Article

Fl. Medit. 30: 347-363
https://doi.org/10.7320/FlMedit30.347
Version of Record published online on 17 December 2020

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Contribution to the seed morphology of some Greek *Campanula* species of sect. *Quinqueloculares* (*Campanulaceae)*

Abstract

Liveri, E., Kalachanis, D., Bareka, P., Grammatikopoulos, G. & Kamari, G.: Contribution to the seed morphology of some Greek *Campanula* species of sect. *Quinqueloculares* (*Campanulaceae*) — Fl. Medit. 30: 347-363. 2020. — ISSN: 1120-4052 printed, 2240-4538 online.

The seed morphology of 16 Greek taxa of *Campanula* section *Quinqueloculares*, 14 of them are endemic to Greece, is studied using Scanning Electron Microscopy. Data on the size, shape, and colour of the seeds are provided and the seed coat morphology is described. The seed morphology is found to be relatively uniform except the seed coat. Two different patterns are described based on the type of striations on the seed surface. The seed coat morphology of the studied taxa is compared to the Turkish relatives of *C.* sect. *Quinqueloculares* highlighting the variation of the section. Overall, seed morphology was found to be an overlooked feature in Greek *Campanula* taxa. Our study sets, for the first time, a framework for the study of seed morphology in Greek *C.* sect. *Quinqueloculares* and additionally supports their complementary role in *Campanula* taxonomy and systematics.

Key words: *Campanula*, micromorphology, Scanning Electron Microscopy, seed coat.

Introduction

Campanula L. comprises ca. 420 species with circumboreal distribution (Lammers 2007). Eurasia, especially the area from Balkans to eastern Caucasus hosts most of the *Campanula* diversity (Tutin & al. 1976; Oganesian 2008; Castroviejo & al. 2010). The endemism hotspots for *Campanula* are located in Eastern Mediterranean region, Balkan Peninsula, Caucasus and Turkey (Damboldt 1978; Gagnidze 2005; Borsch & al. 2009). Greece represents an intriguing part of the Eastern Mediterranean diversity hotspot including ca. 96 *Campanula* taxa of which ca. 60 are Greek endemics (in Dimopoulos & al. 2013, 2020).

Over half of the Greek endemic *Campanula* taxa belong to *Campanula* section *Quinqueloculares* (Boiss.) Phitos (Liveri & al. 2019). In total, *C.* section *Quinqueloculares* includes ca. 39 species (ca. 47 specific and subspecific taxa) distributed in Greece and coastal Turkey (Phitos 1969, 2016) with the exception of *C. medium* L., growing as native in France and Italy (Castroviejo & al. 2010; Bartolucci & al. 2018), as well as *C. lyrata*

