

CYTOGENETIC STUDIES IN SPERGULARIA: IX

Summary and conclusions

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ABSTRACT. The results of a biosystematic study involving thirteen species of *Spergularia* are summarized. The species range from perennial, large-flowered, very polliniferous out-breeders to small-flowered, inbreeding annuals showing great economy in pollen production; figures for pollen output, pollen/seed ratio, etc., are given for most species. Chromosome numbers range from diploid ($2x = 18$) to octoploid level ($8x = 72$), and a number of species have races of different ploidy levels, e.g. *S. rubra*, *S. purpurea*, and *S. media*. No significant differences in chiasma frequency between out- and inbreeders were observed but differences in ploidy level may account for this.

An extensive programme of interspecific hybridization resulted in the synthesis of twenty-eight different F_1 interspecific hybrids and showed that seed incompatibility and seedling lethality were important barriers to hybridization in many interspecific combinations. Most of the F_1 hybrids were completely sterile, showing abnormalities in staminal development and meiotic irregularities leading to pollen abortion, but in a few combinations some fertility occurred. One of these partially fertile hybrids, the triploid *S. nicaeensis* x *purpurea* ($2x$), gave rise to fertile, true-breeding, tetraploid lines which represent synthetic species. Intraspecific hybridization of stocks of *S. marina* and *S. media* produced some sterile hybrids and demonstrated the existence of barriers to gene exchange within these species.

Analysis of the patterns of meiotic association in the interspecific hybrids reveals that the capacity for both allo- and autosyndesis is very widespread (as demonstrated for instance by occurrence of trivalents in triploid hybrids), and it is concluded that homology exists between all genomes and subgenomes studied. The corollary of this is that the polyploids are autopolyploids or segmental allopolyploids and not genomic allopolyploids. A hypothesis is put forward to explain the patterns of meiotic association in hybrids of *S. marina* by the presence of a suppressor of homoeologous pairing which can be countered by an association promoter.

INTRODUCTION, BREEDING SYSTEMS AND CYTOLOGY

The present communication discusses and summarizes the results of a biosystematic study in *Spergularia* which was carried out over a number of years and reported in a series of papers (Ratter, 1964 onwards). Previously unpublished data on breeding systems, chiasma frequencies and other aspects are also presented.

There are approximately fifty species of *Spergularia* with two distinct centres of distribution: 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 thirteen species listed below were available for study; apart from *S. macrotheca*, which is of exclusively New World distribution, they belong to the Mediterranean group or are more or less cosmopolitan. A number of stocks of most of these species were used and details of provenance can be found in the original papers.

	2n	Distribution	Habit
<i>S. bocconii</i> (Scheele) Aschers. & Graebn.	36	SW Europe and Mediterranean region	Slender annual
<i>S. capillacea</i> (Kindb. & Lange) Willk.	18	Portugal & NW Spain	Slender annual to short-lived perennial
<i>S. diandra</i> (Guss.) Heldr. & Sart.	18	Mediterranean region, S Europe and extending far into Asia	Slender annual
<i>S. fimbriata</i> Boiss.	18	SW Spain, S Portugal, Morocco, Canary Is	Robust perennial
<i>S. heldreichii</i> (Fouc.) Simon & Monnier	36	Mediterranean region extending to the Atlantic coast of France	Slender annual
<i>S. macrotheca</i> (Hornem.) Heynh.	36, 72	W coast of Central & N America; Guadalupe Is, Mexico	Robust perennial
<i>S. marina</i> (L.) Griseb. (<i>S. salina</i> J. & C. Presl)	36	± cosmopolitan	Annual to short-lived perennial
<i>S. media</i> (L.) C. Presl (<i>S. marginata</i> Kittel)	18, 36	± cosmopolitan	Robust perennial
<i>S. nicaeensis</i> Sarato ex Burnat	36	Mediterranean region	Short-lived perennial
<i>S. purpurea</i> (Pers.) G. Don (<i>S. longipes</i> Rouy)	18, 36	Mediterranean region	Slender annual
<i>S. rubra</i> (L.) J. & C. Presl	18, 36, 54	Widespread in N hemisphere	Annual to short-lived perennial
<i>S. rupicola</i> Lebel ex Le Jolis	36	Atlantic coast of Europe	Robust perennial
<i>S. tangerina</i> P. Monnier	18	Iberian peninsula, S France	Slender annual

Data on the methods used in the investigation were given in previous papers (see Ratter, 1965a) and it is only necessary to mention here that most of the experimental work was done in a cool glasshouse at the Royal Botanic Garden, Edinburgh.

A few notes on floral structure will be useful before proceeding to the next section. The flower of *Spergularia* conforms to the typical basic pattern of the Alsinoideae. The perianth is pentamerous and the androecium basically diplostemonous, although reduction in staminal number occurs in some species. The gynoecium is tricarpellary and at the summit of the ovary bears three elongate stigmas which are usually free from each other. These organs are termed stigmas rather than styles since in most species the stigmatic papillae extend along their inner surfaces almost to the base (fig. 1b). As discussed later, autogamy commonly occurs by the reflexing stigmas touching dehiscent anthers. Nectar is secreted on the receptacle and in large-flowered species, where its production is most copious, lies as little drops around the bases of the filaments.

All the species studied are self-compatible, as is normal in Caryophyllaceae, and give good seed-set when self-pollinated. As will be discussed in the next section, self-pollination occurs automatically in some species but has to be carried out artificially in others when no insect visitors are present.

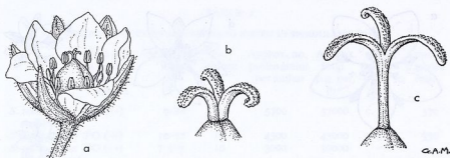


FIG. 1. a, flower of *Spergularia media* to show disposition of parts; b, free-spreading stigmas of *S. media*, N Atlantic race, (note receptive papillae on inner surfaces extending nearly to the base); c, stigmas of *S. media* ssp. *tunetana* showing coherence below to produce a united style.

The next section is based on deductions made from examination of flowers in the glasshouse; no systematic observations of pollination in the field have been made. It was noted, however, that hoverflies seem particularly attracted to the larger-flowered species; they enter the glasshouse, presumably attracted by the foetid scent of massed *Spergularia* flowers, and have also been observed on many occasions in the field visiting the flowers of *S. rupicola* and *S. media*.

