Phenotypic variability in *Scutellaria brevibracteata* subsp. *icarica* on the Ikaria Island (Eastern Aegean)

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Abstract. The aim of this work is to highlight the phenotypic variability of *Scutellaria brevibracteata* subsp. *icarica* on the Aegean Island of Ikaria. While studying the various subpopulations of *S. brevibracteata* subsp. *icarica* found on the Island at different altitudes and in different locations, it has been found that the phenotypic expression of this species is strongly linked to the type of substrate and to terrestrial and atmospheric water sources. In particular, the subpopulation from the southwestern part of the Island that grows on granite soil has manifested several unique features that clearly distinguish it from the other Ikarian subpopulations, and which could justify assigning it to a particular ecotype.

Key words: bedrock composition, phenotypic variability, *Scutellaria brevibracteata* subsp. *icarica*, water sources

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Introduction

Scutellaria is one of the largest genera of the *Lamiaceae,* with 400–500 species worldwide. This genus predominantly occurs in the temperate regions and shows high species diversity mainly in the E Mediterranean and the Irano-Turanian Region (Paton 1990; Salimov & al. 2021). In the Balkan Peninsula, the genus *Scutellaria* is represented by two major complexes of the *S. albida* and *S. rubicunda* groups, two representatives of the *S. orientalis* group, and other distinct species. The *S. albida* group is characterized by tall and robust plants with large bracts, scutellum, and cauline leaves. Flowers are white or cream, usually with spots on the lower corolla lip, although this pattern may vary between populations. The ecology of these species is mainly linked to mesophilic habitats with an elevation range from sea level to mountainous areas (Bothmer 1985). Compared to the *S. albida* group, the *S. rubicunda* group has shorter plants, smaller bracts, cauline leaves and scutellum. The colour of the flowers is pale bluish purple, usually with purple spots on the lower lip. The indumentum is highly variable. The species of this group are confined to higher mountainous regions in a more xeric habitat than the species of the *albida* group (Bothmer 1985). The range of *S. albida s.l.* extends from North Italy to North and Central Balkan Peninsula, North Ana-

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tolia and Crimea. In Greece, it mainly occurs in the eastern part of the mainland and on several islands. It is represented by the following taxa here: *S. albida* L. subsp. *albida*, *S. albida* subsp. *vacillans* (Rech. f.) Bothmer, *S. albida* subsp. *velenovskyi* (Rech. f.) Greuter & Burdet, *S. goulimyi* Rech. f., and *S. sporadum* Bothmer (Dimopoulos & al. 2018). The *S. rubicunda* group has a more restricted distribution than the *S. albida* group, occurring in West and Central Greece and on the East Aegean Islands, some of the Ionian Islands and Sicily. The *S. rubicunda* group comprises the following species: *S. rubicunda* Hornem endemic to Sicily; *S. brevibracteata* subsp. *icarica* (Rech. fil.) Greuter & Burdet occurring in the East Aegean Islands of Samos and Ikaria; *S. rupestris* Boiss. & Heldr. *s.l.* occurring on the Greek mainland and some islands. It is represented by eight subspecies: *S. rupestris* subsp. *adenotricha* (Boiss. & Heldr.) Greuter & Burdet, *S. rupestris* subsp. *caroli-henrici* Bothmer, *S. rupestris* subsp. *cephalonica* (Rech. f.) Greuter & Burdet, *S. rupestris* subsp. *cytherea* (Rech. f.) Greuter & Burdet, *S. rupestris* subsp. *olympica* Bothmer, *S. rupestris* subsp. *parnassica* (Boiss.) Greuter & Burdet, *S. rupestris* subsp. *rechingeri* Bothmer, and *S. rupestris* Boiss. & Heldr. subsp. *rupestris*. To these major groups, the equally complex *S. orientalis* L. group is added, present in the Balkans, Anatolia, Lebanon, and Iran. In Greece, it consists of two subspecies: *S. orientalis* subsp. *alpina* (Boiss.) O. Schwarz and *S. orientalis* subsp. *pinnatifida* J.R. Edm. In addition to these groups, there are also such distinct species as *S. alpina* L., S. *altissima* L., *S. columnae* All., *S. galericulata* L., *S. hastifolia* L., S. *hirta* Sm., and *S. sieberi* Benth (Dimopoulos & al. 2018).

