

Fig. 1. A-D. Shape of caulin leaves – A-B: *S. integrifolia* subsp. *greuteri* (K. Persson, 5.4.1985) – A: lower caulin leaf; B: upper caulin leaf. – C-D: *S. sedoides* subsp. *rundmarkii* (Oxelman & Tollsten 1195) – C: lower caulin leaf; D: upper caulin leaf. – E-I. Shape of gonophores and capsules – E: *S. sedoides* subsp. *sedoides* (Oxelman 2216); F: *S. pentelica* (Oxelman 2215); G: *S. haussknechtii* (Oxelman & Tollsten 1451); H: *S. laconica* (Oxelman & Tollsten 1362); I: *S. integrifolia* subsp. *elaphonesiaca* (Jagel 48).



ancestor. The ranking decisions have been guided by pragmatic criteria, i.e. species rank has been assigned to taxa which can be fairly easily recognised by gross morphology. This is exemplified by *S. integriflora*, where the four subspecies form discrete geographic and phylogenetic entities (Oxelman 1995). Three of the subspecies (subsp. *integriflora*, subsp. *greuteri*, and subsp. *elaphonesiaca*) are well separated by morphological characters, but subsp. *lidenii* is very similar to subsp. *integriflora*.

From the above it is evident that no attention has been paid to the so called "biological" species concept. This concept has been applied in two very different contexts (Lidén & Oxelman 1989, 1990). Of these, one is concerned with the level of organisation (i.e. "gene pool continuum") and is simply irrelevant to taxonomy as it does not apply to the same hierarchy. The other stresses the crossability criterion as decisive for species delimitation. Although certainly not sufficient for grouping taxa into a taxonomic hierarchy, the crossability (or, rather, incompatibility) criterion could be used for ranking entities into species (Mishler & Donoghue 1982). However, the results of artificial crossings made in this group indicate that vital F<sub>1</sub>-progeny can be obtained with many different taxon pairs as parents. Most taxa covered in this study have narrow geographic distributions and sympatry is a rare phenomenon. Adoption of the incompatibility criterion would thus result in very broad species definitions, with loss of much information.

#### 4. Morphology of the *Silene sedoides*-group

##### Habit

An annual life cycle characterizes all taxa. As in most annuals in *Silene*, the main shoot terminates with a cyme, which is the first inflorescence appearing on the plant. Several axillary shoots are usually produced, especially if the plant is ascending. These shoots, which may comprise of one to several vegetative internodes, each terminate also in an inflorescence. Material cultivated in the greenhouse from seeds of *S. haussknechtii* (Oxelman & Tollsten 1451), however, produced non-flowering and flowering shoots simultaneously. This indicates that *S. haussknechtii* is a winter annual.

##### Indumentum

All taxa in the group possess multicellular hairs on most of their green parts. These hairs are often glandular. A progression can be observed from glabrous cotyledons to sparsely hairy basal leaves to rather densely hairy inflorescences.

##### Leaves

Fleshy or succulent leaves characterize all members of the group. Fleshy leaves are defined as flat but soft (although fragile) and juicy. Succulent leaves, present only in *S. sedoides*, are thicker and more rounded in cross-section.

The leaf shape shows a gradual progression from spatulate in basal leaves to obovate in cauline leaves. The taxa differ in the position of the stem region, in which this change occurs and in the shape of the terminal leaves (Fig. 1A-D). In *S. integriflora*, the transformation from spatulate to obovate leaves occurs relatively early and the terminal leaves are usually ovate. The other species usually have obovate or oblong terminal leaves. Small, depauperate specimens of all taxa have less developed "petioles".

##### Inflorescence

The inflorescence is a compound dichasium with more or less unequal branching. In *S. sedoides* subsp. *sedoides*, the branching is sometimes entirely monochasial. The terminal



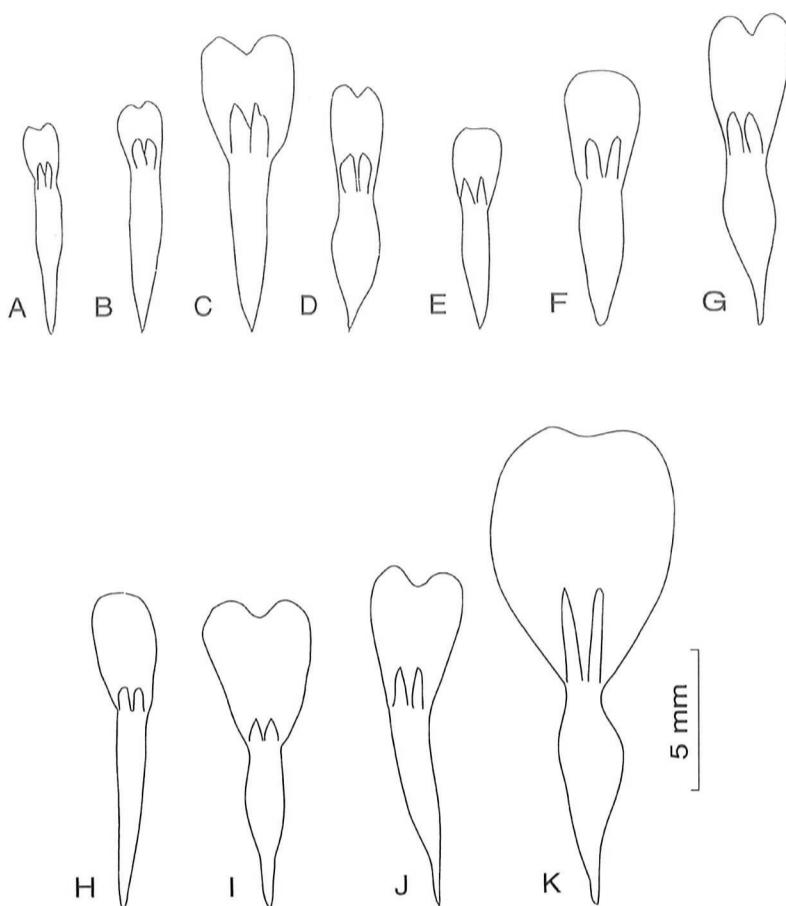


Fig. 2. Shape of petals – A: *S. sedoides* subsp. *sedoides* (Oxelman 2216); B: *S. sedoides* subsp. *sedoides* (Oxelman 2212); C: *S. sedoides* subsp. *runemarkii* (Oxelman & Tollsten 1195); D: *S. aegaea* (Oxelman 2214); E: *S. pentelica* (Oxelman 2217); F: *S. haussknechtii* (Oxelman & Tollsten 1451); G: *S. laconica* (Oxelman & Tollsten 1362); H: *S. integriflora* subsp. *elaphoneisiaca* (Jagel 48); I: *S. integriflora* subsp. *greuteri* (K. Persson, 5.4.1985); J: *S. integriflora* subsp. *lidenii* (herbarium material, Oxelman et al. 2117); K: *S. integriflora* subsp. *integriflora* (Oxelman & Tollsten 1057).

inflorescence is easily identified in upright plants, but may be hard to discern in ascending plants producing many axillary shoots. The taxa presumably differ in the number of orders a single inflorescence is able to produce. For diagnostic purposes, however, this character is difficult to use, because it is greatly affected by plant age and environmental conditions.

#### Flowers

Calyx shape varies from cylindrical to narrowly obconical or narrowly clavate in flower. The ripening capsule often enlarges the calyx to a clavate outline. The calyx teeth have



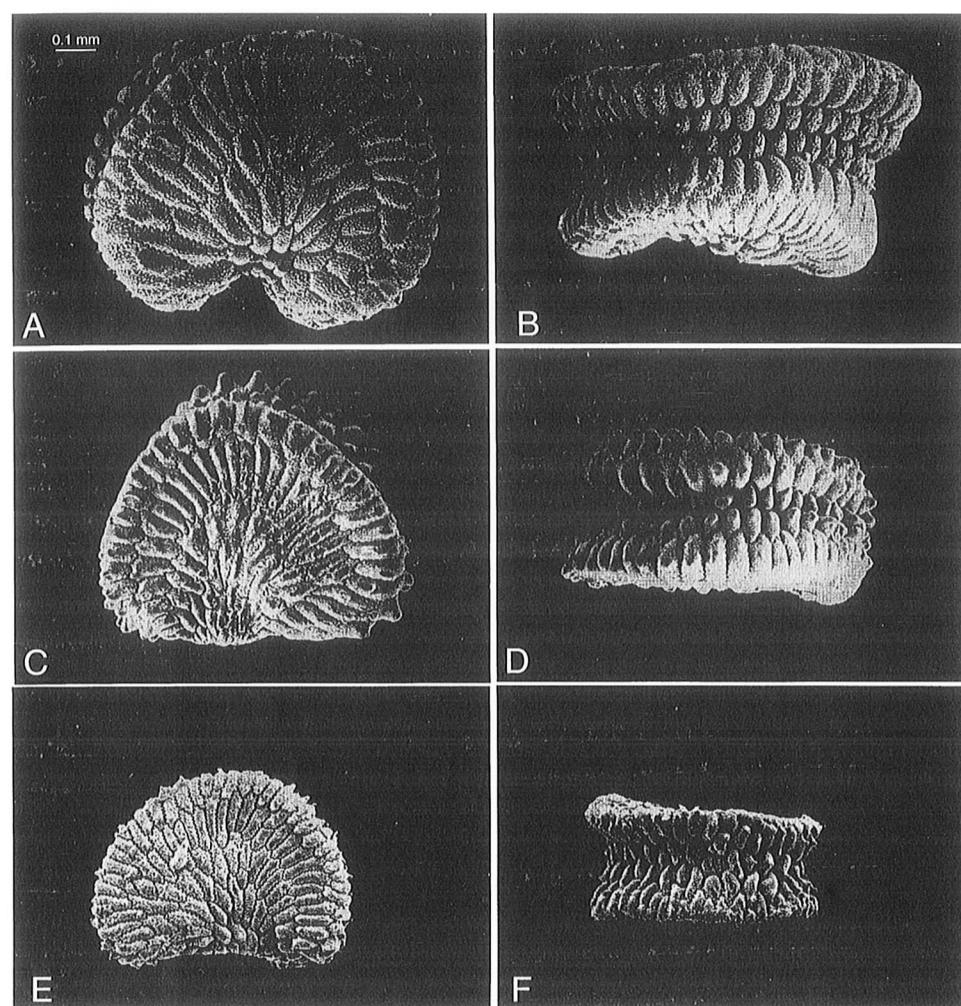


Fig. 3. Seeds – A-B: *S. integrifolia* subsp. *integrifolia* (Oxelman & Tollsten 389); C-D: *S. haussknechtii* (Hartvig et al. 6742); E-F: *S. pentelica* (Stamatiadou 18894).

membranous margins and the shapes of these margins appear to be unequal in a regular way, leading to a zygomorphic shape of the calyx. Whether these margins are entire or ciliate-pubescent is of taxonomic significance within the group.

As in many *Silene* taxa, some flowers have reduced male organs. These female flowers have shorter gonophores and calyces and smaller petals than hermaphrodites (Coode & Cullen 1967, Bocquet 1968, Meusel & Werner 1978–1979). On the other hand, the gynoecium in female flowers can be larger than in hermaphrodite flowers. The outlines of petals and coronal scales are of taxonomic significance in the group; some of the variation is shown in Fig. 2.