BREEDING SYSTEM. Some of the most obvious characters differing amongst the species studied are related to breeding system and longevity. There is a continuous series ranging from long-lived, robust herbs with thick woody rootstocks and large, conspicuous, very polliniferous flowers, well-suited to insect attraction, to small annuals with tiny, inconspicuous flowers producing very little pollen (fig. 2). As would be expected, the former occupy fairly stable habitats and the latter are weeds of open places. Data on pollen output, flower size, etc., for most of the species are given in Table 1.

S. fimbriata represents one of the most extreme outbreeding perennials. Its flowers are about 11 mm in diameter and have ten large stamens (fig. 2a). They are slightly protandrous and the stigmas stand rather erect and seldom reflex sufficiently to touch the anthers of the same flower, so that at least under glasshouse conditions, autogamy almost always fails to occur.* *S. diandra*, a very small annual, represents the inbreeding extreme. Its tiny, inconspicuous flowers, about 3.5 mm in diameter (fig. 2j), usually have only two stamens and are self-pollinated by the dehiscent anthers touching the receptive stigmas before the bud opens. As shown in Table 1, the pollen-output and the ratio of pollen grains to seeds produced by each flower is spectacularly different in these contrasting species.

Most of the other species fall between the extremes represented by *S. fimbriata* and *S. diandra* and probably have breeding systems in which there is normally a mixture of both out- and inbreeding. The size of flower and particularly the pollen output probably give a fair guide to the relative

* In another extreme outbreeder, *S. media* ssp. *tunetana* (Maire) P. Monnier (= *Spergula tunetana* Maire), spreading of the stigmas is much reduced by their coherence below to form a united style (fig. 1c): a structural refinement which greatly reduces the chance of autogamy.

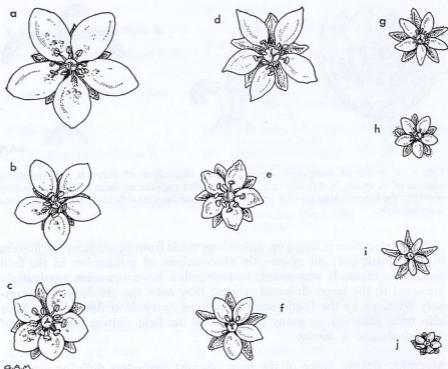


FIG. 2. Flowers of outbreeding, inbreeding and intermediate species of *Sparganium* showing range in flower-size and androecial development (the latter correlated with pollen output); *S. fimbriata* and *S. diandra* represent the out- and inbreeding extremes respectively (see text and Table 1). a, *S. fimbriata*; b, *S. purpurea*; c, *S. media*, Sahara race; d, *S. media*, N Atlantic race; e, *S. nicaeensis*; f, *S. marina*; g, *S. bocconii*, Spanish stock; h, *S. bocconii*, Montpellier stock; i, *S. tangerina*; j, *S. diandra*. Drawn from a photograph, $\times 2\frac{1}{2}$.

importance of these two processes in different species (see Table 1). In most cases, autogamy can occur by the reflexing stigmas touching the anthers. In larger-flowered perennial species, such as *S. rupicola*, there is a phase after the opening of the flower when the stigmas have not yet reflexed sufficiently to touch the anthers and are therefore available for cross-pollination. In smaller-flowered, weedy species such as *S. bocconii*, however, stigmas have normally been pollinated before the opening of the flower-buds.

S. media and *S. marina* are the only species for which estimates of occurrence of out- and inbreeding in the field are available. They are rather similar, nearly cosmopolitan species which in northern Europe grow almost exclusively in maritime habitats. *S. media* is a perennial with thick rootstock and flowers about 9 mm in diameter bearing ten stamens, each containing on average 3500 pollen grains (see Table 1). In contrast, *S. marina* is an annual to short-lived perennial with a relatively slender taproot, flowers about 6 mm in diameter, staminal number reduced to between one and six (most frequently three), and an average of 900 pollen grains per anther. As might be expected, *S. marina* shows a greater degree of weediness than *S. media*: it tends to grow mostly in open habitats by the sea, bare areas on salt marshes, etc., whilst

TABLE 1

POLLEN PRODUCTION AND BREEDING SYSTEM IN SPERGULARIA SPECIES

	Life cycle & putative breeding system	Fl. diam mm	Av. stamen no.	Approx. no. pollengrains per anther	Approx. total p.g. per fl.	Av. seeds per caps	Approx. p.g./seed ratio
<i>S. media</i>	PO (—)	9-10	10	5700	57000	c. 100	570
ssp. <i>tunetana</i>							
<i>S. fimbriata</i>	PO (—)	10-12	10	4500	45000	130	350
<i>S. macrotheca</i>	PO (—)	7.5-9	10	3000	30000	—	—
(Guadalupe)							
<i>S. purpurea</i>	AO (—)	8-9	10	4000 (2600-4900)	40000	—	—
<i>S. rupicola</i>	P(MO) (+)	8-11	10	3800 (2200-5000)	38000	—	—
<i>S. media</i>	P(MO) (+)	8-11	10	3500	35000	116	300
<i>S. nicaeensis</i>	(A-P)M (+)	7	10	1000 (650-1320)	10000	70	140
<i>S. heldreichii</i>	AM (+)	6	7	1000	7000	51	135
<i>S. rubra</i>	(A-P)M (+)	7	10	500	5000	—	—
<i>S. marina</i>	(A-P)M (+)	6-7	3	900 (550-1360)	2700	60	45
<i>S. bocconii</i>	A(MI) (+)	4.5-6	4	190	760	50	15
<i>S. diandra</i>	AI (+)	3.5	2	65 (16-190)	130	21	6.5

A, annual; P, perennial; (A-P), annual—short-lived perennial; I, inbreeding; M, mixed in- and outbreeding; (MI), mixed, but primarily adapted to inbreeding; (MO), mixed, but primarily adapted to outbreeding; O, probably mainly outbreeding; (+), autogamy normally occurs under glasshouse conditions; (—), autogamy normally fails under glasshouse conditions.

The pollen output per anther was actually counted and *not* estimated. Figures showing the range are given where there was great variation in numbers of pollen grains observed in different anthers.

Autogamy did not occur in the Guadalupe stock of *S. macrotheca* but normally took place in two Californian stocks for which detailed figures are not available.

