Notes RBG Edinb. 43(2): 283–297 (1986)

SPERGULA AND SPERGULARIA IN THE BRITISH ISLES

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ABSTRACT. A Flora account, accompanied by notes on reproductive biology, biosystematics and hybridization, is given for *Spergula* and *Spergularia* (Caryophyllaceae) in the British Isles.

The following account was prepared for the now discontinued *Flora of Great Britain and Ireland* project. The information was obtained from various sources and is published here since it is not available elsewhere in collected form. The format follows that of the projected Flora.

Recorded distributions are given in Perring & Walters (1976), *Atlas of the British Flora* (Ed. 2).

SPERGULA L.

Sp. Pl. 440 (1753). (Lectotype species: *S. arvensis* L.).

Annual (rarely perennial*) herbs. Stems ascending, often decumbent and much branched at the base. Leaves linear, obtuse, decussate; stipules scarious, not united to surround the node, deciduous; leaf-fascicles (short leafy lateral branches) borne on both sides at each node. Perianth 5-merous; sepals free, green with scarious margins; petals white, entire; stamens 5–10; styles 5 (less commonly 3*). Capsule ovoid to subglobose, dehiscing by 5-valves (less commonly 3*). Seeds often winged.

Habitat & Distribution. Sandy or peaty soils; fields, waste places, pine groves, etc. One species, *Spergula arvensis*, is nearly cosmopolitan as a weed of cultivated ground. The other four species are found in Europe, the Mediterranean region, the Middle East (extending into Pakistan), and North Africa (extending into Macaronesia).

Reproductive Biology. The majority of species are inbreeding annuals—detailed information is available for *S. arvensis* (q.v.). The largely autogamous breeding-system has also been investigated in the non-British *S. fallax* (Ratter, 1968).

Taxonomy & Biosystematics. Five or six species. Some authors have united *Spergula* and *Spergularia* but there are sufficient diagnostic characters to maintain the distinction of the two genera—see under *Spergularia*. The basic number of the genus is $x = 9$ and all three species for which the chromosome number is known are diploids ($2n = 18$).

Friedrich, H. C. (1962). In Rechinger fil. (ed.) *Hegi Illustrierte Flora von Mitteleuropa* ed. 2. 3.2:775–782.

Griffiths, B. M. (1922). Growth experiments on Spergula and Plantago. *J. Bot. Lond.* 60:228–230.

Moss, C. E. (1920). *The Cambridge British Flora* 3:15–17. Cambridge.

*Only in non-British species.

New, J. K. (1958). A population study of Spergula arvensis, 1. Two clines and their significance. *Ann. Bot., Lond.*, n.s. 22:457–477.
New, J. K. (1959). A population study of Spergula arvensis, 2. Genetics and breeding behaviour. *Ann. Bot., Lond.*, n.s. 23:23–33.
New, J. K. (1961). Spergula arvensis L., in Biological flora of the British Isles. *J. Ecol.* 49:205–215.
New, J. K. (1978). Change and stability of clines in Spergularia arvensis L. (corn spurrey) after 20 years. *Watsonia* 12:137–143.
New, J. K. & Herriott, J. C. (1981). Moisture for germination as a factor affecting the distribution of the seedcoat morphs of Spergula arvensis L. *Watsonia* 13:323–324.
Ratter, J. A. (1968). The chromosome numbers of Spergula fallax and Hypertelis bowkeriana. *Notes RBG Edinb.* 28: 189–190.

Seeds subglobose, keeled or with a narrow wing; leaves channelled beneath . . . . . 1. *S. arvensis*
Seeds compressed, broadly winged; leaves not channelled beneath 2. *S. morisonii*

1. S. arvensis L., Sp. Pl. 440 (1753).
Spergula sativa Boenn., Prodr. Fl. Monast. 135 (1824); *Spergula vulgaris* Boenn., Prodr. Fl. Monast. 135 (1824).
Vernacular Name. Corn Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:464 (1961); Ross-Craig, *Drawings Br. Pl.* 5:pl. 61 (1951).

Annual herb with ascending geniculate stems, 4–50cm, usually branched at the base. Leaves 1–4cm, linear, fleshy, channelled beneath. Stem and leaves slightly to strongly viscid with glandular hairs which when abundant cause the plants to appear grey-green instead of grass-green. Inflorescence a cymose panicle with small ± scarious bracts. Sepals 2·5–4mm, ovate obtuse, ± glandular-hairy. Petals white, obovate, obtuse, slightly exceeding the sepals. Stamens 5–10. Capsule 4–5mm, ovoid-conical, exceeding the sepals. Seeds subglobose, 1·1–1·4mm, with a very narrow-wing or ridge, covered with club-shaped papillae or minutely tuberculate. $2n = 18$.

Habitat & Distribution. Native. Distributed throughout the British Isles. A locally abundant calcifuge weed of arable land, particularly on light sandy and on peaty soils. It is almost cosmopolitan in its world distribution, although only occurring at higher altitudes in the tropics.

Reproductive Biology. Mainly inbreeding due to automatic self-pollination of the flowers—the length of the stamens being such that pollen is shed on to the stigmas when the flowers are closed. New (1959) has estimated that at least 97% selfing occurs in nature, basing her calculations on the percentages in ten populations of plants heterozygous for the papillose v. non-papillose seed character. As in *Spergularia*, the flowers produce an unpleasant odour particularly attractive to hoverflies, but other insects are very occasionally seen working the flowers—insect visits must bring about the up to 3% outcrossing estimated by New. Flowering is from mid June to September.

