

Seed morphology and anatomy of the Mediterranean pentamerous species of *Erica* (Ericaceae)

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Abstract: The species of the “Pentapera group” are distinguished from the rest of the European and Mediterranean *Erica* L. species by having 5 corolla lobes and sepals instead of 4, and 10 stamens instead of 8. The genus *Pentapera* Klotzsch was proposed for these taxa but recent studies regards it as part of *Erica*. Two species are recognised: *Erica sicula* Guss. and *E. bocquetii* (Peşmen) P.F.Stevens, and 3 subspecies have been described within *E. sicula*. This taxonomic treatment is still under discussion and relationships with other species have been poorly discussed.

Seed morphology of the 2 species and the 3 subspecies was studied by means of scanning electron microscope techniques. Characters concerning size and shape of seeds, and primary and secondary ornamentation were observed and measured. Anatomy of the seed coat was analysed in 2 populations of *E. sicula* subsp. *libanotica* (C.Barbey) P.F.Stevens using a light microscope, and seed coat thickness and cell junctions were measured.

Seeds range from 0.45 to 0.8 mm; shape is ellipsoid, oblong, or obovoid with a lateral wing; primary ornamentation is striate while secondary ornamentation shows smooth outer anticlinal walls and indented or smooth outer periclinal walls. Clear differences were found for the studied taxa. The seeds of *E. bocquetii* have the lowest values for size and lack an indented surface; this is shared with *E. sicula* subsp. *libanotica*. *E. sicula* subsp. *sicula* has an indented surface and *E. sicula* subsp. *cyrenaica* Brullo & Furnari has smaller, rounder seeds.

Compared to the rest of the northern *Erica* species, seed coat sections reveal similarities with *E. arborea* L. and *E. australis* L., and seed morphology relate this group with *E. ciliaris* L. but most of all with *E. arborea*

Key words: *Erica*, *Pentapera*, Ericaceae, seed morphology, seed anatomy, taxonomy, SEM

Introduction

Erica sicula Guss. was described by Gussone (1821) as a new species characterised by having 5 corolla lobes and sepals, a pentalocular ovary, and 10 stamens. Klotzsch (1838) proposed a new genus, *Pentapera* Klotzsch, for this species based on the

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distinct characters opposed to the genus *Erica* L., which has flower parts in fours, a tetralocular ovary, and 8 stamens. This treatment was widely used for some time but actually *Pentapera* is considered part of *Erica* (Webb & Rix, 1972; Stevens, 1978; Brullo & Furnari, 1979; Pignatti, 1982; Meikle, 1985; Greuter

et al., 1986; McClintock, 1980, 1989; Oliver, 2000; Nelson, 2007). According to recent systematic interpretations, the existence of other *Erica* species with different numbers of flower parts, stamens, or ovary loci supports this interpretation (Stevens, 1978; Oliver, 2000).

Erica sicula has a very widespread distribution, occurring in several Mediterranean localities (Figure 1). Three subspecies have been described according to this disjunctive geographic distribution: *E. sicula* subsp. *libanotica* (C.Barbey) P.F.Stevens stands for plants from Lebanon, Cyprus, and Turkey; subsp. *cyrenaica* Brullo & Furnari was described for the Libyan populations (Brullo & Furnari, 1979); and the Sicilian plants would then remain as subsp. *sicula* (Yaltirik, 1967; Stevens, 1978; Brullo & Furnari, 1979; McClintock, 1980; Browicz, 1983; Greuter et al., 1986). *Erica sicula* subsp. *libanotica* was first described as a variety by Barbey & Barbey (1882), as having longer, slender stems and an almost glabrous corolla. Previously, Boissier (1875) had noted the morphological differences between the Lebanese plants and those from Sicily. Yaltirik (1967) proposed it as a subspecies under the genus *Pentapera*. Stevens (1978) raised it to a subspecific rank under *Erica* and added the longer, narrower leaves and the dark pink corolla as diagnostic characters. Plants from Cyprus

and Turkey have been included in this subspecies, although Peşmen (1968), McClintock (1980), and Meikle (1985) doubt this interpretation. *Erica sicula* subsp. *cyrenaica* has smaller flowering parts (sepals, corolla, style, stamens, and anthers) and a corolla narrower at its mouth than *E. sicula* subsp. *sicula* (Brullo & Furnari, 1979). The infraspecific taxonomy of *E. sicula* is still under discussion (McClintock, 1980).