S. media is more common in such habitats as the fairly stable *Puccinellia* turf community of salt-marshes. Sterk carried out an extensive study of the biosystematics of these two species in the Netherlands and made meticulous observations of floral biology (Sterk 1969a,b,c,d). He demonstrated that the *S. media* flower was well-suited to allogamy while that of *S. marina* was strongly adapted to autogamy. Using genetic markers, Sterk & Dijkhuisen (1972) studied the occurrence of outbreeding in experimental plots and then making allowance for different environmental conditions, stand density, etc., extrapolated their figures to give an estimate of outbreeding in the field. The estimate for populations of *S. media* was 8 to 15%, and for those of *S. marina* 1 to 2%. These figures refer to the rather bleak Dutch salt-marshes and it seems likely that the occurrence of outbreeding will be higher under conditions where weather is more favourable for insect visitation, e.g. in the Mediterranean area.

There is evidence indicating that some outbreeding occurs in *S. bocconii*, a tiny-flowered, weedy annual which comes second to *S. diandra* in paucity of pollen output (Table 1). Working on populations of this species from the south of France, Dr P. Monnier observed introgression with *S. nicaeensis*,

a species which sometimes grows in the same habitats (Monnier, pers. comm.). Cross-pollination must therefore occur sufficiently often in *S. bocconii* to allow gene exchange to take place between the two species.

The species studied therefore demonstrate a range from long-lived, large-flowered, very polliniferous outbreeders to small-flowered, inbreeding annuals showing great economy in their production of pollen. Similar series are well-known in such genera as *Bromus* (Stebbins, 1957), *Senecio* (Gibbs, Milne & Vargas Carrillo, 1975), *Stellaria* and *Trifolium*, and there is general agreement that evolution has normally proceeded from perennial outbreeder to annual inbreeder. Examination of herbarium specimens or even descriptions of *Spergularia* species not available as living material can give much information as to probable breeding system. *S. gamostyla* Pomel, for instance, a robust N African perennial known only from the type collection, has a united style, and it seems probable that as in the related *S. media* ssp. *tunetana* this prevents the stigmas from touching the anthers of the same flower, thus indicating adaptation to outbreeding.

S. purpurea seems to represent an exception to the normal evolutionary trend in the genus in that it is an annual of open places with flowers strongly adapted to allogamy (Table 1). The flowers are similar to those of *S. fimbriata*, although somewhat smaller and, as in that species, the stigmas do not usually reflex sufficiently to touch the anthers so that autogamy seldom occurs. Other evidence indicating an outbreeding system in *S. purpurea* comes from the great variability of plants grown in culture from field-collected seed, demonstrating the existence of a high level of heterozygosity.

CYTOLOGY OF THE SPECIES. Chromosome numbers are listed on p. 412. They have previously been considered in some detail in Ratter (1964) and therefore are only mentioned briefly here.

The Old World and cosmopolitan species which have been studied are all diploids, tetraploids or hexaploids based on $x = 9$. The Guadalupe Island, Mexico, race of *S. macrotheca* is an octoploid ($2n = 72$) and thus the highest polyploid yet found in the genus. Other collections of *S. macrotheca* from California are tetraploid (Ratter, 1969b).

Since one of my earlier papers (Ratter, 1964) was written, Fernandes & Leitão (1971) have found diploid ($2n = 18$) populations of *S. rubra*, and therefore diploid, tetraploid and hexaploid races of this species are now known. The same authors recorded $2n = 36$ in Portuguese *S. media* but the voucher specimen proved to be *S. marina* when it was examined by Dr P. Monnier (Monnier, 1975). Monnier (1962, 1975) has shown, however, that there are tetraploid races of this predominantly diploid species in N Africa.

The occurrence of polyploid series in *S. purpurea*, *S. rubra* and *S. media* suggests that autopolyploidy may be occurring. Meiosis in tetraploids of *S. purpurea* and in tetraploids and hexaploids of *S. rubra* shows little or no evidence, however, of the type of irregularities typical of raw autopolyploids. Occasional quadrivalents do occur in the tetraploid race of *S. purpurea* (Ratter, 1964) but have not been observed in *S. rubra*. Quadrivalents have also been observed, although they are not common, in the tetraploid species *S. rupicola*, *S. nicaeensis* (Ratter, 1964) and *S. marina* (Rodriguez, 1953; Ratter, 1964). The subject of autopolyploidy is discussed further in later sections of this paper.

Observations on chiasma frequencies are unfortunately very incomplete. Figures for the few taxa where more than ten PMC have been scored are given in Table 2, but even in most of these the number of cells analysed is inadequate. In general, the sparse data fail to show the typical relationship of high chiasma frequency and inbreeding which has been established in a number of genera (Grant, 1958; Jones & Rees, 1966; Stebbins, 1958). Ploidy level, however, might be a possible influencing factor. All the diploids for which figures are available, with the possible exception of *S. media* var. *aptera* (see below), have flowers adapted to outbreeding while the two tetraploids are both predominantly inbreeders. It seems possible that there might be selection for reduced chiasma frequency in the tetraploids to prevent multivalent formation and this would counter the normal increase in chiasma frequency found in inbreeders. It is perhaps significant that the only taxon showing a markedly higher chiasma frequency than the others is *S. media* var. *aptera*, a northern British diploid race which shows features suggesting the beginning of adaptation towards inbreeding (e.g. reduction of flower size and reduction of staminal number from ten to seven or eight).

HYBRIDIZATION

INTERSPECIFIC HYBRIDIZATION. One of the original objects of the study was to determine phylogenetic relationships within the genus by the analysis of meiotic association in hybrids. An extensive programme of interspecific crossing, involving one hundred different combinations, was therefore undertaken. This resulted in the synthesis of 28 different F_1 interspecific hybrids and gave information on the nature of barriers to hybridization in other combinations.

The most important barriers to successful crossing are seed incompatibility and seedling lethality. Seed incompatibility causes the abortion of the developing hybrid embryo at varying stages in development and is perhaps the result of dysfunction of the endosperm. Seedling lethality is found in some combinations involving both *S. rubra* and the related *S. capillacea*. In this condition, normal germination occurs but a lethal chlorosis soon develops and the hybrid seedling dies before more than three pairs of leaves are opened. The data on barriers to hybridization are dealt with fully in Ratter (1973b).

