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Silene subg. *Conoimorpha* (Caryophyllaceae) in Greece

Abstract

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On the basis of calyx morphology, petal shape and colour, and seed structure, eight native Greek taxa are characterized and mapped: *Silene ammophila* subsp. *ammophila*, E. Crete; *S. ammophila* subsp. *carpathae*, Karpathos; *S. sartorii*, Cyclades, E. Attica and Argolis; *S. grisebachii*, N. Aegean; *S. conica*, widespread; *S. subconica*, mainly N.E. Greece, extending to Central Greece and the E. Aegean; *S. lydia*, very scattered in N.E. and E. Central Greece; and *S. macrodonta*, Karpathos and Rhodes. The first four are Greek endemics. *S. grisebachii* is a species recently raised from varietal status. *S. conica* is polymorphic and occurs as a widespread variant with glandular-hairy calyces and a northerly eglandular variant.

Introduction

Silene subg. *Conoimorpha* (Otth) Endl. is a clear-cut taxonomic unit within the polymorphic genus *Silene*, and is sometimes treated as a genus of its own (*Pleconax* Raf., *Conosilene* Fourr.). It is characterized by a peculiar calyx with (15-)20 or more equal, parallel, non-anastomosing veins and by a unique chromosome number of $2n = 2x = 20$ [rarely 22] (as contrasted to $x = 12$ in all other *Silene* species). Other *Silene* species never show the typical calyx shape, conical in fruit, nor the high number (usually 30) of prominent and unbranched calyx veins of the “conoimorphs”. In Greece the subgenus is represented by several taxa, some of which are easily recognized while others, especially in the *S. conica* complex, are critical. They have been assigned to two sections by Greuter (1995), the monospecific *S. sect. Lydiae* Greuter (*S. lydia*) and *S. sect. Conoimorpha* Otth (the other species).

Silene conoidea L. has recently been collected on a roadside in Viotia (specimen: *Phitos & Kamari 23456a*, UPA!), where it was likely introduced by accident (Greuter & Pirker 1997). This may well prove an ephemeral show, and the species has therefore been excluded from our treatment.

The present paper relates the results of work for a diploma thesis (Pirker, unpubl.) in which the variation and taxonomic relevance of calyx morphology, petal shape and col-

our, and seed structure were studied for the native Greek representatives of the subgenus. A fuller descriptive account, taking into consideration other characters as well, with citation of nomenclatural types and with a key for the identification of taxa, has been published elsewhere (Greuter & Pirker 1997).

Material and methods

Herbarium specimens from Greece and neighbouring countries from the herbaria ATH, B, BRNM, C, FI, G, LD, PR, PRC, SOM and UPA, and from the private herbaria of T. Raus and W. Greuter, have been examined. Data for all Greek specimens were entered in the Flora Hellenica Database (Strid 1991).



Fig. 1. Greek distribution of *Silene ammophila* subsp. *ammophila* (Δ), *S. ammophila* subsp. *carpathae* (\blacktriangle), *S. sartorii* (\bullet), *S. grisebachii* (\circ), and *S. lydia* (\blacksquare).

Seed micrographs were made with an I.S.I. Super III A scanning electron microscope. Some of the seeds had to be cleansed for 3 min in distilled water with an ultrasonic cleansing device, Sonorex-Rapid GR 60. After air drying all seeds were directly mounted and sputtered in a low voltage cool sputter coater, Emitech K 550, with a gold-palladium-layer 20 nm thick.

Petal shape was studied both on live, cultivated plants and on herbarium specimens, using the preparation procedure of Melzheimer (1990), suitably modified. For mounting on transparent Astralon foil, dry flowers were soaked for at least 15-20 min, at room temperature, in 50-60 ml water with 1 ml (= 4 drops) of detergent added. The detached petals were spread out in a drop of water directly on Astralon foil cut to the size of a microscope slide. The calyx and reproductive parts were similarly mounted. For permanent conservation a covering foil was added and sealed with colourless nail varnish after removal of the remaining water. Flowers from cultivated plants were mounted directly in the fresh state, without water being added. On preparations made from fresh material, the petal venation is better visible and measurements are more accurate.

Greenhouse cultivated plants were sown in January and grown under an artificial daylight regime of 11 h; they were transplanted to the open in early April, flowering in May. Other samples were directly sown out of doors.