Later, a second species was described under the genus *Pentapera* (Peşmen, 1968) and today is considered as *E. bocquetii* (Peşmen) P.F.Stevens, with leaves in threes (*E. sicula* in fours) and smaller flowers, occurring in the mountains in southern Turkey, Antalya, in clearings of *Cedrus libani* forests (Peşmen, 1968) (Figure 1).

There are only a few brief descriptions published on the seeds of the *Pentapera* group. The first mention on the seeds was given by Klotzsch (1840) for plants from Sicily, which have small, compressed, elongated, yellowish brown, seeds with a reticulate surface pattern. Hooker (1888) described the seeds of *E. sicula* as minute and shiny. Peşmen (1968) in his diagnosis for *E. bocquetii* describes its seeds as compressed, of 0.5×0.3 mm. Meikle (1985) describes seeds of plants from Cyprus as oblong, of 0.8×0.4 mm, shiny and dark brown, and minutely sulcate.

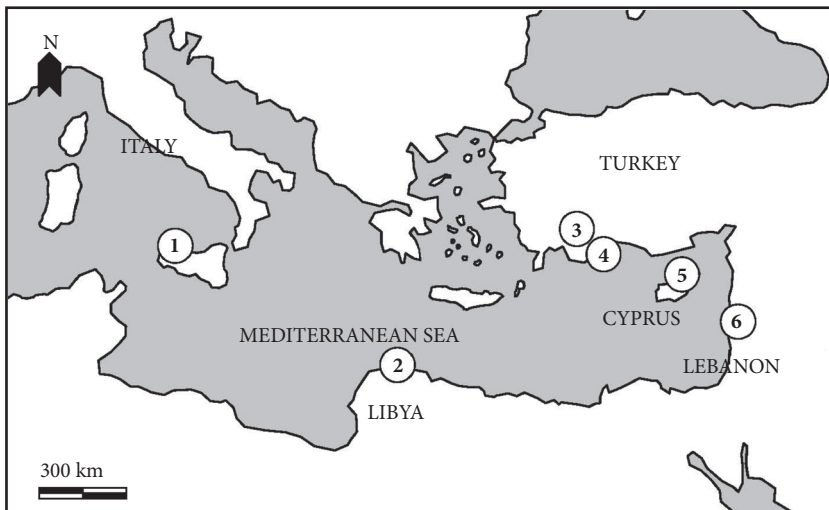


Figure 1. Geographic distribution of the *Pentapera* group. 1- *Erica sicula* subsp. *sicula*, 2- *E. sicula* subsp. *cyrenaica*, 3- *E. bocquetii*, 4- *E. sicula* subsp. *libanotica* (Turkey), 5- *E. sicula* subsp. *libanotica* (Cyprus), 6- *E. sicula* subsp. *libanotica* (Lebanon).

In the present study we examined the seeds of the group to assess differences that can be used as diagnostic characters, and to compare with the rest of the northern heathers. As found in other groups studied, seed morphology and anatomy provide useful taxonomic information that may help to clarify the systematics of this complex and its relationship with other species of the genus.

Materials and methods

Samples from different localities covering the 2 species and the 3 subspecies of *E. sicula* were studied (Table 1). These were collected in the field by the first author in Cyprus, and by the first author, M. Bou Daguer-Kharrat, and B. Doueihy (University Saint Joseph, Beirut, Lebanon) in Lebanon. The Sicilian seeds were donated by C. Gómez-Campo from the ETSIA Seedbank (Universidad Politécnica de Madrid, Madrid, Spain). The rest of the samples were obtained from herbarium sheets. Anatomical studies were only conducted on seeds from Cyprus and Lebanon since large amounts of seeds are needed, and therefore the anatomical characters were not used for taxa delimitation.