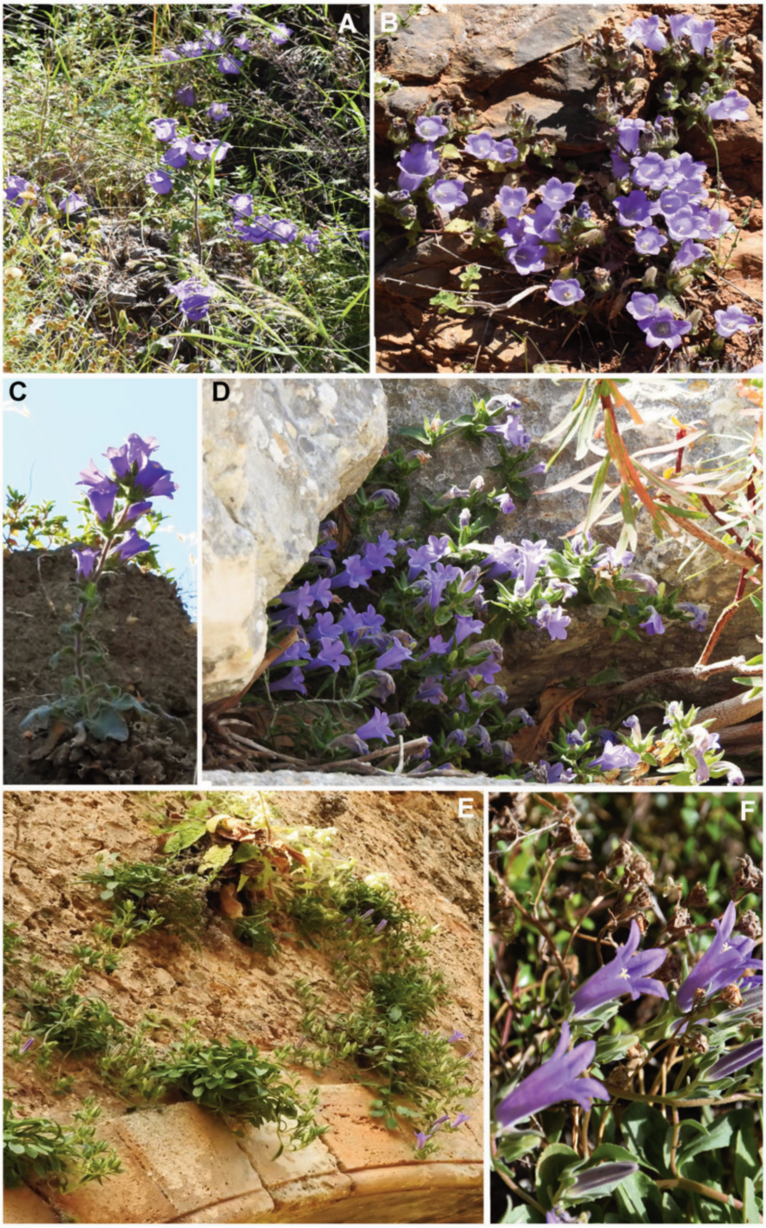

Fig. 1. Representatives of *Campanula* section *Quinqueloculares* from Greece: **A,** *C. pelviformis* growing at roadside banks of New National Road of Agios Nikolaos (Crete), 11.V.2017 and **B,** on rock fissures from Plaka (Crete), 11.V.2017; **C,** *C. nisyria* from Evangelistria (Nisyros), 8.V.2018; **D,** *C. hagielia* on the old walls of castle in Chalki, 5.V.2018; **E,** *C. saxatilis* subsp. *saxatilis* on old walls of Monastery Katholiko (Crete) and **F,** details of the flowers and capsules, 9.V.2017 (Photos by E. Liveri & V. Ketsilis-Rinis).

Lam. and *C. crispa* Lam., of which their distribution extends to the Caucasus and the Middle East (Al-Eisawi 1982; Aghabeigi 1985; Takhtajan 1995; Gagnidze 2005; Aghabeigi & Assadi 2008; Castroviejo & al. 2010).

The species of *Campanula* section *Quinqueloculares* are biennial (monocarpic), or more rarely perennial chasmophytes growing commonly on calcareous cliffs, rock fissures and crevices, old walls (e.g., *Campanula saxatilis* L. subsp. *saxatilis*; Figs 1E, F) (Phitos 1969), and occasionally in rocky places or roadside banks (e.g., *C. pelviformis* Lam.; Figs 1A, B) or schistose rocks cracks (Yıldırım 2013). They are characterized by five-locular ovary, a style with five stigmas, appendages more or less covering the ovary, and a capsule opening with five pores (Phitos 1965, 1969, 2016). Despite the epithet of the section (quinque + loculares = five locules), the number of the ovary locules may vary from three to five (Liveri & al. 2019).

The first mention of this group is found in De Candolle's classic monograph of *Campanulaceae*. De Candolle (1830) divided *Campanula* into two main sections based mainly on calyx morphology: *C.* sect. *Medium* A. DC. and *C.* sect. *Eucodon* A. DC. In his first mentioned section, one subgroup with five locules and five stigmas was recognized including 12 of the known *Quinqueloculares* species. Later, Boissier (1875) also recognized two sections within *Campanula*, almost the same with De Candolle's, but added capsule dehiscence to further define them: *C.* sect. *Medium* and *C.* sect. *Rapunculus* Boiss. For the first time, Boissier (1875) ranked a group of 14 species within *C.* section *Medium* as subsection *Quinqueloculares* Boiss. In 20th century, Charadze (1949) working largely on Caucasian *Campanula* species elevated *Quinqueloculares* to subgenus. Phitos (1963a, 1963b, 1964a, 1964b, 1965, 1969) studied extensively *Quinqueloculares* in Greece and Turkey and established the group as section (in Damboldt 1976). In *Flora of Turkey and the East Aegean Islands*, Damboldt (1978) retained *Quinqueloculares* at sectional level with 10 species, while Oganesian (1995) based on material from Caucasus placed again *Quinqueloculares* at the rank of subgenus.

Campanula section *Quinqueloculares* is characterized by remarkable morphological polymorphism (Fig. 1) as noted by Phitos (1963a, 1963b, 1964a, 1964b, 1965, 1969). His study is based on morphological, phytogeographical and karyological data resulting to the description of 22 new taxa (Phitos 2016; Liveri & al. 2019) and to the identification of three phytogeographically defined groups inside the section (Phitos 1965). Eddie & Ingrouille (1999) tried a phenetic approach to examine the high morphological polymorphism of *C.* sect. *Quinqueloculares* based on leaf and flower features corroborating the extreme morphological variability of the section.

In 21th century, the molecular methods gave new insights into the taxonomy and evolution of this group. The high polyphyly of *Campanula* has been confirmed in many studies (Borsch & al. 2009; Mansion & al. 2012; Crowl & al. 2016; Jones & al. 2017; Yoo & al. 2018; Xu & Hong 2020) presenting two major clusters of *Campanula*: a rapunculoid clade and a *Campanula* s. str. clade (Eddie & al. 2003; Roquet & al. 2008; Cellinese & al. 2009; Haberle & al. 2009). Several species of *C.* sect. *Quinqueloculares* have been included in some of these broader *Campanula* groups (e.g., Roquet & al. 2008; Borsch & al. 2009; Cellinese & al. 2009; Haberle & al. 2009; Mansion & al. 2012; Jones & al. 2017; Silakadze & al. 2019).

According to Liveri & al. (2020), the first phylogenetic study including all the species and subspecies of *C.* sect. *Quinqueloculares* revealed the polyphyly of the traditional section and recovered two strongly-supported clades, which include the majority of species.

Three species (*C. crispa*, *C. medium*, *C. pelia* Bedd.) of *C.* sect. *Quinqueloculares* are resolved outside the main clades, whereas four species from other *Campanula* sections [ie., *C. teucrioides* Boiss. from *C.* sect. *Rupestres* (Boiss.) Charadze] are nested within.