Results

Silene ammophila Boiss. & Heldr. in Boissier, Diagn. Pl. Orient. 8: 82. 1849 ≡ *Conosilene conica* subsp. *ammophila* (Boiss. & Heldr.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 374. 1972 ≡ *Conosilene conica* var. *ammophila* (Boiss. & Heldr.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 374. 1972 ≡ *Pleconax ammophila* (Boiss. & Heldr.) Šourková in Österr. Bot. Z. 119: 579. 1972 ≡ *Pleconax conica* subsp. *ammophila* (Boiss. & Heldr.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974 ≡ *Pleconax conica* var. *ammophila* (Boiss. & Heldr.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974.

Silene ammophila has light pink petals and the smallest calyces in the group, campanulate and with only 15-20 veins. The seeds in side view are circular with a narrow hilar notch (Fig. 5a), and their back is grooved. When the whitish waxy layer has been rubbed off, they are shiny and reddish coloured. The testa cells are smooth and lack tubercles; they are numerous, elongated and narrow on the lateral faces (Fig. 5b), resembling those of *S. sartorii* and *S. grisebachii*. Both subspecies of *S. ammophila* are sandy shore specialists.

Silene ammophila Boiss. & Heldr. subsp. *ammophila*

The petals of *Silene ammophila* subsp. *ammophila* are slightly notched. The fruiting calyx is 5-7 mm long. This taxon has only been collected on the coast and offshore islets of E. Crete (Fig. 1).

Silene ammophila subsp. *carpathae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 278. 1957 ≡ *Conosilene conica* var. *carpathae* (Chowdhuri) Á. Löve & Kjellq. in J.

Indian Bot. Soc. 50A: 374. 1972 \equiv *Pleconax ammophila* subsp. *carpathae* (Chowdhuri)
 Šourková in Österr. Bot. Z. 119: 579. 1972 \equiv *Pleconax conica* var. *carpathae*
 (Chowdhuri) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974 \equiv *Pleconax carpathae*
 (Chowdhuri) Ikonn. in Novosti Sist. Vysš. Rast. 14: 78. 1977.

Silene ammophila subsp. *carpathae* has truncate petal blades (Fig. 4a). The fruiting calyx is 7-9 mm long. The taxon is endemic to the Karpathos island group, but plants from the north-easternmost part of Crete (Paleokastro), here placed in subsp. *ammophila*, are to some extent intermediate between the two subspecies (Fig. 1).