Variation & Biosystematics. Numerous varieties have been described by continental authors but only three are usually recognized for the British Isles, two of which are based largely on the seed coat character:
Var. **vulgaris** (Boenn.) Mert. & Koch, Deutschl. Fl. 3:360 (1831) (*S. vulgaris* Boenn., Prodr. Fl. Monast. 135 (1824)). Seeds brownish-black covered with pale club-shaped papillae, wing narrow or absent.* Stem and leaves less glandular-hairy.
Var. **sativa** (Boenn.) Mert. & Koch, Deutschl. Fl. 3:360 (1831) (*S. sativa* Boenn., Prodr. Fl. Monast. 135 (1824)). Seeds black, dull, minutely tuberculate, narrowly winged. Stem and leaves glandular-hairy, viscous.

New (1959) showed that the seed papilla character is controlled by a single gene with two alleles and that heterozygotes have about half the number of seed-papillae of plants homozygous for the papillate allele. Hairiness, on the other hand, is controlled by many loci and its inheritance is not associated genetically with the seed character. She also discovered (New, 1958, 1961) that 'there is a cline in the frequency of these two seed forms across the British Isles in a north-north-west direction. In the south the papillate form (var. *vulgaris*) is predominant, but with increasing distance north and west it is gradually replaced by the non-papillate form (var. *sativa*). There is also a similar frequency cline in the hairiness character; the slightly hairy form is predominant in the south-east and the densely hairy form is predominant in the north and west. The fact that slight hairiness is broadly associated with papillate seeds and that dense hairiness is associated with non-papillate seeds has meant that the varieties *vulgaris* and *sativa* have often been raised to specific rank. However, in localities where both seed forms and both hairiness forms occur, the slight hairiness is not particularly associated with papillate seeds nor the dense hairiness with non-papillate seeds. There is therefore no adequate justification for specific separation.'†

New (1958, 1981) also demonstrated selective differences which throw light on the distribution of the forms: *a*) the non-papillate form produces a lower proportion of fertile capsules when grown at high temperature and low humidity; *b*) the non-papillate seeds germinate more readily than the papillate seeds at low temperatures, whereas at higher temperatures the reverse is true; and *c*) papillate seeds also have the capacity to germinate at lower water tensions than non-papillate.

Repeating the study after twenty years she showed that the cline for seed-character was still essentially similar but that there had been a south-south-east shift in the hairiness morph which was perhaps attributable to a lowering of summer temperatures (New, 1978).

A third variety occurs in the Channel Islands:
Var. **nana** Linton in J. Bot. Lond. 45:380 (1970) (Illustrations: Moss, *Cambridge British Flora* 3: pl. 15 (1920); McClintock, *The Wild Flowers of*

*However, New (1961) states that she has never seen seeds without a wing.

†As had been done by Boenninghausen (loc. cit.) and which was supported by Griffiths (1922)—the latter, who used the names *S. arvensis* L. and *S. sativa* Boenn., based his conclusion on the observation that the two forms bred true when growing in a mixed population, but we now know that this is due to autogamy rather than to any barrier to hybridization.

Guernsey 80 (1975)). Dwarf ephemeral. Shoots prostrate or decumbent. Leaves very short, 3–13mm. Flowers early, January to March, and grows in native habitats such as the turf of sandy commons and cliffs.

Hybrids. There is no evidence of hybridization with any other species. Crosses between the non-papillate- and the papillate-seeded forms are readily obtained artificially and occur occasionally in nature—there is no evidence of diminished fertility as compared with the parents (New, 1961). Crosses between the densely and medium hairy forms are also readily obtained artificially and most probably occur in nature.

Diagnostic characters. Distinguished from *S. morisonii* by the narrowly winged or ridged, as opposed to broad-winged, seeds, and the leaves having a channel on the lower surface.

2. S. morisonii Boreau in Duchartre, Rev. Bot. 2:424 (1847).
S. pentandra auct. non L.; *S. vernalis* auct.
Illustration. Hegi Illustrierte Flora von Mitteleuropa 2nd ed. 111/2 part 5:779 (fig. 333) (1962).

Annual herb with ascending stems, 5–30cm, glabrous or sparsely glandular-pubescent. Leaves 1–2cm, linear, not channelled beneath, ± glandular; leaf-fascicles dense, conspicuously shorter than the internodes. Sepals 4mm, ovate, acuminate; petals white, about equalling the sepals, ovate, obtuse, overlapping at their margins. Stamens 5–10. Capsule 5mm, slightly exceeding the sepals. Seeds 1–1·5mm (including wing), laterally compressed, with a brownish striate wing narrower than the seed. $2n = 18$.

Habitat & Distribution. Probably introduced. Found in 1943 in Sussex, on sandy cultivated ground on the heathland between Crowborough and Tunbridge Wells. C Europe from Spain, N Italy, and Hungary northwards to S Scandinavia, Germany and Poland; NW Africa.

Reproductive Biology. Probably mainly autogamous.

Variation & Biosystematics. Forms and a variety of the species have been recognized on the continent (Friedrich, 1962). The species is diploid ($2n = 18$).