Seed characters, comparing to other plant organs, are considered less affected by changing environmental conditions (Zorić & al. 2010) and thus essential for classification (Barthlott 1981; Bonilla-Barbosa & al. 2000; Eriksson & al. 2000). Netolitzky (1926) was the first to notice that the structure of the seed coat is characteristic of a family in general and has taxonomic value. Takhtajan (1991) also pointed out that, even for phylogenetic correlations between families and genera, the structure of the seed coat might be important. Scanning electron microscopy data may be useful to delimit taxa at the species level, or sometimes as indicators of suprageneric groupings (Barthlott 1981, 1984; Behnke & Barthlott 1983), while variation in seed coat surface sculpturing among taxa could be correlated to ecological aspects (Barthlott 1981).

Studies on seed morphology of *Campanula* and *Campanulaceae* in general are limited. The first systematic studies of seed surface morphology in *Campanulaceae* were made by Eddie (1984, 1997) and concluded to correlation among testa patterns and ecology and may be useful for recognition at species level, but of little value at the generic level. The usefulness of seed morphology as a character in the systematics of *Campanulaceae* was studied in taxa from Europe (Geslot 1980), North America (Shetler & Morin 1986), India (Haridasan & Mukherjee 1988), Turkey (Akcin 2009; Alçitepe 2010), South Africa (Cupido & al. 2011). All the previous studies demonstrated the potential taxonomic value of seed morphology.

The seed morphology of *Campanula* sect. *Quinqueloculares* has been investigated in nine species from Turkey (Akcin 2009; Alçitepe 2010). Akcin (2009), who used *Campanula* species from several sections, states that micromorphological features of seed surface are useful in species delimitation and, also, suggests the broad investigation of the seeds of other *Campanula* taxa, in order to understand if such surface patterns are consistent and can differentiate taxa. Alçitepe (2010) examined the most of *C.* sect. *Quinqueloculares* in Turkey and concluded that seed coat morphology could be used as taxonomic trait in species delimitation but in combination with other morphological traits.

The current study aims to describe the seed morphology of some Greek *Campanula* species of sect. *Quinqueloculares* and evaluate their taxonomic significance.

Material and Methods

During 2016-2018 plant material of *Campanula* section *Quinqueloculares* was collected from Greece and stored in the herbarium of University of Patras (UPA). A list of the 16 collected taxa, collection localities and voucher numbers are provided in Table 1. Approximately 15 mature seeds of each taxon were analyzed. Seeds were taken from mature capsules collected in the field or from herbarium specimens. The seed samples were mounted on SEM stubs using double-sided adhesive tape and sputter coated with gold (Au). Coated seeds were observed with a Scanning Electron Microscope type JSM 6300 of the company JEOL in the Laboratory of Electron Microscopy and Microanalysis of University of Patras (L.E.M.M.). The terminology follows Barthlott (1981) and Simpson (2016). All the measurements were obtained from the SEM microphotographs.

Table 1. List of studied *Campanula* taxa (section *Quinqueloculares*) and specimen information. Greek endemics are indicated with an (*) asterisk.

Taxon	Specimen information
C. anchusiflora Sm.	Greece/Aegean Islands: Isl. Hydra, village Kamini, rock fissures, 10 m., 27 Apr 2016, *E. Liveri & V. Ketsilis-Rinis 189* (UPA 24629)
C. andrewsii subsp. ***hirsutula*** Phitos	Greece/Peloponnisos: Castle of Monemvasia, walls and rock fissures, 0-5 m., 21 May 2016, *E. Liveri & V. Ketsilis-Rinis 225*
C. carpatha Halácsy	Greece/Aegean Islands: Isl. Karpathos, Mertonas, rock fissures, 300 m., 14 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 271*
C. celsii subsp. ***carystea*** Phitos	Greece/Aegean Islands: Isl. Evia, *D. Phitos & G. Kamari 3825*
C. constantinii Beauverd & Topali	Greece/Aegean Islands: Isl. Evia, Mt. Xerovouni, *G. Kofinas s.n.*
C. cymaea Phitos	Greece/Aegean Islands: Isl. Evia, old walls, 115 m., Niochori-Vrysi, 6 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 294*
C. euboica Phitos	Greece/Aegean Islands: Isl. Evia, village Agios Georgios, rock fissures, 5 m., 5 May 2017, *E. Liveri, V. Ketsilis & N. Cellinese 292* (UPA 24639)
C. hagielia Boiss.	Greece/Aegean Islands: Isl. Rodos, Lindos, rock fissures, 5 m., 7 May 2018, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 306*
	Greece/Aegean Islands: Isl. Chalki, Castle of Chalki, old walls, 5-10 m., 5 May 2018, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 305*
C. kamariana Kyriak., Liveri & Phitos	Greece/Lakonia: south of village Itilo, castle of Kelefa, 17 Jun 2018, *E. Liveri & V. Ketsilis-Rinis 237*
C. lyrata subsp. ***icarica*** Phitos	Greece/Aegean Islands: Isl. Samos, Marathokampos-Kastania, 12 May 2018, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 307*
C. merxmuelleri Phitos	Greece/Aegean Islands: Isl. Skyros, Mt. Kochilas, 430 m., 7 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 291* (UPA 24649)
C. nisyria Papatsou & Phitos	Greece/Aegean Islands: Isl. Nisyros, village Evangelistria, 8 May 2018, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 303* (UPA 24650)
C. pelviformis Lam.	Greece/Aegean Islands: Isl. Crete, 42o km of New National Road Heraklio-Agios Nikolaos, roadside banks, 120 m., 11 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 295*
	Greece/Aegean Islands: Isl. Crete, Plaka-Vrouxas, rock fissures, 190 m., 11 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 296*

Table 1. continued.