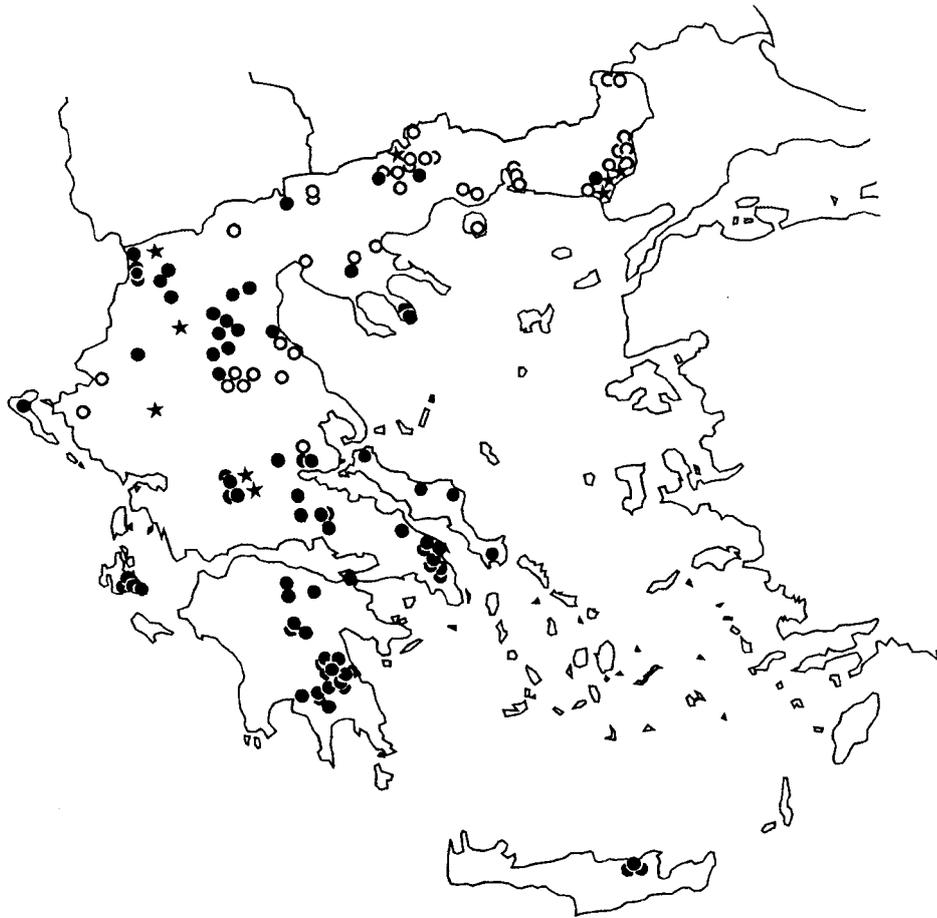


Fig. 2. Greek distribution of *Silene conica*: variant with glandular-hairy calyx (●), variant with eglandular-hairy calyx (○), and mixed populations with both glandular and eglandular hairy calyces (★).

Silene sartorii Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 5: 53. 1856 ≡ *Silene conica* subsp. *sartorii* (Boiss. & Heldr.) Chater & Walters in Feddes Repert. Spec. Nov. Regni Veg. 69: 49. 1964 ≡ *Conosilene conica* var. *sartorii* (Boiss. & Heldr.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 373. 1972 ≡ *Pleconax sartorii* (Boiss. & Heldr.) Šourková in Österr. Bot. Z. 119: 580. 1972 ≡ *Pleconax conica* var. *sartorii* (Boiss. & Heldr.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974.

Silene sartorii has bright purple, obcordate-cuneate petal blades (Fig. 4b). The scarcely inflated calyx (with 30 veins, as in the four following species) is typically rounded at the base in fruit and 10-13 mm long. The seeds (Fig. 5c) resemble those of *S. ammophila* in shape and colour but have a wider hilar notch and are dorsally flat to grooved. The numerous, narrow lateral testa cells (Fig. 5d) are smooth and lack tubercles. This species is endemic to the Cyclades and some sandy shores of Attica and the Argolis (Fig. 1). Records from Rhodes (Carlström 1987) are errors for *S. macrodonta*.

Silene grisebachii (Davidov) Pirker & Greuter, in Willdenowia 25: 137. 1995 ≡ *Silene subconica* var. *grisebachii* Davidov in Trav. Soc. Bulg. Sci. Nat. 8: 53. 1915 ≡ *Silene subconica* subsp. *grisebachii* (Davidov) Jordanov & Panov in Jordanov, Fl. Nar. Rep. Bălg. 3: 512. 1966 ≡ *Pleconax subconica* subsp. *grisebachii* (Davidov) Šourková in Österr. Bot. Z. 119: 580. 1972.

Silene grisebachii has long-exserted petal claws. It differs from the following three species chiefly in its seeds. In petal shape and size (Fig. 4c) it is rather similar to *S. subconica*, but petal venation corresponds more closely to that of *S. sartorii*. In the narrow, scarcely inflated calyx (mostly 15-18 mm long) it shows a superficial resemblance to *S. macrodonta*. The seeds resemble those of *S. ammophila* in colour; in side view (Fig. 5e) they are circular to cordate or somewhat irregular, and their back is flat to grooved. The numerous, narrow lateral testa cells (Fig. 5f) are sparsely and very minutely granular (much less so than in *S. conica* and *S. subconica*). This again is a sand shore specialist, occurring on the northern periphery of the Aegean sea (Fig. 1).

Silene conica L., Sp. Pl.: 418. 1753 ≡ *Conosilene conica* (L.) Fourr. in Ann. Soc. Linn. Lyon 16: 344. 1868 ≡ *Pleconax conica* (L.) Šourková in Österr. Bot. Z. 119: 579. 1972.
= *Silene conica* var. *glandulosa* Caldesi in Nuovo Giorn. Bot. Ital. 11: 339. 1879.

