

Systematics and distribution patterns of the Balkan species of *Eryngium* (*Apiaceae*, *Saniculoideae*)

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Abstract. The Balkan species of genus *Eryngium* (*Apiaceae*, *Saniculoideae*) are 11 in number distributed over six sections. Sectional classification of the genus in the Balkans is presented here. Although most of these sections are common to adjacent Anatolia (except for the endemic *E. sect. Astantiifolia*), only three widespread species actually grow in both regions. Distribution maps of each Balkan species are supplied. Ecological aspects proved useful for their understanding. Most Balkan species of *Eryngium* are fairly old (except for the widespread ones) and obviously result from early immigration and evolution in the region.

Keywords: *Apiaceae*, Balkan, *Eryngium*, phytogeography, sectional classification

Introduction

Genus *Eryngium* L. (*Apiaceae*, *Saniculoideae*) comprises about 250 species growing in Eurasia, North Africa, North and South America, and Australia. It is the most species-rich genus of the *Apiaceae* (Pimenov & Leonov 1993: 3) and includes about four-fifths of the *Saniculoideae*. The latest monograph on *Eryngium* is now over 90 years old (Wolff 1913). Many regional treatments in the Floras were published subsequently, including that of Davis (1972) for Turkey, Pimenov & Tamamschjan (1987) for the Flora Iranica, and Mathias & Constance (1941) for North America. However, a modern treatment of the group is still lacking, which was my reason for starting a project to revise the whole genus *Eryngium*, making use of the modern biosystematic criteria like chromosome numbers, ecology, chorology, and molecular data.

About 60 of the 250 *Eryngium* species occur in West Eurasia and North Africa. Their monographic treatment is in its final phase and will be published soon. This paper deals with the Balkan species and their systematic and biogeographic position. They grow in a region located between two major centres of diversity: Anatolia and the Western Mediterranean. The two possibilities to explain their diversity, recent immigration and in-situ evolution, are discussed.

A sectional classification of the Balkan species of *Eryngium* subg. *Eryngium* is presented, in order to demonstrate their relationship to each other and to the rest of the Old World species. It is based on conventional morphological characters. The basal leaves provide the main characteristics. Other important features are those of the involucre leaves and bracts. Chromosome numbers – not discussed here – are also characteristic for some sections like *E. sect. Campestris* and sect. *Palmito*. The form of

the fruits and petals is more important on subgeneric level.

As it was already pointed out by Froebe (1964), the seemingly simple umbel of *Eryngium* is in fact a reduced double umbel, and each flower a reduced umbellule. The small leaves at the base of the flowers are thus the bracts of the umbel (and not the bracteoles as commonly stated). The lowermost bracts are enlarged to form an additional involucre, which together with the umbel forms the capitulum. To distinguish them from the inner bracts (since they are a different and an important character), they are called “involucral leaves” in the present study.

Distribution maps of the species, some of which are the first ever published, show the biogeographic characteristics. Ecological data collected in the revision process proved helpful for the understanding of the species and their distribution.

These partial results of the full revision are published in advance in the present paper.

Material and methods

Distribution maps are mostly based on herbarium data from several institutions (ANK, B, BM, C, E, G, GAZI, GOE, HUB, K, JE, LD, LE, M, MA, MARSSJ, MPU, P, PR, STU, W, WU). Floristic data were only used for easy-to-identify species and from reliable sources. Doubtful records were excluded. Neighbouring localities have been mapped as one dot, depending on map scale and dot size. The base map was created by means of a free mapping programme of M. Weinelt (www.aquarius.geomar.de). The maps were downloaded and modified with the Corel Draw programme.

Ecological data were collected in the field by means of phytosociological relevés, and to some extent also from literature. In this paper, they are not presented in detail, but a short ecological characterisation is included for each species.

Results

A new subgeneric classification of the genus has been presented by Wörz (2005). It recognises five subgenera, three of which grow exclusively in the New World and Australia and one predominantly in North and South America, with a few species in the

Mediterranean. *Eryngium* subg. *Eryngium* is restricted to West Eurasia and North Africa. It is well defined, consisting of perennials growing mostly in dry habitats. The basal leaves are palmately divided, sometimes secondarily trifoliolate, or with pinnate segments. All 11 Balkan species belong to this subgenus. In the following presentation, they are further classified in six sections (Table 1), based on Wolff (1913). *Eryngium* sect. *Astrantiifolia* is endemic to the Balkans. Three species, *E. campestre*, *E. creticum* and *E. maritimum*, are widespread in Eurasia, five others (in bold letters in the Table) are endemic.

Table 1. The sections of *Eryngium* distributed on the Balkan Peninsula. (The underlined species occur in the Balkans; the endemics are in bold.)

Sections	Species
<i>Campestris</i> subsect. <i>Campestris</i>	<u><i>amethystinum</i></u> , <i>amorginum</i> , <i>billardierei</i> , <u><i>campestre</i></u> , <i>desertorum</i> , <u><i>glomeratum</i></u> , <i>hainesii</i> , <i>polycephalum</i> , <i>thyrsoides</i>
<i>Palmito</i>	<i>palmito</i> , <i>serbicum</i> , <i>ternatum</i> , <i>trisectum</i> , <i>wanaturi</i>
<i>Alpina</i>	<u><i>alpinum</i></u> , <i>bornmuelleri</i> , <i>giganteum</i>
<i>Plana</i>	<i>antiatlanticum</i> , <i>bithynicum</i> , <i>caeruleum</i> , <u><i>creticum</i></u> , <i>dichotomum</i> , <i>falcatum</i> , <i>planum</i> , <i>tricuspidatum</i> , <i>triquetrum</i> , <i>variifolium</i>
<i>Astrantiifolia</i>	<u><i>palmatum</i></u> , <u><i>wiegandii</i></u>
<i>Eryngium</i>	<u><i>maritimum</i></u>

Eryngium sect. *Campestris* H. Wolff in Engler, Pflanzenr. IV.228 (Heft 61): 108, 140. 1913.

subsect. *Campestris*

= *Eryngium* sect. *Campestris* H. Wolff subsect. *Eucampestris* H. Wolff in Engler, Pflanzenr. IV.228 (Heft 61): 141, 146. 1913.