#### Capsule

The ovary has three carpels and three basal dissepiments. The capsule is membranous, i.e. soft and translucent, in *S. sedoides* and semimembranous in *S. aegaea*. All other taxa have firm and opaque capsule walls. In hydrated condition, the capsule shape is oblong or (narrowly) ovoid (Fig. 1E-I). The dry capsule dehisces with six recurved teeth.

#### Seeds

The seeds are reniform with flattened lateral faces and a dorsal furrow. Often the dorsal testa cells have mamillae or tubercles. Fig. 3 shows the main seed types. Testa cell margin shape, a character utilized by Melzheimer (1977), appears to be of little importance in the *S. sedoides* group.

#### 5. Breeding systems and reproductive biology

The flowers are normally protandrous and bisexual. According to both field and greenhouse studies (Oxelman 1990), the protandry is sufficient for preventing autodeposition of pollen on the stigma only in *S. integriflora* subsp. *integriflora*. The degree of protandry, defined as the number of days from anther dehiscence to the exposure of the stigmatic surface, varies from an almost simultaneous onset of the male and female phases in some flowers of *S. sedoides* subsp. *sedoides* to four days in *S. integriflora* subsp. *integriflora*, where the male and female phases are as a rule completely separated. All taxa are self-compatible, and no reduction in seed germinability or plant vigour has been observed over several generations of inbreeding in any of the taxa. In an experimental study in the greenhouse, no significant difference in seed production or germinability between *S. integriflora* subsp. *integriflora* seeds sired from self- and cross-pollinations was found. Female flowers did, however, have a slightly higher seed production. This pattern has also been confirmed by field experiments (Oxelman 1990). It is reasonable to surmise that self-pollination plays a significant role in the taxa discussed in this study.

#### 6. Phylogeny and phytogeography

Although the *Silene sedoides*-group appears well defined, its sister-group relationships are more obscure. The most probable sister-group is the *S. insularis*-group (including *S. insularis* Barbey, *S. salamandra* Pamp., *S. delicatula* Boiss., and *S. cryptoneura* Stapf) occurring in the SE Aegean and SW Anatolia. Morphologically, these species share the glandular hairs, general petal form, and inflorescence type with the *S. sedoides*-group. This relationship is, however, only weakly supported by rDNA sequences (Oxelman & Lidén 1995).

The Greek mainland and the islands of the Aegean Sea is a centre both in diversity and abundance for the *Silene sedoides*-group. *S. sedoides* is more widely distributed but particularly common in the Aegean area. All taxa occur in virgin habitats (gravel, screes, etc.) at various altitudes up to the lower alpine zone, except for *S. sedoides*, which is restricted to the marine supralittoral zone.

The distribution of the genus *Bellium* L. (Webb 1976) is rather well correlated to that of the *Silene sedoides*-group. The annual *Bellium minutum* L., which has similar ecological preferences as *S. sedoides*, is common in the Cardaegean (H. Runemark, pers. comm.) and outside of Greece restricted to the S Italian islands of Pantelleria, Linosa, and Lampedusa (Webb 1976, Arrigoni 1982). A similar distribution pattern is also found in the *Fumaria macrocarpa*-group (Lidén 1986).



### 7. Taxonomy of the *Silene sedoides*-group

#### 7.1. *Silene* sect. *Sedoideae* Oxelman & Greuter, sect. nova

Plantae annuae, pilis multicellularibus saepe glanduligeris, sursum densioribus obtectae; caules ascendentes vel erecti; folia basalia spatulata, sub fructu saepius emarginata, caulina inferiora spatulata sursum obovata vel elliptica dein ovata. Flores in dichasiis saepe inaequalibus et in ramos monochasiales desinentibus digesti; dichasia terminalia cito evoluta, serius dichasiis axillaribus interdum pluribus aucta. Pedicelli erecti vel patuli, sub fructu calycem aequantes plures superantes. Calyx 5–17 mm longus, sub anthesi cylindricus vel obconicus vel subclavatus, maturitate cylindricus vel clavatus, 10-nervius nervis lateralibus indistinctis, dentibus hyalino-marginatis obtusis sed parte centrali herbacea acuta. Limbus petalorum albus vel roseus, integer vel emarginatus; coronae squamulae albae interdum roseo-marginatae vel rosae, inter se liberae, 1–2.5 mm longae. Staminum filaments glabra, antherae albidae vel violaceentes, inter unguis petalorum inclusae vel exsertae. Styli 3, inclusi vel exserti; capsula ovoidea vel oblonga, ore 6-dentato non constricta. Anthophorum (1–)2–7(–8) mm longum glabrum. Semina reniformia, faciebus planis vel subconvexis striato-rugulosis, dorso canaliculato, umeris obtuse vel acute angularibus; cellulae dorsales saepe mamillatae vel tuberculatae.

Typus sectionis: *Silene sedoides* Poir.

Annuals with an indumentum of multicellular, often glandular hairs, progressively denser upwards the shoot. Stems ascending to erect. Basal leaves spatulate, often withered in fruiting stage. Cauline leaves in a progression series from spatulate to obovate, elliptic or ovate. Branches of the dichasium more or less unequal, sometimes passing into monochasium. Terminal cyme appears first; axillary cymose branches often numerous. Pedicels erect or patent, usually 1–4 times as long as calyx in fruiting stage. Calyx 5–17 mm long, cylindrical to obconical or slightly clavate at anthesis, cylindrical to clavate in fruit, with 10 veins and indistinct secondary veins between them; green part of calyx teeth acute, hyaline marginal part obtuse. Petal limb white to pink, entire to emarginate. Coronal scales white, pink, or whitish with reddish margins, divided to the base, 1–2.5 mm long. Filaments smooth; anthers white or violet, included in or exserted from mouth of corolla. Styles 3, exserted from mouth of corolla or not. Capsule ovoid or oblong, not constricted at the mouth, opening by 6 teeth. Gonophore (1–)2–7(–8) mm long, glabrous. Seeds reniform with flat or slightly convex lateral faces and a dorsal furrow, striate-rugulose; dorsal ridges acute or obtuse, dorsal testa cells often mamillate or tuberculate.

#### 7.2. Key to the taxa recognized

1. Petal limb with a dark spot at the base; capsule membranous; basal leaves fleshy or succulent, subglabrous . . . . . 1. *S. sedoides*
- Petal limb without a dark spot at the base; capsule relatively firm and opaque, rarely semimembranous; basal leaves fleshy, sparsely hairy . . . . . 2
2. Capsule 6 mm long or more, oblong; caulin leaves obovate to ovate; anthers lilac; hyaline margin of calyx teeth smooth or shortly and sparsely hairy . . . . . 6. *S. integripetala*
- Capsule 6 mm long or less, ovoid or oblong; caulin leaves spatulate to obovate; anthers white or pale lilac; hyaline margin of calyx teeth ciliate-fringed and often glandular . . . . . 3
3. Petals entire, darker beneath; seeds brownish black, tuberculate . . . . . 4. *S. haussknechii*
- Petals emarginate or entire, paler beneath. Seeds greyish black, dorsal testa cells often mamillate . . . . . 4



4. Capsule slightly longer (<1.5×) than gonophore; uppermost internode of stem at least twice as long as subtending leaves; calyx narrowly clavate in flower; coronal scales usually inflated . . . . . 5. *S. laconica*
- Capsule distinctly longer (>2×) than gonophore; uppermost internode of stem less than three times as long as subtending leaves; calyx narrowly oboconical in flower; coronal scales usually not inflated . . . . . 5
5. Petals emarginate; seeds with obtuse ridges on back; capsule slightly membranous, narrowly ovate . . . . . 2. *S. aegaea*
- Petals entire; seeds with acute ridges on back; capsule relatively firm and opaque, oblong . . . . . 3. *S. pentelica*

### 7.3. Taxa recognized

- 1. *Silene sedoides* Poir., Voy. Barbarie 2: 164 (1789).**  
 Lectotype (designated by Talavera & Muñoz Garmendia in Anales Jard. Bot. Madrid 45: 431 (1989)); [N Africa (Tunisia or NE Algeria?)], Poiret (PLA; iso- G!, P!).  
 = *S. ramosissima* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 297 (1809) non Desf. (1798), nom. illeg. – Lectotype (designated here): [Greece, Kriti], “in rupibus maritimis Cretae”, Sibthorp (K!, iso- OXF).  
 = *S. sedoides* var. *laxa* Hausskn. in Mitth. Thüring. Bot. Vereins 5: 51 (1893) – Lectotype (designated here): [Greece, Peloponnisos], “Peninsula Methana”, 5. 1885, Haussknecht (JE!, iso- JE!).  
 = *S. sedoides* var. *pachyphylla* Hausskn. in Mitth. Thüring. Bot. Vereins 5: 51 (1893). – Lectotype (designated here): [Greece, Attiki], “Laurion ad Kamariza”, 10. 5. 1885, Haussknecht (JE!, iso- JE!).  
 = *S. sedoides* var. *pallescens* Vierh. in Österr. Bot. Z. 84: 145 (1935). – Lectotype (designated here): [Greece, Kriti], “Distrikt Sphakia, im Sande an der Küste nächst Hagios Paulos”, 8. 4. 1904, Dörfler 719 (JE!, iso- GB!).

Stems ascending. Basal leaves (0.5–)1–3(–4) cm long, subglabrous. Cauline leaves spatulate to (narrowly) obovate. Flowers in dichasial cymes passing into monochasia. Hyaline margin of calyx teeth usually with many, sometimes glandular hairs, rarely smooth. Petal limb white to pink, usually emarginate, rarely entire, with a dark spot at base, upright when becoming withered. Coronal scales obliquely triangular, sometimes dentate, white. Anthers white. Capsule twice to several times as long as the gonophore, narrowly ovate, membranous. Gonophore usually swollen when capsule mature. Seeds with flat or slightly convex lateral faces and rounded dorsal ridges; testa cells smooth or mamillate.

Flowering time: April to July.

Ecology: Rocky, stony and sandy places in the maritime supralittoral zone, rarely above this zone, and then a ruderal plant.

#### Key to the subspecies

1. Petal limb white or pink, 1–2(–3) mm long; calyx cylindrical in flower . . . . . 1a. subsp. *sedoides*
- Petal limb deep pink, 3–4 mm long; calyx narrowly oboconical in flower . . . . . 1b. subsp. *runemarkii*



1a. *S. sedoides* subsp. *sedoides* – Fig. 1E, 2A, 2B.

Stems 1–4(–12) cm long. Leaves usually succulent. Uppermost stem internode 1–2 times as long as subtending leaves. Flowers in cymes with dichasial branching in the lower 1–2 orders, then passing into monochasia. Lowest internodes of inflorescence 0.7–2.5 times as long as lowermost pedicel. Pedicels 5–7(–25) mm long, usually equalling or shorter than calyx in fruit, patent and upturned at apex in fruit. Calyx cylindrical in flower, cylindrical to slightly clavate in fruit, 5–7(–8) mm long. Petal limb white to pink, 1–2(–3) mm long, longer than broad, usually emarginate, rarely entire; coronal scales 0.7–1.5 mm long, white. Anthers 0.4–1.0 mm long, included in corolla tube. Gonophore 0.8–2.2 mm long. Capsule twice to several times as long as the gonophore. Seeds 0.5–0.6 mm wide.

Chromosome number:  $2n = 24$  (Malea peninsula, Vinglafia, *Runemark & Svensson* 48140 (LD); previous counts: Damboldt & Phitos (1966); Kithira, *Phitos* 1527 (M!); Abdel Bari (1973); Mallorca, *Ferguson & Ferguson* 2236 (BM!); Montmollin (1986); Crete, Akroteri, *Montmollin* (UPA!)).

