-ellipsoidal, ovoid-subsquare); (3) seed surface (smooth, irregularly pitted, tuberculate-rugulose, shallowly pitted and wrinkled, longitudinally grooved with or without pits, longitudinally sulcate and rugulose-tuberculate, foveolate-reticulate); (4) capsule shape (conical, subglobose, oblong-conical, ovoid-conical, woody globose (i.e. strongly lignified and indurated) and hexahedral, rounded-oblong); (5) capsule surface (smooth, vesiculate, tuberculate or verrucose, granulate at least on keel, papillose); and (6) shape of caruncle (conical, reniform, patelliform, petasiform, longitudinally sulcate, absent).

RESULTS

Seeds and fruits in Iranian perennial euphorbia species

A list of the studied species, with their infrageneric and section placement, habitat, growing season, flowering and fruiting time, distribution and chorotype, is presented in Table 1. The qualitative and quantitative morphological characters of 47 taxa based on the examination of 264 herbarium specimens listed in Appendix 1 are presented in Tables 2–5. Scanning electron micrographs of all studied species are provided in Figures 1–42. Stereomicroscope images of seeds and capsules (colour in online version only) are displayed in Figures 43–133. Identification keys based on macro- and micromorphological features of seeds and capsules have been prepared for both sections and species.

General description

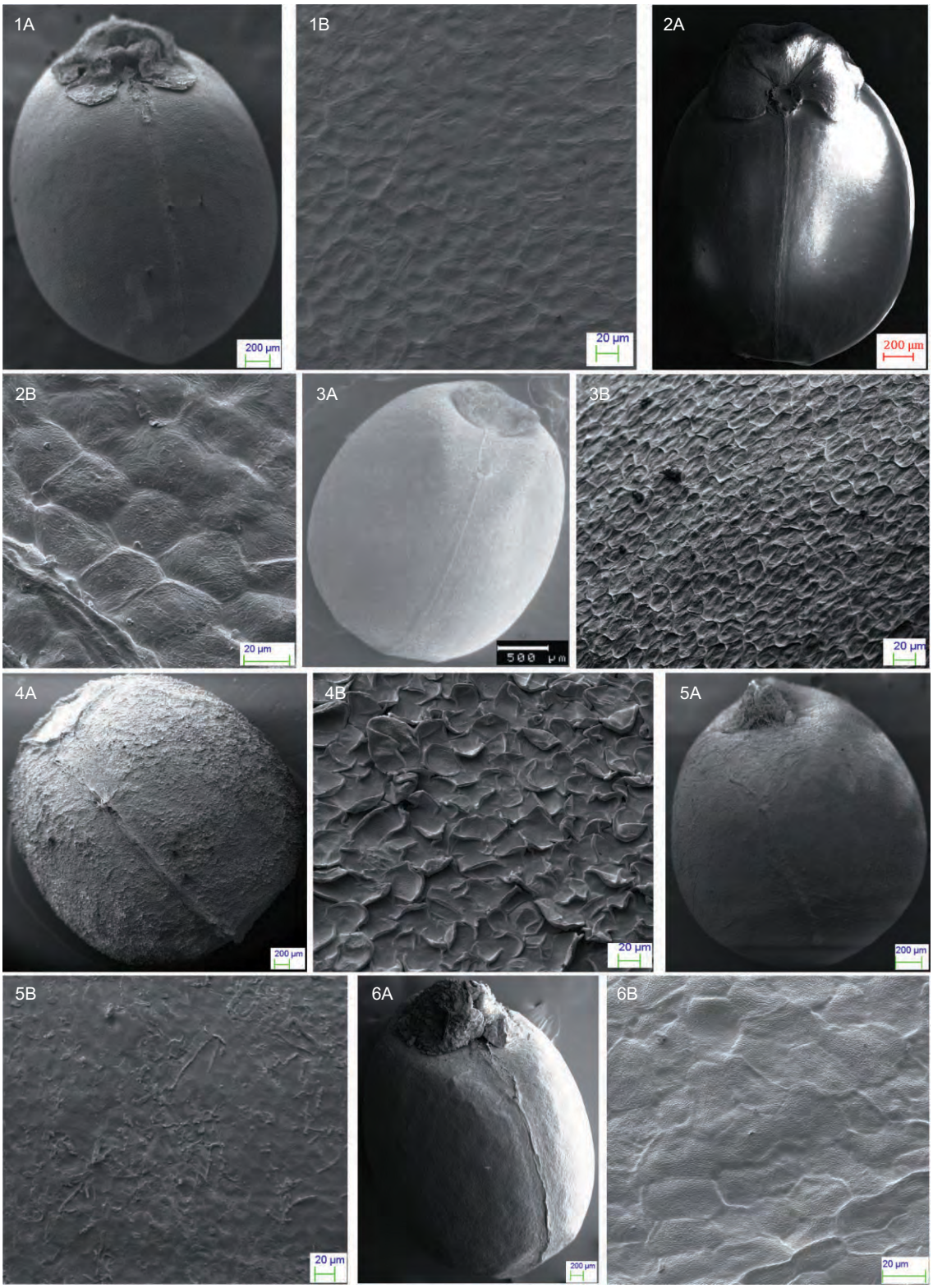
According to the morphometric measurements, the two longest capsules (*c*. 9.9–10 mm long) occurred in *E. craspedia* and *E. denticulata* Lam. (section *Myrsiniteae*; Table 3, Fig. 128). The two shortest capsules (*c*. 2.9 and 3 mm long) were observed in *E. mazandaranica* Pahlevani and *E. seguieriana* Neck., respectively (Table 3, Figs 93, 124). The widest capsule (*c*. 9 mm wide) was seen in *E. macrocarpa* Boiss. & Buhse (Table 3, Fig. 92), followed by *E. craspedia* and *E. denticulata* (*c*. 8 and 8.6 mm wide, respectively) (Table 3, Fig. 128). The narrowest capsule (*c*. 3 mm wide) was observed in *E. glareosa* (Table 3, Fig 114), followed by *E. erythradenia* Boiss., *E. seguieriana*, *E. spartiformis* Mobayen and *E. sulphurea* sp. nov. with capsules about 3.3 mm wide (Table 3, Figs 112, 124–126). The longest and shortest pedicels (*c*. 5.2 and 1 mm long) were seen in *E. osyridea* and *E. sulphurea* sp. nov., respectively (Table 3, Figs 109, 126). The longest styles (*c*. 3 and 2.5 mm long) were seen in *E. craspedia*, *E. denticulata* and *E. myrsinites* (section *Myrsiniteae*; Table 3, Figs 128, 131) and the shortest ones (*c*. 0.65 mm long) were observed in *E. bungei* Boiss., *E. caeladenia* Boiss. and *E. ferdowsiana* sp. nov. (section *Sclerocyathium*; Table 3, Figs 96–98).

The shortest seeds of Iranian perennial *Euphorbia* (*c*. 1.9 and 2 mm long) are those of *E. deltobracteata* (section *Herpetorrhizae* subsection *Aucheriae* Geltman & Pahlevani; Table 5, Figs 21A, B, 64) and *E. seguieriana* (section *Pithyusa*; Table 5, Figs 33A, B, 79), respectively, and the longest ones (*c*. 5.4 and 5 mm long) are those of *E. craspedia* and *E. denticulata* (section *Myrsiniteae*; Figs 37A, 38A, 83, 84), respectively. The narrowest seed (*c*. 1.2 mm wide) was observed in *E. deltobracteata* (Table 5, Figs 21A, 64), followed by *E. seguieriana* and *E. aucheri* Boiss. with seeds *c*. 1.5 mm wide (Table 5, Figs 33A, 79 and 20A, 63, respectively). The two widest seeds were observed in *E. macrocarpa* (*c*. 4 mm wide) and *E. craspedia* (*c*. 3.8 mm wide) (Table 5, Figs 4A, 46 and 37A, 83, respectively). The longest caruncle (*c*. 3.45 mm long) was observed in *E. connata* (Table 5, Figs 12A, 53), followed by *E. heteradena* Jaub. & Spach and *E. marschalliana* (*c*. 1.9 mm) (Table 5, Figs 11A, 54 and 39A, 85, respectively). The two shortest and narrowest caruncles (*c*. 0.30 and 0.35 mm long, *c*. 0.4 mm wide) were seen in *E. macrocarpa* and *E. mazandaranica*, respectively (section *Helioscopia*; Table 5, Figs 4A, 46 and 5A, 47, respectively). The widest caruncle (*c*. 2.8 mm) was also observed in *E. connata* (Table 5, Figs 12A, 53), followed by *E. heteradena* and *E. denticulata* (Table 5, Figs 11A, 54 and 38A, 84, respectively).

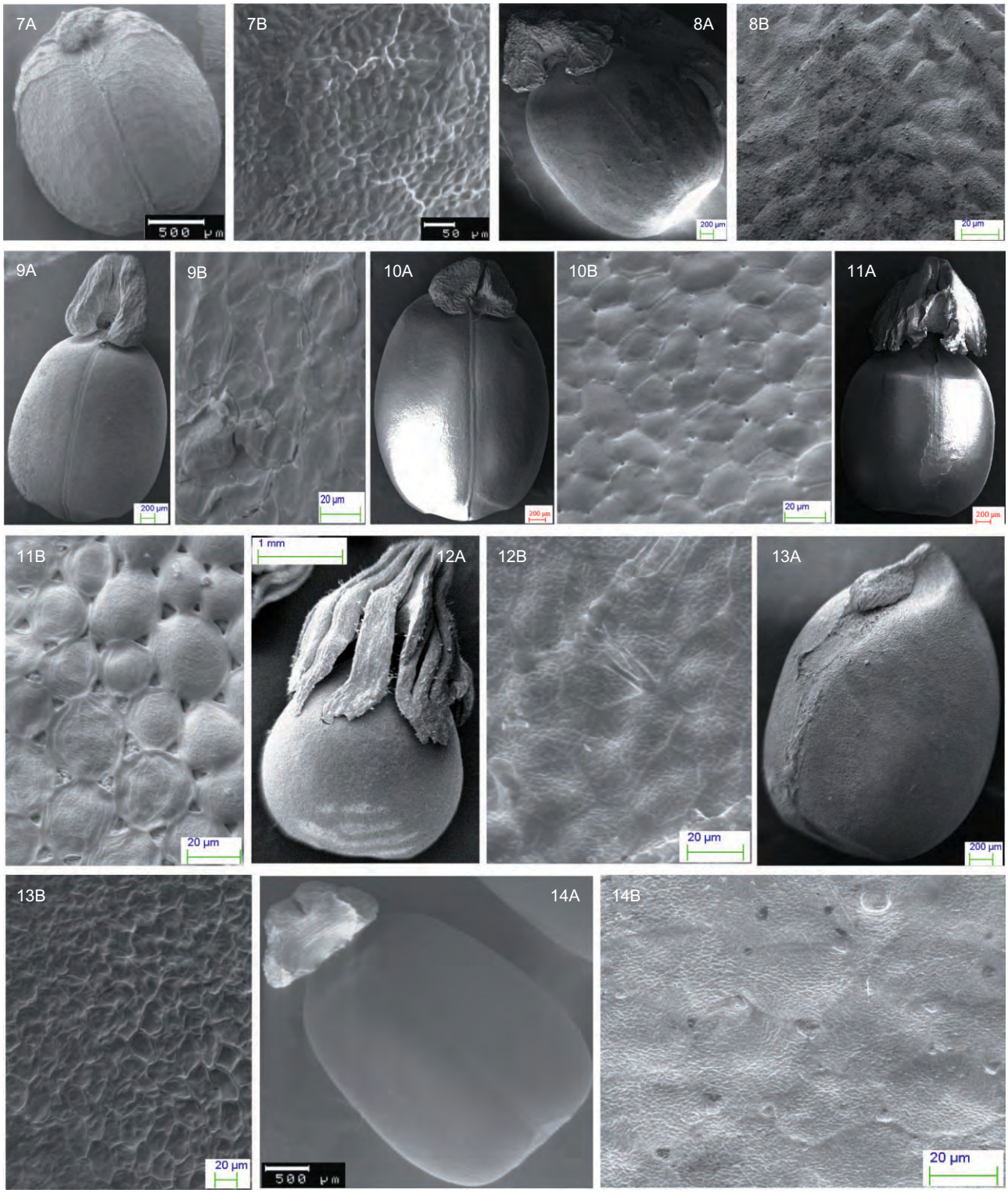
Molecular phylogenetic study

The BI and ML analyses retrieved essentially the same clades and both retrieved the species of Iranian *Euphorbia* subgenus *Esula* as a well-supported clade (Fig. 134). Section *Lagascae* is sister to all other clades, followed by section *Helioscopia*. The remaining 11 sections fall into two major clades, the first comprising sections *Myrsiniteae* and *Pithyusa*, and the second consisting of a grade beginning with sections *Sclerocyathium*, *Calyptratae* and *Chylogala*, followed by the *Szovitsiae–Esula* clade (Fig. 134).

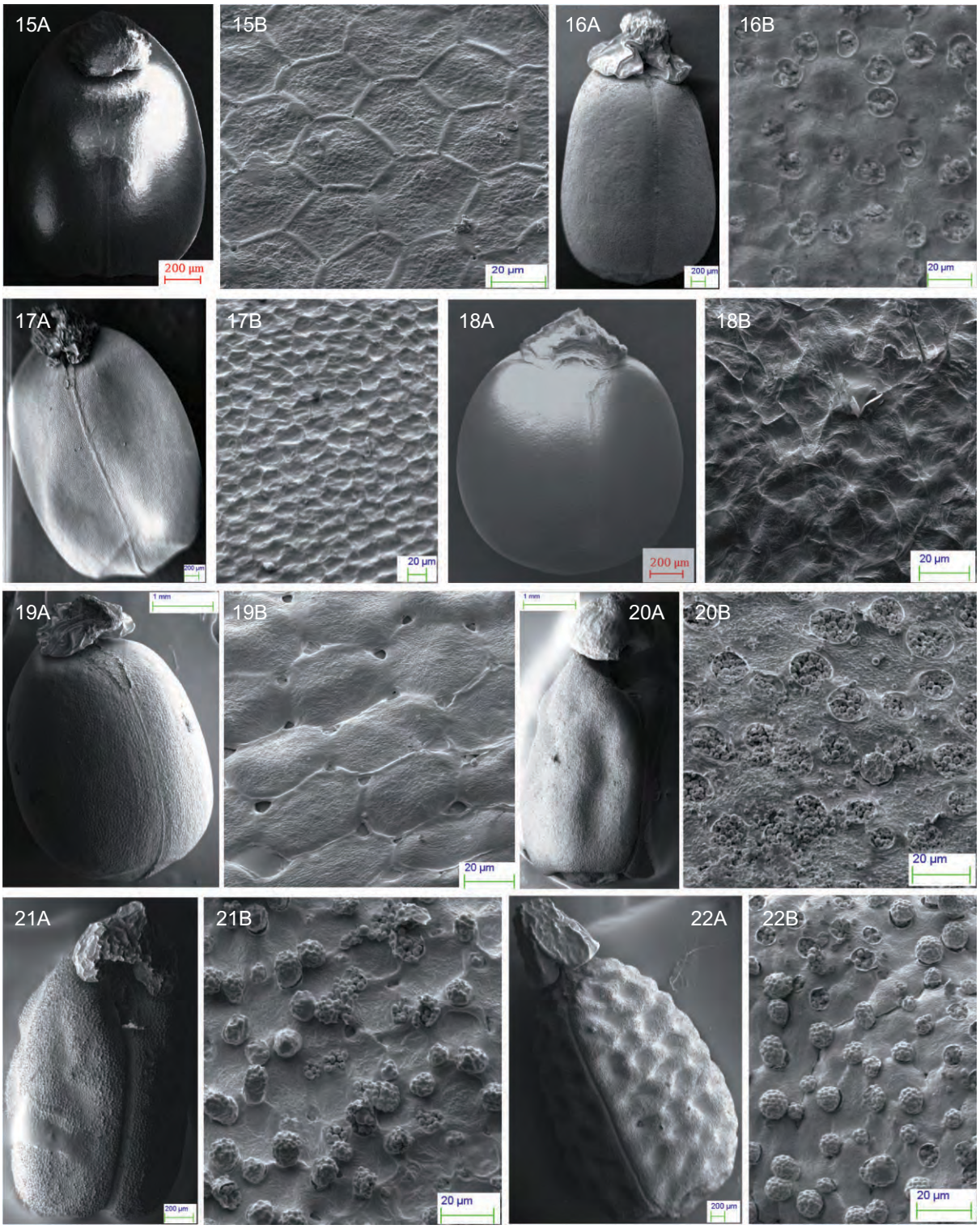
In addition to the Iranian species analysed in Riina *et al*. (2013), we analysed eight more species from Iran. *Euphorbia eriophora* section *Helioscopia* had been sequenced only for ITS in the previous study (Riina *et al*., 2013), whereas we generated ITS and *ndhF* markers, confirming its position. Our tree topology and position of all taxa were almost identical with those of Riina *et al*. (2013). *Euphorbia grisophylla*, an endemic species in eastern Turkey and western Iran, was retrieved in section *Helioscopia*. *Euphorbia glareosa*, a new record for Iran, was sister to an accession of this species from Austria, and both were sister to *E. seguieriana* in section *Pithyusa*.



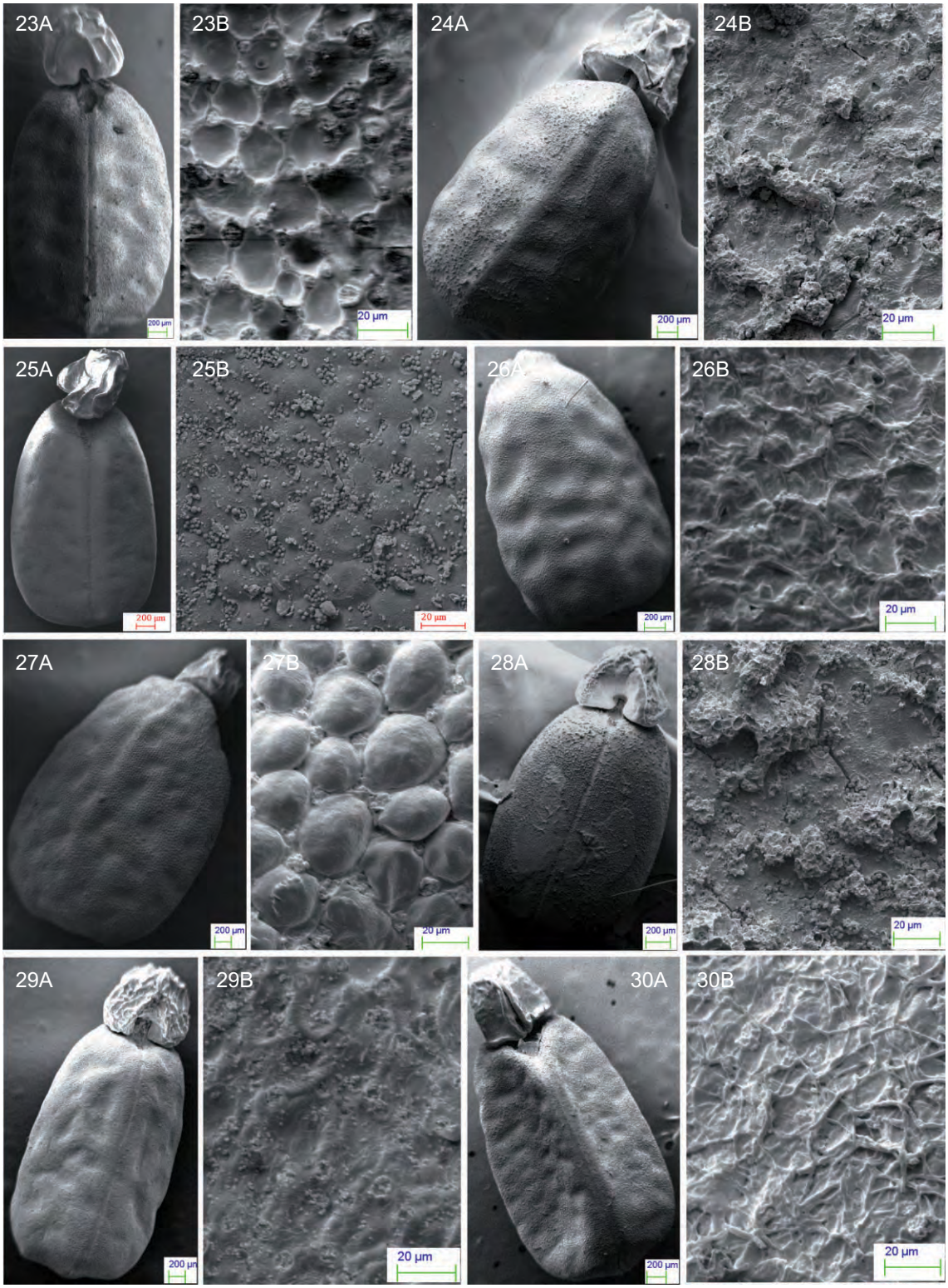
Figures 1–6. Scanning electron micrographs of seeds of six Iranian perennial *Euphorbia* section *Helioscopia*. Scale bar values in µm (unless otherwise indicated) are given in parentheses after the species name. Fig. 1. *E. altissima* ssp. *altissima* (A, 200; B, 20). Fig. 2. *E. condylocarpa* (A, 200; B, 20). Fig. 3. *E. grisophylla* (A, 500; B, 20). Fig. 4. *E. macrocarpa* (A, 200; B, 20). Fig. 5. *E. mazandaranica* (A, 200; B, 20). Fig. 6. *E. orientalis* (A, 200; B, 20).



Figures 7–14. Scanning electron micrographs of seeds of eight Iranian perennial *Euphorbia* (Fig. 7, section *Helioscopia*; Figs 8–10, section *Sclerocyathium*; Fig. 11, section *Chylogala*; Fig. 12, section *Calyptratae*; Figs 13, 14, section *Patellares*). Scale bar values in µm (unless otherwise indicated) are given in parentheses after the species name. Fig. 7. *E. squamosa* (A, 500; B, 50). Fig. 8. *E. bungei* (A, 200; B, 20). Fig. 9. *E. caeladenia* (A, 200; B, 20). Fig. 10. ***E. ferdowsiana*** (A, 200; B, 20). Fig. 11. *E. heteradena* (A, 200; B, 20). Fig. 12. *E. connata* (A, 1 mm; B, 20). Fig. 13. *E. amygdaloides* (A, 200; B, 20). Fig. 14. *E. erubescens* (A, 500; B, 20).



Figures 15–22. Scanning electron micrographs of seeds of eight Iranian perennial *Euphorbia* (Fig. 15, section *Patellares*; Figs 16–19, section *Esula*; Figs 20, 21, section *Herpetorrhizae*; Fig. 22, section *Pithyusa*). Scale bar values in µm (unless otherwise indicated) are given in parentheses after the species name. Fig. 15. *E. macroceras* (A, 200; B, 20). Fig. 16. *E. buhsei* (A, 200; B, 20). Fig. 17. *E. hebecarpa* (A, 200; B, 20). Fig. 18. *E. iberica* (A, 200; B, 20). Fig. 19. *E. virgata* (A, 1 mm; B, 20). Fig. 20. *E. aucheri* (A, 1 mm; B, 20). Fig. 21. *E. deltobracteata* (A, 200; B, 20). Fig. 22. *E. cheiradenia* (A, 200; B, 20).



Figures 23–30. Scanning electron micrographs of seeds of eight Iranian perennial *Euphorbia* section *Pithyusa*. Scale bar values in µm (unless otherwise indicated) are given in parentheses after the species name. Fig. 23. *E. erythradenia* (A, 200; B, 20). Fig. 24. *E. gedrosiaca* (A, 200; B, 20). Fig. 25. *E. glareosa* (A, 200; B, 20). Fig. 26. *E. gypsicola* (A, 200; B, 20). Fig. 27. *E. kopetdaghi* (A, 200; B, 20). Fig. 28. *E. macroclada* (A, 200; B, 20). Fig. 29. *E. malleata* (A, 200; B, 20). Fig. 30. *E. plebeia* (A, 200; B, 20).

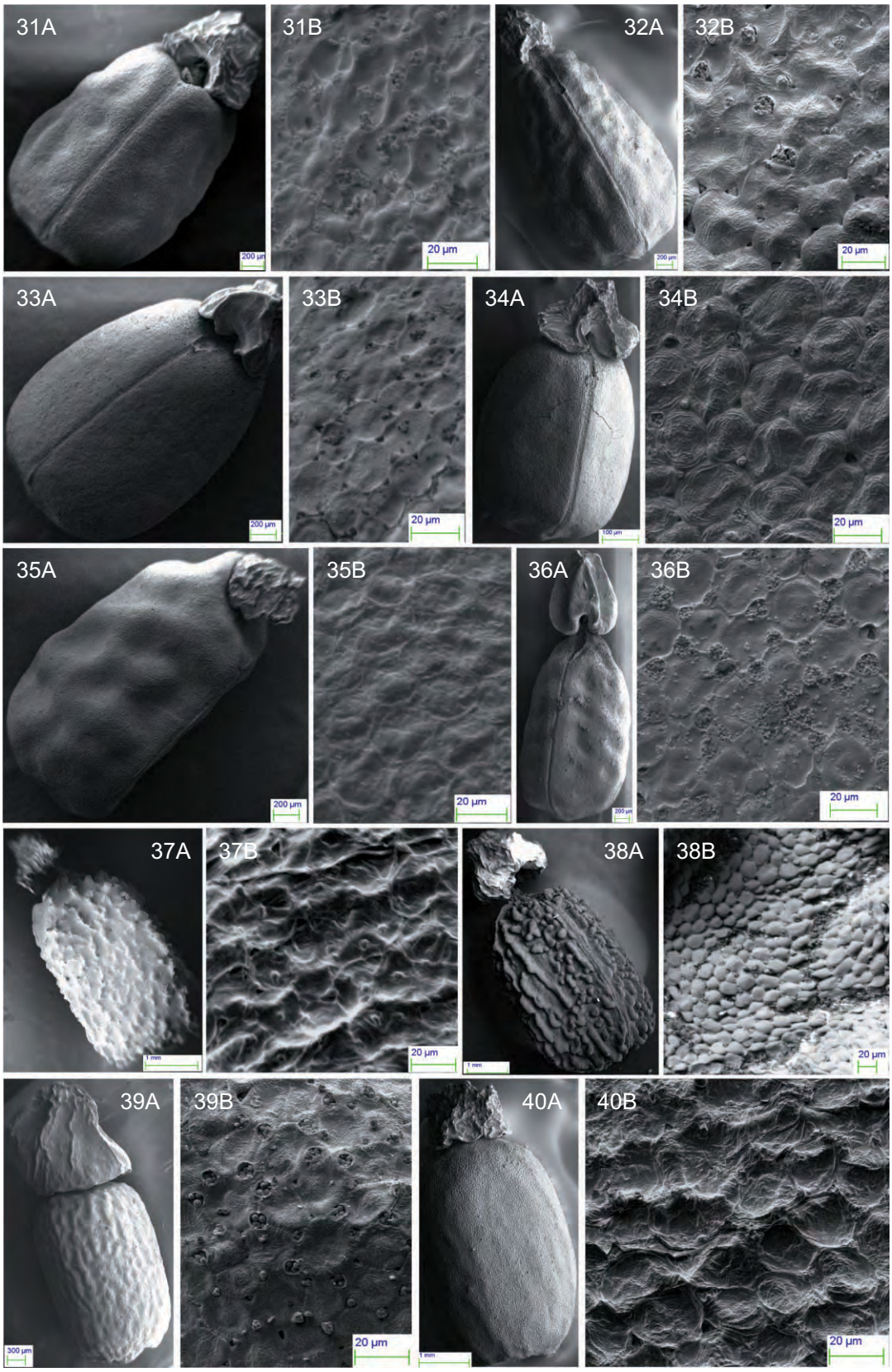
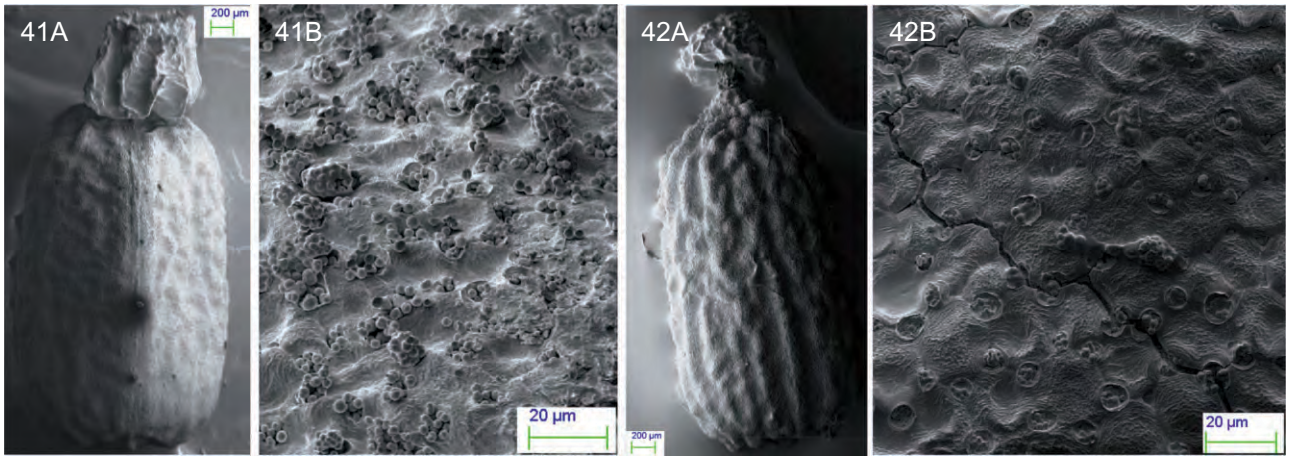


Figure 31–40. See caption on next page.

Figures 31–40. Scanning electron micrographs of seeds of ten Iranian perennial *Euphorbia* (Figs 31–36, section *Pithyusa*; Figs 37–40, section *Myrsiniteae*). Scale bar values in μm (unless otherwise indicated) are given in parentheses after the species name. Fig. 31. *E. polycaulis* (A, 200; B, 20). Fig. 32. *E. sahendii* (A, 200; B, 20). Fig. 33. *E. seguieriana* (A, 200; B, 20). Fig. 34. *E. spartiformis* (A, 100; B, 20). Fig. 35. ***E. sulphurea*** (A, 200; B, 20). Fig. 36. *E. teheranica* (A, 200; B, 20). Fig. 37. *E. craspedia* (A, 1 mm; B, 20). Fig. 38. *E. denticulata* (A, 1 mm; B, 20). Fig. 39. *E. marschalliana* (A, 300; B, 20). Fig. 40. *E. monostyla* (A, 1 mm; B, 20).



Figures 41–42. Scanning electron micrographs of seeds of two Iranian perennial *Euphorbia* section *Myrsiniteae*. Scale bar values in μm (unless otherwise indicated) are given in parentheses after the species name. Fig. 41. *E. myrsinites* (A, 200; B, 20). Fig. 42. *E. spinidens* (A, 200; B, 20).

Euphorbia monostyla, a species from section *Myrsiniteae*, was unresolved with other species of the section in a sister group position to *E. aleppica*. The molecular phylogenetic analysis confirmed the placement of *E. chamaepeplus* in section *Tithymalus* according to morphological characters, as sister to *E. peplus* and *E. peploides* Gouan. *Euphorbia aulacosperma*, recently reported as a new record for Iran (Pahlevani & Akhani, 2011), was retrieved in section *Arvales*. *Euphorbia sulphurea* sp. nov. and *E. ferdowsiana* sp. nov. were retrieved in sections *Pithyusa* and *Sclerocyathium*, respectively (Fig. 134).

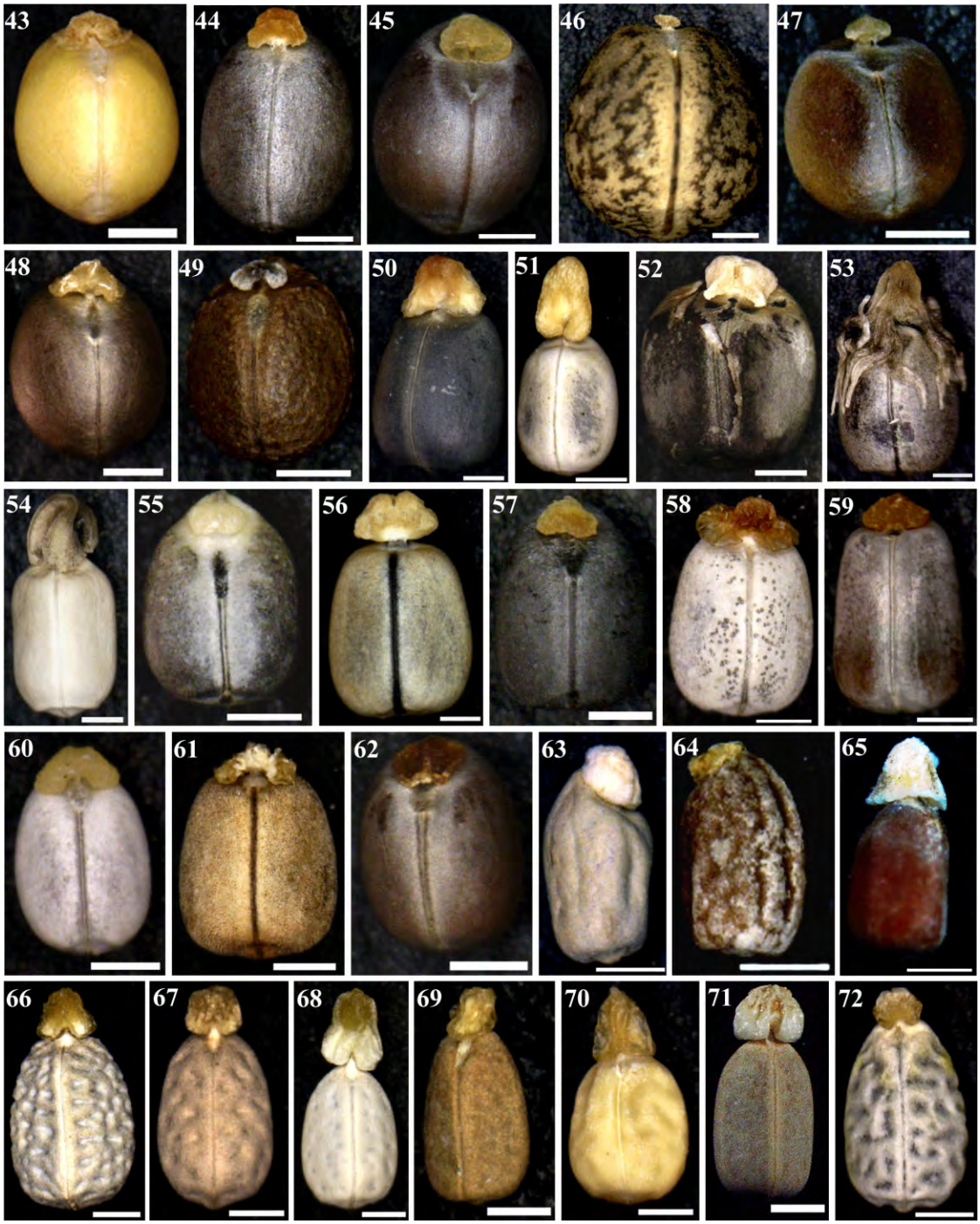
ENUMERATION OF NEW SPECIES AND NEW RECORD

During the course of our phylogenetic and morphological studies in subgenus *Esula*, two new rare and endemic species, *Euphorbia sulphurea* Pahlevani and *E. ferdowsiana* Pahlevani, were discovered. A new record for *E. glareosa* in Iran was reported. Our studies revealed that the report of *E. sogdiana* Pop. from Iran (Pahlevani *et al.*, 2011b) represents a misidentification of *E. kopetdaghi* (Prokh.) Prokh. In addition, *E. gaubae* (Soják) Radcl.-Sm. (*E. halophila* Bornm. & Gauba) falls within the range of variation of *E. buhsei* and is therefore formally placed in synonymy of this species.

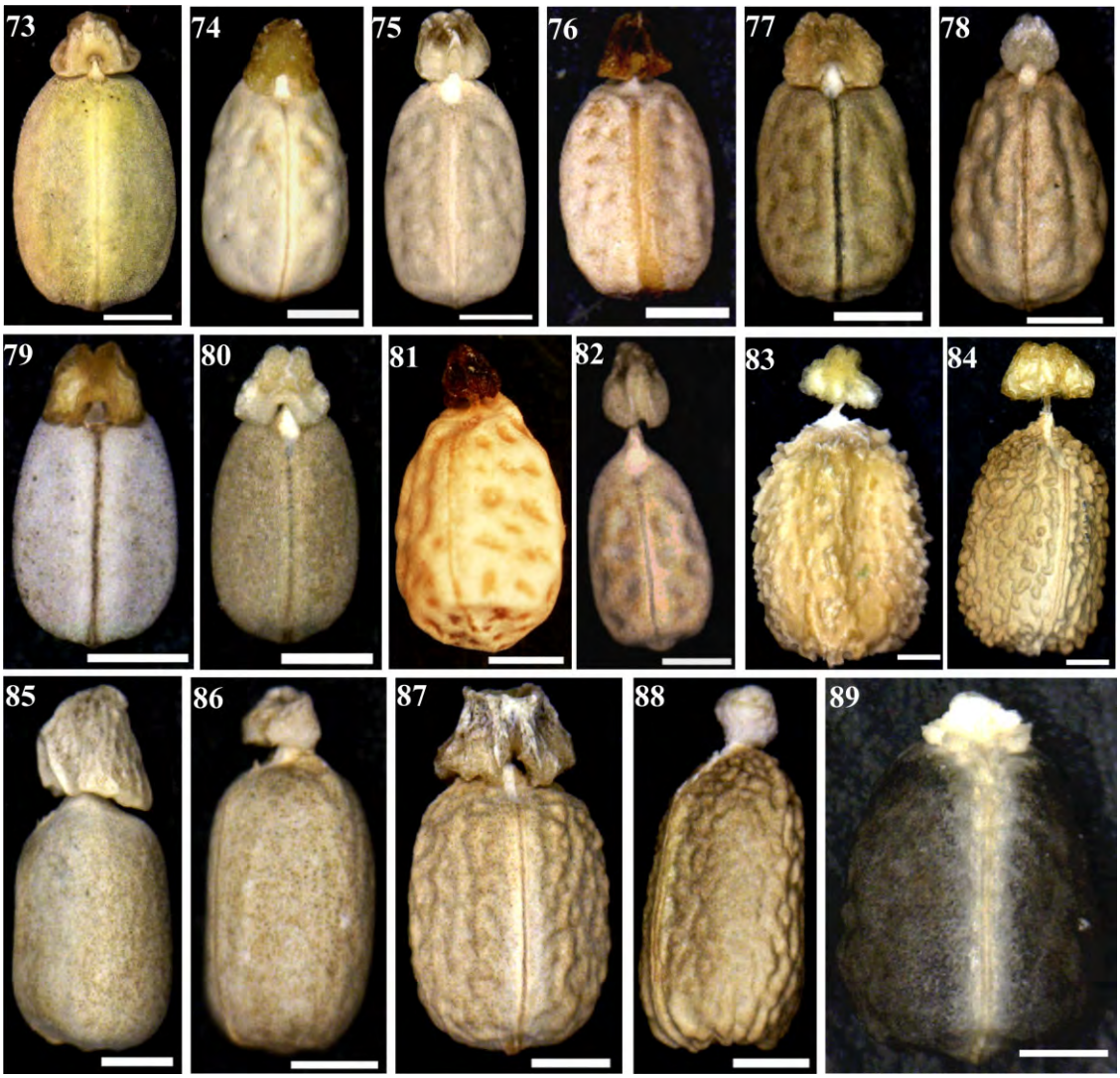
Euphorbia sulphurea *Pahlevani* ***sp. nov.***
(Figs 35A, B, 81, seeds; Fig. 126, capsule)
Type: IRAN. Sistan & Baluchestan: Zahedan to Khash, Tamendan, Taftan Mt., 3700–3900 m, 23.v.2009, *Pahlevani & Bahramishad 55151* (Holotype: IRAN; Isotype: W).

Diagnosis: Most closely related to *E. spartiformis*, but differing by non-spiny branches, non-cushion-form habit, absence of woody stems and lamellate bark, ray and ray leaves two or three (four) (terminal rays not falsely dichotomous), glands denticulate instead of bicornate and pitted ornaments on seed surface in contrast with smooth ones in *E. spartiformis*.

Description: Sparingly pilose to subglabrous perennial herbs, to 12 cm, much branched from base, ascending-procumbent, single stems not branched. Cauline leaves attenuate at the base, sessile to subsessile, ovate to suborbicular, 4–13 × 3–7 mm, obtuse to rarely subacute at apex, entire and usually purplish at margin. Inflorescence terminal rays, two or three; ray leaves ovate, 4.0–9.0 × 3.5–5.0 mm, apex obtuse or mucronulate, margin obscurely dentate and cartilaginous, truncate at the base; raylet leaves ovate-rhombic, apex mucronulate, margin cartilaginous, subentire to denticulate, truncate at the base.



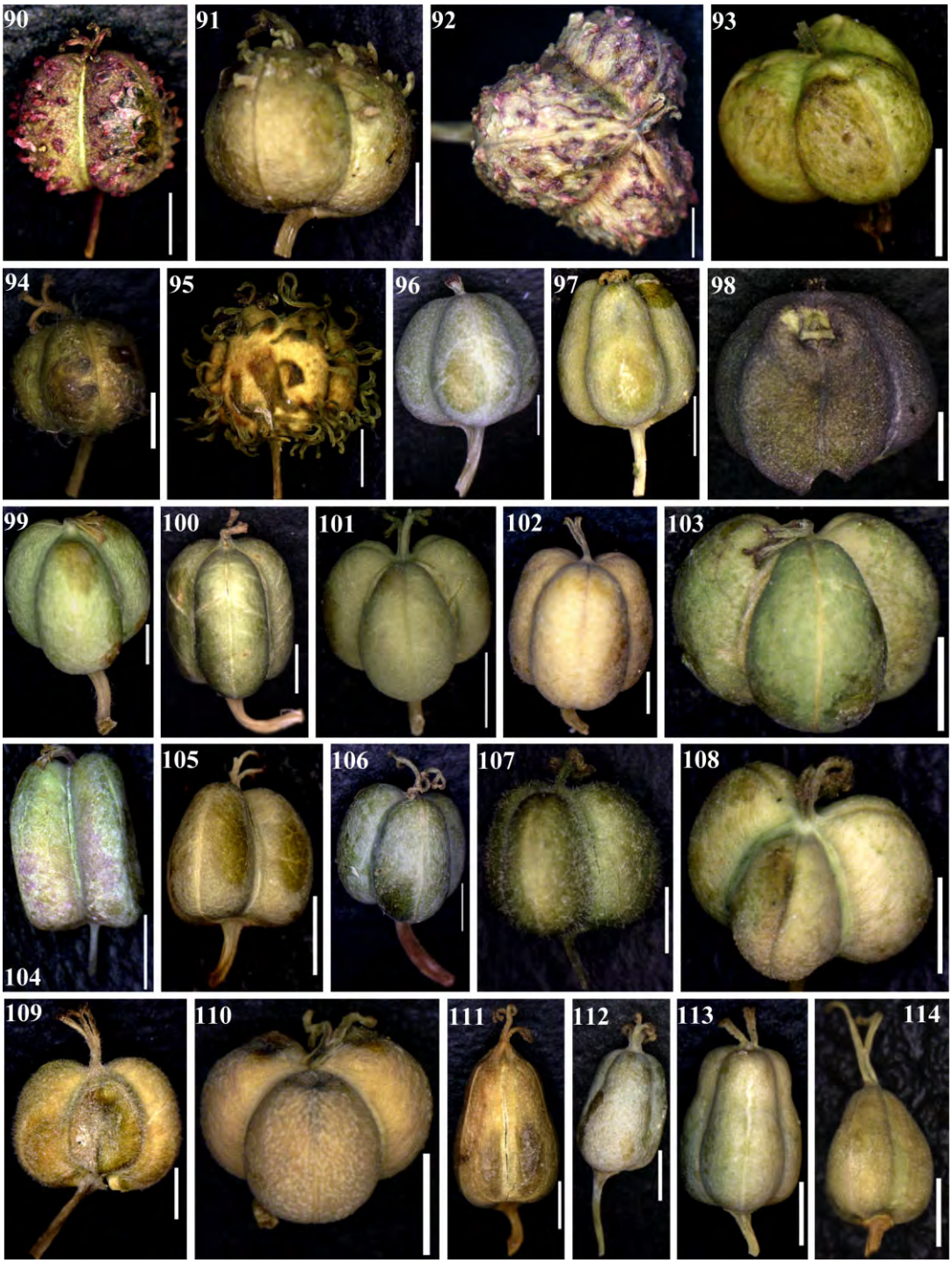
Figures 43–72. Stereomicroscopic micrographs of seeds of 30 Iranian perennial *Euphorbia* (Figs 43–49, section *Heliosco-pia*; Figs 50–52, section *Sclerocyathium*; Fig. 53, section *Calyptratae*; Fig. 54, section *Chylogala*; Figs 55–57, section *Patellares*; Figs 58–62, section *Esula*; Figs 63, 64, section *Herpetorrhizae*; Figs 65–72, section *Pithyusa*). Scale bar values equal 1 mm in all figures. Fig. 43. *E. altissima* ssp. *altissima*. Fig. 44. *E. condylocarpa*. Fig. 45. *E. grisophylla*. Fig. 46. *E. macrocarpa*. Fig. 47. *E. mazandaranica*. Fig. 48. *E. orientalis*. Fig. 49. *E. squamosa*. Fig. 50. *E. bungei*. Fig. 51. *E. caeladenia*. Fig. 52. ***E. ferdowsiana***. Fig. 53. *E. connata*. Fig. 54. *E. heteradena*. Fig. 55. *E. amygdaloides*. Fig. 56. *E. erubescens*. Fig. 57. *E. macroceras*. Fig. 58. *E. buhsei*. Fig. 59. *E. hebecarpa*. Fig. 60. *E. iberica*. Fig. 61. *E. osyridea*. Fig. 62. *E. virgata*. Fig. 63. *E. aucheri*. Fig. 64. *E. deltobracteata*. Fig. 65. *E. acanthodes*. Fig. 66. *E. cheiradenia*. Fig. 67. *E. erythradenia*. Fig. 68. *E. gedrosiaca*. Fig. 69. *E. glareosa*. Fig. 70. *E. gypsicola*. Fig. 71. *E. iranshahri*. Fig. 72. *E. kopetdaghi*.



Figures 73–89. Stereomicroscopic micrographs of seeds of 17 Iranian perennial *Euphorbia* (Figs 73–82, section *Pithyusa*; Figs 83–88, section *Myrsiniteae*; Fig. 89, subgenus *Athymalus*). Scale bar values equal 1 mm in all figures. Fig. 73. *E. macroclada*. Fig. 74. *E. malleata*. Fig. 75. *E. microsciadia*. Fig. 76. *E. plebeia*. Fig. 77. *E. polycaulis*. Fig. 78. *E. sahendii*. Fig. 79. *E. seguieriana*. Fig. 80. *E. spartiformis*. Fig. 81. ***E. sulphurea***. Fig. 82. *E. teheranica*. Fig. 83. *E. craspedia*. Fig. 84. *E. denticulata*. Fig. 85. *E. marschalliana*. Fig. 86. *E. monostyla*. Fig. 87. *E. myrsinites*. Fig. 88. *E. spinidens*. Fig. 89. *E. larica*.

Cyathial lobes oblong-lanceolate, usually reddish; glands crescent, ochreous to brownish, denticulate to shortly bicornate or rarely hornless. Capsules conical, 3.1–3.5 × 2.7–3.0 mm, smooth, sparsely pilose to glabrous. Seeds ovoid, 2.5–2.8 × 1.6–1.8 mm, irregularly pitted, grey to brown; caruncle conical, 0.4–0.7 mm long, brown to ochreous.