Type: *E. campestre* L.

Perennials, basal leaves trifoliolate with trisect to trifid segments, or segments irregularly pinnate or incised, or leaves more or less pinnate; segments mostly decurrent on rachis; involucral leaves mostly with an additional whorl of spines at the base of the capitula; fruits densely covered with long acuminate to filiform, white appendages (occasionally missing), ovoid to conical.

Included species:

Eryngium amethystinum L., *E. amorginum* Rech. f., *E. billardierei* F. Delaroché, *E. campestre*, *E. desertorum* Zohary, *E. glomeratum* Lam., *E. hainesii* C.C.

Towns., *E. polycephalum* Hausskn. ex H. Wolff, *E. thyrsoideum* Boiss.

Wolff (1913) divided his sect. *Campestris* into three subsections, two of which grow in the West Mediterranean and are not closely related to the species of the subsection "Eucampestris". They differ in the form of the basal leaves, the involucre leaves and partially in the synflorescence. Therefore, *Eryngium* sect. *Campestris* subsection. *Eucampestris* deserves the rank of a section in its own right and is discussed in this paper accordingly.

Balkan species:

Eryngium amethystinum

This circumadriatic distributed species shows some morphological differentiation within the Balkan Peninsula: specimens from the southern part (Greece, S Macedonia, Albania) have more narrow leaf segments and grow in drier habitats as compared to the North and Central Balkan and Italian populations (Fig. 1). They have been considered as a separate species, *E. multifidum* Sm. However, considering that transitions are common, and, although the difference in the leaf segments is fairly conspicuous, this is their only difference and therefore a variety rank is more adequate. It must be named *E. amethystinum* var. *tenuifolium* Boiss. & Heldr.

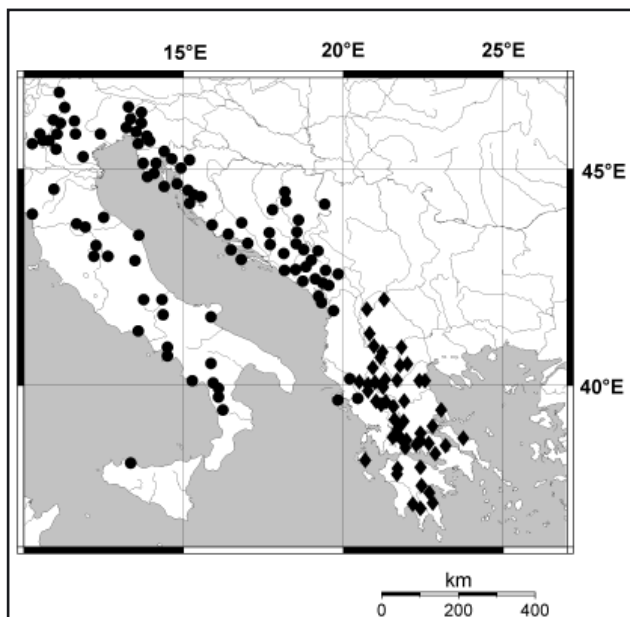


Fig. 1. *Eryngium amethystinum*:
● – var. *amethystinum*; ◆ – var. *tenuifolium* Boiss. & Heldr..

The taxon grows in a well-delimited distribution range (Fig. 1) in open, sun-exposed subalpine and alpine grasslands, meadows, screes and rocky places at much higher altitudes and drier habitats as compared to the *E. amethystinum* var. *amethystinum*. The difference in altitude distribution is much greater than the expected from the more southern location, and the habitat conditions are more or less „alpine“, with lower temperatures, erosion phenomena, and more extreme weather conditions.

Eryngium amorginum

This is an endemic to the Aegean Archipelago and to Crete (Fig. 2). It grows as a chasmophyte in the fissures of calcareous rocks. *Eryngium amorginum* often occurs in shady, wind-exposed, N-facing, maritime limestone cliffs (see for example Phitos & al. 1995: 256), occasionally on inland limestone gorges and rock walls (Monastiraki Gorge in Crete). In one single place on Crete the species was found in a pine forest on deep soil. Such behaviour is occasionally manifested by chasmophytes, as recorded by Greuter (1975b: 185f). The distribution range is similar to the ranges of *Seseli gummiferum* and *Senecio bicolor* presented by Runemark (1969: 117), which are considered as Pliocene remnants. The same is likely to be true for *E. amorginum*. Apart from the unrelated *E. ternatum* from Crete, *E. amorginum* is the only chasmophyte in the genus.