Distribution: Spread all over the E and C Mediterranean area (Fig. 4). A very common plant in Greece but apparently less common in the rest of its distribution area. The most western record from around Mascara in NW Algeria has not been confirmed since 1844.

## Representative specimens

Spain: Mallorca: Headland of Es Carregadir, S of Cala Ratjada [3°27'E, 39°43'N], cult. in Cambridge Bot. Gard., *Ferguson & Ferguson* 2236 (BM). – Menorca: Cabo Dartuch, wind-exposed rocky ground by the sea, 30. 5. 1969, *Dahlgren et al.* 873 (LD). – Girona: L'Escala, Calo Mongo in lapidosis calcareis juxta marem, 15. 5. 1978, *Molero & Pujadas* (G, M).

France: Bouches-du-Rhône, Marseille, sur la partie nord du col de la Madrague du Motredon, 7. 6. 1876, *Autheman* (G, GB, JE, LD, S, UPS).

Italy: Mainland: Etruria merid. marit. in calcar. lit. sept. promontorii Argentarii (ad Torre di Cala grande), 14. 5. 1883, *Forsyth* 1568 (LD); Apulia. Otrantu in scopolis prop. Nova Hellito [?], 28. 5. 1924, *Lacaita* (BM, GB); Japygia inter scopules ad Caput Leucœ, calcar., 22. 5. 1875, *Porta & Rigo* 294 (BM, C, G, GB, JE, K, M); maritime rocks near Gallipoli, 5. 1881, *Groves* 1568 (BM). – Sicily: Catania, 21. 5. 1844, *Nyman* 543 (C, S, UPS); 10 km S of Siracusa, rocky ledges above sea, 10 m, 12. 5. 1979, *Davis & Sutton* 62923 (BM); Franquerville, Palermo, *Lange* (C); Sferracavallo presso Palermo, 10. 7. 1840, *Heldreich* (G, P, S); Messina, *Spitzberger* (S); c. 30 km NE of Trapani, Castelluzzo, calcareous pavement overblown with sand, 22. 5. 1979, *Davis & Sutton* 63617 (BM). – Isole Egadi: Favignana, près de Puula Soltale [= Punta Sottile?], pelaires maritimes, 14. 6. 1983, *Charpin et al.* 18169 (G); Marettimo, in arenosis maritimis, 5. 1901, *Ross* (E, G, GB, K, JE, LD, M, S). – Lampedusa: 19. 4. 1884, *Rouy* 1574 (LD). – Linosa: 22. 4. 1884, *Rouy* 1573 (LD). – Pantelleria, 4. 1890, *Ross* (JE, M).

Malta: Cominotto, 20. 4. 1874, *Duthie* 41874 (BM, K); Chain Joffiah, 5. 5. 1872, *Wright* (herb.) 79 (K).

Croatia: Auf Felsen am Meerstrande auf der Halbinsel Lopad bei Gravosa, 4. 6. 1926, *Koch* (UPS); Lesina, *Novak* (LD); Istrien. Klippen bei Lusin piccolo, Kalk, 5 m, 28. 5. 1876, *Freyn* (JE, LD); ibid., 5. 1842, *Sendtner* 2497 (BM, K, S, UPS); Scoglio Pomo, 3. 6. 1911, *Ginzberger & Teyber* (BM, GB); ibid., San Andrea, 27. 5. 1876, *Spreitzenhofer* (UPS); Marinkova, Lagger (S, UPS); in Quarznus auf dem Scoglio Cosiach, 13. 5. 1804, *Anken* (BM, GB); Mt. Osero, am Felsen, *Noè* 120 (G, S).

Albania: Saranda, 25. 6. 1959, *Meyer* 3309 (JE); ibid., 9. 7. 1932, *Alston* (BM, K).



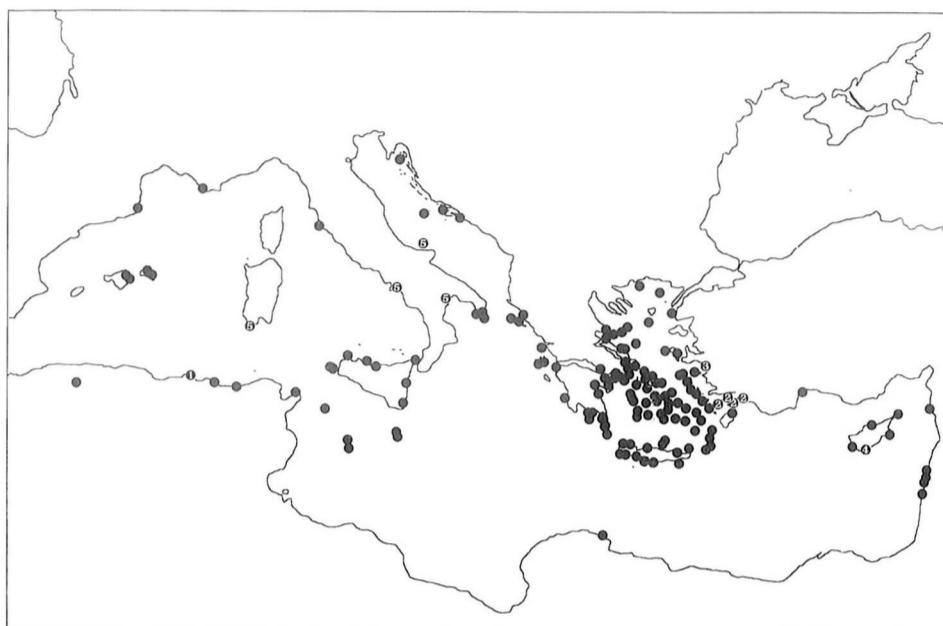


Fig. 4. Distribution of *S. sedoides* subsp. *sedoides* – Numbered dots represent literature records. 1 = Maire (1963); 2 = Carlström (1987); 3 = Coode & Cullen (1967); 4 = Meikle (1977); 5 = Jalas & Suominen (1986).

Greece: Ionian islands: Kerkira: Ile de Nido, 27. 5. 1891, *Bicknell* (BM, K, UPS). – Levkas: Cap Zuana, 15. 5. 1878, *Spreitzenhofer* (B). – Kefallinia: in campis ad 'Hagios Theodoros'. arenosis maritimis, 11. 5. 1926, *Bornmüller* 199 (BM, G, JE, LD, K, S). Peloponnisos: Akhaia: Ad litoream Kounoupeli dict., in saxosis maritimis, [21°21'E, 38°06'N], 30. 5. 1968, *Phitos* 9308 (UPA). – Ilia: In arenosis maritimis Liutzi, 1. 6. 1889, *Heldreich* (G). – Messinia: Agia Kiriaki, coastal sands, [21°35'E, 37°07'N], 20. 4. 1971, *Stamatiadou* 11975 (ATH). – Argolis: Cher. Methanon, in saxosis calc., 25. 5. 1885, *Haussknecht* (JE). – Korinthia: Lake Vouliagmeni, shore, [22°52'E, 38°02'N], 2. 6. 1986, \**Oxelman & Tollsten* 1385 (GB). – Arkadhes: 3 km N Tiros, rocky sea-shore on limestone, [22°50'E, 37°17'N], 27. 4. 1986, *Oxelman & Tollsten* 1045 (GB). – Lakonia: Malea Halbinsel, SW Küste Vinglafia, West, 20. 4. 1991, \**Jagel* 49 (B); ibid., saline and sand N of Elaphonisos, [22°58'E, 36°31'N], 2. 5. 1982, \**Runemark & Svensson* 48140 (LD); sandy saline in W part of Ormos Neapoleos, facing the island of Elaphonisos, [22°59'E, 36°31'N], 8. 5. 1985, \**Oxelman & Tollsten* 982 (GB); Agios Marinas, c. 5 km S of Agios Nikolaos, cliffs near the shore, [23°04'E, 36°28'N], 7. 5. 1985, \**Oxelman & Tollsten* 979 (GB); seashore cliffs about 2 km W of Agios Marinas, [23°03'E, 36°28'N], 2. 7. 1993, \**Oxelman* 2226 (GB); Elafonisos, Phrygana im Osten, 19. 4. 1991, *Jagel* 6 (MB); Akr. Taenaron, [22°29'E, 36°23'N], *Rechinger* 20110 (G). Central Greece: Magnisia: Paltsi, Xynovrisi, Sandstrand, 23. 5. 1972, *Raus* 481 (ATH). – Attiki: Just N of Laurion, rocky sea-shore, [24°03'E, 37°44'N], 10. 5. 1985, \**Oxelman & Tollsten* 1021 (GB); 2 km S Fokea, limestone cliffs near the shore, [23°55'E, 37°42'N], 10. 5.



1985, \**Oxelman & Tollsten 1009* (GB); Saronida, limestone cliffs near the shore, [23°54'E, 37°45'N], 10. 5. 1985, \**Oxelman & Tollsten 1007* (GB); in saxosis peninsulae Manychiae ad Pireum, 6. 1856, *Heldreich* (BM, C, G, JE, K, M, S, UPS).

W Aegean islands: Aiyna: Platakia, sea-shore, 13. 4. 1969, *Charitomidou* (B-Gr). – Andiki-thira: In litoreis, [23°18'E, 35°52'N], 6. 5. 1964, *Phitos & Rechinger 1504* (M). – Kithira: 1 km NE Agios Ioannis Theologos, dry river bed near the seashore, [23°03'E, 36°12'N], 22. 5. 1986, \**Oxelman & Tollsten 1176* (GB); 1 km W Moni Mirtidion, calcareous rocks, 10–30 m, [22°55'E, 36°12'N], 23. 5. 1986, \**Oxelman & Tollsten 1184* (GB). – Evvoia: Ditio pagi Platana, in loco xylithiotico, in arenosis maritimis, [24°07'E, 38°36'N], 11. 4. 1977, *Phitos 15263* (M, UPA); in Petalium ins. Xevonia, 6. 5. 1880, *Heldreich* (BM, GB). – Sporadhes: Alonisos, in rup., maritimis, 15. 5. 1965, *Phitos 2154* (M, UPA); Giura, [24°10'E, 39°23'N], 25. 5. 1896, *Leonis* (G, JE, LD); Kira Panagia, in declivibus insulae minutae (Reiser-insel) in sin. Agios Petros sitae, calc., 10. 5. 1927, *Rechinger 1034* (BM, LD); Skiathos, in arenosis litoreis, prope portum Linaria [23°29'E, 39°10'N], 8. 5. 1963, *Phitos 746* (M); Skopelos, ad muris urbis Skopelos, ad viam litream, [23°44'E, 39°07'N], 19. 5. 1965; *Phitos 2566* (M, UPA); Skiros, the island of Irinia, 19. 4. 1971, *Snogerup & Gustafsson 42527* (LD).

N Aegean islands: Samothraki: Paleopolis, coastal sands, [25°32'E, 40°31'N], 6. 6. 1970, *Stamatiadou 9424* (ATH). – Thasos: Vathy, in sand pockets among rocks of the sea shore, [24°40'E, 40°41'N], 25. 5. 1935, *Tedd 1575* (K). – Limnos: Ag. Evstratios, near the seashore 5 km E-ESE of the harbour, sand and eroded schist, 0–2 m, [25°02'E, 39°32'N], 23. 5. 1988, *Snogerup & Snogerup 5884* (B).