Diagnostic characters. Distinguished from *S. arvensis* by the broad-winged seeds and the short-leaves without a channel on the undersurface. It differs from the very similar *S. pentandra* L., which is common in S and C Europe, in the seed being wider than its brownish-wing (as opposed to the seed being ± as wide as its transparent, shining wing) and the petals being ovate, obtuse and contiguous (as opposed to lanceolate, acute and non-contiguous).

SPERGULARIA (Pers.) J. & C. Presl

Fl. Čechica 94 (1819)—nom. conserv. (Type species: *S. rubra* (L.) J. & C. Presl).
Arenaria L., Sp. Pl. 423 (1753)—pro min. parte; *Alsine* L., Sp. Pl. 272 (1753)—pro parte; *Buda* Adans., Fam. Pl. 2:507 (1763); *Lepigonum* Fries, Fl. Suec. Mant. 3:32 (1842).

Herbs, sometimes woody at the base. Stems erect, decumbent or procumbent, dilated at the nodes, somewhat flattened. Leaves linear, decussate, often fleshy, with pale scarious stipules united to surround the node, forming ± triangular structures on either side of the stem; leaf-fascicles (short leafy lateral branches) when present borne only at one side at each node. Perianth 5-merous; sepals free, green, with scarious margins; petals entire; stamens 1–10; styles 3. Capsule dehiscing by 3 valves. Seeds often winged.

Habitat & Distribution. The genus contains about 50 species and is widely distributed in both northern and southern hemispheres. There are two main centres of diversity: the Mediterranean region and a rather diffuse New World area from temperate South America along the west coast of South and Central America northwards to California. In addition to species more or less confined to these centres, there are others such as *S. marina* and *S. media* which are almost cosmopolitan. The principal habitats are coastal rocks, sands, and salt-marshes, inland desert and saline areas, and waste places.

Reproductive Biology. The genus contains large-flowered species, adapted to outbreeding, with abundant production of pollen and nectar, and tiny-flowered species which are inbreeders and have a greatly reduced pollen-output. Between these two extremes there are species exhibiting a complete range of intermediate conditions and breeding systems which are compromises between out- and inbreeding. As might be expected, outbreeding species are usually long-lived perennials of relatively stable habitats, whilst the extreme inbreeders are ephemeral weeds. In the British flora the former group is exemplified by *S. rupicola* and the latter by *S. bocconii*—the approximate total production of pollen-grains per flower is 38000 in the former and 750 in the latter, and the pollen grain/seed ratio about 350/1 and 15/1 respectively. The other British species lie at various intermediate stages between these two. All species investigated are self-compatible, and all British species can be self-pollinated by the stigmas reflexing and touching the anthers of the same flower. Nectar is secreted on the receptacle and in the large-flowered species, where its production is most copious, lies as little drops around the bases of the staminal filaments. The flowers have a rather unpleasant foetid scent and are very attractive to hoverflies.

Details of the breeding system of a number of species and associated evolutionary trends are given in Ratter (1976).

Hybrids. Only one natural interspecific hybrid, *S. marina* × *rupicola*, occurs in the British Isles, although others have been reported erroneously. Four other interspecific hybrids involving the British species were synthesized in an extensive biosystematic study of the genus (summarized in Ratter, 1976). All hybrids, both natural and synthetic, between British species are completely infertile as a result of chromosomal sterility.

Seed-incompatibility, involving the abortion of the developing hybrid embryo, and lethal chlorosis of seedlings of interspecific hybrids of *S. rubra* are important barriers to hybridization in the genus (Ratter, 1973b).

The wild hybrid is described under *S. rupicola* and comments on synthetic and putative hybrids are given under the relevant species.

Taxonomy & Biosystematics. Some authors have united *Spergularia* and *Spergula*, but the two genera can be separated on stipular and anatomical characters, as well as on a striking difference in facies caused by *Spergularia* producing only one axillary leaf-fascicle (short lateral shoot) at each node, whereas *Spergula* produces two. The two genera are also separated in most cases by style number (always three in *Spergularia*, but usually five in *Spergula*) and on other lesser characters, so there is a good case for maintaining their distinctness.

The basis number of the genus is x=9 and the most frequent chromosome numbers are 2n=18 and 36, but hexaploids (2n=54) and octoploids (2n=72) are known. Cytological data are presented in Ratter (1964) and briefly summarized in Ratter (1976). Interspecific hybrids show great variation in meiosis: in some there is a regular production of bivalents whilst in others there is much irregularity and associated chromosomal sterility.

Blackburn, K. B. & Morton, J. K. (1957). The incidence of polyploidy in Caryophyllaceae of Britain and of Portugal. *New Phytol.* 56:344–351.

Lousley, J. E. (1935). Short notes on some interesting British plants. *J. Bot. Lond.* 73:256–260.

Lousley, J. E. (1936). Spergularia Bocconei (Soleir.) Steudel × S. salina Presl. *Rep. Bot. Soc. Exch. Club Brit. Isles* 9:25.

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Monnier, P. (1975a). Systématique et biosystématique du genre Spergularia dans le bassin méditerranéen occidental (essai de taxonomie synthetique). III. I. Série du Spergularia marginata (DC.) Kittel (=groupe Pterospermae). *Candollea* 30:121–155.