Studies of the genus *Scutellaria* in Greece

The first extensive study of this genus in the Mediterranean area was that of Rechinger (1941), followed by further taxonomic studies with descriptions of additional taxa (Greuter & Rechinger 1967). Subsequently, Bothmer analyzed extensively this genus for several years, and the two critical major groups occurring in the Balkan Peninsula in particular: *S. albida* s.l. and *S. rubicunda* s.l. Bothmer carried out extensive biosystematic studies of both groups (Bothmer 1969, 1981, 1985, 1987, 1991) and not only of the morphological variability of wild and cultivated plants, but also via interpopulation crossing experiments. Bothmer observed a similar differentiation pattern in both *S. albida* and *S. rubicunda* groups, since local variation was present in both groups, giving rise to distinct populations or systems of populations in some restricted areas (Bothmer 1985, 1987). However, the morphological variation has been even more complicated in the *S. rubicunda* group, which makes taxonomic considerations very difficult. The species included in the *S. rubicunda* complex were distinguished by the following features: decumbent and basally branched plants; triangular, truncate, cordate or cuneate leaves with crenate to serrate margins, small bracts, much shorter than or seldom equalling the calyx, with acute or obtuse apex and entire margins; violet or purple corolla, seldom white; indumentum consisting of different types of glandular and eglandular hairs (Rechinger 1941). *Scutellaria rubicunda* and *S. rupestris s.l.* constituted a monophyletic group, but the former has been genetically differentiated due to geographical isolation. For this reason, the Sicilian form was treated as a separate species, *S. rubicunda* Hornem (Bothmer 1987; Greuter 1984). Even populations from the East Aegean Islands of Samos and Ikaria included in the *S. rubicunda* complex were found to be more closely related to the Anatolian species *S. brevibracteata* Stapf. than to the Greek forms and have been treated as *S. brevibracteata* subsp. *icarica* (Rech. fil.) Greuter & Burdet (Bothmer 1991). Rechinger was the first to argue that the Samos and Ikaria populations should be included with the Anatolian species *Scutellaria brevibracteata* Stapf. (Rechinger 1941) and, indeed, the crossing experiments carried out subsequently by Bothmer have outlined the strict sterility barriers between the Samian and Ikarian populations of *S. brevibracteata* subsp. *icarica* and the Central Greek populations of *Scutellaria*, highlighting their closeness with the Anatolian *S. brevibracteata* (Bothmer 1987).

Study area

Ikaria lies in the East Aegean and is located 10 km westwards of Samos and 23 km eastwards of Mykonos. It has an area of 255 km² and is rectangular in shape, with W-NW and E-SE axis directions. The mountain range of Atheras, with the tallest peak Efanos (1040 m a.s.l.), stretches 40 km from west to east and has a steep southern side with precipitous cliffs, and a flatter northern side. Ikaria has deep gorges carved out by its major rivers with permanent flow, Halaris and Myrsonas.

From a geological point of view, three tectonic units are recognized on the Island: 1) the non-metamorphic Fanari Unit, corresponding to a series of Miocene to Pliocene sandstones, conglomerates and ophiolitic molasses (Photiades 2002); 2) the Agios Kirykos Unit (formerly called the Messaria Unit by Kokkalas & Aydin (2013), consisting of alternating marble and metapelite layers, metamorphosed into greenschist facies; 3) the Ikaria Unit, composed of an association of metasediments, including micaschist, marble layers and minor metabasite occurrences.

Three main granitic intrusions are recognized on Ikaria: two small intrusions in Xylosyrtis (S-E) and Karkinagri (S-W), and the large Raches intrusion. The western half of the island is composed of Raches granites from the Miocene era. This type of granite of calc-alkaline composition belongs to the Miocene magmatic arc of potassic plutons, parallel to the Hellenic Trench (Altherr & al. 1982). Mineral assemblage consists of feldspar phenocrysts, zoned plagioclase, quartz, biotite and hornblende, with accessory phases such as red allanite, apatite, sphene, titanomagnetite, zircon, tourmaline or garnet (Laurent & al. 2015) (Fig. 1).