Seeds were collected and stored under cold and dry conditions following the procedures of the University of Santiago de Compostela Seedbank. Whenever possible, 15 seeds from each population were measured using a video camera connected to a binocular scope. Images were treated by means of UTHSCSA Image tool software (Wilcox et al., 2010). Area (a), perimeter (p), major axis length, minor axis length, elongation (major axis/minor axis), and sinuosity ($4\pi a/p^2$) were measured for each seed; mean and standard deviation were calculated for each population.

For SEM pictures, 5-10 dry seeds from 5 populations were mounted on metal stubs using double-sided sticky tape and gold coated. Pictures of whole seeds and details were taken of 3 seeds of each population. Three testa cells were randomly chosen and measures taken in the same way as for the whole seed. Images are presented for *E. sicula* subsp. *sicula* (Figure 2), subsp. *cyrenaica* (Figure 2), *E. bocquetii* (Figure 2), and subsp. *libanotica* from Cyprus (Figure 3), Lebanon (Figure 3), and Turkey (Figure 3).

Histological techniques were as in Fagúndez et al. (2010). Seeds sectioned for light microscopy studies

Table 1. Taxa studied with (population name), sampling locality, date of collection and provenience (herbarium, seed bank or field collection) of the material.

Taxa (pop. name)	Locality	Date	Provenience
<i>E. sicula</i> subsp. <i>sicula</i>	ITALY: Sicily, Trapani, Mt. Cofano	1985	E.T.S.I.A. Seed bank, Madrid
<i>E. sicula</i> subsp. <i>cyrenaica</i>	LIBYA: Ras Al-Hilal	1954	Guichard (BM 915300)
<i>E. sicula</i> subsp. <i>libanotica</i> (Lebanon 1)	LEBANON: Nahr Ibrahim valley	2009	M Bou Daguer-Kharrat
<i>E. sicula</i> subsp. <i>libanotica</i> (Lebanon 2)	LEBANON: Aakoura	2010	J Fagúndez 3248 & B Doueihy (SANT)
<i>E. sicula</i> subsp. <i>libanotica</i> (Cyprus)	CYPRUS: Kyrenia, Alevkaya	2009	J Fagúndez 3198, 3199 (SANT)
<i>E. sicula</i> subsp. <i>libanotica</i> (Turkey)	TURKEY: Antalya, Kesme Boğaz	1992	Turland 596 (BM)
<i>E. bocquetii</i>	TURKEY: Elmali	1989	McClintock et al (BM 916288 and K)