Tables 3 and 4 list the F_1 interspecific hybrids and give data on meiotic associations and fertility. The hybrids are all morphologically intermediate between their parental species and no matrocliny has been observed where reciprocal hybrids have been produced. Most hybrids are very vigorous and extremely floriferous (since they are usually highly sterile and therefore lack the normal check to flowering caused by fruit production). Stamens of most hybrids are abnormally small and this can be used as a quick spot character in identification. The condition is most marked in *S. media* x *capillacea* where the stamens are represented by tiny club-shaped primordia in which the archesporium does not develop (Ratter, 1969b). The stamens of all other hybrids, even when extremely small, are morphologically normal and contain an archesporium in which meiosis and pollen formation takes place. Similar abnormalities of the stamens of hybrids have been recorded by other workers in very diverse families, e.g. in *Paeonia* (Saunders & Stebbins, 1938) and in *Elymus condensatus* x *glaucus* (Stebbins & Walters, 1949). Meiotic

TABLE 2

CHIASMA FREQUENCIES AT MI IN SOME SPECIES AND INTRASPECIFIC HYBRIDS

	Ploidy level	Breeding system	Stock	Xma. frequ. per biv.	No. of PMC scored
<i>S. fimbriata</i>	2X	O	Rabat	1.47	20
<i>S. media</i> ssp. <i>tunetana</i>	2X	O	Tunis	1.30	26
<i>S. media</i>	2X	O/I	Aragon	1.44	11
	2X	O/I	Anglesey	1.54	11
(v. <i>aptera</i>)	2X	?	Glasson	1.72	27
	2X		Clevedon x Montpellier	1.30	18
	2X		Istanbul x Aragon	1.33	19
	2X		Glasson x Istanbul	1.25	41
<i>S. media</i> x <i>media</i> ssp. <i>tunetana</i>	2X		Anglesey x Tunis	1.40	15
	2X		Montpellier x Tunis	1.30	36
<i>S. marina</i>	4X	I	S Atlantic	1.46	14
<i>S. bocconii</i>	4X	I	Montpellier	1.47	22
	4X		Denia x Montpellier	1.54	22

O, predominantly outbreeding; I, predominantly inbreeding; O/I, mixture of out- and inbreeding. Breeding system symbols are not given for hybrids.

TABLE 3

TRIPLOID INTERSPECIFIC HYBRIDS (F₁)

	Max. no. trivalents per PMC	% PMC cont. 2 or more trivalents	Commonest meiotic configurations	Fertility %	Reference
<i>S. bocconii</i> x <i>fimbriata</i>	4	6	9 ₁₁ 9 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁	0	1965a
<i>S. heldreichii</i> x <i>fimbriata</i>	4	12	9 ₁₁ 9 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁ , 8 ₁₁ 11 ₁	0	1965a
<i>S. nicaeensis</i> x <i>fimbriata</i>	3	8	8 ₁₁ 11 ₁ , 7 ₁₁ 113 ₁ , 1 ₁₁₁ 7 ₁₁ 10 ₁	0	1965a
<i>S. purpurea</i> (4X) x <i>fimbriata</i>	3	c.1	9 ₁₁ 9 ₁	0	1965a
<i>S. rupicola</i> x <i>fimbriata</i>	4	21	9 ₁₁ 9 ₁ , 7 ₁₁ 113 ₁ , 8 ₁₁ 11 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁ , 1 ₁₁₁ 7 ₁₁ 10 ₁ , 2 ₁₁₁ 7 ₁₁ 7 ₁ , 2 ₁₁₁ 5 ₁₁ 11 ₁ , 9 ₁₁ 9 ₁ , 7 ₁₁ 113 ₁	0	1965a
<i>S. bocconii</i> x <i>purpurea</i> (2X)	2	8		0	1965a
<i>S. nicaeensis</i> x <i>purpurea</i> (2X)	5	44	9 ₁₁ 9 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁ , 2 ₁₁₁ 7 ₁₁ 7 ₁ , 3 ₁₁₁ 6 ₁₁ 6 ₁	<0.1%	1965a
<i>S. rubra</i> (4X) x <i>capillacea</i>	5	75	3 ₁₁₁ 6 ₁₁ 6 ₁ , 3 ₁₁₁ 7 ₁₁ 4 ₁ , 2 ₁₁₁ 7 ₁₁ 7 ₁ , 4 ₁₁₁ 5 ₁₁ 5 ₁	0	1969a
<i>S. rupicola</i> x <i>capillacea</i>	4	34	8 ₁₁ 11 ₁ , 7 ₁₁ 113 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁ , 1 ₁₁₁ 7 ₁₁ 10 ₁ , 2 ₁₁₁ 6 ₁₁ 9 ₁ , 4 ₁₁₁ 4 ₁₁ 7 ₁	0	1969a
<i>S. media</i> x <i>purpurea</i> (4X)	1	0	9 ₁₁ 9 ₁ , 10 ₁₁ 7 ₁ , 1 ₁₁₁ 8 ₁₁ 8 ₁	<0.2%	1969b