Material and methods

The specimens used for this study were collected during three research sessions in August 2018, August 2021 and late June 2022, and have been stored in the first author's personal herbarium. Samples of *Scutellaria* were collected by the authors from several sites

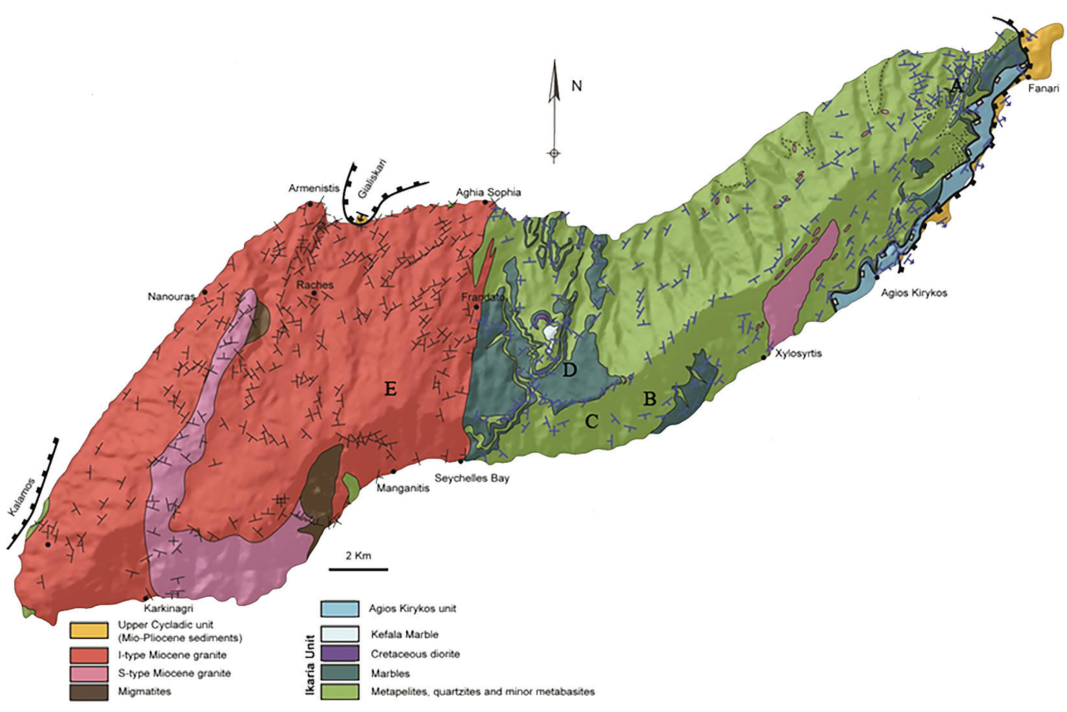

Fig. 1. Geological map of Ikaria (modified by Laurent & al. 2015), with indication of the collection sites: A = Perdiki; B = Vaoni; C = Plagia; D = Koskina; E = Megalophos, Selladia, Zizokabos.

from different altitudes, microclimates and substrates, listed here: Perdiki 380 m (northeast) limestone and marble; Koskina 600 m (centre) limestone and marble; Vaoni 200 m (south - centre) metamorphic rocks (metapelites, quartzites and metabasites); Plagia 200 m (south - centre) metamorphic rocks (metapelites, quartzites and metabasites); Megalophos, Selladi, Zizokabos 700-883 m (southwest) granite and granodiorite. For the study of *Scutellaria brevibracteata* subsp. *icarica,* the following literature was used: Rechinger (1941, 1944), Bothmer (1969, 1981, 1985, 1987, 1991), Edmondson (1982), Greuter (1984), Christodoulakis (1996). Information regarding the distribution of the genus *Scutellaria* in Greece has been extracted from Strid (2016) and the Flora of Greece web database (Dimopoulos & al. 2018). The Lund (LD) Herbarium database (https://www.biomus.lu.se/en/botanical-collections) was consulted for examination of the stored specimens of *Scutellaria brevibracteata* subsp. *icarica* collected on Ikaria and Samos (last access 01/10/2022). Examination of the main morphological features (such as indumentum, size and shape of calyx, corolla and leaves for identification) was carried out using a binocular stereomicroscope. The main information on the geology of Ikaria was extrapolated from Laurent & al. (2015). Place names mentioned in the text follow the map of Ikaria produced by the Terrain Cartography Group (2016).