***C. rupestris** Sm.	Greece/Viotia: Livadia, rock fissures, 200-300 m., 5 May 2016, *E. Liveri, A. A. Crowl & N. Cellinese 209* (UPA 24653)
C. saxatilis** L. subsp. ***saxatilis	Greece/Aegean Islands: Isl. Crete, Plakias beach, rock fissures, 0-20 m., 29 May 2016, *E. Liveri & S. Samaropoulou 229*
	Greece/Aegean Islands: Isl. Crete, Akrotiri Peninsula, old walls, 75 m., 9 May 2017, *E. Liveri, V. Ketsilis-Rinis & N. Cellinese 288* (UPA 24654)
C. topaliana** subsp. ***delphica Phitos	Greece/Phokida: close to Delphi, rock fissures, 450 m., 9 Apr 2017, *E. Liveri & V. Ketsilis-Rinis 258*

Results

All the studied taxa of *Campanula* sect. *Quinqueloculares* show small seeds varying in length from 0.52 to 0.92 mm and width from 0.26 to 0.43 mm. The smallest seed is observed in *Campanula euboica* Phitos both in length and width (Figs 3: 3A, 3B). The longest seed is observed in *C. cymaea* Phitos (Figs 3: 2A, 2B) whereas the widest in *C. topaliana* subsp. *delphica* Phitos (Figs 6: 2A,2 B). Generally, the seeds are glabrous, oblong to elliptic/obelliptic in outline, while the seed colour varies from light to dark brown.

The seed surface cells are elongated with straight and raised boundaries, relatively thick radial walls and an often-distinct lumen, which is essentially linear. These characteristics give a striate appearance to the seed coat. The surface of the outer cell wall (surface of the cuticle) exhibits a micro-ornamentation called striate. The nearness of striations on the seeds' surface varies among the taxa resulting to two seed surface sculpturing patterns: a) regularly striate and b) narrowly striate seed coat pattern. The first seed coat pattern (a) characterizes four species of *Campanula* sect. *Quinqueloculares*: *C. euboica* (Figs 3: 3A, 3B), *C. hagielia* Boiss. (Figs 3: 4A, 4B), *C. kamariana* Kyriak., Liveri & Phitos (Figs 4: 1A, 1B) and *C. nisyria* Papatsou & Phitos (Figs 5: 1A, 1B). The second seed coat pattern (b), which is the most common among the Greek taxa, characterizes eleven taxa: *C. anchusiflora* Sm. (Figs 2: 1A, 2B), *C. andrewsii* subsp. *hirsutula* Phitos (Figs 2: 2A, 2B), *C. carpatha* Halácsy (Figs 2: 3A, 3B), *C. celsii* subsp. *carystea* Phitos (Figs 2: 4A, 4B), *C. constantinii* Beauverd & Topali (Figs 3: 1A, 1B), *C. cymaea* (Figs 3: 2A, 2B), *C. lyrata* subsp. *icarica* Phitos (Figs 4: 2A, 2B), *C. merxmuelleri* Phitos (Figs 4: 3A, 3B), *C. pelviformis* (Figs 5: 2A, 2B), *C. rupestris* Sm. (Figs 5: 3A, 3B) and *C. topaliana* subsp. *delphica* (Figs 6: 2A, 2B). *Campanula saxatilis* subsp. *saxatilis* (Figs 6: 1A, 1B, 1C, 1D) shows both patterns in material from two different populations whereas *Campanula nisyria* (Figs 5: 1A, 1B) shows regular but evidently shallow striations on its seeds.

A summary of the results on seed morphology data of the studied taxa are given in Table 2.