Affinity and plant geography: Euphorbia sulphurea is a geographically isolated and morphologically distinct species known only from the type locality in the alpine zone of the Taftan massif, the isolated mountain system with the highest peak in south-eastern Iran. Our molecular phylogenetic tree (Fig. 134) clearly indicates its position in section *Pithyusa*, with *E. spartiformis* as its sister species (Pahlevani *et al*., 2011b). These species and *E. erythradenia*, *E. gedrosiaca* Rech.f., Aell. & Esfand. and *E. plebeia* form a distinct and supported clade in section *Pithyusa*. Their synapomorphy is the presence of only one to three (four) terminal rays. Only *E. sulphurea* and *E. gedrosiaca* have an eastern range up to Iranian Baluchestan; the other species are endemics of the montane zone of the south-eastern parts of the Zagros Mountains.



Figures 90–114. Stereomicroscopic micrographs of capsules of 25 Iranian perennial *Euphorbia* (Figs 90–95, section *Helioscopia*; Figs 96–98, section *Sclerocyathium*; Fig. 99, section *Calyptratae*; Fig. 100, section *Chylogala*; Figs 101–103, section *Patellares*; Figs 104, 105, section *Herpetorrhizae*; Figs 106–110, section *Esula*; Figs 111–114, section *Pithyusa*). Scale bar values equal 2 mm in all figures. Fig. 90. *E. condylocarpa*. Fig. 91. *E. grisophylla*. Fig. 92. *E. macrocarpa*. Fig. 93. *E. mazandaranica*. Fig. 94. *E. orientalis*. Fig. 95. *E. squamosa*. Fig. 96. *E. bungei*. Fig. 97. *E. caeladenia*. Fig. 98. ***E. ferdowsiana***. Fig. 99. *E. connata*. Fig. 100. *E. heteradena*. Fig. 101. *E. amygdaloides*. Fig. 102. *E. erubescens*. Fig. 103. *E. macroceras*. Fig. 104. *E. aucheri*. Fig. 105. *E. deltobracteata*. Fig. 106. *E. buhsei*. Fig. 107. *E. hebecarpa*. Fig. 108. *E. iberica*. Fig. 109. *E. osyridea*. Fig. 110. *E. virgata*. Fig. 111. *E. cheiradenia*. Fig. 112. *E. erythradenia*. Fig. 113. *E. gedrosiaca*. Fig. 114. *E. glareosa*.

Figures 115–133. Stereomicroscopic micrographs of capsules of 19 Iranian perennial *Euphorbia* (Figs 115–127, section *Pithyusa*; Figs 128–132, section *Myrsiniteae*; Fig. 133, subgenus *Athymalus*). Scale bar values equal 2 mm in all figures. Fig. 115. *E. gypsicola*. Fig. 116. *E. iranshahri*. Fig. 117. *E. kopetdaghi*. Fig. 118. *E. macroclada*. Fig. 119. *E. malleata*. Fig. 120. *E. microsciadia*. Fig. 121. *E. plebeia*. Fig. 122. *E. polycaulis*. Fig. 123. *E. sahendii*. Fig. 124. *E. seguieriana*. Fig. 125. *E. spartiformis*. Fig. 126. ***E. sulphurea***. Fig. 127. *E. teheranica*. Fig. 128. *E. denticulata*; Fig. 129. *E. marschalliana*. Fig. 130. *E. monostyla*. Fig. 131. *E. myrsinites*. Fig. 132. *E. spinidens*. Fig. 133. *E. larica*.

Ecology and conservation status: Euphorbia sulphurea was found in the alpine zone of the volcanic peak of Taftan at 3700–3900 m elevation on sulphur beds. Highly active sulphur-encrusted fumaroles occur at the summit of the cone. The earlier collection of this curious plant dates back to Alfons and Agnes Gabriel in 1937, who collected the plant between 2000 and 3000 m according to the label data. As the new collection with accurate elevation data indicates its restriction to the summit of the peak, it remains open to confirmation whether this species can also be found at lower elevations.

Euphorbia sulphurea is extremely rare and only a few specimens were found near the summit of the peak, despite an intensive search. The fragile habitat on the sulphur-emitting substrate and its rarity suggest the evaluation of this species as 'critically endangered' (CR) according to the International Union for Conservation of Nature (IUCN) threatened categories (IUCN, 2010).

Additional specimens examined: IRAN: Sistan & Baluchestan: Zahedan to Khash, Tamendan, Taftan Mt., 2700–3800 m, 29.v.1985, *Mozaffarian* (53068 TARI); Kuhe Garoh, in Taftan massive, 2000–3000 m, 8.vi.1937, *Alfons & Agnes Gabriel* (115 B).

Etymology: The epithet '*sulphurea*' refers to its habitat on the sulphur-encrusted fumaroles of the volcanic summit.

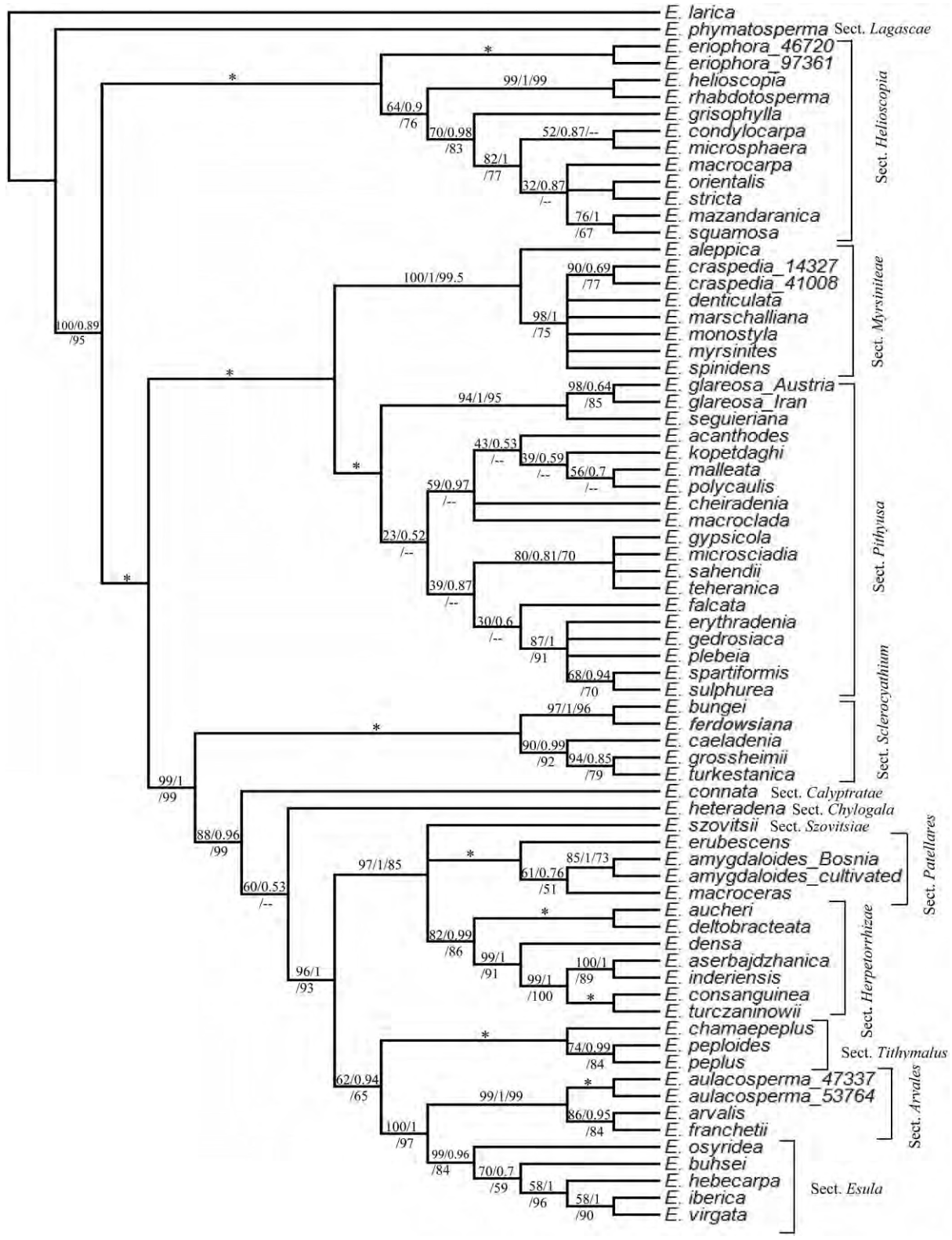


Figure 134. The cladogram from Bayesian analysis of the combined ITS + *ndhF* dataset of Iranian *Euphorbia* subgenus *Esula* with outgroup (*E. larica* subgenus *Athymalus*). Maximum likelihood bootstrap values, Bayesian posterior probabilities and maximum probability bootstrap percentages are indicated above the branches, respectively, separated by a slash mark (fully supported branches are indicated with an asterisk).

Euphorbia ferdowsiana *Pahlevani* ***sp. nov.***
(Figs 10A, B, 52, seeds; Fig. 98, capsule)
Type: IRAN: Khorasan: W of Mashhad, Golmakan, Cheshme sabz, Binaloud Mt., 2300 m, 3.viii.1992. *Ayatollahi & Zangooei 22585* (Holotype: IRAN; Isotypes: FUMH; Hb. Akhani).

Diagnosis: Euphorbia ferdowsiana is closely related to *E. bungei.* It differs from the latter by purplish (instead of green) stems and leaves, ovate to orbiculate and cordate and entire cauline leaves in contrast with ovate to deltoid or linear-oblong and denticulate ones, maroon (instead of green to yellow) cyathial glands, shorter styles (0.4–0.7 mm long instead of 0.65–1.20 mm long) and the caruncle furnished with two ligulate arms at the base in contrast with caruncle lacking arms in *E. bungei*.

Description: Perennial herbs, 12–20 cm high, ascending to procumbent, glabrous. Cauline leaves ovate to orbiculate, reddish to purplish, 1.5–3.3 × 1.5–2.8 cm, sessile, cordate at base, rounded to subacute at apex, entire or slightly undulate at margin. Terminal rays two (three), once or twice dichotomously branched, rarely with axillary rays. Ray leaves similar to cauline leaves in shape and size. Raylet leaves ovate to lanceolate, truncate at base, acute to subacute or obtuse at apex, entire at margin. Cyathial involucre campanulate, 3–4 mm in diameter with dentate bracts; glands elliptic and rounded, hornless, dark reddish to dark purplish. Capsules trilobate, 4.8–6.0 × 4.0–6.5 mm, glabrous, smooth, purplish. Seeds compressed-ovate, 3.0–3.5 × 3.0 mm, smooth, greyish-brown; caruncle conical with two ligulate arms at the base, 1 × 2 mm, yellowish.

Affinity and plant geography: The newly discovered species belongs to section *Sclerocyathium* and is sister to *E. bungei* (Fig. 134).

Species of section *Sclerocyathium* are Irano-Turanian elements with a core distribution in the eastern parts of Iran and Afghanistan up to central Asia and north-western China. *Euphorbia ferdowsiana* has been found only at the type locality in the high mountain zone of the Binaloud massif. Phytogeographically, this area belongs to the Khorasan-Kopetdagh province of the Irano-Turanian region (Memariani, Zarrinpour & Akhani, 2014).

Euphorbia ferdowsiana was misidentified and reported as *E. rosularis* Fed. by Nasseh & Joharchi (2004).

Ecology and conservation status: Euphorbia ferdowsiana was found only on the eastern slopes of the Binaloud Mountains at elevations between 2100 and 2700 m. It grows on scree soil of the rocky substrate. It has a conspicuous camouflage with the colour of the stones, probably to avoid herbivory. So far, it is known only from a limited area despite intensive floristic studies in the Binaloud Mountains (Memariani *et al*., 2014). Because of its rarity and restricted occurrence at the type location, it is suggested to evaluate its conservation status as 'critically endangered' (CR) according to IUCN threatened categories (IUCN, 2010).

Additional specimens examined: IRAN: Khorasan: Mashhad, end of Zoshk, Binaloud Mt., 2200 m, 9.xi.1991, *Joharchi & Zangooei* (21323 FUMH, IRAN); W of Mashhad, Kang, slopes of Binaloud, 2100 m, 25.vi.1996, *Faghihnia & Zangooei* (27607 FUMH, IRAN).

Etymology: Euphorbia ferdowsiana is named in honour of Hakim Abolghasem Ferdowsi Tusi, the greatest Iranian epic poet (AD 940–1020), author of the epic of Shahnameh, who lived in Khorasan province in which the species occurs.

Description of subgenera and sections in Iranian perennial Euphorbia

Based on carpology (capsule size, capsule shape and surface), pedicel and style size, and seed morphology (seed size, seed shape, surface ornamentation, presence or absence of a caruncle, and shape and size of the caruncle) (Tables 2–5), the following ten seed and capsule morphotypes are recognized, which are in agreement with the recent molecular phylogenetic study (Riina *et al*., 2013) and with our extended molecular data.

Subgenus *Esula*: the perennial species of Iranian members of this subgenus are divided into nine sections as follows.

1. Section *Helioscopia* is the largest section of the subgenus, with *c*. 135 species distributed mostly in the Northern Hemisphere of the Old World (Riina *et al*., 2013). There are 12 species of section *Helioscopia* in Iran, seven of which are perennial (Table 1), and the remaining species are annual (Pahlevani & Riina, 2014).
   Capsules subglobose, shallowly to deeply trilobate, 2.45–8.40 × 3–10 mm, usually green, tuberculate, verrucose or rarely smooth, glabrous or hairy (Figs 90–95), pedicel *c*. 0.7–5.2 mm long, style short to long (0.8–3.0 mm long). Seeds ellipsoidal, smooth, mostly shiny and dark brown, *c*. 2.0–5.1 × 1.9–4.9 mm, epidermal cells isodiametric to tetra-pentagonal, randomly distributed, without

elements on the surface; caruncle reniform (Figs 1A–7B, 43–49). The mostly warty and tuberculous capsules, ellipsoidal seeds and reniform caruncles are important traits separating section *Helioscopia* from the other groups.

2. Section *Sclerocyathium* is a rather small group with *c*. ten species distributed mostly in south-western Asia and central Asia; five species occur in Iran, including three perennials (Table 1) and two annuals (*E. grossheimii* and *E. turkestanica* Regel).
   Capsules conical, shallowly trilobate, 4.6–7.7 × 4.0–8.7 mm, glaucous, glabrous, smooth (Figs 96–98), pedicel 2.0–5.9 mm long, style short (0.65–1.20 mm long). Seeds ovoid, smooth, greyish, sometimes spotted, *c*. 2.65–4.50 × 1.80–3.80 mm, epidermal cells usually elongated tetragonal, without any elements on the surface, caruncle conical (Figs 8A–10B, 50–52). The short style is the most important feature in this group.
3. Section *Chylogala* is a small group consisting of *E. alaica* (Prokh.) Prokh., *E. retusa* Forssk., *E. serrata* L. and *E. heteradena*, occurring in the Mediterranean region, south-western and central Asia to northern Pamir-Alay; only the last species is represented in Iran (Geltman, 2013).
   Capsules rounded-oblong-trilobate, 5.8–9.5 × 5.0–8.4 mm, smooth, glabrous to glaucous to some extent, mostly greenish-yellow (Fig. 100), pedicel 1.85–7.50 mm long, style rather long (1.2–2.5 mm) and light brown. Seeds ovoid-subsquare, smooth, greyish, 3.0–4.6 × 2.4–3.8 mm, epidermal cells rounded, with granulate elements in the triangle-shaped pores between epidermal cells; caruncle long (1.2–2.7 mm long), longitudinally sulcate and fluted (Figs 11A, B, 54). The shape of the capsule, seed, caruncle and epidermal cells are the most distinguishable features in this group.
4. Section *Calyptratae* was recently described (Riina *et al*., 2013) as a small group consisting only of two desert-adapted species, *E. connata* endemic to southern Iran and *E. calyptrata* from North Africa to Mauritania.
   Capsules conical, shallowly trilobate, 5.9–8.2 × 5.0–7.7 mm, smooth, glabrous, with prominent reticulate veins on the surface (Fig. 99), pedicel 2.3–7.5 mm long and hairy, style rather long (1.4–2.5 mm long). Seeds ovoid, smooth, dark grey to brown, 3.30–4.20 × 2.55–3.90 mm, epidermal cells penta-hexagonal, randomly distributed, without any elements on the surface; caruncle long (2.0–3.5 mm long), longitudinally sulcate and fluted (Figs 12A, B, 53). The special shape of the caruncle and the hairy pedicel are the two most obvious characters in this small group.
5. Section *Patellares* is a group with *c*. 14 species mostly distributed in the Mediterranean region, parts of the central European mountains, the Balkan Peninsula, Anatolia and Caucasus up to the Iranian highlands. Species in this group grow mostly in forests, mountain meadows and rocky slopes. There are three species, *E. amygdaloides* L., *E. erubescens* Boiss. and *E. macroceras* Fisch. & C.A.Mey., in Iran.
   Capsules subglobose, deeply trilobate, 3.20–8.20 × 3.25–8.30 mm, smooth, glabrous or pilose (Figs 101–103), pedicel 1.3–6.4 mm long, style medium to long (1.0–2.7 mm long). Seeds ovoid, smooth, pale to dark grey, *c*. 2.35–5.00 × 2.00–3.90 mm, epidermal cells penta-hexagonal, randomly distributed, without any elements on the surface, caruncle patelliform (Figs 13A–15B, 55–57). The patelliform caruncle is an important feature separating the group from the others.
6. Section *Esula* is the second largest section of subgenus *Esula*, and the most problematic and complex taxa are embedded in this group. The 96 perennial herbs or, occasionally, small shrubs in the section are mostly distributed and diversified in temperate Eurasia. There are five species in Iran (*E. buhsei* Boiss., *E. hebecarpa* Boiss., *E. iberica* Boiss., *E. osyridea* and *E. virgata* Waldst. & Kit.).
   Capsules subglobose, 3.0–6.4 × 3.4–7.7 mm, smooth, mostly granulate at least on the keels, glabrous or pilose (Figs 106–110), pedicel 1.4–9.5 mm long, style medium to long (1.0–3.4 mm long). Seeds ovoid, smooth, grey to brown, 1.8–3.7 × 1.7–3.0 mm, epidermal cells elongated polygonal, with several rounded pores around the epidermal cells, filled by granulate elements; caruncle petasiform (similar to broad-brimmed felt hat) (Figs 16A–19B, 58–62). Deeply rounded-trilobate capsules with a granulate surface at least on the keel and the petasiform caruncle characterize this group.
7. Section *Herpetorrhizae* includes 12 species with distributions from Iraq through Iran extending to Afghanistan, Pakistan, up to central Asia and western China. These are divided into ten species belonging to subsection *Oppositifoliae* Boiss. (annual species, six in Iran) and two to subsection *Aucheriae* (perennial species, both in Iran).
   Capsules oblong-conical, 3.0–4.9 × 2.8–4.4 mm, smooth, glabrous, glaucous (Figs 104, 105), pedicel 1.0–3.4 mm long, style short to medium (0.8–1.5 mm long). Seeds are pseudo-hexahedral, shallowly pitted and wrinkled, pale grey, 1.8–3.2 × 1.0–2.0 mm, epidermal cells penta-hexagonal, randomly distributed, with six or seven rounded pores around each penta- or hexagonal cell filled by

granulate elements, caruncle conical (Figs 20A, 21B, 63, 64).

8. Section *Pithyusa* is the third largest section in the subgenus with more than 50 taxa, most of which are distributed in south-western Asia with many local endemics, among them 20 species occurring in Iran (Pahlevani *et al*., 2011b). Members of the section are mostly perennial herbs; however, there are two annual species, *E. falcata* L. and *E. gaillardotii* Boiss. & Blanche in section *Pithyusa*.
   Capsules conical, *c*. 2.5–8.0 × 2.5–6.7 mm, smooth, glabrous or pilose, rarely papillose (Figs 111–127), pedicel *c*. 0.9–6.0 mm long, style short to long (0.8–3.0 mm long). Seeds ovoid, irregularly pitted or, rarely, smooth, grey to brown, 1.7–4.4 × 1.3–3.3 mm; epidermal cells penta-hexagonal or sometimes rounded, with granulate elements, caruncle conical (Figs 22A–36B, 65–82).
9. Section *Myrsiniteae* is a taxonomically difficult section of *c*. 15 taxa distributed in the Mediterranean region, the Caucasus and the Iranian highlands, with seven species occurring in Iran (Pahlevani, Geltman & Riina, 2011a). The species constitute perennial herbs or small subshrubs with the exception of the single annual species, *E. aleppica*.
   Capsules large, ovoid-conical, 4.7–11.5 × 4.0–10.0 mm, vesiculate, glaucous, bluish (Figs 128–132), pedicel 1.6–7.2 mm long, style long (1.2–3.5 mm long) and reddish. Seeds ovoid-quadrangular, tuberculate-rugulose to smooth, light grey to brown, 2.80–5.60 × 1.65–4.00 mm, epidermal cells tetrahedral, to some extent rounded, with granulate elements between them; caruncle conical (Figs 37A–42B, 83–88). The size, shape and vesiculate surface of the fruit, seed shape and surface, and style size and colour are the most distinguishable features separating this section from the others.
10. Subgenus *Athymalus* is the smallest of the four subgenera of *Euphorbia* with *c*. 150 species and ten sections, most of which have an African distribution, with only section *Balsamis* Webb & Berthelot represented by *E. larica* in southern to south-eastern Iran to Oman and the United Arab Emirates and probably Yemen (Govaerts, Frodin & Radcliffe-Smith, 2000).
   Capsules woody and globose with six segments, 6.0–8.0 × 6.0–8.9 mm, smooth, glabrous, light green to yellow (Fig. 133), pedicel 1.6–4.9 mm long, style medium to rather long (1.25–2.10 mm long). Seeds ovoid-subsquare, obscurely tuberculate-rugulose, dark grey to brown, *c*. 2.90–4.30 × 2.35–3.45 mm, epidermal cells deeply unequal-rounded without any elements on the surface, ecarunculate (Fig. 89).

DISCUSSION

Taxonomic and phylogenetic importance of seed and capsule morphology

This study indicates and confirms that not only the macro- and micromorphology of seeds (Pahlevani & Akhani, 2011), but also carpology, contribute useful characters to the taxonomy and identification of the perennial *Euphorbia* taxa from subgeneric to species level (Tables 2–5, Figs 1–133). Carpology in this group is at least as important as seed morphology, especially at the sectional level. Among the examined parameters, capsule size and shape, seed size and the ornamentation of the seed surface are correlated better with phylogeny than the other features (Figs 135, 136). Although seed morphology was useful to differentiate the Iranian annual *Euphorbia* spp. (Pahlevani & Akhani, 2011), recent molecular data (Riina *et al*., 2013) have suggested some changes in the classification of this group. According to older classifications of the genus, life cycle was always considered as an important character in the classification and identification of *Euphorbia* (Boissier, 1879; Parsa, 1949; Rechinger, 1964; Rechinger & Schiman-Czeika, 1964; Prokhanov, 1974; Radcliffe-Smith, 1980, 1982, 1986). However, although life cycle is a distinctive indicator for certain sections, variation in life cycle is not always congruent with new molecular phylogenetic classifications (Frajman & Schönswetter, 2011; Horn *et al*., 2012; Riina *et al*., 2013).

Character evolution of seed and capsule morphology

Carpology

Although the outgroup *E. larica*, a member of subgenus *Athymalus*, is characterized by woody globose capsules, fruits of subgenus *Esula* are never woody and can take various shapes. Members of sections *Helioscopia*, *Patellares*, *Esula*, *Szovitsiae*, *Tithymalus* and *Arvales* are characterized by subglobose capsule shape and a rounded keel (Figs 90–95, 101–103, 106–110, 135A). Sections *Patellares* and *Esula* are recognized by having deeper and narrower lobes than section *Helioscopia* (Figs 90–95, 101–103). Subglobose capsule shape has independently evolved three times in clades *Helioscopia*, *Szovitsiae-Patellares* and *Tithymalus-Esula* (Fig. 135A). *Euphorbia peplus* and *E. peploides* are distinguished by winged keels in section *Tithymalus*. Conical capsules occur in sections *Pithyusa*, *Sclerocyathium* and *Calyptratae* (Figs 96–99, 111–127, 135A; Table 2). Species of section *Herpetorrhizae* show synapomorphy of oblong-conical capsules (Figs 104, 105) and seem to have evolved from subglobose ones. Ovoid-conical capsules are found in sections *Myrsiniteae* and *Lagascae*

KEY TO SECTIONS

1. Capsules lignified, globose; seeds ecarunculate ..... subgenus *Athymalus* (*E. larica*)
1. Capsules not lignified, not globose; seeds carunculate ..... 2 (subgenus *Esula*)
2. Capsules tuberculate or verrucose, rarely smooth or with few warts (*E. altissima* and *E. mazandaranica*) ..... 1 section *Helioscopia*
2. Capsules smooth, without any warts on the surface 3
3. Capsules ovoid-conical, obviously trigonous, bluish, vesiculate; seeds ovoid-quadrangular ..... 9 section *Myrsiniteae*
3. Capsules and seeds not as above 4
4. Capsules distinctly conical 5
4. Capsules oblong-conical, subglobose or rounded-oblong 7
5. Seeds smooth, without any element on the surface 6
5. Seeds irregularly pitted, rarely smooth or obscurely pitted, with granulate elements at high magnification ..... 8 section *Pithyusa*
6. Style 0.65–1.20 mm long; caruncle conical, 0.65–1.90 mm long ..... 2 section *Sclerocyathium*
6. Style 1.4–2.5 mm long; caruncle longitudinally sulcate and fluted, 2.6–4.2 mm long ..... 4 section *Calyptratae* (*E. connata*)
7. Capsules oblong-conical; seeds pseudo-hexahedral, shallowly tuberculate and wrinkled, caruncle oblique ..... 7 section *Herpetorrhizae* subsection *Aucheriae*
7. Capsules subglobose or rounded-oblong; seeds ovoid, ovoid-ellipsoidal or ovoid-subsquare, smooth, caruncle erect 8
8. Capsules rounded-oblong; seeds ovoid-subsquare, caruncle longitudinally sulcate and fluted ..... 3 section *Chylogala* (*E. heteradena*)
8. Capsules subglobose; seeds ovoid or ovoid-ellipsoidal, caruncle patelliform or petasiform 9
9. Capsules granulate at least on the keels; seeds with granulate elements on surface, caruncle petasiform ..... 6 section *Esula*
9. Capsules not granulate; seeds without any elements on the surface, caruncle patelliform ..... 5 section *Patellares*

(Fig. 135A), and are most distinctive in section *Myrsiniteae*. Only section *Chylogala*, represented by *E. heteradena*, is distinguished by a unique rounded-oblong capsule (Fig. 135A).

Capsule surface characters are also well correlated with the clades derived from BI analysis (Fig. 135B). The vesiculate surfaces of section *Myrsiniteae* and the granulate surfaces of section *Esula* are synapomorphies congruent with the phylogenetic tree. The perennial species and the annual *E. stricta* (Figs 90–95), all section *Helioscopia*, and characterized by tuberculate or verrucose surfaces, are also monophyletic, whereas most annual species of the section are smooth. Reversals to smooth surfaces have taken place several times, e.g. in the perennial species *E. mazandaranica* and *E. altissima*. *Euphorbia eriophora* is unique among species in section *Helioscopia* because of its long pilose capsules (Pahlevani & Riina, 2014: Fig. 4). Smooth surfaces seem to constitute the primitive state and have been retained in *Herpetorrhizae*, *Chylogala*, *Calyptratae*, *Pithyusa*, *Tithymalus* and *Sclerocyathium*. All species with pilose capsules in section *Pithyusa* (*E. gypsicola*, *E. sahendii* and *E. teheranica*) are monophyletic (Fig. 134). Papillose surfaces, in contrast, have evolved several times in section *Pithyusa* (e.g. *E. glareosa*, *E. macroclada* Boiss. and *E. polycaulis* Boiss.) (Figs 111–127).

Seed morphology

Most of the seed shape character states are somewhat homoplasious, but particular states seem to be synapomorphic for specific groups (Fig. 136A). Among 13 sections existing in the Iranian leafy spurges, six sections have ovoid seeds as the most common shape (Figs 8A–15A, 22A–36A, 50–57, 65–82). Sections *Helioscopia*, *Myrsiniteae* and *Esula* are distinguished from the other groups by ellipsoidal, ovoid-quadrangular and ovoid-ellipsoidal seeds shapes, respectively (Figs 1A–7A, 43–49; 37A–42A, 83–88; 16A–19A, 58–62). The case of the annual *E. aleppica* with ovoid seeds in *Myrsiniteae* indicates that the change in life form has been paralleled by a change in seed shape. Sections *Herpetorrhizae* and *Tithymalus* possess pseudo-hexahedral and hexahedral seed shapes, respectively (Figs 20A, 21A, 63–64; Pahlevani & Akhani, 2011: figs 16A–C, 17A, 18A, B, 23A, 24A, 25A, 26A, 28A). Although these shapes are superficially similar, true hexahedral seeds are only formed in *Tithymalus*, whereas they appear hexahedral because of two ridges on the seeds in *Herpetorrhizae*.

KEY TO SPECIES

Section 1: *Helioscopia*

1. Capsules completely tuberculate or verrucose 2
1. Capsules smooth or with few warts 5
2. Capsules 8–10 mm wide (diameter); seeds 3.6–4.9 mm wide ..... *E. macrocarpa*
2. Capsules < 6.8 mm wide (diameter); seeds up to 3.3 mm wide 3
3. Style up to 1.4 mm long ..... *E. condylocarpa*
3. Style 1.8–3.0 mm long 4
4. Capsule surface covered with long cylindrical-filiform warts, glabrous ..... *E. squamosa*
4. Capsule surface with two rows of short tubercles on each lobe, pilose to subglabrous ..... *E. orientalis*
5. Capsules 6.0–7.4 mm wide (diameter); seeds 3.6–3.9 × 3.0–3.4 mm ..... *E. grisophylla*
5. Capsules up to 4.6 mm wide (diameter); seeds 2.00–2.80 × 1.90–2.45 mm 6
6. Capsules 4.5–4.9 mm long; seeds 2.7–2.9 mm long, caruncle 0.8–1.2 mm long ..... *E. altissima* ssp. *altissima*
6. Capsules 2.5–3.4 mm long; seeds 2.0–2.5 mm long, caruncle 0.3–0.6 mm long ..... *E. mazandaranica*

Section 2: *Sclerocyathium*

1. Caruncle at least half as long as seeds ..... *E. caeladenia*
1. Caruncle shorter than one-third of seed length 2
2. Capsules green, pedicel *c.* 2–6 mm long, style *c.* 0.7–1.2 mm long ..... *E. bungei*
2. Capsules dark red to purplish, pedicel *c.* 1.0–2.2 mm long, style *c.* 0.4–0.7 mm long ..... *E. ferdowsiana*

Sections 3 and 4 (sections *Chylogala* and *Calyptratae*, respectively)

These sections are monotypic.

Section 5: *Patellares*

1. Capsules 6.3–8.3 mm long; seeds 3.9–5.0 mm long ..... *E. erubescens*
1. Capsules 3.2–4.4 mm long; seeds 2.3–3.2 mm long 2
2. Seeds with acute tip; caruncle invisible from back of seed ..... *E. amygdaloides*
2. Seeds with flat tip; caruncle visible from back of seed ..... *E. macroceras*

Section 6: *Esula*

1. Capsules pilose or villose 2
1. Capsules glabrous 3
2. Capsules intensely granulate with long pedicel (3.5–9.5 mm), seed index 1.18 ..... *E. osyridea*
2. Capsules granulate on the keels only with shorter pedicel (1.6–3.5 mm), seed index 1.34 ..... *E. hebecarpa*
3. Caruncle width two times greater than length ..... *E. iberica*
3. Caruncle width two times less than length 4
4. Capsules 3.0–4.4 mm long; seeds 2.0–2.8 mm long ..... *E. virgata*
4. Capsules 4.6–5.7 mm long; seeds 2.7–3.7 mm long ..... *E. buhsei*

Section 7: *Herpetorrhizae*, subsection *Aucheriae*

1. Seeds 1.8–2.0 × 1.0–1.3 mm, surface densely papillose, flat at the end ..... *E. deltobracteata*
1. Seeds 2.25–3.20 × 1.20–2.00 mm, surface sparsely papillose, protruding at the end ..... *E. aucheri*

Section 8: *Pithyusa*

1. Capsules pilose, villose or pruinose-papillose....2
1. Capsules glabrous or rarely sparingly pilose....6
2. Capsules pruinose-papillose....3
2. Capsules pilose to villose, never papillose....5
3. Capsules villose, 5.0–8.0 × 5.0–6.7 mm....*E. macroclada*
3. Capsules glabrous, 3.2–5.2 × 2.5–4.5 mm....4
4. Capsules mostly purplish; seeds irregularly pitted....*E. polycaulis*
4. Capsules yellowish-green; seeds smooth....*E. glareosa*
5. Caruncle 1.00–1.40 × 0.65–1.15 mm....*E. gypsicola*
5. Caruncle 0.75–0.90 × 0.79–1.00 mm....*E. sahendii*
6. Caruncle at least half as long as seeds....7
6. Caruncle shorter than one-third of seed length....8
7. Capsules sparsely pilose or rarely glabrous; caruncle distinctly stipitate....*E. teheranica*
7. Capsules glabrous; caruncle sessile or indistinctly stipitate....*E. gedrosiaca*
8. Seeds smooth....9
8. Seeds irregularly pitted....12
9. Capsules sharply keeled....*E. iranshahri*
9. Capsules obtusely keeled....10
10. Capsules compressed conical, 2.5–3.7 × 2.5–3.7 mm; caruncle 0.4–0.8 mm long....*E. seguieriana*
10. Capsules elongated conical 3.50–4.50 × 2.60–3.95 mm; caruncle 0.8–1.3 mm long....11
11. Seeds 2.8–3.0 × 1.7–2.0 mm, light brown....*E. acanthodes*
11. Seeds 2.1–2.7 × 1.4–2.0 mm, grey....*E. spartiformis*
12. Capsules 3.1–3.9 × 2.7–3.5 mm....*E. sulphurea*
12. Capsules 4.0–6.8 × 3.5–5.2 mm long (rarely < 4 mm long in *E. malleata* or *E. kopetdaghi* and 3.2 mm wide in *E. malleata*)....13
13. Capsules sharply keeled....14
13. Capsules obtusely keeled....16
14. Seeds intensely and deeply wrinkled....*E. cheiradenia*
14. Seeds superficially pitted....15
15. Capsules grey to olive green....*E. plebeia*
15. Capsules light yellow....*E. malleata*
16. Capsules elongated-conical, intensely glaucous....*E. erythradenia*
16. Capsules not elongated, not glaucous or obscurely glaucous....17
17. Seeds with numerous deep pits; caruncle obtusely conical....*E. kopetdaghi*
17. Seeds with a few shallow pits, caruncle mostly acutely conical....*E. microsciadia*

Section 9: *Myrsiniteae*

1. Capsules 8.6–11.5 × 6.8–10.0 mm; seeds 4.5–5.6 × 2.9–4.0 mm....2
1. Capsules 4.7–7.6 × 4.0–6.7 mm; seeds 2.80–4.40 × 1.65–2.70 mm....3
2. Seeds tuberculate-rugulose; caruncle stipitate....*E. denticulata*
2. Seeds tuberculate; caruncle indistinctly stipitate or sessile....*E. craspedia*
3. Caruncle 0.5–1.0 × 0.5–1.1 mm....4
3. Caruncle 1.00–2.55 × 1.20–2.35 mm....5
4. Seeds smooth....*E. monostyla*
4. Seeds vermiculate-rugulose and tuberculate....*E. spinidens*
5. Seeds smooth or shallowly rugulose; caruncle broadly conical, acute....*E. marschalliana*
5. Seeds tuberculate-rugulose; caruncle truncate conical, concave....*E. myrsinites*

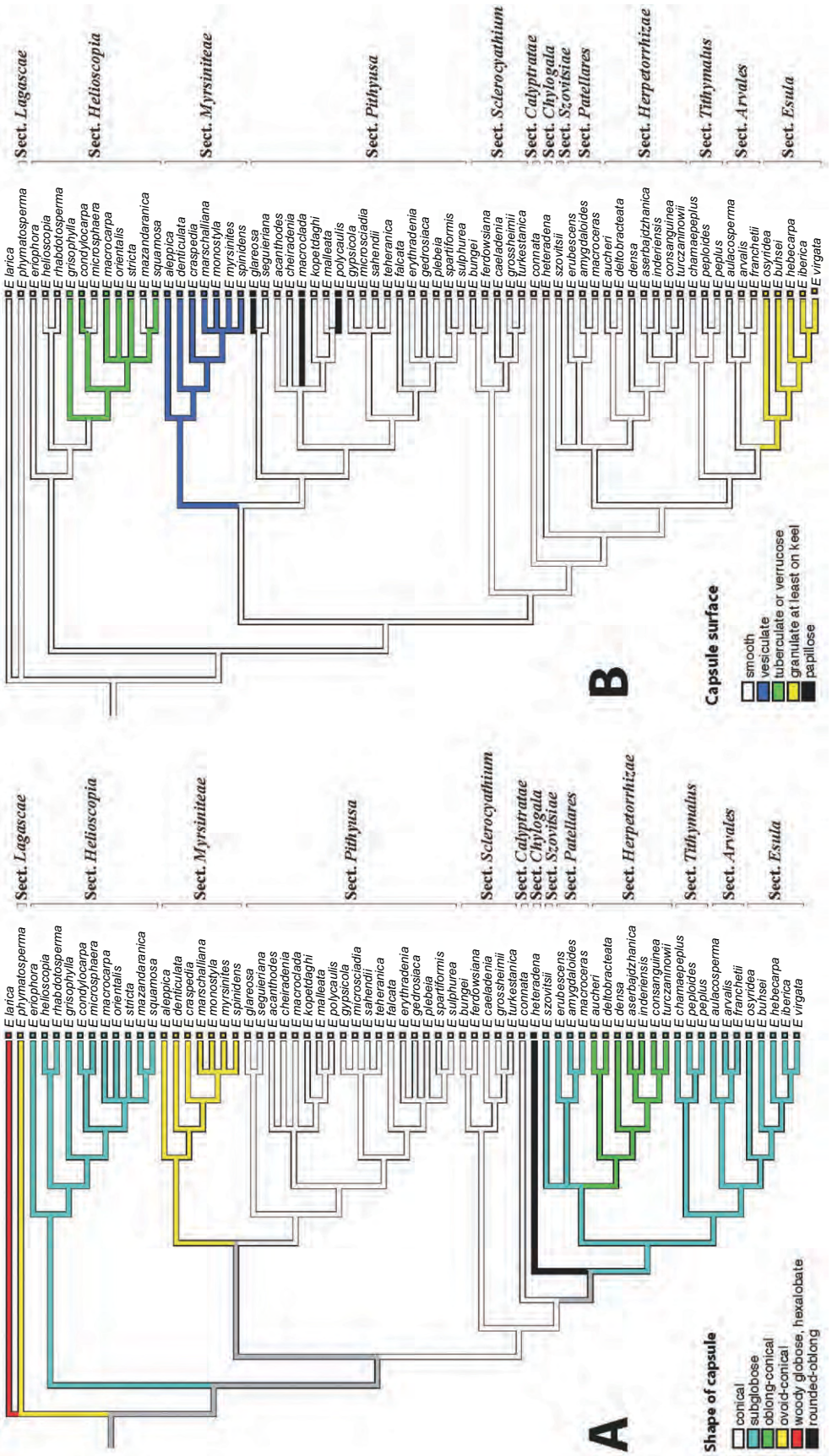


Figure 135. A, B, Evolutionary states of two selected capsule characters (A, capsule shape; B, capsule surface) mapped on the Bayesian tree of combined nrITS + *ndhF* sequences of 67 Iranian species of *Euphorbia* subgenus *Esula*.

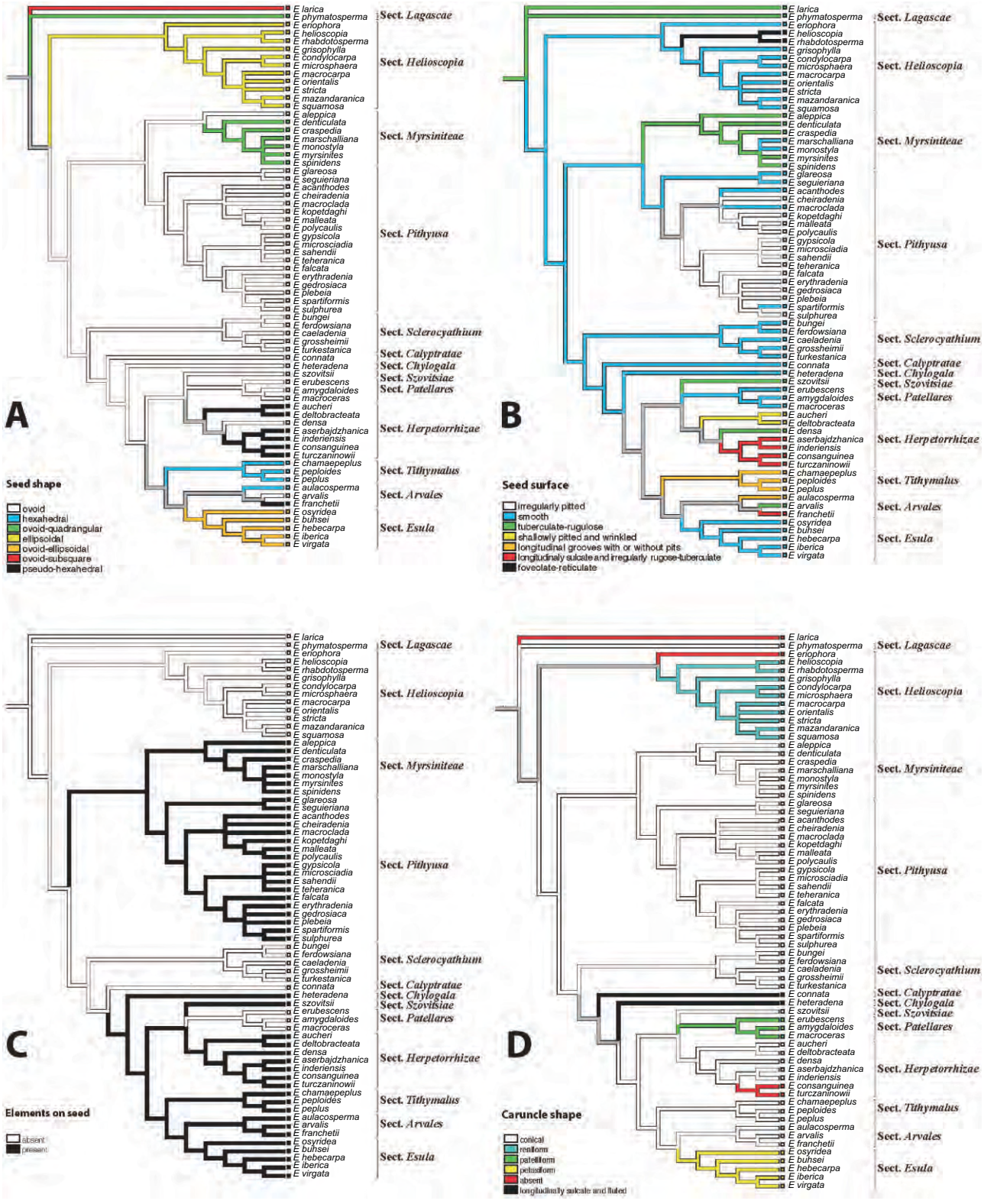


Figure 136. A–D, Evolutionary states of four selected seed characters (A, seed shape; B, seed surface; C, presence or absence of elements on seed; D, caruncle shape) mapped on the Bayesian tree of combined nrITS + *ndhF* sequences of 67 Iranian species of *Euphorbia* subgenus *Esula*.

In *E. densa* (section *Herpetorrhizae*), with ovoid seeds, a reversal from the pseudo-hexahedral shape has possibly taken place (Fig. 136A). Section *Arvales* is unusual because its three annual Iranian members have completely different seed shapes: *E. aulacosperma* displays hexahedral, *E. franchetii* pseudo-hexahedral and *E. arvalis* ovoid seeds (Fig. 136A; Pahlevani & Akhani, 2011: figs 14A, 15A, 15C, 22A, B). Incongruence between seed shape in this group could indicate reticulate evolution which has already been reported in other groups of *Euphorbia* (Yang & Berry, 2011).

Seed surface structure seems to be highly homoplasious in *Euphorbia* subgenus *Esula*. Smooth surfaces are the most common type, present in sections *Patellares*, *Esula*, *Chylogala*, *Calyptratae* and *Sclerocyathium*. It is also the most frequent type in section *Helioscopia*, in which two species, *E. helioscopia* and *E. rhabdotosperma*, have evolved a unique ornamentation type, foveolate-reticulate seeds. For section *Pithyusa*, irregularly pitted seeds are characteristic, with the two first-branching species, *E. glareosa* and *E. seguieriana*, still displaying smooth seeds, and several reversals to smooth seeds (*E. acanthodes*, *E. macroclada*, *E. spartiformis*). Reversals to smooth seeds have also taken place in section *Myrsiniteae* (*E. marschalliana*, *E. monostyla*), which is otherwise characterized by tuberculate-rugose seeds. As the latter seed type is also found in the outgroup, it can be speculated that the common ancestor of subgenus *Esula* possessed tuberculate-rugose seeds (Fig. 136B). Shallowly to deeply rugulose-wrinkled or irregularly rugose-tuberculate and longitudinally sulcate seeds are synapomorphic in section *Herpetorrhizae*. Section *Tithymalus* is uniform with regard to seed ornamentation, displaying two longitudinal grooves on ventral sides and several pits on dorsal sides. This feature on the seed surface occurs only on the Old World species of section *Tithymalus* (Peirson *et al*., 2014). Section *Arvales,* in contrast, is as heterogeneous in seed ornamentation as it is in seed shape.

Granulate elements are absent from the outgroup, and have apparently evolved in subgenus *Esula* twice, once in the *Myrsiniteae–Pithyusa* clade (Figs 22B–42B; Pahlevani & Akhani, 2011: fig 21C, D) and once in the *Chylogala–Szovitsiae–Patellares–Herpetorrhizae–Tithymalus–Arvales–Esula* clade (Figs 11B, 16B–21B; Pahlevani & Akhani, 2011: figs 13B, 15B, 16B, 17C, 18D, 19C, 20D, 22C, 23B, 25B, 26C, 27B, 28C), with a reversal to the absence of granulate elements in section *Patellares* (Fig. 136C).

Caruncle shape shows a strong phylogenetic pattern (Fig. 136D). In the outgroup, a caruncle is absent, as in many members of subgenera *Euphorbia* and *Chamaesyce*; therefore, the presence of a caruncle might constitute a synapomorphy for subgenus *Esula*. The most frequent conical caruncles are found in sections *Lagascae*, *Myrsiniteae–Pithyusa* and *Sclerocyathium*, *Szovitsiae*, *Herpetorrhizae*, *Tithymalus* and *Arvales* (Figs 50–52, 63–88). In sections *Esula* and *Patellares*, special caruncle shapes have evolved, namely petasiform and patelliform caruncles, respectively. Section *Herpetorrhizae* shows the synapomorphy of an oblique position of the caruncle (Figs 20A, 21B, 63, 64; Pahlevani & Akhani, 2011: figs 16A, 18A, 19A, B, 23A, 26A). Ecarunculate or small and caducous caruncles (*E. aleppica*) have evolved several times from carunculate seeds (sections *Helioscopia*, *Myrsiniteae* and *Herpetorrhizae* and species of subgenera *Chamaesyce* and *Athymalus*). *Euphorbia eriophora* with no caruncle is retrieved as sister to the remaining species (Pahlevani & Akhani, 2011: fig 29A). It seems that ecarunculate seeds are a plesiomorphic feature in section *Helioscopia*, occurring in the earliest branching clades (see Riina *et al*., 2013). Generally, absent or small and unsteady caruncles seem to be a plesiomorphic feature in some sections of subgenus *Esula*.

Thus, although some homoplasy has been observed in most seed and fruit characters studied here, these characters, especially in combination, have considerable predictive power for the correct placement of species, especially when considered together with other morphological characters.

