Breeding systems and relationships of the *Cerastium tomentosum* group

Rozmnožovací systémy a příbuzenské vztahy ve skupině *Cerastium tomentosum*

Mohammad K. Khalaf [1] & Clive A. Stace [2]

Dedicated to the memory of Josef Holub

[1]*Department of Biology, College of Arts and Science, Al-al Bayt University, P. O. Box 772, Aljubayha, Amman, Jordan;* [2]*Department of Biology, University of Leicester, Leicester LE1 7RH, England, e-mail: CAS7@leicester.ac.uk*

Khalaf M. K. & Stace C. A. (2000): Breeding systems and relationships of the *Cerastium tomentosum* group. – Preslia, Praha, 72: 323–344.

A programme of artificial hybridization, involving seven species of the *Cerastium tomentosum* group at four levels of ploidy from tetraploid to 16-ploid, produced viable F1 seed in 22 (49%) of the 45 combinations. Eleven (24%) of these gave rise to mature F1 plants, of which three were fertile. Greatest success was with the octoploid × tetraploid and octoploid × octoploid crosses, of which 50% gave mature plants, including all three fertile F1 combinations. Of the latter *C. tomentosum* × *C. grandiflorum* is octoploid, but *C. tomentosum* × *C. biebersteinii* and × *C. gibraltaricum* are hexaploids ($2n = 54$), a chromosome number not known in any wild plants of this group but evidently one capable of producing viable gametes despite apparently irregular meioses. Hybrids between the *C. tomentosum* group and species of the *C. alpinum*, *C. arvense*, *C. banaticum* and *C. latifolium* groups were equally successful in producing viable F1 seed and mature F1 plants. The octoploid *C. tomentosum* × *C. arvense* hybrid was fertile, again despite irregular meiosis, but later generations can probably develop a perfectly regular meiosis as occurs in wild hybrids between these species that occur in south-eastern England (where *C. tomentosum* has become naturalised). In nature the species studied rarely hybridise due to geographical isolation. Most plants are self-compatible but strongly protandrous, and many exhibit varying degrees of male sterility. It is suggested that the five above 'groups' should be recognised as a single undivided taxon (subsection *Cerastium*).

Keywords: *Cerastium*, *Caryophyllaceae*, breeding systems, hybridization, wild hybrids, chromosome numbers, isolating mechanisms, Mediterranean Basin, England

Introduction

Classification of Cerastium

The genus *Cerastium* L. (type species: *C. arvense* L.) contains probably fewer than 100 species of rather small annuals and perennials, almost cosmopolitan in distribution but most diverse in Europe and western Asia, especially the Mediterranean region. Most modern classifications represent modifications of that of Fenzl (1840), and are perhaps best represented by the scheme of Schischkin (1936), a summary of which follows:

Subgenus *Dichodon* (Bartl.) Fenzl
Subgenus *Eucerastium* (Boiss.) Pax (= *Cerastium*)
    Section *Strephodon* Ser.
    Section *Schizodon* (Fenzl) Schischk.

Section *Orthodon* Ser. (= *Cerastium*)
  Subsection *Fugacia* (Fenzl) Pax et K. Hoffm.
  Subsection *Perennia* (Fenzl.) Pax et K. Hoffm. (= *Cerastium*)
    Series *Lasiostemona* (Fenzl) Schischk.
    Series *Leiostemona* (Fenzl) Schischk.
    Series *Alpina* (Borza) Schischk.
    Series *Arvensia* (Hayek) Schischk. (= *Cerastium*)
    Series *Grandiflora* (Borza) Schischk.

The five series cover, respectively, the following species groups: *C. purpurascens* Adams group, *C. fontanum* Baumg. group, *C. alpinum* L. group, *C. arvense* L. group, and *C. tomentosum* L. group. Later Söllner (1954) modified the above classification by removing series *Leiostemona* from subsection *Perennia* to create a third subsection *Caespitosa* Pax et K. Hoffm. Nevertheless Söllner still recognised five (unnamed) groups in subsection *Perennia*, which comprised the *C. alpinum*, *C. arvense*, *C. banaticum* (Rochel) Heuff. *C. latifolium* L. and *C. tomentosum* groups. These five groups of species, and the *C. fontanum* group (series *Leiostemona* or subsection *Caespitosa*) are the subject of the present paper. Our research project focused on the *C. tomentosum* group, but the other five were included in the crossing experiments as widespread outgroups of varying degrees of similarity to the main group.

None of the above six groups is easily delimited. The most important work on the *C. tomentosum* group is that of Buschmann (1938), who diagnosed it by its perennial habit, presence of many non-flowering axillary shoots, relatively large flowers and presence of (usually very dense) long white hairs. It can be considered for present purposes to consist of the nine species (nos 8–16 or 9–17, respectively) treated by Jalas et al. (1964, 1993) in Flora Europaea, the seven species (nos 44–50, one in common with Europe) treated by Schischkin (1936) in Flora URSS, possibly two species (nos 13–14) treated by Cullen (1967) in Flora of Turkey, one species (no. 29) treated by Ayasligil (1984) in the Supplement to the last, and one other species (*C. macrocalyx* Buschm.). Of these 18 species, seven from Europe and one from Ukraine (Crimea), as well as *C. arvense*, *C. banaticum*, *C. alpinum*, *C. latifolium*, *C. carinthiacum* Vest and *C. fontanum*, were available as living plants to be used in the crossing experiments (Appendix 1).

A character that has been much used to separate taxa above the level of species in the perennial groups is whether the testa is strongly tuberculate and tightly fused to, or scarcely tuberculate and only loosely attached to the inner part of the seed. This distinction was first noticed by Fenzl (1842), who termed the former state chondrospermous and the latter physospermous. The value of this character above the species level is, however, doubtful. *Cerastium arvense*, *C. alpinum*, *C. fontanum* and all but two of the *C. tomentosum* group have chondrospermous seeds, but *C. gibraltaricum* Boiss. and *C. boissierianum* Greuter et Burdet of the *C. tomentosum* group, and *C. arcticum* Lange and *C. nigrescens* (H. C. Watson) Edmondston ex H. C. Watson of the *C. alpinum* group have physospermous seeds.

The Cerastium tomentosum group

The approximate distribution of the *C. tomentosum* group is shown in Fig. 1. Most of the species used in this study are largely allopatric (Appendix 1).