Kikladhes: Andros: S Gavron, 22. 4. 1984, \**Dahl 118 & 122* (GB); the islet of Stakala Vrakhos, c. 0.5 km S of Akra Gria [24°57'E, 37°54'N], 24. 5. 1968, *Snogerup & Bothmer 33168* (LD). – Kea: Ormos Poles, E of old Karthea [24°20'E, 37°33'N], 6. 6. 1968, *Snogerup & Bothmer 34442* (LD). – Kithnos: In litoreis, 17. 5. 1964, *Phitos 1782* (M). – Serifos: Ormos Avesalos, [24°26'E, 37°10'N], 28. 4. 1967, *Runemark & Bentzer 28055* (LD). – Milos: Spilia Varytini, 5. 7. 948, *Goulimyi* (K). – Sifnos: 2–3 km S of Akr. Khondropo, [24°41'E, 36°57'N], 12. 4. 1967, *Runemark & Bentzer 25312* (LD). – Naxos: Kavos Kouroupia, W of the village Velgon, maritime cliffs, 28. 6. 1993, *Oxelman 2220* (GB). – Paros: Antiparos, Despotiko, bay on the S-part, [25°00'E, 36°57'N], 21. 4. 1967, *Runemark & Bentzer 26943* (LD). – Siros: C. 1.5 km ENE-E Mitikas, 200–250 m, [24°55'E, 37°28'N], 30. 5. 1968, *Snogerup & Engstrand 33832* (LD). – Amorgos: About 3 km SW of Aegiali, roadside gravel by the Lamios valley, 50 m, [25°58'E, 36°53'N], 30. 6. 1993, *Oxelman 2222* (GB). – Thira: Athionos, Küstenfelsen, 20 m, [25°26'E, 36°23'N], 29. 9. 1988, *Raus 13394* (B). – Tinos: about 4 km SE the village Tinos, Ormos Agios Ioannis, cliffs and phrygana by the shore [25°13'E, 37°32'N], 6. 6. 1986, \**Oxelman & Tollsten 1408* (GB); ibid., ad litora maris, 15. 4. 1889, *Heldreich 1015* (BM, JE, K, LD, M, UPS).

E Aegean islands: Khios: Sandy shore near harbour, [26°09'E, 38°22'N], 30. 4. 1961, *Gathorne-Hardy 21/1961* (E). – Psara: Ad sinum Limnos litoris meridionalis, in arenosis litoreis, [25°36'E, 38°33'N], 21. 4. 1973, *Greuter 10886* (B-Gr, E, G). – Ikaria: Soil crevices in schistose cliffs about 0.5 km SE Evdilos, [26°11'E, 37°38'N], 26. 6. 1993, \**Oxelman 2212* (GB); ibid., in maritimis pagi Evdilos [mixed with *S. aegaea*], [26°11'E, 37°38'N], 29. 4. 1989, \**Christodoulakis 2826β* (UPA); therma, cliffs on the W side of the small harbour [26°18'E, 37°37'N], 26. 6. 1993, \**Oxelman 2216* (GB); prope pagum Armenistis, in arenosis maritimis, 30. 5. 1991, \**Christodoulakis 3241* (UPA). – Samos: About 4 km W of Agios Konstantinos, soil crevices on rocky beach, 25. 6. 1993, \**Oxelman 2210* (GB). – Kalimnos: Masouri, calcareous cliffs near the shore [26°56'E, 37°00'N], 14. 5. 1985, \**Oxelman & Tollsten 1030* (GB). – Leros: About 2 km WNW of Agios Marina, calcareous cliffs near the shore,



[26°48'E, 37°09'N], 12. 5. 1985, \*Oxelman & Tollsten 1022 (GB). — Rodhos: Sables maritimes près Rhodes, [28°14'E, 36°27'N], 14. 5. 1870, Bourgeau (E, G, G-BOIS, K, LD). — Karpathos: Küste gegenüber der Stomata-Halbinsel, 12. 5. 1981, \*Pleger 368 (B, B-Gr, UPA). Kriti: Kissamos, les sables, [23°39'E, 35°30'N], 12. 4. 1884, Reverchon (BM, G, GB, K, LD, UPS); peninsula Korikos, rocky beach by the lagoon S of Balos, 0–150 m, [23°35'E, 35°34'N], 21. 4. 1992, \*Oxelman et al. 2122 (GB); Chora Sfakion, in rupibus ad mare, [24°08'E, 35°12'N], 17. 6. 1969, \*Wängsjö & Wängsjö 3141 (LD); ins. Chrysax [= Gaidaronisi, 25°43'E, 34°52'N], 13. 5. 1942, Rechinger 13123 (LD, M, S); in saxosis calc. infra monasterium Toplu, [26°12'E, 35°14'N], 4. 5. 1942, Rechinger 12662 (BM, LD, M); Hagios Vasilis, Insel Paximadha (minor), 16. 5. 1904, Dörfler 999 (BM, GB).

Turkey: Adalia, in rupestribus secus mare, 7. 5. 1860, Bourgeau 50 (C, E, G, G-BOIS, JE, K); Bozcaada, ins. Tenedos in mani Ogaico prope litus, 8. 5. 1910, Ostenfeld 164 (C).

Cyprus: Cap St. André, am sandigen Strande, Sintenis 243 (G, G-BOIS, K, LD); Cape Greco, 2. 4. 1958, MacDonald 57, 100 (K); Kyrenia Castle, ditches, 5. 4. 1941, Davis 3047 (E, K); peninsula Karpasia, inter Ayios Thyrnos et Ronnas bay, 17. 4. 1974, Wängsjö & Wängsjö 5265 (LD); Reg. Famagusta, Ayia Napa, stenig mark med röd lera nära stranden, 11. 4. 1974, Wängsjö & Wängsjö 5142 (LD); Rizokarposo, 1. 5. 1922, Haradjian 224 (G, K, S).

Syria: Djoumeh, in rupibus calcareis juxta mare, 8. 6. 1932, Samuelsson 2194 (S); Lattakieh, in rupibus litoralibus, [35°47'E, 35°31'N], 17. 5. 1933, Wall (S).

Lebanon: Beyrouth, 7. 5. 1933, Gombault 2190 (S); Cap Roumeh N de Saïda, 21. 5. 1811, Gaillardot 164 (E, G-BOIS); Ras en Nakura, sand, 1. 5. 1913, Dinsmore 3267 (E, G, K, LD, S).

Libya: Derna, 14. 4. 1888, Taubert 376 (E, G, JE).

Tunisia: SW Kap Bon nordwestlich El Haouaria, Ghar El Kebir, Hänge um den antiken Sandsteinbruch, 18. 4. 1982, Poelt (M).

Algeria: La Calle, falaises maritimes, 18. 5. 1919, Clavé 2971 (G); ex Numidia [probably today's Algeria], Poiret (G, P); Mascara. Plain d'Egris, 5. 1844, D R [= Durieu?] (P).

**1b. *S. sedoides* subsp. *runemarkii* Oxelman subsp. *nova*** — Fig. 1C-D, 2C, 5.

Holotypus: [Greece, Peloponnisos], "Laconia, Maleas peninsula southernmost part, c. 5 km S of Velanidio", 1. 5. 1982, Runemark & Svensson 48061 (LD!, iso- LD!).

A subsp. *sedoides* pedicellis longioribus calyce sub anthesi obconico petalis majoribus saturate roseis (nec albis nec pallide roseis) antheris ex calyce protrudentibus differt.

Stems 2–15(–20) cm long. Leaves fleshy to succulent. Uppermost stem internode 1.5–3 times as long as subtending leaves. Flowers in uneven dichasial cymes of 3–6 orders. Lowest internodes of inflorescence 1.3–2.5 times as long as lowermost pedicel. Pedicels 4–25 mm long, usually equal to or longer than calyx in fruit, erect or patent. Calyx obconical in flower, slightly clavate in fruit, 6–8 mm long. Petal limb deep pink, 3–4 mm, about 1.5 times as long as broad, emarginate. Coronal scales 1.5–2.0 mm, pinkish white. Anthers 0.9–1.3 mm, slightly exserted from corolla mouth but not exceeding coronal scales. Gonophore 2–3 mm long. Capsule twice as long as the gonophore. Seeds 0.6–0.7 mm wide.

Chromosome number:  $2n = 24$  (southernmost part of Malea peninsula, Oxelman & Tollsten 1195 (GB)).

Distribution: Confined to coastal cliffs and gravel on the southernmost part of the Malea peninsula (Fig. 6). Forms transitional to subsp. *sedoides* occur at Velanidio only a few km N on the E coast (Oxelman & Tollsten 967).



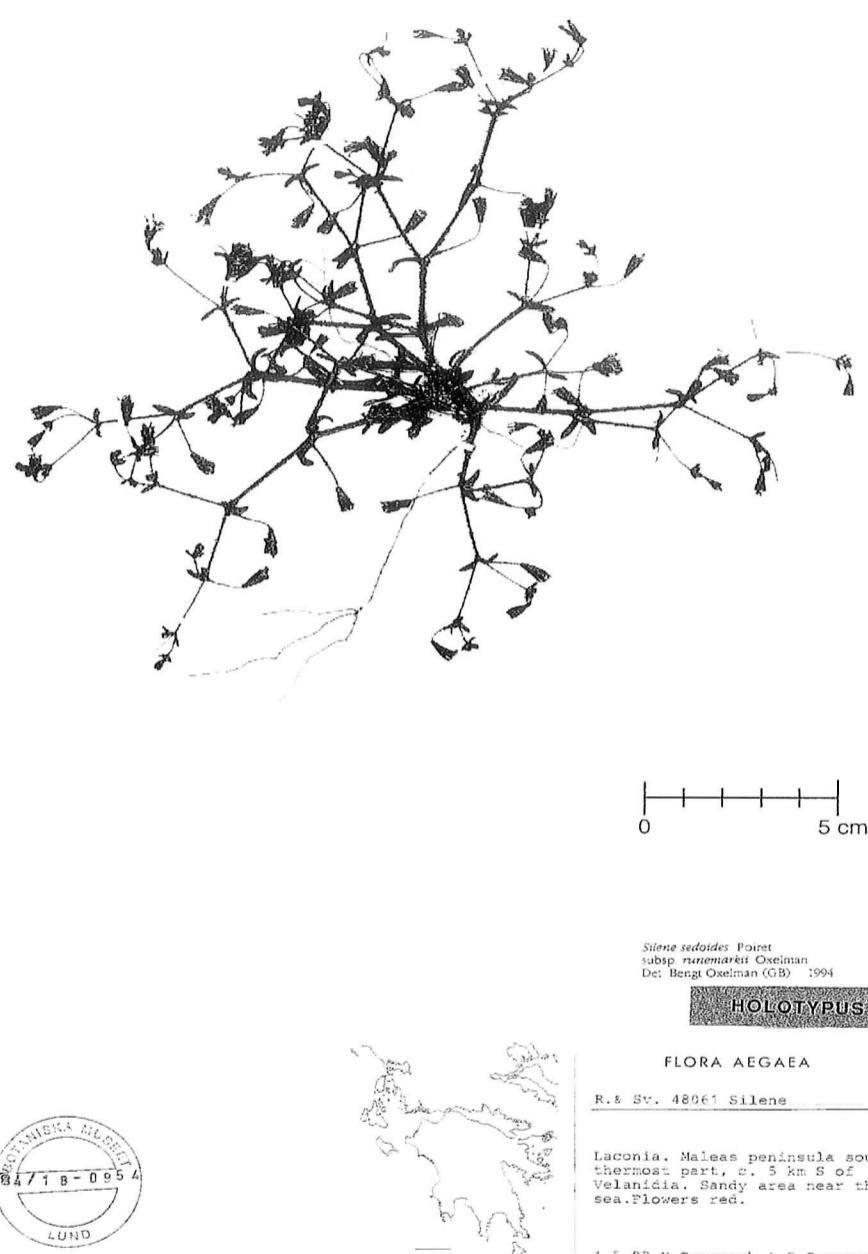


Fig. 5. *S. sedoides* subsp. *runemarkii* (holotype, LD).