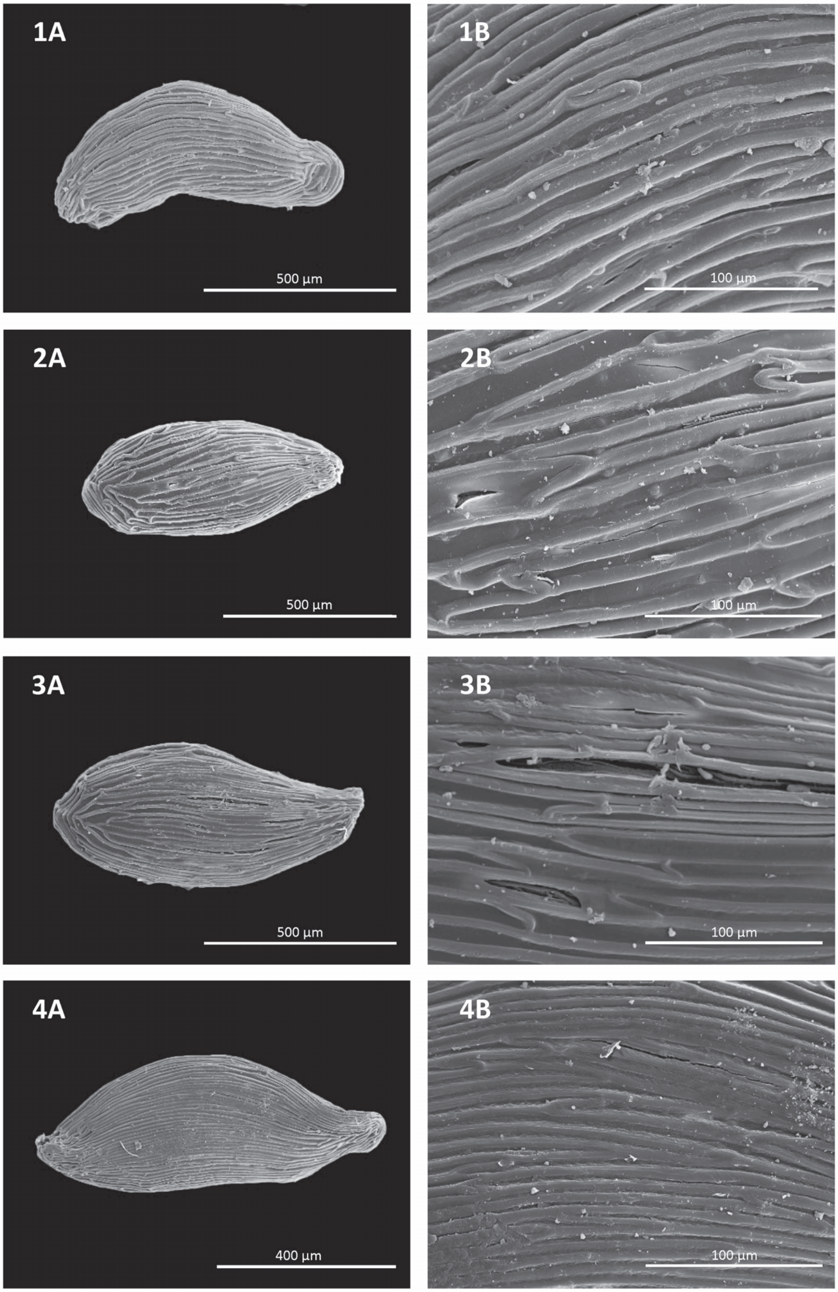

Fig. 2. Seed morphology (A) and seed coat surface (B) of the studied *Campanula* section *Quinqueloculares* taxa in SEM: **1A, B,** *C. anchusiflora*; **2A, B,** *C. andrewsii* subsp. *hirsutula*; **3A, B,** *C. carpatha*; **4A, B,** *C. celsii* subsp. *carystea*.

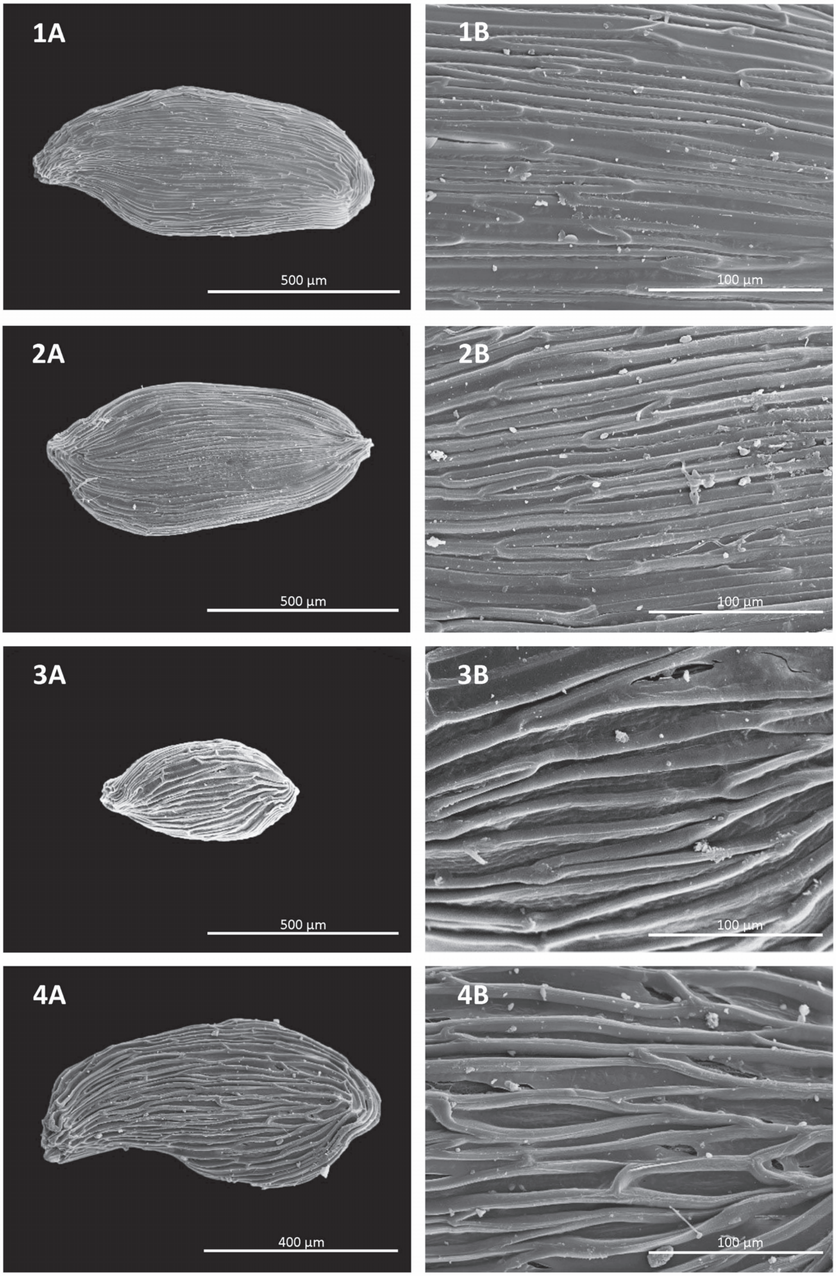

Fig. 3. Seed morphology (A) and seed coat surface (B) of the studied *Campanula* section *Quinqueloculares* taxa in SEM: **1A, B,** *C. constantinii*; **2A, B,** *C. cymaea*; **3A, B,** *C. euboica*; **4A, B,** *C. hagielia.*