TABLE 4

DIPLOID, TETRAPLOID AND PENTAPLOID F₁ HYBRIDS

	2n	Max. no. multi- valents per PMC	PMC cont. 2 or more multi- valents %	Max. assoc- iation observed	Commonest meiotic configurations	Seed fertility %	Reference
<i>S. media</i> <i>x capillacea</i>	18	—	—	—	No meiosis (see p. 417)	0	1969b
<i>S. media</i> <i>x media</i> ssp. <i>tunetana</i>	18	0	0	9 ₁₁	9 ₁₁	1-5	1973a
<i>S. bocconii</i> <i>x heldreichii</i> (& reciprocal)	36	1	c.2	18 ₁₁	18 ₁₁ , 17 ₁₁ 2 ₁ , 16 ₁₁ 4 ₁	0	1965a
<i>S. bocconii</i> <i>x nicaeensis</i> (& reciprocal)	36	1	c.5	18 ₁₁	16 ₁₁ 4 ₁ , 15 ₁₁ 6 ₁ , 14 ₁₁ 8 ₁	0-10	1965a
<i>S. bocconii</i> <i>x rupicola</i>	36	2	20	17 ₁₁ 2 ₁	14 ₁₁ 8 ₁ , 15 ₁₁ 6 ₁	0	1965a
<i>S. heldreichii</i> <i>x purpurea</i> (4x) (& reciprocal)	36	7	51	5 _{iv} 1 ₁₁₁ 6 ₁₁ 1 ₁ , 18 ₁₁	18 ₁₁	20-25	1969a
<i>S. nicaeensis</i> <i>x heldreichii</i> (& reciprocal)	36	2	c.4	18 ₁₁	16 ₁₁ 4 ₁ , 15 ₁₁ 6 ₁ , 14 ₁₁ 8 ₁ , 13 ₁₁ 10 ₁	0	1965a
<i>S. nicaeensis</i> <i>x purpurea</i> (4x)	36	2	c.20	18 ₁₁	18 ₁₁	5	1965a
<i>S. nicaeensis</i> <i>x rupicola</i>	36	1	<0.2	18 ₁₁	15 ₁₁ 6 ₁ , 16 ₁₁ 4 ₁ , 13 ₁₁ 10 ₁ , 12 ₁₁ 12 ₁	0	1965a
<i>S. rupicola</i> <i>x purpurea</i> (4x)	36	2	27	18 ₁₁	18 ₁₁	5	1965a
<i>S. marina</i> (Falkland Is) <i>x marina</i> (Istanbul)	36	0	—	18 ₁₁	18 ₁₁	<0.5	1973a
<i>S. marina</i> <i>x bocconii</i> (& reciprocal)	36	—	—	10 ₁₁ 16 ₁	9 ₁₁ 18 ₁	0	1965b
<i>S. marina</i> <i>x nicaeensis</i>	36	3	10	13 ₁₁ 10 ₁	10 ₁₁ 16 ₁ , 9 ₁₁ 18 ₁ , 8 ₁₁ 20 ₁	0	1965b
<i>S. marina</i> <i>x purpurea</i> (4x)	36	1	c.4	18 ₁₁	18 ₁₁	c.0.5	1965b
<i>S. marina</i> <i>x rubra</i> (4x) (& reciprocal)	36	1	c.1	9 ₁₁ 18 ₁	5 ₁₁ 26 ₁ , 4 ₁₁ 28 ₁ , 3 ₁₁ 30 ₁ , 2 ₁₁ 32 ₁	0	1965b
<i>S. marina</i> <i>x rupicola</i> (& reciprocal)	36	—	—	18 ₁₁	9 ₁₁ 18 ₁ , 8 ₁₁ 20 ₁	0	1965b
<i>S. media</i> <i>x rupicola</i> (p. 424)	36	7	70	3 _{iv} 4 ₁₁₁ 4 ₁₁ 4 ₁	5 ₁₁ 8 ₁₁ 5 ₁ , 5 ₁₁ 6 ₁₁ 9 ₁ , 4 ₁₁ 8 ₁₁ 8 ₁ , 3 ₁₁ 9 ₁₁ 9 ₁ , 12 ₁₁ 12 ₁	0	1969b
<i>S. rubra</i> (6x) <i>x</i> <i>purpurea</i> (2x)	36	6	c.33	1 _v 1 _{iv} 4 ₁₁₁ 5 ₁₁ 5 ₁ , 18 ₁₁	18 ₁₁	consider- able	1969a
<i>S. bocconii</i> <i>x rubra</i> (6x)	45	4	c.50	2 ₁₁₁ 1 ₁ 5 ₁₁ 9 ₁	—	0	1969a
<i>S. media</i> ssp. <i>tunetana</i> <i>x macrotheca</i> (8x)	45	5	c.50	1 _{iv} 4 ₁₁₁ 14 ₁₁ 1 ₁	—	0	1969b

TABLE 5

CHROMOSOME NUMBERS AND FERTILITY OF F_2 HYBRIDS

	F_1 2n	F_2 2n	Fertility %	Reference
<i>S. bocconii</i> x <i>nicaeensis</i>	36	36,40	1—c.30	1965a
<i>S. heldreichii</i> x <i>purpurea</i> (4x) (and reciprocal)	36	36,37	0—c.5	1969a
<i>S. marina</i> x <i>purpurea</i> (4x)	36	36,37	0—c.5	1965b
<i>S. rupicola</i> x <i>purpurea</i> (4x)	36	36,38,39	1—c.3	1965a
<i>S. rubra</i> (6x) x <i>purpurea</i> (2x)	36	36,37,72	0—c.30	1969a
<i>S. media</i> x <i>purpurea</i> (4x)	27	32,33,41	not recorded	1969b
		42,43,44, \pm 45, 46,47,48.		
<i>S. nicaeensis</i> x <i>purpurea</i> (2x)	27	24,30,32, 33,34,35, 44,54	0—c.50 to 60	1972
<i>S. nicaeensis</i> x <i>purpurea</i> (4x)	36	36	c.10—c.70	—

irregularities leading to total or partial pollen abortion characterize most interspecific hybrids and have been considered in some detail in previous papers (e.g. Ratter, 1965a,b); consequently hybrid sterility is an extremely important barrier to interspecific gene exchange in the genus (see Tables 3 and 4 for fertility figures of hybrids).

An F_2 and sometimes later generations were raised in all but one case where the F_2 hybrid showed any fertility. Table 5 lists the F_2 hybrids and gives cytological and fertility data. A notable fact is that in all but one case *S. purpurea*, in its diploid or tetraploid form, is one of the parents. In some cases, e.g. *S. nicaeensis* x *purpurea* (2x), *S. nicaeensis* x *purpurea* (4x) and *S. bocconii* x *nicaeensis*, F_2 hybrids show a fair level of fertility. The degree of segregation towards the parental species varies considerably in different F_2 hybrids. Of the tetraploid hybrids where the parents make equal chromosomal contributions (i.e. are of the same ploidy level), *S. bocconii* x *nicaeensis* and *S. marina* x *purpurea* (4x) show a complete range through a series of intermediate forms to plants almost indistinguishable from the parental species, while *S. heldreichii* x *purpurea* (4x) and *S. nicaeensis* x *purpurea* (4x) show considerable uniformity and are all rather like the F_1 (although showing some evidence of segregation in petal length and colour); and *S. rupicola* x *purpurea* (4x) falls between these two extremes. The situation is more complicated in the other hybrids where the parental genetic contribution is unequal.

Hybrid lines descended from *S. nicaeensis* x *purpurea* (2x) were grown to the F_4 (Ratter, 1972). These lines, although descended from a triploid hybrid, were tetraploid and notable for their fertility and morphological stability. They were morphologically quite distinct from the parental species and it was concluded that they represent synthetic species. Their origin must have involved considerable recombination of the genomes of *S. nicaeensis* and diploid *S. purpurea*.