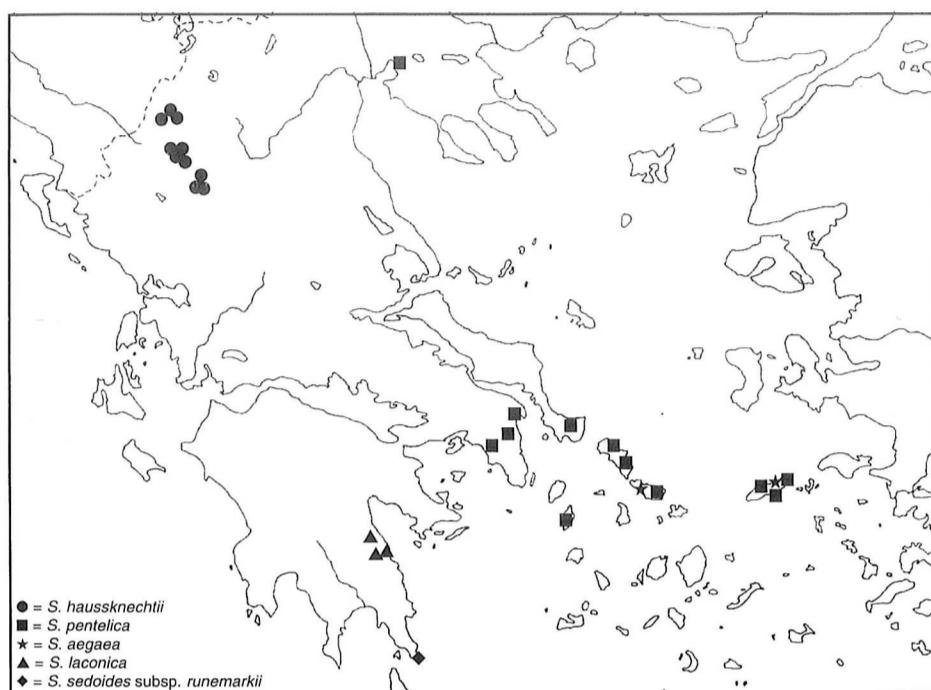


Fig. 6. Distribution of *S. haussknechtii*, *S. pentelica*, *S. aegaea*, *S. laconica*, and *S. sedoides* subsp. *runemarkii*.

Specimens examined

Greece: Peloponnisos, Maleas peninsula, southernmost part, c. 5 km S of Velanidia, sandy area near the sea, [23°09'E, 36°27'N], 1. 5. 1982, \*Runemark & Svensson 48061 (LD); ibid., 24. 5. 1986, \*Oxelman & Tollsten 1195 (GB).

**2. *S. aegaea* Oxelman, spec. nova – Fig. 2D, 7.**

Holotype: [Greece, E Aegean], “Ikaria. S of Evthelo”, 24. 4. 1958, Runemark & Snogerup 6729 (LD!).

Habitu, pedicellis, et absentia macularum petalorum *Silene pentelicae*, seminibus petalis emarginatis *S. sedoidi* similis, sed partibus omnibus leviter majoribus, capsulis foliisque magnitudine et textura inter ambobus intermediis.

Stems ascending or erect, 2–8(–20) cm long. Leaves fleshy to succulent, subglabrous or sparsely glandular hairy. Basal leaves (0.5–)1–3(–4) cm long, with the hairs mostly confined to the margins. Cauline leaves spatulate to (narrowly) obovate. Uppermost stem internode 1–3 times as long as subtending leaves. Flowers in uneven dichasial cymes of 3–6 orders. Lowest internodes of inflorescence 1.0–1.5 times as long as lowermost pedicel. Pedicels upright, 3–25 mm long, of first order 1.5–3 times the length of calyx in fruit, of higher orders 0.5–1.5 times the length of calyx. Calyx cylindrical to narrowly clavate in flower, clavate in fruit, 7–9 mm long. Hyaline margin of calyx teeth usually with many, sometimes glandular hairs. Petal



limb pink, paler beneath, without a dark spot at the base, upright when becoming withered, 2–3(–4) mm, emarginate. Coronal scales 1.0–1.5 mm, obliquely triangular, sometimes dentate, white. Anthers white, 0.7–1.0 mm, included in corolla mouth. Gonophore 2–3 mm long. Capsule narrowly ovoid, semimembranous, twice as long as the gonophore, enclosed within the calyx. Seeds greyish black, 0.7–0.8 mm wide, reniform, dorsally grooved with rounded ridges, dorsal testa cells smooth or mamillate, lateral testa cells smooth.

Flowering time: April to June.

Chromosome number:  $2n =$  presumably 48 (Ikaria, Evdilos, Oxelman 2214 (GB); approximate counts range between 45–50).

Ancestry: Based on both morphological and molecular evidence (Oxelman 1995), *S. aegaea* appears to be of allopolyploid origin, with ancestors of *S. sedoides* and *S. pentelica* as putative parents. It is similar to *S. pentelica* in habit, stem length, inflorescence branching, pedicel orientation, pedicel length and lack of basal spot on petal. With *S. sedoides* subsp. *sedoides* it shares the character states emarginate petals, upright wilting petals and rounded dorsal seed ridges. It is intermediate in leaf texture, capsule form, and capsule texture. It is, however, slightly larger than both in pedicel length, calyx length, capsule length, and seed size.

Ecology: Occurring in gravelly habitats just above the supralittoral zone. At the type locality, *S. aegaea* grows in roadside vegetation dominated by *Cichorium spinosum* L. and *Crithmum maritimum* L. Although *S. sedoides* subsp. *sedoides* grows in the extreme littoral rocky zone at a distance of just a few meters, the taxa appear to occupy different ecological niches.

Distribution: Endemic to the islands Ikaria and Tinos (Fig. 6), with the type locality as the only one known after the 19th century. I have failed to find it on Tinos.

#### Specimens examined

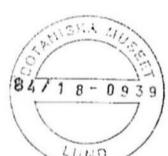
Greece: Ikaria: SE of the village Evdilos, 20–40 m, [26°11'E, 37°38'N], 4. 5. 1976, \*Stamatiadou 19108bis (ATH); ibid., 29. 4. 1989, \*Christodoulakis 2826 (UPA, mixed with *S. sedoides* subsp. *sedoides*); ibid., 24. 4. 1958, Runemark & Snogerup 6729 (LD); ibid., 26. 6. 1993, \*Oxelman 2214 (GB). – Tinos: 12.–17. 4. 1889, Heldreich (BM, JE, K); ibid., 15. 4. 1889, Heldreich 1015 (BM, K, LD, UPS); ibid., 8. 4. 1898, Leonis 129 (M).

Note: On most sheets of Heldreich's collections the species is mixed with *S. sedoides* subsp. *sedoides*. There are also some plants on these sheets which seem to be referable to *S. pentelica*. One specimen in M collected by Heldreich on Tinos in April, 1900, is labelled "Silene Aegaea". The extant material is insufficient for certain determination of its specific identity, but the label might indicate that Heldreich became aware of the distinctiveness of the plants described as *Silene aegaea* here.

**3. *S. pentelica* Boiss., Diagn. Pl. Orient., ser. 1, 8: 74 (1849) – Fig. 1F, 2E, 3E-F.**  
 ≡ *S. sedoides* var. *pentelica* (Boiss.) Rohrb., Monogr. Silene 164 (1869) ≡ *S. sedoides* subsp. *pentelica* (Boiss.) Nyman, Conspl. Fl. Eur. 94 (1878). – Lectotype (designated here): [Greece, Attiki], "Pentelicus", 5. 1842, Boissier (G-BOIS!, iso- C!, G!, K!).

Stems ascending or erect, 2–8(–20) cm long. Leaves fleshy, sparsely glandular hairy. Basal leaves (0.5–)1–3(–4) cm long. Cauline leaves spatulate to (narrowly) obovate. Uppermost





**HOLOTYPUS**

*Silene aegaea* Heldr. ex Oxelman

Det. Bengt Oxelman (GB) 1994

**FLORA AEGAEA**

R. & S. 6729 *Silene pententiformis* Boiss.

Ikaria. S of Evthelo, near the shore



24.4 1958 Hans Runemark and Sven Snogerup  
Botanical Museum, Lund, Sweden

Fig. 7. *S. aegaea* (holotype, LD).



stem internode 0.8–3 times as long as subtending leaves. Flowers in dichasial cymes of 3–6 orders. Lowest internodes of inflorescence 1.0–3.5 times as long as lowermost pedicel. Pedicels patent to upright, 3–20 mm long, pedicels of first order 1–2 times as long as calyx in fruit, pedicels of higher orders equal to or shorter than calyx. Calyx cylindrical to oboconical in flower, clavate in fruit, 6–8 mm long. Hyaline margin of calyx teeth usually with many, sometimes glandular hairs. Petal limb pink, paler beneath, 2–3(–4) mm, usually entire (truncate), rarely emarginate, not erect when wilting. Coronal scales 0.8–1.5 mm, obliquely triangular, sometimes dentate, white. Anthers white, 0.6–1.0 mm, included in corolla mouth. Gonophore 2–4 mm long. Capsule oblong, firm and opaque, 1.5–3 times as long as the gonophore, (3–)4–6 mm long, enclosed within or somewhat exserted from calyx. Seeds greyish black, 0.6–0.7 mm in diameter, reniform, dorsally grooved with sharp ridges, dorsally smooth or mamillate, laterally flat or slightly concave and smooth.

Flowering time: April to July.

Chromosome number:  $2n = 24$  (Ikaria, Karavostamo, Oxelman 2217 (GB), previous count: Constantinidis & Kamari (1994)).

Ecology: Occurring in gravelly habitats above the littoral zone up to c. 1000 m.

Note: The locus classicus population differs from other populations in that the capsule is exserted by 1–2 mm from the calyx. Evidence from RAPD-data suggests that the population from Pendelli is sister to the island populations (Oxelman 1995).

Distribution: Endemic to Greece (Fig. 6). Presently known from Attiki, Evvia, Andros and Ikaria. The record from Livadhia (Williams 1896) requires confirmation. The Tošev collection from Thessaloniki is probably erroneously labelled (W. Greuter, pers. comm.).