Evolutionary role of seed and fruit characters and dispersal mechanism in Euphorbia

Members of subgenus *Esula* are diplochorous, dispersing their seeds first via an explosive capsule mechanism, and second via myrmecochory (Pemberton & Irving, 1990).

The explosive seed dispersal mechanism in *Euphorbia* distributes the seeds to distances from several centimetres to more than 10 m (Narbona, Arista & Ortiz, 2005). The differences in explosive dispersal distance between species depend both on seed mass and caruncle retention. However, other features, such as seed projection angle, seed projection height, seed drag and initial seed velocity, are functional and important to primary seed dispersal (Garrison, Miller & Raspet, 2000). *Euphorbia* has capsules with explosive dehiscence produced by different orientation of the cells of the mechanical wall. Diaspores with morphological adaptation to ant transport are the most common secondary seed dispersal of plants (Mayer, Ölzant & Fischer, 2005), and myrmecochory is known in more than 80 plant families, including more than 3000 species worldwide (Beattie & Hughes, 2002). Indeed, there are two reasons why some species are carunculate and others are ecarunculate or with a tiny caruncle. According to

Narbona *et al*. (2005), who studied two species of section *Pithyusa*, ballistic seed projection is more efficient in terms of distance in seeds with tiny, caducous caruncles or without caruncles than in seeds with gross caruncles. Indeed, large seeds or seeds with caruncles are usually dispersed by secondary seed dispersal involving ants (myrmecochory). Ants are attracted to the elaiosome to feed on the lipid-rich caruncle, and the diaspores themselves are then usually abandoned, intact and viable, either in the ant nest or outside the nest on waste piles or near the ant midden as a safe site for germination (Mayer *et al*., 2005). As seen in Figures 1–91, species of sections *Helioscopia* and *Esula* (Figs 45–51, 60–64) with small caruncles may be dispersed mostly by an explosive mechanism, whereas sections *Sclerocyathium*, *Calyptratae*, *Chylogala* and *Myrsiniteae* (Figs 52–56, 85–90), with large seeds and caruncles, are probably more likely to be dispersed via myrmecochory. In the remaining sections, such as *Pithyusa*, *Patellares* and *Herpetorrhizae*, both seed dispersal patterns will probably be observed as a result of the existence of rather large and small caruncles. Elaiosomes are a striking example of convergence in seed plants and are derived from different parts of the fruit, seed or, rarely, floral parts of the plant. Caruncles in *Euphorbia* are derived from the exostome part of the seed (Mayer *et al*., 2005). Ecarunculate seeds, such as those of *E. eriophora*, *E. consanguinea* Schrenk and *E. turczaninowii* Kar. & Kir., probably disperse via autochory and ants may play a small role in seed dispersal. The absence of a caruncle in *E. consanguinea* and *E. turczaninowii* seems to be the result of secondary loss in adaptation to their habitat of sandy dunes (Fig. 136D), in contrast with the previous speculation that ecarunculate seeds are an important phylogenetic and classification character (Pahlevani & Akhani, 2011; Salmaki *et al*., 2011). There seems to be a strong correlation between seed traits and habitat preferences of the species. All species occurring in forests (*E. amygdaloides*, *E. macroceras*, *E. mazandaranica* and *E. squamosa*) have small seeds with smooth seed surfaces, lacking granulate elements, and tiny caruncles. Such seeds have further projecting distances, roll more easily and also penetrate the soil more easily. In contrast, desert species, such as *E. connata*, *E. caeladenia* and *E. heteradena*, have large seeds with large caruncles. Observations by the first author in natural habitats confirm the importance of long caruncles in the dispersal of seeds by large ants. In other words, they are adapted to secondary seed dispersal by ants (myrmecochory). It is conceivable that species of ant are also affected by seed dispersal patterns and that this symbiosis plays an important role in evolution and speciation.

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APPENDIX 1

List of voucher specimens used for seed and capsule morphological studies.

Euphorbia acanthodes **Akhani Iran. Ilam:** 34 km Dehloran to Mehran, 31.iii.2001, *Akhani* 14782 (IRAN, Hb. Akhani).

Euphorbia altissima ssp. altissima **Boiss. Iran. West Azarbaijan:** Urmieh, road of Talatappeh towards Urmieh, Gol-e Marz village, 27.vii.1990, *Izadpanah & Taheri* 68340 (TARI).

Euphorbia amygdaloides **L. Iran. Mazandaran:** Sangdeh, Abshar, 20 km to Abshar, 19.v.1999, *Termeh & Eskandari* 47219 (IRAN); Tonekabon, Galesh Mahalleh, 24 km Tonekabon, 11.v.1985, *Termeh & Matin* 47283 (IRAN); **Golestan:** 27 km Kord Kuy to Radkan, Deraz Now, 19.iv.2006, *Sajedi & Bahramishad* 47256 (IRAN); Gorgan, Kord Kuy, 7 km E Radkan, Asal Donbaleh, region of Jahan Nama, 26.v.1985 *Moussavi & Tehrani* 47262 (IRAN); Ramian, Jangal Jameh Shuran, 20.v.1990, *Delghandi & Daneshpajuh* 47417 (IRAN); Gorgan, Shamushak Forest, 13.v.2007, *Pahlevani*, *Eskandari & Shirzadian* 47659 (IRAN).

Euphorbia aucheri **Boiss. Iran. Esfahan:** Semirom, Kuhe Sourmandeh, 7.vi.1974, *Iranshahr* 17661 (IRAN); Khansar, Ghaleh Bala Mohammad, Golestan Kuh, 9.vii.1984, *Moussavi & Tehrani* 44511 (IRAN); Semirom, Pashmakou, 27.vii.2009, *Pahlevani & Bahramishad* 53347 (IRAN); **Mazandaran:** Polur, Lar, Gozal Darreh Mt., 10.vii.1982, *Termeh*, *Moussavi & Tehrani* 47232 (IRAN); **Tehran:** Damavand, Havir, Daryacheh Tar, 26.viii.2009, *Eskandari* 54111 (IRAN); **East Azarbaijan:** Tabriz to Marand, Payam, Mishodagh, 15.vi.2010, *Pahlevani & Asef* 54558 (IRAN); **Kohkilouyeh:** Yassuj, Sepidar, Savers Mt., 8.vi.2011, *Amini Rad & Torabi* 56538 (IRAN); *c.* 50 km E of Dehdasht, kuh-e Niel, 21.vii.1983, *Assadi & Abouhamzeh* 46507 (TARI); **North Khorasan:** Ashkhaneh, Tangeh Raz, 10.v.2012, *Fritsch*, *Eskandari & Bahramishad* 58611 (IRAN); **Markazi:** Arak, Shahzand, Hafteh-o Emarat, Alim-abad, kuh-e Alvand, 8.vii.1985, *Mozaffarian* 63936 (TARI).

Euphorbia buhsei **Boiss. Iran. Tehran:** 36 km S. Tehran to Qom, 4.v.1974, *Iranshahr & Riedl* 17767 (IRAN); **Semnan:** 20 km E Semnan, Chasht Khoran to Kuhe Warzom, 20.v.1982, *Termeh & Zargani* 44517 (IRAN); 17 km Momen-abad to Firouzkuh, 29.v.2012, *Pahlevani* 57193 (IRAN); **Khorasan:** Mashhad to Chenaran, Akhlamad, Binaloud Mt., 15.vii.2005, *Djavadi*, *Eskandari & Torabi* 47265 (IRAN); Neyshabur, Bujan, 28.vi.2007, *Pahlevani*, *Amini Rad & Torabi* 47351 (IRAN); Quchan to Chenaran, Radkan, Baru, 17.vi.2002, *Djavadi & Sadeghi* 47413 (IRAN); **Kerman:** 92 km Bam to Kerman, 3.v.2008, *Pahlevani*, *Amini Rad & Torabi* 47481 (IRAN); Negar, Ghaleh Asgar, 25.v.2009, *Pahlevani & Bahramishad* 53824 (IRAN); 70 km Kerman to Bam, around the Jupar Mt., 21.v.2009, *Pahlevani & Bahramishad* 53830 (IRAN); **Sistan & Baluchestan:** Khash to Zahedan, Tamandan, Paylak, Taftan Mt., 23.v.2009, *Pahlevani & Bahramishad* 53823 (IRAN); **Esfahan:** S Esfahan, towards Shahreza, Kolah Ghazi Protected Area, 31.v.2012, *Pahlevani* 57188 (IRAN).

Euphorbia bungei **Boiss. Iran. Semnan:** Damghan to Shahrud, Mehmandust, Tazareh, Kuhe Sefid Shekar, 22.v.1982, *Termeh & Zargani* 44520 (IRAN); 31 km W Semnan, Sorkheh, Momen-abad, 19.v.1982, *Termeh & Zargani* 44521 (IRAN); Shahrud, Reserch Center, 25.vi.2007, *Pahlevani*, *Amini Rad & Torabi* 47343 (IRAN); **Tehran:** 17 km NE of Simin Dasht, Roud Afshan, 9.vi.1998, *Moussavi & Karavar* 47341 (IRAN); **Esfahan:** Shahin Shahr, Chal Siah, Ghamishlu Protected Area, 10.vi.1992, *Termeh & Matin* 47394 (IRAN); **Golestan:** Shahpasand to Bojnurd, Dasht-e Almeh, 6.vi.1975, *Termeh* 47405 (IRAN); Shahpasand to Bojnurd, Almeh (Golestan National Park), 10.vi.1975, *Termeh* 47406 (IRAN); **Khorasan:** Shirvan, Namanlu, Kuhe Goloul, 14.vi.1975, *Termeh* 47927 (IRAN); *c.* 30 km between Esfarayen & Bojnurd, Assadli neck Mt., 29.vi.1984, *Mozaffarian* 48713 (TARI); From Torbat-e Heydarieh to Mashhad, *c.* 5 km to Kameh Sofla, 20.v.2003, *Assadi & Amirabadi* 84829 (TARI).

Euphorbia caeladenia **Boiss. Iran. Sistan & Baluchestan:** Khash to Saravan, Gosht, 25.iv.2004, *Amini Rad & Torabi* 47304 (IRAN); Baluchestan, Khash, 16.iv.1965, *Sharif & Dezfoulian* 47949 (IRAN); Baluchestan, 60 km Khash to Zahedan, 4 km to Eskel Abad, 22.v.2009, *Pahlevani & Bahramishad* 53777 (IRAN); Baluchestan, 10 km Zahedan to Khash, 22.v.2009, *Pahlevani & Bahramishad* 53828 (IRAN); Baluchestan, 25 km Eskel Abad, 15.iv.1973, *Sojak* 2152 (IRAN); Baluchestan, 65 km from Zahedan on the road to Khash, 25.iv.1977, *Assadi* 22774 (TARI); Baluchestan, Khash, 27.iv.1977, *Assadi* 22959 (TARI).

Euphorbia cheiradenia **Boiss. & Hohen. Iran. Tehran:** Karaj, Gachsar to Gajereh, Varang Rud, 8.vii.1977, *Termeh & Matin* 18024 (IRAN); Karaj, Velayat Rud to Varang Rud, 29.iv.2004, *Sajedi* 44530 (IRAN); Tehran, 5 km to Firuzkuh, 20.vi.1992, *Tehrani* 47439 (IRAN); Damavand, Havir, Daryacheh Tar, 26.viii.2009, *Eskandari* 54110 (IRAN); **Hamedan:** Abbas Abad, Kuhe Alvand, 11.vii.1974, *Termeh & Moussavi* 18031 (IRAN); **Kordestan:** Bijar, Kuhe Hamzeh Arab, 1.vii.1971, *Termeh* 18033 (IRAN); 15 km Sanandaj to Marivan, 29.vi.2010, *Amini Rad & Torabi* 54582 (IRAN); **Bakhtiari:** Farsan, Deh Cheshmeh, Kuhe Pir Ghar, 21.v.1991, *Delghandi*, *Abbasi & Tehrani* 47465 (IRAN); Dashtak to Cheri, 13.vi.1973, *Iranshahr & Moussavi* 47902 (IRAN); **Esfahan:** Fereydoun Shahr, Choghyourt, 20.vi.2010, *Djavadi & Ghanbari* 54487 (IRAN).

Euphorbia condylocarpa **M. Bieb. Iran. Ilam:** Kuhe Rino, 3.v.1968, *Iranshahr* 17713 (IRAN); **Fars:** Arjan-Parishan Protected Area, Old Road Kazeroun to Shiraz, Gardaneh Galu Khaje, 8.v.2007, *Ghasemi* 47339 (IRAN); **Zanjan:** 70 km Zanjan to Gilvan, 3.v.2011, *Pahlevani & Fritsch* 56262 (IRAN).

Euphorbia connata **Boiss. Iran. Kerman:** 30 km Kerman to Bam, 5.v.1972, *Leonard* 17720 (IRAN); Rayen, Ghariatol Arab, 20.vi.1976, *Moussavi & Tehrani* 18039 (IRAN); 5 km Kerman to Bam, 4.v.2008, *Pahlevani*, *Amini Rad & Torabi* 47480 (IRAN); Baft to Orzuyeh, 25.v.2009, *Pahlevani & Bahramishad* 53785 (IRAN); Baft to Esfandaqeh, in valley of Halil Rud, 50 km SE of Baft, 10.vi.1977, *Assadi et al*. 1797 (TARI); Shahr-e Babak, 23.iv.1985, *Mozaffarian* 49593 (TARI).

Euphorbia craspedia **Boiss. Iran. Lorestan:** 65 km Khorram Abad to Pol Dokhtar, 12.iv.2009, *Amini Rad & Torabi* 53650 (IRAN).

Euphorbia deltobracteata **(Prokh.) Prokh. Iran. Golestan:** Golestan National Park, Soulgerd to Darreh Khersou, 22.vi.1993, *Matin & Termeh* 47323 (IRAN); Golestan National Park, 2–3 km E of Sharleq towards Almeh, 22.v.1995, *Akhani* 10773 (M).

Euphorbia denticulata **Lam. Iran. Kermanshah:** Kuhe Parrow, Road Chalabeh, 14.v.2008, *Sajedi*, *Javadi & Torabi* 47528 (IRAN); Paveh, Khaneghah Village to Atashgah Mt., 17.v.2007, *Abbasi* 47764 (IRAN); Nojivaran, Paru Mt., 14.v.2009, *Asef & Torabi* 53789 (IRAN); **Tehran:** Savejbulagh, 30.v.1997, *Akbari* 34375 (FAR, IRAN); Savejbulagh, Kuhsiran, 30.v.1997, *Rasoulinia* 56926 (FAR, IRAN); **West Azarbaijan:** Urmieh, Movana, Marmisho, 2.vii.2012, *Amini Rad & Torabi* 58613 (IRAN).

Euphorbia erubescens **Boiss. Iran. Fars:** Ardakan, 19.vii.1964, *Haghighi* 17820 (IRAN); Fahlian to Hossein Abad, 1.vi.1973, *Iranshahr & Moussavi* 18108 (IRAN); **Kohkiluyeh:** Yasouj to Ardakan, 25.vii.1987, *Termeh*, *Delghandi & Tehrani* 47988 (IRAN); Yasouj to Kakan, Cheshmeh Piri, 29.vi.1967, *Zalpour* 17825 (IRAN); Sisakht, Cheshmeh Mishi, 2.vii.2008, *Eskandari*, *Javadi & Torabi* 51492 (IRAN).

Euphorbia erythradenia **Boiss. Iran. Fars:** 20 km Neyriz to Estahban, 27.v.2009, *Pahlevani & Bahramishad* 53336 (IRAN); Estahban, Eij Mt., 28.v.2009, *Pahlevani & Bahramishad* 53337 (IRAN).

Euphorbia ferdowsiana **Pahlevani Iran. Khorasan:** Mashhad, Zoshk, Binaloud Mt., 9.xi.1991, *Joharchi & Zangooei* 21323 (FUMH, IRAN); W Mashhad, Golmakan, Cheshmeh sabz, 3.viii.1992, *Ayatollahi & Zangooei* 22585 (FUMH); Mashhad, Kang, Binaloud Mt., 25.vi.1996, *Faghihnia & Zangooei* 27607 (FUMH, IRAN).

Euphorbia gedrosiaca **Rech. f., Aell. & Esfand. Iran. Yazd:** 12 km Chah Kharbozeh to Anarak, 17.v.1975, *Iranshahr* 18127 (IRAN); **Esfahan:** 40–45 km S Esfahan, Kolah Ghazi Protected Area, 8.vi.1992, *Termeh & Matin* 47474 (IRAN); S Esfahan, towards Shahreza, Kolah Ghazi Protected Area, 31.v.2012, *Pahlevani* 57190 (IRAN); **Semnan:** Khan Khodi, Ghaleh Bala, 4.vi.2007, *Amini Rad* 47810 (IRAN); **Sistan & Baluchestan:** 140 km Khash to Zahedan, 22.v.2009, *Pahlevani & Bahramishad* 53344 (IRAN); Baluchestan: 95 km Khash to Zahedan, 22.v.2009, *Pahlevani & Bahramishad* 53350 (IRAN).

Euphorbia glareosa **Pall. ex M. Bieb. Iran. West Azarbaijan:** 30 km NW Khoy, 2.vii.1965, *Rechinger* 32663 (M); **Armenia. Kotay:** Hrazdan, valley of river Hrazdan, Bjni, 17.vi.2004, *Fayvush et al*. 04–0509 (M).

Euphorbia grisophylla **M.S. Khan Iran. Kordestan:** Sanandaj to Kamiaran, Avalan Mt., 7.vi.2009, *Maroofi* 55797 (IRAN).

Euphorbia gypsicola **Rech. f. & Aellen Iran. Semnan:** 31 km W Semnan, Sorkheh, Momen Abad, 19.v.1982, *Termeh & Zargani* 44552 (IRAN); Momen Abad, 10 km NE Momen Abad, 2.v.1994, *Termeh*, *Moussavi & Tehrani* 52805 (IRAN).

Euphorbia hebecarpa **Boiss. Iran. Markazi:** Khansar, Damaneh Kuhe Darreh Dabbeh, 12.vi.1990, *Termeh*, *Moussavi & Tehrani* 47239 (IRAN); **Kerman:** Shahdad, 40 km Kerman, Kuhe Tunel, 21.vii.1989, *Termeh*, *Delghandi & Tehrani* 47292 (IRAN); Kerman, Kuh-e Hezar, 20 km SW of Rayen, Zehrud Bala, 4.vi.1977, *J.R.Edmondson & A.G.Miller* 1631 (TARI); **Lorestan:** Brujerd, Kuhe Garrow, 18.viii.1973, *Moussavi & Sateii* 47926 (IRAN); Dorud, Oshtorankuh, 18.v.1983, *Mozaffarian & Sardabi* 42469 (TARI); **Esfahan:** Semirom, Pashmakou, 27.vii.2009, *Pahlevani & Bahramishad* 53348 (IRAN); N side of Kuh-e Dena, above the village Noghol, 15.vii.1983, *Assadi & Abouhamzeh* 46088 (TARI); N side of Kuh-e Dena, Gardaneh-Bijan, 16.vii.1983,

Assadi & Abouhamzeh 46148 (TARI); **Kohkilouyeh:** Dehdasht, Sar Faryab, Nil Mt., 10.vi.2011, *Amini Rad & Torabi* 56540 (IRAN).

***Euphorbia heteradena* Jaub. & Spach Iran. Hamedan:** Hamedan to Avaj, 4.vi.1966, *Zargani* 17790 (IRAN); **Esfahan:** Chelgerd to Daran, Komitak, 19.vi.1973, *Iranshahr & Moussavi* 18089 (IRAN); Farydan, Khoygan, Kuhe Sangbaran, 14.vi.1990, *Termeh*, *Moussavi & Tehrani* 47240 (IRAN); S Esfahan, towards Shahreza, Kolah Ghazi Protected Area, 31.v.2012, *Pahlevani* 57189 (IRAN); **West Azarbaijan:** Urmieh, Kabudan Island, 21.v.1998, *Termeh*, *Sangari & Tehrani* 47228 (IRAN); **Zanjan:** Zanjan to Bijar, 40 km to Bijar, 30.vi.1971, *Termeh* 47408 (IRAN); **Kerman:** 92 km Bam to Kerman, 3.v.2008, *Pahlevani*, *Amini Rad* & *Torabi* 47482 (IRAN); Negar, Ghaleh Asgar, 25.v.2009, *Pahlevani & Bahramishad* 53825 (IRAN); **East Azarbaijan:** Jolfa, Aras River side, 9.vi.2007, *Pahlevani & Asef* 47797 (IRAN); Jolfa, Daran, Kiamaki Mt., 21.vi.2009, *Amini Rad* 53273 (IRAN); **Fars:** 20 km From Neyriz to Estahban, 27.v.2009, *Pahlevani & Bahramishad* 53339 (IRAN); Arsanjan, Pasargad, 29.v.2009, *Pahlevani & Bahramishad* 53831 (IRAN).

***Euphorbia iberica* Boiss. Iran. East Azarbaijan:** Arasbaran Protected Area, Kalale Sofla, 8.vi.2007, *Pahlevani & Asef* 47836 (IRAN); Arasbaran Protected Area, Khomarlu, 9.vi.2007, *Pahlevani & Asef* 47880 (IRAN); **West Azarbaijan:** Khoy, Avrin Mt., 19.vii.2011, *Amini Rad & Torabi* 56640 (IRAN).

***Euphorbia iranshahri* Pahlevani Iran. Esfahan:** Semirom, Kuhe Pashmaku, 6.vi.1974, *Iranshahr* 18016 (IRAN); **Fars:** Abadeh, Shahr Mian, 10.vi.1969, *Termeh & Izadyar* 47938 (IRAN); **Bakhtiari:** Gandoman, 6.vi.1973, *Iranshahr & Moussavi* 18122 (IRAN); 12 km E Borujen, Fara Donbeh, 31.v.1974, *Iranshahr* 18118 (IRAN); 21 km Lordegan to Gushaki, 5.vi.1973, *Iranshahr & Moussavi* 18119 (IRAN).

***Euphorbia kopetdaghi* (Prokh.) Prokh. Iran. Khorasan:** Shirvan, Namanlu, Kuhe Goloul, 14.vi.1975, *Termeh* 17648 (IRAN); 2 km Chekneh, Soltan Abad to Quchan, 18.vi.1975, *Termeh* 17649 (IRAN); Shirvan, Ziarat to Beyg, 12.vi.1975, *Termeh* 18117 (IRAN); W Bojnourd, between Darkesh & Havar, 13.vi.2001, *Joharchi* 33791 (FUMH); Shirvan, Namanlu, Goloul, Cheshmeh Gabri, 19.vii.1986, *Termeh*, *Moussavi & Tehrani* 47284 (IRAN); Kopedagh, 48 km NE Shirvan, 7.vii.1973, *Edmondson* 47790 (IRAN); **Golestan:** Golestan National Park, Almeh, Soulgerd, 22.vi.1993, *Termeh & Matin* 47320 (IRAN); Golestan National Park, 11 km Soulgerd, 16.vii.1991, *Termeh & Matin* 47456 (IRAN).

***Euphorbia larica* Boiss. Iran. Hormozgan:** 38 km from Minab to Jask, 28.ii.1982, *Mozaffarian et al*. 37969 (TARI); 15 km from Bandar-Abbas to Sirjan, 21.iv.1983, *Assadi & Sardabi* 42065 (TARI); 35 km from Senderk to Araghin, Deh-e Ziaraton, 9.v.1983, *Mozaffarian* 44492 (TARI); Bandar-Abbas, Geno Mt., 14.iv.2007, *Pahlevani & Torabi* 47668 (IRAN); Bandar-Abbas, 15 km after Hamiran, 21.iii.1985, *Maasoumi & Abouhamzeh* 52062 (TARI); Bandar-Abbas, Ghotb-abad, 13.iii.2009, *Pahlevani*, *Eskandari & Bahramishad* 53583 (IRAN); Bandar-Abbas, Ghotb-abad, Gohreh, 12.vi.2012, *Pahlevani*.

***Euphorbia macrocarpa* Boiss. & Buhse Iran. Lorestan:** Khorram Abad, Sefid Dasht, Baghbanan, 60 km Khorram Abad, 12.vi.1974, *Iranshahr* 55345 (IRAN); **Kordestan:** 15 km Baneh to Saghez, Vazaneh Mt., 13.vi.2007, *Maroofi & Karegar* 55861 (IRAN); 34 km from Chenareh to Baneh, 25.vi.2003, *Assadi* 85085 (TARI); 36 km from Sanandaj to Kamiaran, Nashur valley, 15.vi.1987, *Assadi* 60617 (TARI); **Kermanshah:** between Kermanshah & Paveh, before Shamshir, Mansour-Aghai village, kuh-e Shahoo, 2.vii.2005, *Assadi & Mehregan* 89152 (TARI); Kermanshah towards Paveh, Shamshir village, Shahoo Mt., 16.vii.2010, *Pahlevani & Asef*; Paveh, above the village Shamshir, base of Shahoo Mt., 18.vi.1987, *Assadi* 60749 (TARI); **West Azarbaijan:** Silvaneh, Jermi, 17.vi.2012, *Eskandari & Bahramishad* 58609 (IRAN).

***Euphorbia macroceras* Fisch. & C.A. Mey. Iran. Mazandaran:** Kelardasht, Kordichal to Mazuchal, 22.vii.1983, *Termeh & Zargani* 47241 (IRAN); **Gilan:** 30 km Khalkhal to Asalem, 16.vi.2007, *Pahlevani* 47356 (IRAN).

***Euphorbia macroclada* Boiss. Iran. Kermanshah:** Kazaran, Branand Sofla, Dalahu, Kuhe Gol Zard, 15.viii.1973, *Moussavi & Satei* 18104 (IRAN); Kermanshah, Kuhe Parow, 17.viii.1973, *Moussavi & Satei* 18106 (IRAN); Kermanshah, 55 km Kangavar to Hamedan, 24.vii.2010, *Pahlevani & Asef* 54789 (IRAN); Kermanshah, Ravansar, 8 km to Paveh, Shamshir Village, Shahoo Mt., 26.vii.2010, *Pahlevani & Asef* 54792 (IRAN); **Hamedan:** 35 km N Nahavand Mt., 15.vii.1974, *Termeh & Moussavi* 44566 (IRAN); **West Azarbaijan:** 70 km Mahabad to Urmieh, 17.vii.1997, *Sangari & Tehrani* 44584 (IRAN); 14 km Khoy to Qotur, 20.viii.2007, *Pahlevani & Amini Rad* 47783 (IRAN); **Ilam:** Ilam to Saleh Abad, Mahdi Abad, 23.vi.2007, *Eskandari*, *Shirzadian*& *Bahramishad* 47348 (IRAN); **Lorestan:** Borujerd, Tangeh Loveh, Absardeh, 22 km SW Borujerd, 21.viii.1997, *Moussavi Tehrani* 47870 (IRAN).

***Euphorbia malleata* Boiss. Iran. Yazd:** Mehriz, Asiab Anjirak (Mazrir-abad), 19.viii.1990, *Dehghanizadeh* 134 (HSBU); **Esfahan:** 25 km SW Natanz, Karkas Mt., 24.vii.2003, *Akhani* 17148 (IRAN, Hb. Akhani); Kashan, Abiyaneh, Tordal, 7.vii.1984, *Moussavi & Tehrani* 44540 (IRAN); Kashan, Abiyaneh, anonymous, 47928 (IRAN); Natanz, Keshe Village,

Karkas Mt., 26.vii.2009, *Pahlevani & Bahramishad* 53334 (IRAN); Natanz, Keshe Village, around the Karkas Mt., 26.vii.2009, *Pahlevani & Bahramishad* 53358 (IRAN); Natanz, Targh, Keshe Village, Karkas Mt., 24.viii.2010, *Pahlevani & Bahramishad* 54891 (IRAN); Kashan, Ghamsar, Ghohroud, 25.viii.2010, *Pahlevani & Bahramishad* 54893 (IRAN).

Euphorbia marschalliana **Boiss. Iran. East Azarbaijan:** Tabriz, Shater Ali, 27.v.1971, *Iranshahr* 18114 (IRAN); 5 km Tasuj to Shabestar, Sea Shores, 23.v.1997, *Termeh*, *Sangari & Tehrani* 44569 (IRAN); 10 km Marand to Jolfa, 13.vi.2007, *Pahlevani & Asef* 47882 (IRAN); 75 km Tabriz to Ahar, 11.vi.2007, *Pahlevani & Asef* 47883 (IRAN); 10 km Oskou to Kandovan, 14.vi.2010, *Pahlevani & Asef* 54574 (IRAN); Ajabshir, W Danalou Village, 11.v.2011, *Pahlevani & Fritsch* 56265 (IRAN); Lake Urmieh, Ashk Island, 3–5.vi.1983, *Zehzad* 83374 (HSBU); Urmieh, Golmankhaneh port, 1.vi.1983, *Zehzad* 831025 (HSBU); Marand, Galinghieh, Kuh-e Lachinghieh, 8.v.1996, *Ehsani* 13477 (FAR, IRAN); **West Azarbaijan:** Maku, Buralan, 22.viii.2007, *Pahlevani & Amini Rad* 47791 (IRAN).

Euphorbia mazandaranica **Pahlevani Iran. Mazandaran:** Shirgah forest, 35 km to Ghaemshahr, 13.v.1993, *Soleimani* 4114 (FAR, IRAN); 5 km Chalus to Karaj, Fian Park, 22.v.2008, *Pahlevani & Eskandari* 47539 (IRAN); same locality, 17.v.2007, *Pahlevani & Eskandari* 55150 (IRAN).

Euphorbia microsciadia **Boiss. Iran. Esfahan:** 12 km W Boin, Daran to Aligudarz, 10.vi.1974, *Iranshahr* 18017 (IRAN); Esfahan, Ghaleh Baba Mohammad, Golestan Kuh, 9.vii.1984, *Moussavi & Tehrani* 47306 (IRAN); Shahreza, 10 km Borujen, 31.v.1974, *Iranshahr* 47896 (IRAN); Shahreza to Semirom, 3 km Malek Cham, 15.v.2010, *Asef & Torabi* 55426 (IRAN); Mehrgherd, Sakkez, 20.vi.1986, *Zehzad* 862073 (HSBU); **Yazd:** 60–70 km W Ardestan, Abiazand to Rahmat Abad, 27.v.1974, *Iranshahr* 47900 (IRAN); **Fars:** Ardakan, 19.vii.1964, *Haghighi* 47946 (IRAN); Abadeh to Shahreza (Dasht), 2.vi.1969, *Termeh & Izadyar* 47947 (IRAN); 10 km Abadeh to Shahreza, 29.v.2009, *Pahlevani & Bahramishad* 53826 (IRAN); **Bakhtiari:** Shahr-e Kord, 19.vi.1986, *Zehzad* 862684 (HSBU).

Euphorbia monostyla **Prokh. Iran. Khorasan:** Jangal Golestan, Dasht-e Kalpush, 16.iv.1995, *Tehrani & Karavar* 47220 (IRAN); Golestan National Park, Dasht-e Kalpush to Ghez Ghaleh, 15.v.1992, *Matin & Termeh* 47987 (IRAN); **Golestan:** Jangal Golestan, Tunel, 29.iv.1978, *Daneshpajuh* 47976 (IRAN).

Euphorbia myrsinites **L. Iran. Tehran:** Karaj to Qazvin, Khur to Fashand, 22.v.1976, *Moussavi & Tehrani* 17828 (IRAN); 33 km Karaj to Qazvin, Aghasht, 18.v.1975, *Termeh & Matin* 18196 (IRAN); Karaj, Baraghan, 26.v.1984, *Moussavi & Karavar* 47441 (IRAN); **Qazvin:** Qazvin to Moallem Kelaye, 17 km NE Qazvin, Chenar Khani, 1.vi.1997, *Moussavi*, *Tehrani & Karavar* 47872 (IRAN); **Zanjan:** Dandi to Takab, Anguran mine, Belgheis Mt., 6.vi.2012, *Amini Rad & Torabi* 58612 (IRAN).

Euphorbia orientalis **L. Iran. Tehran:** 6 km Fasham to Lashgarak, 2.vii.1975, *Moussavi* 17851 (IRAN); between Karaj & Tehran, Kuh-e Dashteh, 22.vi.1985, *Assadi et al*., 55283 (TARI); **West Azarbaijan:** Maku, Buralan, 22.viii.2007, *Pahlevani & Amini Rad* 47794 (IRAN); **East Azarbaijan:** Ahar, Godjebel Mt., 13.viii.1968, *Termeh* 47951 (IRAN).

Euphorbia osyridea **Boiss. Iran. Hormozgan:** Marz, Mamanak, Kuhe Sefid (Bashagerd), 12.iii.1978, *Moussavi & Tehrani* 17860 (IRAN); **Bushehr:** 13 miles Asalouyeh to Bandar Taheri, 21.ii.1975, *Iranshahr & Termeh* 18142 (IRAN); Borazjan, Dalaki to Bushkan, from Tange Eram between Faryab & Kheyrak (Abegarm Shekarak, Kheyrak), 25.iv.1995, *Mozaffarian* 74157 (TARI); **Sistan & Baluchestan:** Baluchestan**,** 60–63 km from Iranshahr on road to Khash, 6.iii.1977, *Runemark et al*. 22226 (TARI); Baluchestan, 20 km from Khash to Iranshahr, 12.iv.1983, *Mozaffarian* 42794 (TARI); Baluchestan, Khash to Mirjaveh, Sangun, Ladiz, 27 km N Doruk, 29.iv.1983, *Termeh*, *Moussavi & Tehrani* 47245 (IRAN); Baluchestan, Khash, Karvandar, 85 km N Iranshahr, 28.ii.2000, *Moussavi*, *Sangari & Tehrani* 47387 (IRAN); **South Khorasan:** 100 km E of Birjand, Ahangaran Mt., 7 km NNW of Zeidan, 1.vi.1977, *Runemark & Sardabi* 23721 (TARI); between Taybad & Khaf, after Karat, 18.v.2003, *Assadi & Amirabadi* 84627 (TARI); **Fars:** 8 km S of Lar, 16.iii.1983, *Assadi & Sardabi* 41721 (TARI).

Euphorbia plebeia **Boiss. Iran. Fars:** Kuh-e Delu, 10.vi.1842, *T.Kotschy* 469 (W).

Euphorbia polycaulis **Boiss. Iran. Markazi:** Arak, 6 km S of Arak, W of Senejan, Farajollah Mt., 29.v.1986, *Akhani* 1395 (HSBU); Arak, Lateh Dar, 11.v.2008, *Sajedi*, *Javadi & Torabi* 51408 (IRAN); Arak, Shazand, 12.v.2008, *Sajedi*, *Javadi & Torabi* 51409 (IRAN); **Zanjan:** Qazvin to Hamedan, Soltan Bulagh, 15.vi.1956, *Sabeti* 17727 (IRAN); Zanjan, Mahneshan, Taghi Kandi Mt., 24.vi.1983, *Moussavi*, *Habibi & Tehrani* 47468 (IRAN); **Tehran:** Karaj, Eshtehard, Kuhe Kordha, 23.v.1968, *Termeh* 17730 (IRAN); Taleghan, Kuhhaye Assalak, 17.viii.1991, *Termeh*, *Moussavi & Tehrani* 47385 (IRAN); **Esfahan:** Kashan, Ghamsar, Ghazaan, 19.v.1970, *Iranshahr* 18052 (IRAN); 87 km W Najaf Abad to Daran, 10.vi.1974, *Iranshahr* 18055 (IRAN); Khansar, Ghaleh Bala Mohammad, Golestan Kuh, 9.vii.1984, *Moussavi & Tehrani* 44539 (IRAN); Golpayegan, Golestan Kuh, 31.v.2000, *Djavadi & Ghanbari* 47204 (IRAN); Kashan, Ghamsar, Ghohroud, Kargez

Mt., 25.viii.2010, *Pahlevani & Bahramishad* 54892 (IRAN).

Euphorbia sahendii **Bornm. Iran. East Azarbaijan:** Tabriz to Bostan Abad, Iranagh Matanagh, Ghoush Goli, Sahand Mt., 17.viii.2007, *Pahlevani & Amini Rad* 47845 (IRAN).

Euphorbia seguieriana **Neck. Iran. East Azarbaijan:** Tabriz, Osku, Kandovan, Anish, kuhe Nour, 8.viii.1984, *Termeh & Moussavi* 47295 (IRAN); Bostan Abad, Pishiklu to Chini Bulagh, 4 km Pishiklu, 1.viii.1984, *Termeh & Moussavi* 47297 (IRAN); Asheghlu to Siah Rud, 5 km Siah Rud, 9.vi.2007, *Pahlevani & Asef* 47806 (IRAN); **Ardebil:** Namin, Anbaran Olia, 14.ix.2007, *Eskandari & Torabi* 47840 (IRAN); Ardebil, Meshkin Shahr, Anzan, 12.ix.2007, *Eskandari & Torabi* 47841 (IRAN).

Euphorbia spartiformis **Mobayen Iran. Hormozgan:** Bandar Abbas to Sirjan, Ghotb Abad, Kuhe Tunel, 9.iii.1971, *Iranshahr & Termeh* 18096 (IRAN); 55 km Haji Abad to Bandar Abbas, Kuhe Tunel, Tangeh Zagh, 13.iii.2009, *Pahlevani*, *Eskandari & Bahramishad* 55156 (IRAN).

Euphorbia spinidens **Bornm. ex Prokh. Iran. Khorasan:** Fariman, Shahan Garmab, Aftar, Sefidsang, 25.iv.1984, *Ayatollahi & Mahvan* 10824 (FUMH, IRAN); Sarakhs, Bazengan Road, 27.iv.1984, *Rezaei & Mahvan* 10877 (FUMH, IRAN); 37 km Mashhad to Kalat, 30.iv.2005, *Safavi* 47458 (IRAN); Mozduran to Sarakhs, 1.vi.2001, *Djavadi & Ghanbari* 47929 (IRAN); Chenaran, Boghmeg Village, *Basiri* 55372 (IRAN); Bojnurd, Arkan Village, Zarghum, Aladagh Mt., 26.v.2007, *Gholipour* 47861 (IRAN).

Euphorbia squamosa **Willd. Iran. East Azarbaijan:** Arasbaran Protected Area, Oskolou to Ilankesh, 18.vi.2010, *Pahlevani & Asef* 54570 (IRAN); Arasbaran Protected Area, Doghrun & Kalan Mts., 14.vii.1977, *Assadi & Sardabi* 24139 (TARI); Arasbaran Protected Area, Kalan, along Barazeh-Tchay valley, 1.vii.1983, *Zehzad & Madjnonian* 83953 (HSBU); **Ardebil:** Khalkhal to Asalem, 17 km to Asalem, 23.vi.2010, *Pahlevani & Asef* 54565 (IRAN).

Euphorbia sulphurea **Pahlevani Iran. Sistan & Baluchestan:** Kuh-e Garoh, in Taftan massive, 8.vi.1937, Alfons & Agnes Gabriel 115 (B); Zahedan to Khash, Tamendan, Taftan Mt., 29.v.1985, *Mozaffarian* 53068 (TARI).

Euphorbia teheranica **Boiss. Iran. Tehran:** 15 km SE Tehran to Amin Abad, 17.v.1974, *Rechinger & Iranshahr* 18180 (IRAN); Karaj, Qazvin road, Soheilieh, Ramandeh village, 10.vi.2009, *Pahlevani* 53852 (IRAN); Tehran, S of Park-e Chitgar, 12.vi.1994, *Sharifi* 4417 (FAR, IRAN); Tehran, Evin, at the hills to the NW of the National University of Iran (Melli) campus, 20.vi.1982, *Zehzad & Azizian* 82680 (HSBU); *c.* 75 km S of Tehran on road to Qom, 13.v.1974, *Wendelbo & Foroughi* 11389 (TARI); **Semnan:** 30 miles E Semnan, 7.vii.1972, *Iranshahr* 44548 (IRAN); Semnan, 20 km Momen-abad from Firouzkuh, 29.v.2012, *Pahlevani* 57192 (IRAN).

Euphorbia virgata **Waldst. & Kit. Iran. Tehran:** 20 km NE Karaj to Chalus, 20.vi.1977, *Eghtedari* 17993 (IRAN); 5 km Firuzkuh to Semnan, 26.vi.2007, *Pahlevani*, *Amini Rad & Torabi* 47354 (IRAN); **Hamedan:** *c.* 16 km from Ganjnameh to Tuyserkan, 9.vii.1981, *Assadi & Mozaffarian* 36891 (TARI); **Semnan:** *c.* 50 km N of Semnan, Mt. above Hiku, 29.vii.1982, *Assadi & Mozaffarian* 40738 (TARI); **Kordestan:** Bijar, Kuhe Hamzeh Arab, 1.vii.1971, *Termeh* 44200 (IRAN); **East Azarbaijan:** 18 km Tabriz to Marand, 27.vii.1971, *Termeh* 44512 (IRAN); Ahar, Kuhe Garma Douz, 1.viii.1968, *Termeh* 47950 (IRAN); **Zanjan:** 140 km SE Zanjan to Hamedan, Kuhe Takht, 6.vii.1974, *Termeh & Moussavi* 44515 (IRAN); **Lorestan:** Borujerd, Vanaee, 29.vi.2007, *Eskandari*, *Shirzadian & Bahramishad* 47346 (IRAN); **West Azarbaijan:** 10 km E Urmieh, Golmarz, 19.vi.2012, *Eskandari & Bahramishad* 58610 (IRAN).

APPENDIX 2

List of species used in the phylogenetic analysis of *Euphorbia* in Iran with their classification according to recent molecular phylogeny by Riina *et al*. (2013), vouchers for newly generated sequences and GenBank accession numbers.

Taxon	Section and subsection	Locality	Voucher	ITS Gen	*ndhF* Gen
E. acanthodes Akhani	*Pithyusa*	Iran		KC212160	–
E. aleppica L.	*Myrsiniteae*	Iran		KC212166	KC212438
E. amygdaloides L.	*Patellares*	Bosnia		JN010024	KC212439
E. amygdaloides L.	*Patellares*	USA, cultivated		JN250111	JN249101
E. arvalis ssp. *arvalis* Boiss. & Heldr.	*Arvales*	Iran		KC212177	KC212442
E. aserbajdzhanica Bordz.	*Herpetorrhizae* § *Oppositifoliae*	Iran		KC212180	KC212444
E. aucheri Boiss.	*Herpetorrhizae* § *Aucheriae*	Iran		KC212181	KC212446
E. aulacosperma Boiss.	*Arvales*	Iran: Mazandaran, Kelardasht, Sardabe Rud to Telochal, 18.v.2007	*Pahlevani & Eskandari 47337 (IRAN)*	LN680638	LN680647
E. aulacosperma Boiss.	*Arvales*	Iran: Semnan, Parvar Protected Area, Molla Deh, Hiku, 27.v.2009	*Eskandari 53764 (IRAN)*	LN680639	LN680648
E. buhsei Boiss.	*Esula*	Turkmenistan		KC212197	–
E. bungei Boiss.	*Sclerocyathium*	Iran		KC212199	KC212460
E. caeladenia Boiss.	*Sclerocyathium*	Iran		KC212200	KC212461
E. chamaepeplus Boiss. & Gaill.	*Tithymalus*	Jordan: Maan, 17.iv.2000	*M. Staudinger 209a18 (W)*	LN680640	LN680649
E. cheiradenia Boiss. & Hohen.	*Pithyusa*	Iran		KC212471	–
E. condylocarpa M. Bieb.	*Helioscopia*	Iran		KC212208	KC212473
E. connata Boiss.	*Calyptratea*	Iran		KC212211	KC212475
E. consanguinea Schrenk	*Herpetorrhizae* § *Oppositifoliae*	Turkmenistan		KC212212	–
E. craspedia Boiss. (sub. *E. denticulata* Lam.)	*Myrsiniteae*	Iran		–	KC212488
E. craspedia Boiss.	*Myrsiniteae*	Iran		KC212213	KC212477
E. deltobracteata (Prokh.) Prokh.	*Herpetorrhizae* § *Aucheriae*	Iran		KC212218	KC212482
E. densa Schrenk	*Herpetorrhizae* § *Oppositifoliae*	Iran		KC212220	KC212483
E. denticulata Lam.	*Myrsiniteae*	Iran		HQ900601	–
E. eriophora Boiss.	*Helioscopia*	Iran		KC212238	–
E. eriophora Boiss.	*Helioscopia*	Iran: Chaharmahale Bakhtiari, Farsan, Dehe Cheshme toward Gushe village, 7.vi.2010	*V. Mozaffarian 97361 (TARI)*	LN680641	LN680650
E. erubescens Boiss.	*Patellares*	Iran		KC212240	KC212501
E. erythradenia Boiss.	*Pithyusa*	Iran		KC212241	–
E. falcata L.	*Pithyusa*	Bulgaria		JN010046	KC212507
E. franchetii B. Fedtsch.	*Arvales*	Iran		KC212256	KC212516
E. ferdowsiana Pahlevani	*Sclerocyathium*	Iran: Khorasan, W of Mashhad, Golmakan, Cheshme sabz, Binaloud Mt., 3.viii.1992	*Ayatollahi & Zangoei 22585 (IRAN)*	LN680642	LN680651
E. gedrosiaca Rech.f., Aellen & Esfand.	*Pithyusa*	Iran		KC212259	–
E. glareosa Pall. ex M.Bieb.	*Pithyusa*	Austria		JN010050	KC212522
E. glareosa Pall. ex M.Bieb.	*Pithyusa*	Iran: W. Azerbaijan, Maku, 5.v.1971	*K. Rechinger 39198 (W)*	LN680643	LN680652

Appendix 2 *Continued*

Taxon	Section and subsection	Locality	Voucher	ITS Gen	*ndhF* Gen
E. grisophylla M.S.Khan	*Helioscopia*	Iran: Sanandaj to Kamiaran, Avalan Mt., 7.vi.2009	*Maroofi 55797 (IRAN)*	LN680644	LN680653
E. grossheimii (Prokh.) Prokh.	*Sclerocyathium*	Iran		KC212266	KC212529
E. gypsicola Rech.f. & Aellen	*Pithyusa*	Iran		KC212268	KC212530
E. hebecarpa Boiss.	*Esula*	Iran		KC212270	KC212532
E. helioscopia L.	*Helioscopia*	Austria		JN010052	KC212533
E. heteradena Jaub. & Spach	*Chylogala*	Iran		KC212273	KC212537
E. iberica Boiss.	*Esula*	Iran		KC212275	KC212540
E. inderiensis Less. ex Kar. & Kir.	*Herpetorrhizae* § *Oppositifoliae*	Iran		KC212277	KC212544
E. kopetdaghi (Prokh.) Prokh.	*Pithyusa*	Turkmenistan		JN250177	JN249167
E. larica Boiss.	Subgen. *Athymalus*	Oman		HQ900620	KC212430
E. macrocarpa Boiss. & Buhse	*Helioscopia*	Iran		KC212297	KC212558
E. macroceras Fisch. & C.A.Mey	*Patellares*	Georgia		JN010062	KC212560
E. macroclada Boiss.	*Pithyusa*	Iran		–	KC212562
E. malleata Boiss.	*Pithyusa*	Iran		–	KC212563
E. marschalliana Boiss.	*Myrsiniteae*	Iran		JF732971	–
E. mazandaranica Pahlevani	*Helioscopia*	Iran		KC212304	KC212567
E. microsciadia Boiss.	*Pithyusa*	Iran		KC212312	KC212572
E. microsphaera Boiss.	*Helioscopia*	Iran		KC212313	–
E. monostyla Prokh.	*Myrsiniteae*	Iran: Golestan, Maravetappeh, 14.v.2009	*Pahlevani 53763 (IRAN)*	LN680645	LN680654
E. myrsinites L.	*Myrsiniteae*	Bosnia		JN010069	KC212576
E. orientalis L.	*Helioscopia*	Cultivated		EU659764	–
E. osyridea Boiss.	*Esula*	Iran		KC212326	–
E. peplus var. *minima* DC.	*Tithymalus*	Croatia		JN010076	KC212597
E. peplus var. *peplus* L.	*Tithymalus*	Spain		HQ900643	–
E. phymatosperma Boiss. & Gaill.	*Lagascea*	Iran		KC212336	KC212599
E. plebeia Boiss.	*Pithyusa*	Iran		JF732978	–
E. polycaulis Boiss. & Hohen.	*Pithyusa*	Iran		KC212342	KC212604
E. rhabdotosperma Radcl.-Sm.	*Helioscopia*	Georgia		KC212360	KC212618
E. sahendi Bornm.	*Pithyusa*	Iran		KC212365	KC212621
E. seguieriana Neck.	*Pithyusa*	France		KC212377	KC212631
E. spartiformis Mobayen	*Pithyusa*	Iran		KC212379	–
E. spinidens Bornm. ex Prokh.	*Myrsiniteae*	Iran		–	KC212638
E. squamosa Willd.	*Helioscopia*	Russia		GU937804	–
E. stricta L.	*Helioscopia*	Bosnia		JN010104	KC212649
E. sulphurea Pahlevani	*Pithyusa*	Iran: Sistan & Baluchestan, Tamendan, Taftan Mts., 23.v.2009	*Pahlevani & Bahramishad 55151 (IRAN)*	LN680646	LN680655
E. szovitsii Fisch. & C.A.Mey.	*Szovitsiae*	Iran		KC212402	KC212654
E. teheranica Boiss.	*Pithyusa*	Iran		KC212406	KC212658
E. turczaninowii Kar. & Kir.	*Herpetorrhizae* § *Oppositifoliae*	Iran		KC212416	KC212668
E. turkestanica Regel.	*Sclerocyathium*	Turkmenistan		KC212417	–
E. virgata Waldst. & Kit.	*Esula*	Iran		KC212423	KC212681

§, subsection.

