

Fig. 1. A-D. Shape of cauline leaves – A-B: *S. integripetala* subsp. *greuteri* (K. Persson, 5.4.1985) – A: lower cauline leaf; B: upper cauline leaf. – C-D: *S. sedoides* subsp. *runemarkii* (Oxelman & Tollsten 1195) – C: lower cauline leaf; D: upper cauline 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. integripetala* subsp. *elaphonesiaca* (Jagel 48).



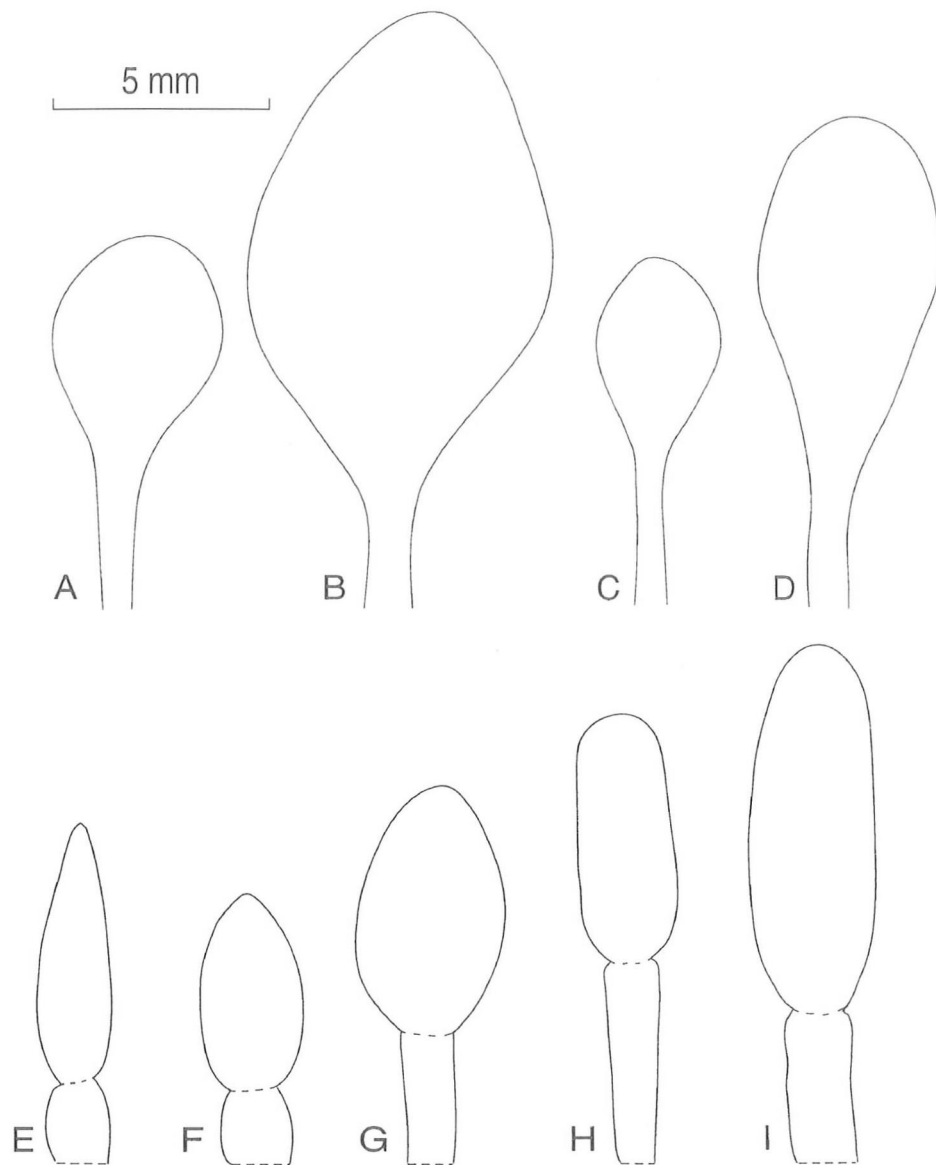


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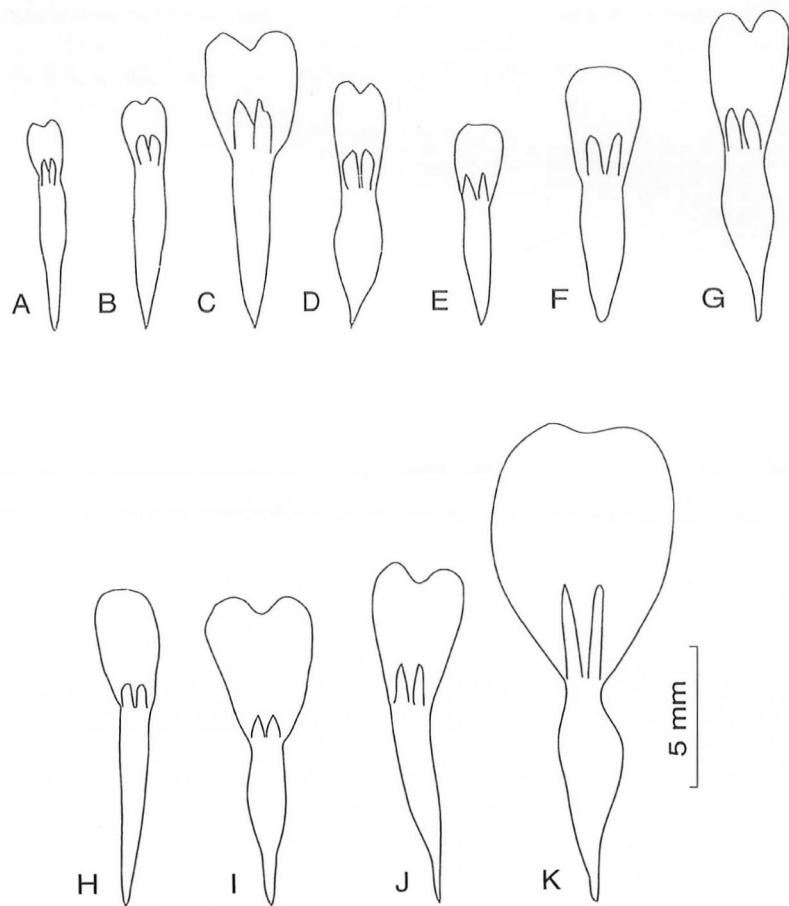