Monnier, P. (1975b). Op. cit. III. 3. Section des 'Heterospermae' (=Série de S. salina). *Naturalia monspeliensia, sér. Bot.* 25:65–87.

Moss, C.E. (1920). *The Cambridge British Flora 3*:17–23. Cambridge.

Ratter, J. A. (1964). Cytogenetic studies in Spergularia: I, cytology of the old world species. *Notes RBG Edinb.* 25:293–303.

Ratter, J. A. (1965a). Op. cit.: II, an attempt to discover cytogenetic relationships of some species. *ibid.* 26:203–223.

Ratter, J. A. (1965b). Op. cit. III, some interspecific hybrids involving S. marina (L). Griseb. *ibid.* 26:224–236.

Ratter, J. A. (1969a). Op. cit.: IV, some further interspecific hybrids. *ibid.* 29:213–223.

Ratter, J. A. (1969b). Op cit.: V, some interspecific hybrids involving S. media (L.) C. Presl. *ibid.* 29:225–232.

Ratter, J. A. (1972). Op. cit.: VI, the evolution of true breeding, fertile tetraploids from a triploid interspecific hybrid. *ibid.* 32:117–125.

Ratter, J. A. (1973a). Op. cit.: VII, cryptic speciation in S. media (L.) C. Presl and S. marina (L.) Griseb, *ibid.* 32:291–296.

Ratter, J. A. (1973b). Op. cit.: VIII, barriers to the production of viable interspecific hybrids. *ibid.* 32:297–301.

Ratter, J. A. (1975). Spergularia, in Stace, C. A. (ed.), *Hybridization and the Flora of the British Isles,* pp. 176–178. London.

Ratter, J. A. (1976). Cytogenetic studies in Spergularia: IX, summary and conclusions. *Notes RBG Edinb.* 34:411–428.

Salisbury, E. J. (1958). Spergularia salina and Spergularia marginata and their heteromorphic seeds. *Kew Bull.* 13:41–51.

Sterk, A. A. (1969a). Biosystematic studies on Spergularia media and S. marina in the Netherlands: I, the morphological variability of S. media. *Acta Bot. Neerl.* 18:325–338.

Sterk, A. A. (1969b). Op. cit.: II, the morphological variability of S. marina. *ibid.* 18:467–476.

Sterk, A. A. (1969c). cit.: III, the variability of S. media and S. marina in relation to the environment, *ibid.* 18:561–577.

Sterk, A. A. (1969d). Op. cit.: IV, reproduction, dissemination, karyogenetics and taxonomy, *ibid.* 18:639–650.

Sterk, A. A. & Dijkhuizen, L. (1972). The relation between the genetic determination and the ecological significance of the seed wing in Spergularia media and S. marina. *ibid.* 21:481–490.

KEY TO THE SPECIES

1. Perennials with thick woody rootstocks; sepals 4mm or more . 2
+ Annuals or short-lived perennials with slender taproots; sepals usually less than 4mm 4

2. Plant densely glandular-pubescent throughout; petals concolorous pink; stamens 10; seeds black, unwinged; maritime cliffs, rocks and walls in the S & W . . . . . 3. *S. rupicola*
+ Plant glabrous, or glandular-hairy only above; petals uniformly white, or pink with a white base; stamens 10 or less; seeds brown, often winged; salt-marshes or other maritime habitats and inland saline areas 3

3. Stamens 10 (rarely 9, 8 or 7); capsule 7–10mm; seeds usually all with entire scarious wing, more rarely all unwinged or dimorphic 4. *S. media*
+ Stamens 1–5 (rarely –8); capsule 3–6mm; seeds all unwinged, or a few seeds at the base of the capsules with broad scarious wings with erose margins . . . . . 5. *S. marina*

4. Stipules lanceolate-acuminate, silvery; leaves awned; stamens usually 10; petals uniformly pink . . . . . 1. *S. rubra*
+ Stipules broadly triangular, scarious; leaves mucronate; stamens less than 10; petals white with pink tips, or entirely white . . . 5

5. Leaves fleshy; capsule usually more than 4mm; seeds unwinged or with some winged seeds present, seed-body at least 0·6mm; widespread in salt-marshes and waste places near the sea . . . 5. *S. marina*
+ Leaves not fleshy; capsule less than 4mm; seeds unwinged, 0·3–0·45mm; rare casual of ruderal habitats near the sea, Cornwall, Suffolk and Channel Is. . . . . 2. *S. bocconii*

1. S. rubra (L.) J. & C. Presl, Fl. Čechica 94 (1819).
Arenaria rubra L. ∝ *campestris* L., Sp. Pl. 423 (1753), (described from Europe—in Europae arenosis collibus); *Alsine rubra* (L.) Crantz, Institutiones 2:407 (1766); *Buda rubra* (L.) Dumort., Fl. Belg. 110 (1827); *Lepigonum rubrum* (L.) Fries, Fl. Suec. Mant. 3:33 (1842); *Spergularia campestris* (L.) Aschers. in Bot. Zeit. 17:292 (1859) non Willk. & Lange.
Vernacular Name. Sand Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:458 (1961); Ross-Craig, *Drawings Br. Pl.* 5: pl. 62 (1951).