Publication 3

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ORIGINAL ARTICLE

Molecular and morphological studies disentangle species complex in *Euphorbia* sect. *Esula* (Euphorbiaceae) from Iran, including two new species

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Abstract Southwest Asia is one of the most important centers of diversity for leafy spurges (*Euphorbia* subgen. *Esula*), and Iran is one of the richest countries both for species and endemics in the subgenus. Section *Esula*, the second largest of the 21 sections of this subgenus, comprises *c*. 96 taxonomically and phylogenetically poorly understood species with complicated patterns of morphological variation. The *Euphorbia osyridea* alliance is an Iranian-centered group harboring the well-known endemic and semi-endemic species, *E. buhsei*, *E. osyridea*, and two poorly understood and yet undescribed taxa. In a phylogenetic framework based on nuclear ribosomal ITS (internal transcribed spacer) and plastid *ndh*F sequences, inter-simple sequence repeat (ISSR) polymorphisms were used to investigate genetic structure and genetic diversity in seven populations of the endemic and semi-endemic species of *E. osyridea* alliance. Phenetic analysis (principal component analysis) was used to assess morphological differentiation of the alliance. Neither nuclear nor plastid sequences provided sufficient resolution to disentangle the diversification patterns within the *E. osyridea* alliance. The combined evaluation of phylogenetic study, ISSR analysis, and morphological data confirmed that studied populations of *E. osyridea* alliance can be divided into four different groups including two new endemic species, *E. khabrica* sp. nov. and *E. austro-iranica* sp. nov. Typification, description, data on distribution and habitats, key to species as well as pertinent comments are given.

Keywords DNA finger printing · Endemic · *Euphorbia* · Genetic structure · ISSR · Phylogeny

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Introduction

The cosmopolitan genus *Euphorbia* L. (Euphorbiaceae), with approximately 2000 species, represents one of the largest genera within angiosperms (Webster 1994; Govaerts et al. 2000). Members of this genus are adapted to a wide range of habitats, occurring from the rainforest to very hot and dry deserts or severe environments in alpine regions (Pearcy and Troughton 1975; Pahlevani et al. 2015). The morphological diversity in *Euphorbia* varies from ephemeral species to up to 20-m-tall phanerophytes (Horn et al. 2012). Recent molecular studies have revealed four main evolutionary lineages within *Euphorbia*, corresponding to four monophyletic subgenera: *Euphorbia*, *Chamaesyce* Raf., *Athymalus* Neck. ex Reichb., and *Esula* Pers. (Steinmann and Porter 2002; Bruyns et al. 2006; Zimmermann et al. 2010; Horn et al. 2012). Following

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molecular infrageneric studies, some species-level relationships and sectional divisions have been developed for all four subgenera (Yang et al. 2012; Dorsey et al. 2013; Peirson et al. 2013; Riina et al. 2013; Peirson et al. 2014).

Subgenus *Esula* or leafy spurges with roughly 485 species and 21 sections are mostly distributed in the temperate regions of the northern hemisphere in the Old World with hot spots in SW and Central Asia, Caucasus, and the Mediterranean region (Riina et al. 2013; Pahlevani and Riina 2014; Geltman 2015). These plants are mostly perennial (*c*. 387 species) and annual (*c*. 70 species) herbs and rarely shrubs, subshrubs, or succulents (28 species). Of the 21 sections of subgenus *Esula*, 18 with approximately 260 species occur in SW Asia and the Mediterranean region, an area considered as cradle for lineage diversification in many different groups of flowering plants (Takhtajan 1987; Geltman 2015). Turkey and Iran are the most species-rich countries with *c*. 83 and 76 species, respectively. Among the four subgenera, leafy spurges are considered as the most uniform group in growth form and morphology (Horn et al. 2012); therefore, recognition and identification especially at species level are often difficult in both nature and herbarium.

Section *Esula* with *c*. 96 species is the second largest section of subgenus *Esula* after sect. *Helioscopia* with *c*. 136 species (Riina et al. 2013; Hand et al. 2015). Species of sect. *Esula* are usually perennial herbs, or occasionally small shrubs, most of which are native to Eurasia and few species to Africa and New Zealand (Kuzmanov 1964; Radcliffe-Smith and Tutin 1968; Molero and Rovira 1992; Riina et al. 2013; Geltman 2015). Most problematic and notorious species in subgenus *Esula* belong to sect. *Esula* and constitute either invasive plants outside their natural habitats or weeds in their native regions (Crompton et al. 1990; DiTomaso and Healy 2007; Pahlevani 2007). One of the most outstanding examples is *E. virgata* Waldst. & Kit. which was introduced to North America from Europe and Asia since the nineteenth century with contaminated seed grains. This species then spread to some parts of Canada (Hanson and Rudd 1933; Carmichael and Selbo 1999). It occupies a wide range of habitats including meadows, rangelands, fields, pastures, recreational parks, roadsides, and disturbed areas. It is also toxic to some animals and reduces the livestock and cattle carrying capacity of pasture and rangeland by 20–50%. Some species of sect. *Esula* in the New World have been targeted for extensive biological control programs in both Canada and the USA (Harris 1984; Watson 1985). Likewise, some hybrids have been reported between species of this group, making their taxonomy difficult (Hegi and Beger 1924; Zimmermann 1924; Soo 1925, 1930; Prodan 1953). On the other hand, sect. *Esula* also harbors some rare and isolated species with very fragile habitats and restricted areas requiring coherent plans for their conservation (Pahlevani et al. 2015). Seven species of sect. *Esula*: *E. hebecarpa*, *E. iberica*, *E. virgata*, *E. buhsei*, and *E. osyridea*, as well as two new species described in this paper (*E. austro-iranica* sp. nov. and *E. khabrica* sp. nov.) occur in Iran. Of these, five (*E. hebecarpa*, *E. buhsei*, *E. osyridea* and *E. khabrica* and *E. austro-iranica*) are endemic to some parts of SW Asia, and the last four are informally known as the morphologically closely related *Osyridea* group. *Euphorbia iberica* is more widespread in the Caucasus, NW Iran, and parts of Turkey and Iraq while *E. virgata* constitutes a very widespread weedy species.

Recent molecular phylogenetic works using ITS, *ndh*F, and *trnT-trnF* of some species of sect. *Esula* (Frajman and Schönswetter 2011; Riina et al. 2013) show that not only morphology, but also phylogeny is poorly understood because resolution using the above markers is insufficient (Fig. 5d in Riina et al. 2013). To resolve these relationships, other complementary methods such as DNA fingerprinting could be useful. Recently, DNA fingerprinting markers have been employed successfully for studies of natural populations of plants, fungi, insects, and some animal groups (Wolfe 2005). They are also suited to disentangle the genetic and ecogeographical variation within species. Among the various DNA fingerprinting markers, ISSR markers (inter-simple sequence repeat) have been introduced in 1994 (Gupta et al. 1994; Zietkiewicz et al. 1994) for studies of cultivated plants, but later ISSR was used for many different kinds of biological studies such as hybridization, population and conservation genetics, systematics, and taxonomy applied to natural populations (Wolfe et al. 1998; Esselman et al. 1999; Crawford et al. 2001; Culley and Wolfe 2001; Wolfe and Randle 2001; Mort et al. 2003; Archibald et al. 2004; Agarwal et al. 2008; Cichorz et al. 2014). So far, DNA fingerprinting methods have been used only three times in *Euphorbia*, including RAPD, microsatellite, and AFLP markers (Morden and Gregoritza 2006; Durka 2009; Hastilestari et al. 2013). Among those markers, RAPD is less informative and reproducible than ISSR (Jones et al. 1997), while the two other methods need fresh plant material and involve costly laboratory procedures. Thus, this is the first time ISSR markers are used for taxonomic purposes in *Euphorbia*.

Iran is a vast country with approximately 1.65 million km^2 and is the fifth largest country in Asia with mostly arid and semiarid climates. Topographical and bioclimatical diversity has created interesting and complex ecosystems with rich miscellaneous plant species (Hedge and Wendelbo 1978). More than 54% of the country is covered with mountainous regions comprising 16,000 mountains (Anonymous 2002). A depression about 26 m below sea level at the Caspian sea shore, freshwater and saltwater

lakes, rift valleys, volcanic cones (Taftan and Sabalan peaks), sandy dunes, gypsum hills, and hammadas altogether make the plateau of Iran one of the largest centers of speciation for arid flora in the holarctic region (Zohary 1963). Iran is well known as a bridge between three continents: Europe, Asia, and Africa. This situation plus plenty of mountains, unique geobotanical situation, as well as different bioclimatic zones, created a large number of areas with high degrees of endemism and subendemism, many of them with protected status. There are approximately 7400 species in Iran, distributed in three phytogeographical zones: the Irano-Turanian, Euro-Siberian and Saharo-Arabian (sensu Zohary 1973) or Sudano-Zambezian (sensu Takhtajan 1986) zones, of which the two last ones are related to N Iran near the Caspian Sea and S Iran near the Persian Gulf, respectively.

The present paper endeavors to clarify the systematics of sect. *Esula* in Iran and aims (1) to test whether ISSR markers are useful to separate closely related species in *Euphorbia*; (2) to evaluate genetic diversity between Iranian populations in the *Osyridea* group of sect. *Esula* with ITS, *ndh*F, and ISSR fingerprinting; (3) to study morphological and phenetic relationships using principal component analysis; and (4) to provide a key to all Iranian species of sect. *Esula*. Based on our results, we describe two morphologically and phylogenetically distinct populations as two new species.

Materials and methods

Morphological study

Plant material

Eighteen populations of four species of *E. buhsei*, *E. austro-iranica* sp. nov., *E. khabrica* sp. nov., and *E. osyridea* were used for morphometric and phenetic analyses. Selected herbarium specimens or newly collected specimens from different parts of Iran (if available) were used to cover the taxonomic and geographic range of the group. Details of localities as well as voucher specimens are given in the taxonomic treatment below and in Table 1.

Morphometry

Based on the available literature and on our own unpublished results, 23 quantitative (13) and qualitative (10) morphological characters were used for morphometric and phenetic analysis (Table 2). The characters and character states were determined by the examination of all materials of the mentioned species housed in IRAN and TARI herbaria as well as newly collected specimens (Table 1). All repetitions (2–9) of each population were measured for selected morphological characters, and for quantitative features, the mean of all repetitions was taken to represent each population. Both quantitative and qualitative characters were coded as binary state (Table 1).

Phenetic analysis

The data matrix was scored using binary coding, and a dissimilarity matrix of morphological characters was calculated using the Statistical Package for the Social Sciences (SPSS) software package version 18 (George and Mallery 2010). In order to determine the most variable characters among species, factor analysis based on PCA (principal component analysis) was performed on standardized data and Varimax rotation was carried out to provide minimum number of influencing variables on each factor making results interpretation easier (Manly 1991). A scatter graph was prepared to show phenetic relationships among the studied taxa.

Phylogenetic studies

Plant material

Fourteen individuals of four species (*E. austro-iranica* sp. nov., *E. buhsei*, *E. khabrica* sp. nov., and *E. osyridea*) were considered for molecular analyses (Online Resources 1, 2). The specimens studied were from herbarium materials or newly collected samples. The DNA sequence dataset was complemented with 47 existing accessions of sect. *Esula* used by Riina et al. (2013) as well as *E. lathyris* as outgroup (Online Resources 1, 2). In total, ITS sequences of 62 accessions and *ndh*F sequences of 63 accessions comprising 48 species were analyzed.

ITS and ndhF sequence analysis

Total genomic DNA of four species, *E. buhsei*, *E. osyridea*, *E. austro-iranica* sp. nov., and *E. khabrica* sp. nov. with several populations (Online Resources 1, 2), were extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions, but adjusted by applying 5 µl of proteinase K at 20 mg/ml to deactivate the secondary compounds that occur in the genus (Barres et al. 2011). For total DNA isolation and amplification of the ITS region, we followed the protocol described in Kryukov et al. (2010), Barres et al. (2011), Riina et al. (2013), and Pahlevani et al. (2015). We tried to amplify the chloroplast *ndh*F gene as two overlapping fragments using primers 536f and 1318r (Olmstead and Sweere 1994) for the 5′ region, and primers 1000f (Riina et al. 2013) and 2110ri (Steinmann and Porter 2002) for the

Table 1 Basic morphological data matrix of taxa of four *Euphorbia* section *Esula*

Taxa	Province/voucher	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
E. austro-iranica	Baluchestan, *Moussavi* and *Tehrani 47288* (IRAN)	1	1	1	1	1	1	1	0	2	1	0	0	1	0	0	0	1	0	1	0	0	1	1
E. austro-iranica	Hormozgan, *Iranshahr* and *Moussavi 17859* (IRAN)	1	1	1	1	1	1	1	0	2	1	0	0	1	1	0	0	1	0	1	0	0	1	1
E. austro-iranica	Kerman, *Iranshahr* and *Termeh 18138* (IRAN)	1	1	1	1	1	1	1	0	2	1	0	0	1	0	0	0	1	0	0	0	0	1	1
E. austro-iranica	Baluchestan, *Runemark* et al. *22226* (TARI)	1	1	2	1	1	1	1	0	2	1	0	0	1	1	0	0	1	0	0	0	0	1	1
E. buhsei	Tehran, *Iranshahr* and *Riedl 17767* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	2	0	1	1	2	0	0	0	0	0
E. buhsei	Yazd, *Eskandari 54351* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	3	0	1	1	2	0	0	0	0	0
E. buhsei	Baluchestan, *Pahlevani* and *Bahramishad 53823* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	2	0	1	1	2	0	0	0	0	0
E. buhsei	Fars, *Pahlevani* and *Bahramishad 53341* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	3	0	1	1	2	0	0	0	0	0
E. buhsei	Khorasan, *Pahlevani* et al. *47351* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	3	0	1	1	2	0	0	0	0	0
E. buhsei	Esfahan, *Pahlevani 57188* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	2	0	1	1	2	0	0	0	0	0
E. buhsei	Semnan, *Pahlevani 57193* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	2	0	1	1	2	0	0	0	0	0
E. buhsei	Kerman, *Pahlevani* and *Bahramishad 53830* (IRAN)	2	2	2	1	2	1	1	0	1	0	1	1	1	2	0	1	1	2	0	0	0	0	0
E. khabrica	Kerman, *Pahlevani* and *Bahramishad 55152* (IRAN)	2	3	2	2	3	2	1	2	0	0	1	1	2	4	1	2	2	3	2	1	1	0	2
E. osyridea	Baluchestan, *Moussavi* et al. *47387* (IRAN)	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	1	1	0	0	1	1
E. osyridea	Fars, *Iranshahr* and *Termeh 18134* (IRAN)	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	1	1	0	0	1	1
E. osyridea	Bushehr, *Kashkouli 17861* (IRAN)	0	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0	0	1	1	0	0	1	1
E. osyridea	Hormozgan, *Iranshahr* and *Moussavi 18140* (IRAN)	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	1	1	0	0	1	1
E. osyridea	S Khorasan, *Eskandari* and *Torabi 47655* (IRAN)	0	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0	0	1	1	0	0	1	1

Description and coding of characters and states from Table 2

3′ region. However, the second part of *ndh*F could not be amplified from our material, so that only ITS and the first part of *ndh*F are included for the specimens newly sequenced.

Data assembly and phylogenetic analyses

Sequences were edited and pre-aligned using CodonCode Aligner v.3.7.1 and subsequently adjusted manually. Sequence alignments were performed with Mesquite v.2.75 (Maddison and Maddison 2011) using the OPAL package (Wheeler and Kececioglu 2007). RAxML (Stamatakis et al. 2008) was used to conduct maximum likelihood (ML) phylogenetic analyses on the ITS, *ndh*F, and combined ITS + *ndh*F datasets. The nucleotide substitution model was set to GTR + γ as recommended by the RaxML manual; 100 ML bootstrap replicates were performed, followed by a thorough search for the best tree. For Bayesian (BI) analysis of ITS, *ndh*F, and the combined dataset, we used MrBayes v.3.1.2 (Huelsenbeck and

Table 2 Morphological characters and character states used in the phenetic analysis

No.	Characters	Character states
1	Life form	Shrub (0); shrublet (1); perennial herb (2)
2	Height of plant (cm)	More than 120 (0); 50–100 (1); 20–50 (2); less than 20 (3)
3	Stem color	Grayish (0); reddish-brown (1); greenish (2)
4	Stem indumentum	Tomentose (0); glabrous (1); pubescent to glabrescent (2)
5	Stem base diameter (mm)	3.5–5 (0); 3–3.5 (1); 1.8–3 (2); less than 1.5 (3)
6	Leaf shape	Linear-lanceolate (0); oblong-lanceolate to oblong (1); elliptic-oblong or elliptic-ovate (2)
7	Leaf apex	Acute (0); obtuse (1)
8	Leaf indumentum	Glabrous (0); tomentose (1); pilose (2)
9	Leaf width (mm)	6–10 (0); 3–5.5 (1); 1.5–3 (2)
10	Position of rays	Terminal (0); axillary (1)
11	Ray number	1–4 (0); 4–8 (1)
12	Ray-leaf number	2–4 (0); 4–8 (1)
13	Indumentum of cyathium	Hairy (0); glabrous (1); pubinervis to glabrescent (2)
14	Glands shape and color	Trapeziform, lacerate, light brown (0), lunate, lacerate to bilobate, ochreous (1); lunate, 2-horned, ochreous (2); trapeziform, truncate, brown (3); lunate, two-horned, dark purplish (4)
15	Capsule length (mm)	More than 3.7 (0); less than 3.5 (1)
16	Capsule width (mm)	More than 4.5 (0); 3.8–4.5 (1); less than 3.8 (2)
17	Capsule surface	Tomentose (0); glabrous (1); pilose to glabrescent (2)
18	Pedicel length (mm)	4.5–6 (0); 3.3–4.3 (1); 2.1–3 (2); less than 1.1 (3)
19	Style length (mm)	2–2.5 (0); 1.7–2 (1); less than 1.4 (2)
20	Seed length (mm)	2.7–3.5 (0); less than 2.7 (1)
21	Seed width (mm)	2.1–2.5 (0); less than 2 (1)
22	Caruncle length (mm)	0.8–1 (0); up to 0.6 (1)
23	Caruncle width (mm)	1.3–1.9 (0); 0.9–1.2 (1); 0.6–0.8 (2)

Ronquist 2001; Ronquist and Huelsenbeck 2003), using the nucleotide substitution model GTR + I+γ for ITS and *ndh*F following Riina et al. (2013). The process included four runs with four chains each run for 10,000,000 generations, saving one tree every 1000 generations. A relative burnin of 0.5 was set so that only the last 5000 trees of each run were used to estimate the 50% majority rule consensus tree and the Bayesian posterior probabilities.

ISSR genomic fingerprinting

Plant material

Seven populations of two known species of *Euphorbia* sect. *Esula* (*E. buhsei,* three populations; *E. osyridea,* two populations) and two newly described species (*E. austro-iranica,* one population; *E. khabrica,* one population) as well as a population of *E. mazandaranica* (sect. *Helioscopia*) as outgroup were sampled from seven Iranian provinces (Table 3). The specimens were sampled either from the field or from herbaria. For each population, ten individuals were collected, five of which were randomly selected. Whole plants and leaf tissues from each individual were collected. Leaves were placed in sealed plastic bags with silica gel for immediate drying and chilled (−30 °C) until DNA was extracted. The specimens were prepared based on established herbarium techniques, and voucher specimens were deposited in IRAN herbarium. All voucher data are indicated in Table 3.

Nucleic acid extraction and ISSR analysis

Total genomic DNA was isolated from dried leaf sections (up to 5 mm in square) using the NucleoMag^{TM} 96 Plant extraction kit (Machery-Nagel, Düren, Germany) and the FastPrep-24^{TM} Instrument (MP Biomedicals, Santa Ana, CA, USA) as described in Feulner et al. (2013).

Table 3 Voucher of population and individuals of four Iranian *Euphorbia* species section *Esula* used in ISSR DNA fingerprinting experiment

Taxon	Locality/coordinates	Individuals	Voucher	Habitat
E. buhsei	Semnan: 17 km Momen-abad to Firouzkuh; 35°36′N, 53°07′E	5	29 May 2012, *Pahlevani 57193* (IRAN)	Rocky slopes on gypsum hills
E. buhsei	S Khorasan: Birjand, N of Aryanshahr (Sedeh); 33°21′N, 59°15′E	5	6 May 2012, *Joharchi 44743* (FUMH)	Rocky slopes
E. buhsei	Esfahan: S Esfahan to Shahreza, Kolah-Ghazi Protected Area; 32°25′N, 51°47′E	5	31 May 2012, *Pahlevani 57188* (IRAN)	Rocky slopes
E. osyridea	S Khorasan: SW Torbate Jam, Miansara Mts.; 35°10′N, 60°17′E	5	23 May 2012, *Joharchi 34036* (FUMH)	Rocky slopes
E. osyridea	Hormozgan: Bandar-abbas, Kuh-e Geno; 27°25′N, 56°09′E	5	4 Apr 2012, *Pahlevani 1a*	Rocky slopes
E. austro-iranica	Baluchestan: Iranshahr to Bazman, 30 km NW Bazman, Govanz; 28°01′N, 60°04′E	5	22 Feb 1997, *Moussavi* and *Tehrani 47288* (IRAN)	Stony mountains
E. khabrica	Kerman: Baft, Khabr Protected Area, Dahaney-e Bahre Anjir; 28°51′N, 56°23′E	4	25 May 2009, *Pahlevani* and *Bahramishad 55152* (IRAN)	Rocky mountains on screes

For inter-simple sequence repeat (ISSR) analysis (Gupta et al. 1994), an initial set of 31 SSR primers (University of British Columbia primer set #9, Li et al. 2006) was analyzed by agarose gel electrophoresis for the appearance of polymorphic fragment patterns using genomic DNA from five selected plant samples. To find clear and reproducible bands, all primers were firstly evaluated based on band quality (clear, rather clear, unclear, negative and smear) and quantity (below 600 bp, between 600 and 1000 bp and above 1000 bp) using the GeneTools software (Synoptics Ltd.). Primers producing bands below 600 bp and between 600 and 1000 bp were considered superior to primers producing bands above 1000 bp. Six primers were selected for subsequent analysis, carrying a fluorescent label at the 5′-end (Table 4). ISSR fragments were amplified using 1 µl of purified genomic DNA, 10 µM SSR primer (for primer and annealing temperature, see Table 4), and the KAPA3G Plant Kit (Peqlab, Erlangen, Germany) in a 12.5 µl reaction volume (PCR profile: initial activation 95 °C/3 min, followed by 35–40 cycles at 95 °C/30 s, primer-specific annealing temperature/30 s, extension at 72 °C/30 s, followed by a final extension step at 72 °C/5 min). A combination of three ISSR reaction products (Table 4) was separated by capillary electrophoresis (CEQ 8000 Genetic Analysis System, Beckman-Coulter, Krefeld, Germany; now: ABSciex, Darmstadt, Germany) and scored using GeneMarker 1.95 (SoftGenetics, USA).

ISSR data analysis

A neighbor joining (NJ) analysis of the presence–absence (presence = 1 and absence = 0) matrix was conducted (Nei Li distance), followed by bootstrap (BS) analysis after internode rooting with 1000 replicates using the program TREECON (Van de Peer and De Wachter 1994). The tree was rooted with an *E. mazandaranica* individual from sect. *Helioscopia*. The number and the percentage of polymorphic loci, Nei's gene diversity, and Nei's genetic distance were calculated with the program POPGENE (Yeh and Yang 1999).

Results

Principal component analysis

Twenty-three vegetative and reproductive characters were identified for numerical analysis and phenetic relationships of existing Iranian populations of four *Euphorbia* species of sect. *Esula* (Table 2). Principal component analysis summarized the phenetic relationships between the taxa and displayed them in a non-hierarchical way (Fig. 1). Factor analysis of morphological data showed that the first three factors are responsible for about 97% of the total variance. The first factor accounts for *c*. 65% of total variance in which characters such as number of rays and ray-leaves, gland shape and color, and pedicel length revealed the highest positive correlation (>0.8). The second factor explains about 22.5% of total variance in which characters like stem indumentum, leaf shape and apex, indumentum of cyathium, and capsule surface showed the highest correlation (>0.9). Finally, the third factor accounts for almost 10% of total variance including characters with the highest correlation such as leaf indumentum, capsule length, and seed size (>0.9). Factor one separated populations of *E. osyridea* and *E. austro-iranica* from other populations of *E. buhsei* and *E. khabrica*, whereas factor two distinguished *E. osyridea* and *E. khabrica* from the other populations of *E. buhsei* and *E. austro-iranica*. Factor three also separated the single *E. khabrica* population from

Table 4 List of primers used in the ISSR experiment and subsequent selected ones with other information

SSR primer	Annealing temp. (°C)	Combined for CE	5′ Label
TF807	53		
TF810	51	Euphorbia 2	DY-751
TF815	51		
TF834	53	Euphorbia 1	BMN-6
TF835	53		
TF840	51		
TF842	53		
TF844	53		
TF857	51		
TF864	51		
TF931	48		
TF932	58		
UBC807	51		
UBC809	51		
UBC812	45		
UBC822	51		
UBC840	48	Euphorbia 2	BMN-5
UBC841	51		
UBC842	56	Euphorbia 1	DY-751
UBC845	45		
UBC848	51		
UBC850	45		
UBC857	45		
UBC859	45		
UBC861	58		
UBC881	51	Euphorbia 2	BMN-6
UBC885	45		
UBC888	51	Euphorbia 1	BMN-5
UBC889	51		
UBC890	56		
UBC891	51		

TF primers: (Li et al. 2006); UBC primers: University of British Columbia primer set #9

the other populations studied (Fig. 1). The most negative correlation indicated in factor one includes position of rays, leaf width, and caruncle length (<−0.8). The most important diagnostic characters of all four studied species are indicated in Table 5.

Phylogenetic studies

The maximum likelihood and Bayesian analyses revealed an identical result with both ITS and *ndh*F data. However, the inferred phylogenies differed between the nuclear ITS and *ndh*F plastid data. The *ndh*F and the combined ITS + *ndh*F trees indicated polytomies and unresolved

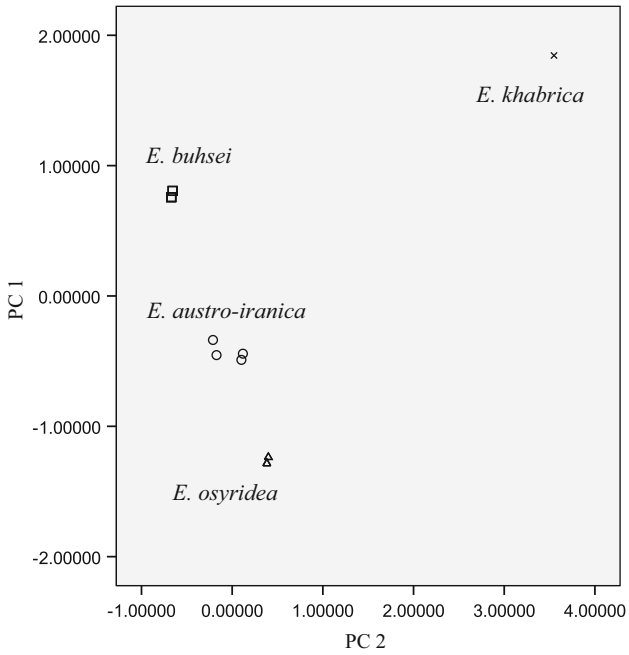

Fig. 1 Principal component analysis (PCA) of 18 populations of *Euphorbia austro-iranica*, *E. buhsei*, *E. khabrica*, and *E. osyridea* based on morphological characters

positions in almost all groups of sect. *Esula* (not shown). In the ITS tree, the samples of the four species of the *E. osyridea* alliance formed a monophyletic group (BS 59%, PP 0.64), sister to other clades of sect. *Esula* (Fig. 2). In this tree, the samples of *E. khabrica* sp. nov. form a monophyletic group, but support is weak for both ML and BI analyses (BS 63%, PP 0.73). The only other grouping consists of three accessions of *E. osyridea* from Hormozgan, whose monophyly is well supported (BS 95%, PP 1). All other accessions remain unresolved.

ISSR genomic fingerprinting

ISSR genomic fingerprinting with six primers revealed a total of 169 bands for 34 individuals of four species of *E. osyridea* alliance from sect. *Esula* (Table 3). The size of amplified bands ranged from approximately 200 to about 2500 bp. Number and percentage of polymorphic loci are indicated in Table 6. The range of polymorphic loci of *E. osyridea* alliance populations varied between 22 (13%) in *E. khabrica* and 43 (25.4%) in *E. osyridea*. The number of polymorphic loci in populations of *E. buhsei* ranged from 23 (13.6%) in population Khorasan to 35 (20.7%) in population Esfahan (Table 6).

In the neighbor joining tree (Fig. 3), all studied accessions (Table 3) were divided into four main groups, *E. buhsei*, *E. osyridea*, *E. austro-iranica* sp. nov., and *E. khabrica* sp. nov. Individuals of *E. khabrica* and *E. austro-iranica* were more strongly dissimilar than the individuals

Table 5 Diagnostic characters of two new species *Euphorbia austro-iranica* and *E. khabrica* compared to close relative species *E. buhsei* and *E. osyridea*

Taxa	*E. austro-iranica*	*E. buhsei*	*E. khabrica*	*E. osyridea*
Height of plant and life form	50–100 cm, shrublets	20–50 cm, perennial herbs	<20 cm, perennial herbs	>120 cm, shrubs
Main stem diameter	3–4.3 mm	1.8–3 mm	1–1.5 mm	3.6–5 mm
Stem indumentum	Glabrous	Glabrous	Puberulent, pilose to glabrescent	Tomentose
Leaf shape	Oblong-lanceolate or rarely linear-lanceolate	Oblong-lanceolate	Elliptic to ovate-oblong	Linear-lanceolate
Leaf indumentum	Glabrous	Glabrous or rarely pilose	Pubescent to glabrescent	Tomentose
Main rays	Axillary	Terminal	Terminal	Axillary
Ray no.	(1) 2–3 (4)	(4) 5–8	(2) 3 (5)	(1) 2–4
Ray-leaf no.	2–4	(4) 5–7	(3) 5	2–4
Cyathium indumentum	Glabrous	Glabrous	Pubinervis or rarely glabrescent	Tomentose
Glands color	Brown to ochreous	Ochreous	Dark purplish	Light brown to ochreous
Pedicel length	4–9 mm	2–4.7 mm	1.1–1.5 mm	4–7.2 mm
Capsule length	3.9–5.2 mm	3.5–5 mm	2.8–3.5 mm	4.2–5.2 mm
Style length	1.7–2.6 mm	1.8–3 mm	1–1.5 mm	1.3–2.5 mm

of *E. buhsei* and *E. osyridea* and were separated with strong supports (BS 100 for *E. khabrica* and 93 for *E. austro-iranica*). The closest group to *E. osyridea* was *E. buhsei* but with weak support (BS 42).

Nei's gene diversity

Nei's gene diversity (NGD) of the studied taxa and populations of *E. osyridea* alliance are shown in Table 6. The NGD values varied between 0.042 in *E. buhsei* from Khorasan and 0.089 in *E. osyridea* from Hormozgan Province (Table 6). NGD was rather similar in the populations of *E. osyridea* from Hormozgan and Khorasan (0.089 and 0.083, respectively) and NGD for *E. khabrica* sp. nov., *E. buhsei* from Semnan and Khorasan were also in the same range (0.046, 0.048, and 0.042, respectively). Both *E. buhsei* from Esfahan and *E. austro-iranica* sp. nov. from Baluchestan with NGD values of 0.062 and 0.056, respectively, were higher than NGD values of other populations of *E. buhsei* as well as *E. khabrica* sp. nov. Genetic diversity of two populations of *E. osyridea* from S Khorasan and Hormozgan was about twice the genetic diversity of other studied taxa. In general, genetic diversity values in this group were relatively low (Table 6).

Nei's genetic distance

Generally, Nei's genetic distance (Ds) between intraspecific populations was predominantly lower than between specific populations (Table 7). Among three studied populations of *E. buhsei*, the highest genetic distance was between populations of Esfahan and S Khorasan (Ds = 0.022).

The lowest Nei's genetic distance was found between Esfahan and Semnan populations of *E. buhsei* (0.014), whereas the highest was detected between *E. austro-iranica* sp. nov. (Baluchestan population) and *E. khabrica* sp. nov. (Kerman population, Ds = 0.162) (Table 7). Based on Ds analysis, the widest genetic distance was observed between *E. khabrica* sp. nov. and the studied species *E. austro-iranica* sp. nov., *E. buhsei* and *E. osyridea* with different populations (Ds = 0.112–0.162). The closest population to both *E. austro-iranica* sp. nov. and *E. khabrica* sp. nov. was *E. buhsei* from Semnan Province (Table 7; Fig. 3). In comparison, the genetic distances between *E. khabrica* sp. nov. and populations of *E. buhsei* and *E. osyridea* were higher than those between *E. austro-iranica* sp. nov. and the species *E. buhsei* and *E. osyridea*. In other words, *E. austro-iranica* sp. nov. is more closely related to both *E. buhsei* and *E. osyridea* than to *E. khabrica* (Table 7).

Population specificity was low in *E. buhsei*, especially in populations of Esfahan and Semnan Provinces, while the population of S Khorasan was more isolated in the ISSR NJ tree (Fig. 3). This pattern also occurred in *E. osyridea* populations of Hormozgan and S Khorasan Provinces, in fact there is no high population differentiation among studied specimens (Fig. 3).

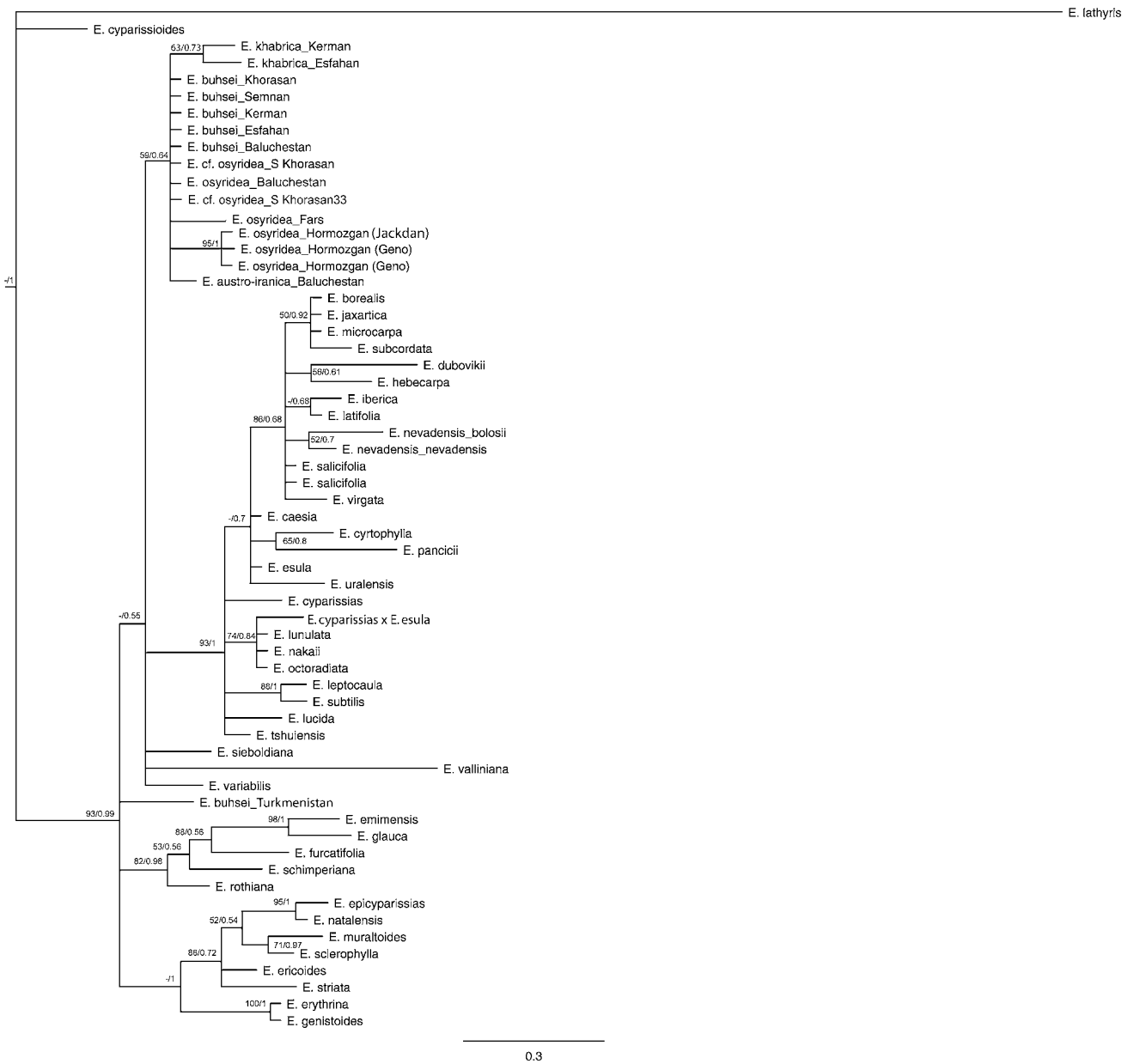

Fig. 2 Majority rule consensus from Bayesian inference of the ITS dataset of section *Esula* with *Euphorbia lathyris* (sect. *Lathyris*) as outgroup. Maximum likelihood bootstrap values, Bayesian posterior probabilities are indicated above branches, separated by a slash

Discussion

The *Euphorbia osyridea* alliance in sect. *Esula* (*E. austro-iranica*, *E. buhsei*, *E. khabrica*, *E. osyridea*) is centered in Iran, but *E. buhsei* ranges from Iran to S of Turkmenistan on the borderline of Iran and *E. osyridea* also occurs in W of Pakistan and Afghanistan. The two new species, *E. austro-iranica* and *E. khabrica*, are isolated species, endemic to the Irano-Turanian region of Iran where *E. khabrica* occurs with some subalpine to alpine species of southern Zagros and *E. austro-iranica* occurs on the hills and mounds from S to SE Iran. As indicated in Fig. 2, all these Irano-Turanian species with limited distribution form a monophyletic group. The distribution and phylogenetic pattern along with morphological characters support this monophyly.

In a previous molecular study (Riina et al. 2013), one accession of *E. osyridea* and two accessions of *E. buhsei* were analyzed with the ITS marker only, whereas here we generated ITS and *ndh*F sequences which confirmed *E. osyridea* and the Iranian *E. buhsei* phylogenetic position (Fig. 2). Strangely, the accession of *E. buhsei* from Turkmenistan was retrieved in a different position from the above-mentioned accessions (Fig. 2). Thus, the

Table 6 Number and percentage of polymorphic loci, Nei's gene diversity, and standard deviation of *Euphorbia* taxa for ISSR marker

Taxa & populations	Neis gene diversity	Percentage of polymorphic loci (%)	Number of polymorphic loci	Standard deviation
*E. khabrica*_K	0.0464	13.02	22	0.1299
*E. buhsei*_S	0.0487	18.34	31	0.1132
*E. buhsei*_KH	0.0422	13.61	23	0.1162
*E. buhsei*_E	0.0627	20.71	35	0.1345
*E. osyridea*_H	0.0890	25.44	43	0.1624
*E. osyridea*_KH	0.0833	24.85	42	0.1557
*E. austro-iranica*_B	0.0562	14.20	24	0.1453

B: Sistan & Baluchestan; E: Esfahan; H: Hormozgan; K: Kerman; KH: South Khorasan; S: Semnan

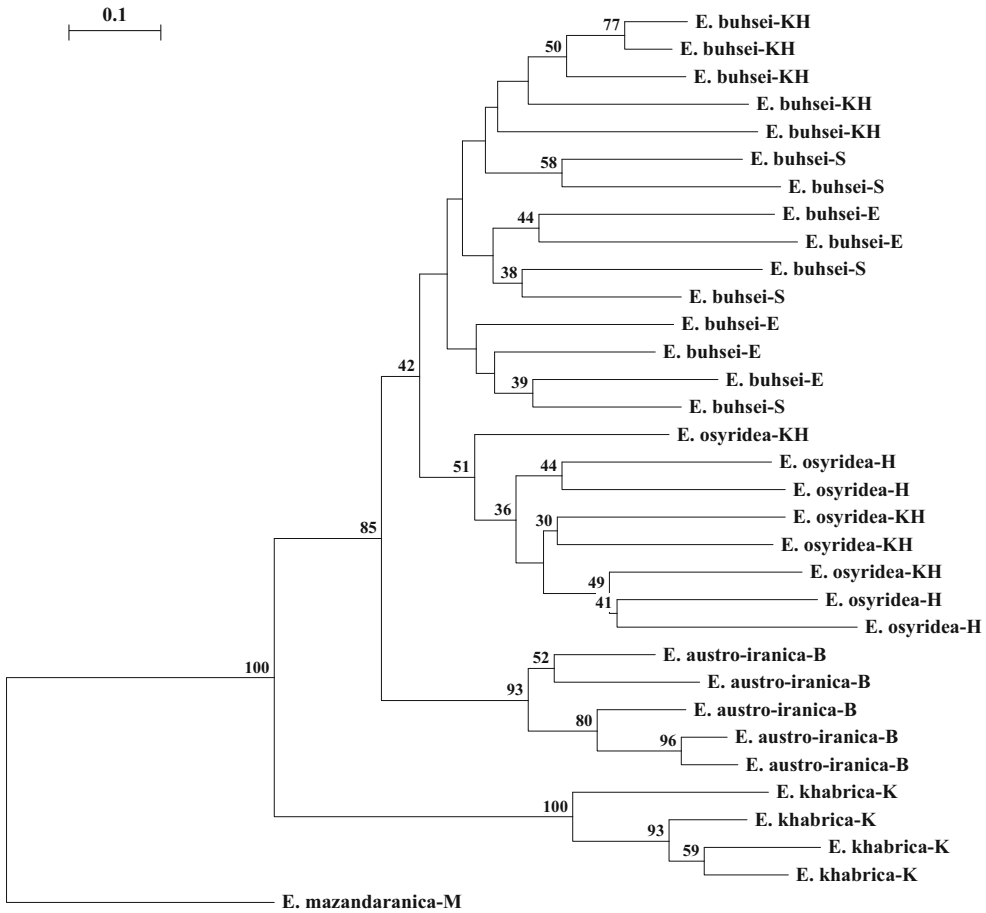

Fig. 3 Neighbor joining tree with Nei Li distance and bootstrap values with 1000 replicates using TREECON

Turkmenistanian taxon considered as *E. buhsei* might be a misidentified known or unknown species. Boissier (1862) places *E. osyridea* in an unranked subsect. *Osyrideae* Boiss. According to the ITS analysis (Fig. 2), all accessions of *E. osyridea* alliance including *E. buhsei*, *E. khabrica*, and *E. austro-iranica* form a monophyletic group which could be considered as a new subsection.

Neither nuclear nor plastid sequences, nor their combination were sufficient to disentangle the diversification patterns within the *E. osyridea* alliance. This could be related to the rapid evolution in sect. *Esula,* which is one of the youngest groups in the subgenus (Horn et al. 2014). The phenomenon of incongruence between chloroplast and nuclear DNA data occurs in other groups of angiosperms with rapid evolution (Fehrer et al. 2007). Because ITS and *ndh*F sequence data were insufficient to resolve species boundaries, we will concentrate the discussion on the results of our ISSR and morphological analyses.

Table 7 Nei's standard genetic distance between the taxa of *Euphorbia* section *Esula* (*E. osyridea* aggregate)

	*E. khabrica*_K	*E. buhsei*_S	*E. buhsei*_KH	*E. buhsei*_E	*E. osyridea*_H	*E. osyridea*_KH
*E. khabrica*_K	–					
*E. buhsei*_S	0.1123	–				
*E. buhsei*_KH	0.1217	0.0197	–			
*E. buhsei*_E	0.1201	0.0145	0.0220	–		
*E. osyridea*_H	0.1367	0.0548	0.0488	0.0550	–	
*E. osyridea*_KH	0.1506	0.0589	0.0527	0.0547	0.0294	–
*E. austro-iranica*_B	0.1624	0.0706	0.0798	0.0747	0.0921	0.1010

B: Sistan and Baluchestan; E: Esfahan; H: Hormozgan; K: Kerman; KH: South Khorasan; S: Semnan

Two closely related species in this group (*E. osyridea* alliance) that have already been reported are *E. osyridiformis* Parsa and *E. gulestanica* Podlech from S Iran and Afghanistan, respectively. After close examination of morphological features of immature type specimen of *E. osyridiformis*, as well as its protologue (Parsa 1948), we determined that it falls within the range of variation in *E. hebecarpa* and is therefore placed in synonymy. *Euphorbia gulestanica* is a species with poor information about its habitat, habit, phylogeny, and ecology. It is only known from the type and has not been collected again (Podlech 1981). The type specimen is immature without any seed or mature capsule. More morphological and molecular studies are needed to determine its phylogenetic position.

Detailed morphological examination of herbarium material kept under the name "*E. osyridea*" revealed that the specimens do not belong to the same species, indicating that the concept of Radcliffe-Smith (1986) for *E. osyridea* includes morphologically and genetically heterogeneous populations. The results of our ISSR and morphology studies (Figs. 1, 3) indicate that the populations of *E. osyridea* can be divided into two obviously different groups, of which the first one is here considered *E. osyridea* sensu Boissier (Boissier 1846) and the second one is reported here as a new species, *E. austro-iranica* sp. nov. Although *E. austro-iranica* is morphologically more similar to *E. osyridea*, it is genetically more closely related to *E. buhsei* (Table 7; Fig. 3). The most important morphological difference between the two species is the tomentose indument of stem, leaf and capsule in *E. osyridea*, which is absent in *E. austro-iranica* (Table 5). Leaf shape and leaf apex can also serve as distinguishing features between *E. austro-iranica* and *E. osyridea*. The overall aspect of their habit and the presence of axillary rays (no terminal rays) make them to appear more similar to each other than to the other species in this group; however, the factor analysis of our phenetic study indicated that position of rays had negative correlation in comparison with other studied characters. On the other hand, a shrub or shrublet life form in these two species cannot be considered a synapomorphic character because several more species in other clades of sect. *Esula* are also shrubs or shrublets. The presence of axillary rays alone (without terminal rays) is uncommon in other species of *Euphorbia* subgen. *Esula*, and it has been never reported in other taxa.

Based on our phylogenetic tree (Fig. 2), there are some differences between populations of *E. osyridea* from Fars, Hormozgan, and Baluchestan which could be due to hybridization between *E. buhsei* and *E. osyridea* or to the existence of microspecies in this aggregate.

Nei's Gene Diversity (NGD) of the studied populations was low to intermediate (0.042–0.130) which can be attributed to the low number of individuals analyzed. It is remarkable that Ds values of *E. austro-iranica* sp. nov. to *E. buhsei* populations (Ds = 0.070–0.079) were lower than to *E. osyridea* populations (Ds = 0.092–0.101) which is in contrast to the morphological results of the taxa.