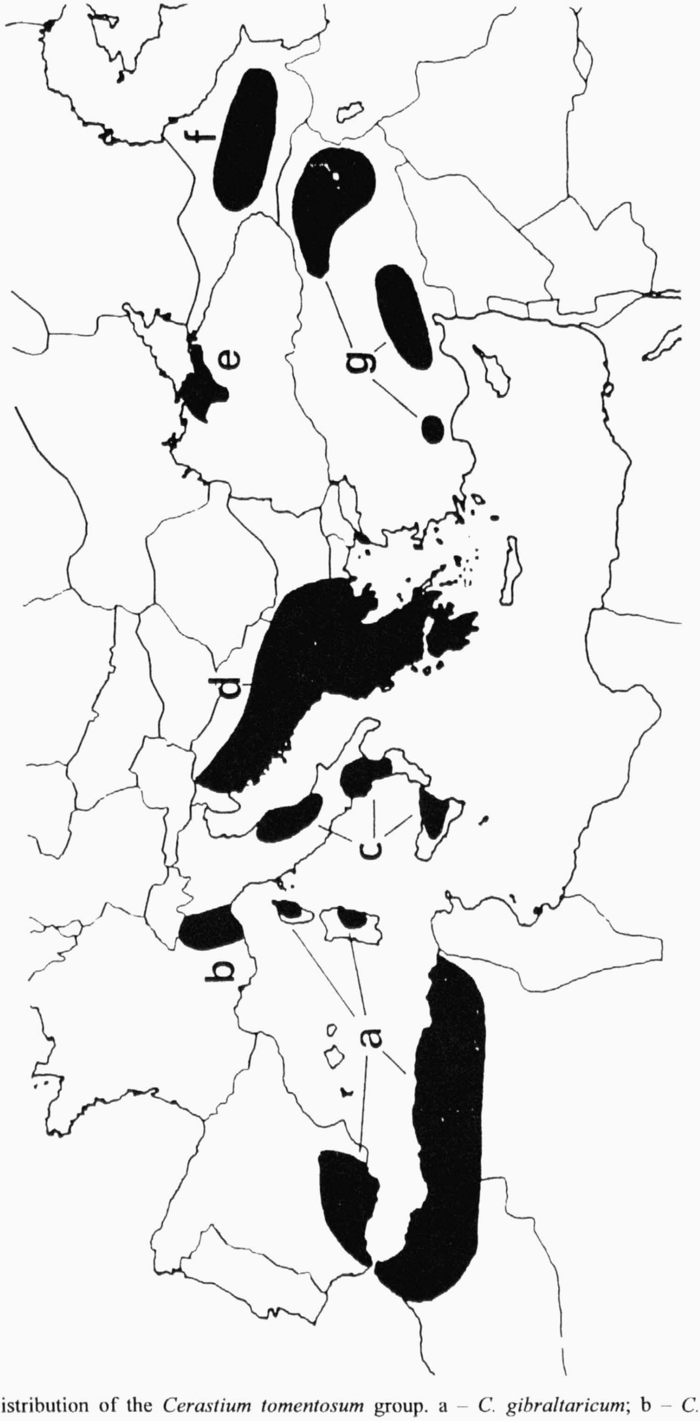

Fig. 1. – Distribution of the *Cerastium tomentosum* group. a – *C. gibraltaricum*; b – *C. lineare*; c – *C. tomentosum*, d – *C. decalvans*, *C. candidissimum*, *C. grandiflorum* and *C. moesiacum*; e – *C. biebersteinii*; f – up to seven species in Fl. URSS; g – three species in Fl. Turkey. Partly adapted from Jalas & Suominen (1983).

C. tomentosum itself is an extremely variable taxon, but is endemic to Italy and Sicily, where no other taxa in the *C. tomentosum* group occur. Of all its variations, specimens from higher altitudes on Mt Etna, Sicily, are the most distinct in having only sparse hairs, narrower leaves, shorter petals and capsules and smaller seeds; we have distinguished it in our experiments as var. *minus* C. Presl (var. *aetnaeum* Jan). *C. tomentosum* var. *tomentosum* has been introduced to central and northern Europe as a garden ornamental. From here it has escaped into the wild and in places has become extremely well naturalised not only in marginal and disturbed ground but sometimes in natural habitats, such as sandy grassland and maritime sand-dunes. It has caused taxonomic problems in two ways. Firstly it has quite frequently hybridised with the native *C. arvense* (in eastern and south-eastern England and one part of central Scotland) to produce plants that superficially resemble the Balkan *C. decalvans* Schlosser et Vuk. and which have been wrongly so called. Secondly there are several reports of the introduction to gardens of the Crimean *C. biebersteinii* DC., and the variability of *C. tomentosum* has often been partly explained by determination of some naturalised plants as this or as various Balkan species of the group. Despite this, in our extensive observations of wild populations of *C. tomentosum* in Britain we have never encountered any of the Balkan or Crimean species. The only living *C. biebersteinii* that we have seen is that grown from seeds from the Crimea or from Botanic Gardens (Appendix 1).

The Spanish plants were considered as two species (*C. gibraltaricum* and *C. boissierianum*, earlier known as *C. boissieri* Gren.) by Jalas et al. (1964, 1993), but Talavera (1987) treated them as a single species which Rico (1990) divided into three varieties: var. *gibraltaricum*, var. *lanuginosum* (Gren.) F. N. Williams (*C. boissierianum*), and var. *viridulum* (Pau) Font Quer. We have followed the latter and differentiated between vars. *gibraltaricum* and *lanuginosum* (we believe that var. *viridulum* possibly represents hybrids with *C. arvense*).

Hybrids between *C. tomentosum* and *C. arvense* have also arisen spontaneously in many European botanic gardens (England, France, Germany, Poland, Romania and Switzerland, and probably elsewhere), and in the wild where the two taxa are naturalised in Sweden (Karlsson 1997) and Canada (Morton 1975). Strid (1986) stated that intermediates, which might be hybrids, occur in Greece between *C. candidissimum* Correns and *C. banaticum*, and between *C. decalvans* and *C. banaticum*.

The *C. tomentosum* group contains a range of chromosome numbers from $2n = 36$ to $2n = 144$ (data extracted from the standard chromosome number compilations and our results). Whether $2n = 36$ should be considered the diploid or the tetraploid level is a moot point. Only one (uncorroborated) count of $2n = 18$ exists in the genus, for *C. lithospermifolium* Fisch., a perennial member of section *Strephodon* from Siberia (Krogulevich 1971). On this basis the number $2n = 36$ should be considered as tetraploid, and it will be so-called in this paper. However, for the six groups of the genus under study here, it is effectively diploid. The tetraploid to 16-ploid counts in the *C. tomentosum* group evidently represent several polyploid series: *C. tomentosum* itself occurs as tetraploids, octoploids and dodecaploids; *C. biebersteinii* as tetraploids and octoploids; *C. decalvans* as tetraploids, octoploids and 14-ploids; *C. banaticum* as octoploids, 14-ploids and 16-ploids; and *C. gibraltaricum* as tetraploids, octoploids and dodecaploids. The chromosome counts of all the accessions used in our hybridization experiments are given in Appendix 1.

The Cerastium alpinum group

Only *C. alpinum* itself is considered here. This species is well distributed in the mountains of western, central and northern Europe, and is sympatric with members of the *C. tomentosum* group only in the western Alps and northern Balkans (Jalas & Suominen 1983). Probably *C. alpinum* is always octoploid, and dodecaploid counts are cases of confusion with *C. arcticum* or *C. nigrescens* (Brysting 1999).

The Cerastium arvense group

Only *C. arvense* itself is considered here. This species is largely sympatric with the taxa of the *C. tomentosum* group except for its absence from the Mediterranean islands, southern Greece, the Crimea and the Caucasus (Jalas & Suominen 1983). Tetraploid, octoploid and decaploid counts have been reported.

The Cerastium latifolium group

The tetraploids *C. latifolium* and *C. carinthiacum* were included in our experiments. Both are plants of the Alps, the former in the west and the latter in the east, where they are sympatric with *C. alpinum* and *C. arvense*. *Cerastium latifolium* also has outlying localities in the Apennines, where it is probably sympatric with *C. tomentosum*. Members of this group resemble those of the *C. alpinum* group apart from their lack of long shaggy hairs.

The Cerastium banaticum group

Only *C. banaticum* is considered here. It is a 16-ploid distributed in the southern and eastern parts of the Balkan Peninsula, where it is sympatric with four species of the *C. tomentosum* group and with *C. arvense*. It is morphologically rather close to the *C. arvense* group.

The Cerastium fontanum group

Only *C. fontanum* itself is considered here. It is very widespread in Europe and probably sympatric with all the other groups throughout their ranges. Chromosome number reports range from octoploid to 20-ploid.

The crossing experiments described in this paper were carried out as part of a programme (Khalaf 1993) to investigate the reality of the *C. tomentosum* group and the genetical inter-relationships of the species within that group.

Materials and Methods

Materials

Accessions were obtained as plants or seeds by collecting in the wild, from correspondents in Continental Europe, and by the seed-exchange schemes (frequently material from the last of these sources was misidentified).

Seeds and plants

Seed accessions were germinated at 15–19 °C in a 3 : 7 : 2 loam: peat: grit mixture under a light regime of 16 hr light/8 hr dark. Germination occurred between 4 and 7 days; seedlings were potted on and after 1–2 months were transferred to an unheated glasshouse where they were kept permanently. Plants of most of the taxa used flowered much more profusely after vernalization over winter in the cold glasshouse, but *C. alpinum* and *C. fontanum* did not require vernalization. Seeds obtained from pollination experiments were treated in the same way except that they were sown on moist filter paper in an incubator at 20 °C and transferred after 1 day to a cold-room at 4 °C for vernalization; germination occurred in the cold-room after 3–7 days. Vouchers of all accessions at flowering are deposited in LTR.

Chromosome counts

Root-tips were obtained from fresh stem-cuttings after 10–15 days; these possessed larger meristems and a higher mitotic index than root-tips gathered from mature plants or from seedlings. They were pretreated in 50% saturated aqueous paradichlorbenzene, washed in tap-water, fixed for 3 hr in ethanoic acid : ethanol (1: 3), washed again and stored in 70% IMS. After storage they were rewashed, hydrolysed in 5N HCl at room temperature for 3–6 min, washed in 70% ethanol, and transferred to a drop of 45% ethanoic acid on a slide. The meristematic region was dissected from the rest of the tissue and transferred into a drop of 2% aqueous aceto-orcein on another slide. The meristem was dissected apart and squashed in the usual way and then gently heated over a spirit lamp to flatten the cells, and the coverslip was sealed with rubber solution. Suitable spreads were photographed.