Annual to perennial herb with slender to somewhat woody tap-root; shoots 5–25cm, usually many, procumbent, diffuse, ± glandular-hairy. Leaves 4–25mm, awned, not fleshy, very fasciculate; stipules lanceolate, acuminate, silvery, very conspicuous on the young shoots. Inflorescence glandular-hairy, usually with bracts almost as long as foliage leaves, pedicels usually longer than calyces. Sepals 3–4mm, glandular-hairy; petals about as long as the sepals, uniformly pink. Stamens (5–)10. Capsule 4–5mm, about equalling the sepals. Seeds 0·45–0·55mm, dark brown, subtrigonous, tuberculate. 2n = 36.

Habitat & Distribution. Native. Throughout the British Isles except for the Outer Hebrides, Orkney and Shetland. Widely distributed in Europe and the northern hemisphere, and introduced into Australia. Dry sandy and gravelly soils, not halophilous, paths, cracks of pavements, etc., ascending to over 2000m in the Alps.

Reproductive Biology. Probably mainly inbreeding due to automatic self-pollination of the flowers, but with some outbreeding taking place. Generally there is no reduction in stamen number such as occurs in many inbreeding species, and the average pollen output per flower is 5000 grains—more than 10 times the number produced by the extreme inbreeders of the genus. The flowering period is very long, extending from May to October, and seed production is also prolonged, commencing in June.

Variation & Biosystematics. S. rubra is very variable in size, ranging from tiny plants in the cracks of pavements to many-stemmed prostrate mats up to 50cm or more in diameter. All British plants so far recorded have been tetraploid, 2n = 36, but a hexaploid race (2n = 54) is widespread in the Mediterranean area.

Hybrids. There are no records of wild hybrids. Artificial crossing with *S. marina*, *S. media* and *S. rupicola* produces abundant seeds, but although there is good germination the seedlings in almost all cases develop a lethal chlorosis (Ratter, 1973b). Viable hybrids were produced by only a single combination of stocks of *S. rubra* and *S. marina* (Ratter, 1965b). The synthetic hybrids were vigorous and intermediate in morphology between the parents, but with abnormally small stamens, a very irregular meiosis (the commonest numbers of bivalents at first meiotic metaphase were two to five—a low number when 2n = 36), and total pollen and seed sterility. Like all sterile *Spergularia* hybrids, they showed the very long straggling inflorescences which result from continuous flowering without the normal check caused by fruit production.

Diagnostic characters. Leaves awned; stipules lanceolate, acuminate, silvery; petals uniformly pink; stamens 10; seeds dark brown, unwinged.

2. S. bocconii (Scheele) Aschers. & Graebn., Syn. Mitteleur. Fl. 5(1):849 (1919).
Alsine bocconii Scheele in Flora 26:431 (1843) (described from Europe); [*S. rubra β atheniensis* Heldr. & Start. in sched.—from Athens]; *Lepigonum campestre* Kindb., Monogr. Lepig. 35 (1863) (syntypes from Mediterranean area and Ethiopia); *S. atheniensis* (Heldr. & Sart.) Aschers. in Schweinfurth, Beitr. Fl. Aethiop. 305 (1867); *S. campestris* (Kindb.) Willk. & Lange, Prodr. Fl. Hisp. 3:165 (1880) non Aschers.
Vernacular Name. Bocconi's Sand Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:460 (1961).

Annual or biennial herb with slender tap-root; shoots 5–25cm, slender, prostrate or ascending, densely glandular-hairy above. Leaves 3–20mm, glandular-hairy, mucronate, not fasciculate; stipules triangular, not acuminate. Inflorescence often secund; upper bracts much reduced; pedicels usually shorter than calyces. Sepals 2–3·5mm, glandular-hairy. Petals pink with white base, or entirely white, somewhat shorter than or equalling the sepals. Stamens (0–)2–5(–8). Capsule 2–3·5mm, equalling or shorter than the sepals. Seeds 0·35–0·45mm, pale grey-brown, finely tuberculate. $2n = 36$.

Habitat & Distribution. Introduced. V.c. 2 (E Cornwall), 25 (E Suffolk), and Channel Islands—previous records from other vice-counties have all been misidentifications of *S. rubra*. *S. bocconii* occurs in ruderal habitats by the sea, harbours, etc. In the Mediterranean area the species is very common as a weed on wharf-sides and other open places by the sea and there is little doubt that it has been introduced by shipping to the few isolated localities in the south of the British Isles where it occurs.

Reproductive Biology. Predominantly inbreeding by self-pollination of the inconspicuous flowers. The stamen number is much reduced and the total number of pollen grains produced per flower is only about 750: the pollen grain/seed ratio is only 15/1. However, there is evidence to indicate that some outbreeding occurs in this species in the Mediterranean area (Ratter, 1976, p.415). Flowering is recorded from May to September and probably extends for as long as there are favourable conditions.

Variation & Biosystematics. Very variable in size according to habitat. All stocks studied, including that from Par, E Cornwall are tetraploid, $2n = 36$.