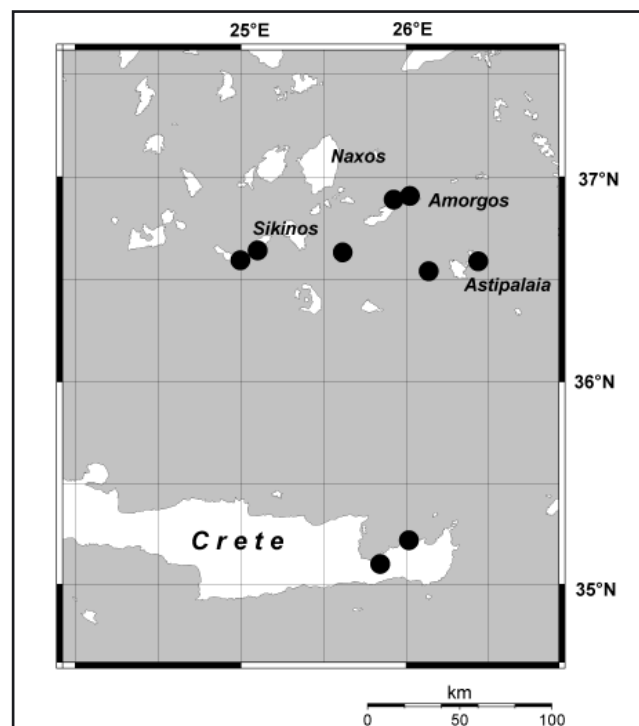


Fig. 2. *Eryngium amorginum*.

Eryngium campestre

A widespread species occurring all over Europe. A distribution map is presented in Meusel & al. (1978). The species is common all over the Balkan Peninsula and grows in a broad range of usually dry, open and sunny habitats, including crop fields or man-disturbed places.

Eryngium glomeratum

This is an East Mediterranean species, with a main distribution range in South Turkey, Lebanon, Palestine, and Israel (Fig. 3). It is crossing the border to the Balkan area in the southeast of the Aegean Islands and with one population on Crete, the latter often considered as doubtful, although it was recorded for the first time in 1962 in a collection of Runemark (No. 18463, LD). However, this Crete population consists of many individuals within a large slope and it is certainly not introduced recently. The locality is at the track from Liopetra to the sea below the saddle, 150 m, 35°12'41,3" N, 26°1'3,2" E. The species grows in rocky places, mostly but not exclusively on limestone, in the case of Liopetra on andesite.

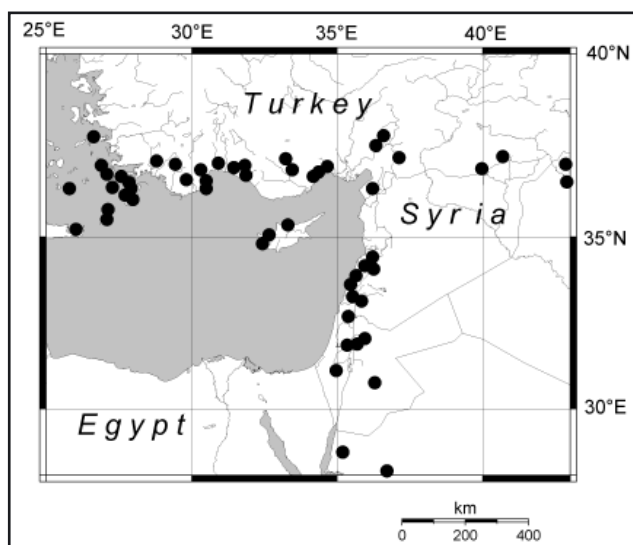


Fig. 3. *Eryngium glomeratum* subsp. *glomeratum*.

Eryngium* sect. *Palmito H. Wolff in Engler, Pflanzenr.

IV.228 (Heft 61): 107, 137. 1913.

Type: *E. palmito* Boiss. & Heldr.

Basal and cauline leaves at least partly long-petiolate, palmatipartite with grass-like segments, sometimes undivided linear-lanceolate; synflorescence paniculate; bracts about as long as flowers incl. fruits.

Included species:

Eryngium palmito, *E. serbicum* Pančić, *E. ternatum* Poir., *E. trisectum* Wörz & Duman, *E. wanaturi* Woronow.

This section is remarkable for its grass-like leaf segments and many relict distributions (Fig. 4). It includes some habitat specializations like the serpentine plants. Two species occur on the Balkan Peninsula, both are endemics. All other species of this section grow in Turkey.

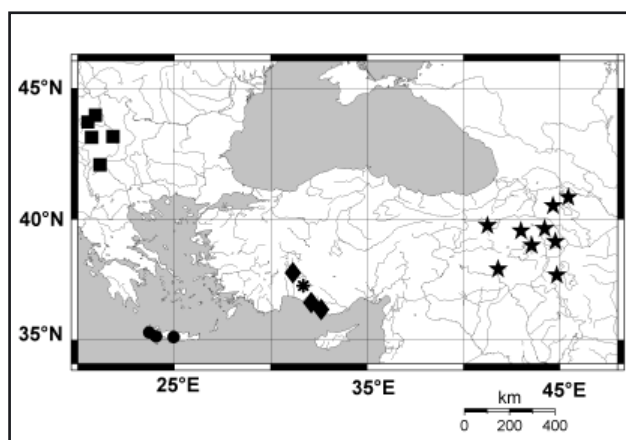


Fig. 4. *Eryngium* sect. *Palmito*:

◆ *Eryngium palmito*; ■ *Eryngium serbicum*; ● *Eryngium ternatum*; * *Eryngium trisectum*; ★ *Eryngium wanaturi*.