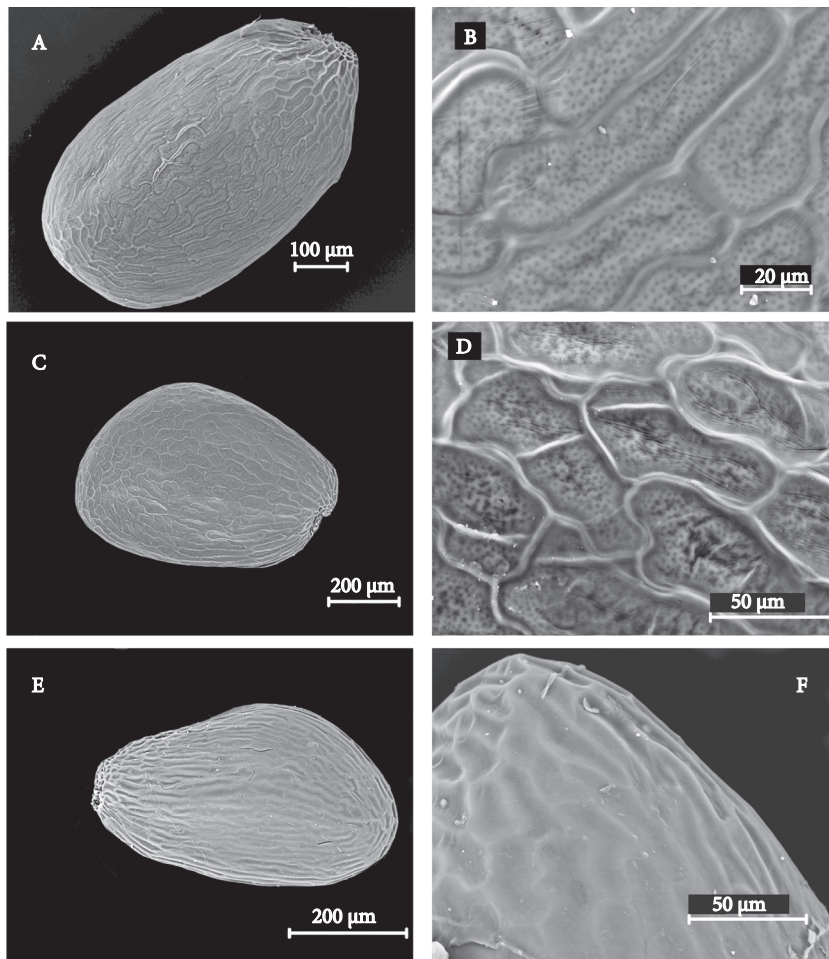


Figure 2. SEM pictures of the seeds of: A and B - *Erica sicala* subsp. *sicala*, C and D - *Erica sicala* subsp. *cyrenaica*, E and F - *Erica bocquetii*. A, C, and E: general view of a seed, B, D, and F: detail of surface cells. Note the indented pattern in B and D and the smooth pattern of F.

were first fixed in FAA for at least 48 h, dehydrated in an ethanol-tertiary butanol series (Johansen, 1940; Fagúndez et al., 2010), and embedded in paraffin (Paraplast plus). Sections were cut at 3 μm with a Micron HM-355 microtome. Four slides were mounted for each sample. The slides were studied and photographed with a digital camera Optikam PRO 3 adjusted to an Optika B-350 microscope. The software used for image analysis was Optika Vision Pro 2.7. Ten measures of each population were performed for inner periclinal wall thickness, and mean and standard deviation were calculated.

One-way analysis of variance (ANOVA) was conducted for every variable measured using SPSS 9.0 for Windows. Homogeneous subgroups were

calculated using the Student-Newman-Keuls test ($P < 0.05$).

Nomenclature follows Berggren (1981) and Barthlott (1984) for seed morphology, and Werker (1997) for anatomical descriptions.

Results

Seed morphology

Values of size and shape of seeds are given in Table 2. Every character had significant differences between populations according to one-way ANOVA ($P < 0.01$), although numbers of seeds per population are not homogeneous and thus the results must be