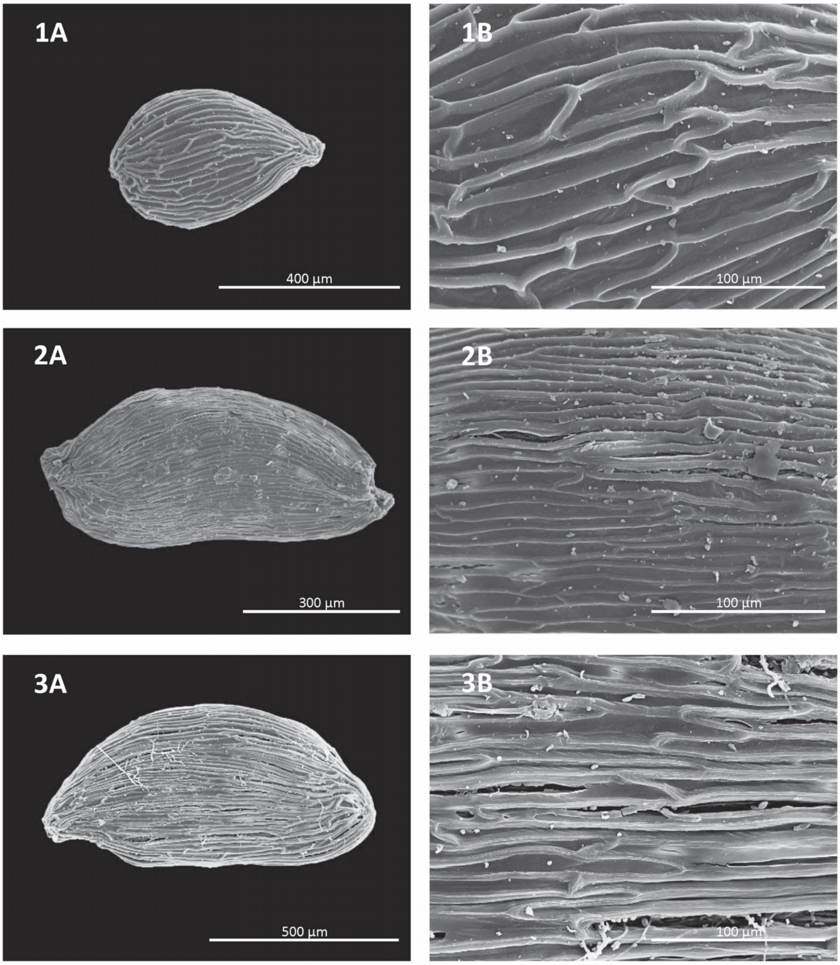

Fig. 4. Seed morphology (A) and seed coat surface (B) of the studied *Campanula* section *Quinqueloculares* taxa in SEM: **1A, B,** *C. kamariana*; **2A, B,** *C. lyrata* subsp. *icarica*; **3A, B,** *C. merxmuelleri*.

Discussion

In the current study, the seed morphology of 16 species and subspecies belonging to *Campanula* section *Quinqueloculares* from Greece are studied for the first time. In general, the seeds of *C.* sect. *Quinqueloculares* are small in size, oblong to elliptic/obelliptic varying in colour from light to dark brown. Although the seed coat morphology is striate in all investigated taxa, two different patterns related to the nearness of striation are revealed: a) regularly striate and b) narrowly striate.