Balkan species:***Eryngium serbicum***

Endemic to the central Balkan Peninsula (Fig. 5), this species grows mostly but not exclusively on serpentine. The nearest relatives are *E. palmito*. and – not surprisingly – *E. trisectum*, which is the second serpentine plant of this section. *E. serbicum* occurs in grasslands and in open pine forests. The species is considered as an old transregional endemic (Stevanović & al. 2003: 165)

Eryngium ternatum

Endemic to Crete, this species is a typical chasmo-phyte growing in rock fissures of calcareous rocks in the narrow gorges of the island. It mostly occurs on bedded limestone, often under overhanging rocks, well away from grazing animals. The microclimate is cooler, more humid and more shaded as compared to the surroundings. It is a special habitat in which many relict species and other endemics

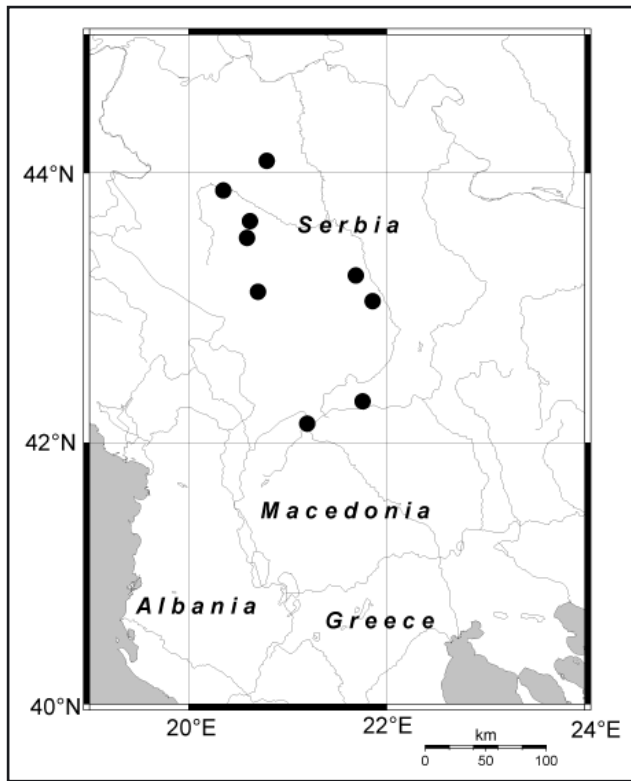


Fig. 5. *Eryngium serbicum*.

are found. *E. ternatum* is a Carpathian relict element sensu Greuter (1971, 1975a) and was first mapped by Turland & al. (1993) and it is the base of Fig. 6.

Eryngium* sect. *Alpina H. Wolff in Engler, Pflanzenr. IV.228 (Heft 61): 107, 123. 1913.

Type: *E. alpinum* L.

Basal leaves undivided, cordate, spineless; involucre leaves broad, with pinnate or reticulate venation. Plants of high altitudes.

Included species:

Eryngium alpinum, *E. bornmuelleri* Nábělek, *E. giganteum* M. Bieb.

Balkan species:

Eryngium alpinum

The distribution area of this species (Fig. 7) suggests possible separation of the species in two refuge areas during the Ice Ages: one in the SW Alps, the other on the Balkan

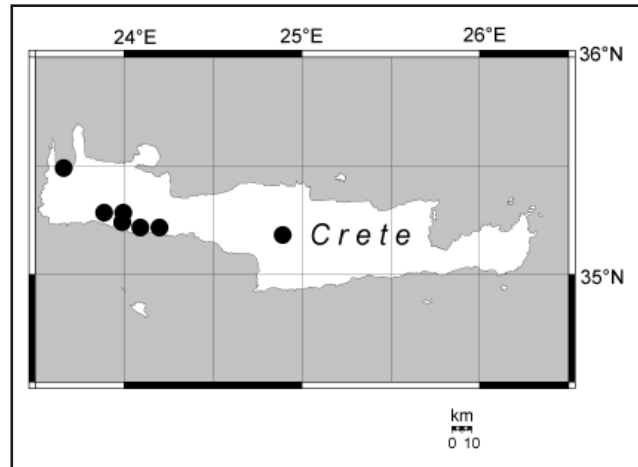


Fig. 6. *Eryngium ternatum*, based on Turland & al. (1993).

Peninsula. A possible post-glacial recolonization of the Alps from both sides may explain the significant gap in the central part of the mountain range. Large ice-free open areas lacking a forest cover in the Balkan part of the distribution area (as already suggested by Büdel 1949) may support this view. However, if this separation has really happened, morphological differences between the two populations should be expected. In fact, the specimens from both parts of the distribution range are identical and this does not support the hypothesis.

Eryngium alpinum is one of the few species of *Eryngium* subg. *Eryngium* that grow in moist or even wet conditions, mostly in tall herb communities on more or less well-watered ground and well-supplied with nutrients.