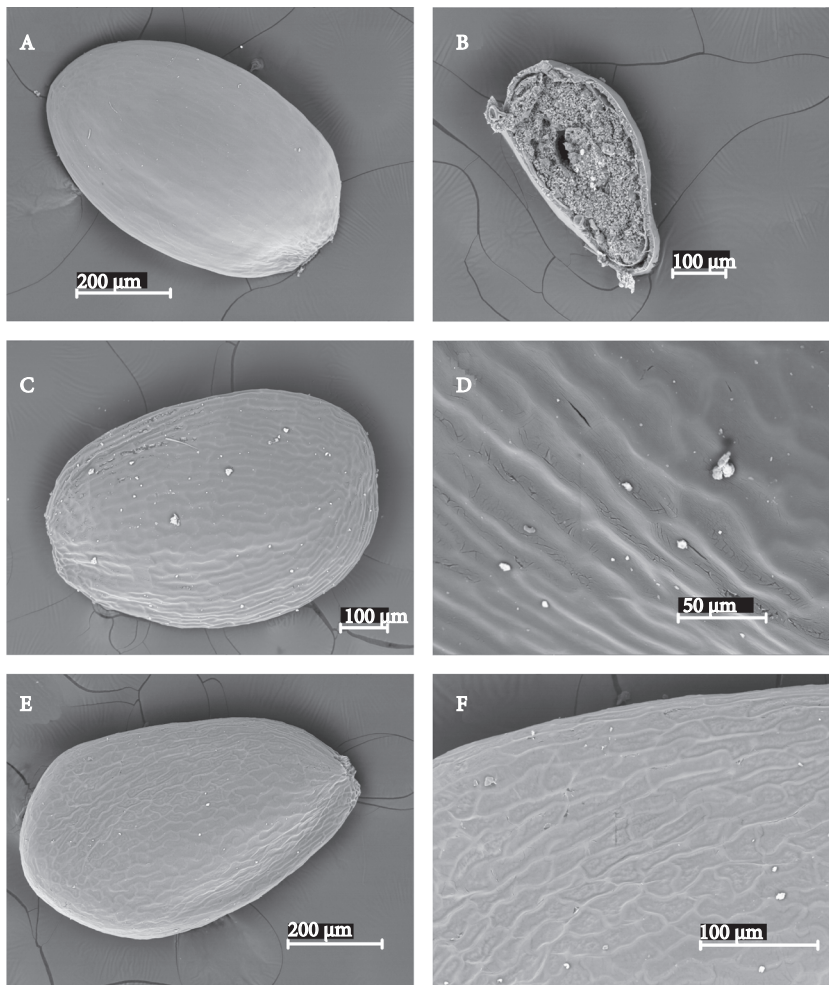


Figure 3. SEM pictures of the seeds of: A and B - *Erica sicula* subsp. *libanotica* from Cyprus, C and D - *Erica sicula* subsp. *libanotica* from Lebanon, E and F - *Erica sicula* subsp. *libanotica* from Turkey. A, C, and E: general view of a seed. B: transverse section of a seed. D and F: detail of surface cells. Note the lateral wing in A, B, C, and E.

treated with caution. Seed size (major axis length) range from values lower than 0.5 mm in *E. bocquetii* samples to c. 0.8 in *E. sicula* subsp. *libanotica* from Lebanon. Homogeneous subgroups group together seeds of *E. sicula* from Sicily, Turkey, Cyprus, and Lebanon, with mean values of 0.72-0.76, while those from Libya show lower values of 0.65 and share a subgroup with seeds from Sicily, Cyprus, and one of the Lebanese samples. There is an overlap for all the *E. sicula* samples, clearly larger than those of *E. bocquetii*. Axis ratio (elongation) values are variable, between 1.5 and 2 (ratio 2:1 to 3:2) with lower values (rounder seeds) in seeds from Libya (*E. sicula* subsp.

cyrenaica), which forms a homogeneous subgroup against the rest of the species except for one of the samples from Lebanon (*E. sicula* subsp. *libanotica*), which belongs to both subgroups. Values of area, perimeter, and sinuosity are in accordance with main axis values.

The outline of the seeds is oblong (Figure 2), elliptic (Figure 3), or obovate (Figures 2-3), frequently asymmetric in its main axis (Figure 2). The third axis values are low, and seeds are clearly compressed (Figure 3), frequently with a lateral wing as a result of the lateral position of the embryo (Figure 3). The seeds are bright reddish brown or similar, and

Table 2. Mean \pm standard deviation and maximum-minimum values of the populations studied. Taxa with (population name), N is number of seeds. All measures in mm except for area (mm²), seed coat thickness (μ m), elongation and sinuosity. Different letters are for homogeneous subgroups by means of the Student-Newman-Keuls test, $p < 0.05$. Seed coat thickness calculated after 10 measures from 6-8 seeds.