Most of the F_2 hybrids are euploid (see the original publications for details) but there are also many aneuploids and polyploids. Although most of the aneuploids only differ from the euploid number by one or two, there

are some examples showing major deviations, e.g. vigorous F_2 plants produced by the triploid ($2n = 27$) F_1 of *S. nicaeensis* x *purpurea* ($2x$) with $2n = 24, 30$ and 32 (Table 5). Such deviations from the normal at fairly low ploidy levels appear to indicate considerable tolerance of chromosomal unbalance.

BACKCROSSES. Backcrosses of hybrids with their parental species were produced in a number of cases.

S. bocconii x *nicæensis* F_1 hybrids were used as female parents in crosses with both parents to produce backcross progenies of variable, but generally rather high, fertility. The production of good seed by *S. bocconii* x *nicæensis* F_1 x *S. bocconii* varied from approximately 30% to 100% of that normal for *S. bocconii*. In *S. bocconii* x *nicæensis* F_1 x *S. nicaeensis* the figure was rather lower, varying from about 50% of that normal for *S. nicaeensis* to nil. The morphology conformed to expectations in that it normally approached that of the parental species used in the backcross but retained some characters of the other parent. There were, however, segregants in the large F_2 generations produced by selfing the F_1 hybrid which showed as close an approach to the morphology of one or other parent as did the backcrosses. Meiosis in the few backcross hybrids examined cytologically was regular with formation of eighteen bivalents. These synthetic backcrosses provide an experimental model reproducing the initial stages of the introgression between *S. bocconii* and *S. nicaeensis* observed by Dr P. Monnier in the field (see p. 416). Gene exchange between the two species occurs across a barrier of partial hybrid sterility, showing that they are at an ecospecific level of differentiation from each other.

F_1 and F_4 hybrids of *S. nicaeensis* x *purpurea* ($2x$) were backcrossed to *S. nicaeensis*, using the latter as pollen parent (Ratter, 1972, pp. 121-122). Fertility was very variable in the backcross progeny involving the F_1 hybrid, as might be expected with a triploid hybrid as female parent. Crosses of the highly fertile, tetraploid F_4 hybrids with *S. nicaeensis* produced fertile offspring morphologically close to *S. nicaeensis* but showing some characters of the hybrid parent.

S. nicaeensis x *purpurea* ($4x$) was backcrossed as female parent to *S. purpurea* ($4x$) and produced rather uniform progeny, as would be expected, morphologically closer to *S. purpurea* than the F_2 generation produced by selfing the F_1 hybrid.

INTRASPECIFIC HYBRIDS. A number of interstock hybrids were synthesized in *S. marina* and *S. media* and the results reported by Ratter (1973a).

Hybrids between stocks of *S. marina* from Europe and the Falkland Islands resembled interspecific hybrids in their small hybrid-type androecium and low fertility, while those between European stocks were of normal fertility and morphology.

All interstock hybrids of *S. media* showed some degree of androecial abnormality and reduced fertility, but in the hybrids involving ssp. *tunetana* this was extreme and the plants showed the characters typical of sterile interspecific hybrids. Data on this hybrid and also the intraspecific *S. marina* hybrid involving the Falkland Islands stock are included in Table 4.

In the *S. marina* hybrids involving the Falkland Islands stock and in *S. media* x *media* ssp. *tunetana*, meiosis is regular and all chromosomes associate as bivalents. The chiasma frequencies of 1.3 and 1.4 per bivalent recorded in *S. media* x *media* ssp. *tunetana* (Table 2) are similar to those occurring in the parental stocks and do not suggest any reduced homology of the parental genomes. The situation in the *S. marina* hybrids is similar with a chiasma frequency of between 1.4 and 1.5 per bivalent (this figure is not recorded in Table 2 since it is based on the scores from less than ten PMC). Chromosomal sterility, as shown by obvious meiotic abnormalities, is not therefore the cause of the lack of fertility of these hybrids. Pollen fertility, however, is very low, presumably as a result of genetic unbalance, and this together with the failure of autogamy because of the small size of the stamens accounts for the observed sterility.

As discussed in Ratter (1973a, p. 295), the Falkland Islands' *marina* stock and *S. media* ssp. *tunetana* are more strongly genetically isolated from the other stocks of their species than some morphologically dissimilar species are from each other, e.g. *S. bocconii* and *S. nicdaensis*, *S. marina* and *S. purpurea* (4x). This genetic separation of the Falkland Islands' *S. marina* is rather surprising since it is morphologically indistinguishable from N European races of the same species. *S. media* ssp. *tunetana*, on the other hand, shows a number of morphological differences from the other stocks with which it was crossed and has been recognized by Maire (1963) as a separate species under the name *Spergula tunetana* Maire. Monnier (1975), however, prefers to consider it as a subspecies of the very variable *S. media* aggregate.

Interstock hybrids were also produced in *S. bocconii* but all showed fertility comparable with their parents.

CHROMOSOME ASSOCIATION IN F_1 INTERSPECIFIC HYBRIDS. Details of the meiotic analyses of all 28 F_1 interspecific hybrids have already been published (Ratter 1965a,b; 1969a,b; 1972; 1973a). The object of the present account is to bring together and summarize the information and discuss the salient features which emerge.

TRIPLOID HYBRIDS. The triploid F_1 hybrids provide a suitable starting point for discussion. They are listed in Table 3 which also gives data on the commonest meiotic configurations and the frequency of trivalents.

The occurrence of trivalents provides the key to the interpretation of the pattern of chromosome association. There is good evidence to indicate that trivalents originate by normal association of the equivalent chromosomes of the three genomes present (Ratter, 1965a, p. 209). Their occurrence therefore demonstrates not only genomic homology between the diploid and tetraploid parental species but also of the two subgenomes of the tetraploid. An objection could be raised, however, that too much emphasis should not be placed on evidence of homology based on trivalents since they occur in high numbers in a relatively low percentage of cells. For instance, even in *S. rubra* x *capillacea*, the triploid hybrid where trivalents are commonest, there are only about 5% of PMC with 5 trivalents, 14% with 4, and 30% with 3. High percentages of trivalents, however, would not be expected in hybrids of

species with chiasma frequencies generally below 1.5 per bivalent and furthermore preferential pairing might also play a role in reducing their numbers.* It is important to remember in this connection the obvious fact that the configurations showing the highest degree of association are the most significant in revealing genomic homology.