Silene conica has saturate pink (rarely white), cuneate-obcordate petal blades with a wide apical sinus (Fig. 4e-f). In N. Greece, where it may grow side by side with *S. subconica*, the calyx indumentum is normally eglandular, but elsewhere it is consistently glandular (Fig. 2); the distinctly inflated calyx is (10-)13-17(-19) mm long in fruit in the glandular variant but usually larger (mostly 15-20 mm long) in the eglandular variant. The reniform, flat-backed seeds (Fig. 5i, l) are covered by a greyish waxy bloom that may either be persistent or easily wiped off, and if so the seed colour is reddish brown. They are variable in structure, with or without tubercles; the lateral testa cells are proportionately wider and distinctly less numerous than in the taxa described before, and show various degrees of granularity (Fig. 5k, m). This is a grassland species occurring both in

weedy situations and semi-natural submediterranean therophyte communities; at least in northern Greece it shows a clear preference for siliceous substrates and is absent from limestone areas.

Silene subconica Friv. in Flora 18: 334. 1835 \equiv *Silene conica* subsp. *subconica* (Friv.) Fiori & Béguinot, Sched. Fl. Ital. Exsicc. 3: 363 [& in sched. No. 2864]. 1927 \equiv *Conosilene conica* var. *subconica* (Friv.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 374. 1972 \equiv *Pleconax subconica* (Friv.) Šourková in Österr. Bot. Z. 119: 580. 1972 \equiv *Pleconax conica* var. *subconica* (Friv.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974.
 \equiv *Silene juvenalis* Delile, Sem. Hort. Monspel. 1836: 28. 1837 \equiv *Silene subconica* var. *juvenalis* (Delile) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30 (1): 259. 1924 \equiv *Pleconax juvenalis* (Delile) Ikonn. in Novosti Sist. Vysš. Rast. 14: 76. 1977.



Fig. 3. Greek distribution of *Silene subconica* (●) and *S. macrodonta* (□).

Table 1. Provenances of the petal preparations of Fig. 4. For provenances marked with an asterisk (*), preparations were made from live plants raised from seeds; otherwise dry flowers from the herbarium specimen were used. (TR = herb. T. Raus.)

<i>Silene</i>	Fig.	Locality	Date	Collector (Herbarium)
<i>ammophila</i> subsp. <i>carpathae</i>	a	Karpathos: Kasos, N. coast	24 Apr 1982	Raus & Pleger 5717 (B)*
<i>sartorii</i>	b	Thira: Thira, N. coast	24 May 1990	Raus & Sipman 14994 (B)*
<i>grisebachii</i>	c	Volos: Paltsi	7 Jun 1974	Raus 2019 (TR)
<i>lydia</i>	d	Larisa: Mt. Ossa above Ambelakia	2 May 1992	Anagnostopoulos & Athanasiou 2398 (UPA)
<i>conica</i>	e	Serres: S.W. of Hrisopji	25 Jun 1989	Willing 7285 (B)*
<i>conica</i>	f	Grevena/Voion: Mt Vourinos	22 Jul 1989	Höner 1594 & Potthoff 1215 (B)*
<i>subconica</i>	g	Ajia: Kato Kalamaki	8 May 1974	Raus 1453 (TR)
<i>macrodongta</i>	h	Turkey: E. of Antalya	14 Apr 1959	Hennipman & al. 348 (B)

= *Silene tempskyana* Freyn & Sint. in Bull. Herb. Boissier 5: 584. 1897 = *Pleconax tempskyana* (Freyn & Sint.) Šourková in Österr. Bot. Z. 119: 580. 1972.

Silene subconica is unique in its pale pink or white, large, obcordate petal blades with a narrow apical sinus (Fig. 4g). The calyx indumentum is always glandular and the calyx in fruit is distinctly inflated, often vesicular and (10-)15-20 mm long. When forming mixed stands with *S. conica* it maintains its distinctive features, and no intermediates have been observed.

The cordate to reniform, flat-backed seeds (Fig. 5n, p) agree with those of *Silene conica* in all characters and show a virtually identical range of variation (Fig. 5o, q). The species has the same habitat preferences as *S. conica* but is absent from W. and S. Greece (Fig. 3). Plants from the E. Aegean islands (Lesvos, Samos, Kalimnos, Nisiros) have a narrower, less inflated fruiting calyx and superficially resemble *S. grisebachii* but the seeds, when present, make their attribution to *S. subconica* reasonably safe.

Silene macrodongta Boiss., Diagn. Pl. Orient. 1: 37. 1843 = *Conosilene conica* subsp. *macrodongta* (Boiss.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 374. 1972 = *Pleconax macrodongta* (Boiss.) Šourková in Österr. Bot. Z. 119: 580. 1972 = *Pleconax conica* subsp. *macrodongta* (Boiss.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974.