Hybrids. There are no genuine records in Britain of wild hybrids of this species, although artificial crossing with *S. rupicola* and *S. marina* has produced vigorous hybrids (see Ratter, 1965a & b, 1976). These synthetic hybrids have abnormally small stamens and show abnormalities of meiosis leading to pollen abortion—they are completely infertile and produce the characteristic long straggling inflorescences of sterile *Spergularia* hybrids. Wild hybrids of *S. bocconii* × *marina* were reported from Par E, Cornwall (v.c. 2) and Jersey (Lousley, 1935, 1936) but did not show the characters of the synthetic hybrid; examination of the specimens reveals, in fact, that they are large, robust plants of *S. bocconii*.

Diagnostic characters. Stipules triangular, not acuminate; small flowers with generally reduced number of stamens; small, unwinged, light grey-brown seeds.

3. S. rupicola [Lebel ex] Le Jolis, Mém. Soc. Nat. Sci. Cherbourg 7:274 (1860) (described from France).
S. rupestris Lebel, Rech. Pl. Manch 12 (1848)—n.v. (described from France); *Alsine rupicola* (Lebel ex Le Jolis) Hiern in Journ. Bot. 37:318 (1899).
Vernacular name. Rock Sea-Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:461 (1961); Ross-Craig, *Drawings Br. Pl.* 5: pl. 64 (1951).

Perennial herb with stout woody rootstock; shoots 5–35cm, usually sticky glandular-hairy throughout, decumbent or ascending, somewhat woody below, often massed to form a tussock. Leaves 5–15mm, fleshy, linear, mucronate, glandular-hairy, with a lateral fascicle (reduced lateral branch) at each node; stipules ovate-triangular, somewhat silvery. Inflorescence densely glandular-hairy. Sepals 4–4·5mm, glandular-hairy; petals uniformly pink, about equalling the sepals. Stamens 10. Capsule 4·5–7mm, equalling or somewhat exceeding the sepals. Seeds 0·5–0·7mm, dark brown to black, unwinged, regularly tuberculate. 2n = 36.

Habitat & Distribution. Native. Limited to the Channel Islands, the south and west of England, Wales, the Isle of Man, the west of Scotland, including the Inner and Outer Hebrides, and Ireland. It grows, often in dense tussocks or hanging masses, on cliffs, walls and rocky places by the sea.

Reproductive Biology. Well-adapted for outbreeding with conspicuous nectariferous flowers each producing approximately 38000 pollen grains from 10 stamens, and having a pollen grain/seed ratio of about 350/1. Hoverflies can be seen visiting the flowers on sunny days, but no doubt a great deal of self-pollination and inbreeding also takes place, particularly in dull weather. Flowering is very abundant and proceeds from June to September.

Variation & Biosystematics. Always a long-lived perennial but varying considerably in size according to its habitat. Almost glabrous plants (var. *glabrescens* [Lebel ex] Brébisson) do occur but are rare. The species is tetraploid (2n = 36).

Hybrids. The hybrid *S. marina* × *rupicola* (*S* × *symeana,* Druce *nom. nud.*) has been found in three localities: three plants on the west breakwater at Par harbour, E Cornwall, v.c. 2; one plant on the harbour pier at Lyme Regis, Dorset, v.c. 9; and nine plants on the top of a sea-cliff at Stackpole Head, Pembrokeshire, v.c. 45 (Ratter, 1975). In all cases the hybrids occurred in mixed populations of the parental species. The hybrids are vigorous, prostrate perennials intermediate in morphology between the parental species. They are very floriferous and produce long, straggling, many-flowered inflorescences which never bear any capsules. The flowers are notable for the very small stamens which lie in a ring about the base of the ovary. The pollen is completely abortive and the

hybrid is absolutely sterile. Artificial hybrids can be made quite easily with either parent as the female; they are identical to the wild hybrids. At meiosis there are c.9 bivalents and 18 univalents at first meiotic metaphase, and further irregularities at later meiotic stages.

Synthetic hybrids with *S. bocconii* and *S. media* have been produced using *S. rupicola* as pollen parent. In both cases the hybrids were completely sterile (see under *S. bocconii* for *S. bocconii* × *rupicola*). *S. media* × *rupicola* was tetraploid, not triploid as expected from the parental chromosome numbers, indicating that the *S. media* egg nucleus must have been diploid; the hybrid showed meiotic irregularities including the production of many multivalents (Ratter, 1969b). Synthetic hybrid seedlings of *S. rupicola* × *rubra* (and reciprocal) develop a lethal chlorosis (see under *S. rubra*).

Diagnostic characters. Robust habit; stout rootstock; densely glandular-hairy shoots; large flowers with uniformly pink petals; dark-brown to black unwinged seeds.

4. S. media (L.) C. Presl, *Fl. Sicula* 161 (1826).
Arenaria media L., Sp. Pl. ed. 2, 606 (1762) (described from Europe—in Germania, Gallia); *Arenaria maritima* Allioni in Mel. Phil. Mat. Roy. Turin 5:87 (1774) (described from Europe–Turin?); *Arenaria marginata* DC. in Lamarck & De Candolle, Fl. Fr. 4:793 (1805) (described from France); *Spergularia marginata* (DC.) Kittel, Taschenbuch ed. 2, 1003 (1844); *Spergularia maritima* (Allioni) Chiovenda in Ann. Bot. Roma 10:22 (1912).