Results and discussion

Scutellaria brevibracteata subsp. *icarica* on the Ikaria Island shows a high degree of variability in ecology and morphology (habitus, indumentum, size of stems, leaves and inflorescence), as already was pointed out by Rechinger (1941) and Bothmer (1969, 1981, 1987) in relation to altitude. At first, Rechinger distinguished to distinguish the two populations of *S. brevibracteata* from Samos and Ikaria. He described for Ikaria *Scutellaria icarica* Rech. fil., subsequently reduced to a subspecies of *S. rubicunda* Hornem (*Scutellaria rubicunda* subsp. *icarica* (Rech. fil.) Rech. fil.), and for Samos *Scutellaria rubicunda* subsp. *samia* Rech. fil. (Rechinger 1941). The distinction between the populations of the two islands arose from the material collected by Rechinger on Ikaria on Mt. Atheras (950 m). At that altitude, a low-growing form of *Scutellaria* occurred and, indeed, specimens collected later by Runemark and Snogerup from Mt. Atheras (1000 m) had the same habitus (LD 1472568) (Fig. 2). That low-growing form had led Rechinger to think that the Ikarian population had diverged from the Samian population. After some subsequent research that assumption was disproved, but it showed how the Ikarian specimens from lower altitudes resembled those of Samos (Bothmer 1969). The fact still remained, however, that Rechinger had detected re-

Fig. 2. Specimens of *Scutellaria brevibracteata* subsp. *icarica* collected by Runemark and Snogerup 1958 on Mount Atheras preserved in the Lund Herbarium (reproduced with the permission of the Director of the Biological Museum of Lund).

markable variability within the species.

Our research has also highlighted notable differences within this species on Ikaria, related to the type of substrate, water source availability and microclimate, and hence, the aim of this work has been to emphasize the phenotypic variability of *S. brevibracteata* subsp. *icarica* on the Aegean Island of Ikaria.

The ecologically adaptive value of leaf traits in various ecosystems is well known. Reduction in leaf and stem size and presence of a marked pubescence are the plant's response to a stressful environment. Small leaf size is related to the conductance of the leaf boundary layer to heat and water vapor transfer (Gates 1965), and may also be due to overall limitation of carbon in these types of environments (Niinimets & al. 2007). The small leaf size also reduces boundary-layer resistance and helps maintain favourable leaf temperatures and higher photosynthetic water-use efficiency under the combination of high solar radiation and low water availability (Parkhurst & Loucks 1972; Givnish & Vermeij 1976; Navarro & al. 2010); it is also more resistant to wind damage (Dolph & Dilcher 1980). Furthermore, marked pubescence, especially at the leaf level in very dry environments, is a strategy of the plants providing photo-protective mechanisms (Ehleringer 1984; Sanquist & Ehlelinger 1997) for reduction of transpiration (Jordan & al. 2008) and for increasing water-use efficiency by promoting condensation. Leaf surface features, such as hairs, may play a substantial role in dew harvesting, since dense trichome covers promote capillary condensation at lower values of relative humidity 'early condensation' and are able to store water (droplets) and delay the drying process of the leaf (Konrad & al. 2015).

Based on our observations, geology and geomorphology (bedrock composition and bedrock hydrology), and physical environment (incident radiation, moisture, temperature, and wind) are factors closely linked to variations in phenotypic expression of *S. brevibracteata* subsp. *icarica*. On the basis of our field observations, as well as on earlier collections on Ikaria done by Rechinger, Runemark, Snogerup, Bothmer, and Strid, it transpired that the species can be found in the northeastern section of the island and in the area following the ridge of the Atheras Mountain Range. However, it has been mainly found along the entire southern side, the rockiest part of the island, with less water and poor tree and shrub cover. *Scutellaria brevibracteata* subsp. *icarica* has not been found on the northern side of Ikaria, which is much richer in vegetation, thanks to the presence of permanent rivers. This presumes that the species tolerates high temperatures well and grows in south-facing environments with poor vegetation cover and almost no watercourses.

