Cytogenetic relationships between lowland and montane species of the *Campanula rotundifolia* L. group

II. Tetraploid *C. rotundifolia* L. s. str. as well as *C. polymorpha* Witasek and *C. scheuchzeri* Vill. from Poland

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INTRODUCTION

The present study is a continuation of investigations on the cytogenetic relationships within the polyploid *C. rotundifolia* L.s.l. complex. It is aimed at the elucidation of the relations between the tetraploid taxa occurring in Poland: *C. rotundifolia* L. s. str., *C. polymorpha* Witasek and *C. scheuchzeri* Vill. Since so far no diploid and hexaploid forms have been found in Poland, *C. rotundifolia* s. str. is considered as a tetraploid taxon. Nevertheless, the existence of these unknown forms in Poland cannot be excluded.

Diploid forms have been collected in the environs of Moscow (Böcher 1960), Pskov (Gadella 1962, 1964) as well as in Czechoslovakia (Gadella 1962, 1964; Kovanda 1966a, b). All these regions, however, have never undergone glaciation. The territory of Poland. stripped by being glaciated of its previous vegetation, had more chances of being colonized by polyploids according to the theory of Stebbins (1956) which found confirmation in the investigations of other authors (Rollins and Manton, in discussion on Merxmüller's paper 1958; Johnson and Packer 1965).

Tetraploid forms of *C. rotundifolia* s. str. are common on the entire Polish lowland and in the lower zones of the Carpathian and Sudetic Mts. In the subalpine zone of these mountains there occurs, moreover, another tetraploid species of the same group, *C. polymorpha* Witasek and at the level above ca. 1400 m a.s.l. also the tetraploid *C. scheuchzeri* Vill. (Witasek 1902, 1906; Hruby 1930, 1934, 1950; Szafer, Kulczyński and Pawłowski 1953).

MATERIAL AND METHOD

As in the preceding work (Bielawska 1964) the plants for investigation and crosses originated from natural habitats and were cultivated on an experimental plot of the Department of General Genetics of the

Polish Academy of Sciences in Warsaw in possibly uniform conditions, though not too favourable, especially for mountain plants. All the descriptions and measurements were made as before on living plants and not on herbarium specimens. The following characters were taken into account: height of stems, number of flowers per stem, length and width of lower stem leaves on young shoots, length of corolla, depth of incision
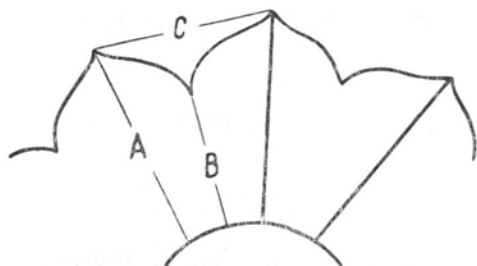

Fig. 1. The scheme of the corolla

of corolla lobes, and distance between their tips, length of calyx teeth, pollen and seed fertility and date of the beginning of flowering. Moreover, if necessary, the following features were included in the description: occurrence of pubescence, colour of flowers and pollen, type of branching of shoots and type of foliage, shape of endings of stem leaves and a number of other morphological features only sporadically taken into account in descriptions. The details regarding measurement or determination of the characters studied and the methods of crossing and obtaining seeds by self-pollination are described in the preceding paper (Bielawski 1964). The scheme of the corolla (fig. 1) given above illustrates the way of calculation of the coefficients characterizing the corolla $\left(\dfrac{A}{C} \right.$ — coefficient of corolla enlargement, $\dfrac{A-B}{A}$ — coefficient of corolla incision). Coefficient of shape of stem leaves is a ratio of length and width of stem leaves on young shoots.

The seed fertility is given in terms of mean number of seeds set per capsule in free pollination, as calculated from five capsules.

Cytological examination was also performed to determine the number of chromosomes. Their small size and lack of differentiation did not allow a closer analysis. The methods applied are described in the previous paper.

Not all traits were taken into account in the analysis of the particular crosses.

PARENTAL FORMS

The plants used for the crosses were treated exclusively as representatives of the respective taxa, since the material was too sparse to allow

Table 1

Comparison of some characters within the tetraploid taxa of *C. rotundifolia* L.s.l. group