Arenaria media L. is typified by Linn. herb No. 585/23 (lectotype chosen by Rossbach in *Rhodora* 42:121–122, 1940) which, although not a typical specimen, clearly belongs to this species. The name therefore has priority over *Arenaria maritima* Allioni, and therefore *Spergularia media* (L.) C. Presl rather than *Spergularia maritima* (Allioni) Chiovenda is the correct name for the species.
Vernacular Name. Greater Sea-Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:462 (1961); Ross-Craig, *Drawings Br. Pl.* 5: pl. 66 (1951).

Perennial herb with stout woody rootstock; shoots 5–40cm, glabrous throughout or glandular-hairy in the inflorescence. Leaves 1–2·5cm, fleshy, mucronate at the tip; stipules broadly triangular, not silvery or acuminate at the tip. Sepals (4–)4·5–5(–6)mm, glabrous or glandular hairy; petals white, or white with pink tips, equalling or somewhat exceeding the sepals. Stamens 10 (rarely 7–9). Capsule 7–9mm, much exceeding the calyx. Seeds 0·7–1mm (excluding wing), broadly or narrowly winged, with the wing-margin entire or only slightly divided, or more rarely the wing reduced to narrow membranous fragments or ridges only visible under magnification, or completely absent; testa usually smooth, rarely sparsely tuberculate in winged seeds, frequently densely tuberculate in totally unwinged seeds. $2n = 18$.

Habitat & Distribution. Native. A common species of salt-marshes and other places by the sea, occurring in suitable habitats all round the coasts

of the British Isles. It is widespread throughout the northern and southern hemispheres and shows great diversity in western North Africa where many races occur (Monnier, 1975).

Reproductive Biology. Well-adapted for outbreeding with conspicuous, nectariferous flowers each producing approximately 35000 pollen grains and having a pollen grain/seed ratio of about 300/1 (Ratter, 1976). Hoverflies can be seen visiting the flowers on sunny days but a great deal of self-pollination and inbreeding also takes place, particularly in dull weather. Meticulous observations of floral biology made in the Netherlands demonstrated that the flower is well-suited to allogamy (Sterk, 1969a, b, c, d), but despite this outbreeding in the field was estimated at only 8–15%. Flowering is normally from June to late September.

Variation & Biosystematics. Much attention has been paid to the seed-wing in *S. media*. Many Floras state that the species produces only winged seeds, but in fact the character is very variable: populations differ in percentages of winged and unwinged seeds and the ratio of the two types produced by a single plant can vary according to the time of year, the number of unwinged seeds increasing at the end of the season (Salisbury, 1958). In Britain the great majority of populations have winged seeds* almost entirely, but in some populations, particularly in the north of the country, plants producing mainly unwinged or very narrowly winged seeds are common. The form with unwinged or narrowly winged seeds has been described as var. *angustata* Clavaud (*Fl. Gironde* 1:179 (1882), under the synonym *S. marginata* (DC.) Kittel) and var. *apterum* Marshall (*J. Bot. Lond.* 35:268 (1901), under the synonym *Lepigonum marinum* Wahl.), the type material of the latter coming from the Kyle of Tongue, Sutherland (v.c. 108). It tends to have smaller flowers and shorter capsules than is normal for the species, and the staminal number is often reduced to eight or nine; it is, however, completely interfertile with the wing-seeded form. Sterk (1969a) examined Dutch populations of *S. media* in detail and found that they also varied in the percentage of winged and unwinged seeds, with capsules of unwinged or narrowly winged seeds predominating in some northern populations. Inheritance of seed-wing was also studied (Sterk & Dijkhuizen, 1972) and it was discovered that 'winged' is dominant to 'unwinged'; the same workers also found a correlation between occurrence of wing-seeded plants in stable habitats and unwinged in unstable habitats. Environmental conditions can also produce considerable phenotypic variation in the development of the wing in genetically broad-winged seeds.

There is also considerable variation in indumentum. Glabrous forms are very common in the British Isles, but plants with glandular-hairy inflorescences and even sometimes vegetative shoots occur. The glandular-hairy form has been described under the synonym *Buda media* Dumort. as var. *glandulosa* Druce (*Rep. Bot. Soc. Exch. Club. Brit. Isles* 1:599, 1901).

*On superficial examination they generally give the impression of having winged seeds *entirely*, since the unwinged are borne at the apex of the placental column and are the first to be lost at dehiscence and thus easily overlooked.

British and other European plants are diploid (2n = 18), apart from one anomalous count of 2n = 36 (Blackburn & Morton, 1957), but tetraploid races occur in N Africa (Monnier, 1962, 1975). Hybrids between British and some Mediterranean stocks of the species show much reduced fertility and other features characteristic of interspecific *Spergularia* hybrids, indicating that barriers to gene flow occur between races of this very widespread species (Ratter, 1973a).

Dr Monnier, University of Montpellier, has made detailed studies of the *S. media* complex in S Europe and N Africa, where much more diversity is shown than in N Europe. Many of his observations are summarized in Monnier (1962 & 1975).

Hybrids. S. media × *marina* (*S.* × *morei* Druce, nom. nud.) has been reported from v.c. 5/6 (Somerset), 10 (Isle of Wight), 16 (E Kent), Jersey and from western parts of Europe and N Africa. Experimental investigations have shown, however, that hybridization of the two species is completely blocked by a barrier of seed incompatibility, the young embryos aborting at an early stage of development (Ratter, 1973b). The reputed wild hybrids were individuals of *S. marina* with dimorphic (winged and unwinged) seeds, or specimens of *S. media* with unwinged seeds.