Meiosis

Meiosis was found to take place ten to fifteen days before anthesis in the cold glasshouse. Meiosis is synchronized within each anther, but the 10 anthers of a flower are not regularly synchronized. Flower buds at the appropriate stage were fixed in ethanoic acid : ethanol (1: 3) at between 11.30 and 13.00 and stored at 4 °C until needed. Anthers were dissected in a drop of 2% aqueous aceto-orcein on a slide and the anther remains discarded. A cover-slip was placed over the anther contents and the pollen mother cells were separated by gentle tapping and heating. The coverslip was sealed with rubber solution and suitable spreads were photographed.

Emasculation

All hybridizations were carried out by pollinating emasculated flowers. Floral buds were emasculated one day before they would have opened and pollen release would have occurred. The buds were opened carefully by hand and the ten anthers removed with fine forceps sterilised with 95% ethanol. The emasculated flowers were then covered with a pollen-proof bag, which was briefly removed in succeeding days to enable other flowers on the same inflorescence to be emasculated; any flowers that were not successfully emasculated were cut off and discarded.

Hand-pollination

Stigmas of emasculated flowers were receptive 7–10 days after emasculation, as shown by their bending outwards and the development of papillae. Flowers are therefore strongly protandrous. Anthers were taken from flowers just before they had dehisced, slightly squeezed with the forceps to expose the pollen and placed directly on to the stigmas of recipient flowers. In some cases pollen-donor anthers were kept in petri-dishes at room temperature until suitable emasculated flowers were available; experiments showed that the pollen remained viable for about 17 days. The inflorescences were rebagged after pollination; as soon as all the stigmas in an inflorescence had lost their fresh appearance (hence were no longer receptive) the bags were discarded.

Pollen stainability

Anthers were collected at about the time of their natural dehiscence and dissected in a drop of Muntzing's acetocarmine. The percentage of full, well-stained grains was calculated from a total of a minimum of 500 grains.

Testing for breeding system

In order to test for breeding system the following experiments were performed:
1. To test for autogamy – unemasculated flowers were bagged before anthesis.
2. To test for self-incompatibility – (a) unemasculated flowers were bagged before anthesis and then pollinated by hand using pollen from the same flower or from other flowers of the same plant; and (b) emasculated flowers of the same plant were bagged before anthesis and then pollinated by hand with pollen from different accessions of the same taxon.
3. To test for autonomous agamospermy – emasculated flowers were bagged before anthesis.

Successful fertilization was measured as number of seeds set per capsule.

Testing for crossability

Emasculated flowers were bagged before anthesis and then pollinated by hand with pollen from a range of other accessions of the same and of different taxa.

Results

Chromosome numbers

Counts were made of all the accessions used in the hybridization experiments; all agreed with previously published reports. Within the *C. tomentosum* group, *C. biebersteinii*, *C. candidissimum*, *C. decalvans* and *C. gibraltaricum* (both varieties) were tetraploids ($2n = 36$), *C. grandiflorum* and *C. tomentosum* var. *minus* were octoploids ($2n = 72$), *C. moesiacum* was 16-ploid ($2n = 144$), and *C. tomentosum* var. *tomentosum* was tetraploid, octoploid and dodecaploid (2n = 36, 72, 108). Several accessions of octoploid *C. tomentosum* var. *tomentosum* had from one to nine B-chromosomes, and some accessions of *C. grandiflorum* had from one to five B-chromosomes.

Cerastium arvense was tetraploid or octoploid (2n = 36, 72), *C. banaticum* was 16-ploid (2a = 144), *C. carinthiacum* and *C. latifolium* were tetraploid (2n = 36) and *C. alpinum* was octoploid (2n = 72). The *C. fontanum* utilized was 16-ploid.

Breeding system in the Cerastium tomentosum group

A summary of the results from the experiments testing for autogamy and self-incompatibility in the *C. tomentosum* group is given in Table 1.

Table 1. – Results of self-pollination and intra-taxon cross-pollination experiments in the *Cerastium tomentosum* group. Abbreviations: caps. = capsule; fls. = flowers; prod. = produced; SC = self-compatible; SI = self-incompatible.

	Unassisted self-pollination			Artificial self-pollination			Intraspecific cross-pollination			Self- compatibility	
Taxon (no. of accessions used)	No. fls. used	No. caps. prod.	Mean seed -set	No. fls. used	No. caps. prod.	Mean seed -set	No. fls. used	No. caps. prod.	Mean seed -set	Range	Mean
TETRAPLOIDS											
C. biebersteinii (2)	31	1	4	15	11	9	11	11	11	73–75%	74%
C. candidissimum (2)	20	0	0	23	22	11	15	15	13	71–100%	85%
C. decalvans (2)	26	12	3	15	22	7	—	—	—	—	—
C. gibraltaricum var. *gibraltaricum* (1)	17	0	0	6	3	5	—	—	—	—	—
C. gibraltaricum var. *lanuginosum* (3)	39	1	3	31	27	8	23	22	12	50–100%	66%
C. tomentosum var. *tomentosum* (2)	27	0	0	26	7	12	14	14	8	100–100%	100%
OCTOPLOIDS											
C. grandiflorum (2)	35	18	5	27	22	9	13	12	26	30–60%	35%
C. tomentosum var. *minus* (3)	59	0	0	20	9	14	23	21	18	41–100%	78%
C. tomentosum var. *tomentosum* (SC) (16)	164	11	3	209	132	12	86	71	15	38–100%	80%
C. tomentosum var. *tomentosum* (SI) (2)	19	0	0	10	0	0	11	7	12	0–0%	0%
DODECAPLOIDS											
C. tomentosum var. *tomentosum* (2)	35	0	0	50	34	6	8	7	11	50–80%	55%
16-PLOIDS											
C. moesiacum (3)	11	0	0	11	0	0	14	14	5	0–0%	0%

No seed was set from flowers that were emasculated and not subsequently hand-pollinated, indicating the absence of autonomous apomixis.

A comparison of seed-set following (a) artificial selfing of unemasculated flowers and (b) intra-taxon cross-pollination of emasculated flowers was used to calculate the percentage self-incompatibility of each accession. Most accessions exhibited self-compatibility at levels between 30% and 100%. The only exceptions were two of the 18 octoploid accessions of *C. tomentosum* var. *tomentosum*, and all three accessions of *C. moesiacum*, which showed 100% self-incompatibility. These results reinforced our earlier decision to carry out all artificial hybridizations on emasculated flowers.

The proportion of flowers producing seed, and the number of seeds produced in each capsule, was invariably lower following unassisted autogamy than following artificial self-pollination. Observations on flower development showed that the anthers dehisce several days before the stigmas are receptive in all the taxa investigated, and that even after anther dehiscence the anthers and stigmas are well separated. However, the flowers begin to close two to three days after the stigmas are ripe, and as they do so the sepals push any remaining pollen from the anthers on to the stigmas. The amount of pollen remaining varies according to the number of insect visitors that the flower has received, but all the pollen is likely to be viable since we found viability to last for more than two weeks. Hence, in self-compatible plants (which constitute the great majority), some self-fertilization is likely, especially if the flowers are shaken by wind or by visiting insects. However, intra-specific cross-pollination always results in a higher seed-set, and it is likely that when crossing has taken place the level of selfing will be below that achieved in our unassisted autogamy experiments.

Intraspecific crosses between varieties and between ploidy levels within the Cerastium tomentosum group

Crosses were made reciprocally between the two varieties of *C. gibraltaricum* (vars. *gibraltaricum* and *lanuginosum*, both tetraploid) and reciprocally in all six combinations between the two varieties of *C. tomentosum* (octoploid var. *minus*; tetraploid, octoploid and dodecaploid var. *tomentosum*). Crosses were also made reciprocally in five of the six possible combinations between the three cytotypes of *C. tomentosum* var. *tomentosum* (only the dodecaploid × tetraploid was not attempted). Results are summarised in Table 2.

All the above crosses were successful. All flowers used in crosses between the two varieties of *C. gibraltaricum* produced capsules with a similar number of seeds to capsules produced from intravarietal crosses within this species, and the seed proved to be 80–93% viable. Moreover this seed produced many mature plants which showed full fertility.

In the intervarietal crosses within *C. tomentosum* 28.6–76.2% of flowers crossed produced capsules containing seeds with a viability of 57.5–94.3%. Within the octoploid level the intervarietal hybrids grew well and produced fully fertile flowers, but in the octoploid × tetraploid and octoploid × dodecaploid crosses mature plants developed which either did not flower or produced only sterile flowers.

Results of crosses between the three cytotypes of *C. tomentosum* var. *tomentosum* produced a similar level of seed-set to the last and, although precise figures were not recorded, the fertility of the F1 plants also followed a similar pattern, i. e. crosses between ploidy levels gave rise to only sterile F1 plants.