Taxa (p. name)	N	Area	Perimeter	Major axis length	Minor axis length	Elongation	Sinuosity	Seed coat thickness
<i>E. sicula</i> subsp. <i>sicula</i> (Sicily)	6	0.24 \pm 0.04 b (0.17-0.27)	2.01 \pm 0.13 b (1.81-2.09)	0.72 \pm 0.05 bc (0.63-0.77)	0.42 \pm 0.06 b (0.33-0.49)	1.72 \pm 0.16 b (1.51-1.91)	0.73 \pm 0.06 a (0.63-0.79)	
<i>E. sicula</i> subsp. <i>cyrenaica</i> (Libya)	6	0.24 \pm 0.04 b (0.19-0.28)	1.91 \pm 0.15 b (1.69-2.08)	0.65 \pm 0.07 b (0.57-0.75)	0.47 \pm 0.06 cd (0.43-0.51)	1.37 \pm 0.09 a (1.24-1.5)	0.81 \pm 0.04 b (0.76-0.85)	
<i>E. sicula</i> subsp. <i>libanotica</i> (Turkey)	3	0.26 bc	2.03 \pm 0.01 b (2.02-2.04)	0.76 \pm 0.01 c (0.75-0.77)	0.45 \pm 0.01 bc (0.44-0.46)	1.69 \pm 0.06 b (1.63-1.75)	0.79 \pm 0.01 b (0.78-0.8)	
<i>E. sicula</i> subsp. <i>libanotica</i> (Cyprus)	12	0.24 \pm 0.02 b (0.21-0.27)	1.94 \pm 0.06 b (1.83-2.04)	0.72 \pm 0.03 bc (0.66-0.78)	0.43 \pm 0.03 b (0.36-0.46)	1.71 \pm 0.2 b (1.51-2.06)	0.8 \pm 0.04 b (0.73-0.85)	7.96 \pm 1.47 (6-10.1)
<i>E. sicula</i> subsp. <i>libanotica</i> (Leban. 1)	14	0.29 \pm 0.04 c (0.22-0.35)	2.09 \pm 0.14 b (1.88-2.34)	0.74 \pm 0.04 c (0.68-0.82)	0.49 \pm 0.04 d (0.42-0.58)	1.52 \pm 0.1 ab (1.37-1.62)	0.82 \pm 0.02 b (0.78-0.85)	7.94 \pm 0.63 (7.1-8.8)
<i>E. sicula</i> subsp. <i>libanotica</i> (Leban. 2)	23	0.24 \pm 0.04 b (0.15-0.33)	2.01 \pm 0.2 b (1.63-2.47)	0.73 \pm 0.09 bc (0.57-0.89)	0.42 \pm 0.03 b (0.33-0.47)	1.73 \pm 0.17 b (1.38-2.05)	0.73 \pm 0.05 a (0.62-0.84)	
<i>E. bocquetii</i>	17	0.12 \pm 0.02 a (0.09-0.15)	1.43 \pm 0.1 a (1.27-1.59)	0.52 \pm 0.03 a (0.47-0.56)	0.3 \pm 0.03 a (0.23-0.38)	1.73 \pm 0.16 b (1.4-2.14)	0.76 \pm 0.04 ab (0.65-0.83)	

sometimes variegated, darker on the surrounding hilum region.

The surface pattern (primary ornamentation) of the seed is slightly striate, with slightly prominent outer walls that are curved or sinuate. The secondary ornamentation is either smooth in seeds from Lebanon, Turkey, or Cyprus of *E. sicula* subsp. *libanotica* (Figure 3) and of *E. bocquetii* (Figure 2), or indented in seeds from Sicily (subsp. *sicula*) and Libya (subsp. *cyrenaica*) (Figure 2). This key character is conservative and has been tested in several seeds from each sample.

Seed coat anatomy

Several seeds of *E. sicula* subsp. *libanotica* from Cyprus and Lebanon were analysed, and the results were similar for both populations. The seed coat is formed by a single cell layer, and all cells collapsed at maturity. The thin outer walls collapse over the thick inner periclinal wall, which is densely pitted, and the outer walls are moderately thin (Figure 4). Cell boundaries are not raised, with a continuum between neighbouring cells and no prominent anticlinal walls are present (type A according to Fagúndez et al., 2010) (Figure 4). The inner periclinal walls are c. 8