As indicated in Table 7, genetic distance between *E. austro-iranica*, a population of Baluchestan which was previously considered to be *E. osyridea*, and two more populations of *E. osyridea* was clearly higher (0.092 and 0.101) than that between *E. osyridea* accessions of Hormozgan and S Khorasan (0.029), indicating genetical differentiation between *E. austro-iranica* and *E. osyridea*. As Ds revealed (Table 7), genetic distance between *E. khabrica* and three other populations of *E. buhsei* was lower than that between *E. khabrica* and three populations of *E. austro-iranica* and *E. osyridea*, a result corroborated by PCA and morphological analysis (Fig. 1).

Taxonomic treatment

Euphorbia* sect. *Esula (Pers.) Dumort., Fl., Belg.: 87. 1827.—Type: *Euphorbia esula* L. = *Euphorbia* sect. *Wentsai* J.S.Ma & C.Y.Wu in Collect. Bot. (Barcelona) 21: 116. 1993.—Type: *Euphorbia yanjinensis* W.T.Wang.

Perennial herbs or occasionally shrublets to shrubs, glabrous or hairy. Cauline leaves alternate, linear, linear-lanceolate to elliptic or ovate, margin entire, venation

pinnate, mostly prominent. Raylet leaves 2, free. Cyathial glands 4, semilunate or trapezoidal, margin entire, with 2 horn-like appendages or lacerate. Capsule subglobose or nearly so, deeply trilobate, minutely granulate or smooth, glabrous, pilose or tomentose. Seeds ovoid-ellipsoidal or subspherical, mostly smooth, rarely foveolate, grayish to brown, carunculate. $2n = 18, 20, 36, 40, 56, 60, 64$. Section description sensu Riina et al. (2013).

Euphorbia austro-iranica Pahlevani, **sp. nov.**— HOLOTYPE: Iran, Sistan & Baluchestan, Iranshahr to Bazman, 30 km NW of Bazman, Govanz, 1500 m a. s. l., 22 Feb 1997, *Moussavi* and *Tehrani 47288/5* (IRAN!; isotypes: IRAN!, B!) (Fig. 4).

Diagnosis: It is most closely related to *E. osyridea* but, differing from the latter by shrublet habit (not shrub), glabrous and reddish-brown stems (not tomentose and grayish), oblong-lanceolate leaves (rarely linear-lanceolate), glabrous leaves (not tomentose), glabrous cyathium (not tomentose), glabrous or rarely glabrescent capsules (not tomentose).

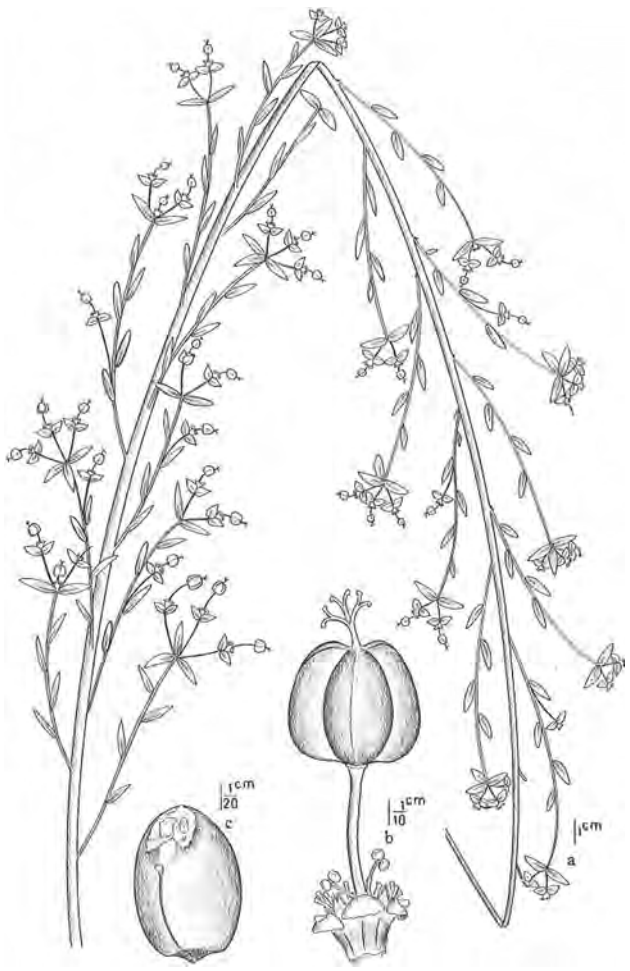

Fig. 4 *Euphorbia austro-iranica*, **a** habit; **b** cyathium and capsule; **c** seed. After *Moussavi* and *Tehrani 47288* (IRAN)

Description: An erect, glabrous with reddish-brown stem shrublet, up to 100 cm height arising from a rather thick woody stock (3–4.3 mm). Cauline leaves oblong-lanceolate to rarely linear-lanceolate, 9–36 × 1.8–4.2 mm, glabrous, apex obtuse, attenuate to the base, entire, sessile. Rays in the axillary shoots only, (1) 2–3 (4); ray-leaves 2–4, oblong-lanceolate, 10–15 × 2.5–4 mm, apex obtuse to subacute, tapered to the base, entire and sessile. Raylet leaves 2, ovate-rhombic to transversely ovate, 5–7 × 3.8–5 mm, apex mucronulate, truncate to rounded at the base, entire and sessile. Cyathia: involucre campanulate, lobes dentate, glabrous or glabrescent; glands 4, ochreous to brown, trapeziform to lunate, lacerate to entire outwards. Capsules subglobose, 3.9–5.2 × 4.5–5.6 mm, deeply trilobate, glabrous or rarely glabrescent, mostly granulate. Seeds ovoid-ellipsoidal, 2.7–3 × 2–2.5 mm, smooth; caruncle petasiform, compressed, 0.4–0.5 × 1–1.3 mm.

Additional specimens examined: **IRAN.** Kerman, Djiroft to Esfandagheh, 1700 m a. s. l., 20 Mar 1971, *Iranshahr* and *Termeh 18138* (IRAN); Kerman, Djiroft, Marz, Mamanak, Kuh-e Sefid (Bashagerd), 1000–1450 m a. s. l., 12 Mar 1978, *Moussavi* and *Tehrani 17860* (IRAN); Baluchestan, 60–63 km from Iranshahr on road to Khash, 1100–1200 m a. s. l., 6 Mar 1977, *Runemark*, *Assadi* and *Sardabi 22226* (TARI); Baluchestan, ad viam Bazman-Eskelabad, ca 63 km NNE, a vico Bazman, 14 Apr 1973, *Sojak 2089* (PR); Hormozgan, Bashagerd, Gourichi, 1000 m a. s. l., 20 Feb 1973, *Iranshahr* and *Moussavi 17859* (IRAN).

Etymology: The epithet "austro-iranica" has been selected because the new species is distributed in southern Iran.

Phenology: Flowering and fruiting from the end of February to April.

Distribution and ecology: *Euphorbia austro-iranica* is known from S to SE Iran on hills and mountainous regions at 1000–1700 m altitude, but precise knowledge of its habitat, ecology, and distribution is still needed (Fig. 5).

Conservation status: Even though the known populations of *E. austro-iranica* are not isolated in a particular or fragile habitat like some rare species of *Euphorbia* (Pahlevani et al. 2015), several factors such as small number of populations, distribution restricted to Iran, road construction, grazing as well as drought in the area of distribution lead us to classify it as vulnerable (VU) according to "IUCN Red list category" (IUCN 2014).

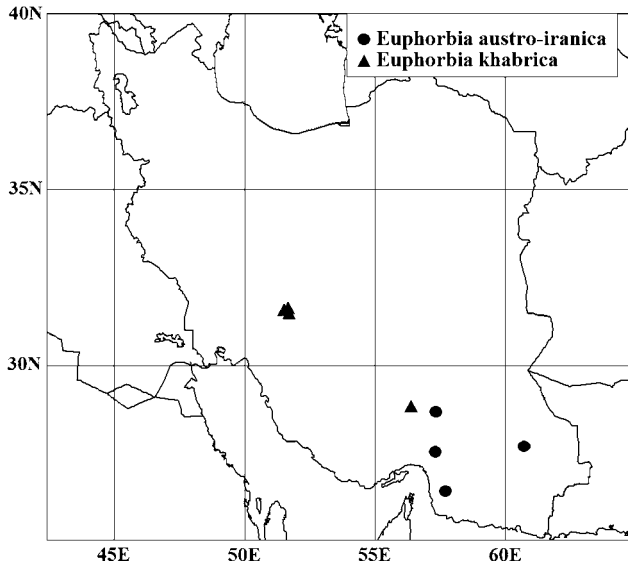

Fig. 5 Geographical distribution of *Euphorbia austro-iranica* and *E. khabrica*

Notes: *Euphorbia austro-iranica* has been also collected among populations of the closely related species *E. osyridea*, but in addition to their morphological and genetic differentiation, flowering and fruiting times are also different. *Euphorbia osyridea* starts flowering approximately four weeks earlier than *E. austro-iranica* in places where the two grow together. ITS sequences (Fig. 2) placed *E. austro-iranica* in sect. *Esula*, near other populations of *E. osyridea*, whereas ISSR analysis placed it sister to *E. buhsei* + *E. osyridea* (Fig. 3).

Euphorbia buhsei Boiss. in DC., Prodr. 15, 2: 167 (1862) ≡ *Tithymalus buhsei* (Boiss.) Prokh., Consp. Syst. *Tithym*. Asiae Mediae 166 (1933) ≡ *Galarhoeus buhsei* (Boiss.) Prokh., Trudy Kuibyshevsk. Bot. Sada, 1: 46 (1941).—LECTOTYPE (**designated here**): IRAN. LT (Rechinger, Schiman-Czeika, 1964; h.d.): "Persia, prope Rescht [Rasht] et Rischm [Rashm], Mar 1847, *Buhse 1247*" (G-BOISS!). Rechinger and Schiman-Czeika (1964) selected as "type" the Buhse collection from Raschm, but did not mention the herbarium and herbarium number.

=*Euphorbia buhsei* var. *lasiostemon* Boiss. In DC., Prodr. 15, 2: 167 (1862).—LECTOTYPE (**designated here**): Persiae orientalis, prope Shahroud, 21 May 1858, *Bunge 14* G-Boiss (image!).

=*Euphorbia kopetdaghensis* Korovin ex Prokh., Consp. Syst. *Tithymalus* As. Med. 166 (1933), **nom. inval.** [Art. 50]

=*Euphorbia halophila* Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 61 (1939), **nom. illeg.** [Art. 52]

= *Euphorbia gaubae* (Soják) Radcl.-Sm., Kew Bull. 36: 216 (1981) ≡ Tithymalus gaubae Soják, Čas. Nar. Mus., Odd. Prir. 140: 172 (1972).—LECTOTYPE (**designated here**): Persia borealis, Keredj [Karaj], ad Mardabad, 15 Jun 1935, *Gauba 1062* (B100367981!; isolectotype: B100367982!).

=*Euphorbia halophila* var. *velutina* Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 47: 62 (1939)

= *Euphorbia gaubae* var. *velutina* (Bornm. & Gauba) Oudejans, Collect. Bot. (Barcelona), 21: 184 (1992, publ. 1993).—LECTOTYPE (**designated here**): Persia borealis, Keredj [Karaj], bei Mardabad, 18 Apr 1935, *Gauba 1064* (IRAN!).

Description: Perennial herbs, glabrous or rarely sporadically pilose, 20–50 cm height. Stems 1.8–3 mm diameter. Cauline leaves oblong to oblong-lanceolate, 7–45 × 2–6.5 mm, glabrous, sessile, base attenuate to subtruncate, apex obtuse to subacute, margin entire. Terminal rays (4) 5–7 (8), once or twice dichotomous, elongated or not, axillary rays 0–10. Ray-leaves ovate-oblong, 5–8, apex subacute to acute, raylet leaves ovate-deltoid to rhombic. Cyathia: involucre campanulate-turbinate, 2 mm in diameter, lobes deltoid, mostly lacerate; glands semilunate to trapeziform, hornless, obscurely lacerate or with two short horns, ochreous to brownish. Capsules subglobose, deeply trilobate, 3.5–5 × 3.7–4.5 mm, glabrous, granulate at least on the keel. Seeds ovoid-ellipsoidal, smooth, 2.5–3 × 1.9–2.4 mm, light grayish to dark grayish, caruncle petasiform, 0.8–1 × 1.2–1.9 mm.

Chromosome number: $2n = 2x = 20$ (Sheidai et al. 2010).

Phenology: Flowering and fruiting from the end of May to mid-July.

Distribution and ecology: Based on Govaerts et al. (2000), *E. buhsei* occurs from Iran to Mongolia (Afghanistan, Iran, Mongolia, Turkmenistan, and Uzbekistan); however, after studying most SW and C Asian species-rich herbaria including, B, BM, E, G, K, M, MSB, PR, W, WU as well as the Iranian herbaria IRAN, TARI, HSBU, TUH, FUMH, FAR, and other local herbaria, the distribution of *E. buhsei* is limited to N, NE, E, C, S, SE Iran, and Turkmenistan (Nasimova 1983). However, *E. buhsei* was reported for flora of Uzbekistan (Pazij 1959) from Kashka-Darya region vicinity of Guzar, and from a single specimen from Afghanistan by Rechinger and Schiman-Czeika (1964) (Afghanistan, Bamian, Darreh-i Shikar, 46 km S Doab, 2100 m a. s. l., *Hedge and Wendelbo 3359* E!) which the latter one was misidentification of *E. ecorniculata* Kitam. For a more precise distribution and to confirm the presence of the species in Uzbekistan and Afghanistan, other C Asian herbaria should be consulted. *Euphorbia buhsei* usually occurs among *Astragalus* and *Artemisia* communities in rocky mountain slopes, gypsum hills and occasionally in halophyte communities.

Additional specimens examined: **IRAN.** Khorasan, Neyshabour, Akhlamad, Darreh-Abshar, 1600–1800 m a. s. l., 30 May 1948, *Rechinger* et al. *4564* (IRAN, M, W); Khorasan, Inter Mashhad et Torbat-e Heydariyeh, 10–11 Jul 1937, *Rechinger 1556* (W); Khorasan, Mashhad to Neyshabour, Pivejan, 1630–2000 m, 21 Jun 2002, *Djavadi* and *Sadeghi 47415* (IRAN); Khorasan, 82–90 km S Mashhad, between Kafar-Chaleh and Robat-e Sefid (Serpentin), 1520 m, 7 May 1975, *Iranshahr 18128*, *Rechinger 57340* (IRAN, B, W); Khorasan, Robat Sefid, 1800–2000 m, 27 May 1948, *Rechinger* et al. *4443* (IRAN, K, W); Khorasan, Esfarayen to Sabzevar, Hesari, Kuh-e Shah-e Jahan (protected area), 1400–1750 m, 17 Jun 1975, *Termeh 17999* (IRAN); Khorasan, Neyshabour, Boujan, 1750 m, 28 Jun 2007, *Pahlevani* et al. *47351* (IRAN); Khorasan, 12–20 km N Kashmar, 1150–1700 m, 4 May 1975, *Iranshahr 18005* (IRAN); Khorassan, 13 km N Kashmar versus Rivash, 1300–1400 m, 4 May 1975, *Rechinger 51187* (B, M, W, WU); Khorasan, Mashhad to Chenaran, Akhlamad (Binaloud Mts.), 1400 m, 15 Jun 2005, *Djavadi* et al. *47265* (IRAN); Khorassan, In montibus serpentinicis inter Torbat-e Heydariyeh et Assadabad, 27 May 1948, *Rechinger* et al. *4417* (B, E, IRAN, K, W); Khorasan, Robat-e Sefid, inter Mashhad et Torbat-e Heydariyeh, 1600–1700 m, 29 May 1977, *Rechinger 55867* (B, W); Khorasan, 74 km to Mashhad, from Kalat-e Naderi, 950 m, 27 Apr 1986, *Assadi* and *Maasoumi 55859* (TARI); N Khorasan, Ghoochan to Chenaran, Radkan, Barou, 900–1100 m, 17 Jun 2002, *Djavadi* and *Sadeghi 47413* (IRAN); N Khorasan, ca 25 km SW Darreh-Gaz, Tandooreh National Park, Chehel-Mehr, 1200 m, 29 May 1984, *Assadi* and *Maasoumi 50795* (TARI); N Khorasan, Between Ghoochan and Darreh-Gaz, Tandooreh National Park, between Shekarab and Chehel-Mehr, 1600–1900 m, 28 May 1984, *Assadi* and *Maasoumi 50714*, *50693* (TARI); S Khorasan, 18 km to Birjand, from Ghayen,1900 m, 19 May 2003, *Assadi* and *Amirabadi 84753* (TARI); S Khorasan, Birjand to Ghaen, 26 May 1948, *Rechinger* et al. *4186* (B, IRAN, W); Kerman, Baghin to Sanghur, 27 Apr 1948, *Rechinger* et al. *2881* (IRAN, K, W); Kerman, 100 km S Yazd versus Kerman, 25 Mar 1965, *Rechinger 27137* (W); Kerman, kuh-e Tagh-Ali, 2000 m, 16 Apr 1892, *Bornmüller 4697* (B, E, K, W, WU); Kerman, Zarand to Koohbanan, Shahrak-e Taleghani, Babatangol, 1800 m, 11 Apr 2007, *Pahlevani* and *Torabi 47697* (IRAN); Kerman, Tahrud, inter Kerman et Bam, 1500 m, 6 May 1948, *Rechinger* et al. *3605* (B, E, IRAN, K, M, W); Kerman, Baft, Khabr Protected Area, Korikou, 2300 m, 26 May 2009, *Pahlevani* and *Bahramishad 53342* (IRAN); Kerman, 92 km Bam toward Kerman, 3 May 2008, *Pahlevani* et al. *47481* (IRAN); Kerman, inter Kerman et Bam, Nehbid [Neybid], 2250 m, 6 May 1948, *Rechinger* et al. *3569* (IRAN, W); Kerman, Kuh-e Jebalbarez to Jiroft, 8–10 May 1948, *Rechinger* et al. *3843*, *2904*, *5756* (IRAN, M, W); Kerman, Khabr va Rouchun Protected region, 50 km SSW of Baft, E side of Kuh-e Khabr, 12 km E of Khabr, 2850 m, 8 Jun 77, *Assadi* et al. *1709* (TARI); Kerman, near Sarcheshmeh, 2300 m, 3 Jun 1986, *Assadi* and *Bazgosha 56406* (TARI); Kerman, W Dasht-e Lut, 10 km N Guk, 2100 m, 20 May 1972, *Leonard 6266* (IRAN); Kerman, 70 km Kerman to Bam, around Jupar Mt., 2700 m, 21 May 2009, *Pahlevani* and *Bahramishad 53830* (IRAN); Kerman, Kermanshahan, 1700 m, 11 Apr 1892, *Bornmüller 4699* (B, K); Kerman, Negar, Ghale Asgar, 2565 m, 25 May 2009, *Pahlevani* and *Bahramishad 53824* (IRAN); Kerman, Zarand, 100 km to Koohbanan, 2100 m, 11 Apr 2007, *Pahlevani* and *Torabi 47698* (IRAN); Kerman, ca 50 km W of Ravar mountain above the Homkar coal mine, 2350–2700 m, 1 Jun 1986, *Assadi* and *Bazgosha 56243* (TARI); Semnan, 66 km SE Semnan, Anjirab, 1500 m, 2 May 1974, *Iranshahr* and *Riedl 17998*, *15983* (IRAN, MSB, W); Semnan, Turan Protected region, Kuh-e Molahadi, N part, 1200–1300 m, 6 May 1978, *Freitag* and *Mozaffarian 28878* (TARI); Semnan, Touran Protected Area, SE of Shahrud, E side of Kuh-e Yazdu pass at road Ghazazan-Ahmad-abad, 1280 m, 8 May 1978, *Freitag 15167* (B); Semnan, Shahroud, 40 km E Shahrud, 1250 m, 26 Apr 1975, *Iranshahr 18003* (IRAN); Semnan, 17 km Momen-abad to Firouzkuh, 29 May 2012, *Pahlevani 57193* (IRAN); Semnan, 20 km E of Semnan, Momen-abad, 1200–1300 m, 24 Apr 1975, *Iranshahr 44498* (IRAN); Semnan, Damghan-Semnan, in deserto gypsaceo 2–7 km supra Sorkheh prope Semnan, 1300–1400 m, 24 Apr 1975, *Rechinger 50206* (W); Semnan, Shahroud-Bastum, 14 km S Zeydar versus Biarjomand, 1300 m, 26 Apr 1975, *Rechinger 50278* (W); Semnan, Turan Protected Area, Qaleh Bala, 1120 m, 27 Apr 1975, *Rechinger 50342*, *Iranshahr 44518* (IRAN, TARI, W); Semnan, Zidar to Biarjomand, 1450 m, 1 May 1984, *Eghbali 47223* (IRAN); Semnan, Toward Firouzkuh, 5 km SE Momen-abad, 1100 m, 3 May 1997, *Moussavi* and *Tehrani 54524* (IRAN); Semnan, Damghan, 33 km NE Semnan versus Damghan, 1600–1700 m, 25 Apr 1975, *Rechinger 50247* (B, M, W, WU); Semnan, between Damghan and Semnan, 1200 m, 24 May 1978, *Dini* and *Bazargan 32916* (TARI); Semnan, Touran Protected Area, W and most part of Shtoran kuh, 1300–1500 m, 24 Apr 1978, *Freitag* and *Mozaffarian 28458* (TARI); Semnan, 24 km SE of Shahrud, Armeyan, Jowdaneh kuh, on road to Biarjomand, 1540 m, 22 Apr 1978, *Freitag* and *Mozaffarian 28330*, *14596* (B, TARI); Yazd, Taft, Darreh-Gahan, 2100–2400 m, 1 May 2010, *Eskandari 54351* (IRAN); Yazd, Khormiz, 5 km SW of Mehriz, NE of Kuh-e Khoseh, 1700 m, 27 May 1977, *Aryavand* et al. *1482* (TARI); Yazd, 15–20 km Anarak, 1250 m, 17 May 1975, *Rechinger 52012* (B, W); Yazd, Shirkuh Mt., 2000 m, 6 Apr 1892, *Bornmüller 4698* (B, K, W, WU); Yazd, 54 km from Bafgh

to Sheitoor, near Gazestan, 2200 m, 28 May 1986, *Assadi* and *Bazgosha 56050* (TARI); Yazd, ca 50 km E of Bafgh, mountains above the village Hamsook, 30 May 1985 *Assadi* and *Bazgosha 56094* (TARI); Esfahan, Kolah-Ghazi Wildlife Park, 30–50 km S Esfahan, 1700 m, 29 May 1974, *Iranshahr 18000*, *Rechinger 46728* (B, IRAN, W); Esfahan, N Najafabad, 25 km W Esfahan, 1800 m, 2 May 1953, *Soder 213* (W); Esfahan, Kashan, Ghamsar, Ghazaan, 19 May 1970, *Iranshahr 17991* (IRAN); Esfahan, SE of Esfahan, 11 Apr 1962, *Furse 1362* (W); Esfahan, Kashan, Ravand Khiarsareh, 1550 m, 22 Apr 1974, *Dini* and *Bazargan 8008* (TARI); Esfahan, ca 22 km from Kashan to Natanz, 1200 m, 28 May 1986, *Assadi* and *Bazgosha 55963* (TARI); Esfahan, in semideserto 6 km occid.-boreo-occid., a vico Kermanshahan (ca 85 km ab oppido Yazd), 1610 m, 21 Mar 1973, *Sojak 112* (PR); Esfahan, S Esfahan toward Shahreza, Kolah-Ghazi Protected Area, 1670 m, 31 May 2012, *Pahlevani 57188* (IRAN); Esfahan, Kashan, Abyaneh, Tordal, 2000–2220 m, 7 Jul 1984, *Moussavi* and *Tehrani 44516* (IRAN); Esfahan, Ardestan, Hombar, 1550 m, 17 Apr 1975, *Foroughi 15982* (TARI); Esfahan, Kashan, Mooteh Protected region, In Mt. Mooteh, 1950–2000 m, 31 May 1974, *Rechinger 46853* (B, M, W, WU); Baluchestan, Tamendan, Kuh-e Taftan, 2100–2300 m, 18 Apr 1973, *Sojak 2419*, *2420*, *2421*, *2425,* (IRAN, PR); Baluchestan, Khash to Zahedan, Tamendan, Paylak, Taftan Mt., 2500–2900 m, 23 May 2009, *Pahlevani* and *Bahramishad 53823* (IRAN); Baluchestan, Kuh-e Taftan from Tamendan and Paylak, 2700–3800 m, 29 May 1985, *Mozaffarian 53102* (TARI); Baluchestan, Kuh-e Taftan, Sardarya, 2500–2650 m, 17 May 1985, *Valizadeh* and *Maasoumi 1187* (TARI); Baluchestan, Taftan Mt. Region, N of Anjirak, 2600–2800 m, 28 May 1985, *Mozaffarian 53048* (TARI); Baluchestan, inter Zahedan et Khash, 1300–1600 m, 15 May 1948, *Rechinger* et al. *4214*, *4279* (IRAN, W); Fars, 20 km from Neyriz to Estahban, 1920–2100 m, 27 May 2009, *Pahlevani* and *Bahramishad 53345* (IRAN); Fars, Estahban, Eij Mt., 2500 m, 28 May 2009, *Pahlevani* and *Bahramishad 53341* (IRAN); Fars, entre Abadeh et Dulatabad [Dolatabad], 1500–2000 m, 26 Apr 1956, *Schmid 5302* (E, K, W); Fars, Eghlid, Sedeh, Tange Boragh to Khaniman, 1900 m, 26 Apr 2009, *Eskandari* and *Bahramishad 53758* (IRAN); Fars, Prope ruinas Persepolis [Fars, Shiraz, Persepolis], Apr 1842, *Kotschy 878* (G, K, P, W); Alborz, Montes Elburs centr. [Alborz], Karadj, in montibus Kuh-e Dasht, 1600 m, 7 Jun 1937, *Rechinger 799* (W); Alborz, Karadj, In montibus ad pagum Kalak, 17 May 1937, *Rechinger 101* (K, W); Alborz, Karaj, Kalak, 2040 m, 5 May 1973, *Mousavi 23548* (TARI); same locality, 1200 m, 27 Jul 1970, *Babakhanlou 7684* (TARI); Alborz, Karaj, the valley of Kan, 1500 m, 10 Apr 1977, *Runemark* and *Varnecke 25469* (TARI); Alborz, Karaj, Garm Darreh, 1500 m, 7 May 1978, *Assadi 27523* (TARI); Alborz, Between Tehran and Karaj, above Kalak, 1500–1900 m, 9 May 1978, *Assadi* and *Mozaffarian 27626* (TARI); Alborz, Karaj, Sarvedar, Karaj valley, 1500 m, 5 Jun 1974, *Foroughi* et al. *12310* (TARI); Qazvin, Keredj [Karaj], *s.d. Gauba 2257* (W); Alborz, Karaj, Kalak, 1500 m, 4 May 1934, *Gauba 1063* (B); Tehran, Inter Kan et Sangan, 15–20 km NW Tehran, 1400–1800 m, 22 Apr 1977, *Rechinger 54520*, *54529* (B, M, W, WU); Tehran, Vardavard valley, 1800 m, 27 May 1974, *Wendelbo* et al. *11738* (W); Tehran, 55 km E Tehran, Rudshur, 1000 m, 31 May 1966, *Pabot 8220* (TARI); Tehran, Rudshur Protected station, 1040 m, 9 Apr 1973, *Dini* and *Bazargan 7598* (TARI); Tehran, Hasanabad on the road to Ghom, 2150 m, 18 Apr 1975, *Foroughi 15994* (TARI); Tehran, 21 km NW Tehran, Kan-Solughan road, 1600 m, 22 May 1974, *Amin* and *Bazargan 18534* (TARI); Tehran-Karaj, the valley of Kan, 1500 m, 10 Apr 1977, *Runemark* and *Varnecke 25470* (TARI); Tehran, 84 km Tehran-Qom road, 1500 m, 18 May 1974, *Amin* and *Bazargan 18257* (TARI); Tehran, Jajroud, 1550 m, 7 Jun 1972, *Dini* and *Arazm 7685* (TARI); Tehran, ca 20 km S of Damavand, between Tamisiun and Aselun, 1550–1650 m, 22 Jun 1985, *Mozaffarian 53913* (TARI); Tehran, Parandak, 1080 m, 14 Apr 1973, *Babakhanlou* and *Amin 7509* (TARI); Saveh toward Zavieh and Shirin-abad, 1250 m, 9 May 1974, *Dini* and *Bazargan 8293* (TARI); Tehran, 36 km S Tehran to Qom, 1100 m, 4 May 1974, *Iranshahr* and *Riedl 17767* (IRAN); Tehran Mountain NW of Tehran, Suleghun valley, 1600 m, 1 May 1979, *Assadi* et al. *33632* (TARI).

Euphorbia hebecarpa Boiss., Diagn. Pl. Orient. 7: 90 (1846) ≡ *Tithymalus hebecarpus* (Boiss.) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 88 (1860).—LECTOTYPE (**designated here**): IRAN, In humidis, pr. p. Duse-Kurd, ad rad. m. Kuh Dena [Fars, Dena Mt.], 6 Jul 1842, *Kotschy* 567 (W0031060!, isolectotypes: BM001050480!, G-DC!, G!, K001080076!, LE [n.v.], OXF [n.v.], P00606729!, W0031059!, W0031061!).

=*Euphorbia osyridiformis* Parsa, Kew Bull. 3: 228 (1948) **syn. nov.**—LECTOTYPE (**designated here**): Persia, Kuh Disch, near Daescht-aerdschen [Dasht-i-Arjan], Shiraz, 29 May 1885, *Stapf s.n.* (K001080077!).

Description: Perennial herbs, woody at the base, up to 85 cm height. Stems 3.5–6 mm diameter, glabrous, mostly with numerous axillary leafy shoots. Cauline leaves elliptic-ovate to linear-lanceolate, 25–110 × 4–30 mm, glabrous, sessile, base cuneate to obtuse, apex acute, subacute to obtuse, margin entire. Terminal rays (6) 8–17, once dichotomous (rarely twice), axillary rays 5–12. Ray-leaves 8–12, obovate, lanceolate to linear-lanceolate, 8–30 × 5–15 mm, base cuneate, rounded to asymmetrical,

apex acute-subacute or obtuse, margin entire, sessile; raylet leaves 2, reniform, rhombic, yellowish, mucronulate. Cyathia: involucre campanulate-turbinate, 2–2.5 mm in diameter, lobes deltoid, lacerate, pubescent; glands lunate, two-medium or long-horned, dark brown. Capsules subglobose, deeply trilobate, 4–6 × 4.3–6.4 mm, pubescent. Seeds ovoid-ellipsoidal, smooth, 2.7–3.7 × 1.8–2.9 mm, light grayish to brown, caruncle petasiform, 0.5–1 × 0.5–1.3 mm.

Phenology: Flowering and fruiting from the end of May to July.

Distribution and ecology: Euphorbia hebecarpa is reported from Iran and once in Iraq (Rechinger and Schiman-Czeika 1964) near the Turkish frontier (Zirva, *Thesiger 1232* BM). After studying mentioned specimen which has been collected from Iraq, we found that the specimen is *E. orientalis*. *Euphorbia hebecarpa* occurs from central Zagros to some parts of southern Zagros in subalpine to alpine regions from 1800–3800 m elevation in rocky slopes.

Additional specimens examined: **IRAN.** Esfahan, Khansar, Damaneh, Kuh-e Darreh-Dabbeh, 2200–2600 m, 12 Jun 1990, *Termeh* et al. *47239* (IRAN); Esfahan, Akhoreh, Choghyourt to Tange Dozdan, 2650 m, 3 Aug 1973, *Moussavi* and *Satei 17995*, *18200* (IRAN); Esfahan, Shahreza to Semirom, Kuh-e Alijough, 2600–3250 m, 11 Jul 1990, *Delghandi* and *Tehrani 47462* (IRAN); Esfahan, Poshtkouh, Masir village, 2450 m, 22 May 1982, *Rahiminejad* and *Nowrouzi 1553* (TARI); Esfahan, Semirom, Kuh-e Pashmakou, 2650–3000 m, 6 Jun 1974, *Iranshahr*, *Rechinger 18094*, *47416*, *47440* (IRAN, B, M, W); Esfahan, In faucibus Darreh-Abshar a Semirom orientem versus, 2450 m, 6 Jun 1974, *Rechinger 47480* (B), Esfahan, N side of Kuh-e Aineh-Ghabri, 2600–2800 m, 8 Aug 1978, *Assadi* and *Mozaffarian 31623* (TARI); Esfahan, Semirom, 35 km Semirom to Chaharrah, 2200 m, 14 May 1985, *Noroozi 3781* (TARI); Esfahan, Semirom, Padena, between Tang-e Rigan and Deh-bid, 1950 m, 11 Jun 1983, *Noroozi 2942* (TARI); Esfahan, Farydan, Khoamis, Kuh-e Barf-Anbar, 2300–2800 m, 21 Jun 1989, *Termeh* et al. *47291* (IRAN); Esfahan, Akhoreh, Makeh-Din, Kuh-e Vanizan, 2800 m, 5 Aug 1973, *Moussavi* and *Satei 47924* (IRAN); Esfahan, Akhoreh, Kuhhaye Akhoreh, 2700 m, 19 Jun 1973, *Iranshahr* and *Moussavi 47996* (IRAN); Esfahan, Semirom, W slope of Pashmakuh, Khosh Makan, 2700 m, 16 Aug 2006, *Aghabeigi* and *Bahramishad 47422* (IRAN); Esfahan, Akhoreh to Choghyort, Kuh-e Ghalin Darreh, 2420–2700 m, 3 Aug 1973, *Moussavi* and *Satei 18092* (IRAN); Esfahan, 55 km Shahreza to Semirom, Dowlat-Gharin, 2650–2750 m, 10 Jun 1984, *Nowroozi* and *Bozorgi 3411* (TARI); Esfahan, Fereydunshahr, near the village Sibak, 2800 m, 20 Jun 1996, *Assadi* and *Khatamsaz 76479* (TARI); Esfahan, Fereydunshahr, Meydanak, Sardabe Sophla, 2550 m, 26 May 1981, *Nowroozi 429* (TARI); Esfahan, Semirom, Padena to Sisakht, Gardaney-e Bijan, 2600 m, 10 Jun 1983, *Nowroozi 2862* (TARI); Esfahan, N side of Kuh-e Dena, Gardaneh-Bijan, 2800 m, 16 Jul 1983, *Assadi* and *Abouhamzeh 46148* (TARI); Esfahan, N side of Kuh-e Dena, above the village Noghol, 2500–3000 m, 15 Jul 1983, *Assadi* and *Abouhamzeh 46088* (TARI); Esfahan, Semirom, Pashmakou, 2820 m, 27 Jul 2009, *Pahlevani* and *Bahramishad 53348* (IRAN); Esfahan, Dena, Gardaney-e Bijan to Sisakht, 2750 m, 24 Jun 1975, *Safayian 24* (TARI); Esfahan, Khafr, Kuh-e Dena, 3000 m, 16 Aug 1972, *Riazi 7029* (TARI); Fars, Abadeh, Eghlid, Kuh-e Padena, 19 Jun 1969, *Iranshahr 18082* (IRAN); Fars, Eghlid, Bel Mt., 2400–2800 m, 1 Jul 2009, *Djavadi* et al. *53267* (IRAN); Fars, Dasht-e Arzhan, 1700 m, 9 Jun 1973, *Sojak 5649*, *5792* (IRAN, PR); Fars, Abadeh to Kakan, 2800 m, 10 Aug 1966, *Myrzayan 18154* (IRAN); Fars, N of Kuh-e Dena, Abmalakh, 2000–2600 m, 5 Aug 1978, *Assadi* and *Mozaffarian 31391* (TARI); Kerman, Baft, Kuh-e Laleh-Zar (versus Ghalleh Shah, 3000–3800 m, 30 May 1975, *Moussavi* and *Tehrani 17796* (IRAN); Kerman, Baft, Gavsoltani, 2500 m, 27 Aug 1975, *Dini* and *Bazargan 30690* (TARI); Kerman, Baft, Kuh-e Lalehzar, 3000–3800 m, 30 May 1975, *Moussavi* and *Tehrani 17787* (IRAN); Kerman, on road of Baft to Ghaleh-Askar, 2500 m, 24 May 1977, *Rajamand* and *Bazargan 33099* (TARI); Kerman, Kuh-e Hezar, 20 km SW of Rayen, 3250 m, 2 Jun 1977, *Edmondson* and *Miller 1578* (TARI); Kerman, Laleh-Zar, Kuh-e Laleh-Zar, 2650–3000 m, 24 Jun 1976, *Moussavi* and *Tehrani 47074* (IRAN); Kerman, Rayen, above the village Babzangi, S slope of Kuh-e Hazar, 3100–3900 m, 29 Jul 2002, *Assadi 83189* (TARI); Kerman, Lalehzar, Khormuj, Kuh-e Faramarz, 2800–3400 m, 27 Jun 1976, *Moussavi* and *Tehrani 18083* (IRAN); Kerman, Kuh-e Hezar, 20 km SW of Rayen, Zehrud Bala, 2700 m, 4 Jun 1977, *Edmondson* and *Miller 1631* (TARI); Kerman, prope Shirinek, montes Lalezar, 2400 m, 9 Jul 1892, *Bornmüller 4703* (B, WU); Kerman, Kuh-e Sirch, 3000 m, 24 May 1892, *Bornmüller 4707* (B); Kerman, Kuh-e Nasr, 3400–3800 m, 4 Jul 1892, *Bornmüller 4706* (B, BM, K, W, WU); Kerman, Kuh-e Lalehzar, 3400–3500 m, 18 Jul 1892, *Bornmüller 4708* (B, BM, K, W, WU); Kerman, Kuh-e Hezar, 3000–3300 m, 15 Jun 1975, *Foroughi* and *Assadi 16233* (TARI); Kerman, Rayen, 2400 m, 24 May 1981, *Manuchehri 282* (TARI); Kerman, Kuh-e Abbas-Ali, 3 Aug 1885, *Stapf s.n.* (K); Kerman to Shahdad, 40 km Kerman, Kuh-e Tunnel, 2500–2650 m, 21 Jul 1989, *Termeh* et al. *47292* (IRAN); Kerman, Negar, Ghale Asgar, 2565 m, 25 May 2009, *Pahlevani* and *Bahramishad 53786* (IRAN); Lorestan, Brujerd, Kuh-e Garrow, 2000–2900 m, 18 Aug 1973, *Moussavi* and *Satei*

47926 (IRAN); Lorestan, Khorram-abad, Kuh-e Hashtad-Pahlou, 2000–2400 m, 15 Jul 1992, *Delghandi* and *Tehrani 47310* (IRAN); Lorestan, Azna, Oshtorankuh, 2700–2800 m, 23 Jul 2011, *Dehshiri 56638* (IRAN); Lorestan, 39 km on road from Khorramabad to Nowjian and Keshvar Mts. S of the road, 2300–2550 m, 28 Jun 1977, *Runemark* and *Lazari 26132* (TARI); Lorestan, on the road from Nurabad to Nahavand, Islamabad, Kuh-e Garrin, 2100–2600 m, 31 Jun 2005, *Assadi* and *Mehregan 89002* (TARI); Lorestan, Oshtorankuh, above the village Tihun, 2000–2500 m, 12 Jul 1981, *Assadi* and *Mozaffarian 37046* (TARI); Lorestan, Dorud, Gahar lake, 2250–2900 m, 15 Aug 1982, *Mozaffarian* and *Sardabi 42245* (TARI); Lorestan, Azna, Oshtorankuh, between Bidestaneh village and Sanboran summit, 3250 m, 23 Jul 2012, *Mahmoodi* and *Hosseini* 98489, 98490, 98473 (TARI); Chaharmahal & Bakhtiari, Kuhrang, Dec 1968, *s.col. 27450* (K); Chaharmahal & Bakhtiari, Zagros Central, 9 km SE du tunnel de Kuhrang, 7 Jul 1959, *Pabot 17795* (IRAN); Chaharmahal & Bakhtiari, Shahre Kord, Ben, Harchegan, 2650 m, 12 Jun 1987, *Mozaffarian 62070* (TARI); Chaharmahal & Bakhtiari, Zardkuh, Haftanan, slope NE, 3500 m, 25 Jul 1973, *Fotovat 10244* (TARI); Chaharmahal & Bakhtiari, Zard-Kuh Mt., 3350 m, 14 Aug 1965, *R. Timmis 133* (K); Chaharmahal & Bakhtiari, Gandomkar, Kuh-e Garreh, 2300–2800 m, 9 Jun 1973, *Iranshahr* and *Moussavi 18103* (IRAN); Chaharmahal & Bakhtiari, Zard-Kuh, 2710 m, *s.d.*, *Mozaffarian 96911* (TARI); Chaharmahal & Bakhtiari, Zardkuh, 2870 m, 25 Jul 1973, *Riazi 10252* (TARI); Chaharmahal & Bakhtiari, Farsan, Deh Cheshmeh, Pir Ghar, 2050 m, 24 Jun 2008, *Eskandari* et al. *51494* (IRAN); Chaharmahal & Bakhtiari, Sabzkuh, 2400–3100 m, 30 Jun 1986, *Mozaffarian 57269* (TARI); Chaharmahal & Bakhtiari, Darreh Bazoft, Chebed, N slope of Kuh-eTaraz, 1700–2300 m, 12 Jul 1986, *Mozaffarian 57834* (TARI); Chaharmahal & Bakhtiari, N slope of Zard-Kuh from Marbor valley, 2300–3950 m, 12 Jul 1986, *Mozaffarian 57758* (TARI); Chaharmahal & Bakhtiari, Gandoman, Vastegan, 2300 m, 26 Jun 2008, *Eskandari* et al. *51493* (IRAN); Chaharmahal & Bakhtiari, Shahre Kord, Naghan, between Doupolan and Gandomkar, Kuh-e Kase–Kase, 2350–2950 m, 26 Jun 1986, *Mozaffarian 54879* (TARI); Chaharmahal & Bakhtiari, N slope of Zard-Kuh, from Marbor valley, 2300–3950 m, 12 Jul 1986, *Mozaffarian 57758* (TARI); Chaharmahal & Bakhtiari, Ardal, Sartang Mahmoud, 1800 m, 8 Jun 1973, *Iranshahr* and *Moussavi 47911* (IRAN); Kohgilouyeh & Boyerahmad, Dehdasht, Sar Faryab, Nil Mt., 2270–2965 m, 10 Jun 2011, *Amini Rad* and *Torabi 56540* (IRAN); Kohgilouye & Boyerahmad, Sisakht, Gardaneh-Bijan, 2900 m, 2 Jul 2008, *Eskandari* et al. *51490* (IRAN); Kohgilouyeh & Boyerahmad, ca 50 km E of Dehdasht, Kuh-e Nil, 2400–3200 m, 21 Jul 1983, *Assadi* and *Abouhamzeh 46494* (TARI); Hamadan, ca 20 km S of Nahavand, Kuh-e Gareu, above Cheshmeh-Gamasab, 2600 m, 10 Jul 1981, *Assadi* and *Mozaffarian 36988* (TARI); Hamadan, Nahavand, on the road to Nurabad, above Gamasab, kuh-e Garin, 2500–3400 m, 27 Jul 1995, *Assadi 75124* (TARI); Yazd, ad Dehbala, in monte Shirkuh, 2300 m, 5 Apr 1892, *Bornmüller 4704* (B, BM, K, W); Yazd, above the village Dehbala, Shirkuh Mt., 2821–3800 m, 14 Jun 2002, *Assadi* and *Ranjbar 82860* (TARI); Yazd, Taft, Hedesh (Deh-Bala), 2300–2600 m, 12 Jun 1976, *Moussavi* and *Tehrani 47075* (IRAN); Yazd, Tezerjan kuh, SE of Shirkuh, 2600 m, 26 May 1977, *Aryavand* et al. *1447* (TARI).

Euphorbia iberica Boiss., Cent. Euphorb. 38 (1860) ≡*Tithymalus ibericus* (Boiss.) Prokh., Consp. Syst. Tithymalus As. Med. 183 (1933). ≡ *Galarhoeus ibericus* (Boiss.) Prokh., Trudy Kuibyshevsk. Bot. Sada 1: 71 (1941).—TYPE: In demissis herbidis humidiusculis prope Helenedorf, May 1835, *R.F. Hohenacker* (lectotype: G-BOISS!, designated by Geltman (2002: 110); isolectotypes: K001080075!, LE [n.v.]).

=*Euphorbia latifolia* Boiss., Cent. Euphorb. 39 (1933).

=*Euphorbia intermedia* Fisch. & C.A.Mey. ex Boiss. in A.P. de Candolle, Prodr., 15: 163 (1862).

=*Euphorbia iberica* var. *intermedia* Boiss. in A.P. de Candolle, Prodr., 15: 163 (1862).

=*Euphorbia kemulariae* Ter-Chatsch., Zametki Sist. Geogr. Rast. 23: 92 (1963).

=*Euphorbia sanasunitensis* Hand.-Mazz., Ann. Naturhist. Mus. Wien, 26: 139 (1912).

=*Euphorbia vedica* Ter-Chatsch., Zametki Sist. Geogr. Rast. 24: 24 (1965).

Description: Perennial herbs, woody at the base, up to 45 cm height. Stems 3–8 mm diameter, glabrous, mostly with densely leafy sterile shoots in the middle. Cauline leaves ovate to broadly ovate-lanceolate, 20–70 × 18–35 mm, glabrous, distinctly pinnately veined beneath, sessile, base rounded to obtuse, apex obtuse or acute, margin entire to repand. Terminal rays 9–15, once dichotomous, axillary rays (0) 5–8. Ray-leaves 5–11, ovate to ovate-lanceolate, 12–25 × 8–22 mm, base truncate, apex obtuse or mucronate, margin entire; raylet leaves 2, reniform, base cordate, apex obtuse, mucronate, more or less yellowish. Cyathia: involucre campanulate-turbinate, 1.5–2 mm in diameter, lobes oblong, truncate, margin fimbriate; glands lunate, two short-horned, dark brown. Capsules subglobose, deeply trilobate, 3–3.9 × 3.5–5.2 mm, glabrous, more or less granulate on keels. Seeds ovoid-ellipsoidal, smooth, 1.8–2.7 × 1.8–2.2 mm, light grayish to brown or motted, caruncle petasiform, 0.45–0.7 mm.

Phenology: Flowering and fruiting from mid-June to August.

Distribution and ecology: *Euphorbia iberica* is reported from Azerbaijan, Armenia, Georgia, Caucasus part of Russia, NW Iran, NE Iraq, E Turkey. It is very rare in Iraq where it has been reported only once (Erbil, Helgurd Mt., near Persia frontier, above Nawanda, 2600–3000 m, 10–14 Aug 1957, *Rechinger 11467a* (W!). *Euphorbia iberica* occurs from the most northern part of Zagros to Caucasus region in subalpine to alpine regions from 2000–3500 m elevation in rocky slopes, dry stony ground and moist meadows.