Scutellaria brevibracteata subsp. *icarica* grows on metamorphic, calcareous and granite substrates with scarce vegetation cover, at 200-1100 m a.s.l. It is a heliophilous species, which, however, seeks a certain degree of moisture in the cracks of step crevices, at the base of rocky cliffs, or under granodiorite boulders where there is higher humidity. Examination of the detected specimens has shown that the geological factors (such as bedrock composition) and physical factors (such as water availability), but not altitude have made the species change its morphology and phenology, namely in flowering time. Considerable phenotypic variability of the species has been observed linked to three different types of bedrock composition: metamorphic rocks, limestone rocks and granite. With regards to morphology, such as the habitus, *S. brevibracteata* subsp. *icarica* has shown best development on metamorphic rocks as opposed to limestone rocks, where it is reduced in size. On granite soil, it is low-growing, with a very underdeveloped floral axis, and poor in flowers. As for the indumentum, the hairs increase in terms of density and length in the specimens that grow on limestone rocks, reaching a noticeable increase in those that grow on granite. Finally, there are also some differences in the phenology of the species. Anthesis occurs from mid-April to June in the subpopulations linked to limestone rocks, and until July in those linked to metamorphic rocks. In the subpopulations growing on granite, the anthesis sets in later and lasts until the end of August. These data show that intraspecific variability is closely related to the type of substrate and availability of water sources. The three different ecological forms found in Ikaria are discussed below (Tab.1).

Phenotype linked to metamorphic rock. From a geological point of view, Vaoni and Plagia on the south-

Table 1. Comparison of the most relevant characters detected among the subpopulations of *Scutellaria brevibracteata* subsp. *icarica* in the Aegean Island of Ikaria, linked to three different kinds of substrates.

Substrate and sites of collection	Metamorphic rocks (Vaoni, Plagia)	Limestone rocks (Perdiki, Koskina)	Granite (Zizokabos, Selladi, Megalophos)
Habitus	Well developed plants, decumbent with several stems with ascending inflorescences (4-20 cm). Internodes in the inflorescence 4-10 mm.	Decumbent plants with short stems ascending to suberect, with few ascending inflorescences (2-8 cm). Internodes in the inflorescence 4-8 mm.	Decumbent plants with several stems, with few ascending inflorescences (1-5 cm). Internodes in the inflorescence 0.5-5 mm. Most of the plants that grow on this type of substrate are quite appressed, with minimum development of the floral axis.
Indumentum of the stem	Stem with dense short and long eglandular hairs (up to 1 mm)	Stem with dense short and long eglandular hairs (up to 2 mm)	Stem with very dense short and long eglandular hairs (up to 2.5 mm)
Indumentum of the floral axis	Inflorescence with short and long eglandular hairs mixed with dense glandular hairs, with small and large glands	Inflorescence with dense short and long eglandular hairs mixed with dense glandular hairs, with small and large glands	Inflorescence with very dense and very long eglandular hairs (especially on the calyx), mixed with dense glandular hairs, with small and large glands
Indumentum of the leaves	Leaves with short eglandular hairs on both surfaces, denser on the lower leaf blade especially along the ribs, with few glandular hairs	Leaves with very dense, short eglandular hairs on both surfaces, denser on the lower leaf blade especially along the ribs. Few glandular hairs are also present on the lower leaf blade.	Leaves with bent and very dense long eglandular hairs on both surfaces.
Size and appearance of the leaves	Leaves triangular or slightly cordate, with crenate or serrate margins, petiole 3-22 mm, leaf blade 8-28 × 4-20 mm	Leaves somewhat triangular with crenate margins, petiole 2-20 mm, leaf blade 4-15 × 3-15 mm	Leaves slightly triangular, cordate to rounded, with shallowly crenate margins, petiole 2-15 mm, leaf blade 2-16 × 2-14
Size of corolla	11	11	5-11 mm
Size of calyx in the fruit stage	5-7 mm	5-6 mm	4-5.5 mm
Size of bracts	2-7 × 1-4 mm	2-6 × 1-3 mm	2-3 × 1-2 mm
Seeds	1.2 × 1	1 × 0.8	1 × 0.6

ern coast of Ikaria are characterized by metapelites, quartzites and metabasites. Here, the climate is hot and windy, but ledges and ravines of cliffs occurring in this area offer microclimate suitable for the rooting of many species. At these sites, *S. brevibracteata* subsp. *icarica* grows in the crevices of vertical cliffs made up of metamorphic rocks with phrygana, in semi shade and with a certain moisture gradient. Its plants are well developed, with several long, creeping stems from which inflorescences up to 20 cm arise. Leaves are triangular or slightly cordate, with crenate or serrate margins (Plagia), and reach 28 mm in length and 20 mm in width. The stem has dense short and long eglandular hairs, and the inflorescence has long eglandular hairs mixed with glandular hairs with small and large glands. The leaves have short eglandular hairs on both surfaces, sparse on the upper leaf blade and denser on the lower, especially along the ribs. Internodes of the inflorescence reach 10 mm. The corolla reaches 11 mm, the tube is white/light purple, the upper lip is bluish-purple, the lower lip is whitish, with dark purple spots at the mouth. The flowering time is mid-April-July (Figs. 3, 4).