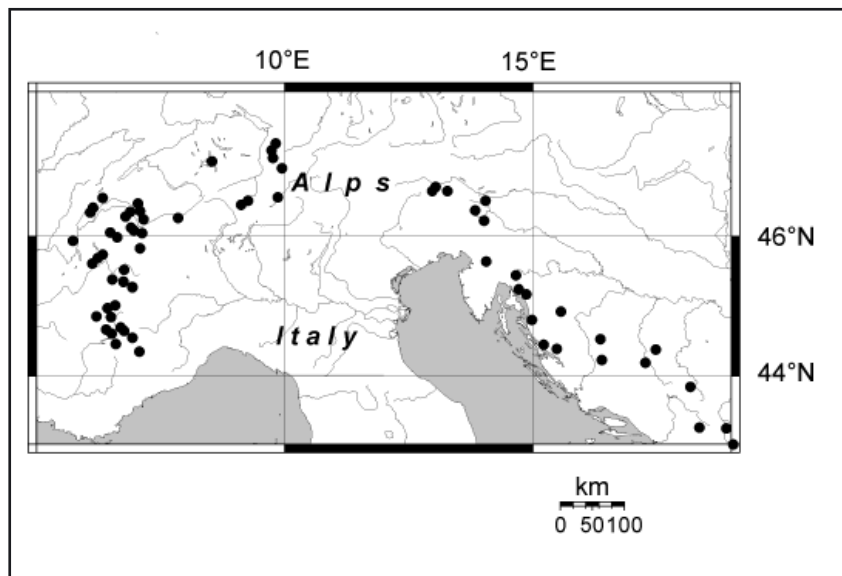


Fig. 7. *Eryngium alpinum*.

Eryngium sect. *Plana* H. Wolff in Engler, Pflanzenr. IV.228 (Heft 61): 107, 126. 1913.

Type: *E. planum* L.

Basal leaves undivided or trifid, not divided to the base, palmately to reticulately, in the upper part seldom pinnately veined, mostly without spines; cauline leaves palmatifid; involucre leaves more than twice as long as umbels (except *E. planum*); bracts tricuspidate or entire.

Included species:

Eryngium antiatlanticum Jury, *E. bithynicum* Boiss., *E. caeruleum* M. Bieb., *E. creticum* Lam., *E. dichotomum* Desf., *E. falcatum* F. Delaroché, *E. planum*, *E. tricuspdatum* L., *E. triquetrum* Vahl, *E. variifolium* Coss.

Balkan species:

Eryngium creticum

Although its name refers to Crete, this biennial, seldom annual species is widespread from the Adriatic Sea eastwards to Iraq (Fig. 8). It grows at lower altitudes, mostly in the Mediterranean zone, in sunny places or in disturbed, man-made habitats and is occasionally found even in the fields and field edges or in the understorey of olive groves. The soils are usually deep and not too poor in nutrients. Within the circummediterranean section *Plana*, *E. creticum* is the only Balkan species. The closest relative is the Caucasian *E. caeruleum*.

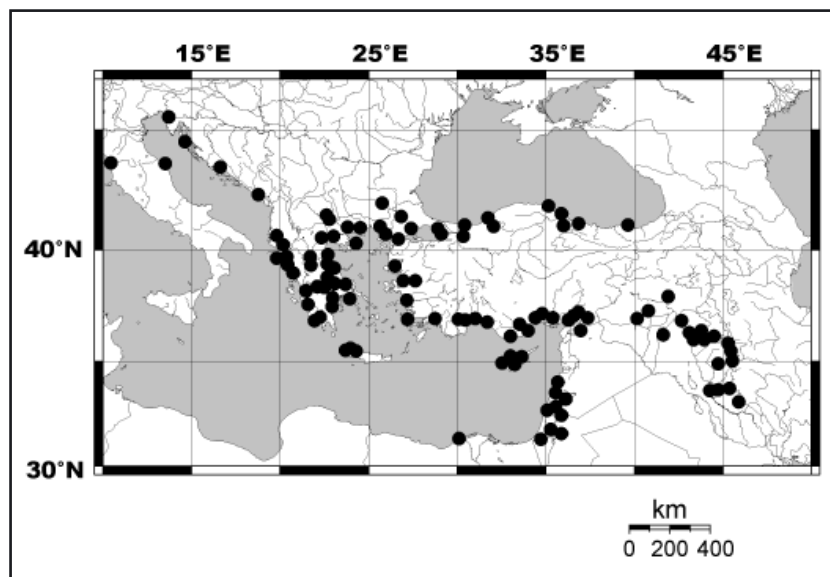


Fig. 8. *Eryngium creticum*.

Eryngium sect. *Astrantiifolia* H. Wolff in Engler, Pflanzenr. IV.228 (Heft 61): 107, 139. 1913.

Type (designated here): *E. palmatum* Pančić & Vis.

Basal leaves palmatisect or trisect, long-petiolate, segments not monocotyloid, bracts tricuspidate, umbels hemisphaerical.

Included species:

Eryngium palmatum, *E. wiegandii* Adamović.

This is the only section endemic to the Balkans. It comprises two species which have been considered as conspecific by Chater (1968). However, Mayer & Micevski (1982) contradicted this view and, in fact, both species are well differentiated morphologically (see the characters in the key below) and ecologically. Yet it is not clear, whether these two species are really closely related to each other. Both grow in forests, a fairly rare habitat type for genus *Eryngium*, since most other species grow in open, sunny sites. The only other typical forest species is *E. falcatum* from S Turkey, which is not related to this section. The forest types, however, are fairly different. Both species do occur from the lower to the upper mountain zone of the central and southern part of the Balkan Peninsula but, in fact, the overlap of the distribution areas is very small.

Eryngium palmatum

This species grows in broad-leaved forests and on their edges. Most of them are beech or hornbeam forests on calcareous soil. The habitats are more or less shady and not too dry. Therefore, the species lacks spines and has a mesophytic habit. It ranges from Central Serbia south to E Albania and N Greece, but is rare in Macedonia (Fig. 9).

Eryngium wiegandii

The pine forest habitats of this species are much drier, less shaded and warmer than the broad-leaved forests of *E. palmatum*. Consequently, this species is more sclerophyllous in its habit. *E. wiegandii* is extant in Macedonia, but more widespread in Serbia and S Croatia, where *E. palmatum* does not occur (Fig. 10). A disjunct population on Mount Olympus in Greece is well

to the south of *E. palmatum* occurrences in the north-
 ern part of the country.