Judging from the evidence provided by trivalents, there appears to be considerable homology between the genome of *S. fimbriata* and both subgenomes of the tetraploid species *S. bocconii*, *S. heldreichii*, *S. nicaeensis*, *S. purpurea* (4x) and *S. rupicola*. Similarly, there seems to be homology between the genome of diploid *S. purpurea* and both subgenomes of *S. bocconii* and *S. nicaeensis*, and between the genome of *S. capillacea* and both subgenomes of *S. rubra* (4x) and *S. rupicola*.

Despite the existence of homology between the three genomes present in most of the hybrids, the majority of PMC show configurations made up principally of bivalents and univalents, often approximating to the association of two genomes with the other remaining unpaired. By the present interpretation such configurations result either from preferential pairing or by chiasma frequency limiting the number of trivalents formed. It is clearly impossible from the evidence available to speculate whether the bivalents are generally auto- or allosyndetic, and in fact they probably represent a mixture of both types of association.

TETRAPLOID HYBRIDS (EXCEPT FOR THOSE INVOLVING *S. MARINA*). F_1 hybrids of thirteen different interspecific combinations of tetraploid parents were synthesized (see Table 4). For convenience consideration of those involving *S. marina* will be reserved until later and the present discussion concerns the remaining eight. In all these hybrids some PMC show the chromosomes associated entirely or almost entirely as bivalents (i.e. 18_{II} or $17_{II} 2_1$). In other PMC, however, the variable number of chromosomes failing to "find" partners indicates that homology is not as high as occurs within a normal species. Quadrivalents are present in a high percentage of PMC of *S. purpurea* (4x) x *S. heldreichii*, sometimes reaching as many as five per cell, and are found in much lower numbers in *S. rupicola* x *S. purpurea* (4x) and some of the other hybrids. Such quadrivalents demonstrate homology of all four genomes present. Trivalents are also common in many of the tetraploid hybrids and particularly those in which fair numbers of quadrivalents occur. Their presence is probably the result of potential quadrivalent formation being prevented by competition in pairing. As in the triploid hybrids, occurrence of multivalents indicates the capacity for both auto- and allosyndesis, but we do not know which type of association is taking place in the bivalents which are present in far greater numbers than multivalents. Thus configurations of eighteen bivalents might represent complete auto- or allosyndesis or a mixture of both types of association.

Two other tetraploid hybrids, produced by crossing species of different ploidy levels, furnish interesting information.

* Occurrence of exceptional octoploid pollen mother cells in the tetraploid hybrids *S. nicaeensis* x *S. rupicola* and *S. marina* x *S. purpurea* (4x) demonstrates how effective such constraints to multivalent formation can be. Despite tetraploid PMC in both these hybrids showing the great majority of chromosomes associated as bivalents, the octoploid cells had no multivalents whatsoever (Ratter, 1965a, p. 219, and 1965b, pp. 229 and 232).

In PMC of the hybrid of hexaploid *S. rubra* and diploid *S. purpurea* most of the configurations are of eighteen bivalents. This must represent the allosyndesis of the *purpurea* genome with a *rubra* subgenome and the auto-syndesis of the other two *rubra* subgenomes. In other PMC of this hybrid trivalents and quadrivalents are present showing that genomic homologies are wider than demonstrated by the cells with eighteen bivalents.*

The tetraploid hybrid *S. media* x *rupicola* was synthesized by crossing the diploid species *S. media* with the tetraploid species *S. rupicola*. The evidence indicates that the aberrant chromosome number is due to fusion of diploid egg-cells of *S. media* with normal pollen of *S. rupicola* (Ratter, 1969b). The complement of this hybrid is therefore made up of two fully homologous genomes of *S. media* and two subgenomes of *S. rupicola*. The meiotic configurations show high numbers of quadrivalents and trivalents, indicating considerable homology of all genomes present. There are also rather high numbers of univalents which are probably the result of competition in pairing.

PENTAPLOID HYBRIDS. *S. media* ssp. *tunetana* x (8x) *macrotheca* shows complex meiotic configurations with frequent occurrence of multivalents, amongst which a 5-valent has been observed (Ratter 1969b). In some cells only one or two univalents are present, indicating that nearly all the chromosomes have found partners at meiosis. Clearly the *tunetana* chromosomes are associating allosyndetically with *macrotheca* chromosomes, whilst *macrotheca* chromosomes are associating autosyndetically amongst themselves.

The pentaploid hybrid *S. bocconii* x (6x) *rubra* is notable for the occurrence of rather large numbers of univalents and little can be deduced from the meiotic analyses (Ratter, 1969a).

GENOMIC HOMOLOGIES. The following scheme can be constructed to relate the homology, or at least the pairing potential, of the genomes of the diploid and tetraploid species involved in the hybridizations.

As previously discussed (p. 423) the genome of the diploid species *S. fimbriata* shows considerable homology with both subgenomes of the tetraploid species *S. bocconii*, *S. heldreichii*, *S. purpurea* (4x) and *S. rupicola*. Similarly there seems to be homology between the genome of diploid *S. purpurea* and both subgenomes of *S. bocconii* and *S. rupicola*; this carries the corollary that the *fimbriata* and *purpurea* genomes are homologous (unfortunately the hybrid of the two species cannot be synthesized so no direct confirmation is possible). Meiosis in *S. media* x *rupicola* shows that the *media* genome is homologous with both subgenomes of *S. rupicola* and thus by inference with the genomes of all other species so far considered. Pairing in the hybrid of *S. media* and the rather dissimilar *S. media* ssp. *tunetana*

* The original data for this hybrid were reported in Ratter (1969a) but since that date more meiotic analyses have been made from another plant of the same parentage. The additional records are of 26 figures showing 18 bivalents and one with 16 bivalents and a quadrivalent. It is one of the few hybrids in which chiasma frequency has been determined: the figure of 1.11 chiasmata per bivalent is the lowest recorded in this investigation and probably explains the paucity of multivalent occurrence. One might speculate that the plant reported in Ratter (1969a) which had many more multivalents in the PMC examined had a higher chiasma frequency.

demonstrates the homology of the genomes of these two diploids and thus adds another genome to the chain of homologies. Finally, the genome of *S. capillacea* shows considerable homology with both subgenomes of *S. rupicola*, indicating that it is equivalent to the other diploid genomes, and since it shows similar association in hybrids with tetraploid *S. rubra* the latter species must also belong to the common pattern of homology. Meiotic patterns occurring in the tetraploid hybrids, apart from some of those involving *S. marina*, are consistent with this postulated scheme of homology. Thus the genomes of all five diploid taxa involved in the hybridizations and the subgenomes of six of the tetraploid taxa show considerable homology. Evidence will be presented later to relate *S. marina* to this pattern.