Phenotype linked to limestone rocks and marble. The specimens collected in Perdiki (northeast) and Koskina (centre) come from elevated areas composed of limestone and marble, with high exposure to strong winds. The plants observed at these sites grow at the base of limestone cliffs or in step crevices with phrygana, in semi shade. They are quite different from those that grow on metamorphic rocks, being smaller in size, with short stems and inflorescence up to 6-8 cm. They differ from the above-mentioned specimens in their somewhat triangular or cordate leaf shape (Koskina) and smaller size (15×15 mm); greater density of the short, eglandular hairs and greater length of the long eglandular hairs of the stem (up to 2 mm); greater pubescence of the indumentum of

Fig. 3. Specimen of *S. brevibracteata* subsp. *icarica* photographed in Vaoni on 27/06/2022.

Fig. 4. Specimen of *S. brevibracteata* subsp. *icarica* collected in Plagia on 2/08/2018 (specimen from Cattaneo's personal herbarium).

the leaves with very dense, short, scabrid eglandular hairs on both surfaces, which are more pronounced on the lower leaf blade, especially along the ribs. Finally, the internodes in the inflorescence reach 8 mm. The flowering time is mid-April - June. The small size of the plant, greater pubescence and slightly reduced phenology are probably the result of reduced water availability, along with the drying effect of the strong wind on the cliffs and rocks (Figs. 5, 6).

Phenotype linked to granite. The specimens collected in the southwestern part of Ikaria, in an area located between the Randis Forest and Melissa Mountain (Megalophos, Selladia, Zizokabos) and composed of Miocene granite, show several features that markedly differentiate them from the other subpopulations that occur on other substrates. This area of Ikaria is impressive for its outstanding granite boulders and for the absence of tree cover. There are harsh climatic conditions there, as summer is very hot and there are no permanent water courses, though dryness is partially balanced by the presence of surface aquifers and the low permeability of granite, which ensure a certain degree of moisture. The ecology of *S. brevibracteata* subsp. *icarica* there is quite different from the other above-mentioned subpopulations, since the species doesn't grow on rocks or cliffs, but on granite soil below granodiorite monoliths, a very low-nutrient substrate, where the herbaceous layer is not made up of phrygana, but of dense monospecific populations of *Pteridium aquilinum,* a species that grows on poor, acid or subacid soils (Fig. 7). Most plants that grow on this type of substrate are prostrate, with minimal development of the floral axis (up to 5 cm) (Figs. 8, 9) and inflorescence that is composed of few flowers with very short internodes (0.5-5 mm). Roots are extremely long and plants are very small, with short stems. The size of the stems, leaves, bracts, and calyx are reduced. Leaves are cordate, rounded or slightly triangular and rather small, with shallowly crenate margins. The size of the corolla ranges from 5 to 11 mm. The lower part of the tube and the upper lip is bluish purple, the lower lip is white or very pale pink, with or without dark purple veins. A notable difference in the other specimens of *S. brevibracteata* subsp. *icarica* collected on Ikaria is in the indumentum. The plants show a dense and woolly

Fig. 5. Specimen of *S. brevibracteata* subsp. *icarica* photographed in Koskina 28/06/2022.

Fig. 6. Specimen of *S. brevibracteata* subsp. *icarica* collected in Perdiki on 26/06/2022 (specimen from Cattaneo's personal herbarium).

pubescence especially on the petioles, where the eglandular hairs reach 2 mm, and on the stems with short and long simple hairs, up to 3 mm in length. The leaves have dense, short and very long, bent, eglandular hairs on both surfaces, with a thickened base. There are few glandular hairs, mostly arranged along the ribs and on the edges of the blade. The calyx shows very dense and long eglandular hairs, and the flowers also have a pubescence consisting of a mix of simple and glandular hairs on the upper lip. With regards to phenology, the flowering time of the subpopulations in this area lasts until late August, thus having a later anthesis, as compared to the subpopulations observed at the other locations on the island.