#### Representative specimens

Greece: Attiki: Pentelicon radices, 5. 1842, Boissier (C, G, G-BOIS, K); ibid., in saxosis ad lapi vicinas marmoris, 22. 4. 1855, Heldreich 491 (BM, C, G, JE, K, M, P, S, UPS); ibid., stony phrygana and burned pine-forest, 700–800 m, 29. 4. 1984, \*Oxelman & Tollsten 185 (GB); Rapelusa b, Marathon, Bretzl (BM); Mt. Hymettos, soil above the town [tower?], 21. 5. 1883, Lacaita (BM). – Evvia: Mt. Ocha, substr. calc. et schist. cristall. in saxosis regionis mediae, 1000 m, 22. 5. 1955, Rechinger 16303 (G, K, M, S); ibid., about 4 km NE Karistos, sandy and schisty ground, 1000 m, [24°27'E, 38°03'N], 4. 6. 1986, \*Oxelman & Tollsten 1387 (GB). – Kikladhes: Andros, Oros Rakhi, 600–800 m, [24°56'E, 37°44'N], 17. 5. 1968, Snogerup & Bothmer 32111 (LD). – Kithnos, 4. 1900, Tuntas (M). – Ikaria: supra pagum Magganitis, alt. c. 250 m, in rupestribus calc., 18. 4. 1989, \*Christodoulakis 3321 (UPA); inter pagos Chrysostomos et Plagia, 31. 5. 1991, \*Christodoulakis 3336 (UPA); prope pagum Ploumari, 5. 6. 1986, \*Christodoulakis 2046 (UPA); schistose gravel by the road, c. 1 km W of Ploumari, 26. 6. 1993, \*Oxelman 2215 (GB); between Ploumari and Mileopo, rocky roadsides, [26°16'E, 37°39'N], 2. 5. 1976, Stamatiadou 18894 (ATH); roadside gravel about 2 km E of Karavostamo, [26°14'E, 37°38'N], 26. 6. 1993, \*Oxelman 2217 (GB). – Makedhonia: in aridis prope Thessalonikis, [22°57'N, 40°38'E], 12. 5. 1899, Tosev (M).

**4. *S. haussknechtii*** Hausskn. in Mitth. Thüring. Bot. Vereins 5: 51 (1893) – Fig. 1G, 2F, 3C-D.  
≡ *S. sedoides* subsp. *haussknechtii* (Hausskn.) Maire & Petitm. in Bull. Soc. Sci. Nancy, ser. 3, 9: 189 (1908).



Lectotype (designated here): [Greece, Pindhos range], "in summo montis Zygos (Lakmon veter.) supra Metzovo", 1350–1500 m, 7. 1885, Haussknecht (JE!, iso- JE!).

Stems ascending or erect, 3–7(–15) cm long. Leaves fleshy, sparsely glandular hairy. Basal leaves (0.5–)1–3(–6) cm long. Cauline leaves spatulate to (narrowly) obovate. Uppermost stem internode 1.5–5 times as long as subtending leaves. Flowers in dichasial cymes of 3–4(–6) unevenly branched orders. Lowermost internodes of inflorescence 1.0–2.5 times as long as lowermost pedicel. Pedicels patent to upright, 4–25 mm long; pedicels of first order at least twice as long as calyx in fruit; pedicels of higher orders (third and more) equal to or shorter than calyx. Calyx obconical in flower, clavate in fruit, 8–10 mm long. Hyaline margin of calyx teeth usually with many, sometimes glandular hairs. Petal limb pink, darker beneath, 3–5 mm, entire. Coronal scales 1–1.5 mm, obliquely triangular, sometimes dentate, white. Anthers white to pale lilac, 0.7–1.2 mm, slightly exserted from corolla mouth. Gonophore 2–4 mm long. Capsule ovoid to ellipsoidal, firm, a little longer to twice as long as the gonophore, 4–5(–6) mm long, enclosed within the calyx. Seeds brownish black, 0.7–0.8 mm in diameter, reniform, dorsally grooved with sharp ridges; dorsal testa cells tuberculate, lateral testa cells smooth.

Flowering time: May to July.

Typification: It is not clear to me if the collections by Heldreich ("Pindhos Tymphaeus: in summit montis Zygos supra Metzovo, 4500'–5000', 19–20. 7. 1885") and by Haussknecht should be considered as duplicates of the same gathering. Therefore, I have decided to treat only the specimens with Haussknecht's labels as types.

Chromosome number:  $2n =$  probably 24 (Dhistraton, Oxelman & Tollsten 1451 (GB); approximate counts ranged between 22–25).

Ecology: Occurring in gravelly habitats on serpentine between ca. 700–2100 m.

Distribution: Endemic to NW Greece (Fig. 6).

#### Representative specimens

Greece: Mt. Smolikas, great SE ravine c. 3 km SW of Samarina, SW-facing steep, rocky slopes and ravines in *Pinus nigra* woodland, serpentine substr., 1300–1550 m, [21°00'E, 40°05'N], 31. 8. 1975, Hartvig & Seberg 5079 (B, B-Gr, C); 1 km W Dhistraton, serpentine gravel, 950 m, [21°01'E, 40°02'N], 9. 6. 1986, \*Oxelman & Tollsten 1451 (GB); Pindhos Tymphaeus, in summis montis Zygos supra Metzovo, 4500'–5000', 19.–20. 7. 1885, Heldreich (E, G, JE, K, LD, UPS); Mt. Bouchetsi (Gramos), 6 km NW of Eptachorion, summit area, gravelly plateau, rocky slopes and screes, serpentine substr., 1600–1700 m, [20°57'E, 40°15'N], 11. 7. 1977, Hartvig et al. 6742 (C).

**5. *S. laconica*** Boiss. & Orph. in Boissier. Diagn. Pl. Orient., ser. 2, 6: 34 (1859) – Fig. 1H, 2G.  
Holotype: [Greece, Peloponnisos], "in monte Malevo Laconiae supra Platanos", 22. 4./4. 5. 1857, *Orphanides* 3359 (G-BOIS!).

Stems ascending or erect, 3–12(–20) cm long. Leaves slightly fleshy, sparsely glandular hairy. Basal leaves (0.5–)1–3(–6) cm long. Cauline leaves spatulate to (narrowly) obovate or elliptic. Uppermost stem internode (2–)3–6(–8) times as long as subtending leaves. Flowers in dichasial cymes of (2–)4–5(–6) orders. Lowermost internodes of inflorescence 0.7–2.5 times as long as lowermost pedicel. Pedicels upright, 8–30 mm long; pedicels of first order



2–3 times as long as calyx in fruit; pedicels of higher orders (third and more) equal to or slightly longer than calyx. Calyx narrowly clavate in flower, clavate in fruit, 8–11 mm long. Hyaline margin of calyx teeth with few short hairs. Petals pink, paler beneath, (2.5–)4–4.5 mm, emarginate or slightly bifid, not erect when wilting. Coronal scales 1.3–1.5 mm, white. Anthers pale lilac, (0.9–)1.0–1.4(–1.5) mm, exserted from corolla mouth by 1–2.5 mm. Gonophore (2.5–)4–5 mm long. Capsule oblong, firm, 4–5(–6) mm long, equalling to slightly longer than the gonophore, enclosed within the calyx. Seeds greyish black, 0.7–0.8 mm wide, reniform, dorsally grooved with rounded ridges, faces flat; dorsal testa cells smooth or mamillate, lateral cells smooth.

Flowering time: April to June.

Note: Specimens collected at the type locality (*Oxelman & Tollsten 851*) did not have the conspicuously small leaves otherwise characterizing this taxon.

Chromosome number:  $2n =$  probably 24 (Moni Elonis, *Oxelman 1897* (GB); approximate counts ranged between 22–24).

Ecology: Occurring in gravelly habitats in the colline and montane zones 10–900 m.

Distribution: Endemic to mount Parnon, on SE Peloponnisos, Greece (Fig. 6).

Representative specimens

Greece: Peloponnisos, Mt. Parnon, 1 km NW Sitaena, roadside gravel, 850–900 m, [22°39'E, 37°19'N], 1. 6. 1986, \**Oxelman & Tollsten 1362* (GB); 1 km NNE Platanos, roadside gravel, 600 m, [22°39'E, 37°20'N], 29. 4. 1985, \**Oxelman & Tollsten 851* (GB); ibid., 4. 5. 1837, *Orphanides 3359* (G-BOIS); Leonidion, dry river bed, [22°53'E, 37°10'N], 27. 4. 1986, \**Oxelman & Tollsten 1053* (GB); ibid., 9. 5. 1982, \**Runemark & Svensson 48473* (LD); about 1 km W Moni Elonis, roadside, 550 m, [22°45'E, 37°08'N], 12. 6. 1991, \**Oxelman 1897* (GB).

**6. *S. integripetala* Bory & Chaub., Exp. Sci. Morée, Bot. 123 (1832).**

Lectotype (designated here): [Greece, Peloponnisos], "Morée", 1826, Bory (P!, iso- G!).

Stems erect. Leaves fleshy, sparsely glandular hairy. Basal leaves (0.5–)1–5(–8) cm long, hairs mostly confined to the margins. Cauline leaves obovate to ovate. Flowers in dichasial cymes. Pedicels upright. Calyx cylindrical in flower, clavate in fruit. Hyaline margin of calyx teeth subentire and often reddish-tinged. Petals not erect when wilting. Anthers lilac. Capsule oblong, firm, (6–)7–9(–10) mm long. Seeds greyish black, reniform, 0.6–0.8 mm wide, dorsally grooved with rounded ridges, faces flat; dorsal testa cells smooth or mamillate, lateral testa cells smooth.

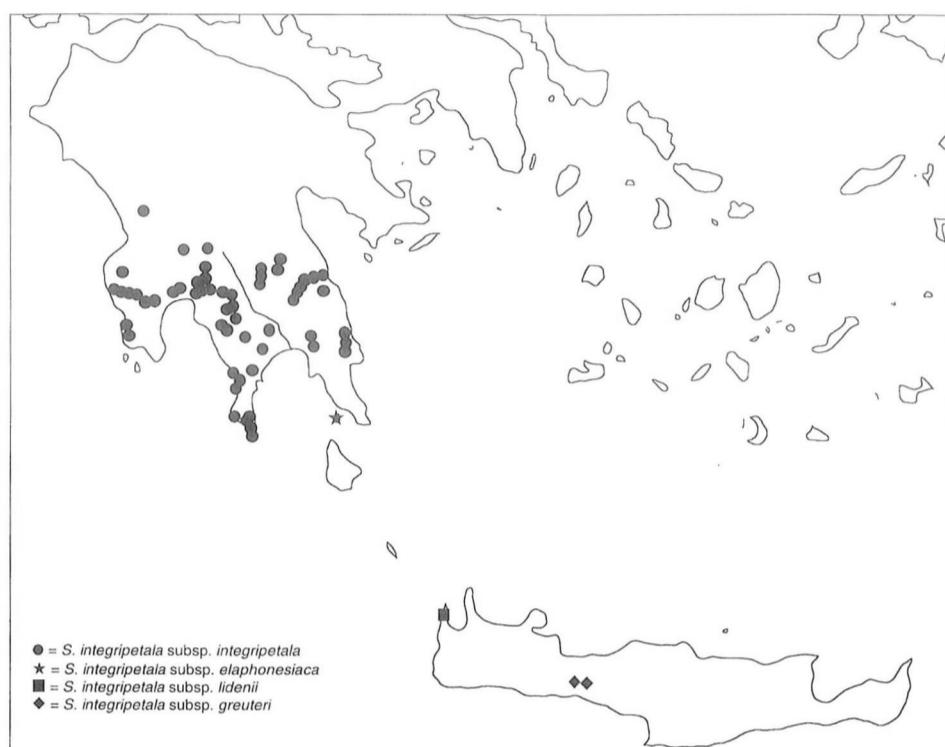
Flowering time: March to June.

Ecology: Occurring in gravelly habitats between ca. 10–1900 m.

Distribution: Endemic to Greece (Fig. 8).

Note: As judged from RAPD-data (Oxelman 1995), the island taxa appear to form a monophyletic group with the Peloponnesian subsp. *integripetala* as sister-group. The superficial similarity between subsp. *integripetala* and subsp. *lidenii* did, however, lead me to the decision to rank all four taxa as subspecies of *S. integripetala*, which both constitutes a bold hypothesis of monophyly and permits easy identification at the species level.