= *Silene pamphylica* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient. 8: 81. 1849 = *Silene macrodongta* var. *pamphylica* (Boiss. & Heldr.) Boiss., Fl. Orient. 1: 581. 1867 = *Pleconax pamphylica* (Boiss. & Heldr.) Ikonn. in Novosti Sist. Vysš. Rast. 14: 77. 1977.

Silene macrodongta is fairly similar in petal shape (Fig. 4a) to *S. lydia*. It differs from all other species by its 50-60 very tightly set calyx veins. The fruiting calyx is 12-16 mm long and scarcely inflated. The seeds in side view are circular with a deep hilar notch

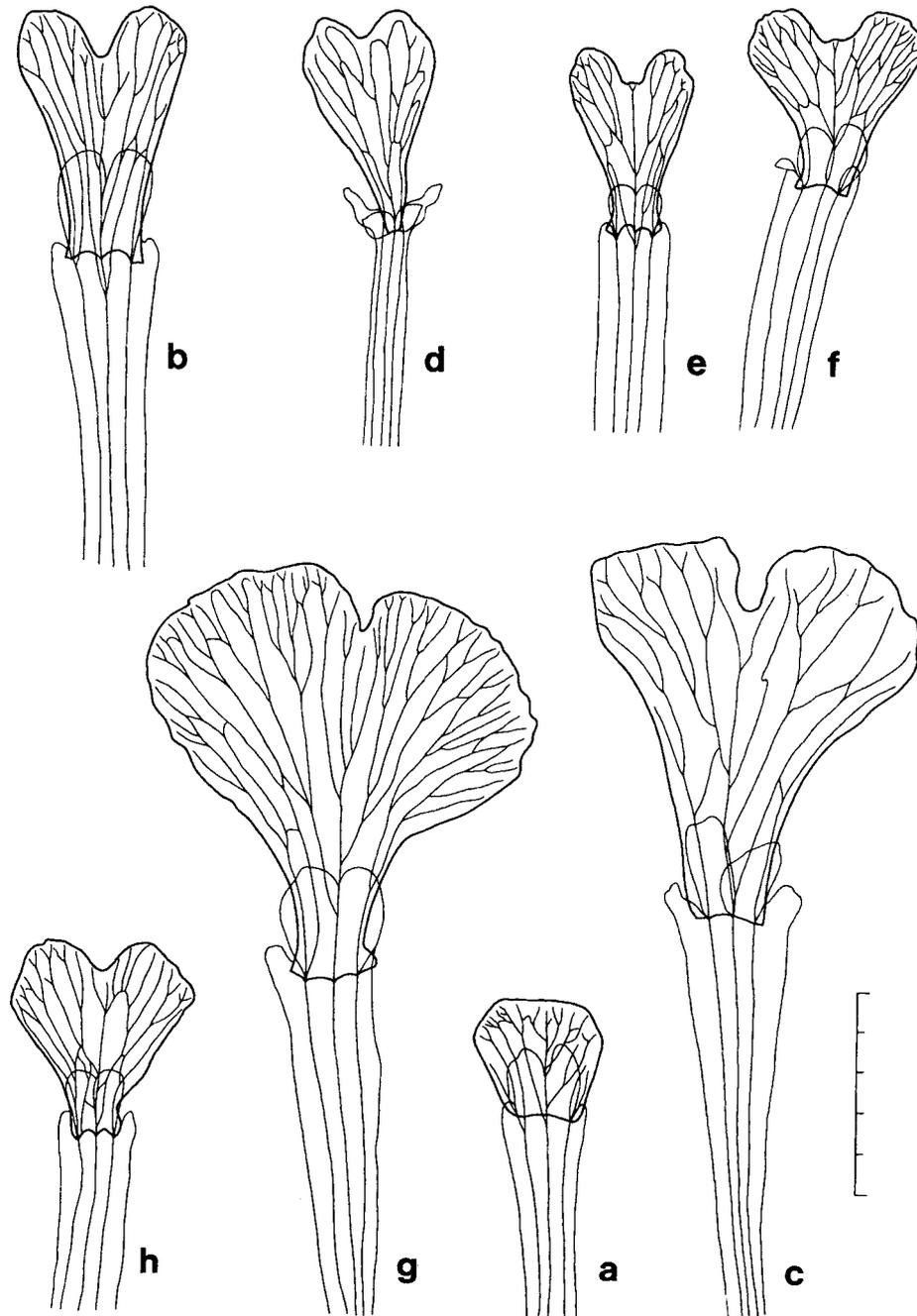


Fig. 4. Petal shapes: **a**, *Silene ammophila* subsp. *carpathae*; **b**, *S. sartorii*; **c**, *S. grisebachii*; **d**, *S. lydia*; **e-f**, *S. conica*; **g**, *S. subconica*; **h**, *S. macrodonta* (see Table 1 for provenances). – Scale = 5 mm.