Eryngium* L. sect. *Eryngium

= *Eryngium* sect. *Halobia* Calestani, Webbia 1: 126. 1905.

Type: *E. maritimum* L.

Perennials with long slender cylindrical roots; involu-
 cral leaves 5–6, broad, reticulately veined; bracts tri-
 cuspidate; fruit scales filiform, withering; plant grow-
 ing on sandy sea shores.

Included species: (single species) *Eryngium maritimum*

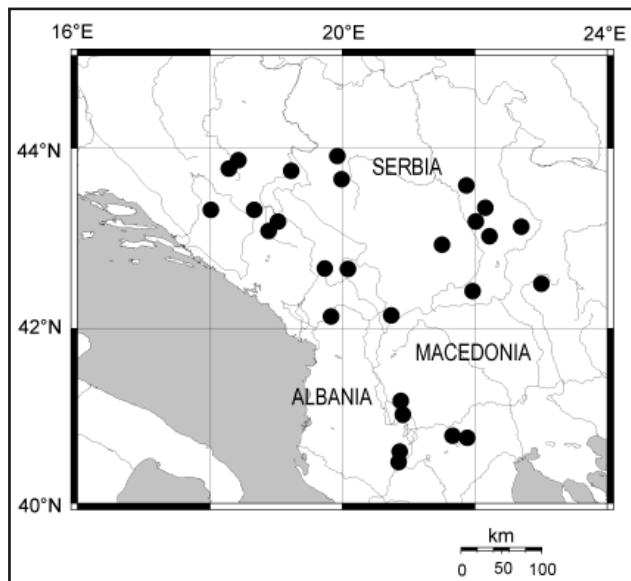


Fig. 9. *Eryngium palmatum*.

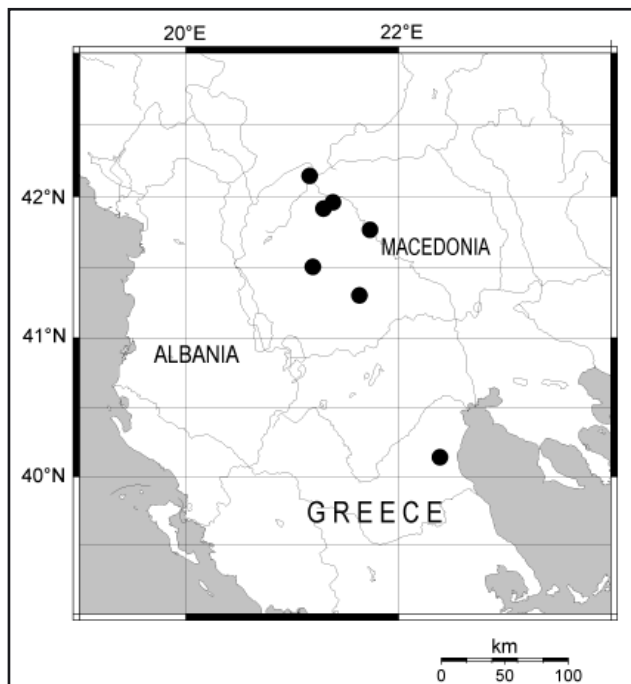


Fig. 10. *Eryngium wiegandii*.

Eryngium maritimum

Its name provides the type of *Eryngium* (lectotypifica-
 tion: see Jarvis & al. 1993: 46). It is a widespread spe-
 cies on coastal sand dunes and usually common along
 the Balkan coasts. For a distribution map see Meusel
 & al. (1978). Endangered by tourism and coastal de-
 velopment.

Discussion

Diversity of the Balkan *Eryngium* species may be ex-
 plained in two different ways: (1) an early immigration
 of the ancestors and an in-situ evolution of the modern
 species, (2) a recent immigration of the species. Table 2
 shows the species and section numbers as compared to
 other regions important for the genus. The relatively low
 number of *Eryngium* species in the Balkans is fairly sur-
 prising, considering the geographical structure and the
 diversity in other groups. Judging by the existence of
 high mountain ranges and many islands, a much greater
 diversity should be expected as in the more terrestri-
 al, but also well-structured regions of Anatolia, Spain
 or Morocco. Although the endemism is fairly high (5
 of 11 species, i. e. 45.5%), the only really local endemic
 with small distribution area is *E. ternatum*. *E. amorgi-
 num* is more widespread across the Aegean, and the
 other three species have a relatively wide distribution
 throughout the southern half of the Peninsula. They
 are old transregional endemics sensu Stevanović & al.
 (2003: 165). A great number of local endemics, so char-
 acteristic for S Anatolia, S Spain or Morocco, do not ex-
 ist on the Balkan Peninsula.

Table 2. Diversity of *Eryngium* on the Balkan Peninsula as
 compared to other regions.