Table 2. – Results of intraspecific inter-ploidy and intervarietal hybridizations in the *Cerastium tomentosum* group. Abbreviations: caps. = capsule; fert. = fertile; flow. = flowering; fls. = flowers; prod. = produced; viab. = viability; *C. g.* = *C. gibraltaricum*; *C. t.* = *C. tomentosum*.

Female parent (no. of accessions used)	Male parent (no. of accessions used)	No. fls. used	No. caps. prod.	Mean seed -set	% seeds viab.	Mature F1 plants	Flow. F1 plants	Fert. F1 plants
TETRAPLOIDS × TETRAPLOIDS								
C. g. var. *gibraltaricum* (1)	*C. g.* var. *lanuginosum* (1)	5	5	12.0	93.3	Yes	Yes	Yes
C. g. var. *lanuginosum* (1)	*C. g.* var. *gibraltaricum* (1)	4	4	8.0	80.0	Yes	Yes	Yes
TETRAPLOIDS × OCTOPLOIDS								
C. t. var. *tomentosum* (3)	*C. t.* var. *tomentosum* (10)	65	54	—	—	—	—	—
C. t. var. *tomentosum* (2)	*C. t.* var. *minus* (5)	23	10	6.6	51.5	?	—	—
TETRAPLOIDS × DODECAPLOIDS								
C. t. var. *tomentosum* (3)	*C. t.* var. *tomentosum* (2)	18	4	?	?	—	—	—
OCTOPLOIDS × TETRAPLOIDS								
C. t. var. *tomentosum* (9)	*C. t.* var. *tomentosum* (3)	53	35	?	?	—	—	—
C. t. var. *minus* (3)	*C. t.* var. *tomentosum* (2)	24	15	5.4	72.2	Yes	Yes	No
OCTOPLOIDS × OCTOPLOIDS								
C. t. var. *tomentosum* (28)	*C. t.* var. *minus* (6)	247	166	15.0	85.6	Yes	Yes	Yes
C. t. var. *minus* (6)	*C. t.* var. *tomentosum* (26)	265	202	13.0	90.5	Yes	Yes	Yes
OCTOPLOIDS × DODECAPLOIDS								
C. t. var. *tomentosum* (15)	*C. t.* var. *tomentosum* (2)	70	48	?	?	—	—	—
C. t. var. *minus* (3)	*C. t.* var. *tomentosum* (2)	21	16	9.0	57.5	Yes	No	—
DODECAPLOIDS × OCTOPLOIDS								
C. t. var. *tomentosum* (1)	*C. t.* var. *tomentosum* (1)	2	1	?	?	—	—	—
C. t. var. *tomentosum* (2)	*C. t.* var. *minus* (2)	7	2	17.5	94.3	—	—	—

There is clearly little if any evidence of internal intraspecific isolating barriers in these two species within one ploidy level; the intervarietal crosses within *C. tomentosum* were as successful as the intravarietal ones. The success rate of crosses between ploidy levels was little different (in terms of capsules producing seeds, number of seeds per capsule, or percentage viability of seeds) from that of crosses within the tetraploid level, but the fertility of F1 plants produced was reduced to nil.

Interspecific crosses within the Cerastium tomentosum group

The results of interspecific hybridization experiments involving the seven species of the *C. tomentosum* group (four tetraploids, one octoploid, one 16-ploid and *C. tomentosum* at tetraploid, octoploid and dodecaploid levels) are summarized in Table 3. Fifty six combinations of taxa representing twelve combinations of ploidy level were involved in the hybridizations. Because of the similarity of results obtained from different varieties of one species, the figures for the two varieties of *C. tomentosum*, and for the two varieties of *C. gibraltaricum*, have each been amalgamated. This reduces the number of combinations of taxa to 45.

Table 3. – Results of interspecific hybridizations in the *Cerastium tomentosum* group. Abbreviations as in Table 2 and: ALP = *C. alpinum*; ARV = *C. arvense*; BAN = *C. banaticum*; BIE = *C. biebersteinii*; CAN = *C. candidissimum*; CAR = *C. carinthiacum*; DEC = *C. decalvans*; FON = *C. fontanum*; GIB = *C. gibraltaricum*; GRA = *C. grandiflorum*; LAT = *C. latifolium*; MOE = *C. moesiacum*; TOM = *C. tomentosum*.

Female parent (no. accessions)	Male parent (no. accessions)	No. fls. used	No. caps. prod.	Mean seed -set	% seeds viab.	Mature F1 plants	Flow. F1 plants	Fert. F1 plants
TETRAPLOID × TETRAPLOID								
BIE (2)	GIB (2)	10	9	8.1	7.8	No	—	—
CAN (1)	BIE (1)	6	5	8.7	53.8	Yes	No	—
CAN (1)	GIB (1)	3	0	—	—	—	—	—
CAN (1)	TOM (1)	4	3	13.0	0.0	—	—	—
DEC (1)	BIE (1)	2	2	2.5	20.0	No	—	—
DEC (1)	GIB (1)	4	2	1.0	0.0	—	—	—
DEC (1)	TOM (1)	5	0	—	—	—	—	—
GIB (1)	BIE (1)	8	0	—	—	—	—	—
GIB (1)	CAN (1)	4	0	—	—	—	—	—
GIB (1)	TOM (1)	4	4	22.5	91.1	Yes	No	—
TOM (1)	BIE (1)	6	0	—	—	—	—	—
TOM (3)	CAN (1)	12	0	—	—	—	—	—
TOM (1)	DEC (1)	5	0	—	—	—	—	—
TOM (3)	GIB (3)	21	14	8.0	93.8	Yes	No	—
TETRAPLOID × OCTOPLOID								
BIE (1)	GRA (1)	3	3	21.3	15.6	Yes	No	—
BIE (1)	TOM (2)	6	5	11.4	7.7	No	—	—
CAN (1)	GRA (1)	3	3	4.3	0.0	—	—	—
CAN (1)	TOM (4)	11	11	9.9	0.0	—	—	—
DEC (1)	GRA (1)	2	1	2.0	0.0	—	—	—
DEC (1)	TOM (5)	21	14	6.4	0.0	—	—	—
GIB (2)	GRA (1)	10	0	—	—	—	—	—
GIB (3)	TOM (16)	108	50	16.0	4.3	Yes	No	—
TOM (1)	GRA (1)	13	9	7.0	100.0	Yes	No	—
TETRAPLOID × DODECAPLOID								
BIE (1)	TOM (1)	4	2	9.0	0.0	—	—	—
CAN (1)	TOM (1)	3	0	—	—	—	—	—
GIB (2)	TOM (2)	9	5	9.3	3.6	No	—	—
TETRAPLOID × 16-PLOID								
TOM (1)	MOE (1)	2	0	—	—	—	—	—
OCTOPLOID × TETRAPLOID								
GRA (1)	BIE (1)	8	0	—	—	—	—	—
GRA (1)	CAN (1)	3	1	1.0	100.0	No	—	—
GRA (1)	GIB (1)	3	2	15.0	30.0	Yes	No	—
GRA (1)	TOM (1)	6	4	9.5	36.8	Yes	No	—
TOM (26)	BIE (2)	145	13	5.6	74.0	Yes	Yes	Yes
TOM (8)	CAN (1)	27	0	—	—	—	—	—
TOM (17)	DEC (1)	103	7	3.7	81.8	No	—	—
TOM (17)	GIB (2)	100	46	3.6	56.0	Yes	Yes	Yes
OCTOPLOID × OCTOPLOID								
GRA (1)	TOM (5)	22	10	4.8	2.3	No	—	—
TOM (3)	GRA (1)	8	4	2.0	87.5	Yes	Yes	Yes

OCTOPLOID × DODECAPLOID								
GRA (1)	TOM (1)	3	2	3.0	33.3	No	—	—
OCTOPLOID × 16-PLOID								
TOM (3)	MOE (1)	11	0	—	—	—	—	—
DODECAPLOID × TETRAPLOID								
TOM (1)	GIB (1)	3	0	—	—	—	—	—
16-PLOID × TETRAPLOID								
MOE (1)	BIE (1)	3	2	2.5	20.0	No	—	—
MOE (1)	GIB (1)	5	3	1.0	0.0	—	—	—
MOE (1)	TOM (1)	3	3	1.0	50.0	No	—	—
16-PLOID × OCTOPLOID								
MOE (1)	TOM (3)	13	3	7.3	59.0	No	—	—
16-PLOID × DODECAPLOID								
MOE (1)	TOM (1)	3	2	2.0	0.0	—	—	—

Measured in terms of the production of hybrid seeds, 31 (69%) of the 45 combinations attempted were successful. In terms of the production of viable (germinated) seeds this figure dropped to 22 (49%), and in terms of the production of mature F1 plants it dropped further to 11 (24%). With regard to the levels of ploidy of the parents, and ignoring the five combinations of ploidy level that were represented by only one taxon combination, the least success was achieved in the tetraploid × tetraploid crosses (only seven out of fourteen produced F1 seed, and only three produced mature F1 plants). There was greater success where one or both of the parents was octoploid or higher, especially where this was the female parent. In both the octoploid × tetraploid and octoploid × octoploid crosses 50% of the taxon combinations produced mature F1 plants. *C. moesiacum* was successful only as a female parent, and *C. decalvans* and *C. candidissimum* were much more successful as female than as male parents. This might be due to a relatively low pollen fertility in these species (see on).