Fig. 2. Shape of petals – A: *S. sedoides* subsp. *sedoides* (Oxelman 2216); B: *S. sedoides* subsp. *sedoides* (Oxelman 2212); C: *S. sedoides* subsp. *runemarkii* (Oxelman & Tollsten 1195); D: *S. aegaea* (Oxelman 2214); E: *S. pentelica* (Oxelman 2217); F: *S. haussknechtii* (Oxelman & Tollsten 1451);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

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. integripetala*, where the four subspecies form discrete geographic and phylogenetic entities (Oxelman 1995). Three of the subspecies (subsp. *integripetala*, subsp. *greuteri*, and subsp. *elaphonesiaca*) are well separated by morphological characters, but subsp. *lidenii* is very similar to subsp. *integripetala*.

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 1951), 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-ovate 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. integripetala*, 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

### 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. integripetala* subsp. *integripetala*. 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. integripetala* subsp. *integripetala*, 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. integripetala* subsp. *integripetala* 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 Cardaean (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).

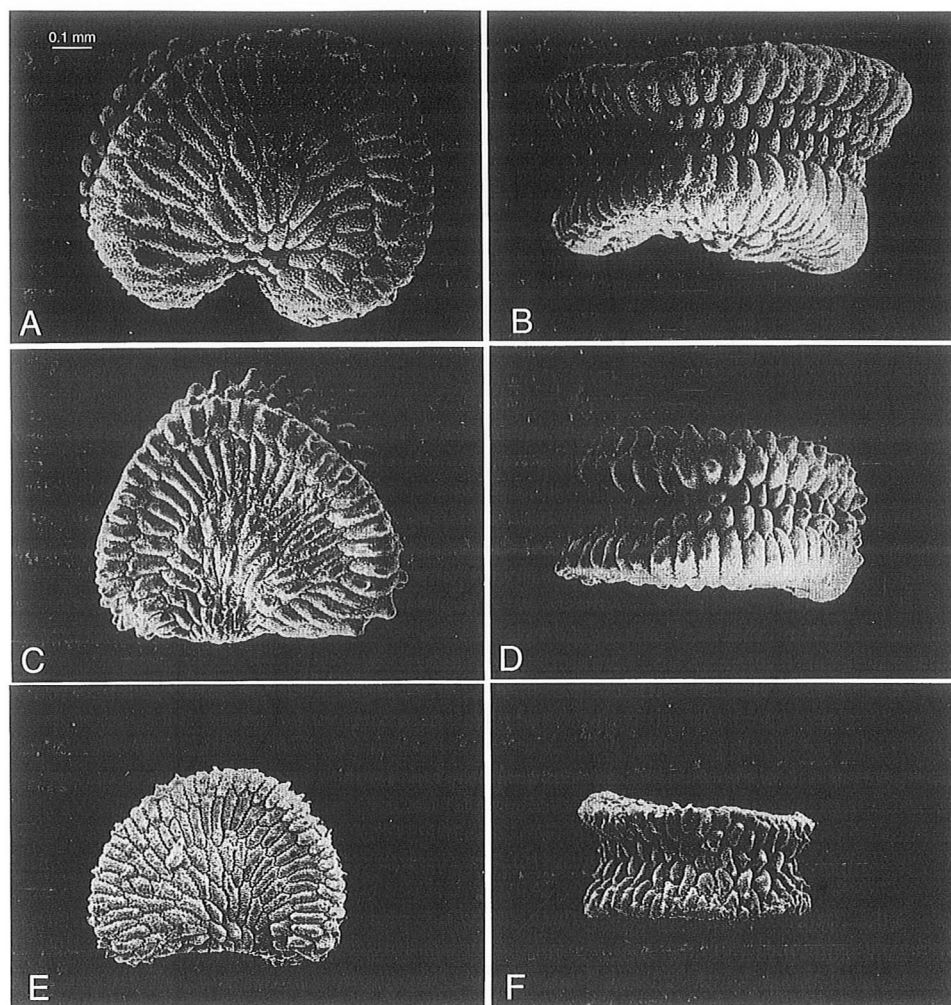


Fig. 3. Seeds – A-B: *S. integripetala* subsp. *integripetala* (Oxelman & Tollsten 389); C-D: *S. haussknechtii* (Harvig et al. 6742); E-F: *S. pentelica* (Stamatiadou 18894).

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.