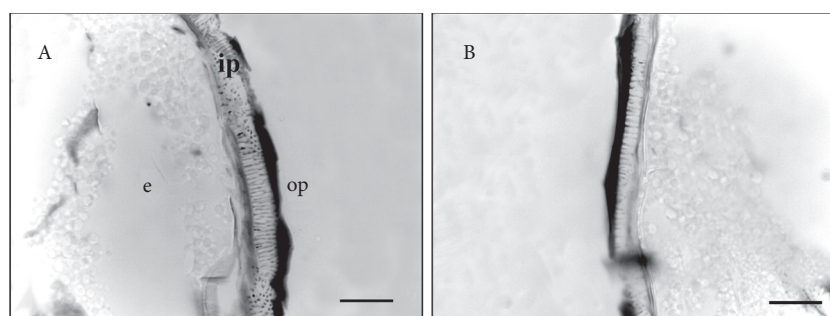


Figure 4. LM pictures of the seed coat of: A - *Erica sicula* subsp. *libanotica* from Cyprus; B - *Erica sicula* subsp. *libanotica* from Lebanon. e - endosperm, ip - inner periclinal wall, op - outer periclinal wall. Scale bar: 20 μ m.

μm thick (Table 2). No differences were found for the 2 populations studied although variation was higher in seeds from Cyprus.

Seed description

Erica group Pentapera: Seeds bright reddish brown sometimes variegated, darker on the hilum region, 0.5-0.8 mm long 0.3-0.45 mm wide, obovate, elliptic or oblong in outline, cross section elliptic or round, main axis ratio 2:1 to 3:2, appendages absent; hilum terminal, seed symmetric from hilum or rarely laterally displaced; primary ornamentation striate with testa cells elongated in the central area, 100 μm long 20 μm wide, shorter and wider towards the polar areas, with around 15 cells in main axis; outer anticlinal walls thin, sinuate, smooth, slightly protruding clearly different from outer periclinal walls, these with a secondary ornamentation indented or smooth; cell boundaries with totally fused outer anticlinal walls; seed coat constituted by a single cell layer with a thin outer layer and a c. 8 μm thick inner layer, this many pitted.

Erica sicula: Seeds 0.65-0.75 mm long 0.35-0.45 mm wide, outer periclinal walls with an indented secondary ornamentation, or smooth.

Erica sicula subsp. sicula: Seeds 0.7-0.75 mm long, 3:2 to 2:1 axis ratio; outer anticlinal walls thin, sinuate, smooth, slightly protruding, clearly different from the outer periclinal walls, these with an indented secondary ornamentation.

Erica sicula subsp. cyrenaica Brullo & Furnari: Seeds 0.65 mm long, 5:4 to 3:2 axis ratio; outer anticlinal walls thin, sinuate, smooth, slightly protruding, clearly different from the outer periclinal walls, these with an indented secondary ornamentation.

Erica sicula subsp. libanotica (incl. Cyprus and Turkey): Seeds 0.7-0.8 mm long, 3:2 to 2:1 axis ratio; outer anticlinal walls smooth, very slightly protruding, continued with the outer periclinal walls, these with a smooth secondary ornamentation.

Erica bocquetii: Seeds 0.5-0.55 mm long 0.3 mm wide, 3:2 to 2:1 axis ratio; outer anticlinal walls smooth, very slightly protruding, continued with the outer periclinal walls, these with a smooth secondary ornamentation.