Only three combinations produced fertile F1 plants, all with octoploid *C. tomentosum* as the female parent. The male parents were *C. biebersteinii* (tetraploid), *C. gibraltaricum* (tetraploid) and *C. grandiflorum* (octoploid). Two of the three fertile F1 hybrids were hexaploids (2n = 54), a level not known to exist in any species. Hybrid fertility is considered in more detail below.

Interspecific crosses between species of the Cerastium tomentosum group and those of other groups

The results of interspecific hybridization experiments involving the seven species of the *C. tomentosum* group (four tetraploids, one octoploid, one 16-ploid and *C. tomentosum* at tetraploid, octoploid and dodecaploid levels) crossed with species of the other five groups are summarized in Table 4. Forty one combinations of taxa representing nine combinations of ploidy level were involved in the hybridizations. Because of the similarity of results obtained from different varieties of one species, the figures for the two varieties of *C. tomentosum*, and for the two varieties of *C. gibraltaricum*, have each been amalgamated. This reduces the number of combinations of taxa to 35.

Table 4. – Results of interspecific hybridizations between taxa of the *Cerastium tomentosum* group and taxa of the *C. arvense*, *C. alpinum*, *C. banaticum*, *C. fontanum* and *C. latifolium* groups. Membership of the latter 5 groups is designated by -arv, -alp, -ban, -fon and -lat respectively. Abbreviations as in Table 3.

Female parent (no. accessions)	Male parent (no. accessions)	No. fls. used	No. caps. prod.	Mean seed -set	% seeds viab.	Mature F1 plants	Flow. F1 plants	Fert. F1 plants
TETRAPLOID × TETRAPLOID								
CAN (1)	ARV-arv (1)	3	2	4.0	0.0	—	—	—
DEC (1)	ARV-arv (1)	4	0	—	—	—	—	—
LAT-lat (1)	BIE (1)	4	1	15.0	0.0	—	—	—
LAT-lat (1)	DEC (1)	5	5	16.7	0.0	—	—	—
LAT-lat (1)	GIB (1)	3	2	21.0	0.0	—	—	—
TETRAPLOID × OCTOPLOID								
ARV-arv (2)	TOM (9)	38	31	13.7	13.1	Yes	No	—
BIE (1)	ARV-arv (2)	6	4	8.0	3.1	No	—	—
CAN (1)	ARV-arv (1)	3	2	13.5	0.0	—	—	—
TOM (1)	ARV-arv (1)	2	2	14.5	13.8	No	—	—
BIE (2)	ALP-alp (2)	4	1	3.0	0.0	—	—	—
CAN (1)	ALP-alp (1)	2	2	14.5	3.4	No	—	—
CAR-lat (1)	TOM (1)	4	4	17.0	14.2	No	—	—
DEC (1)	ALP-alp (1)	7	4	5.5	0.0	—	—	—
LAT-lat (2)	TOM (4)	17	12	7.3	0.0	—	—	—
TETRAPLOID × 16-PLOID								
DEC (1)	BAN-ban (1)	4	1	10.0	60.0	Yes	No	—
BIE (1)	FON-fon (1)	2	2	4.0	0.0	—	—	—
CAN (1)	FON-fon (1)	2	0	—	—	—	—	—
DEC (1)	FON-fon (1)	3	0	—	—	—	—	—
OCTOPLOID × TETRAPLOID								
TOM (1)	ARV-arv (1)	5	5	20.0	70.0	Yes	No	—
ALP-alp (1)	BIE (1)	6	5	11.7	100.0	Yes	No	—
OCTOPLOID × OCTOPLOID								
ARV-arv (2)	TOM (2)	6	6	26.5	100.0	Yes	Yes	Yes
GRA (1)	ARV-arv (1)	5	1	7.0	28.6	No	—	—
TOM (9)	ARV-arv (4)	86	71	12.0	86.3	Yes	Yes	Yes
ALP-alp (8)	TOM (7)	66	60	28.8	54.6	Yes	Yes	No
GRA (1)	ALP-alp (2)	6	5	15.0	30.0	No	—	—
TOM (3)	ALP-alp (5)	23	18	9.6	85.8	Yes	Yes	No
OCTOPLOID × 16-PLOID								
ARV-arv (1)	MOE (1)	8	0	—	—	—	—	—
GRA (1)	BAN-ban (1)	3	1	15.0	0.0	—	—	—
TOM (3)	BAN-ban (1)	10	9	3.6	65.2	No	—	—
GRA (1)	FON-fon (1)	2	0	—	—	—	—	—
TOM (5)	FON-fon (1)	21	0	—	—	—	—	—
16-PLOID × TETRAPLOID								
BAN-ban (1)	BIE (1)	5	0	—	—	—	—	—
BAN-ban (1)	GIB (1)	4	0	—	—	—	—	—
16-PLOID × OCTOPLOID								
BAN-ban (1)	TOM (2)	10	4	7.0	57.1	No	—	—
16-PLOID × DODECAPLOID								
BAN-ban (1)	TOM (1)	4	4	5.5	0.0	—	—	—

The crosses between members of the *C. tomentosum* group on the one hand, and members of the *C. arvense*, *C. banaticum*, *C. carinthiacum* and *C. alpinum* groups on the other hand, were as successful as crosses within the *C. tomentosum* group. 77% of the crosses produced F1 seed, 46% of the total produced viable seed, and 23% produced mature hybrid plants (69, 49 and 24% respectively for the crosses within the *C. tomentosum* group). None of the tetraploid × tetraploid crosses resulted in viable F1 seed production, but seven of the eleven crosses between tetraploids and octoploids, and all six of the octoploid × octoploid crosses, produced viable F1 seed. Three of the second and four of the third of these groups produced mature F1 plants. The only plants to flower were four of the octoploid × octoploid crosses. Of these four, two (the *C. arvense* × *C. tomentosum* reciprocal crosses) were fertile and two (the *C. alpinum* × *C. tomentosum* reciprocal crosses) were sterile. Hybrid fertility is considered in more detail below.

None of the crosses involving *C. latifolium* or *C. fontanum* produced viable F1 seed.

Interspecific crosses between species of the Cerastium arvense, C. banaticum, C. latifolium, C. alpinum and C. fontanum groups

As a comparison with the *C. tomentosum* group results, the results of interspecific hybridization experiments involving six species of the above five groups are presented in Table 5. Fourteen combinations of species representing five combinations of ploidy level were included.

Four of the 14 crosses produced viable F1 seed. These were all crosses between tetraploids and octoploids and all involved octoploid *C. alpinum* as one parent. The three crosses with *C. alpinum* as the female parent (and with *C. arvense*, *C. carinthiacum* and *C. latifolium* as the male parents) all produced mature F1 plants but these did not flower.

Chromosome numbers in hybrids

Chromosome counts of all hybrids that reached maturity were determined, and all were as predicted from those of the two parents. Of the inter-ploidy crosses, tetraploid × octoploid (or reciprocal) crosses were hexaploids ($2n = 54$), and the tetraploid × 16-ploid cross was a decaploid ($2n = 90$).

Meiotic studies

Male meiosis in the parent species was usually found to be highly regular, with all the chromosomes forming rod or ring bivalents. Mean chiasmata number per bivalent (recorded at full terminalization, hence figures are minimal) ranged from 1.33 to 1.61, except for one accession of *C. gibraltaricum* subsp. *gibraltaricum*, which gave the figure of 1.06. Chiasma frequency did not vary with ploidy level. The B-chromosomes did not take part in pairing. Some irregularities were apparent at later stages (mainly laggards and stickiness at anaphase), leading to the formation of irregular tetrads and micronuclei. Such abnormalities, however, were not common, and were often characteristic of particular accessions (see under pollen stainability).