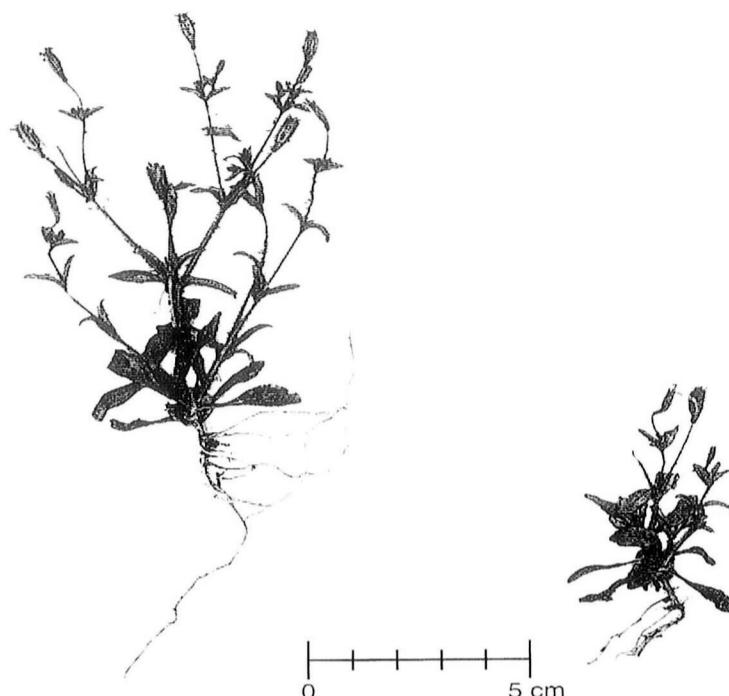
Fig. 8. Distribution of *S. integriflora*.**Key to the subspecies**

1. Capsule (on hermaphrodite flowers) less than 1.5 times as long as gonophore, gonophore usually more than 6 mm . . . . . 6a. subsp. *integriflora*
- Capsule (on hermaphrodite flowers) more than 1.5 times as long as gonophore, gonophore less than 6 mm . . . . . 2
2. Petal limb twice as long as broad, stem leaves narrow, coronal scales 1 mm or less . . . . . 6b. subsp. *elaphonesiaca*
- Petal limb less than 1.5 times as long as broad, stem leaves broad, coronal scales longer than 1 mm . . . . . 3
3. Petal limbs intensely pink, not overlapping, gonophore 3–5 mm . . . . . 6c. subsp. *lidenii*
- Petal limbs pale pink, often overlapping, gonophore 2–3 mm . . . . . 6d. subsp. *greuteri*

**6a. *S. integriflora* subsp. *integriflora* – Fig. 2K, 3A-B.**

Stems (2–)6–20(–40) cm long. Uppermost stem internode (1.5–)2–4(–6) times as long as subtending leaves. Lower cauline leaves obovate, upper oblong, elliptic or ovate. Flowers in many-flowered dichasial cymes of (2–)4–7(–10) orders. Lowermost internodes of inflorescen-





**HOLOTYPUS**  
*Silene integriflora* Bory & Chaub.  
 subsp. *elaphonesiaca* Oxelman  
 Det. Bengt Oxelman (GB) 1994  
 (48)  
 Caryophyllaceae  
*Silene sedoides*  
 Fundort: Griechenland, Peloponnes  
 Lakenien, Elafonisos  
 Plougana Südl. des Gyfels  
 acc.  
 Datum: 20.3.1992  
 leg. et det. A. Jagel  
 08. MRL 1993

Fig. 9. *S. integriflora* subsp. *elaphonesiaca* (holotype, B).



ce 1.5–3.0 times as long as lowermost pedicel. Pedicels 5–50 mm long; pedicels of first order (1–)2–3(–4) times as long as calyx in fruit; pedicels of higher orders (third and more) equal to or shorter than calyx. Calyx (8–)12–15(–19) mm long. Petal limb intensely pink, (4.5–)6–8(–9.5) mm, rounded or truncate at apex, rarely emarginate. Coronal scales 2–2.5 mm, linear, white with pinkish margins. Anthers (1.1–)1.2–1.7(–1.8) mm, exserted from corolla mouth by (0–)1–4(–6) mm. Gonophore (4–)6.5–9.5(–11) mm long. Capsule (6–)7–9(–10) mm long, equalling to a little longer than the gonophore, enclosed within the calyx.

Chromosome number:  $2n = 24$  (Mount Taigetos, *Phitos* 1472 (M!); Damboldt & Phitos (1966)).

Distribution: Endemic to S Peloponnisos (Fig. 8).

Reproductive biology: This subspecies of *S. integrifolia* is the only taxon in the group with poor seed production when excluded from pollinators. It is, however, self-fertile (Oxelman 1990).

#### Representative specimens

Greece: Peloponnisos: Arkadhi: Leonidhi - Kosmas, 15 km nach Leonidhi, Kalkschutt an der Strasse, 560 m, 7. 4. 1979, Greuter & Merxmüller 16965 (B, B-Gr, M, UPA); Leonidion, dry river bed, [22°53'E, 37°10'N], 27. 4. 1986, \*Oxelman & Tollsten 1057 (GB); ibid., 2. 5. 1984, \*Oxelman & Tollsten 387 (GB); road Leonidion - Kosmas, about 4 km S monastery Elonis, grazed land, 1100 m, [22°45'E, 37°07'N], 2. 5. 1984, \*Oxelman & Tollsten 434 (GB); Mt. Taigetos, 1 km SE Dirrachion, calcareous gravel by the forest road, 850 m, [22°14'E, 37°10'N], 26. 5. 1986, \*Oxelman & Tollsten 1252 (GB); ibid., 14. 6. 1991, \*Oxelman 1907 (GB); 5 km N Dirrachion, forest roadside, [22°14'E, 37°16'N], 1. 5. 1986, \*Oxelman & Tollsten 1075 (GB). – Lakonia: Mt. Parnon, 1 km SE Varvitsa, roadside, 900 m, [22°32'E, 37°16'N], 25. 5. 1986, \*Oxelman & Tollsten 1205 (GB); Krioneri, gravelly roadside near the rill from Varvara, 1000 m, [22°24'E, 36°58'N], 13. 6. 1991, \*Oxelman 1903 (GB); 7 km W Tripi, near the road Sparti - Kalamata, roadside gravel, 800 m, [22°20'E, 37°06'N], 9. 5. 1085, \*Oxelman & Tollsten 1005 (GB); Sparta in Alveo torrentium, 4. 1842, Boissier (C, E, G, JE, K, S, UPS); above Kiparissia, hard limestone, small stream and cliffs, [22°59'E, 36°58'N], 6. 5. 1982, \*Runemark & Svensson 48325 (LD); NE Charax, large E-exposed limestone cliffs at the road, [23°00'E, 36°55'N], 5. 1982, \*Runemark & Svensson 48290 (LD); 1 km W Nea Iton, limestone cliffs facing N near the shore, [22°22'E, 36°41'N], 5. 5. 1985, \*Oxelman & Tollsten 930 (GB); Mani peninsula, 1 km SW Gerolimin, stony steppe on limestone plateau, [22°24'E, 36°29'N], 4. 5. 1985, \*Oxelman & Tollsten 907 (GB); ibid., Ormos Diros, recently burned *Euphorbia dendroides*-dominated phrygana, 30 m, [22°23'E, 36°39'N], 4. 5. 1985, \*Oxelman & Tollsten 928 (GB). – Messinia: In collibus apricis et in submontis Kalamata frequens, 20. 4. 1896, Zahn (B, BM, G, GB, JE, K, LD, M, S, UPS); road Sparti - Kalamata, by turn-off road to Neochorion, limestone gravel, [22°16'E, 37°04'N], 3. 5. 1984, \*Oxelman & Tollsten 484 (GB); road Messini - Pilos, Km 18, c. 2 km NE Charavji, roadside, [21°51'E, 37°00'N], 4. 5. 1984, \*Oxelman & Tollsten 540 (GB); Mt. Kiparissias, on the ascent between the villages Kerasea and Mali, 700–900 m, [21°42'E, 37°10'N], 1. 5. 1971, Stamatiadou 12051 (ATH). – Ilia: In ditione pagi Figalia in saxosis (in petrosis), [21°50'E, 37°24'N], 20. 4. 1975, Phitos & Kamari 18469 (B-Gr).

#### 6b. *S. integrifolia* subsp. *elaphonesiaca* Oxelman subsp. *nova* – Fig. II, 2H, 9.

Holotype: [Greece, Peloponnisos, Lakonia], “Elafonisos/Phrygana südl. des Gipfels”, 20. 3. 1991, Jagel 48 (B!).

Petalis foliisque angustis a subspeciebus ceteris differt. Praeterea a subsp. *integrifolia* dichas paucifloris gonophoriorum multo brevioribus distinguenda.



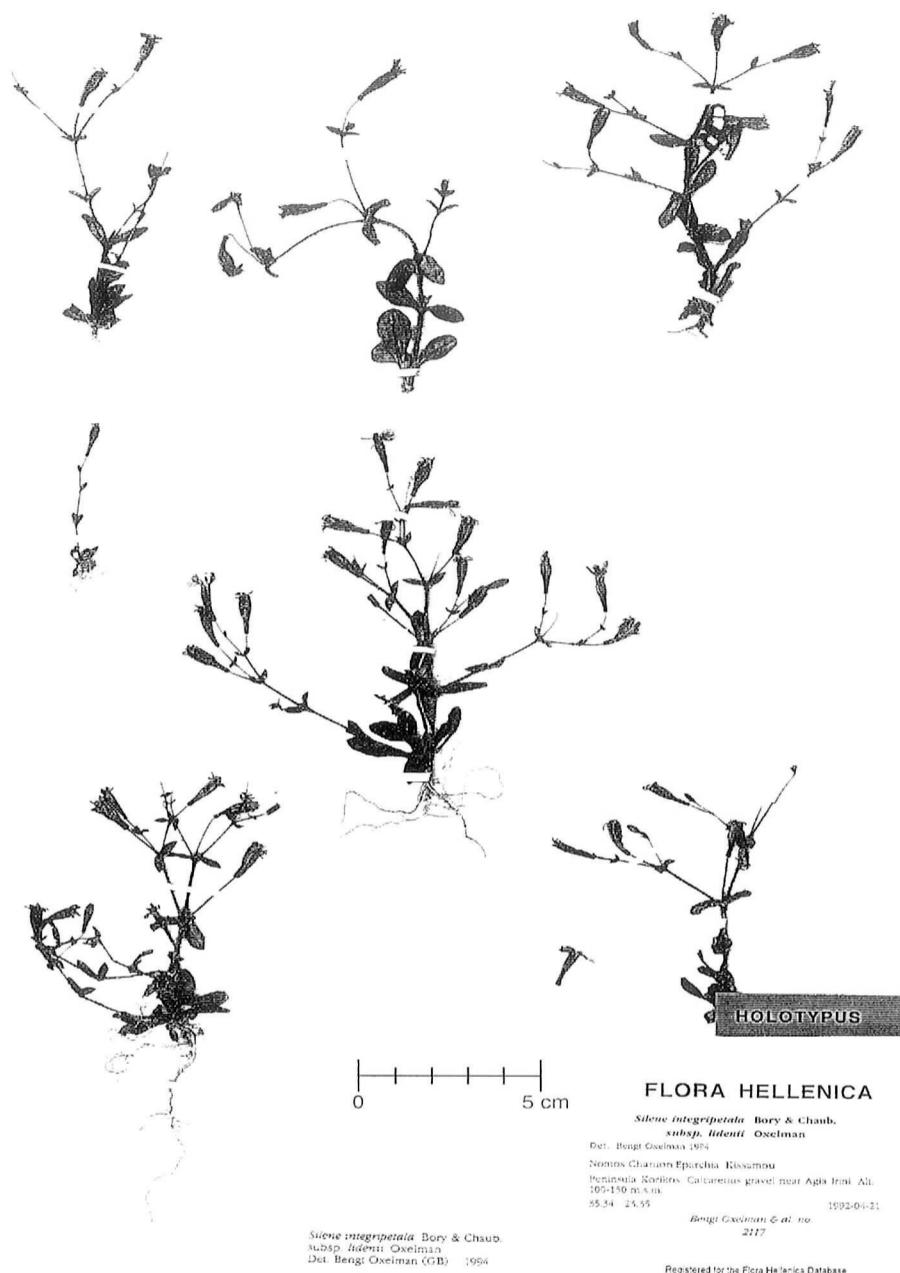


Fig. 10. *S. integrifolia* subsp. *lidenii* (holotype, GB).