Taxon	Height of stems[1] cm	Pubescence of stems[2]	Stem leaves coefficient of shape	Stem leaves en-ding[2]	Flower buds	No. of flowers per stem	Corolla length mm	Corolla coefficient of incision	Corolla coefficient of enlargement	Ratio of calyx teeth length to corolla length	Pollen fertility %	Beginning of flowering on the experimental plot
C. rotundifolia s. str.												
— lowland representatives	35—72 (26—81)	+	8,4—11,5	pointed	erect	13,2—47,2	18,1—23,4	0,31—0,36	1,69—2,00	0,27—0,34	88,5— 98,9[3]	25.V—10.VI
— montane representatives	26—40 (20—46)	—+	8,8—10,6	blunt	erect	10,2—20,6	18,8—23,9	0,33—0,35	1,73—1,95	0,33—0,64	97,7—100,0	25.V—10.VI
C. polymorpha	6—36 (5—43)	—(+)	5,5—16,2	blunt (pointed)	erect	1,8—29,6	17,1—27,1	0,26—0,37	1,55—2,45	0,27—0,46	86,8— 99,0[4]	1.VI—1.VII
C. scheuchzeri	9—25 (8—30)	+(—)	9,3—11,3	pointed (blunt)	pendent	2,0— 8,0	14,6—25,3	0,24—0,34	1,78—2,49	0,26—0,47	77,1— 98,5	10.VI—1.VII

[1] In parenthesis a minimal and maximal value is given. [2] In parenthesis less frequent characters are given. [3] The plant no. 17—49,8%. [4] The plant no. 109—0,0%.

a wider elaboration of variation within these taxa. The range of varia-
tion of some features in the reared plants of each taxon is shown in
Table 1. As seen in this tabulation, most features exhibit a great
variability within the taxa considered, and distinction between them is
difficult. The similarities are mostly more pronounced than the diffe-
rences. *C. scheuchzeri* exhibits the most distinct differences. The degree
of relationship and the differences between the taxa examined found
their reflection in the results of the crosses.

1. *C. rotundifolia* L. s. str.

The plants of this taxon taken for study originate from the Polish
lowland and montane stands in the Tatra (up to ca. 1000 m a.s.l. —
Figs 2—3).

nos. 13, 14, 46 — environs of Warsaw
no. 17   — Pińczów
no. 4   — Zakopane, Antałówka (ca. 900 m a.s.l.)
no. 22   — Zakopane, Dolina Kościeliska valley (ca. 1000 m a.s.l.).

The typical lowland forms are high, mostly with hirsute stems pro-
fusely branched on their entire length and abundantly foliated. Stem
leaves long and sharp; basal leaves dry up before flowering. Inflorescen-
ces multiflorous. Buds erect. Flowers violet with recurved lobes rather
deeply incised. Another more than two times longer than the filament.
Pollen cream-coloured, sometimes greyish, in the latter case young
pollen in the anthers is pale rose. All the plants have a high percentage
of morphologically very good pollen and set seeds profusely after free
pollination. They all produce progeny from artificial self-pollination.

The second group of *C. rotundifolia* s. str. representatives the range
of which overlaps that of *C. polymorpha,* is very interesting. It was not
checked in the field whether we are dealing here with a clinal variation
of character correlated with altitude. On the basis of the present results
it may be only assumed that there exists a reciprocal introgression
between the two taxa. A study of a larger number of stands on these
areas would no doubt contribute to the elucidation of the existing
relationships and it would be worth supplementing in this way the
picture of the variation of *C. rotundifolia.* Investigation of the variation
within the species *C. polymorpha* involves the same problems.