Table 5. – Results of interspecific hybridizations between taxa of the *Cerastium arvense*, *C. alpinum*, *C. banaticum*, *C. fontanum* and *C. latifolium* groups. Membership of the latter 5 groups is designated by -arv, -alp, -ban, -fon and -lat respectively. Abbreviations as in Table 3.

Female parent (no. accessions)	Male parent (no. accessions)	No. fls. used	No. caps. prod.	Mean seed -set	% seeds viab.	Mature F1 plants	Flow. F1 plants	Fert. F1 plants
TETRAPLOID × TETRAPLOID								
ARV-arv (1)	LAT-lat (2)	14	1	21.0	0.0	—	—	—
LAT-lat (1)	ARV-arv (1)	6	5	12.7	0.0	—	—	—
TETRAPLOID × OCTOPLOID								
ARV-arv (2)	ALP-alp (5)	18	3	6.0	50.0	No	—	—
LAT-lat (1)	ALP-alp (1)	3	3	8.5	0.0	—	—	—
TETRAPLOID × 16-PLOID								
ARV-arv (1)	BAN-ban (1)	5	0	—	—	—	—	—
ARV-arv (1)	FON-fon (1)	2	0	—	—	—	—	—
OCTOPLOID × TETRAPLOID								
ARV-arv (2)	ARV-arv (2)	7	4	1.3	0.0	—	—	—
ARV-arv (2)	LAT-lat (1)	9	0	—	—	—	—	—
ALP-alp (7)	ARV-arv (2)	37	37	23.4	78.3	Yes	No	—
ALP-alp (5)	CAR-lat (1)	24	7	2.3	93.8	Yes	No	—
ALP-alp (6)	LAT-lat (1)	33	5	16.5	12.1	Yes	No	—
OCTOPLOID × 16-PLOID								
ARV-arv (1)	FON-fon (1)	4	0	—	—	—	—	—
ALP-alp (5)	BAN-ban (1)	32	0	—	—	—	—	—
ALP-alp (20	FON-fon (1)	4	0	—	—	—	—	—

Chromosome pairing in the hybrids varied from highly regular to highly irregular. Usually 18 bivalents were formed in the tetraploid hybrids between the two varieties of *C. gibraltaricum*, and 36 bivalents in the octoploid hybrids between the two varieties of *C. tomentosum*. In the octoploid hybrids between *C. tomentosum* and *C. arvense* there were few bivalents, with many univalents and some multivalents and clumped chromosomes, but telophase was usually regular with no or few non-segregating chromosomes. However, in the hexaploid hybrids between *C. tomentosum* var. *tomentosum* and either *C. biebersteinii* or *C. gibraltaricum* var. *lanuginosum*, approximately 18 bivalents and 18 univalents were regularly observed. These hexaploid hybrids showed many meiotic irregularities at later stages

Pollen stainability

Pollen stainability was recorded for the species, the natural hybrids and the artificial hybrids as an approximate measure of male fertility (Table 6). Somewhat surprisingly figures of more than 90%, even for wild-collected species, were uncommon.

Table 6. – Pollen stainability in the species and in the natural and artificial hybrids. Abbreviations as in Table 2.

Taxon (no. of accessions)	Percentage pollen stainability
Species:	
TETRAPLOIDS	
C. biebersteinii (4)	75.7–82.1 (mean 78.7)
C. candidissimum (2)	58.1–61.5 (mean 59.8)
C. decalvans (2)	68.8–86.4 (mean 77.6)
C. g. var. *gibraltaricum* (1)	15.5
C. g. var. *lanuginosum* (5)	2.6–53.9 (mean 33.8)
C. t. var. *tomentosum* (4)	65.3–71.8 (mean 67.5)
OCTOPLOIDS	
C. grandiflorum (3)	85.6–88.9 (mean 87.2)
C. t. var. *minus* (4)	61.2–97.5 (mean 85.7)
C. t. var. *tomentosum* (32)	5.4–95.9 (mean 68)
DODECAPLOIDS	
C. t. var. *tomentosum* (3)	66.8–83.5 (mean 74.7)
16-PLOIDS	
C. moesiacum (4)	5.8–10.2 (mean 8.1)
Natural hybrids:	
OCTOPLOID × OCTOPLOID	
C. arvense × *C. tomentosum* (10)	24.8–95.9 (mean 75.9)
Artificial hybrids:	
TETRAPLOID × TETRAPLOID	
C. g. var. *gibraltaricum* × *C. g.* var. *lanuginosum* (1)	94.1
C. g. var. *lanuginosum* × *C. g.* var. *gibraltaricum* (1)	93.7
OCTOPLOID × TETRAPLOID	
C. tomentosum × *C. biebersteinii* (1)	23.7
C. tomentosum × *C. gibraltaricum* (1)	55.5
OCTOPLOID × OCTOPLOID	
C. tomentosum × *C. grandiflorum* (1)	77.4
C. arvense × *C. tomentosum* (1)	35.7
C. tomentosum × *C. arvense* (2)	35.2–89.9 (mean 62.6)
C. t. var. *tomentosum* × *C. t.* var. *minus* (4)	83.3–94.3 (mean 88.8)
C. t. var. *minus* × *C. t.* var. *tomentosum* (1)	92.3

Most species gave mean figures of between 60% and 90%, the conspicuous exceptions being *C. gibraltaricum* (mean of both varieties 30.8%) and the 16-ploid *C. moesiacum* (mean 8.1%). The pollen stainability of the natural octoploid hybrids between *C. arvense* and *C. tomentosum* were well within the ranges of the species.

The mean pollen stainability of the artificial inter-varietal hybrids within *C. gibraltaricum* and *C. tomentosum* was high (88.8–94.1%). Among the interspecific hybrids, three combinations exhibited stainabilities (55.5–77.4%) of the same order as those of the species and the fourth (*C. tomentosum* × *C. biebersteinii*, 35.7%) was somewhat lower, but still providing ample apparently fertile pollen.

The 32 octoploid *C. tomentosum* accessions showed a wide range of pollen stainabilities (5.4–95.9%), five of them being below 50% and only twelve of them above 80%. This lowered male fertility is also apparent at the morphological level, plants exhibiting an interesting series of degrees of male-function, as shown by abortive stamens. In many plants the first (terminal) flower to open is wholly female, and only the later flowers have viable pollen. Such variation was also seen in other species of the *C. tomentosum* group (especially *C. gibraltaricum*), and in *C. arvense* and *C. alpinum* as well.

Discussion

The extent to which the ability of two taxa to hybridise is indicative of taxonomic and evolutionary relationships is debatable. However, the observation that only relatively closely related species are able to form hybrids must certainly show that crossability does have an important significance, even if this is difficult to quantify. Most hybrids, natural or artificial, involve parents within the same genus; intergeneric hybrids are relatively rare, and the existence of interfamily hybrids has not been substantiated (Stace 1975). We consider that the ability to hybridise is indeed an important indication of relationship, but in a relative rather than an absolute manner. Hence the fact that two species form fertile hybrids should not in isolation be used to unite them as one species, or even indicate that they should of necessity belong to the same genus, but such arguments would become far stronger if none of the close relatives of these two species could hybridise among themselves or with the former two (Stace 1986).

A second level of argument concerns the importance that should be attached to the degree of miscibility of two species. It is usually considered that the formation of mature, vigorous F1 plants is in general more significant than the formation of F1 seed that does not germinate, or which germinates but fails to develop into a mature plant, and that the production of a fertile F1 is more significant than that of a sterile one. This view is, however, open to criticism because a number of factors that affect viability and fertility are known to be only tenuously associated with broader evolutionary relationships. Examples of such factors are chromosome number and cytoplasmic/chromosomal compatibility (Stebbins 1958), which can cause a lack of success in hybrids between species (or individuals within one species) that are known to be very closely related.

In the present results we distinguished five levels of hybrid success: the production of F1 seed; the successful germination of F1 seed; the production of mature F1 plants; the production of flowering F1 plants; and the production of fertile F1 plants (Tables 1–5). However, the third category (the production of mature but non-flowering F1 plants) is somewhat artificial, because the project was terminated when the F1 plants were three years old and it is possible that a proportion of the non-flowering plants would have flowered if given longer.