Additional specimens examined: **IRAN.** E Azarbaijan, Tabriz to Bostan-abad, Iranagh-Matanagh road, Ghoush-goli, Sahand Mt., 3400–3700 m, 17 Aug 2007, *Pahlevani* and *Amini Rad 52147* (IRAN); E Azarbaijan, Sarab, Bijand, Bozghush Mt., 2300–2600 m, 6 May 2011, *Pahlevani* and *Fritsch 56259* (IRAN); E Azarbaijan, Kandovan, Arshad-Chaman, Sahand Mt., 3000–3200 m, 14 Jun 2010, *Pahlevani* and *Asef 54569* (IRAN); E Azarabaijan, Kandovan, 12 km from Kandovan to Sahand Mt., before Arshad-Chaman, Soltan-Bulaghi, 3700–3750 m, 26 May 1987, *Sarkarat* and *Olfat 138* (TARI); E Azarbaijan, Ahar, Ghoshehdagh Mt., 2750–2950 m, 10 Jul 2014, *Amini Rad 67051* (IRAN); E Azarbaijan, Oskou to Sahand, Soltan Mts., 2700–2900 m, 23 Jun 1985, *Termeh* et al. *47965* (IRAN); E Azarabaijan, Bozghush Mt., Blucan, 1880 m, 15 Jun 2009, *Mozaffarian* and *Ramezani 94734* (TARI); E Azarabaijan, Arasbaran Protected region, Hejrandust to Makidi, 1400–1700 m, 7 Jun 1976, *Assadi* and *Maasoumi 20143* (TARI); E Azarabaijan, Arasbaran Protected Area, between Doghrun mountain and Saigran-Dagh, 2300–2500 m, 15 Jul 1977, *Assadi* and *Sardabi 24175* (TARI); E Azarabaijan, Arasbaran Protected Area, between Doghrun mountain and Makidi, 2100 m, 26 Aug 1976, *Runemark* and *Assadi 22017* (TARI); E Azarabaijan, Arasbaran Protected region, between Kharil and Makidi, 2000 m, 29 May 1977, *Assadi* and *Vosughi 24890* (TARI); E Azarabaijan, Arasbaran Protected Area, forest above village Kalaleh, 1200 m, 9 Jul 1995, *Assadi 73902* (TARI); E Azarabaijan, Bostan-abad, Atmish-alti, Sahand Mt., 2620 m, 3 Aug 1984, *Termeh* and *Moussavi 47293* (IRAN); Same locality, 3000–3400 m, 5 Aug 1984, *Termeh* and *Moussavi 47472* (IRAN); E Azarbaijan, SE of Sahand Mt., 2300 m, 24 May 1960, *Furse* and *Synge 227* (K, IRAN); E. Azarbaijan, Between Marand and Jolfa, Kiamaki Dagh, 2000 m, 27 Jun 1978, *Assadi* and *Mozaffarian 29954* (TARI); ca 25 km SE of Jolfa, Kiamaki Protected Area, Gheshlagh village, kuh-e Gelenj, 2100–2700 m, 19 Jun 1988, *Assadi* and *Shahsavari 65770* (TARI); Zanjan, Mah-neshan, Alam-Kandy, Ghar-ghalan Mt., 1900–2500 m, 27 Jun 1983, *Moussavi* et al. *47975* (IRAN); Zanjan, Dandy, 25 km to Takht-e Soleiman, Zinc and Lead mine, Belgheis Mt., 2720 m, 4 May 2011, *Pahlevani* and *Fritsch 56269* (IRAN); W Azarbaijan, Khoy, Avrin Mt., 2905–3118 m, 19 Jul 2011, *Amini Rad* and *Torabi 56640* (IRAN); W Azarbaijan, Rezaiyeh, Suluk, 2400 m, 29 Jun 1972, *Sabeti 4853* (TARI); Ardebil, W of Kalour village, 2400 m, 31 May 2014, *Bidarlord 68403* (IRAN).

Euphorbia khabrica Pahlevani, **sp. nov.**—HOLOTYPE: Iran, Kerman, Baft, Khabr Protected Area, Dahaney-e Bahre Anjir (Bahre Anjir valley), 2500 m a. s. l., 28°51′N, 56°23′E, 25 May 2009, *Pahlevani* and *Bahramishad 55152/4* (IRAN!; isotypes: IRAN!, B!) (Figs. 6b, c, 7).

Diagnosis: The species is most closely related to *E. buhsei* Boiss. but differs from it by its stature <18 cm height (not >20 cm), 3–4 (5) rays (not 5–8), stem diameter 1–1.5 mm (not 2–4 mm), puberulent to glabrescent stems (not glabrous), with purplish lateral buds, elliptic to ovate-oblong leaves (not oblong-lanceolate), pubescent leaves with reddish margin (not glabrous), pubinervis to rarely glabrescent cyathia (not glabrous), dark purplish red or rarely brown glands with light reddish horns (not ochreous).

Description: Perennial herbs, woody at the base, up to 16 cm height. Stems 1–1.5 mm diameter, sparse pilose or glabrescens, ascendens. Cauline leaves elliptic or ovate-oblong, 9–25 × 4–10 mm, pilose or glabrescent, petiolate, 0.5–2 mm long, base cuneate to rounded, reddish at the base, apex obtuse to subacute, margin entire, reddish. Terminal rays (2) 3 (5), once dichotomous, without axillary rays. Ray-leaves 5 (3), elliptic-oblong, 11–32 × 5–9 mm, base rounded to cuneate, apex obtuse, margin entire, mostly reddish, sessile to subsessile; raylet leaves 2, elliptic, oblong to ovate or suborbicular, 4–13 × 4–7 mm, base rounded-truncate, apex obtuse or subacute, margin entire, mostly reddish, sessile. Cyathia: involucre campanulate, lobes ovate, interior densely pilose, exterior pubinervis or rarely glabrescent; glands 4, vinaceous (dark purplish red) or rarely dark brown, semilunate, two short-horned, horns pinkish to light red, base pilose. Capsules subglobose, 2.8–3.5 × 2.5–3.8 mm, pilose to glabrescent, pedicel pilose. Seeds ovoid-ellipsoidal, smooth, 2.4–2.7 × 1.8–2 mm, grayish, caruncle petasiform.

Additional specimens examined: **IRAN.** Kerman, Baft, Khabr Protected Area, Dahaney-e Bahre Anjir, 2500 m, 15 May 2010, *Poormirzayee* and *Kuduri 6886*; Esfahan, between Shahreza and Vanak, Sakkez, 2200 m, 6 May 1987, *Zehzad* and *Darrehshuri 87419* (HSBU); N Semi-rom, in declivibus boreo-orientalibus, Kuh-e Surmandeh (Kuh-e Alijuq), calcareous substrate, 2700 m, 7 Jun 1974, *Rechinger 47515* (W).

Etymology: The specific epithet (khabrica) refers to the name of the Khabr Protected Area where the species has been collected.

Fig. 6 Photographs of habit and habitat of *Euphorbia khabrica* in Khabr Protected Area, **a** habitat (Dahaney-e Bahr-e Anjir), **b** close up of cyathium, **c** habit

Phenology: Flowering and fruiting from mid-May to June.

Distribution and ecology: *Euphorbia khabrica* grows on scree and calcareous soil of open, sporadic and xerophytic Juniper forest (*Juniperus polycarpos* K.Koch) (Fig. 6a–c)

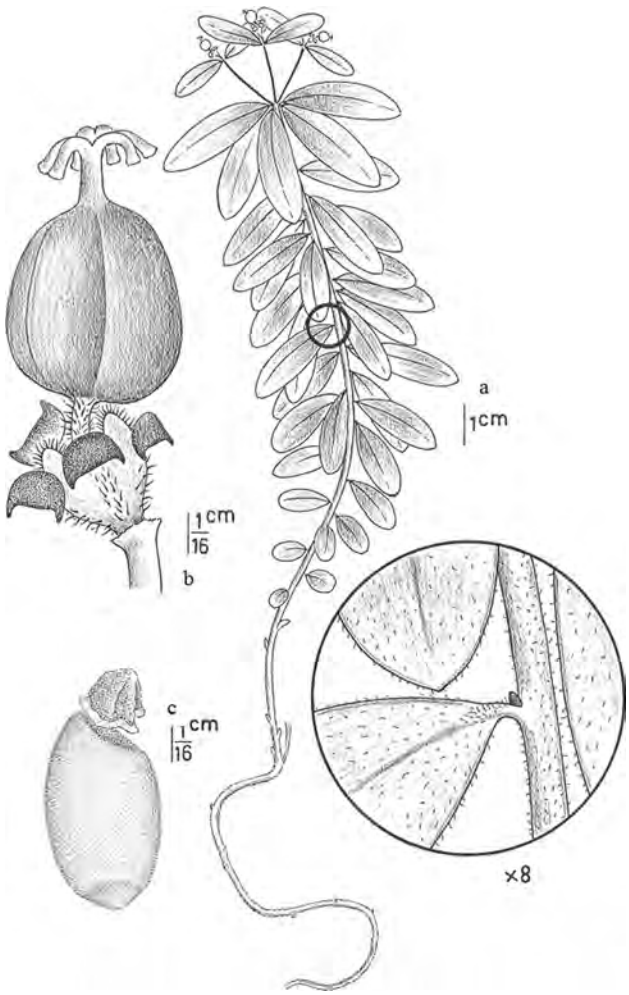

Fig. 7 *Euphorbia khabrica*, **a** habit; **b** cyathium and capsule; **c** seed. After *Pahlevani* and *Bahramishad 55152* (IRAN)

at 2500–2800 m elevation, with several communities of shrubs, chasmophyte, therophyte, and erinaceous species (Online Resource 3). Khabr Protected Area is located in the southern part of Zagros Mountains, and area with a high percentage of endemism from where noticeable angiosperm species have been reported (Hedge and Wendelbo 1978; Rechinger and Wendelbo 1985; Assadi 2006).

Conservation status: *Euphorbia khabrica* is only known from three populations from the type locality, where approximately no more than 10 individuals have been found in a rather small valley (Dahaney-e Bahre Anjir) and two herbarium specimens have been collected from central part of Zagros Mountains in Esfahan Province (Fig. 5). For these reasons and according to the IUCN Red list category (IUCN 2014), this species is considered as "endangered" (EN). In addition to *Euphorbia khabrica*, there are many rare and endemic species in Khabr Protected Area requiring urgent attention (Online Resource 3). Due to road construction, sheep and goats overgrazing, and cultivation

on one hand and global climate changing on the other hand, desertification is steadily spreading toward higher elevations in this region. With this trend, many delicate and sensitive Irano-Turanian species at higher altitudes, especially those that are more mesophytic and palatable, might be at risk of becoming extinct.

Notes: While both *E. buhsei* and *E. osyridea* have been reported from Khabr Protected Area, *E. khabrica* is geographically isolated from them, growing only in one valley (Dahaney-e Bahre Anjir). Some morphological variation has been observed between *E. khabrica* population of Kerman and two more populations from Esfahan Province. One of the most variable characters is indumentum distribution and density. Two herbarium specimens of Esfahan are densely hairy in all parts such as stem, leaves, cyathium as well as capsule, whereas the population of Kerman is scarcely hairy to rather glabrescent. The color of cyathial glands is brown in Esfahan specimens and reddish-purplish in those of Kerman. Both ITS and ISSR trees (Figs. 2, 3) clearly retrieve *E. khabrica* as a distinct unit, and the ISSR tree shows it sister to the three other species.

Euphorbia osyridea Boiss. Diagn. Pl. Or. Nov. 1, 7: 87 (1846) ≡ *Tithymalus osyrideus* (Boiss.) Soják, Čas. Nar. Mus., Odd. Prir., 140: 175 (1972).—LECTOTYPE (**designated here**): IRAN, i.1837, *Aucher-Eloy 5298* (cited as type by Radcliffe-Smith in Flora of Pakistan (172: 167, 1986) (P00606920 [web!], isolectotypes: (BM001050 436!, G!, K000911929!, LE [n.v.], P00606919 [web!], P00606921 [web!], P00606922 [web!], W0031073!).

=*Euphorbia lateriflora* Jaub. & Spach, Ill. Pl. Or. 2 (1845), non Schum. & Thonn. (1827), **nom. illeg.** [Art. 52] ≡ *Tithymalus lateriflorus* Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 81 (1860)

Description: Shrubs, 120–150 cm height, stems tomentose, grayish-green, woody, twiggy and striated, 3.6–5 mm diameter. Cauline leaves linear to linear-lanceolate, 6.5–37 × 1–3.5 mm, tomentose, sessile, tapered to the base, apex acute or subacute, margin entire. Rays present in axillary shoots only, 2–4, once dichotomous. Ray-leaves elliptic-oblanceolate, 2–4 (5), apex mucronulate, acute to subacute, raylet leaves suborbicular, ovate-rhombic to obovate. Cyathia: involucre campanulate, solitary, 3–4 mm in diameter, lobes lacerate; glands semilunate to trapeziform, truncate, lacerate or shortly and broadly 2-horned, brown to ochreous. Capsules subglobose, deeply trilobate, 4.2–5.2 × 4.5–5.7 mm, tomentose. Seeds ovoid-ellipsoidal to rather subspherical, 2.8–3.1 × 2.2–2.5, smooth, dark gray to brown, caruncle petasiform, compressed, 0.4–0.6 × 0.9–1.2 mm.

Phenology: Flowering and fruiting from mid-January to March.

Distribution and ecology: *Euphorbia osyridea* grows on rocky foothills at low to mid-altitude from SW Iran toward W Himalaya.

Notes: Syntypes of *E. osyridea* were collected by Aucher-Eloy in 1837 and by Kotschy in 1842. Radcliffe-Smith (1986) in his Flora of Pakistan considered Aucher-Eloy collection (no. 5298) from P as the holotype and two more sheets deposited in K and G as isotypes. He also indicated Kotschy collection (no. 111) from P as paratype and three more specimens from G, K, W as isoparatypes. However, there are four sheets of Aucher-Eloy in P and three more at BM, LE, W which he did not see. Therefore, here we selected one of these specimens as a lectotype (see type part).

Euphorbia osyridea was included in sect. *Tithymalus* Boiss. subsect. *Osyrideae* Boiss. by Boissier (1862) and confirmed in the same section by Rechinger and Schiman-Czeika (1964). Later, the species was included in Flora of Pakistan (Radcliffe-Smith 1986) without any sectional classification, but with a much enlarged circumscription. In fact, Radcliffe-Smith considered it as a species with a wide range of morphological features different from the original protologue (Boissier 1846). A recent molecular study has shown that the species belongs to sect. *Esula* (Riina et al. 2013). However, the species shows a considerable morphological plasticity and capacity for range expansion. The most variable morphological features of *E. osyridea* group are leaf size, stem indument, morphology of leaves and capsules, height of plant, and number and length of axillary rays.

Additional specimens examined: **IRAN.** Hormozgan, Bandar-Abbas, Kuh-e Geno, 7 Mar 1973, *Iranshahr* and *Moussavi 18140* (IRAN); Same locality, 1500–1800 m, 8 Mar 1984, *Moussavi* et al. *47386* (IRAN); Hormozgan, Bandar-abbas, S side of Kuh-e Geno, 1600 m, 4 Apr 1975, *Wendelbo* and *Foroughi 15427* (TARI); Hormozgan, Bashagerd, Jackdan, 800 m, 17 Feb 1973, *Iranshahr* and *Moussavi 18141* (IRAN); Baluchestan, Gosht to Maksukhteh, 1400 m, 14 Mar 1974, *Iranshahr* and *Ershad 18136* (IRAN); Baluchestan, 10 km Zahedan to Khash, 1650 m, 22 May 2009, *Pahlevani* and *Bahramishad 53829* (IRAN); Baluchestan, Khwash [Khash], 18 Apr 1951, *Popov 51135* (BM); Baluchestan, Saravan, Shastan, 9 Mar 1949, *Mirzayans 17854* (IRAN); Baluchestan, Khash, 16 Feb 1949, *Sharif 17853* (IRAN); Baluchestan, Khash to Iranshahr, 16 May 1948, *Rechinger* et al. *17855* (IRAN); Baluchestan, Khash, 85 km N Iranshahr, Karvandar,

1200 m, 28 Feb 2000, *Moussavi* et al. *47387* (IRAN); Baluchestan, near Suran, 40 km W of Saravan, 30 Mar 1973, *Sojak 724* (IRAN); Baluchestan, 10 km S Khash, 1350 m, 25 Feb 1974 *Iranshahr* and *Ershad 18133* (IRAN); Baluchestan, Khash, 1 Mar 1949, *Mirzayans 17857* (IRAN); Baluchestan, Sarbaz, 7 Mar 1949, *Salavatian 17858* (IRAN); Baluchestan, 15–18 km N Khash, 1300 m, 15 Mar 1974, *Iranshahr* and *Ershad 18137* (IRAN); Baluchestan, Saravan, 3 Mar 1949, *Vakhshouri 17856* (IRAN); Baluchestan, Saravan, 57 km Esfandak road, 1060 m, 13 Mar 1974, *Foroughi 10830* (TARI); Baluchestan, 20 km from Khash to Iranshahr, diviation of Irandegan road, 1420 m, 12 Apr 1983, *Mozaffarian 42794* (TARI); Baluchestan, 55 km from Khash to Iranshahr, 1500 m, 13 Apr 1983, *Mozaffarian 42916* (TARI); Baluchestan, 130 km from Bampour to Iranshahr, Tangey-e Sarhe, 1150–1250 m, 14 Apr 1983, *Mozaffarian 43074* (TARI); Baluchestan, 10 km from Zahedan to Cheshmeh Ziarat, 1570 m, 11 Apr 1983, *Mozaffarian 42727* (TARI); Kerman, 19 km SW Nosratabad, Sipi, 27 Mar 1965, *Rechinger 27191* (B, W, K); Sistan, Ghale-Zaboli, 1150 m, 11 Mar 1974, *Iranshahr* and *Ershad 18135* (IRAN); S Khorassan, Kuh-e Ahangaran, 2200–2800 m, 2 Jun 1977, *Renz 56182* (B); S Khorasan, Ghayen to Haji-abad, Ahangaran, 29 May 2007, *Eskandari* and *Torabi 47655* (IRAN); S Khorasan, 100 km E of Birjand, Ahangaran Mts., 7 km NNW of Zeidan, 2000–2300 m, 1 Jun 1977, Siliceous rock, *Runemark* and *Sardabi 23721* (TARI); Bushehr, Ahram, 15 Apr 1952, *Kashkouli 17861* (IRAN); Bushehr, 13 mile Asalouyeh to Taheri port, 21 Feb 1975, *Iranshahr* and *Termeh 18142* (IRAN); Bushehr, Borazjan, Dalaki to Bushkan from Tange Eram, between Faryab and Kheyrak (Abegarm, Shekarak, Kheyrak), 450–1000 m, 25 Apr 1995, *Mozaffarian 74157* (TARI); Bushehr, 32 km on the road from Kangan to Bandar-e Taheri, s.l., 20 Mar 1985, *Massoumi* and *Abouhamzeh 51984* (TARI); Fars, Farashband, Kuh-e Pir, Konar Malek, 800–1300 m, 4 Mar 1975, *Iranshahr* and *Termeh 18134* (IRAN); Fars, 8 km S of Lar, 1000 m, 16 Mar 1983, *Assadi* and *Sardabi 41721* (TARI); Prope pagum Gere in monte Buschom [Fars: kuh-e Sabzpushan, near Shiraz], 25 Mar 1842, *Kotschy 111* (BM, G [web!], K, P [web!], W).

Euphorbia virgata Waldst. & Kit., Pl. Rar. Hung. 2: 176 (1804) ≡ *Tithymalus virgatus* (Waldst. et Kit.) Klotzsch & Garcke, Fl. N. Mitt. Deutschl. ed. 4: 292 (1858), **nom. illeg.** [Art. 52]. ≡ *Tithymalus boissierianus* Woronow, Herb. Fl. Cauc. 479 (1931). ≡ *Tithymalus hypoleucus* Prokh., Consp. Syst. Tithymalus As. Med. 199 (1933). ≡ *Tithymalus waldsteinii* Soják, Čas. Nar. Mus., Odd. Prir., 140: 177 (1972). ≡ *Tithymalus tommasinianus* (Bertol.) Soják subsp. *waldsteinii* (Soják) Soják, Čas. Nar. Mus., Odd. Prir., 140: 177 (1972).—TYPE: Hungary, Hungarn (PR, lectotype selected by Chrtek in Skočdopolová 1982).

=*Euphorbia boissieriana* (Woronow) Prokh., Fl. URSS 14: 445 (1949).

=*Euphorbia hypoleuca* (Prokh.) Rech.f., Ann. Naturhist. Mus. Wien 56: 212 (1948).

=*Euphorbia virgata* var. *orientalis* Boiss., in A.P. de Candolle Prodr. 15: 160 (1862).

=*Euphorbia virgultosa* Klokov, Fl. RSS Ucr. 7: 631 (1955).

=*Euphorbia waldsteinii* (Soják) Radcl.-Sm., Kew Bull. 36: 216 (1981).

=*Euphorbia kitaibelii* Klokov & Dubovik, Nov. Syst. Pl. Vasc. et Non Vasc. (Kiev) 108 (1977), **nom. nud.** [Art. 50].

=*Euphorbia khorasanica* Saeidi & Ghayormand, Ann. Bot. Fennici 52: 38 (2015), **syn. nov.** (holotype: TUH!, isotype: M).

Description: Perennial herbs, woody at the base, 30–110 cm height. Stems 3–6 mm diameter, erect, glabrous, mostly with axillary shoots arising near middle of stem. Cauline leaves linear, linear-lanceolate or linear-elliptic, (2.5) 3–8.5 × 3–14 (15) mm, glabrous, sessile, base truncate, apex acute to subacute, mucronate, margin entire; leaves of axillary shoots narrower. Terminal rays 6–20, up to three times dichotomous, axillary rays 3–20 (25). Ray-leaves 5–12, linear-lanceolate to ovate, 8–25 × 3–11 mm, base truncate, apex acute to subacute, mucronate, margin entire; raylet leaves 2, ovate-rhombic, ovate-deltoid or reniform, base truncate or shallowly cordate, apex mucronate. Cyathia: involucre campanulate-turbinate, 1.7–2.2 mm in diameter, lobes oblong, truncate; glands semilunate, brownish, medium to long-horned, mostly lobate, stramineous. Capsules subglobose, deeply trilobate, 3–4.4 × 3.8–5.3 mm, glabrous, granulate at least on keels. Seeds ovoid-ellipsoidal, smooth, 2–2.8 × 1.6–2.3 mm, gray to brown, caruncle petasiform, 0.3–0.7 mm.

Phenology: Flowering and fruiting from mid-May to September.

Distribution and ecology: *Euphorbia virgata* occurs in many different kinds of habitat especially in wet places such as riverbanks, fields, orchards, roadsides, grasslands, ditches, marshes, and steppes. It is one of the most invasive plants in North America and a problematic weed in the Old World, and it occupies a wide range of habitats in places where is introduced. *Euphorbia virgata* occurs in most countries of the northern hemisphere from 1000 to 3000 m elevation.

Additional specimens examined: **IRAN.** Ardebil, Moghan, Parsabad to Bilehsavar, 26 km Parsabad, 90 m, 20 May 1971, *Iranshahr 18131* (IRAN); Same specimen, 20 May 1971, *Lamond 40058* (E, W); Ardebil, Aghdagh, 15 Jul 1959, *Brown 2069* (IRAN, K); Ardebil, Meshkin-Shahr, Anzan, 1800 m, 12 Sep 2009, *Eskandari* and *Torabi 47839* (IRAN); Ardebil, Khalkhal, 25 km S of Khalkhal, Bafrajerd village, 2100 m, 10 Jun 2014, *Bidarlord 68405* (IRAN); W Azarbaijan, E of Bazargan, 1520 m, 22 May 1960, *Furse* and *Synge 72* (IRAN, K); W Azarbaijan, Urumieh, 15 May 1986, *Parizi* and *Zargani 47285* (IRAN); W Azarbaijan, Chaldoran, Saadal, Chokhor Kandi, 2900–3030 m, 13 Jul 2015, *Amini Rad* and *Bahramishad 70222* (IRAN); W Azarbaijan, 10 km E of Urumieh, Golmarz village, 19 Jun 2012, *Eskandari* and *Bahramishad 58610* (IRAN); W Azarbaijan, Naghadeh (Soldouz), road Yeddi Goz to Soltan Yaghub, 1335 m, 22 May 2009, *Ozar 62880* (IRAN); W Azarbaijan, 30–35 km SE of Shahindez, near Mahmud-abad, 1500 m, 4 Jun 1974, *Wendelbo* et al. *12167* (TARI); W Azarbaijan, Rezaiyeh, Ghasemlu, 1600 m, 26 Jul 1972, *Sabeti 7021* (TARI); Same locality, 15 Jun 1974, *Barri 1234* (TARI); W Azarbaijan, Urmiyeh, Razhan, Rabat valley, 1900 m, 7 Jul 1973, *Siami 1223* (TARI); W Azarbaijan, Urmiyeh, Kavalak, 1300 m, 19 Jul 1974, *Farbodnia 1286* (TARI); W Azarbaijan, Maku, Kelisakandi, Khan goli, 2500 m, 31 Jun 1973, *Siami 1228* (TARI); E Azarbaijan, Arasbaran Protected Area, Ainalou to Ilankesh, 18 Jun 2010, *Pahlevani* and *Asef 55438* (IRAN); E Azarbaijan, Tasuj to Marand, 18 km S Marand, 1500 m, 27 Jul 1971, *Termeh 44512* (IRAN); E Azarbaijan, Arasbaran, Asheghlou, 3 km after Kalaleh-Sofla, 1300–1315 m, 19 Jun 2009, *Amini Rad 53272* (IRAN); E Azarbaijan, Ahar, Kuh-e Garma Duz, 1 Aug 1968, *Termeh 47950* (IRAN); E Azarbaijan, Asheghlou to Siahroud, 5 km Siahroud, 9 Jun 2007, *Pahlevani* and *Asef 47807* (IRAN); E Azarbaijan, 60 km Siahroud to Jolfa, 9 Jun 2007, *Pahlevani* and *Asef 47805* (IRAN); E Azarbaijan, Mianeh, Dishab village, 9 Jun 1986, *Termeh* and *Daneshpajuh 47272* (IRAN); Zanjan, 78 km from Zanjan to Mianeh, 13 Jun 2010, *Pahlevani* and *Asef 54572* (IRAN); Zanjan, 15 km from Zanjan on the road to Bijar, 1900 m, 30 May 1974, *Wendelbo* et al. *11854* (TARI); Zanjan, Zanjan to Khalkhal, Kaghaz Kanan, 1400–1700 m, 9 Sep 2007, *Eskandari* and *Torabi* (IRAN); Zanjan, Zanjan to Hamadan, 140 km SE Hamadan, Kuh-e Takht, 2000–2150 m, 5 Jul 1974, *Termeh* and *Moussavi 44515* (IRAN); Zanjan, 106 km from Qazvin on Hamadan road, 1730 m, 7 Jun 1965, *Seraj 24725* (TARI); Qazvin, 12 km from Qazvin to Zanjan, 1750 m, 23 Jul 1980, *Vosughi 33699* (TARI); Golestan, Nodeh to Gorgan, 15 Jun 1948, *Rechinger* et al. *5520* (IRAN, W); Golestan, Gonbad, 30 Jun 1964, *Haghighi 17673* (IRAN); Golestan, Park-e Melli Golestan, Tange Rah to Dakal, 930–1120 m, 10 Jun 1994, *Termeh* and *Matin 47389* (IRAN); Golestan, Kalaleh, 19 Jul 1967, *Hashemi 17677* (IRAN); Golestan, Gorgan, Tirtash, 30 Jul 1988, *Montazeri* and *Sateii 44513* (IRAN); Golestan, Bandar Gaz, 28 May 1948, *Sharif 17672* (IRAN); Golestan, between Bandar-e Gaz and Bandar-e Torkaman, s.l., 21 Aug 1996, *Assadi* and *Azadi 76065* (TARI); Mazandaran, Gaduk, Doab, 20 km Pol-Sefid to Ghaemshahr, 930 m, 14 May 2002, *Pahlevani 53772* (IRAN); Mazandaran, Chalus, 10 km Kojur, 17 May 2007, *Pahlevani* and *Eskandari 47670* (IRAN); Mazandaran, Kelar-Dasht, 6–16 Aug 1967, *Zaiiri 17676* (IRAN); Mazandaran, Amol, Panjab, 1000–1200 m, 31 May 2007, *Amini Rad 47809* (IRAN); Tehran, Damavand, 4 Jun 2009, *Pahlevani 53280* (IRAN); Tehran, 30 km from Tehran on Shemshak road, 1930 m, 12 Jun 1973, *Babakhanlou* and *Amin 7474* (TARI); Tehran, Polour, 2350 m, 16 Jun 1973, *Badakhshan* and *Amin 7338* (TARI); Tehran, Kafardareh, 62 km from Karaj to Chalus, 1980 m, 26 Jun 1973, *Babakhanlou* and *Amin 7473* (TARI); Tehran, 46 km from Tehran, between Meigoun and Shemshak, 2200 m, 2 Aug 1972, *Amin* et al. *7337* (TARI); Tehran, Evine, Velenjak Mt., 1700 m, 2 Jun 1972, *Termeh* and *Zargani 47252* (IRAN); Tehran, 50 km S of Qom, Kenijan, 1900 m, 12 Jun 1974, *Amini* and *Bazargan 18846* (TARI); Tehran, Lavasan, SW mountains of Kallan, 2200 m, 25 Apr 1973, *Arazm* and *Bazargan 7340* (TARI); Tehran, Shemshak, N of Darbandsar, 2600–2700 m, 12 Aug 1984, *Mozaffarian* and *Mohammadi 49093* (TARI); Tehran, 31 km NE of Tehran on Shemshak road, 1850 m, 30 Jul 1972, *Babakhanlou* et al. *7463* (TARI); Tehran, 21 km NW Tehran, Kan-Solughan road, 1600 m, 22 May 1974, *Amin* and *Bazargan 18533* (TARI); Tehran, 5 km from Firouzkuh to Semnan, 1990 m, 26 Jun 2007, *Pahlevani* et al. *47354* (IRAN); Tehran, N of Tehran, Yonjezar, 1800 m, 5 Jun 1974, *Amin* and *Bazargan 18567* (TARI); Tehran, between Firuzkuh and Zarindasht, 1500 m, 14 May 1974, *Babakhanlou* and *Amin 18117* (TARI); Tehran, Shemshak, 2280 m, 3 Sep 1971, *Gheissari 2713* (TARI); Tehran, ca 20 km S of Damavand, between Tamisun and Aselun, 1550–1650 m, 22 Jun 1985, *Mozaffarian 53908* (TARI); Tehran, Haraz road, Kahrod, 2050 m, 9 Aug 1971, *Panahi 2577* (TARI); Semnan, ca 50 km N of Semnan, Mt above Hiku, 2400–2700 m, 29 Jul 1982, *Assadi* and *Abouhamzeh 40738* (TARI); Semnan, Shahrud, Tash, 2030 m, 28 Aug 1972, *Rowshan 7015* (TARI); Semnan, Shahmirzad, 1800 m, 20 May 1987, *Mozaffarian 58885* (TARI); Alborz, Karaj, Asara, 15 Jun 1948, *Rechinger* and *Manuchehri 6276* (BM, IRAN, W); Alborz, Karaj to Chalus, 20 km Karaj, 20 Jun 1977, *Eghtedari 17993* (IRAN); Alborz, Karaj, In ditione oppidi Keredj [Karaj], 20 Aug-1 Sep 1948, *K.H.* and *F. Rechinger 6711* (BM); Alborz, Karaj, Taleghan, between road of Hasiran village to Mengolan village, 2000 m, 29 Jun 1984, *Aghabeigi 47676* (TARI); Alborz, Karaj valley,

Nesa, 2290 m, 22 May 1970, *Foroughi 523* (TARI); Alborz, Adaran, Haft Cheshmeh, 15 km from Karaj on Chalus road, 1700 m, 18 Jun 1973, *Babakhanlou* and *Amin 7465* (TARI); Hamadan, Bahar, 15 Jun 1965, *Babaii 17681* (IRAN); Hamadan, Hamadan to Tuyserkan, 3 km to Tuyserkan, 1730 m, 3 Aug 1992, *Termeh* et al. *47188* (IRAN); Hamadan, ca 16 km from Ganjnameh to Tuyserkan, 2200 m, 9 Jul 1981, *Assadi* and *Mozaffarian 36891* (TARI); Lorestan, Borujerd, Vanaiee, 29 Jun 2007, *Eskandari* et al. *47346* (IRAN); Markazi, Arak, 72 km from Saveh toward Nowbaran, Gharghabad and Kahak, 2 May 1985, *Akhani 197* (TARI); Khorasan, Kuh-e Hezar-Masjed, 8 Jun 1948, *Rechinger* et al. *5135* (IRAN, M, W); Khorasan, Neyshabour, Boujan, 1750 m, 28 Jun 2007, *Pahlevani* et al. *47350* (IRAN); Khorasan, Neyshabour, Akhlamad, Darreh-Abshar, 1600–1800 m, 30 May 1948, *Rechinger* et al. *4569* (BM, IRAN, W); N. Khorasan, Esferayen, N slope of Kuh-e Shah Jahan from Darparchin-e bala village, 1700–2500 m, 7 Jun 1984, *Mozaffarian 48485* (TARI); Kordestan, Bijar, Kuh-e Hamzeh-Arab, 2000 m, 1 Jul 1971, *Termeh 44200* (IRAN); Kordestan, ca 25 km SSE of Sanandaj, Mt. above the village Narran, 2200–2600 m, 15 Jun 1987, *Assadi 60485* (TARI); Kordestan, Sanandaj, Sarab-Ghamish, Saral Mt., 2300 m, 27 Jul 2010, *Pahlevani* and *Asef 54794* (IRAN); Kordestan, 20 km from Shevisheh to Marivan, 1500 m, 24 Jun 2003, *Assadi 84945* (TARI); Kordestan, ca 35 km N of Sanandaj, Afrasiab village, Deh-e Gazzan, 1700–2800 m, 29 Jul 1995, *Assadi 75250* (TARI); Chaharmahal & Bakhtiari, Kouhrang, Sheikh Ali khan waterfall, 2450 m, 24 Jun 2008, *Eskandari* et al. *51495* (IRAN); Chaharmahal & Bakhtiari, Farsan, after Babaheidar, opposite to Sefiddane, 2220 m, 3 Jun 2008, *Mozaffarian 96687* (TARI); Chaharmahal & Bakhtiari, Kuhrang, Sefiddivan, 2470 m, 24 Jul 1973, *Riazi 10251* (TARI); Chaharmahal & Bakhtiari, Borujen, Sabzehkuh, 2580 m, 28 Jul 1973, *Riazi 10249* (TARI); Kohgilouyeh & Boyerahmad, between Yasuj and Dehdasht, Dilegoon, kuh-e Savers, 2200–3200 m, 19 Jul 1983, *Assadi* and *Abouhamzeh 46393* (TARI); Gilan, Kalaj-Manjil, 1200 m, 22 May 1973, *Sabeti 7331* (TARI); Fars, 10 km S of Dashte Arjan, Kotale Pirzan pass, 2000 m, 5 Jul 1989, *Zehzad* and *Taheri 67035* (TARI); Esfahan, Semirom, Vanak to Dalan-Kuh, Shams-abad and Ganat, 2200 m, 12 Jun 1984, *Nowroozi* and *Bozorgi 3594* (TARI); Qazvin, Alamout, Aghagir, 1250 m, 23 Jul 1970, *Foroughi 3670* (TARI).

Key to species of *Euphorbia* sect. *Esula* in Iran

1a. Shrubs or shrublets; rays on axillary branches only…… 2

1b. Perennial herbs; terminal rays always present with or without axillary rays…… 3

2a. Shrubs (>120 cm tall); stems mostly grayish, tomentose, leaves linear to linear-lanceolate; capsules mostly tomentose…… *E. osyridea*

2b. Shrublets (50–100 cm tall); stems mostly reddish, glabrous, leaves oblong-lanceolate or rarely linear-lanceolate; capsules mostly glabrous…… *E. austro-iranica*

3a. Plants <18 cm tall; glands dark purple…… *E. khabrica*

3b. Plant ≥20 cm tall; glands ochreous to brown, never purplish…… 4

4a. Capsules pubescent…….. *E. hebecarpa*

4b. Capsules glabrous (rarely sporadically hairy in *E. buhsei*)…… 5

5a. Terminal rays (4) 5–7 (8); capsules 4.6–5.7 mm long; seeds 2.7–3.7 mm long…….. *E. buhsei*

5b. Terminal rays (6) 8–15 (20); capsules 3–4.4 mm long; seeds 1.8–2.8 mm long…… 6

6a. Cauline leaves ovate to broadly ovate-lanceolate, more than 1.7 cm wide (to 3.5 cm), lateral nerves prominent beneath…… *E. iberica*

6b. Cauline leaves linear to linear-lanceolate, not more than 1.5 cm wide, lateral nerves not prominent beneath…… *E. virgata*

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Information on Electronic Supplementary Material

Online Resource 1. Voucher information and GeneBank accession numbers for all sequences used in our analyses. Newly generated sequences are preceded (the accession numbers have been received by EMBL) by an asterisk (*).
Online Resource 2. Dataset and alignment of the ITS sequence using in this study.
Online Resource 3. Species composition of the Euphorbia khabrica community from Kerman, Khabr Protected area, with their habitat, life form, phytochory and distribution.

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Publication 4

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Synopsis of *Euphorbia* subgen. *Esula* sect. *Helioscopia* (Euphorbiaceae) in Iran with the description of *Euphorbia mazandaranica* sp. nov.

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Euphorbia subgen. *Esula* with about 480 species is one of the most diverse and complex lineages of the giant genus *Euphorbia*. Species of this subgenus are usually herbaceous and are mainly distributed in temperate areas of the Northern Hemisphere. This paper updates the taxonomy and distribution of *Euphorbia* (subgen. *Esula*) sect. *Helioscopia* in Iran since the publication of 'Flora Iranica' in 1964. We provide a key, species descriptions, illustrations (for most species), distribution maps, brief characterization of ecology as well as relevant notes for the 12 species of this section occurring in Iran. As a result of this revision, *E. altissima* var. *altissima* is reported as new for the country, and a new species from northern Iran, *Euphorbia mazandaranica*, is described and illustrated. With the exception of *E. helioscopia*, a widespread weed in temperate regions worldwide, the remaining species occur in the Alborz, Zagros and northwestern regions of Iran.

Euphorbia L. is one of the largest genera of flowering plants with about 2000 species (Govaerts et al. 2000, Frodin 2004, Bruyns et al. 2006, Riina and Berry 2011). *Euphorbia* species show a high diversity of growth forms and are distributed on all continents from sea level to 4000 m a.s.l., occupying a great variety of habitats. Southwest Asia is an important center of diversity for *Euphorbia* with about 230 species, most of them in *E.* subgen. *Esula* Pers. (Boissier 1879, Parsa 1949, Prokhanov 1949, Rechinger 1964, Rechinger and Schiman-Czeika 1964, Radcliffe-Smith 1980, 1982, 1986, Collenette 1999, Govaerts et al. 2000, Riina et al. 2013). Subgenus *Esula* comprises ca 480 species of mostly non-succulent herbs and shrubs distributed mainly in the Northern Hemisphere (Horn et al. 2012). Iran has the largest number of taxa in southwest Asia with about 90 species including several endemics and even undescribed species (Rechinger and Schiman-Czeika 1964, Mobayen 1979, Mobayen 1984, Akhani 2004, Nasseh and Joharchi 2004, Djavadi et al. 2006, Nasseh et al. 2006, Pahlevani 2006, Sajedi et al. 2006, Pahlevani 2007, Pahlevani and Riina 2011, Pahlevani and Mozaffarian 2011, Pahlevani et al. 2011b).

Ongoing taxonomic revisions of different groups of *Euphorbia* in Iran as part of the *Euphorbia* Planetary Biodiversity Inventory project (Esser et al. 2009), has raised the number of species occurring in the country from 65 (Rechinger and Schiman-Czeika 1964) to more than 90 (Pahlevani 2007, Pahlevani and Riina 2011, Pahlevani and Mozaffarian 2011, Pahlevani and Akhani 2011, Pahlevani et al. 2011a, 2011b). This taxonomic revision is motivated by the ecological importance of this genus in different Iranian plant communities, the weedy nature of some *Euphorbia* species, as well as the presence of some rare or endemic species in Iran. Many species are rich in chemical compounds, including carcinogenic, skin-irritant, and anti-cancer agents. Lastly, detailed descriptions and illustrations are lacking in the first sixth volumes of 'Flora Iranica' (Rechinger and Schiman-Czeika 1964) where Euphorbiaceae was treated (Akhani 2006). Our goals are to update the taxonomy and geographic distribution of *Euphorbia* sect. *Helioscopia* in Iran since the treatment of 'Flora Iranica' in 1964, and to provide a key and illustrations to facilitate species identification.

Material and methods

Species of sect. *Helioscopia* were revised using existing holdings in Iranian herbaria, especially FAR, IRAN, and TARI, including recently collected specimens by the first author. A few specimens from FUMH, K, M, TUH as well as the private herbarium of Akhani (Herb. Akhani, Dept of Plant Sciences, Univ. of Tehran) were also included. All specimens were studied and identified using relevant

taxonomic literature and floras (Boissier 1879, Prokhanov 1949, Khan 1964, Rechinger and Schiman-Czeika 1964, Radcliffe-Smith and Tutin 1968, Radcliffe-Smith 1980, 1982, 1986, Govaerts et al. 2000, Geltman 2009) and were compared with type collections hold in several herbaria with rich collections from Eurasia. Types were also searched online at JSTOR Plant Science (http://plants.jstor.org) and the Berlin digital herbarium (ww2.bgbm.org/Herbarium). Included in the synopsis of each species are the following details: accepted name, types, synonymy, description, illustration (for most species), brief characterization of ecology, flowering and fruiting time, habitat, distribution map, relevant notes, and examined specimens.

Results and discussion

'Flora Iranica' (Rechinger and Schiman-Czeika 1964) included all together 20 species in *E.* sect. *Helioscopia*, and 12 of them were reported from Iran. According to the present revision, some of those names are synonyms (*E. unilateralis* Blakelock, *E. guestii* Blakelock), two species are not found in Iran despite extensive fieldwork and herbarium research (*E. schottiana* Boiss., *E. coniosperma* Boiss.), and four others belong to different sections or clades within *E.* subgen. *Esula* (*E. bungei* Boiss., *E. gaillardotii* Boiss. & Blanche *E. turkestanica* Regel, *E. phymatosperma* Boiss.). We recognize 12 species of *E.* sect. *Helioscopia* in Iran, including one new record (*E. altissima* var. *altissima*) and one new species (*E. mazandaranica*).

We consider *Euphorbia* subg. *Esula* sect. *Chamaebuxus* Lázaro with ca 95 species (Geltman 2009) part of sect. *Helioscopia* as it has been suggested by recent molecular phylogenetic analyses (Kryukov et al. 2010, Salmaki et al. 2011) where members of sect. *Chamaebuxus* are well embedded within a clade including most species of sect. *Helioscopia*. Boissier (1879) and Rechinger and Schiman-Czeika (1964) treated sect. *Chamaebuxus* as subsect. *Galarhoei* Boiss. and sect. *Tithymalus* Boiss. Prokhanov (1949) treated the group as subgen. *Paralias* sect. *Tulocarpa* (Rafin.) Prokh., divided into three subsections, i.e. *Lutescentes* Prokh., *Purpuratae* Prokh. and *Helioscopiae* Prokh. Radcliffe-Smith (1982) treated sect. *Chamaebuxus* as sect. *Helioscopia* with two subsections separated by their life history: subsect. *Galarhoei* (perennials) and subsect. *Helioscopiae* (annuals). According to recent phylogenetic studies on subgenus *Esula* using DNA sequence data (Kryukov et al. 2010, Barres et al. 2011, Frajman and Schönswetter 2011, Peirson et al. 2014), it is clear that life history in subgen. *Esula* is not phylogenetically stable and thus not a reliable character for infrageneric classification. However, in sect. *Helioscopia* life history is a useful character for distinguishing species. The main feature characterizing sect. *Helioscopia* is the rounded involucral glands with entire margins and without appendages (Rechinger and Schiman-Czeika 1964, Radcliffe-Smith and Tutin 1968, Radcliffe-Smith 1982). However, this feature is also present in species from other lineages within subg. *Esula*. Species of sect. *Helioscopia* are annual or perennial with fruits bearing different kinds of ornaments on their surface and seeds with a smooth and usually shiny surface. Notable exceptions regarding fruit and seed morphology are *E. helioscopia* with ornamented seeds and smooth fruits, and *E. mazandaranica*, *E. microsphaera* and *E. eriophora* with smooth fruits. Based on morphological features, including capsule and seed morphology, a subdivision of sect. *Helioscopia* into several subsections seems appropriate. However, comprehensive molecular phylogenetic studies are underway to further evaluate the taxonomic subdivision of this diverse section of subgen. *Esula*.

Euphorbia schottiana was recorded by Rechinger and Schiman-Czeika (1964) from western Iran (Lorestan Province, Shahbazan). However, after several collection trips to that region and study of most specimens deposited in Iranian herbaria, no specimen of *E. schottiana* has been found. The source of the confusion probably comes from an Iranian Specimen, seen by Rechinger and Schiman-Czeika at W, identified as *E. schottiana* (M. Koie 465). This specimen corresponds to an immature individual of *E. condylocarpa*. *Euphorbia schottiana* is distributed in the Mediterranean region and it is unlikely that it occurs in Iran. The record in 'Flora Iranica' (Rechinger and Schiman-Czeika 1964) is probably a misidentification. For all these reasons, we excluded *E. schottiana* from the present taxonomic treatment. This issue was also discussed by Radcliffe-Smith (1982) who pointed out that the occurrence of *E. schottiana* in Iran seemed rather unlikely. Another doubtful species is *E. gaillardotii*, which is reported from Iran (Govaerts et al. 2000), but so far we have not found any record for that species in the country. It seems that Govaerts et al. (2000) used Parsa (Flore de L' Iran) as their source for this record. Parsa (1949) indicated two *E. gaillardotii* specimens (Lazar 966, 1087 at K) from Isfahan and Soleymanieh to Tehran, respectively. These two specimens could not be located at K for further study; however it should be noticed that Soleymanieh is a city in Iraq. There are many problems with Parsa's work, such as misidentification and wrong information about the geographic distribution of species, not only in Euphorbiaceae but in other families as well (Lamond 1977).

The species *E. phymatosperma*, present in Iran, which used to be treated under sect. *Helioscopia* is excluded from this treatment following our molecular phylogenetic analyses (Riina et al. 2013), which place *E. phymatosperma* in a different lineage outside the sect. *Helioscopia* clade.

Euphorbia L. (1753, p. 157)

Taxonomic synonym: *Tithymalus* Gaertn. (1790, p. 115) nom. cons.

E. subgen. *Esula Pers.* (1806, p. 14).

Type: *E. esula* L.

Usually erect herbs or sometimes dendroid shrubs. Leaves exstipulate, usually alternate, symmetrical at the base, sessile or subsessile. Cyathia in pleiochasial cymes (rays). Glands without petaloid appendages. Seeds usually carunculate.

E. sect. *Helioscopia* Dumort. (1827, p. 87)

Type: *Euphorbia helioscopia* L.
Taxonomic synonym: *E.* sect. *Chamaebuxus* Lázaro (1896, p. 282).

Annual or perennial herbs, rarely subshrubs, tuberous or not, erect or ascendent. Leaves pinnately nerved, membranous, sessile or petiolate. Involucral glands rounded. Capsules usually warty, rarely smooth, glabrous or pilose. Seeds usually smooth, sometimes ornamented, carunculate or rarely ecarunculate.

Key to the Iranian species of *E.* sect. *Helioscopia*

1. Annuals 2
   – Perennials 6
2. Seeds smooth 3
   – Seeds ornamented 5
3. Capsules densely tuberculate ..... 12. *E. stricta*
   – Capsules smooth 4
4. Capsules spherical, glabrous to sparingly pilose; seeds carunculate ..... 8. *E. microsphaera*
   – Capsules obviously trilobate, pilose; seeds ecarunculate ..... 5. *E. eriophora*
5. Seeds foveolate ..... 8. *E. helioscopia*
   – Seeds striate-rugulose ..... 10. *E. rhabdotosperma*
6. Capsules smooth (rarely with a few short warts or granulate), glabrous or rarely sparingly pilose 7
   – Capsules tuberculate or verrucose, glabrous or pilose 8
7. Cauline leaves sessile, linear-lanceolate, 5.5–10.0 × 0.5–1.0 cm, with minutely serrulate and cartilaginous margin; terminal rays 3–4-chotomous ..... 1. *E. altissima* var. *altissima*
   – Cauline leaves petiolate, elliptic-lanceolate to ovate-oblong, 3.5–10.0 × 1.5–4.0 cm, with entire margin; terminal rays 2-chotomous ..... 7. *E. mazandaranica*
8. Cauline leaves cordate-auriculate at base; root a fusiform tuber ..... 3. *E. condylocarpa*
   – Cauline leaves rounded or cuneate; root not forming a tuber 9
9. Stems scaly at base 10
   – Stems not scaly at base 11
10. Axillary rays numerous (>7); capsules 8–10 mm in diameter; seeds 4 mm wide ..... 6. *E. macrocarpa*
    – Axillary rays 0–4; capsules 5.0–6.5 mm diameter; seeds up to 3 mm wide ..... 7. *E. grisophylla*
11. Cauline leaves broadly ovate, up to 3.5 cm at the widest portion, petiolate, white pilose, especially at margin and main vein; terminal rays dichotomous ..... 11. *E. squamosa*
    – Cauline leaves oblong-lanceolate, not more than 2 mm at the widest portion, sessile, glabrous; terminal rays 3–4-chotomous ..... 9. *E. orientalis*

1. *Euphorbia altissima* Boiss. var. *altissima* (Fig. 1)

Based on the same type: *Tithymalus altissimus* (Boiss.) Klotzsch and Garcke (1860, p. 80). **Type:** Hab. ad rivulos Denisleh et Laodiceam in Phrygia australi, legi flor. Jun 1842, P. E. Boissier, s.n (lectotype designated here: G-BOISS!; isolectotypes: GH00282013!, P00552405!, P00552406!).