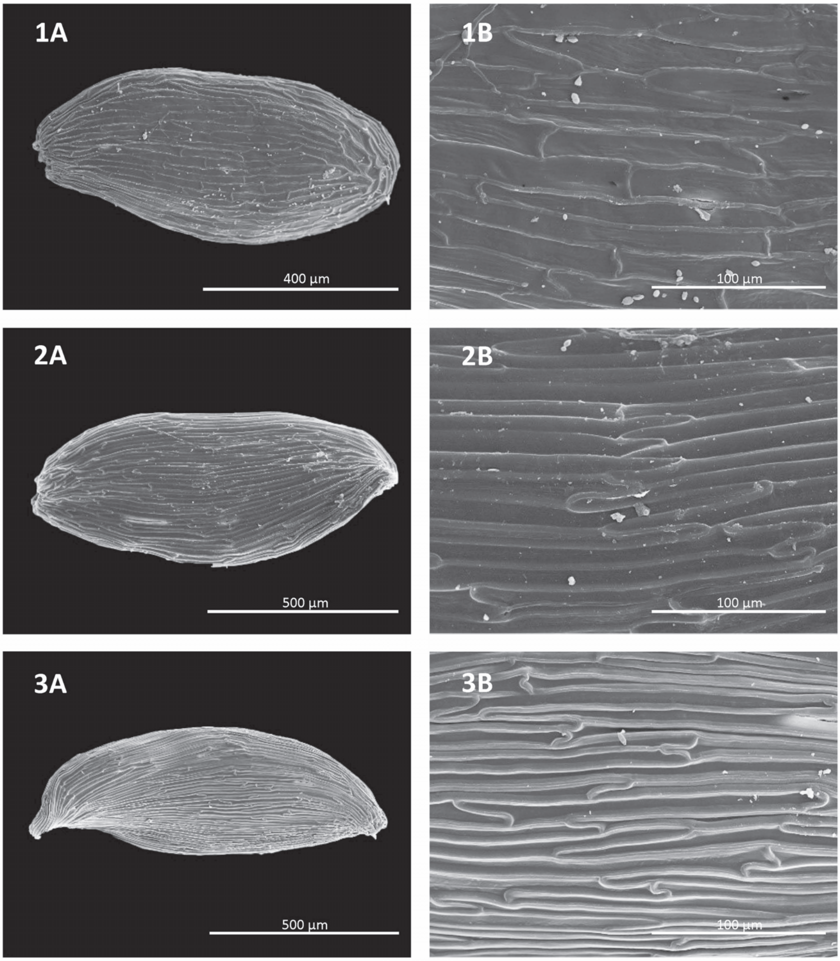

Fig. 5. Seed morphology (A) and seed coat surface (B) of the studied *Campanula* section *Quinqueloculares* taxa in SEM: **1A, B,** *C. nisyria*; **2A, B,** *C. pelviformis*; **3A, B,** *C. rupestris*.

The striate seed coat is common in *Campanula* and particularly in section *Quinqueloculares* from Turkey (Akcin 2009; Alçitepe 2010). This pattern has been recognized by Alçitepe (2010) as Type II including two subtypes (II-a and II-b). The two subtypes coincide with the presented two patterns (a) and (b) in our study. Most of the Turkish *C*. sect. *Quinqueloculares* belong to subtype II-a in contrast to the Greek taxa, which mostly belong to subtype II-b (Table 2). However, Alçitepe (2010) finds one more type of seed coat sculpturing characterized by weakly striate/wavy-striped radial walls presented only in one species, *C. tomentosa* Lam. According to Alçitepe (2010), *Campanula lyrata* subp.

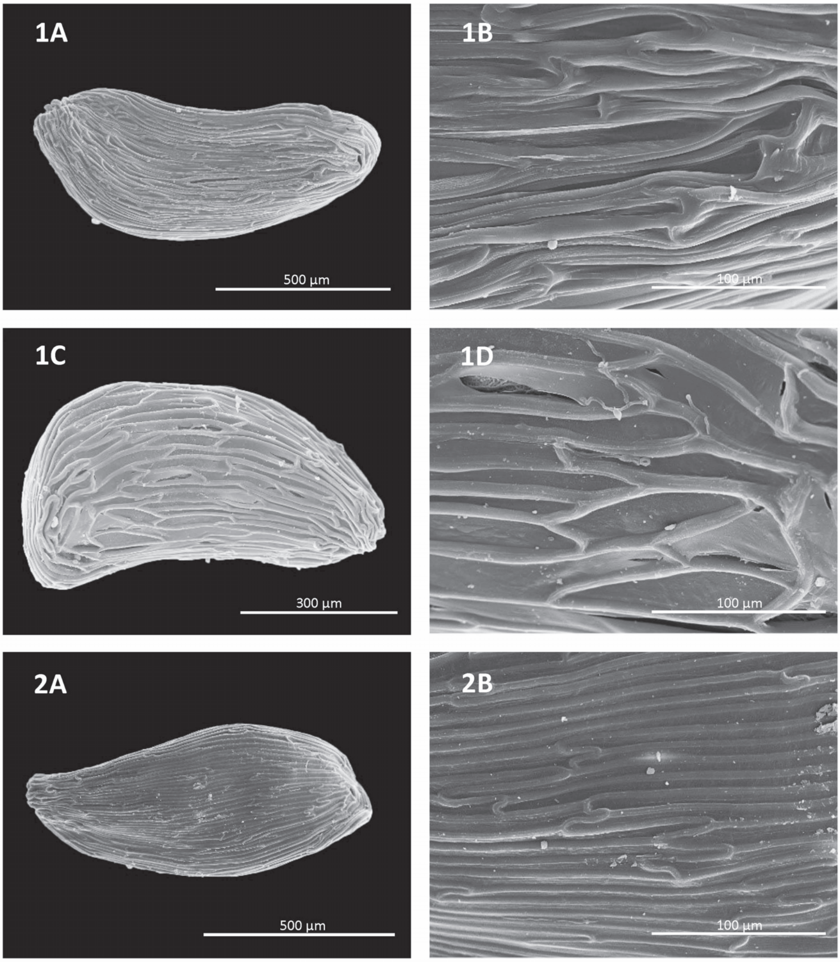

Fig. 6. Seed morphology (A, C) and seed coat surface (B, D) of the studied *Campanula* section *Quinqueloculares* taxa in SEM: **1A, B, C, D,** *C. saxatilis* subsp. *saxatilis*; **2A, B,** *C. topaliana* subsp. *delphica*.

lyrata belong to subtype II-a, but in our study *C. lyrata* subsp. *icarica* (Figs 4: 2A, 2B) falls into the second subtype presenting another difference between the subspecies. Akcin (2009) studies the seed coat morphology of Turkish *Campanula* from five sections belonging to two subgenera but includes only *C. lyrata* subsp. *lyrata* from *C.* sect. *Quinqueloculares* placing it in Type II without mentioning the subtype. Based on the microphotographs of his study (Akcin 2009), we can conclude that it belongs to the second subtype that is in accordance with Alçitepe's (2010) findings.

Table 2. Seed characters of the studied *Campanula* section *Quinqueloculares*. The mean value along with the Standard Deviation (SD) in parenthesis given for length (mm) and width (mm).