Within the *C. tomentosum* group seven species were studied: six species each at one ploidy level, varying from tetraploid to 16-ploid, and *C. tomentosum* at the tetraploid, octoploid and dodecaploid levels. Perhaps the most notable result was the high level of success in terms of interspecific combinations producing F1 seed (69%), or in terms of producing viable F1 seed (49%) or even mature plants (24%). In the octoploid × tetraploid and octoploid × octoploid crosses 50% of the taxon combinations produced mature F1 plants. In crosses between different varieties within *C. tomentosum* and *C. gibraltaricum* at the same ploidy level (octoploid and tetraploid respectively), there was no loss of fertility in the F1 plants. In the interspecific crosses fertile F1 plants were obtained from only three combinations, all with octoploid *C. tomentosum* as the female parent. The male parents were *C. biebersteinii* (tetraploid), *C. gibraltaricum* (tetraploid) and *C. grandiflorum* (octoploid). It should be noted these crosses are all between naturally allopatric taxa. It can be concluded that there is little evidence that there are internal isolating barriers preventing interspecific gene exchange between these four species. A much lower level of success is achieved when the female parent is at the tetraploid level. Crosses between *C. tomentosum* and the other two tetraploid species of the group, *C. candidissimum* and *C. decalvans*, did not produce mature plants. Crosses between plants of *C. tomentosum* at different ploidy levels produced no fertile F1 plants, although our results are not complete. Nevertheless, it appears that crosses between species in the *C. tomentosum* group are at least as successful as crosses between different cytotypes within *C. tomentosum* itself. This evidence on its own could be taken to indicate that the *C. tomentosum* group comprises closely related taxa that form a natural taxon.

However, it is clear that, in terms of hybridization, the species of the *C. tomentosum* group are as closely related to those of the *C. alpinum*, *C. arvense*, *C. banaticum* and *C. latifolium* groups as they are to other species of their own group (see comparable figures under Results). It must therefore be concluded that there is no evidence from the crossability data for the reality of these five groups, but that all five together form a single genetical coenospecies (Turesson 1922) or comparium (Danser 1929). In view of the fact that there is uncertainty about the delimitation of these five groups (the placement of *C. gibraltaricum* and *C. lineare* within or outside the *C. tomentosum* group is particularly debated), it is here suggested that they should be amalgamated to form a single undivided taxon (which must bear the name *Cerastium* at whatever rank is chosen). This corresponds more or less with Söllner's (1954) concept of subsection *Perennia*.

Fertile hybrids were obtained not only between octoploid *C. tomentosum* and two tetraploid and one octoploid species of the *C. tomentosum* group, but also between octoploid *C. tomentosum* and octoploid *C. arvense*. The naturally occurring octoploid hybrids between *C. tomentosum* and *C. arvense* from south-eastern England are also fertile. All these natural and artificial hybrids have the expected euploid chromosome numbers (hexaploid or octoploid), and their pollen stainabilities are mostly within the range of those of the species (Table 6). This is somewhat surprising in view of the results of meiotic analysis of the artificial hybrids, which showed major irregularities in both the hexaploids and the octoploids. Despite this, sufficient euploid pollen and embryo sacs are produced to generate effectively fertile hybrid plants. Moreover there is evidence to suggest that meiosis in these hybrids can, presumably over some generations, become normal. Natural octoploid *C. arvense* × *C. tomentosum* found in extensive maritime dune and shingle populations at Holme and Snettisham, W. Norfolk (south-eastern England) is fertile, and analyses of two plants showed a high degree of meiotic regularity, contrasting with those of the artificial hybrids. One plant regularly formed 36 bivalents at prophase I, and the other had 95.9% pollen stainability and a regular anaphase II; both produced viable seed from selfing. The figure of 95.9% pollen stainability for the latter was actually the highest found in any of the wild hybrids, the other nine plants measured varying down to as low as 24.8%. The mean figure for the wild hybrids (75.9%) is higher than those obtained for artificial hybrids (35.7% and 62.6% for the reciprocal crosses). It seems likely that the Norfolk populations include hybrids of a range of ages and hence of degrees of meiotic regularity. The plants of both species and hybrids are very long-lived (potentially immortal) and the normal mode of reproduction is by rhizomes and stolons, which are well equipped to withstand the shifting substrate. Nevertheless the habitat provides ample new open areas, which enable the continual establishment of newly formed hybrids.

Cerastium arvense is sympatric with members of the *C. tomentosum* group over most of their range except in Crimea (*C. biebersteinii*) and Greece (*C. candidissimum*) (Jalas & Suominen 1983). It would, therefore, not be surprising if natural hybrids were to exist within the natural range of the *C. tomentosum* group. Based purely on herbarium studies, it does seem possible that *C. gibraltaricum* var. *viridulum* from southern Spain and *C. tomentosum* var. *minus* from Sicily might have had such an origin; significantly in both areas the two species concerned have been recorded at the same ploidy level.

Contrasting with the above hybrid, the artificial hybrids between the two octoploids *C. tomentosum* and *C. alpinum* were sterile. In accordance with our views on the relative taxonomic value of crossability, we consider this to be significant. In the wild *C. alpinum* is broadly sympatric with members of the *C. tomentosum* group only in the western Alps (*C. lineare*) and northern Balkans (*C. decalvans*, *C. grandiflorum* and *C. moesiacum*) (Jalas & Suominen 1983). We do not know if they ever occur in mixed populations, but their altitudinal ranges certainly coincide.

Within the *C. tomentosum* group only *C. decalvans*, *C. grandiflorum* and *C. moesiacum* are broadly sympatric. We do not know whether mixed populations occur, but no wild hybrids have been reported to our knowledge. The only combination attempted by us was between *C. decalvans* and *C. grandiflorum*, which produced no viable seeds. None of the crosses between *C. moesiacum* and other species produced mature plants, and this 16-ploid species seems well isolated from all the others. Nevertheless, in view of our production of fertile hybrids between *C. tomentosum* and three other species, it appears that the main isolating barrier in the *C. tomentosum* group is geographical. If *C. tomentosum* occurred with the Spanish *C. gibraltaricum*, the Balkan *C. grandiflorum* or the Crimean *C. biebersteinii* it is likely that wild fertile hybrids and their later generations and backcrosses would occur.

The 16-ploid *C. moesiacum* and some clones of the octoploid *C. tomentosum* are highly self-incompatible, but most clones of *C. tomentosum* and all or most clones of the other species are self-compatible. Out-crossing in the latter is achieved by strong protandry, but selfing can occur when crossing has failed by the action of the closing sepals at the end of the flowering period. The ability to self-fertilize is perhaps important in these plants, where a single clone can occupy a large area, but evenso crossing must be frequent as the flowers are very attractive to insects, particularly large bees. Varying degrees of male-sterility must also mitigate against selfing to some degree, notably in some clones of *C. tomentosum*, but it cannot be of significance in the self-incompatible *C. moesiacum*, which has a consistently low pollen fertility.

Souhrn

Článek přináší výsledky umělých hybridizačních pokusů mezi druhy skupiny *Cerastium tomentosum*. Z různých hybridních kombinací čtyř ploidních hladin, které se v tomto komplexu druhů vyskytují, produkují životaschopná semena kříženci v F1 generaci ve 22 případech (49 %) ze 45 možných kombinací. V jedenácti případech byly vypěstovány dospělé rostliny, z nichž tři byly fertilní. Nejúspěšnější bylo křížení mezi oktoploidními a tetraploidními druhy a v rámci oktoploidních druhů, z nichž byly v 50 % případů vypěstovány dospělé rostliny, včetně všech tří plodných F1 hybridních kombinací. Vzhledem k tomu, že jednotlivé druhy jsou v přírodě geograficky izolovány, dochází k hybridizaci jen velmi vzácně. Snadná křížitelnost nicméně naznačuje, že jednotlivé zmíněné skupiny druhů náleží do jediné subsekce *Cerastium*.

References

Ayasligil Y. (1984): New taxa and records from SW Turkey. – Notes Roy. Bot. Gard. Edinburgh 42: 69–76.

Brysting A. K. (1999): Reticulate evolution and its taxonomical consequences. – Doctoral Dissertation, Faculty of Mathematics and Natural Sciences, University of Oslo, Oslo.

Buschmann A. (1938): Über einige ausdauernde *Cerastium*-Arten aus der Vermandtschaft des *C. tomentosum* L. – Feddes Repert. 43: 118–143.

Cullen J. (1967): *Cerastium* L. – In: Davis P. H. (ed.), Flora of Turkey 2: 73–85, Edinburgh University Press, Edinburgh.

Danser B. H. (1929): Über die Begriffe Komparium, Kommiscuum und Konvivium und über die Entstehungsweiseder Konvivien. – Genetica 11: 399–450.

Fenzl E. (1840): *Cerastium* L. – In: Endlicher S. L. (ed.), Genera Plantarum, p. 969–970, Fr. Beck, Vienna.