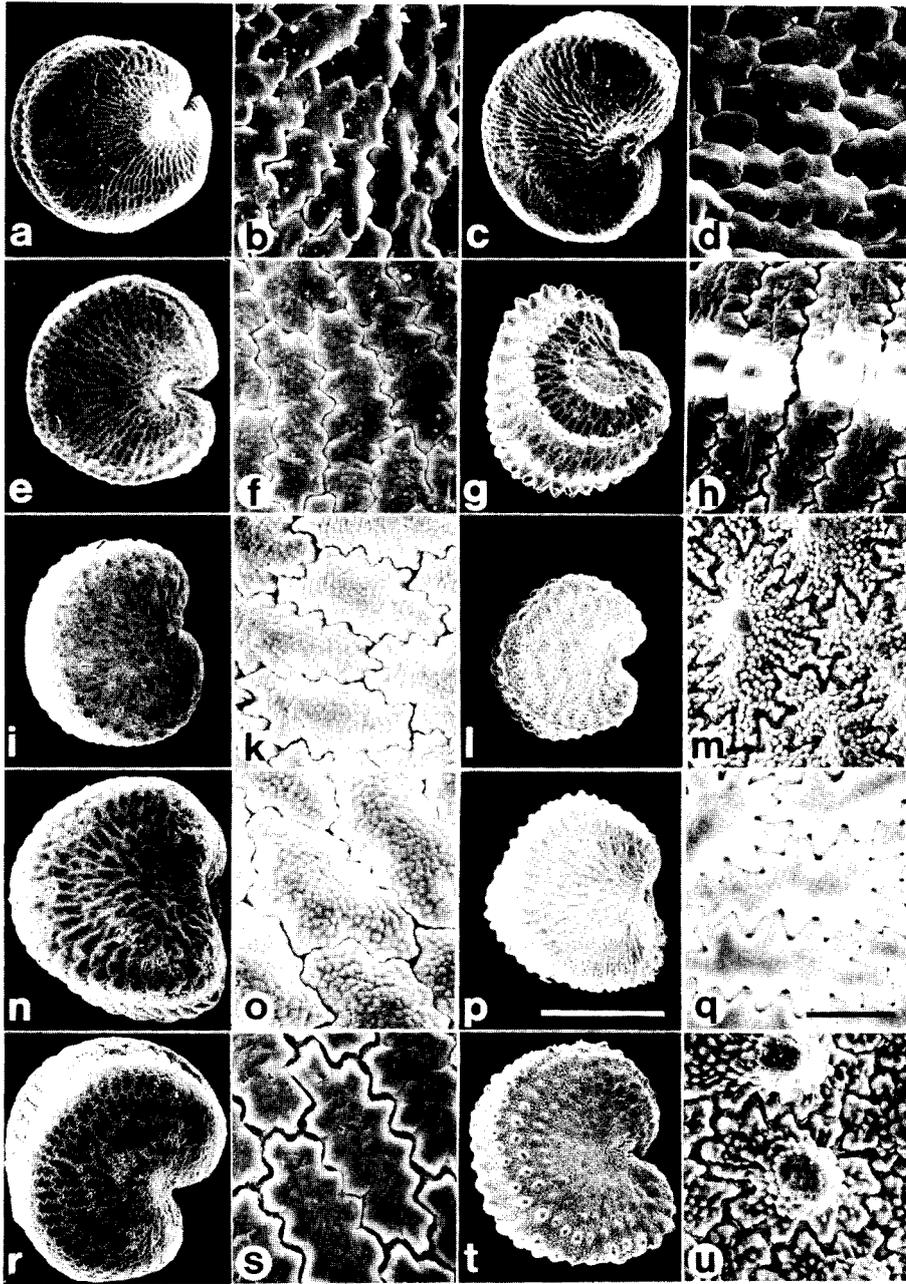


Fig. 5. Scanning electron micrographs of seeds in side view, and details thereof: **a-b**, *Silene amrophila* subsp. *carpathae*; **c-d**, *S. sartorii*; **e-f**, *S. grisebachii*; **g-h**, *S. lydia*; **i-m**, *S. conica*; **n-q**, *S. subconica*; **r-u**, *S. macrodonta* (see Table 2 for provenances). – Scale bars for a, c, e, g, i, l, n, p, r, t = 500 μm , scale bars for b, d, f, h, k, m, o, q, s, u = 50 μm .

(Fig. 5r, t) and a shallowly grooved back. The lateral testa cells (Fig. 5s, u) are proportionately wide, granular and usually tubercled; seeds with smooth testa cells lacking tubercles have only been found in one of the specimens from Rhodes, which is typical *S. macrodonta* in every other respect. *S. macrodonta* is an eastern species, just skirting the Greek border in the south-easternmost corner of the country (Karpathos, Rhodes) where it is a rare member of semi-natural therophyte communities (Fig. 3).

Silene lydia Boiss., Diagn. Pl. Orient. 1: 37. 1843 \equiv *Conosilene conica* subsp. *lydia* (Boiss.) Á. Löve & Kjellq. in J. Indian Bot. Soc. 50A: 374. 1972 \equiv *Pleconax lydia* (Boiss.) Šourková in Österr. Bot. Z. 119: 580. 1972 \equiv *Pleconax conica* subsp. *lydia* (Boiss.) Á. Löve & Kjellq. in Lagasalia 4: 14. 1974.
= *Silene harrisii* Turrill in Bull. Misc. Inform. Kew 1918: 267. 1918.

Silene lydia is the only species in which the corona is concolorous with the purplish pink, shallowly emarginate petal blades (Fig. 4d); in all other taxa the corona is whitish. The species is furthermore unique in its trimorphic calyx indumentum with long, multicellular eglandular and short glandular as well as eglandular hairs; the calyx is usually 15-19 mm long and not inflated. The seeds in side view (Fig. 5g) are almost orbicular, and their back is flat to convex. They are covered by a persistent waxy bloom, yellowish to grey. The lateral testa cells (Fig. 5h) are numerous, narrow and elongate, densely granular, and bear single, prominent tubercles in their centre, which taken together form regular, concentric, almost cristate rows. *S. lydia* has scattered occurrences in N.E. Greece, E. Central Greece, and Attica (Fig. 1). It is a member of semi-natural to weedy therophyte communities.