A hybrid with *S. rupicola* was synthesised and is described under that species, but all other hybridizations with British species are blocked by seed incompatibility or failure of any fruit development.

Diagnostic characters. Robust habit; stout rootstock; large flowers with 10 stamens; large capsule much exceeding the calyx; generally all, or the great majority of, seeds with an entire-margined wing.

5. S. marina (L.) Griseb., Spicel. Fl. Rumel. 1:212 (1843).
Arenaria rubra β marina L., Sp. Pl. 423 (1753) (Described from Europe); *Spergularia salina* J. & C. Presl, Fl. Čechia 95 (1819) (Described from Czechoslovakia); *Lepigonum medium* Wahlb., Fl. Gothob. 46 (1820) (Described from Sweden); *Lepigonum neglectum* Kindb., Syn. Lepigon. 6 (1856); *Spergularia dillenii* Lebel in Mém. Soc. Sci. Cherbourg 14:43 (1868) (type not specified).
Vernacular Name. Lesser Sea-Spurrey.
Illustrations. Butcher, *Illustr. Br. Flora* 1:463 (1961); Ross-Craig, *Drawings Br. Pl.* 5: pl. 65 (1951).

Annual, biennial or rarely short-lived perennial herb with slender or somewhat fleshy stock. Shoots 2–35cm, prostrate or ascending, glabrous throughout or glandular-hairy only in the inflorescence. Leaves 1–2·5cm, fleshy, mucronate at the tip; stipules short, obtuse, forming a sheath, not silvery. Sepals 2·5–4mm, glabrous or glandular-hairy. Petals pink above and white below, rarely entirely white, equalling or more usually slightly shorter than the sepals. Stamens 1–5(–8). Capsule (3–)4–6mm, usually considerably exceeding the sepals. Seeds mainly unwinged but a few winged seeds occur at the base of the capsules; unwinged seeds 0·6–0·7mm, winged 0·7–1·6mm overall with wings varying from a narrow ridge to a breadth of 0·4mm; margin of seed-wing erose to laciniate; testa light brown, strongly tuberculate, weakly tuberculate or smooth. 2n = 36.

Habitat & Distribution. Native. A common species of the upper parts of salt-marshes and of open places near the sea; it also occurs in inland salt areas and occasionally as a casual in waste places. It is found in suitable habitats all round the coasts of the British Isles and is widespread in the northern and southern hemispheres.

Reproductive Biology. The flowers show adaptation to inbreeding in the reduction in number of stamens; however, approximately 2700 pollen grains are produced per flower and the pollen grain/seed ratio is 45/1—much higher than in the extreme inbreeding species (see figures for *S. bocconii*). Sterk & Dijkhuizen (1972) have extrapolated from data obtained on experimental plots and estimate outbreeding at 1–2% in Dutch populations of this species. The higher degree of inbreeding in *S. marina* than *S. media* correlates well with the more weedy habit of the former. Cross-pollination is probably mainly by hoverflies, as in the other British species of *Spergularia.* Flowering is normally from June to September.

Variation & Biosystematics. Plants vary greatly in size according to habitat: small, prostrate individuals with short internodes occur in drier, weedy situations, such as ash-paths and gravel-heaps near the sea, while much larger plants occur in more sheltered places such as hollows in the upper salt-marsh. Longevity is also correlated with habitat: the small weedy plants are annual whilst those in more sheltered habitats frequently perennate. Many populations are of entirely glabrous plants, but in others glandular-hairy inflorescences occur. Seed characters are very variable: some populations have only unwinged seeds, but in the majority at least some capsules have a few winged seeds at the base; seeds may also be smooth or tuberculate. Various authors have given specific or subspecific recognition based on seed variation and have thus caused taxonomic confusion.

Sterk & Dijkhuizen (1972) worked on the genetics of seed-wing inheritance and found that 'unwinged' is dominant to 'winged'—the opposite of the situation in *S. media.* They relate occurrence of winged seeds to stable habitats and conclude that such seeds are rare in *S. marina* since it is a plant of unstable types of environment.

Interspecific hybridization experiments involving European and Falkland Islands strains of *S. marina* have demonstrated the occurrence of a barrier to gene exchange, the hybrids showing reduced fertility and other characters typical of interspecific *Spergularia* hybrids (Ratter, 1973a). Thus in, *S. marina*, as in *S. media*, some incipient speciation between races has taken place.

The chromosome number is tetraploid ($2n=36$) and some quadrivalent formation occurs at meiosis (Ratter, 1964).

Hybrids. S. marina × *rupicola* occurs in the wild, and synthetic hybrids with *S. rubra* and *S. bocconii* have been produced; the cross with *S. media* is blocked by seed incompatibility—all these hybrids are discussed under the other parental species involved.

The majority of interspecific hybrids involving *S. marina* show a high number of univalents at meiosis and there is evidence to indicate that, as

in *Triticum aestivum*, the species has a genetic factor preventing autosyndesis of its own chromosomes in hybrids (Ratter, 1976).

Diagnostic characters. Less robust habit than *S. media* and smaller flowers with staminal number reduced generally to 2–5; small unwinged seeds, sometimes mixed with a few winged seeds; seed-wing when present with an erose or laciniate margin.