Fenzl E. (1842): *Cerastium* L. – In: Ledebour C. (ed.), Flora Rossica 1: 396–416, E. Schweizerbart, Stuttgart.

Jalas J., Sell P. D. & Whitehead F. H. (1964): *Cerastium* L. – In: Tutin T. G., Heywood V. H. et al. (eds.), Flora Europaea 1: 136–145, Cambridge University Press, Cambridge.

Jalas J., Wyse Jackson M. B., Sell P. D. & Whitehead F. H. (1993): *Cerastium* L. – In: Tutin T. G., Heywood V. H. et al. (eds.), Flora Europaea, Ed. 2, 1: 164–175, Cambridge University Press, Cambridge.

Jalas J. & Suominen J. (1983): *Cerastium* L. – In: Atlas Florae Europaeae 6: 85–119, Societas Biologia Vanamo, Helsinki.

Karlsson T. (1997): Förteckning över svenska kärlväxter. – Svensk Bot. Tidskr. 91: 241–560.

Khalaf M. K. (1993): Biosystematic studies in *Cerastium tomentosum* group (*Caryophyllaceae*). – PhD Thesis, Faculty of Science, University of Leicester, Leicester.

Krogulevich R. E. (1971): The role of polyploidy in the genesis of the alpine flora of the Stanovoye Nagorye mountains. – In: The ecology of the flora of the Trans-Baikal region, Irkutsk. [not seen]

Morton J. K. (1975): *Cerastium* L. – In: Stace C. A. (ed.), Hybridization and the flora of the British Isles, p. 171–174, Academic Press, London.

Rico E. (1990): *Cerastium* L. – In: Castroviejo S. et al. (eds.), Flora Iberica 2: 260–283, Real Jardín Botánico, Madrid.

Schischkin B. K. (1936): *Cerastium* L. – In: Komarov V. L. & Schiskin B. K. (eds.), Flora URSS 6: 430–466, Izdateľstvo Akademii Nauk SSSR, Moscow & Leningrad.

Söllner R. (1954): Recherches cytotaxonomiques sur le genre *Cerastium*. – Bull. Soc. Bot. Suisse 64: 221–354.

Stace C. A. (ed.) (1975): Hybridization and the flora of the British Isles. – Academic Press, London.

Stace C. A. (1986): Hybridization and plant taxonomy. – Symb. Bot. Upsal. 27 (2): 9–18.

Stebbins G. L. (1958): The inviability, weakness and sterility of interspecific hybrids. – Advances in Genetics 9: 147–215.

Strid A. (1986): *Cerastium* L. – In: Strid A. (ed.), Mountain flora of Greece 1: 110–122, Cambridge University Press, Cambridge.

Talavera S. (1987): *Cerastium* L. – In: Valdés B., Talavera S. & Fernández-Galiano E. (eds.), Flora vascular de Andalucía Occidental 1: 237–240, Ketres Editora, Barcelona.

Turesson G. (1922): The genotypical response of the plant species to the habitat. – Hereditas 3: 211–350.

Received 6 April
Accepted 23 May

Appendix 1. – List of accessions of *Cerastium* taxa used in the hybridization experiments, with chromosome numbers as determined in this study.

***Cerastium tomentosum* group**

- *Cerastium biebersteinii* – tetraploid (2n = 36)
  - CER 81 – South Crimea, Ukraine
- *Cerastium candidissimum* – tetraploid (2n = 36)
  - CER 51–1400 m, Parnon, Peliponnisos, Greece
- *Cerastium decalvans* – tetraploid (2n = 36)
  - CER 66 – Botanic Garden material, ex Switzerland
- *Cerastium gibraltaricum* var. *gibraltaricum* – tetraploid (2n = 36)
  - CER 121–240 m, Gibraltar
- *Cerastium gibraltaricum* var. *lanuginosum* – tetraploid (2n = 36)
  - CER 69 – Botanic Garden material, ex Switzerland
- *Cerastium grandiflorum* – octoploid (2n = 72)
  - CER 39 – Croatia
- *Cerastium moesiacum* – 16-ploid (2n = 144)
  - CER 83 – Botanic Garden material, ex Germany
  - CER 177 – Botanic Garden material, ex Germany
- *Cerastium tomentosum* var. *minus* – octoploid (2n = 72)
  - CER 38 – Etna, Sicily
  - CER 44–1800 m, Etna, Sicily
  - CER 56–2000 m, Etna, Sicily
- *Cerastium tomentosum* var. *tomentosum* – tetraploid (2n = 36)
  - CER 37 – Botanic Garden material, ex Switzerland
- *Cerastium tomentosum* var. *tomentosum* – octoploid (2n = 72)
  - CER 1 – Botanic Garden material, ex Czech Republic
  - CER 2 – Botanic Garden material, ex Czech Republic
  - CER 3 – Botanic Garden material, ex England
  - CER 4 – Gorebridge, Midlothian, Scotland (+ 1–3 B-chrs)
  - CER 5 – Blackford Quarry, Midlothian, Scotland (+ 5 B-chrs)
  - CER 7 – Botanic Garden material, ex England
  - CER 8 – Botanic Garden material, ex Poland
  - CER 9 – Botanic Garden material, ex Poland
  - CER 16 – Botanic Garden material, ex Netherlands
  - CER 20 – Snettisham, W. Norfolk, England
  - CER 21 – Snettisham, W. Norfolk, England
  - CER 25 – Snettisham, W. Norfolk, England
  - CER 26 – Snettisham, W. Norfolk, England (+ 2 B-chrs)
  - CER 31 – Holme, W. Norfolk, England
  - CER 33 – Botanic Garden material, ex Spain (+ 2 B-chrs)
  - CER 36 – Botanic Garden material, ex Switzerland (+ 0–2 B-chrs)
  - CER 45 – Botanic Garden material, ex France
  - CER 57 – Botanic Garden material, ex Poland
  - CER 60 – Botanic Garden material, ex Germany (+ 0–4 B-chrs)
  - CER 62 – Botanic Garden material, ex Germany (+ 2 B-chrs)
  - CER 64 – Botanic Garden material, ex Germany (+ 0–2 B-chrs)
  - CER 78 – Botanic Garden material, ex Romania
  - CER 88 – Botanic Garden material, ex Hungary
  - CER 91 – Botanic Garden material, ex Switzerland
  - CER 94 – Botanic Garden material, ex Hungary
  - CER 95 – Botanic Garden material, ex Hungary
  - CER 98 – Botanic Garden material, ex Hungary
  - CER 100 – Botanic Garden material, ex Hungary
  - CER 102 – Botanic Garden material, ex Hungary
- *Cerastium tomentosum* var. *tomentosum* – dodecaploid (2n = 108)
  - CER 65 – Botanic Garden material, ex Switzerland

Cerastium alpinum **group**

- *Cerastium alpinum* – octoploid (2n = 72)
  - CER 14–750 m, Lom, Opland, Norway
  - CER 15–1000 m, Abisco, Norrbotten, Sweden
  - CER 17 – Botanic Garden material, ex Netherlands
  - CER 18 – Botanic Garden material, ex Netherlands
  - CER 35 – Botanic Garden material, ex Switzerland
  - CER 47 – Botanic Garden material, ex France
  - CER 48–2000 m, Pyrénées Atlantiques, France
  - CER 63 – Botanic Garden material, ex Germany
  - CER 82 – Botanic Garden material, ex Germany
  - CER 99 – Botanic Garden material, ex Hungary

Cerastium arvense **group**

- *Cerastium arvense* – octoploid (2n = 72)
  - CER 27 – Snettisham, W. Norfolk, England
  - CER 29 – Holme, W. Norfolk, England
  - CER 55–2350 m, Valle di Gressoney, Italy
  - CER 75 – Botanic Garden material, ex Romania
  - CER 80 – Botanic Garden material, ex Romania

Cerastium banaticum **group**

- *Cerastium banaticum* – 16-ploid (2n = 144)
  - CER 50–2250 m, Makedonia, Greece
  - CER 70 – Botanic Garden material, ex Switzerland

Cerastium fontanum **group**

- *Cerastium fontanum* – 16-ploid (2n = 144)
  - CER 22 – Snettisham, W. Norfolk, England
  - CER 53 – Eschwege, Germany

Cerastium latifolium **group**

- *Cerastium carinthiacum* – tetraploid (2n = 36)
  - CER 42–1700 m, Insubria, Italy
- *Cerastium latifolium* – tetraploid (2n = 36)
  - CER 41–2000 m, Valais, Switzerland
  - CER 61 – Botanic Garden material, ex Germany