Stems 4–6(–10) cm long. Uppermost stem internode 1(–3) times as long as subtending leaves. Lower cauline leaves narrowly obovate, upper narrowly oblong or elliptic. Flowers in dichasial cymes of (1–)2–3(–4) orders. Lowermost internodes of inflorescence 0.6–1.2 times as long as lowermost pedicel. Pedicels 7–25 mm long; pedicels of first order 1.5–2.5 times as long as calyx in fruit; pedicels of higher orders (third and more) as long as or shorter than calyx. Calyx 8–10 mm long. Petal limb pale pink, 2.5–4 mm, narrowly oblong, rounded at apex. Coronal scales 0.7–0.9 mm, obtusely triangular, white. Anthers 0.7–0.8 mm, exserted from corolla mouth by 1–2 mm. Gonophore (1–)2–3 mm long. Capsule 6–7 mm long, 2–3 times as long as long as the gonophore, enclosed within the calyx.

Flowering time: March to May.

Chromosome number:  $2n =$  probably 24 (*Jagel* 48 (B); approximate counts ranged between 22–24).

Distribution: Endemic to the island of Elafonisos S of the Peloponnisos (Fig. 8).

Specimens examined

Greece: Elafonisos: 13. 4. 1991, *Jagel* 53 (B); Phrygana südl. des Gipfels, 20. 3. 1991, \**Jagel* 48 (B); Phrygana im Osten der Insel, 21. 4. 1991, \**Jagel* 7 (MB); Phrygana unterhalb des Gipfels, 22. 3. 1991, *Jagel* 47 (B).

**6c. *S. integriflora* subsp. *lidenii* Oxelman subsp. *nova*** – Fig. 2J, 10.

Holotype: [Greece, Kriti, Kissamos], “Peninsula Korikos, near Agia Irini”, 100–150 m, 21. 4. 1992, *Oxelman et al.* 2117 (GB!), iso-B!

A subsp. *integriflora* floribus minoribus gonophoris brevioribus, a subsp. *greuteri* petalis intense roseis gonophoris longioribus, a subsp. *elaphonesiacaca* foliis petalisque latioribus gonophoris longioribus differt.

Stem 3–10(–20) cm long. Uppermost stem internode 1–2(–3) times as long as subtending leaves. Lower cauline leaves obovate, upper oblong, elliptic or ovate. Flowers in dichasial cymes of (2–)3–4(–5) orders. Lowermost internodes of inflorescence 0.7–1.5 times as long as lowermost pedicel. Pedicels 7–20(–30) mm long; pedicels of first order 1.5–2(–3) times as long as calyx in fruit; pedicels of higher orders (third and more) shorter than calyx. Calyx 10–14 mm long. Petal limb intensely pink, 4–6 mm, obovate, emarginate; coronal scales 1.4–1.5 mm, white or pinkish, linear. Anthers 1.1–1.3 mm, exserted from corolla mouth by 1–2 mm. Gonophore 3–5 mm long. Capsule 7–9 mm long, 1.5–2 times as long as long as the gonophore, enclosed within the calyx.

Flowering time: April to May.

Chromosome number:  $2n = 24$  (*Oxelman* 2117 (GB)).

Distribution: Endemic to the Gramvousa peninsula on NW Kriti (Fig. 8).

Specimen examined

Greece: Kriti: Peninsula Korikos, calcareous gravel near Agia Irini, 100–150 m, [35°34'N, 23°35'E], 21. 4. 1992, \**Oxelman* 2117 (B, GB).

**6d. *S. integriflora* subsp. *greuteri* (Phitos) Akeroyd in Bot. J. Linn. Soc. 97: 341 (1988) – Fig. 1A-B, 2I.**

≡ *S. greuteri* Phitos in Bot. Hron. 2: 53 (1983). – Holotype: [Greece, Kriti, Rethimni], “prope



pagum Mariou, in fauibus Kourtaliotiko". 350 m. 13. 4. 1982. *Tzanoudakis* 7067 (UPA!, iso-B-Gr, UPA!).

Stem 1.5–9(–20) cm long. Uppermost stem internode (0.7–)1–1.5(–2.5) times as long as subtending leaves. Lower cauline leaves obovate, upper elliptic or ovate. Flowers in dichasial cymes of (1–)2–3(–4) orders. Lowermost internodes of inflorescence 0.5–1.5 times as long as lowermost pedicel. Pedicels 7–24 mm long; pedicels of first order 1–2 times as long as calyx in fruit; pedicels of higher orders (third and more) shorter than calyx. Calyx (8–)10–11(–12) mm long. Petal limb pale pink, (4–)4.5–5.5(–6) mm, obovate, emarginate; limbs often overlapping. Coronal scales 1.2–1.4 mm, obtusely triangular, white. Anthers (0.7–)1.0–1.4(–1.5) mm, exserted from corolla mouth by 1–2 mm. Gonophore 2.5–3 mm long. Capsule (6–)7–8 mm long, 2–3 times as long as the gonophore, often slightly exceeding the calyx.

Flowering time: April to June.

Chromosome number:  $2n = 24$  (Kourtaloutiko gorge, *K. Persson* (GB)); approximate counts ranged between 24–25).

Distribution: Endemic to the Kourtaliotiko and Kotsifou gorges in W Central Kriti (Fig. 8).

#### Representative specimens

Greece: Kriti: Kotsifou gorge, about 2 km NNW Mirthios, calcareous cliffs and gravel, 200–300 m, [24°24'E, 35°11'N], 22. 4. 1992, \*Oxelman et al. 2140 (B, GB); prope pagum Mariou, in fauibus Kourtaliotiko, in glareosis, 350 m, [24°25'E, 35°12'N], 13. 4. 1982, *Tzanoudakis* 7067 (UPA); Kourtaloutiko gorge, gravel and scree in E-facing slopes, 200–250 m, 5. 4. 1985, \**K. Persson* (GB); Kourtaliotiko gorge, about 2 km NE of Asomatos, calcareous cliffs and gravel, 250 m, [24°27'E, 35°12'N], 22. 4. 1992, \*Oxelman et al. 2126 (GB).

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#### 9. References

- Abdel Bari, E. 1973: Cytological studies in the genus *Silene* L. – New Phytol. **72**: 833–838.
- Arrigoni, P. V. 1982: *Bellium* L., p. 28. – In: Pignatti, S. (ed.), Flora d'Italia **3**. – Bologna.
- Bocquet, G. 1968: Physolychnidum morphologica catalecta. – Candollea **23**: 151–176.
- Carlström, A. 1987: A survey of the flora and phytogeography of Rodhos, Simi, Tilos and the Marmaris peninsula (SE Greece, SW Turkey). – Ph.D. thesis, Lund.



- Chowdhuri, P. K. 1957: Studies in the genus *Silene*. – Notes Roy. Bot. Gard. Edinburgh **22**: 221–278.
- Constantinidis, T. & Kamari, G. 1994: Reports, p. 290–295. – In: Kamari, G., Felber, F. & Garbari, F. (eds.), Mediterranean chromosome number reports 4. – Fl. Medit. **4**: 233–301.
- Coode, M. J. & Cullen, J. 1967: *Silene* L., p. 179–242. – In: Davis, P. H. (ed.), Flora of Turkey 2. – Edinburgh.
- Damboldt, J. & Phitos, D. 1966: Ein Beitrag zur Zytotaxonomie der Gattung *Silene* L. in Griechenland. – Österr. Bot. Z. **113**: 169–175.
- Holmgren, K. P., Holmgren, N. H. & Barnett, L. C. 1990: Index herbariorum I: The herbaria of the world, ed. 8. – Regnum Veg. **120**.
- Jalas, J. & Suominen, J. 1986: Atlas florae europaea 7. *Caryophyllaceae (Sileneoideae)*. – Helsinki.
- Lidén, M. 1986: Synopsis of *Fumarioideae* (*Papaveraceae*) with a monograph of the tribe *Fumarieae*. – Opera Bot. **88**.
- & Oxelman, B. 1989: Species – pattern or process? – Taxon **38**: 228–232.
- & — 1990: Species – evolutionary actors or evolutionary products? – Taxon **39**: 449.
- Maire, R. 1963: Flore de l’Afrique du Nord **10**. – Paris.
- Meikle, R. D. 1977: Flora of Cyprus **1**. – Kew.
- Melzheimer, V. 1977: Biosystematische Revision einiger *Silene*-Arten (*Caryophyllaceae*) der Balkanhalbinsel (Griechenland). – Bot. Jahrb. Syst. **98**: 1–92.
- Meusel, H. & Werner, K. 1978–1979: *Silene* L., p. 1043–1153. – In: Hegi, Illustrierte Flora von Mitteleuropa, ed. 2, **3(2)**. – Berlin.
- Mishler, B. D. & Donoghue, M. J. 1982: Species concepts: a case of pluralism. – Syst. Zool. **41**: 491–503.
- Montmollin, B. de 1986: Etude cytotaxonomique de la Crète. III. Nombres chromosomiques. – Candollea **41**: 431–439.
- Oxelman, B. 1990: Studies on the reproductive biology of *Silene integrifolia* Bory & Chaub. (*Caryophyllaceae*). – Thesis, Göteborg.
- 1995: RAPD patterns, nrDNA ITS sequences, and morphological patterns in the *Silene sedoides*-group (*Caryophyllaceae*). – Manuscript.
- & Lidén, M. 1995: Generic boundaries in the tribe *Sileneae* (*Caryophyllaceae*) as inferred by nuclear rDNA sequences. – Manuscript.
- Rohrbach, P. 1869: Monographie der Gattung *Silene* L. – Leipzig.
- Runemark, H. 1969: Reproductive drift, a neglected principle in reproductive biology. – Bot. Not. **122**: 90–129.
- Stearn, W. T. 1983: Botanical Latin. – London.
- Talavera, S. & Muñoz Garmendia, F. 1989: Sinopsis del género *Silene* L. (*Caryophyllaceae*) en la península Ibérica y Baleares. – Anales Jard. Bot. Madrid **45**: 407–460.
- Webb, D. A. 1976: *Bellium* L., p. 112. – In: Tutin, T. G. et al. (eds.), Flora europaea **4**. – Cambridge.
- Williams, F. N. 1896: A revision of the genus *Silene* L. – J. Linn. Soc. Bot. **32**: 1–196.

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