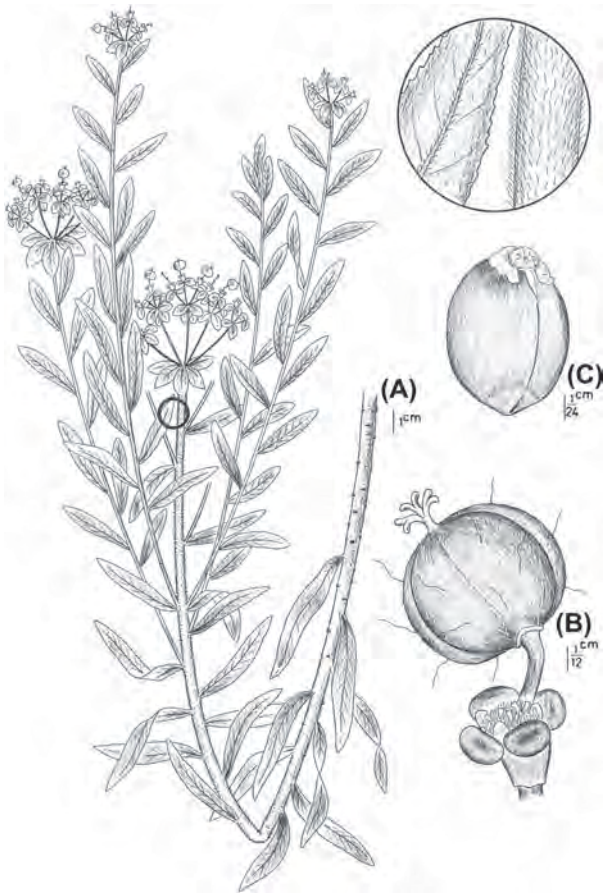

Figure 1. *Euphorbia altissima* var. *altissima*. (A) habit, (B) cyathium and fruit, (C) seed. Drawn from voucher specimen from west Azarbaijan: road of Talatappeh towards Urmieh, Gol-e Marz village, TARI 68340.

Perennial herbs, up to 2 m high. Stems erect, pilose or villous, with violet spots. Cauline leaves linear-lanceolate to elliptic-lanceolate, hirsute, 5.5–10.0 × 0.5–1.0 cm, sessile, with tapering base and acute apex, mucronate, with serrulate margin and prominent white midrib. Terminal rays 4–7, 3- or 4-chotomous, once dichotomous; axillary rays 0–5. Ray leaves like cauline leaves but smaller, 1.0–1.5 × 0.5–1.0 cm, sessile, cuneate or truncate at base, subacute at apex, mucronate, with serrulate to subentire margin. Raylet leaves ovate-rotundate, cuneate-truncate at base, cuspidate at apex, with serrulate margin. Cyathia: involucre turbinate, 2.0–2.5 mm in diameter, lobes short-oblong; glands elliptic and rounded, brownish. Capsules subglobulose, trilobate, 5.0–5.5 mm in diameter, smooth or granulate, glabrous or rarely sparingly pilose. Seeds ellipsoidal, 2.5 mm long (excluding the caruncle), smooth, dark brown; caruncle reniform, 0.25 mm long, yellowish. Flowering and fruiting in June to August.

Habitat
In moist depressions, on the banks of small irrigation ditches, pools, springs and streams, in fields, at 700–1400 m a.s.l.

Distribution
Old World: Iran (northwest), northern Iraq, Turkey, Syria, Lebanon, Cyprus. An Irano–Turanian element (Fig. 2). Not previously reported from Iran.

Specimen examined
Iran. West Azerbaijan: road of Talatappeh towards Urmieh, Gol-e Marz village, Izadpanah and Taheri 68340 (TARI).

2. *Euphorbia condylocarpa* M. Bieb. (1808, p. 377) (Fig. 3)

Basionym: *Tithymalus condylocarpus* (M. Bieb.) Klotzsch and Garcke (1859, publ. 1860, p. 78). **Type:** Turkey, in Montosis Caucasi, circa acidulam Narzana, s.d., Marschall von Bieberstein s.n. (LE, n.v.).
Taxonomic synonyms: *Euphorbia amplexicaulis* Ledeb. (1850, p. 567) nom. illeg., non Hook. f. 1847 – *Euphorbia cardiophylla* Boiss. & Heldr. (1853, p.107). – *Tithymalus amplexicaulis* Klotzsch & Garcke (1859, publ. 1860, p. 80). – *Tithymalus cardiophyllus* (Boiss. & Heldr.) Klotzsch & Garcke (1859, publ. 1860, p. 78).

Perennial herbs, 10–35 cm high, with a fusiform-cylindrical tuber; stems prostrate, decumbent or erect, glabrous. Cauline leaves oblong, elliptic-oblong or linear-lanceolate, 1.5–3.5 × 0.5–1.5 cm, sessile, at base auriculate-cordate or dilated-cordate and amplexicaul only in one side, obtuse to subacute at apex, with entire, subentire or serrate margin. Terminal rays 3–6, unbranched or once dichotomous; axillary rays 3–10. Ray leaves triangular-lanceolate or oblong-triangular, 1.0–1.5 × 0.5–1.0 cm, sessile, cuneate or truncate at base, obtuse-acute at apex, with entire-serrate margin. Raylet leaves rhombic-reniform, wider than long, cuneate-truncate at base, cuspidate or not at apex, with more or less serrate or subentire margin. Cyathia: involucre subglobular-turbinate, 2.0–2.5 mm in diameter, with short-oblong lobes; glands elliptic and rounded, brownish. Capsules subglobulose, trilobate, 4.0–5.5 (6.0) mm in diameter, covered with subglobular-conical processes, glabrous. Seeds compressed ellipsoidal, 3.0–3.5 mm long (excluding the caruncle), smooth, dark brown; caruncle reniform, 0.5 mm long, yellowish. Flowering and fruiting in April to May.

Habitat
Mountain slopes, oak forests, meadows, rocky slopes and steppe forests on limestone, at 1500–2500 m a.s.l.

Distribution
Old World: Iran (north, northwest, west and southwest), northern Iraq, Turkey, Caucasus (Georgia, Armenia, Azerbaijan and Russia). An Irano–Turanian element, restricted to the Zagros, Alborz and Arasbaran protected area ranges in Iran (Fig. 2).

Specimens examined
Iran. East Azerbaijan: Arasbaran protected area, between Kalaleh and Mahmoud-abad, Assadi 73941 (TARI); Arasbaran protected area, west part of Makidi, Assadi and Masoumi 20255 (TARI); Kalibar, from Makidi to Vinagh, Wendelbo and Assadi 17062 (TARI); Arasbaran protected area, between Doghrun Mt and Saigran-Dagh, Assadi and Sardabi 24170 (TARI); Fars: Kuh-e-Bamu, northeast of

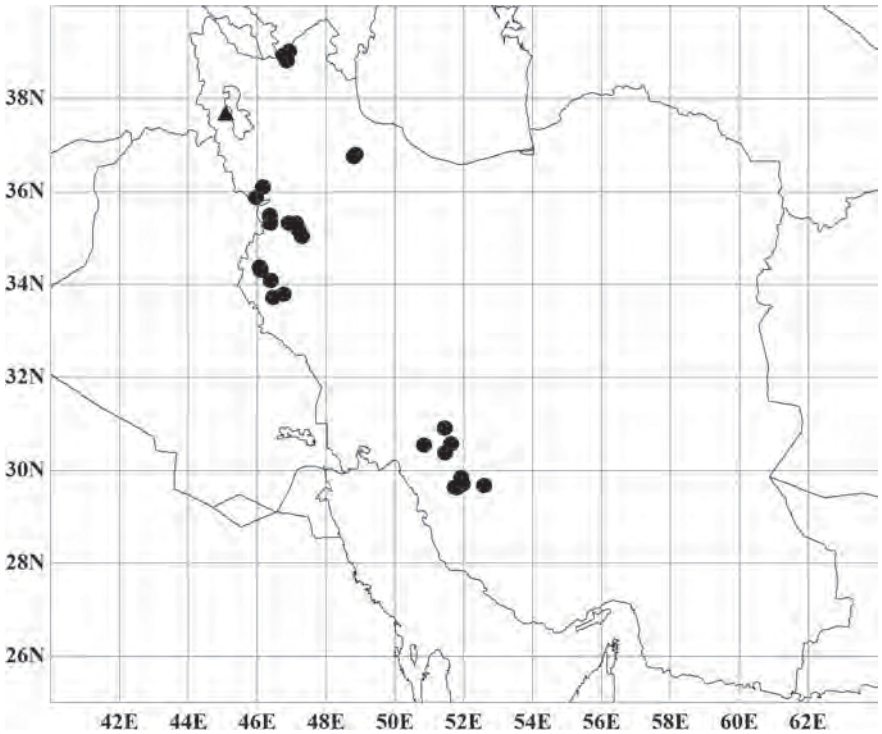

Figure 2. Distribution of *Euphorbia altissima* (triangle) var. *altissima* and *E. condylocarpa* (circle) in Iran.

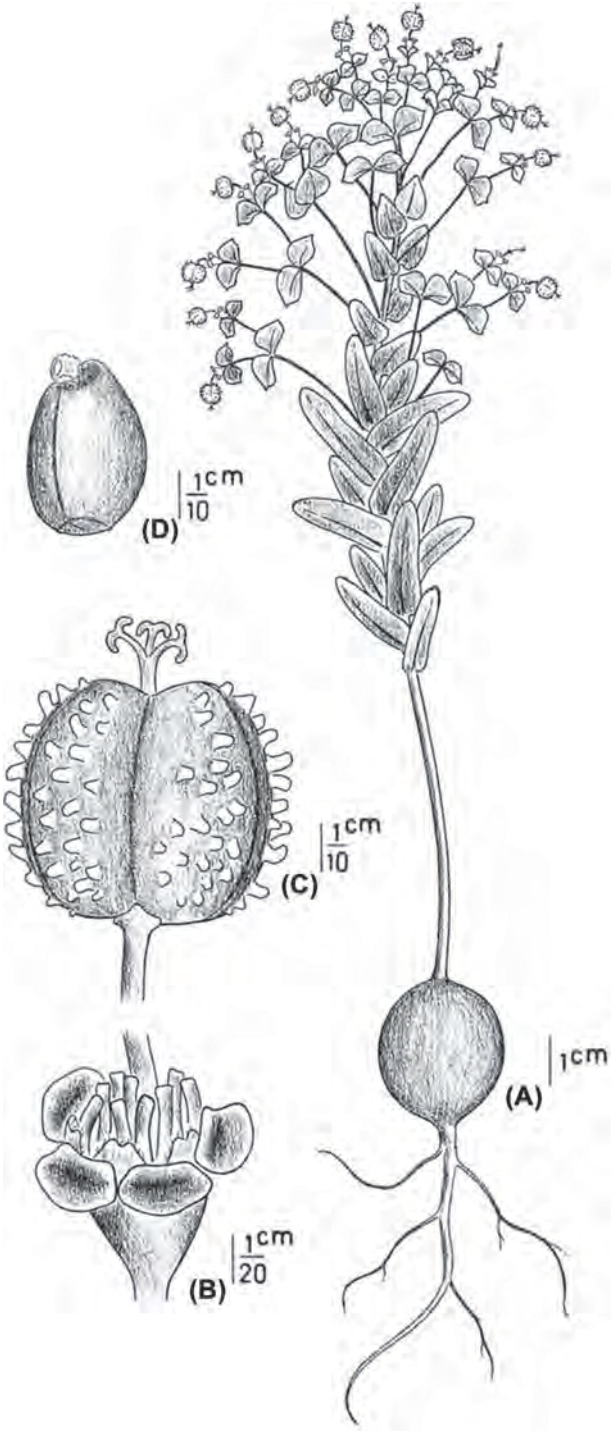

Figure 3. *Euphorbia condylocarpa.* (A) habit, (B) cyathium, (C) fruit, (D) seed. Drawn from voucher specimen from Zanjan, 70 km from Zanjan to Gilvan, IRAN 56262.

Shiraz, Archibald 1408 (K); Ridges south of Kuh Chang, east of Kazerun, Archibald 1296 (K); 23 km from Babameidan to Yasuj, Assadi and Aboohamze 38425 (TARI); Arjan-Parishan protected area, gardane-ye galu Khajei, Ghasemi 47339 (IRAN); Kazeroon, Kotale Pirezan, Riazi 4867 (TARI); Shiraz, Kotel-e Pirzan protected area, 2 km after Dasht-e Arjan on the new road of Kazeroun, Salmaki and Zarre 39955 (TUH); Gilan: Manjil to Zanjan, Badamestan, Iranshahr 17994 (IRAN); Ilam: Reno, Iranshahr 17713 (IRAN); Kohgiluye and Boyerahmad: ca 12 km from Yasuj to Ardakhan, before Vaz (Varag) village, Davis and Bokhari D56479 (K); Yasuj, Sisakht, Foroughi 4851 (TARI); Neck Mt, between Churam and Gachsaran, Mozaffarian 77298 (TARI); Kurdistan: Marivan to Saghez, 65 km Marivan, Sajedi and Bahramishad 47340 (IRAN); Baneh, Naheni Mt, Fattah and Khaledian 2381 (TARI); southeast of Sanandaj, 40 km from Sanandaj, Garawa, Fattahi and Khaledian 403

(TARI); Sarvabad, west of Sanandaj, 98 km from Sananadaj, Fattahi and Khaledian 701 (TARI); east of Sanandaj, 12 km to Sanandaj, Fattahi and Khaledian 1296 (TARI); Zanjan: 70 km from Zanjan to Gilvan, Pahlevani and Fritsch 56262 (IRAN).

3. *Euphorbia eriophora* Boiss. (1844, p. 51) (Fig. 4)

Based on the same type: *Tithymalus eriophorus* (Boiss.) Klotzsch and Garcke (1859, publ. 1860, p. 65). **Type:** Turkey (C2): In agris Cariae interioris segetes, specimen

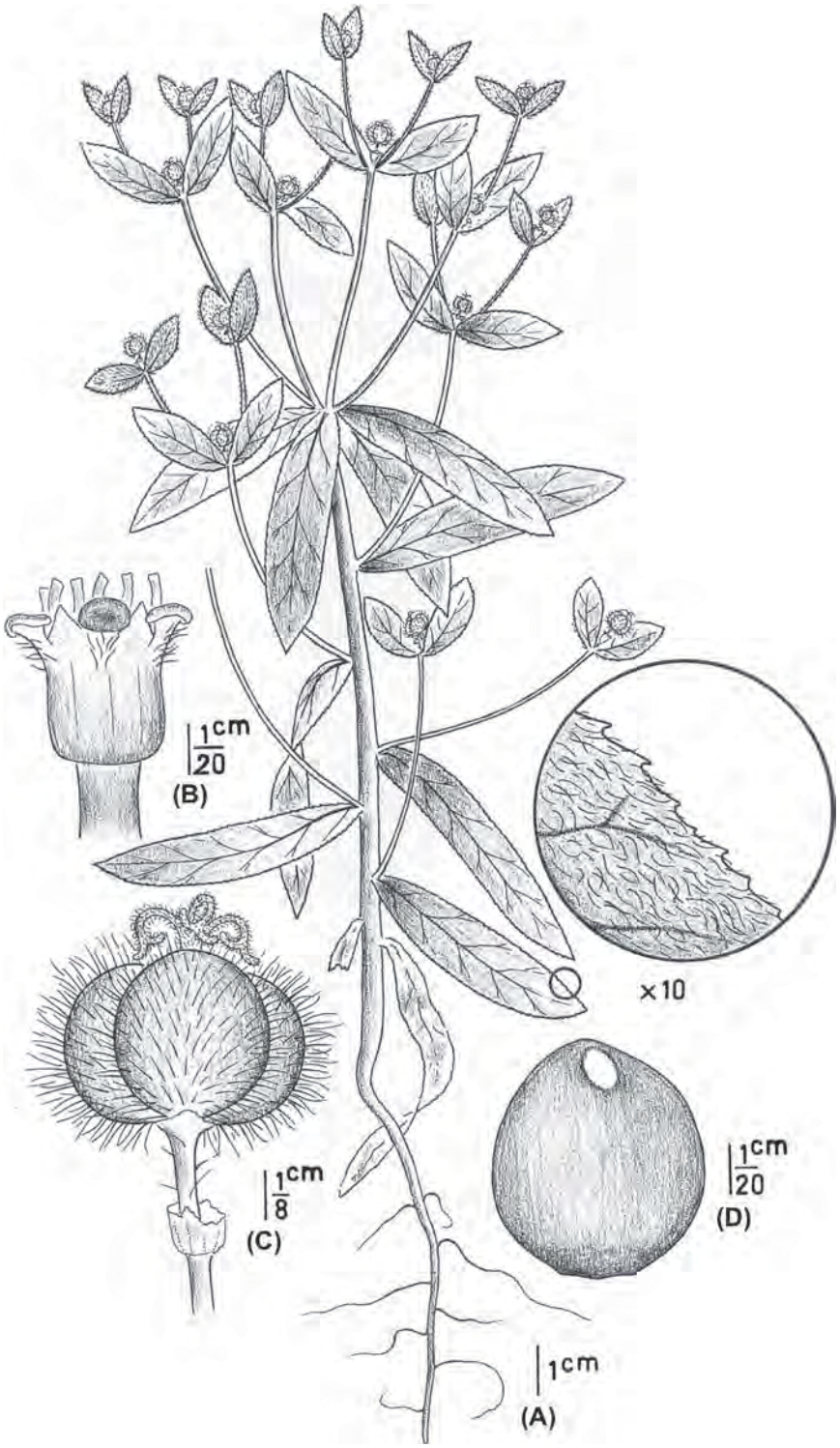

Figure 4. *Euphorbia eriophora*. (A) habit, (B) cyathium, (C) fruit, (D) seed. Drawn from voucher specimen from east Azerbaijan: Mianeh, Ghaflankuh, IRAN 46720.

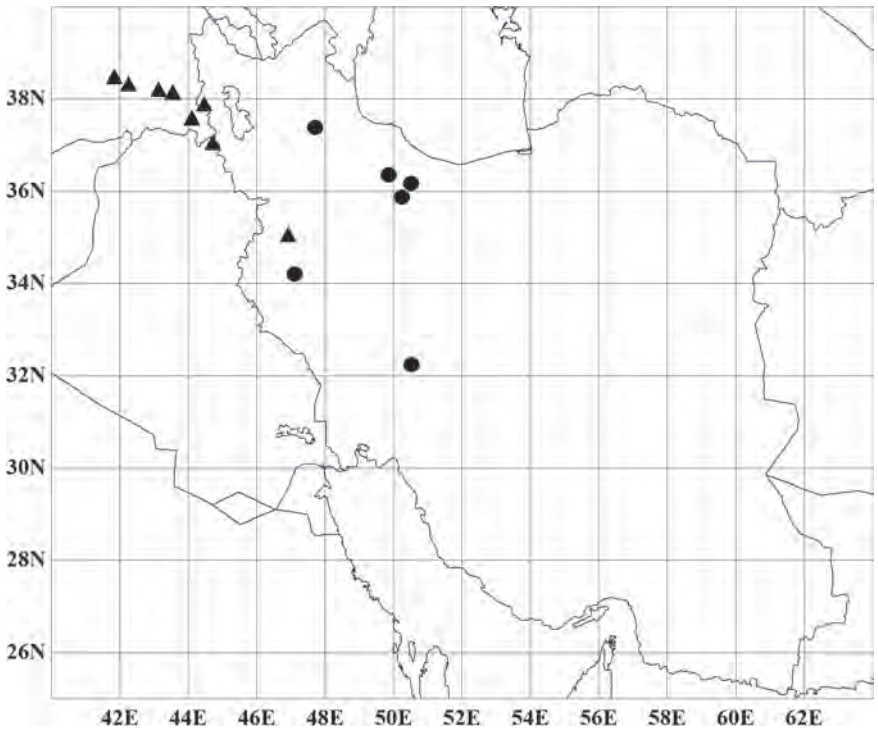

Figure 5. Distribution of *Euphorbia eriophora* (circle) and *E. grisophylla* (triangle) in Iran.

unicum, in planitie ad meridiem Cadmi [Honaz dag], Jun 1842, Boissier s.n. (holotype: G-BOISS!).
Taxonomic synonym: *Euphorbia lasiocarpa* K. Koch. (1849, p. 721), nom. illeg., non Klotzsch 1843.

Annual herbs, up to 45 cm high, pilose or villous. Cauline leaves oblanceolate, 1.5–6.0 × 0.5–1.5 cm, sessile, tapering at base, acute or subacute at apex, with serrulate margin, pilose. Terminal rays 3 (4), three times dichotomous; axillary rays 0–4. Ray leaves ovate-lanceolate, 2.5–5.5 × 1.0–1.5 cm, sessile, rounded or cuneate at base, acute at apex, with serrulate margin. Raylet-leaves oblong-ovate to ovate-lanceolate, cuneate or rounded at base, mucronate at apex, with serrulate margin. Cyathia: involucre campanulate, 1.0–1.5 mm in diameter; glands elliptic and rounded, light brown. Capsules strongly trilobate, 5.0–5.5 mm in diameter, smooth, villous. Seeds ellipsoidal-subglobose, 2.3–2.6 mm long, smooth, grayish–brown; without caruncle. Flowering and fruiting in May to June.

Habitat
On steppic clay plains and in fallow fields at 500–1500 m a.s.l.

Distribution
Old World: northern, northwestern and western Iran, northern Iraq, Armenia, Azerbaijan (Nakhichevan) and Turkey. An Irano–Turanian element, restricted to the Zagros, Alborz and Caucasus regions. *Euphorbia eriophora* is very rare in Iran (Fig. 5).

Specimens examined
Iran. East Azerbaijan: Mianeh, Ghaflankuh, Iranshahr 46720 (IRAN); Ghazvin: Sarkisian 37938 (IRAN); Kermanshah: anonymous 47693 (IRAN); Chaharmahal va Bakhtiari: Farsan, Dehe Cheshme toward Gushe village, Mozaffarian 97361 (TARI); Alborz: 98 km west of Karaj, Foroughian and Hariri 7625 (TARI); Taleghan, Varkash, Amin and Bazargan 19714 (TARI).

4. *Euphorbia grisophylla* M. S. Khan. (1964, p. 94)

Based on the same type: *Tithymalus grisophyllus* (M. S. Khan) Soják (1972, p. 140). **Type:** Turkey (C10), Prov. Hakari, Cilo dag, in gorge between Cilo yayla and Diz deresi, 8000 ft, rocky slope, 10 Aug 1954, Davis and Polunin 24250 (holotype: E00359918!, isotypes: BM000951563!, K!).

Perennial herbs, up to 90 cm high, arising from a woody stock; stems several, usually simple, sparingly pubescent-pilose to subglabrous, scaly at base. Cauline leaves ovate-oblong, lanceolate or broadly ovate, 3.0–5.5 × 1.0–2.5 cm, subsessile, truncate, cuneate or sometimes subcordate at base, acute or obtuse at apex, with entire margin. Terminal rays 5, once or twice dichotomous; axillary rays 0–4. Ray leaves ovate, broadly ovate or ovate-rhombic, 2–3 × 1.5–2.5 cm, sessile, truncate at base, acute or sometimes cuspidate at apex, with entire-undulate margin. Raylet leaves ovate-deltoid to suborbicular, truncate or shallowly cordate at base, cuspidate and yellowish at apex, with entire margin. Cyathia: involucre campanulate-turbinate, 2 mm in diameter, with oblong-lanceolate lobes; glands elliptic and rounded, brownish. Capsules trilobate, 5.0–6.5 mm in diameter, covered with conic-cylindrical warts, glabrous. Seeds broadly ellipsoidal, up to 4 mm long, smooth or rarely flecked blackish, gray-brownish; caruncle reniform, 0.5 mm long, yellowish. Flowering and fruiting in May to July.

Habitat
Dry rocky igneous and limestone slopes, screes, at 1800–3000 m a.s.l.

Distribution
Old World: western Iran and eastern Turkey. An Irano–Turanian element, restricted to the Zagros Mts (Fig. 5). This species was previously only known from eastern Turkey, but a new record from west Iran (Maroofi 55797) was recently found and illustrated (Pahlevani et al. 2011b).

Specimens examined
Iran. Kurdistan: Sanandaj to Kamiaran, Avalan Mt, Maroofi 55797 (IRAN).

5. *Euphorbia helioscopia* L. (1753 p. 459)

Based on the same type: *Tithymalus helioscopius* (L.) Hill (1768, p. 3). – *Galarhoeus helioscopius* (L.) Haw. (1812, p. 152). – *Euphorbion helioscopium* (L.) St.-Lag. (1880, p. 126). **Type:** Habitat in Europae cultis, Herb. Linn. no. 630.49 (lectotype: LINN, designated by Jafri and El-Gadi (1982, p. 33).

Annual herbs, up to 40 cm high, glabrous or sparingly pilose. Cauline leaves obovate-spathulate, 1.0–3.5 × 0.5–2.0 cm, sessile, attenuate at base, obtuse or retuse at apex, with serrulate margin in the upper half. Terminal rays 5, at first trichotomous, then once or twice dichotomous; axillary rays absent. Ray leaves obovate, 1.0–2.5 × 0.5–1.8 cm, sessile, attenuate at base, obtuse at apex, with margin serrulate in upper half. Raylet leaves obliquely obovate, asymmetric or rounded at base, obtuse at apex, with margin serrulate in upper half or more. Cyathia: involucre turbinate, 1.5–2.0 mm in diameter; glands elliptic and rounded, light brown. Capsules trilobate, 2.5–3.5 mm in diameter, with smooth surface, glabrous. Seeds ovoid, 1.6–2.0 mm long, foveolate-reticulate, dark brown; caruncle flattened, transversely ovate, 0.4–0.6 mm long, straw yellow. Flowering and fruiting almost all over the year in the absence of severely cold conditions.

Habitat
Ruderal weed in disturbed and cultivated areas and city gardens, streamsides; from sea level to 2500 m a.s.l.

Distribution
Old World and introduced into the New World: a cosmopolitan weed (Fig. 6).

Specimens examined
Iran. Alborz: Shahriar, Esmaieli 17407 (FAR); Karaj, Hesarak, Salavati et al 20923 (FAR); Baluchestan:

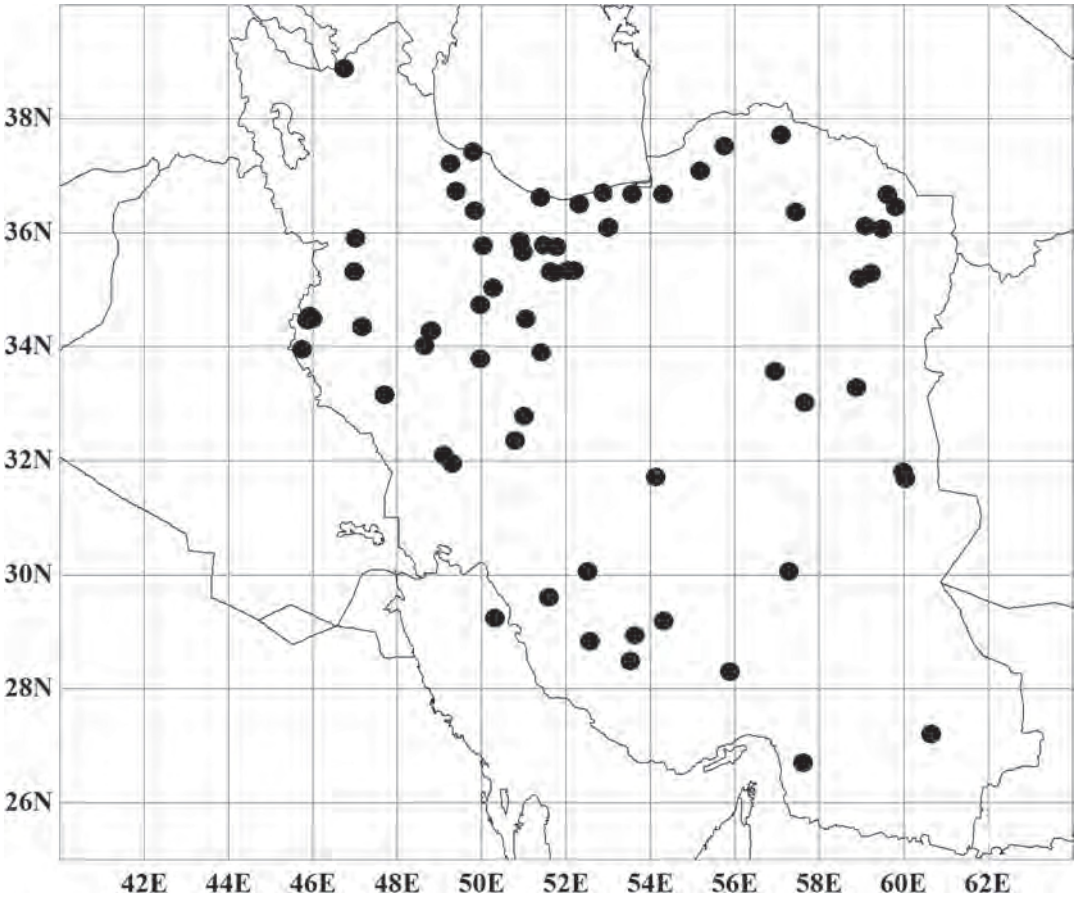

Figure 6. Distribution of *Euphorbia helioscopia* in Iran.

Iranshahr, Manouchehri 17773 (IRAN); Bushehr: Kazeroun, Kaskan, Rasti 4250 (FAR); Persian gulf, Khark Island, Termeh and Moussavi 18080 (IRAN); Chaharmahale-Bakhtiari: Shahrekord, Rokh pass, Khodarahmi 4435 (FAR); east Azerbaijan: Arasbaran protected area, Vaighan to Shabkhaneh, Pahlevani and Asef 54568 (IRAN); Esfahan: Kashan, Saghar-abad village, Tamaddon 34959 (FAR); Varche, Adadsuzan 4423 (FAR); Fars: Fasa, Gholamzadeh 4386 (FAR); Firouz-abad, Kashkouli 17776 (IRAN); Jahrum, Sadeghi 4112 (FAR); Neyriz, Palangan, Shamsi 4488 (FAR); Gilan: Fouman, Asfia 4213 (FAR); near Sefidrud, 100 m to Mangil dam, Ghadimi 4269 (FAR); Zibakenar, Razaee 25913 (FAR); Golestan: Gorgan, 73 km Shahpasand, Termeh 47991 (IRAN); Hamedan: Malayer, Mosaddeghi 4506 (FAR); Hormozgan: Bashagerd, Ghurichi, Iranshahr and Moussavi 44555 (IRAN); Bandar-abbas, Hajiabad, Mozaffarian 52119 (TARI); Kerman: Mahan, Susanzadeh 4330 (FAR). Kermanshah: Rijab, Iranshahr and Dezfoulian 17771 (IRAN); Taghbostan, Alizadeh et al. 17450 (FAR); Pol-e Zahab, 8 km northeast of Pol-e Zahab, Berimvand village, Hatami 2286 (TARI); Khuzestan: Masjed-Soleiman to Lali, Tougah, Iranshahr and Termeh 18079 (IRAN); Kordestan: Sanandaj, Divandarreh, Asef and Torabi 53797 (IRAN); Lorestan: Borujerd, Malayer road, Amini 4142 (FAR); Khorram-abad, Pol-Dokhtar, Ershadi 26274 (FAR); 20 km of Boroujerd, Oshtorinan, Gamshidi 29662 (FAR); Mazandaran: Jouybar, Larim village, Kianmehr 27163 (FAR); Gaduk, Doab, 5 km to Pol-Sefid, Pahlevani 53766 (IRAN); Behshahr, east Behshahr, Rasuli 13516 (FAR); Amol, near forest, Rudgarian 4184 (FAR); Nowshahr, Chalus road, anonymous 4268 (FAR); Sangdeh, Pol-e Sefid, Domanchik 31466 (TARI); northern Khorasan: northwest Bojnourd, 1 km to west of Shirindarreh dam, Memariani and Zangooei 41918 (FUMH); Qazvin, Boien-Zahra, Mirhosseini 29383 (FAR); Alamout region, Vaghfi 4245 (FAR); Qom: Saveh, Garzan, Toghroud plain, Mohammadi 32425 (FAR); Razavi Khorasan: Torbat-e Heydarieh, Doroudgar 42019 (FAR); Ferdows road, 20 km to Mashhad, Jahanbakhsh 17422 (FAR); 10 km Shadmehr to Kashmar, Ghuch-palang Mt, Faghihnia and Zangooei 26668 (FUMH); northeast of Mashhad, between Pasakuh and Tabadkan, Faghihnia and Zangooei 24977 (FUMH); north of Neyshabur, Somea, Faghihnia and Zangooei 20912 (FUMH); Mashhad, around Kardeh dam, Jahanbakhsh 4408 (FAR); Semnan: Garmsar, Eyvanekey, Shahbodaghi 4494 (FAR); Delbar, Turan, anonymous 4498 (FAR); southern Khorasan: Tabas, northwest of Nayband, Faghihnia and Salehi 31999 (FUMH); Nehbandan, Shusf, Faghihnia and Zangooei 21512 (FUMH); Birjand, Amin-abad, Faghihnia and Zangooei 30362 (FUMH); Between Dayhuk-e Tabas and Ravar-e Kerman, northeast of Nayband, Joharchi and Zangooei 11934 (FUMH); 2 km Ghaen, around Ghanat-e Shahek, Zokaie 375 (FUMH); Tabas, Cheshme Deh-Cheruk, Zokaie 734 (FUMH); Tehran: Gageroud, Ashrafzade 4427 (FAR); Varamin, Manuchehri 17770 (IRAN); Darabad, Nemati 17961 (FAR); Yazd: 40 km to west Yazd, Farashah, Javadi 28647 (FAR); Markazi, Tafresh, Valadabad, Amin and Bazargan 18683 (TARI).

6. *Euphorbia macrocarpa* Boiss. & Buhse (1860, p. 197) (Fig. 7)

Based on the same type: *Tithymalus macrocarpus* (Boiss. & Buhse) Prokh. in V. L. Komarov (1949, p. 350), nom. illeg., non (Benth.) Croizat 1937. – *Tithymalus notabilis* Soják (1972, p. 174).
Type: Persia, Ssamam, 1847 [1 Jun 1848], Buhse s.n. (holotype: G-BOISS!, isotypes: LE!, BR0000005106370!).

Perennial herbs, up to 70 cm high, arising from a woody stock; stems several, simple, sparingly pilose to subglabrous, scaly at base. Cauline leaves lanceolate to oblong, 4.0–7.5 × 1.0–1.8 cm, sessile, rounded to subcordate at base, acute or obtuse at apex, with margin entire or sometimes shallowly denticulate in the distal half of upper leaves. Terminal rays 5–7, dichotomous; axillary rays numerous. Ray leaves ovate to oblong, 2.0–2.5 × 1.0–1.5 cm, sessile, rounded at base, obtuse at apex, with entire margin. Raylet leaves ovate-rhombic to suborbicular, rounded or cuneate at base, obtuse at apex, with entire margin. Cyathia: involucre turbinate, 2–3 mm in diameter, with oblong-lanceolate lobes; glands elliptic and rounded, brownish. Capsules trilobate, 8–10 mm in diameter, their surface densely covered with warts, glabrous. Seeds subglobose, 4 mm long, smooth, gray–brown; caruncle minute. Flowering and fruiting time in May to June.

Habitat
Rocky limestone and serpentine slopes, open ground in oak forests, old volcanic craters, at 1800–3000 m a.s.l.

Distribution
Old World: northern, northwestern and western Iran, eastern Turkey, northern Iraq and Azerbaijan. An Irano–Turanian element, restricted to the Zagros and Alborz Mts (Fig. 8).

Specimens examined
Iran. Kermanshah: Paveh, above the village Shemshir, base of Shahu Mt, Assadi 60749 (TARI); Between Kermanshah and Paveh, before Shamshir, Mansour-Aghai village, kuh-e Shahu, Assadi and Mehregan 89152 (TARI); road of Songhor to Bisotun, Kamijeh, Hamzehee and Asri 87826 (TARI); Kurdistan: 36 km from Sanandaj to Kamiaran, Nashur valley, Assadi 60617 (TARI); ca 15 km from Baneh to Saghez, Vazaneh Mt, Maroofi and Karegar 55861 (IRAN); ca 35 km from Saghez to Baneh, Piromaran village, Nacarouz Mt, Maroofi and Naseri 6141; northwest of Sanandaj, Saral Mt, near Hanegelan village, Maroofi and Rastegar 8570; ca 50 km northwest Sanandaj, Saral, Mozaffarian 71575 (TARI); south of Baneh, 15 km from Baneh to Sanandaj, Fattahi and Bolooki 1409 (TARI); 34 km from Chenareh to Baneh, Assadi 85085 (TARI); on the road of Nosud to Marivan, 6 km to Daraki-Lakhani, Salmaki and Zarre 39561 (TUH); Lorestan: between Khorram-abad and Sepid-dasht, Baghbanan, 60 km to Khorram-abad, Iranshahr 55345 (IRAN); On the road from Nurabad to Nahavand, Islamabad, kuh-e Garin, Assadi and Mehregan 88995 (TARI); Borujerd, Vanai area, kuh-Garin, Assadi and Mehregan 89082 (TARI); west Azerbaijan: south of Urumieh, Gharehaghaj, Balanaj, Kokia village, Ghasemloo valley, Pahlevani and Fritsch 56267 (IRAN).

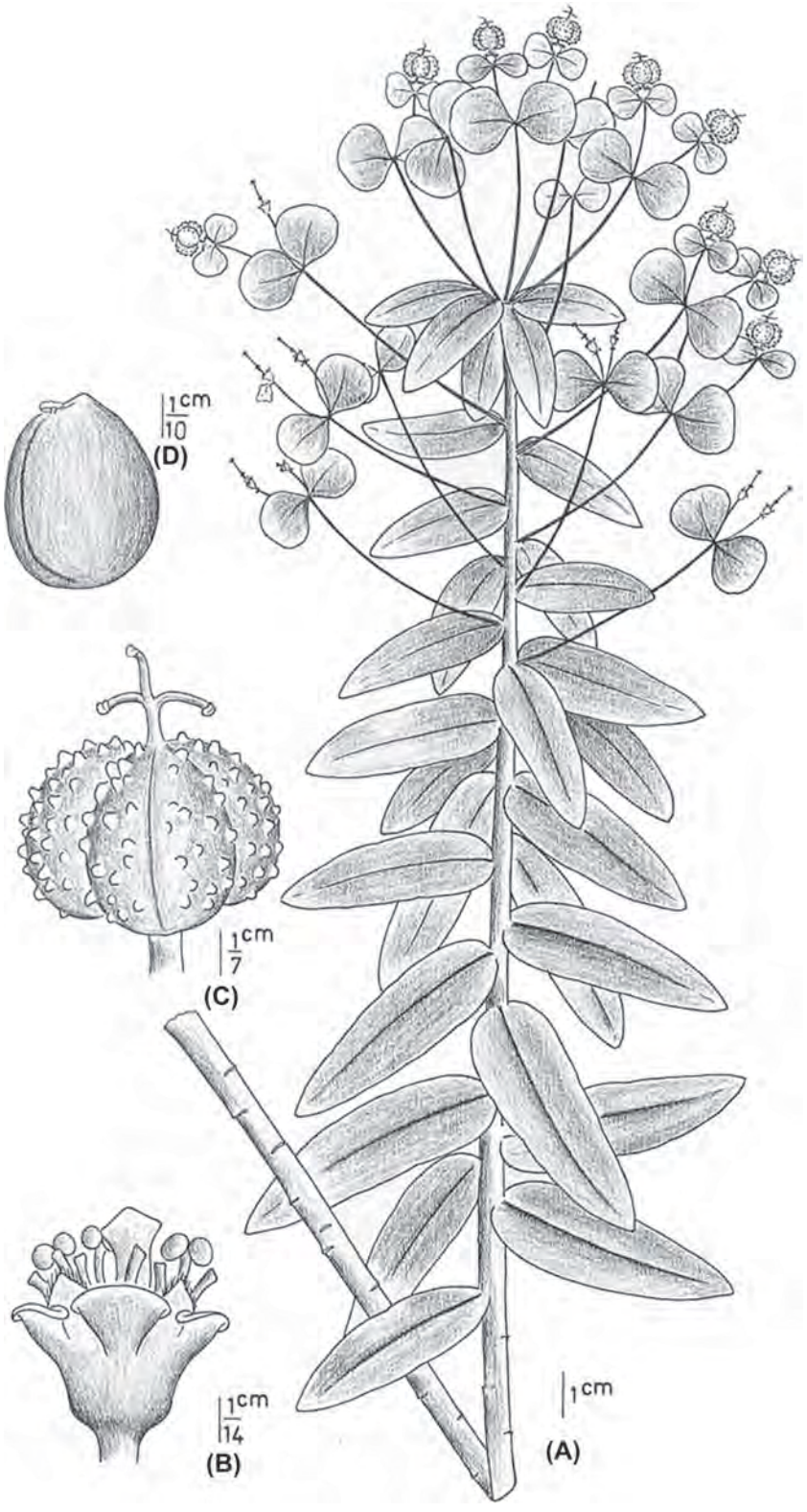

Figure 7. *Euphorbia macrocarpa*. (A) habit, (B) cyathium, (C) fruit, (D) seed. Drawn from voucher specimen from Lorestan: between Khorram-abad and Sepid-dasht, Baghbanan, 60 km to Khorram-abad, IRAN 55345.

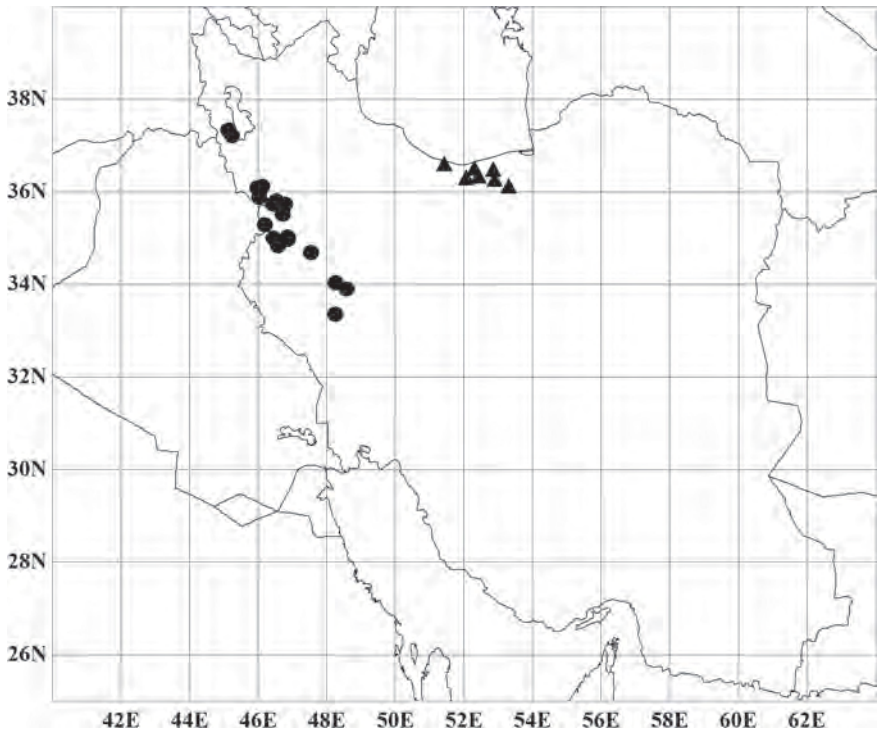

Figure 8. Distribution of *Euphorbia macrocarpa* (circle) and *E. mazandaranica* (triangle) in Iran.

7. *Euphorbia mazandaranica* Pahlevani sp. nov. (Fig. 9–10)

Ab E. microsphaerae Boiss. habito perenni (non annuo), foliis caulinis petiolatis (non sessilibus), subaxillaribus pilosis (non glabris), margine integris (non denticulatis); umbellae radiis bifidis (non trifidis); involucellorum phyllis integris (non denticulatis), capsula trisulcata (non globosa) differt.

Type: Iran. Mazandaran, 5 km to Chalus, in the forest, 110 m a.s.l., 36°37'N, 51°25'E, 17 May 2007, Pahlevani and Eskandari 55150 (holotype: IRAN, isotype: IRAN).

Etymology

Euphorbia mazandaranica is named after the Mazandaran province where the species occurs.

Description

Perennial herbs, up to 45 cm high, arising from a woody rootstock; stems single or several, usually 4, simple, usually reddish, sparingly pilose to subglabrous. Cauline leaves elliptic-lanceolate, ovate-oblong, 3.5–10.0 × 1.5–4.0 cm, with 3–5 mm long, sometimes subwinged petiole, attenuate at base, subacute , acute or obtuse at apex, with entire margin, glabrous on the adaxial side, pilose on the abaxial side, especially on the midrib. Terminal rays (4) 5, unequal in length (6–18 cm), dichotomous; axillary rays 0–5. Ray leaves like cauline leaves in all aspects but usually larger. Raylet leaves deltoid-ovate or rhombic-ovate, the most distal ones suborbicular, truncate to rounded at base, rounded, obtuse or sometimes emarginate at apex, with entire margin. Cyathia: involucre turbinate or campanulate, 2 mm in diameter; glands elliptic and rounded, brownish or yellowish. Capsules trilobate, 3–4 mm in diameter, their surface smooth or rarely granulate or with a few short warts, glabrous to subglabrous. Seeds ellipsoidal, 2.0–2.5 mm long, smooth, brownish; caruncle minute (0.25–0.50 mm long), light yellow. Flowering and fruiting in April to May (at least one month earlier than *E. squamosa*).

Habitat

Forest vegetation from see level to 1450 m a.s.l., including *Fagus orientalis*, *Quercus castaneifolia*, *Acer velutinum* forest (1200 m a.s.l.), and *Quercus petraea*, *Populus caspica*, *Carpinus betulus*, *Pterocarya fraxinifolia* forest (0–150 m a.s.l.).

Distribution

Old World: the species is endemic to the northern forests of Iran (Fig. 8). An Hyrcano–Euxine element.

Similar species

Besides its resemblance to *E. microsphaera*, *E. mazandaranica* is also in close morphological affinity with another perennial spurge, *E. squamosa*. The most important diagnostic characters differentiating these three species are given in Table 1. *Euphorbia squamosa* is distributed from forest areas of the Gilan province to the northwest (Arasbaran protected area) in the east Azarbaijan province and extends to the Caucasus region (Russia, Georgia, Armenia, Azerbaijan, northeast Turkey, northwest Iran), whereas *E. mazandaranica* is restricted to forest areas of the Mazandaran province.