The web of homologies just described shows the truth of the tentative conclusion reached during later stages of the study that, given the right conditions, any *Spergularia* genome will pair with any other. The hybrids involving higher polyploid taxa also support this conclusion: as already discussed (p. 424) the high levels of association observed in *S. rubra* (6x) x *purpurea* (2x) and in *S. media* ssp. *tunetana* x *macrotheca* (8x) represent a mixture of auto- and allosyndesis.

There are, of course, varying degrees of homology and studies of pairing in F_1 hybrids often fail to differentiate them. As is well known, chromosomes of different species may be sufficiently similar to pair and yet contain many cryptic structural differences. There is little evidence to indicate whether or not the 'homologous' genomes of different *Spergularia* species are made up of chromosomes differentiated in this way. As already discussed (p. 422), chiasma frequencies in *S. media* x *media* ssp. *tunetana* suggest structural equivalence between the chromosomes of these taxa, and the apparent interchangeability of chromosomes between genomes in F_2 and later generation hybrids of *S. bocconii* x *nicaeensis* and *S. nicaeensis* x *purpurea* (2x) (see Ratter, 1965a, p. 209, and 1972, p. 123) must also indicate a very high level of homology of the genomes involved. On the other hand, the frequency of univalents observed in some hybrids may be the result of partial erosion of homology.

The homology (whether complete or partial) of all genomes and subgenomes studied and the consequent capacity for autosyndesis which has been demonstrated in almost all the polyploid species shows that the latter are either autopolyploids or segmental allopolyploids. The occurrence of morphologically indistinguishable, or almost indistinguishable, diploid and tetraploid races of *S. purpurea*, and diploid, tetraploid and hexaploid races of *S. rubra* suggests that autopolyploidy is occurring in these species (see also p. 416). In other cases, however, considerable numbers of univalents occur in most PMC of hybrids, e.g. *S. bocconii* x *rupicola* and *S. nicaeensis* x *heldreichii* (Ratter, 1965a, and Table 4), which would not be expected if the parents were autopolyploids with a very strong capacity for autosyndesis, and these species are possibly segmental allopolyploids. On the other hand, diploidization of an autopolyploid to eliminate meiotic irregularities causing reduction in fertility could also bring about failure of autosyndesis in hybrids.

HYBRIDS OF *S. MARINA*. The pattern of chromosome association found in four tetraploid hybrids of *S. marina* is completely different from that occurring in tetraploid hybrids involving other species (Ratter, 1965b). In *S. rupicola* x

marina, *S. nicaeensis* x *marina* and *S. bocconii* x *marina* the most common meiotic configurations approximate to $9_{11} 18_1$, that is the pairing of two sub-genomes with the other two remaining unpaired, while in *S. rubra* (4x) x *marina* there is considerably less association and $5_{11} 26_1$ is the commonest configuration. Since the capacity for autosyndesis has been demonstrated in *S. bocconii*, *S. nicaeensis*, *S. rubra* (4x) and *S. rupicola*, it seems reasonable to suggest that chromosomes of these species form the bivalents while the univalents represent in the main chromosomes of *S. marina*. Another tetraploid hybrid of *S. marina*, however, shows a very different pattern of association. Almost all the PMC of *S. marina* x *purpurea* (4x) show regular production of eighteen bivalents and the hybrid even shows some fertility.

Since it is improbable on morphological grounds that *S. purpurea* is any more closely related to *S. marina* than are the other species involved in the hybrids, it seems unlikely that differential homology resulting from such processes as chromosome restructuring is responsible for the contrasting patterns of association, and the following hypothesis is put forward to explain the observations. It represents a considerable revision of some of the views expressed in Ratter (1965b).

The pattern of chromosome association in all hybrids of *S. marina*, apart from *S. marina* x *purpurea* (4x), could be explained if the species is a segmental allopolyploid with a genetically controlled system which suppresses homoeologous pairing, as in *Triticum aestivum* (Riley & Chapman, 1958). Such a system would have the effect of suppressing quadrivalent formation in *S. marina* and would also prevent autosyndesis of its chromosomes in hybrids. If, on the other hand, *S. purpurea* (4x) possessed a system which actively promoted chromosome pairing to such an extent that the antihomoeologous pairing suppressor of *S. marina* were inhibited, we should get the pattern of pairing observed in *S. marina* x *purpurea* (4x). There is some evidence available that the genotype of *S. purpurea* (4x) has such an effect in promoting chromosome association, since tetraploid hybrids of this species, such as *S. heldreichii* x *purpurea* (4x) and *S. rupicola* x *purpurea* (4x), produce higher numbers of quadrivalents than is normal in other hybrids. A comparable interrelationship of systems suppressing and promoting homoeologous chromosome pairing has been demonstrated by Feldman & Mello-Sampayo (1967) and Mello-Sampayo (1971) in the hybrids of *Triticum aestivum* with *Aegilops longissima* and *A. speltoides*.

A significant piece of information is provided by the observation of a single aberrant meiotic configuration in *S. marina* x *rupicola*. This configuration had all chromosomes paired as bivalents, in contrast to the normal $9_{11} 18_1$, and one might speculate that it was the result of a breakdown of the postulated mechanism suppressing homoeologous association.

CONCLUSIONS

The main evolutionary trends in the morphology of the species of *Spergularia* studied are associated with breeding system and longevity.

Barriers to interspecific hybridization are widespread and even when interspecific hybrids can be synthesized, total sterility usually prevents gene

exchange between the parents. Gene exchange between some species, however, can occur across a barrier of partial hybrid sterility: e.g. *S. bocconii* and *S. nicaeensis*, where the initial stages of introgression observed in the field have been reproduced experimentally. Such species are at an eco-specific level of differentiation from each other.

Evolution of the species studied has involved little erosion of genomic homology. In interspecific hybrids, any genome has the potential to pair with any other, but competition in pairing, preferential pairing, or the presence of a postulated suppressor of homoeologous pairing in *S. marina*, often profoundly affect the type of meiotic configurations observed. The occurrence of such high genomic homology indicates that the polyploids are autopolyploids or segmental allopolyploids despite their cytologically diploid behaviour.

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