Regions	Morocco	Iberian Peninsula	Balkan Peninsula	Turkey
Number of:				
Species	15	15	11	23
Endemics	5	5	5	12
Sections	9	8	6	9
Species of Balkan sections				
<i>Alpina</i>			1	2
<i>Campestris</i> subsect. <i>Campestris</i>	1	1	4	5
<i>Astrantifolia</i>			2	
<i>Eryngium</i>	1	1	1	1
<i>Palmito</i>			2	3
<i>Plana</i>	4	1	1	4

The two endemics of the Greek Islands are both chasmophytes (*E. ternatum*, *E. amorginum*), growing in fairly old and constant rock habitats, especially in gorges. They are „static populations“ sensu Greuter (1972: 173) which undergo an evolutionary standstill. *E. ternatum* is taxonomically isolated, with its nearest relatives growing at great distance. *E. amorginum* is not exclusively growing in gorges, but also on cliffs. Nevertheless, this is a relict habitat and not subject to rapid changes. Therefore, both species are probably remnants of an ancient steppe flora named a xero-mesogaic element („xero-mesogäisches Element“) by Greuter (1970: 240). In a similar way, Runemark (1969: 111) considered the Aegean chasmophytes a remnant of the Pleistocene cliff flora. Therefore, two Aegean chasmophytic *Eryngium* species are old and may indicate the old age of the other Balkan endemics of the genus as well.

Two species are spreading from the Balkans in NW direction, *E. alpinum* and *E. amethystinum*, and they are very different morphologically as well as ecologically. It is difficult to decide whether they are immigrants coming from the north or species radiating from the Balkans into the Alps and the Apennines. *E. amethystinum* var. *tenuifolium* may have evolved from isolated southern populations, possibly during the Pleistocene glacial period. They would have grown in steppe vegetation. In this case, a separation with subsequent reunification of the two varieties of *E. amethystinum* is probable.

The endemic *Eryngium* sect. *Astrantiifolia* comprises forest-inhabiting species, two of the very few understorey species within genus *Eryngium* and probably relicts of a preglacial, more widespread group of forest plants. In fact, the palynological data collected by Bottema (1975) suggest a relict area for the forest species in NW Greece, in which today *E. palmatum* and (nearby) *E. wiegandii* grow. During the last gla-

cial period, this region was covered by steppe vegetation, with forests limited to the higher altitudes. This former vegetation pattern makes the region suitable as a refuge area.

Most sections, however, are common to the nearby region of Anatolia, like *Eryngium* sect. *Campestris* subsect. *Campestris*, *E.* sect. *Palmito*, or *Eryngium* sect. *Alpina*. All these occur both in the Balkans and in Turkey, but they are absent or rare in the West Mediterranean. On the other hand, on species level, only the three widespread *E. campestre*, *E. maritimum*, and *E. creticum* are really common to both regions. This pattern is similar to the one found in *Centaurea* (Wagenitz 1975) and these cases indicate a longer and more separate species evolution on the Balkan Peninsula. Altogether, sectional diversity of *Eryngium* in the Balkans is relatively high: the 11 species are dispersed in 6 sections.

Specialization, the high rate of endemism, comparatively high sectional diversity and distribution patterns all suggest a relatively old age for most Balkan *Eryngium* species. The diversity of the genus in this region seems mostly (except for the three widespread species) to result from early immigration and subsequent in-situ evolution in the area. This immigration came from the east, as the relationships to Anatolian species indicates. The topographical and climatic diversity, as well as the intensive climatic changes during and before the last Ice Age resulted in isolation and some ecological adaptations, as it is visible in a serpentine plant (*E. serbicum*) and in the chasmophytes (*E. ternatum* and *E. amorginum*). The climatic changes and extinctions during the Ice Ages may explain the relatively low species number. Exceptions from the old age are probably the widespread species *E. campestre*, *E. creticum*, and *E. maritimum*, which are migratory elements sensu Greuter (1975a: 18).

Identification key to the Balkan *Eryngium* species

- 1 Basal leaves withered during flowering time 2
- 1* Basal leaves persistent during flowering time 3
- 2 Synflorescence glomerate, paniculate; cauline leaves extremely spiny, pinnate, more than 25 mm long, reflexed *E. glomeratum*
- 2* Synflorescence spreading, dichasial; cauline leaves palmate with tripartite central segments longer than the lateral, conspicuously smaller, 10–25 cm long *E. creticum*

- 3 Basal leaves undivided, cordate, ovate, not spiny, palmately veined 4
- 3* Basal leaves divided, or if undivided, then parallel veined 5
- 4 Capitula few, umbels large, club-shaped; involucre leaves pinnate; basal leaves persistent during flowering time *E. alpinum*
- 4* Capitula numerous, small, orbicular to shortly ovoid; involucre leaves linear to lanceolate, never pinnate, narrow basal leaves mostly withered during flowering time *E. creticum*
- 5 Leaf segments with parallel veins, linear or lanceolate, not spiny 6
- 5* Leaves not as above 7
- 6 Basal and cauline leaves with 4–8 narrow, linear segments; bracts entire *E. serbicum*
- 6* Basal leaves often undivided, cauline leaves with 3 broadly lanceolate segments; bracts tricuspidate *E. ternatum*
7. Basal leaves ovoid or round in shape, palmatisect or trisect to tripartite, never pinnate or trifoliolate-pinnate or with trisect or tripartite segments 8
- 7* Basal leaves trifoliolate with trisect to trifid segments, or segments irregularly pinnate or incised, or leaves more or less pinnate; segments mostly decurrent on rhachis 10
- 8 Basal leaves palmatisect, never tripartite or undivided, not spiny, with 5–7 trifid to pinnatifid, obtuse, dentate segments; cauline leaves palmatifid. *E. palmatum*
- 8* Basal leaves tripartite or trisect, spiny. 9
- 9 Involucre leaves ovoid to elliptical, reticulate veined; umbels large 15–26 mm in diameter; dune species *E. maritimum*
- 9* Involucre leaves lanceolate, 1-veined; umbels small, 5–10 mm in diameter; pine forest species . *E. wiegandii*
- 10 Synflorescence a long, glomerous panicle with long, very spiny, reflexed cauline leaves; basal leaves withered during flowering time. *E. glomeratum*
- 10* Synflorescence dichasial, if paniculate, then dichasial in the uppermost part, always spreading; basal leaves not withered during flowering time 11
- 11 Plant conspicuously blue in the upper, sometimes also in the lower parts, synflorescence paniculate, dichasial to corymbose in the uppermost part *E. amethystinum*
- 11* Plant always green to yellowish-green, synflorescence dichasial, spreading. 12
- 12 Involucre leaves shorter than the umbel, capitula few, about 7; leaf segments broad, rounded at the base, overlapping. *E. amorginum*
- 12* Involucre leaves longer than the umbel, capitula numerous; leaf segments more narrow, not rounded at the base and not overlapping *E. campestre*