Discussion

Petal shape and colour are perhaps the best suited characters for distinguishing between the species, especially when combined with calyx venation and indumentum. Unfortunately, much of the flower features is lost in herbarium specimens, which doubtless accounts for their having been so neglected in the past.

Seed surface is very variable within some of the taxa, sometimes even within populations, especially as regards the presence and size of tubercles. Nevertheless, three seed types can be recognized which characterize species groups: (A) the *Silene sartorii* type, found in *S. sartorii*, *S. ammophila* and *S. grisebachii*, with seeds always lacking tubercles and with numerous, narrow cells on the lateral faces; (B) the *S. conica* type, found in *S. conica*, *S. subconica* and *S. macrodonta*, in which the cells of the lateral faces are less numerous, less regular, and comparatively wide; and (C) the *S. lydia* type, only found in that species, with numerous narrow cells laterally, each bearing a prominent tubercle in the middle, so that the tubercles form dense, regular concentric rows. Type B seeds are variable as to tuberculation, cell margins and surface microstructure within all three species concerned.

The usefulness of seed surface microstructure for the purpose of taxon definition and identification has sometimes been overrated, and variation has not been sufficiently taken into account (see e.g. Melzheimer 1977, 1980). Except for *Silene lydia*, seed characters

alone do not permit identification of species. There seems to be no correlation between intraspecific variation of seed surface characters and other morphological features. However, the variability itself appears to be characteristic of certain species (and a certain seed type) and to lack in others. The fact that the three sandy shore specialists share the same, uniform seed type may also be of some relevance, both taxonomically (monophyletic group?) and ecologically (seed dispersal?).

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