Taxon	Length	Width	Shape	Surface	Colour
C. anchusiflora	0.72 (0.12)	0.34 (0.02)	Elliptic to obelliptic	Narrowly striate	Light brown
C. andrewsii subsp. ***hirsutula***	0.70 (0.05)	0.27 (0.02)	Obelliptic to oblong	Narrowly striate	Brown
C. carpatha	0.75 (0.06)	0.39 (0.03)	Elliptic to obelliptic	Narrowly striate	Light brown
C. celsii subsp. ***carystea***	0.74 (0.05)	0.30 (0.03)	Elliptic to obelliptic	Narrowly striate	Brown
C. constantinii	0.87 (0.06)	0.36 (0.03)	Oblong	Narrowly striate	Brown
C. cymaea	0.89 (0.04)	0.43 (0.04)	Oblong	Narrowly striate	Brown
C. euboica	0.52 (0.05)	0.26 (0.04)	Elliptic	Regularly striate	Brown
C. hagielia	0.70 (0.04)	0.30 (0.02)	Oblong	Regularly striate	Light brown
	0.57 (0.03)	0.31 (0.02)	Elliptic	Regularly striate	Light brown
C. kamariana	0.56 (0.06)	0.31 (0.05)	Elliptic to obelliptic	Regularly striate	Brown
C. lyrata subsp. ***icarica***	0.65 (0.1)	0.30 (0.02)	Oblong	Narrowly striate	Light brown
C. merxmuelleri	0.88 (0.8)	0.39 (0.04)	Elliptic to obelliptic	Narrowly striate	Brown
C. nisyria	0.76 (0.03)	0.34 (0.03)	Oblong to elliptic	Regularly striate (shallow striations)	Dark brown
C. pelviformis	0.89 (0.08)	0.39 (0.04)	Oblong to elliptic	Narrowly striate	Brown
	0.54 (0.07)	0.29 (0.05)	Oblong to elliptic	Narrowly striate	Brown
C. rupestris	0.89 (0.06)	0.33 (0.02)	Oblong	Narrowly striate	Light brown
C. saxatilis subsp. ***saxatilis***	0.90 (0.12)	0.42 (0.05)	Oblong	Narrowly striate	Brown
	0.76 (0.11)	0.36 (0.03)	Oblong to obelliptic	Regularly striate	Brown
C. topaliana subsp. ***delphica***	0.92 (0.11)	0.41 (0.05)	Oblong	Narrowly striate	Brown

The studied material of *C.* sect. *Quinqueloculares* from Greece even if seems uniform concerning the size, shape and colour of the seeds, varies considerably in seed coat morphology giving further insights in species relationships. Our findings present the variation characterizing this section from micro-morphological point of view and provide also taxonomic interpretation in some cases. For example, we observe that the striation pattern may even differ within the same subspecies (e.g. the Cretan endemic *C. saxatilis* subsp. *saxatilis*; Figs 6: 1A, 1B, 1C, 1D) emphasizing the need for a more extensive study.

In the case of *C. hagielia* (distributed in East Aegean Islands and coastal Turkey) and *C. nisyria* (one-island endemic), which recently were considered synonyms (Strid 2016), the differences in seed coat sculpturing (Figs 3: 4A, 4B and Figs 5: 1A, 1B, respectively), combined with some other taxonomically important morphological features, support the distinction of these two species (Papatsou & Phitos 1975; Damboldt 1978). Concerning the morphology, *C. nisyria* is a long hirsute/scabrid plant with flowers sessile/subsessile, solitary or 2-3 together, forming a long spike-like inflorescence (Fig. 1C) whereas *C. hagielia* is softly hirsute/pubescent with terminal and axillary, pedicellate flowers (Fig. 1D). Additionally, molecular data place *C. nisyria* more closely related to other Turkish endemics (ie., *C. iconia* Phitos and *C. sorgerae* Phitos) than to *C. hagielia* (Liveri & al. 2020).

In general, the studied material of *C.* sect. *Quinqueloculares* from Greece and Turkey show similarities concerning seed morphology (size, shape, colour). However, the seed coat pattern shows some differences among Greek and Turkish representatives. Firstly, the weakly striate/wavy-striped seed coat is observed in the Turkish endemic *C. tomentosa* and also the newly described endemic Turkish species *C. phitosiana* Yıldırım & Şentürk (Yıldırım & al. 2020). For the rest of *C.* sect. *Quinqueloculares* species, the striate seed coat pattern predominates. However, the seed coat striation of *C. mugeana* Yıldırım shows transition between the weakly striate/wavy-striped seed coat and prominent striate seed coat patterns (Yıldırım 2013). Although, the most common pattern in Turkey is regularly striate (noticed in more than the half studied taxa), whereas the narrowly striate seed coat pattern is observed for nearly 70% of the studied taxa from Greece.

Concluding, the taxonomic significance of seed morphology of *C.* sect. *Quinqueloculares* can be complementary to other morphological characters. However, its importance should not be underestimated. In contrast, the seed morphology of more *Campanula* species should be studied in order to have a better representation of the genus in Greece. The seed coat morphology probably could be the most useful micro-morphological character, compared to the other seed features, in taxonomy and systematics. Nevertheless, the first necessary step is to broaden our knowledge on seed characteristics.

Acknowledgements

The current study is part of the PhD of the first author and is financed by the General Secretariat for Research and Technology (GSRT) and the Hellenic Foundation for Research and Innovation (HFRI). We would like to thank Dr. A. Seferlis for his technical support on SEM and V. Ketsilis-Rinis for his assistance in the field. Finally, we are grateful to Prof. Emeritus D. Phitos for his invaluable support.

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