Discussion

Systematics of the Pentapera group

Erica sicula and *E. bocquetii* are distinguished by the size and indumentum of the corolla, smaller and almost glabrous in *E. bocquetii*, leaves in whorls of 3 in *E. bocquetii* and 4 in *E. sicula* (Peşmen, 1968; Stevens, 1978; McClintock, 1980). Another character proposed by Stevens (1978) is the lack of small anther appendages in this species, while *E. sicula* has small anther appendages. This character needs confirmation (McClintock, 1980). Seed characters discriminate both species mainly by size of the seeds. Seeds of *E. bocquetii* are around 0.5×0.3 mm, while those of *E. sicula* are clearly larger, c. $0.7-0.8 \times 0.4$ mm with no overlapping measures. The secondary ornamentation shows that *E. sicula* seeds from Sicily and Libya (namely *E. sicula* subsp. *sicula* and *E. sicula* subsp. *cyrenaica*) have indented surface cells. This may be due to thinner outer periclinal walls that collapse to the inner walls and reveal the pitted surface of the inner walls. *E. bocquetii* has thicker walls with a smooth pattern (Figure 2). Values of size and shape are similar for the different populations of *E. sicula*, except for the smaller seeds of *E. sicula* subsp. *cyrenaica* (mean of 0.65 mm), which are also rounder, while seeds from Lebanon (*E. sicula* subsp. *libanotica*) are intermediate for roundness between *E. sicula* subsp. *cyrenaica* and the rest of the samples. Secondary ornamentation of *E. sicula* subsp. *libanotica* from Lebanon, Turkey, and Cyprus is similar to that of *E. bocquetii* seeds, with a smooth surface pattern against the indented outer periclinal walls observed on the seeds of *E. sicula* subsp. *sicula* and subsp. *cyrenaica*. In our observations this character was constant for all seeds observed. According to this, there would be 2 main seed types, corresponding to *E. sicula* subsp. *sicula* and *E. sicula* subsp. *cyrenaica* against plants from *E. sicula* subsp. *libanotica* sensu Stevens (1978), including populations from Lebanon, Turkey, and Cyprus. This last subspecies would also be more closely related to *E. bocquetii* but clearly distinguished by the larger seeds. *E. sicula* subsp. *sicula* and subsp. *cyrenaica* can be discriminated by the size and shape of the seeds, larger and more elongated in subsp. *sicula*. A throughout study must be carried out to determine the taxonomic value of the proposed classification.

The Pentapera group in *Erica*

In published phylogenetic studies within the Ericales (Anderberg, 1993) and the Ericaceae (Kron et al., 2002), floral parts in fives is a primitive state compared with floral parts in fours. The Pentapera group (*Erica sicula*, including the 3 subspecies and *E. bocquetii*) could then retain these plesiomorphic characters within the genus *Erica*, being pentamerous and because of its disperse geographical distribution that has been considered as relictic by some authors (Brullo & Furnari, 1979). This should be carefully considered, as reversals such as pollen grains in tetrads or monads, or presence of anther appendages, are not rare within *Erica* (Oliver, 2000). However, the position of *E. sicula* was unresolved within the European clade in the phylogenetic study performed by McGuire and Kron (2005) using nuclear and chloroplast molecular markers.

The study of the seeds reveals several characters in the Pentapera group shared with *E. arborea* (Fagúndez & Izco, 2010). Both have a striate pattern for primary ornamentation, a lateral wing as the embryo is displaced laterally (Figure 3), seeds are mostly compressed and shape is sometimes obovate in *E. arborea* as in *E. sicula* (Figures 2-3). *E. arborea* is the only species present in both the European and African nucleus and is most probably an early-divergent species (Hansen, 1950). As for the secondary ornamentation, the indented surface of the seeds of *E. sicula* subsp. *sicula* and *E. sicula* subsp. *cyrenaica* has only been observed in *E. ciliaris* (Fagúndez & Izco, 2009) a species with many exclusive characters

within the European species of the genus, some of which are considered primitive by Oliver (2000) such as the basal position of the bract.

The seed coat characters were only observed in *E. sicula* subsp. *libanotica* from Lebanon and Cyprus, and should be tested in the other populations. The seed coat type is close to that of *E. arborea* because of the cell junction type, but mostly to that of *E. australis*, whose outer walls are not as thin as in most of the species (Fagúndez et al., 2010). This is probably related to the secondary ornamentation, and the indented pattern of *E. sicula* subsp. *sicula* and *E. sicula* subsp. *cyrenaica* is probably due to a thinner outer wall. Density of pits in the inner walls is low compared to most of the other species, but not as much as in *E. multiflora* (Fagúndez et al., 2010). The thickness values are close to 8 µm ranges within the most numerous group of the northern species, which have values of 4-10 µm, and includes all the species mentioned above (Fagúndez et al., 2010).

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