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References

- Bottema, S.** 1975. Reconstruction of the Late Quaternary vegetation of Northwestern Greece. – In: **Jordanov, D. & al.** (eds), Problems of the Balkan flora and vegetation. Pp. 58-63. Publishing House Bulg. Acad. Sci., Sofia.
- Büdel, J.** 1949. Die räumliche und zeitliche Gliederung des Eiszeitklimas. – *Naturwissenschaften*, **36**: 133-139.

- Chater, A.O.** 1968. *Eryngium* L. – In: **Tutin, T.G. & al.** (eds), Flora Europaea. Vol. 2, pp. 320-324. Cambridge Univ. Press, Cambridge.
- Davis, P.H.** 1972. 5. *Eryngium* L. – In: **Davis, P.H.** (ed.), Flora of Turkey and the East Aegean Islands. Vol. 4, pp. 292-304. Univ. Press, Edinburgh.
- Froebe, H.A.** 1964. Die Blütenstände der Saniculoideen (*Umbelliferae*). Eine vergleichend-morphologische und entwicklungsgeschichtliche Untersuchung. – Beitr. Biol. Pflanzen, **40**: 325-388.
- Greuter, W.** 1970. Zur Paläogeographie und Florengeschichte der südlichen Ägäis. – Feddes Repert., **81**: 233-242.
- Greuter, W.** 1971. Betrachtungen zur Phytogeographie der Südägäis. – Opera Bot., **30**: 49-64.
- Greuter, W.** 1972. The relict element of the flora of Crete and its evolutionary significance. – In: **Valentine, D.H.** (ed.), Taxonomy, Phytogeography and Evolution. Pp. 161-177. Acad. Press, London & New York.
- Greuter, W.** 1975a. Historical phytogeography of the southern half of the Aegean Area. – In: **Jordanov, D. & al.** (eds), Problems of the Balkan flora and vegetation. Pp. 17-21. Publishing House Bulgarian Acad. Sci., Sofia.
- Greuter, W.** 1975b. Die Insel Kreta – eine geobotanische Skizze. – Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich, **55**: 141-197.
- Jarvis, C.E., Barrie, F.R., Allan, D.M. & Reveal, J.L.** 1993. A List of Linnean Generic Names and their Types. – Regnum Veg., **127**.
- Mathias, M.E. & Constance, L.** 1941. A synopsis of the North American species of *Eryngium*. – Amer. Midl. Naturalist, **25**: 361-387.
- Mayer, E. & Micevski, K.** 1982. Zur taxonomischen Bewertung von *Eryngium wiegandii* Adamović. – Acta Bot. Croat., **41**: 181-186.
- Meusel, H., Jäger, E., Rauschert, S. & Weinert, E.** 1978. Vergleichende Chorologie der zentraleuropäischen Flora. 2, Karten. G. Fischer, Jena.
- Phitos, D., Strid, A., Snogerup, S. & Greuter, W.** 1995. The Red Data Book of Rare and Threatened Plants of Greece. K. Michalas, Athens.
- Pimenov, M.G. & Leonov, M.V.** 1993. The Genera of the *Umbelliferae*. Royal Bot. Gard., Kew.
- Pimenov, M.G. & Tamamschjan, S.G.** 1987. *Eryngium* L. – In: **Rechinger, K.-H.** (ed.), Flora Iranica. Vol. 162, pp. 45-60. Akad. Druck- und Verlagsanstalt, Graz.
- Runemark, H.** 1969. Reproductive drift, a neglected principle in reproductive biology. – Bot. Not., **122**: 90.
- Stevanović, V., Tan, Kit & Iatrou, G.** 2003. Distribution of the endemic Balkan flora on serpentine I. – obligate serpentine endemics. – Pl. Syst. Evol., **242**: 149-170.
- Turland, N.J., Clinton, L. & Press, J.R.** 1993. Flora of the Cretan Area. Annotated Checklist & Atlas. The Nat. Hist. Museum, HMSO, London.
- Wagenitz, G.** 1975. Floristic connections between the Balkan Peninsula and the Near East as exemplified by genus *Centaurea*. – In: **Jordanov, D. & al.** (eds), Problems of the Balkan flora and vegetation. Pp. 223-228. Publishing House Bulgarian Acad. Sci., Sofia.
- Wolff, H.** 1913. *Umbelliferae-Saniculoideae*. – In: **Engler, A.** (ed.), Das Pflanzenreich, IV.228 (Heft 61). W. Engelmann, Berlin.
- Wörz, A.** 2005. A new subgeneric classification of the genus *Eryngium* L. (*Apiaceae* – *Saniculoideae*). – Bot. Jahrb. Syst., **126**: 253-259.