Conclusions

The present study shows that *S. brevibracteata* subsp. *icarica* occurs on the island of Ikaria in varying ecological forms related to different kinds of physical environment. Soil composition, bedrock hydrology and microclimate are among the factors most closely related to this intraspecific variability. This species' ability to exploit water from the rocks and from the atmosphere has allowed it to appear differently both from a morphological and a phenological point of view.

If the differences between the ecological forms of *S. brevibracteata* subsp. *icarica* that grow on metamorphic and limestone rocks are sometimes subtle, the differences between the subpopulations that grow on granite soil are more obvious, leading to the assumption that they are a new ecotype.

The specimens observed in Plagia and Vaoni show best development, thanks to the bedrock composition and the greater moisture availability. On the other hand, the specimens found in Koskina and Perdiki show a slightly different ecological form of *S. brevibracteata* subsp. *icarica*. The limestone rocks, which retain less water, along with the drying effect of the strong winds lead to less water availability for the plants and result in different morphological development and phenology of the species.

Megalophos, Selladia and Zizokabos host a subpopulation of *S. brevibracteata* subsp. *icarica* that

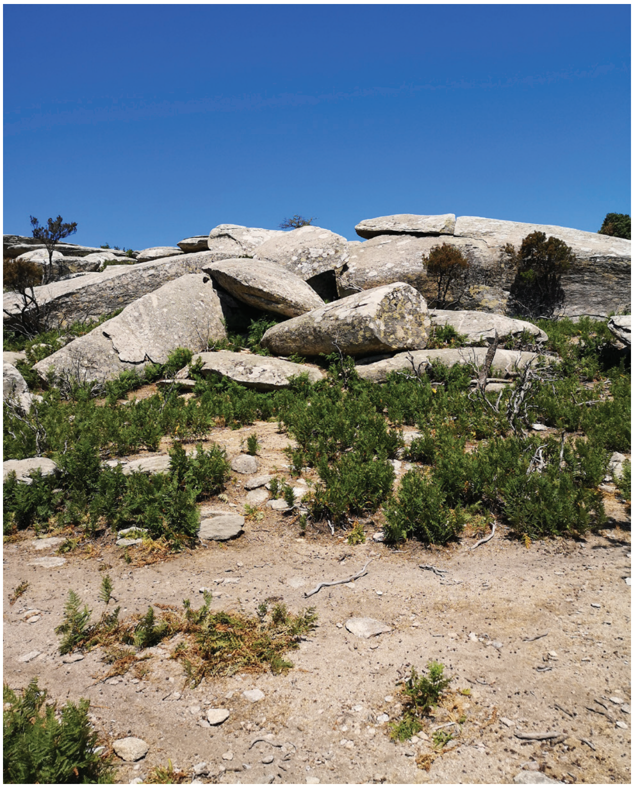

Fig. 7. Typical landscape of the southwest area of Ikaria with granodiorite boulders and populations of *Pteridium aquilinum*.

clearly stands out against the other Ikarian ecological forms, mainly in habitus (low-growing), smaller leaf, stem, calyx and bract size, and indumentum, which features a remarkable pubescence composed of very dense and very long glandular and eglandular hairs, mainly on the floral axis and on the leaves. Furthermore, the ecology and phenology of this subpopulation differs from the others in that it grows on granite soil and the anthesis lasts until late August. The absence of tree cover and watercourses make this area of the island extremely arid and inhospitable.

It is known that edaphic and climatic factors can promote variations in the phenotypic expression of some plant species, giving rise to a simple intraspecific variability. However, extreme environmental conditions linked to aridity and poor soil fertility, as is the case in the southwestern part of Ikaria, limit plant tolerance by exerting strong evolutionary pressures on plant functioning (Navarro & al. 2010). Hence, these harsh environmental conditions may have promoted a different ecotype perfectly adapted to this kind of habitat. The plant has changed its

Fig. 8. Low-growing form of *S. brevibracteata* subsp. *icarica* observed in Selladi.

Fig. 9. Specimens of *S. brevibracteata* subsp. *icarica* collected in Zizokabos on 25/06/2022 (specimen from Cattaneo's personal herbarium).

morphology to make the most of the terrestrial water sources, developing very long roots and growing in the shade of granodiorite monoliths, and taking advantage of atmospheric water by significantly increasing pubescence and reducing leaves and stems. For these reasons, this Ikarian subpopulation of *S. brevibracteata* subsp. *icarica* could be assigned to a particular ecotype.

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