Conservation status

The apparent limited distribution and small populations of *E. mazandaranica* suggest that this species could be

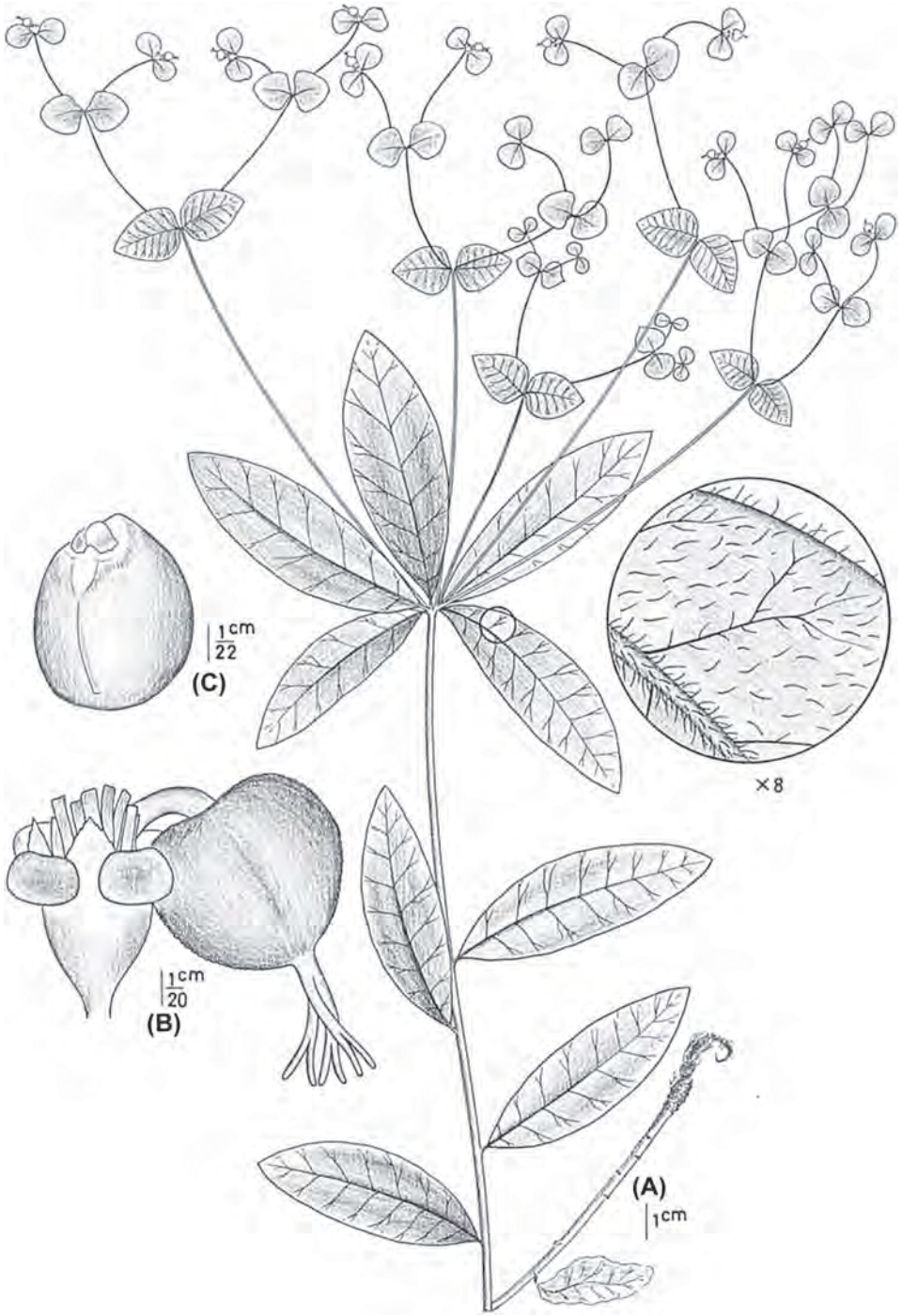

Figure 9. *Euphorbia mazandaranica*. (A) habit, (B) cyathium and fruit, (C) seed. Drawn from voucher specimen from Mazandaran, 5 km to Chalus, IRAN 55150.

threatened; however detailed field studies are needed to determine its conservation status.

Additional specimens examined (paratypes)

Iran. Mazandaran: Amol, Ahmad Chalepey, Baliran village, Amini Rad and Asef 56631 (IRAN); ca 15 km north of Sangdeh on the road to Farim, Assadi 73329 (TARI); Amol, Amol forests, Hashemi moghadam 26135 (FAR); Nur, Chamestan, Vaz, Mozaffarian 72869 (TARI); Ghaemshahr, Niknafs 4153 (FAR); 45 km from tonekabon to Jannat-Rudbar (36 km from the deviation road to Jannat-Rudbar at Tonekabon-Ramsar main road), Salmaki 39758 (M, TUH); Shirgah, 35 km to Ghaemshahr, Soleimani 4113 (FAR); Chalus forest, Termeh and Moussavi 17989 (IRAN).

8. *Euphorbia microsphaera* Boiss. (1846, p. 87) (Fig. 11)

Based on the same type: *Tithymalus microsphaerus* (Boiss.) Klotzsch and Garcke (1860, p. 74). **Type:** Hab. in humidis

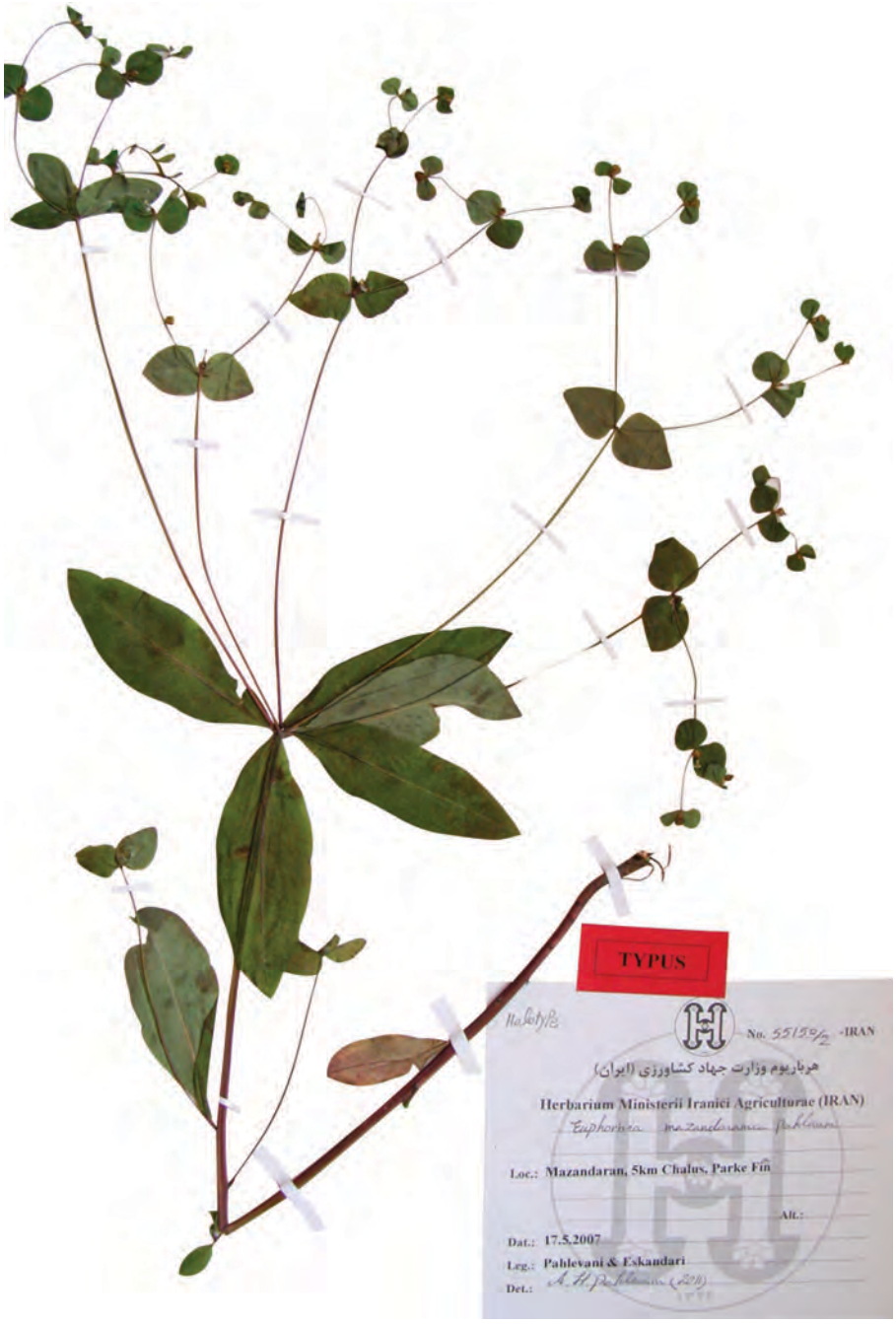

Figure 10. Holotype (IRAN) of *Euphorbia mazandaranica*.

Table 1. Morphological comparison between *Euphorbia mazandaranica* sp. nov., *E. squamosa* and *E. microsphaera*.

Species	*E. mazandaranica*	*E. squamosa*	*E. microsphaera*
Life form	Perennial	Perennial	Annual
Bark	Reddish	Yellowish–green	Yellowish–brown
Margin of cauline leaves	Glabrous, entire–slightly undulate	With prominent white hairs, entire–slightly undulate	Glabrous, serrulate at least in upper half
Terminal rays/Ray-Leaves	4–5	(5)6–9	(4)5–6
Ray-leaves, size	Usually larger or the same size as cauline leaves	Usually smaller than cauline leaves	More or less same size as cauline leaves
Capsule, diameter (mm)	3–4	4.5–5.0	2.5–3.0
Capsule, surface	Smooth or rarely with a few short warts, glabrous–subglabrous	Covered with long cylindric–filiform warts, glabrous	Smooth, glabrous or sparingly pilose

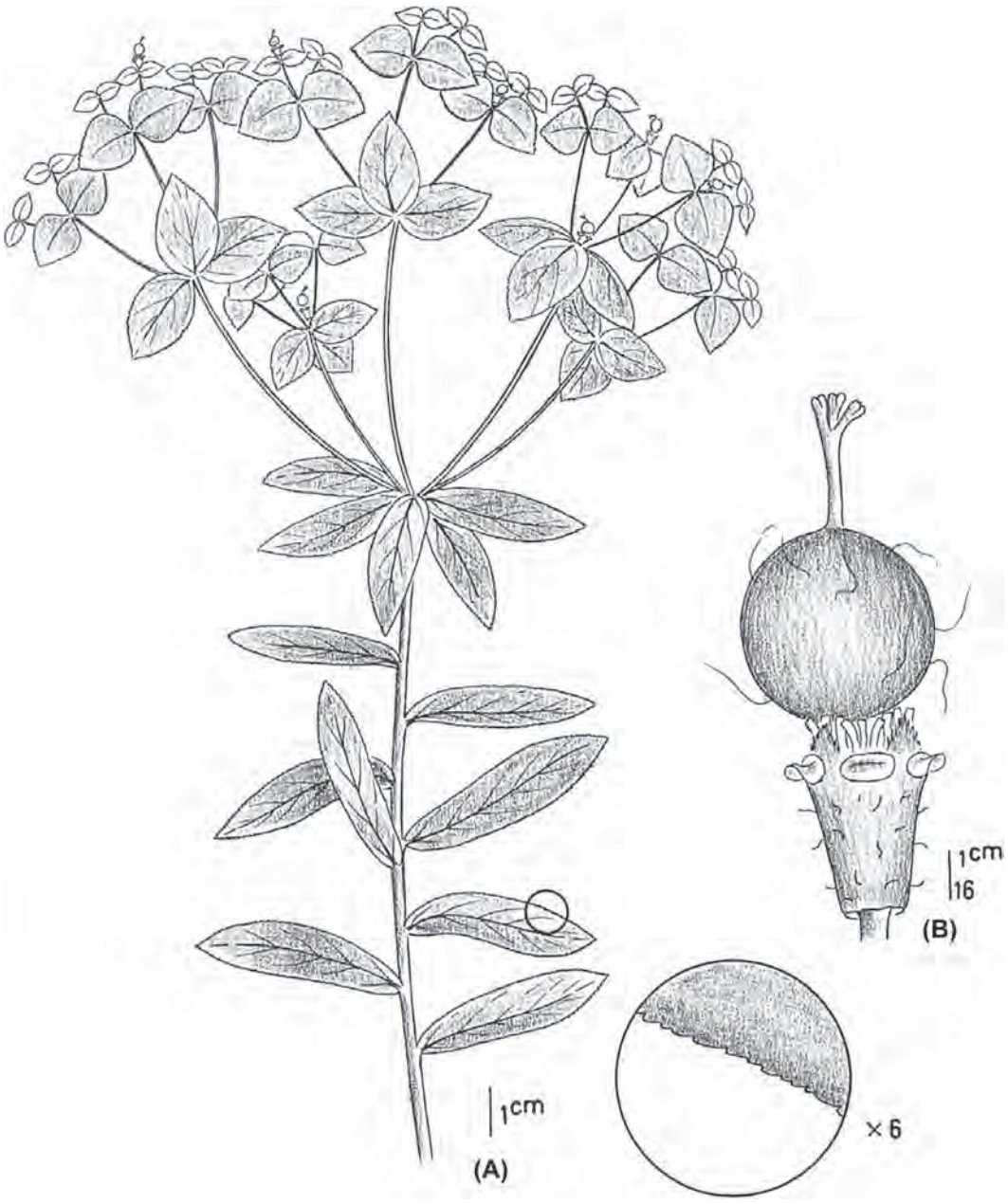

Figure 11. *Euphorbia microsphaera*. (A) habit with detail of leaf margin, (B) cyathium and fruit.

ad radices montis Sabsi-Buschom prope Schiraz, 31 May 1842, Kotschy 448 (holotype: G-BOISS!, isotypes: A00047988!, A00277273!, BM000951541!, CAS00123963!, E00362388!, G-DC!, GOET003734!, JE00002899!, JE00002900!, MPU014907!, MPU014469!, MO-260133!, MO-260134!, MO-260135!, S-G-2584!, US00095369!, WAG0004311!).

Taxonomic synonyms: *Euphorbia mohammerensis* Boiss. in A. P. de Candolle (1862, p. 118), pro syn. – *Euphorbia subtuberculata* C. A. Mey. ex Boiss. in A. P. de Candolle (1862, p. 118). – *Euphorbia unilateralis* Blakelock (1950, publ. 1951, p. 453). – *Tithymalus unilateralis* (Blakelock) Holub (1977 p. 428).

Annual herbs to 70 cm high, glabrous. Cauline leaves oblong-lanceolate to elliptic-lanceolate, 2.5–6.0 × 0.5–1.5 cm, sessile, tapering to a slightly auriculate base, acute, subacute or obtuse at apex, with margin minutely serrulate in upper half. Terminal rays (4) 5 (6), at first 3- or 4-chotomous, then dichotomous; axillary rays absent. Ray leaves like cauline leaves. Raylet leaves ovate-deltoid to ovate-rhombic or elliptic-oblong, rounded, cuneate or rarely slightly cordate at base, acute , subacute or mucronulate at apex, with serrulate margin. Cyathia: involucre turbinate, 1.5–2.0 mm in diameter; glands elliptic and rounded, light brown. Capsules globose to subglobose, not sulcate, 2.5–3.0 mm in diameter, smooth, glabrous or sparingly pilose. Seeds flattened-ellipsoidal,

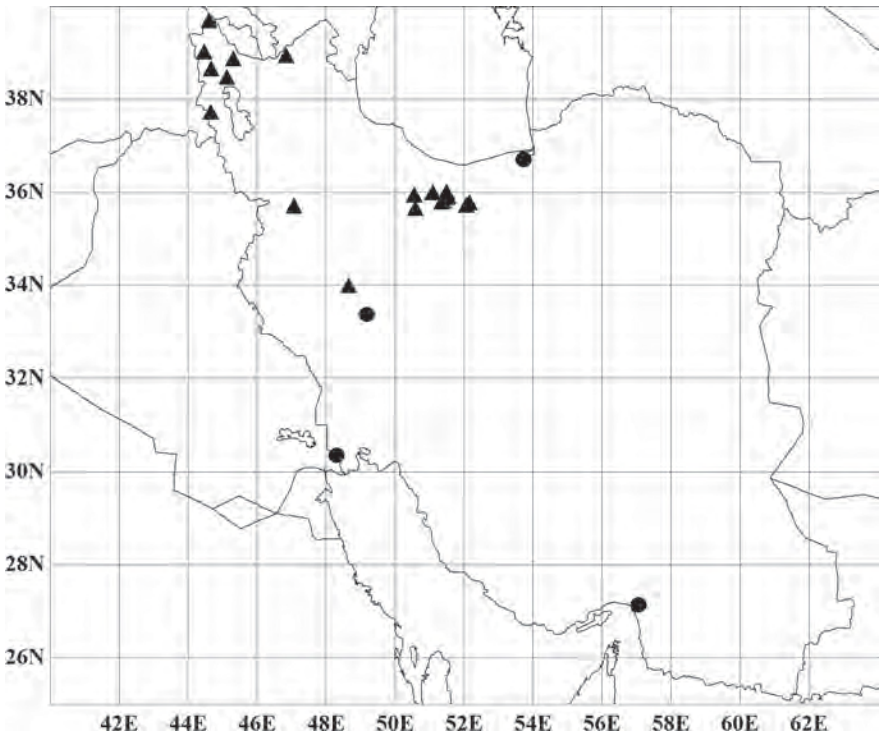

Figure 12. Distribution of *Euphorbia microsphaera* (circle) and *E. orientalis* (triangle) in Iran.

2 mm long (excluding the caruncle), smooth, dark grayish–brown and shiny; caruncle reniform, 0.3–0.4 mm long, yellowish. Flowering and fruiting in April to July.

Habitat

Foothills, marshlands, roadsides, orchards and fields, from sea level to 1900 m a.s.l.

Distribution

Old World: southwest Asia (northern, northwestern, western and southern Iran, Azerbaijan (Talysh), Iraq, Turkey, Palestine, Lebanon, Jordan, Syria) and central Asia (Tajikistan and Uzbekistan). An Irano–Turanian element; in Iran the species is restricted to the Alborz and Zagros Mts (Fig. 12).

Specimens examined

Iran. Mazandaran: Tirtash, Sharif 17841 (IRAN); Hormozgan: Minab, Safavi and Dezfoulian 17840 (IRAN); Golestan: entre Gurgan [Gorgan] et Naudeh [Nodeh], Schmid 5913 (K).

9. *Euphorbia orientalis* L. (1753, p. 460) (Fig. 13)

Based on the same type: *Tithymalus orientalis* (L.) Hill (1768, p. 172/3). – *Galarhoeus orientalis* (L.) Haw. (1812, p. 148). **Type**: Habitat in oriente, Herb. Linn. no. 630.60 (lectotype: LINN, designated by Croizat (1938, p. 98)).
Taxonomic synonyms: *Euphorbia notadenia* Boiss. & Hohen., in P. E. Boissier (1853, p. 111). – *Tithymalus notadenius* (Boiss. & Hohen.) Klotzsch and Garcke (1859, p. 78). – *Euphorbia artvinensis* Bornm. & Woronow (1913, p. 3).

Perennial herbs, ca 1 m high, usually without axillary leafy shoots, glabrous. Cauline leaves linear-lanceolate to elliptic-lanceolate, 3.5–9.0 × 0.8–1.5 cm, sessile, tapering at base, acute to subacute at apex, with entire margin. Terminal rays 5–8, tri or tetrachotomous; axillary rays (0) 3–16. Ray-leaves broadly ovate, elliptic-ovate to elliptic-lanceolate, 2–4 × 0.8–2.0 cm, sessile, truncate to tapering at base, acute or usually cuspidate at apex, with entire margin. Raylet leaves suborbicular, ovate-rhombic to elliptic-ovate, rounded to truncate at base, cuspidate at apex, with entire margin. Cyathia: involucre turbinate, 2–3 mm in diameter; glands elliptic and rounded, brownish. Capsules trilobate, 4.5–5.5 mm in diameter, their surface with two rows of tubercles on each lobe, pilose to subglabrous. Seeds ellipsoidal, 2.5–3.0 mm long, smooth, pinkish–brown; caruncle minute, 0.5 mm long, white–yellowish. Flowering and fruiting in late June to August.

Habitat

Rocky slopes, screes, valleys, dry river-banks, scrubs, metamorphic rocks and steppe forests, at 700–2400 m a.s.l.

Distribution

Old World: northern, northwestern and western Iran, Azerbaijan (Nakhichevan), Armenia, northern Iraq and eastern Turkey. An Irano–Turanian element, restricted to the Zagros and Alborz Mts (Fig. 12).

Specimens examined

Iran. East Azerbaijan: Marakan protected area, ca 10 km northwest of Marakan, Agh-Dagh Mt, Akhani 7688 Hb. Akhani; Arasbaran Protected area, Vaighan to Veinagh, Assadi and Masoumi 20474 (TARI); Ahar, Goijebel Mt, Termeh 47951 (IRAN); west Azerbaijan: ca 18 km northwest of Khoy, on the road to Shurik, Assadi and Olfat 67700 (TARI);

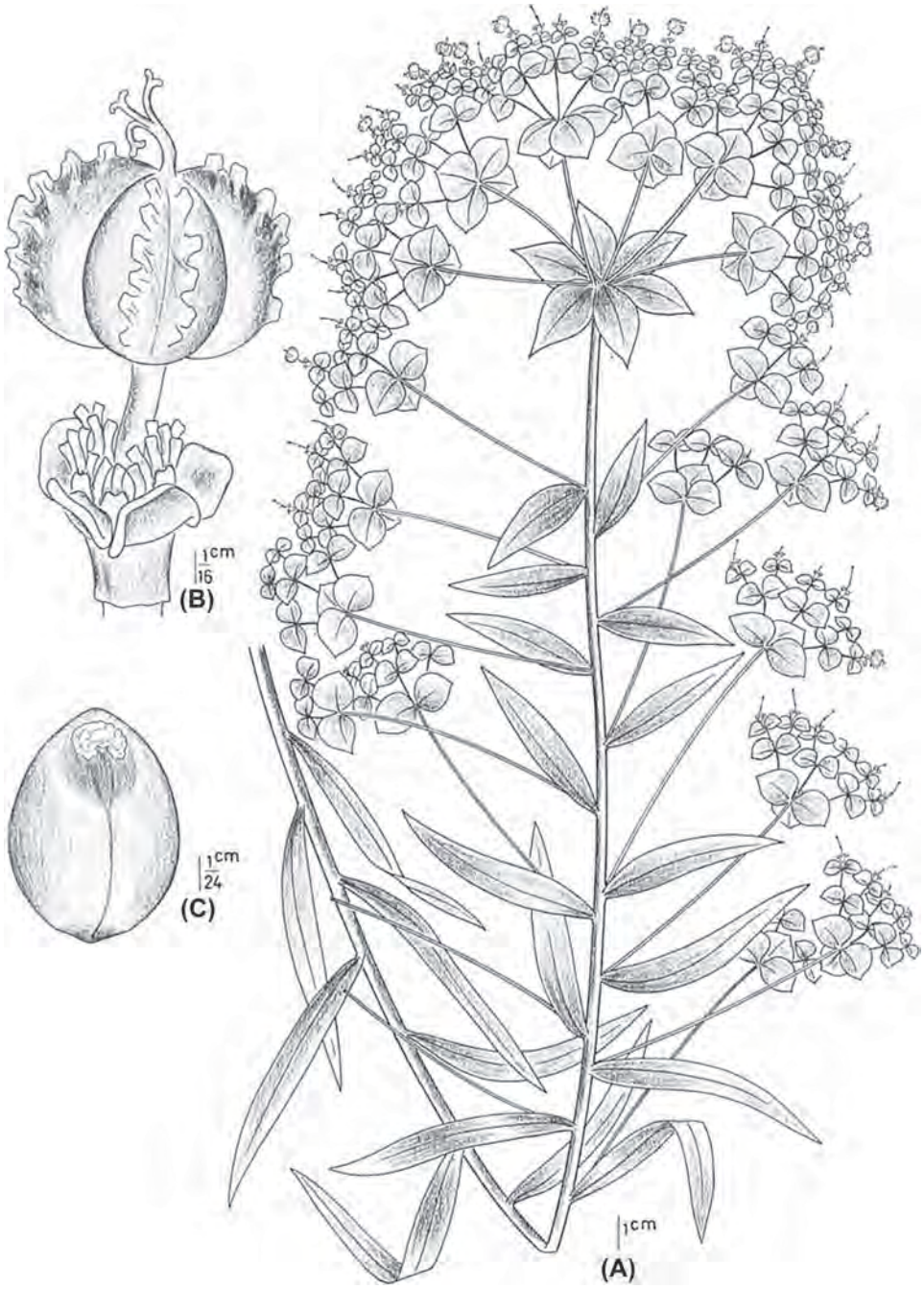

Figure 13. *Euphorbia orientalis*. (A) habit, (B) cyathium and fruit, (C) seed. Drawn from voucher specimen from west Azerbaijan: Makou, Buralan, IRAN 47794/1.

north of Orumieh Lake, Assadi, Taheri and Izadpanah 68485 (TARI); Makou, Buralan, Pahlevani and Amini Rad 47794 (IRAN); Lorestan: Azna, Oshtorankouh, Iranshahr 17850 (IRAN); Tehran: Tehran, Pas-Ghaleh to Touchal Mt, Alava and Termeh 44575 (IRAN); 44 km from Tehran on Shemshak road, Amin 7466 (TARI); north of Tehran, Amin and Bazargan 7562 (TARI); Tehran, Lashgarak to Fasham, 6 km Fasham, Moussavi 17851 (IRAN); Tehran, Darakeh, Ozgol-Chal, Moussavi and Tehrani 44576 (IRAN); Damavand, rocky mountains, north of Veliran village, Mozaffarian 32367 (TARI); Damavand, Dasht-e Mazar, Tizab, Mozaffarian 39891 (TARI); Evine, Darakeh, Haftgel, Termeh and Zargani 47906 (IRAN); Below Ushan, Wendelbo 18650 (TARI); Damavand, just north of the city, Vavin Mt, Garrubar valley, Mozaffarian 54102 (TARI); Alborz: by Neza, 40 km north of Karadj on the riverbank, Anderson and Petersen 166 (K); Karaj, Kouh-e Dashte, Gauba 17852 (IRAN); Savog-bolagh, Rasoulinia 32378 (FAR).

10. *Euphorbia rhabdotosperma* Radcl.-Sm. (1975, p. 129)

Basionym: *Tithymalus rhabdotospermus* (Radcl.-Sm.) Holub (1977, p. 428). **Type:** Turkey, Elmali-Korkuteli, 8 km

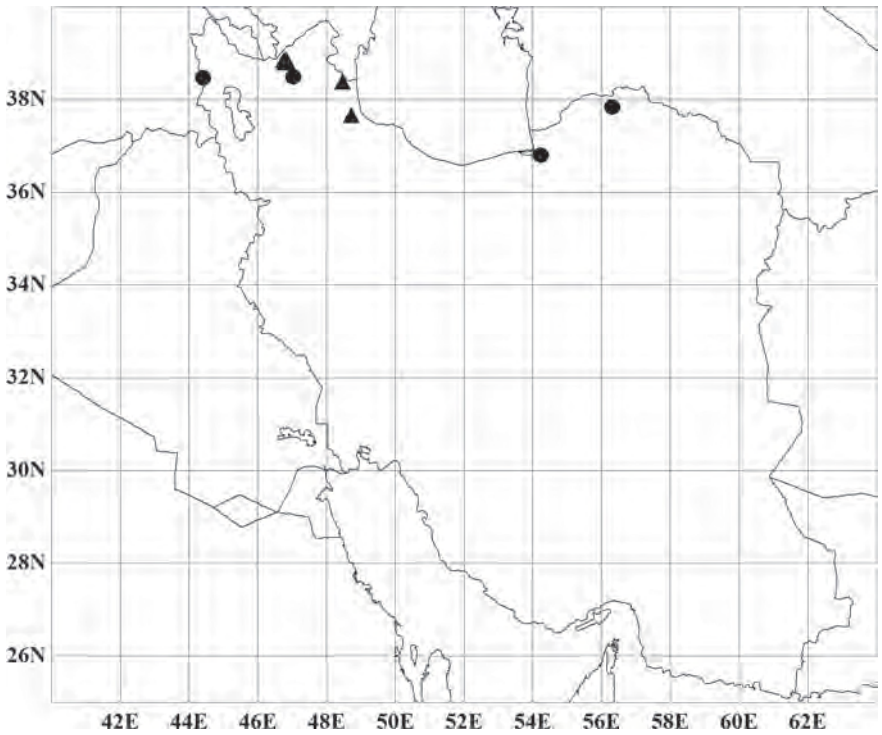

Figure 14. Distribution of *Euphorbia rhabdotosperma* (circle) and *E. squamosa* (triangle) in Iran.

from Elmali, in dry steppe, 1120 m a.s.l., 31 Mar 1962, T. R. Dudley 35223 (holotype: E00359917!, isotype: K!).

Very similar to *E. helioscopia*, but differing in having striate-rugulose seeds, not foveolate-reticulate. Flowering and fruiting time: May to June.

Habitat
Steppes, edge of fields and orchards, at 500–1600 m a.s.l.

Distribution
Old World: Caucasus, east Turkey and northern Iran. An Irano–Turanian element (Fig. 14).

Specimens examined
Iran. East Azarbaijan: Ahar, Purghorban 4165 (FAR); Golestan: Gorgan, Kordkuy, Asal-Donbaleh, Jahan-nema region, Moussavi and Tehrani 47260 (IRAN); northern Khorasan: northwest Bojnurd, 4 km to Ghazanghaye, Memariani and Zangooei 39490 (FUMH); west Azarbaijan: Khoy, Ghotur, Hedayati 26308 (FAR).

11. *Euphorbia squamosa* Willd. (1799, p. 918) (Fig. 15)

Based on the same type: *Tithymalus squamosus* (Willd.) Klotzsch and Garcke (1860, p. 78). – *Keraselma squamosa* (Willd.) Raf. (1838, p. 116). **Type:** Turkey, in Cappadocia, Tournefort s.n. (holotype: B-W09358-010!, isotypes: E00362385, photo)!, P?).
Taxonomic synonyms: *Euphorbia aspera* M. Bieb. (1808, p. 377). – *Euphorbia muricata* M. Bieb. (1808, p. 378). – *Euphorbia muricata* var. *wilhelmsiana* K. Koch (1849, p. 725). – *Tithymalus asper* (M. Bieb.) Klotzsch and Garcke (1860, p. 78). – *Euphorbia talyschensis* Boiss. & Buhse (1860, p. 196). – *Euphorbia aspera* var. *oligadenia* Boiss. in A. P. De Candolle (1862, p. 124). – *Euphorbia aspera* var. *serrata* Boiss. in A. P. De Candolle (1862, p. 124). – *Euphorbia abchazica* Woronow (1912, p. 3). – *Euphorbia squamosa* var. *serrata* (Boiss.) Oudejans (1992, publ. 1993, p. 188). – *Euphorbia squamosa* var. *talyschensis* (Boiss. & Buhse) Oudejans (1992, publ. 1993, p. 188). – *Euphorbia squamosa* var. *wilhelmsiana* (K. Koch) Oudejans (1992, publ. 1993, p. 188).

Perennial herbs, up to 70 cm high, arising from a woody stock; stems few, erect, simple, sparingly pilose. Cauline leaves broadly ovate to elliptic-ovate, 3–11 × 2–4 cm, with 2–9 mm long petiole, attenuate to cuneate at base, obtuse to acute or sometimes mucronulate at apex, with entire margin, glabrous to subglabrous on the adaxial side, white pilose on the abaxial side, especially on midrib and margin. Terminal rays 5–9, once or twice dichotomous; axillary rays (0–1) 2–12. Ray leaves elliptic-ovate to elliptic-lanceolate, 3.0–7.5 × 1.5–3.0 cm, petiolate, attenuate to cuneate at base, acute to subacute at apex, with margin entire to subundulate with whitish hairs. Raylet leaves broadly ovate-deltoid to ovate-rhombic, 1.0–2.5 × 0.8–2.0 cm, truncate to shallowly cordate at base, acute or cuspidate at apex,with entire to subentire margin. Cyathia: involucre turbinate, 1.5–2.0 mm in diameter; glands elliptic and rounded, brownish. Capsules trilobate, 4.5–5.0 mm in diameter, their surface covered with cylindric-filiform warts, glabrous. Seeds ellipsoidal, 2.5–2.8 mm long, smooth, brown to gray; caruncle minute, less than 0.5 mm long, persistent, yellow to white with brown centre. Flowering and fruiting in June to July.

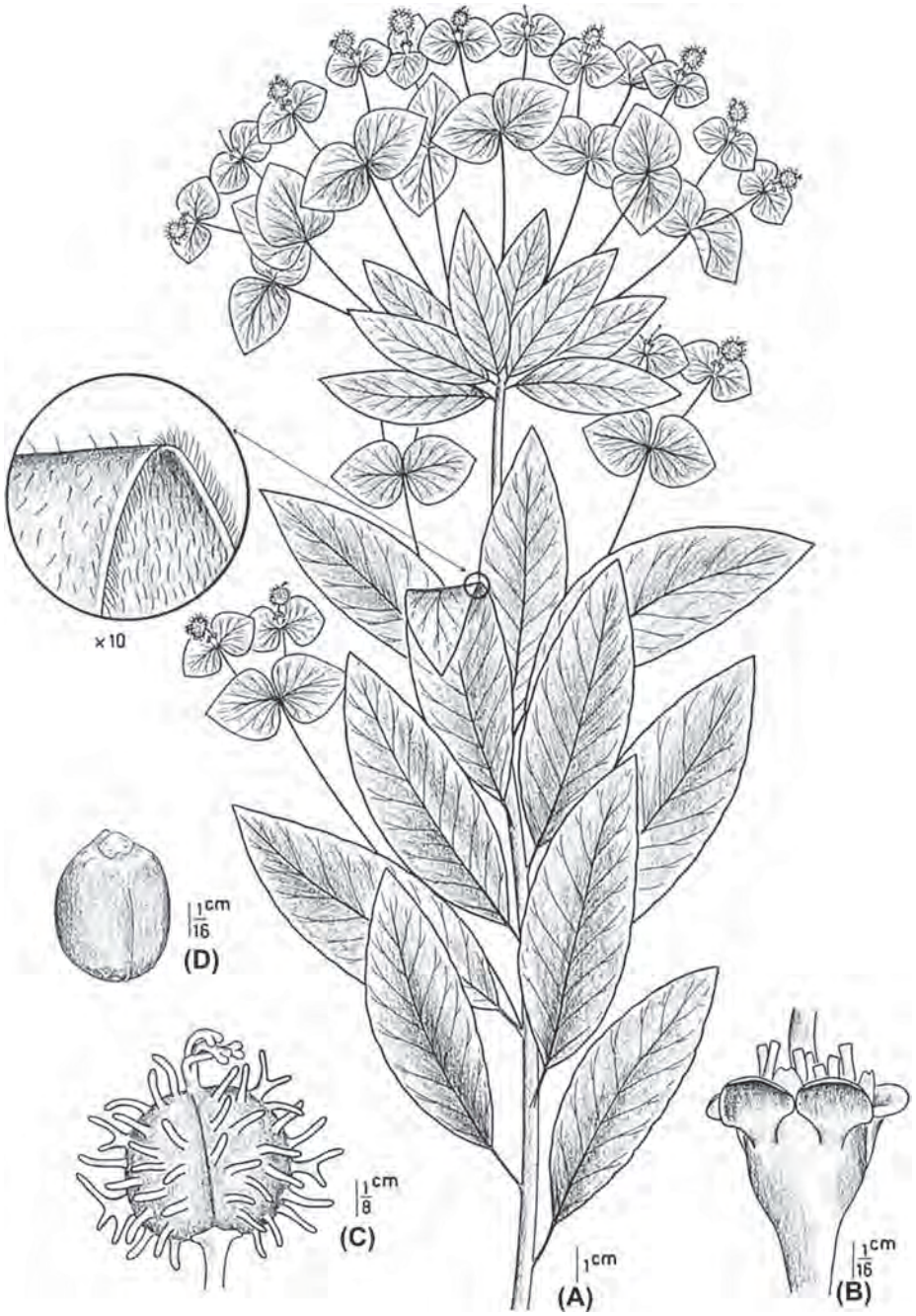

Figure 15. *Euphorbia squamosa*. (A) habit, (B) cyathium, (C) fruit, (D) seed. Drawn from voucher specimen from east Azerbaijan: Arasbaran protected area, Oskolou to Ilankesh, IRAN 54570.

Habitat

In forests (including: *Acer campestre*, *Viburnum lantana*, *Fagus orientalis*, *Quercus* sp.) and sometimes occurring in grassy and calcareous rocky slopes, at 50–2000 m a.s.l.

Distribution

Northern and northwestern Iran, northern Turkey and Caucasus. A Hyrcano–Euxine element (Fig. 14).

Specimens examined

Iran. Ardebil: Ardebil-Astara, Bowles Scholarchip Bot. Expd. 2336 (K); east Azerbaijan: Arasbaran protected area, Doghroun and Kalan Mt, Assadi and Sardabi 24139 (TARI); Arasbaran protected area, Vaighan to Kharil, Assadi and Vosughi 24861 (TARI); Arasbaran protected area, Toopkhaneh road, Hamzehee and Asri 81458 (TARI); Arasbaran protected area, Inalou to Ilankesh, Pahlevani and Asef 47759 (IRAN); Arasbaran protected area, Ilankesh to Oskolou, Pahlevani and Asef 47359, 47795 (IRAN); Gilan: Khalkhal to Asalem, 17 km to Asalem, Pahlevani and Asef 54565 (IRAN); Asalem to Khalkhal, 12 km Assalem, Termeh and Moussavi 17651 (IRAN).

There is only one collection record (Buhse s.n.) of *E. squamosa* cited in 'Flora Iranica' (Rechinger and

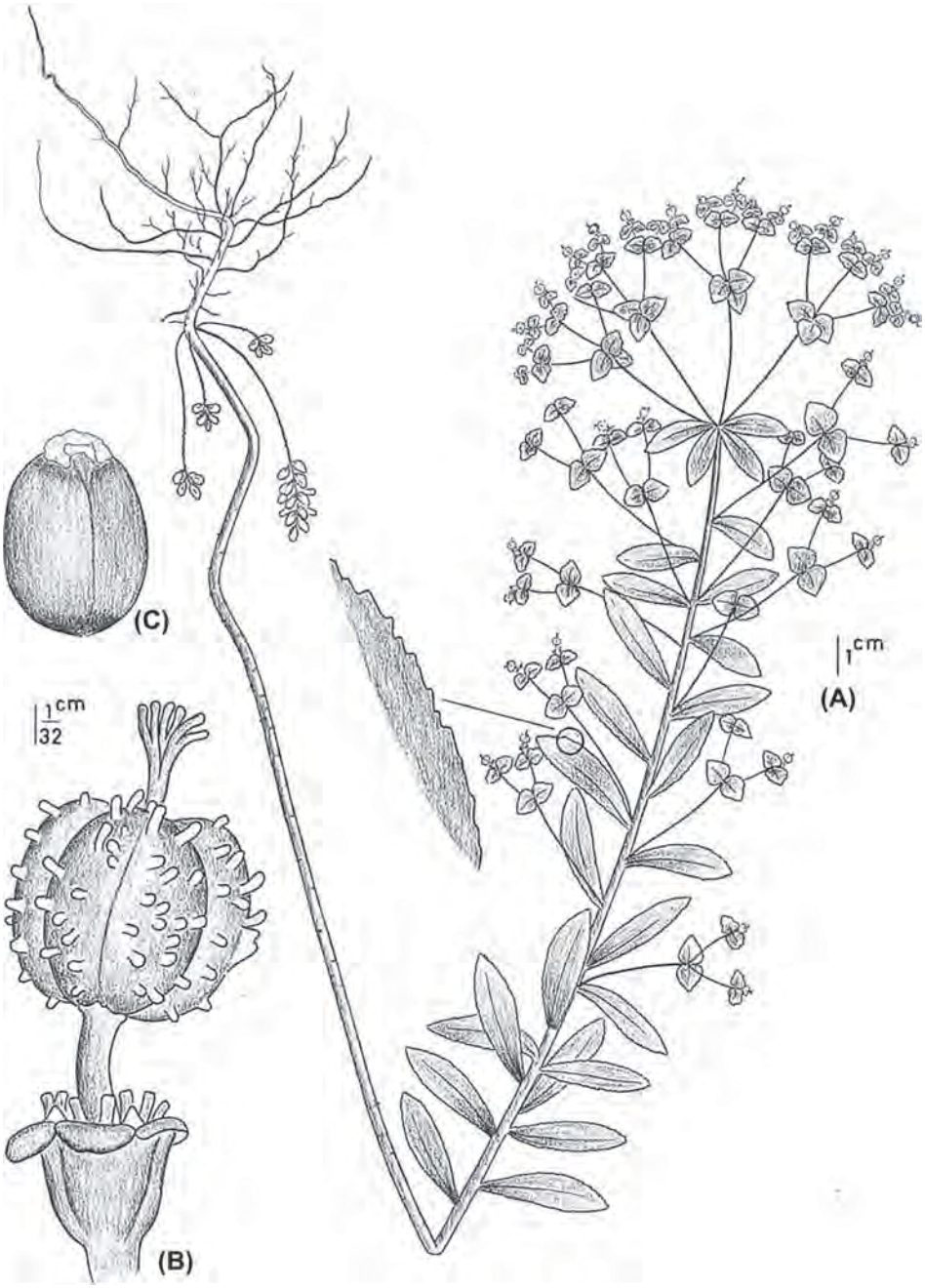

Figure 16. *Euphorbia stricta*. (A) habit, (B) cyathium and fruit, (C) seed. Drawn from voucher specimen from Mazandaran: Chamestan, 3 km Chamestan to Noor, IRAN 53778.

Schimman-Czeika 1964). Khan (1964) indicated that the photo of the type specimen at E was from an unseen specimen at P, which he cited as the holotype. After checking the B–W collection online we found the specimen matching the photo at E, and this sheet (B–W) should be the holotype as indicated above. We did not find any duplicate of the type collection at P, but it is possible that there is a duplicate in that herbarium.

12. *Euphorbia stricta* L. (1759, p. 1049) (Fig. 16)

Based on the same type: *Galarhoeus strictus* (L.) Haw. (1812, p. 151). – *Tithymalus strictus* (L.) Klotzsch and Garcke (1858, p. 290). – *Euphorbia platyphyllos* var. *stricta* (L.) Fiori in A. Fiori et al. (1901, p. 281).

Taxonomic synonyms: *Euphorbia micrantha* Stephan ex Willd. (1799, p. 905). – *Euphorbia serrulata* Thuill. (1799, p. 237). – *Euphorbia platyphyllos* var. *serrulata* (Thuill.) Pers. (1806, p. 18). – *Galarhoeus micranthus* (Stephan ex Willd.) Haw. (1812, p. 152). – *Tithymalus micranthus* (Stephan ex Willd.) Raf. (1838, p. 115). – *Euphorbia foetida* Hoppe ex W. Koch (1844, p. 724), pro syn. – *Euphorbia stricta* subsp. *micrantha* (Stephan ex Willd.) Nyman (1881, p. 651). – *Euphorbia stricta* subsp. *pubescens* Erdner (1911, p. 569). – *Tithymalus serrulatus* (Thuill.) Holub (1970, p. 94).

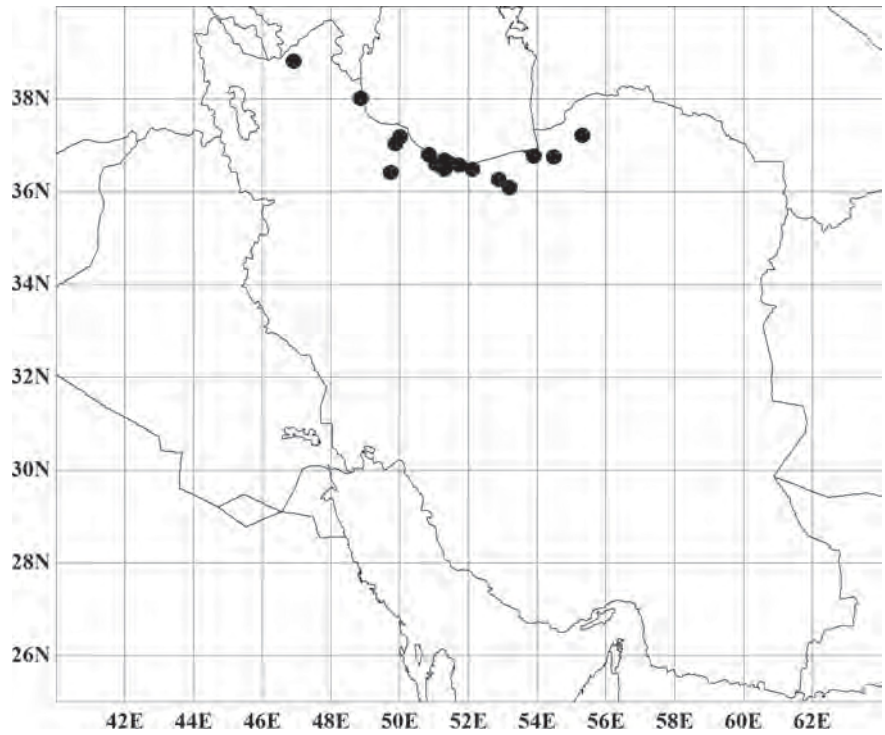

Figure 17. Distribution of *Euphorbia stricta* in Iran.

Annual herbs, 20–60 cm high, glabrous or rarely sparingly pubescent. Cauline leaves oblong-ovate to oblong-oblanceolate, 1.5–5.5 × 0.5–2.0 cm, sessile to subsessile, subamplexicaul or cuneate at base, acute or obtuse at apex, with margin irregularly serrate at upper half. Terminal rays 3 (4–5), trichotomous; axillary rays numerous. Ray leaves like cauline leaves. Raylet leaves ovate-deltoid to ovate-rhombic or suborbicular-reniform, truncate or slightly cordate at base, short cuspidate or obtuse at apex, with serrate margin. Cyathia: involucre campanulate, 1 mm in diameter; glands elliptic and rounded, light brown to yellow. Capsules trilobate, subglobose, 1.5–2.0 mm in diameter, thier surface covered by cylindrical-tuberculate processes, glabrous. Seeds ellipsoidal, 1.3–1.7 mm long, smooth, pinkish–light brown and shiny; caruncle small crescent-shaped, 0.2–0.3 mm long, yellowish. Flowering and fruiting in late May to July.

Habitat

Forests and roadsides from sea level to 2500 m a.s.l.

Distribution

Old World: Europe, Caucasus, Turkey and Iran (northern and northwestern). An Euro–Siberian element (Fig. 17).

Specimens examined

Iran. Golestan: Gorgan, Naharkhoran, Ziarat, Kuh-e Talanbar, Moussavi and Karavar 18160 (IRAN); Minou-Dasht, Sharif 17887 (IRAN); Bandar-e Gaz, Rechinger, Esfandiari and Aellen 17886 (IRAN); Mazandaran: Nowshahr, Shahr-Posht, Sabeti 17714 (IRAN); Chamestan, 3 km Chamestan to Noor, Amini Rad 53778 (IRAN); 8 km Abbass-abad to Kelardasht, Pahlevani and Eskandari 47651 (IRAN); 2 km Nowshahr to Noor, Pahlevani and Eskandari 47654 (IRAN); Chalus, Doab, Veysar, Termeh, Daneshpajuh and Zargani 44603 (IRAN); Pol-e Sefid, Sang-Deh, Miyana, Matin, Daneshpajuh and Fatehi 47246 (IRAN); 25 km Namak-Abroud, Pahlevani and Eskandari 47652 (IRAN); Tonekabon, Shekarak, Shokrgozar 4497 (FAR); Nowshahr, near Sisangan Park, Moallemi 4416 (FAR); Tonekabon, Lashkarak village, anonymous 4496 (FAR); Gilan: Lahijan, Mirkamali 17889 (IRAN); Deylaman, Larukhani to Lanak, Termeh and Daryadel 18161 (IRAN); Lisar valley, Assadi 89450 (TARI); Rasht, Lahijan, Dehkade, Panahkhodahi and Baghani 28649 (FAR); east Azerbaijan: Arasbaran protected area, Makidi, Pahlevani and Asef 47798 (IRAN); Qazvin: About 3 km after Kuhin pass, the first pass from Kuhin toward Loshan, Salmaki 39748 (TUH).

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