The plants of *C. rotundifolia* s. str. from lower montane habitats
(up to ca. 1000 m a.s.l.) are lower, they have bluntly ending and wider
stem leaves and less flowers per stem. Flower buds typically erect.
Flowers larger, somewhat deeper incised with longer sepals. Individuals
with relatively longer filaments and pollen containing anthocyanine occur
rather frequently. The pollen fertility is very high, and the plants set
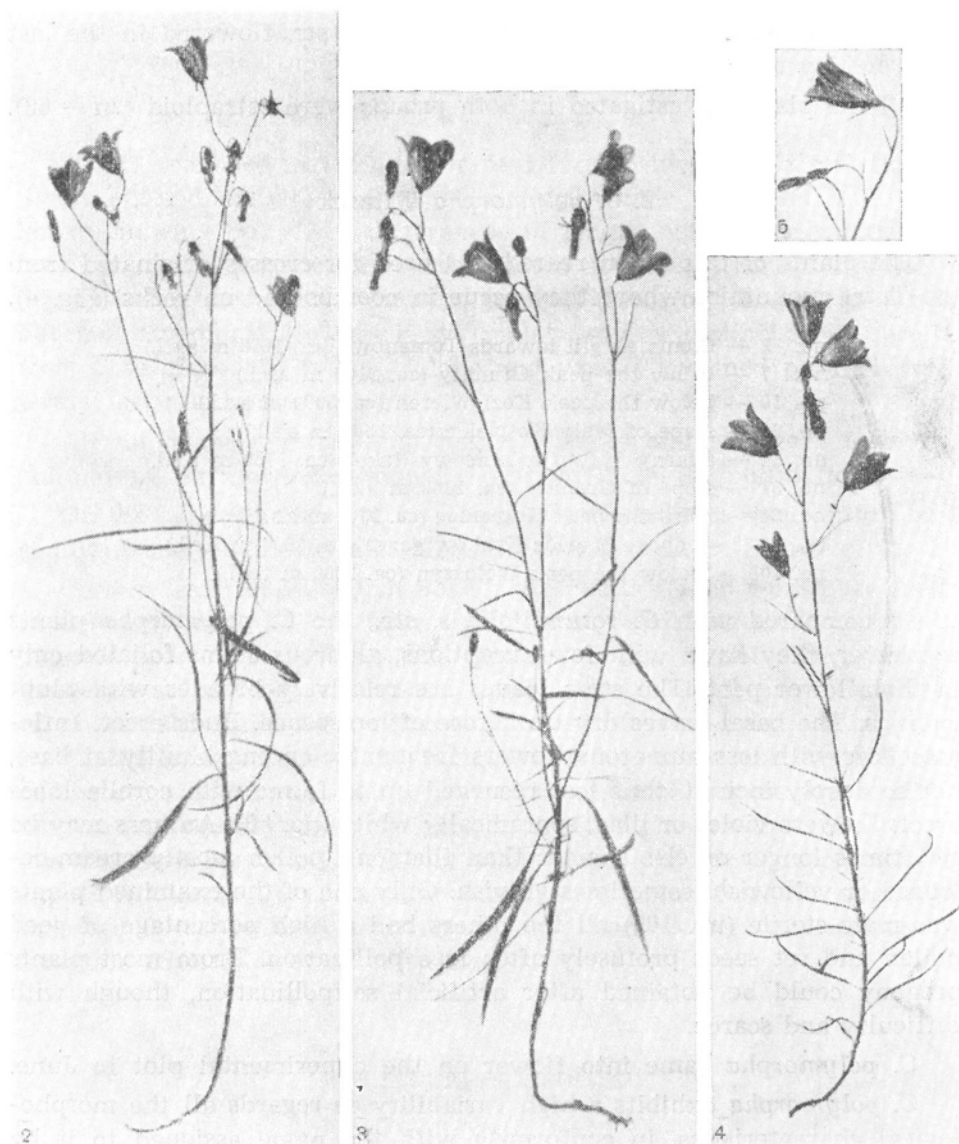seeds profusely after free pollination, they also all produced progeny

Fig. 2. Lowland representative of *Campanula rotundifolia* L.s.str. no. 14
Fig. 3. Montane representative of *Campanula rotundifolia* L.s.str. no. 4
Fig. 4. *Campanula polymorpha* Witasek no. 2
Fig. 5. *Campanula scheuchzeri* Vill. no. 62

when artificially selfpollinated. In Table 1 some characters of both groups of *C. rotundifolia* s. str. from various altitudes are listed for comparison. As seen, the differences occurring between them involve height, type of stem leaves, number of flowers per stem and length of filaments.

On the experimental plot *C. rotundifolia* s. str. flowered in the last days of May or at the beginning of June.

All the plants investigated in both groups were tetraploid (2n = 68).

2. *C. polymorpha* Witasek

The plants of this taxon reared and used for crosses originated from the Tatra mountains where they occur in coombs and on rocks (Fig. 4).

no. 2 — Ciemniak gill towards Tomanowa (ca. 1800 m a.s.l.)
no. 7 — below the peak Granaty (ca. 2100 m a.s.l.)
no. 10 — below the peak Kozi Wierch (ca. 2000 m a.s.l.)
no. 25 — slope of Mały Kościelec (ca. 1800 m a.s.l.)
no. 28 — Czarny Staw Gąsienicowy (lake) (ca. 1700 m a.s.l.)
no. 31 — slope of Granaty (ca. 1800 m a.s.l.)
no. 34 — below the peak Kopieniec (ca. 1300 m a.s.l.)
no. 78,80 — above Wąwóz Kraków gorge (ca. 2000 m a.s.l.)
no. 109 — below the peak Wołoszyn (ca. 2000 m a.s.l.).

As compared with *C. rotundifolia* s. str., the *C. polymorpha* plants are lower, they have, with few exceptions, glabrous stems foliated only in their lower part. The stem leaves are relatively broader with blunt endings. The basal leaves dry up before efflorescence. Buds erect. Inflorescences with less numerous flowers frequently ending bluntly at base, not so deeply incised, thus less recurved up to forms with corolla lobes erect. Flowers violet or lilac, sporadically white (no. 80). Anthers may be two times longer or else shorter than filament, pollen mostly cream-coloured or yellowish, sometimes greyish. Only one of the examined plants was male-sterile (no. 109) all the others had a high percentage of good pollen and set seeds profusely after free pollination. From most plants progeny could be obtained after artificial selfpollination, though with difficulty and scarce.

C. polymorpha came into flower on the experimental plot in June.

C. polymorpha exhibits a high variability as regards all the morphological characteristics, in conformity with the name assigned to it by W i t a s e k. Even populations occurring in the same mountain valleys are not uniform and each cluster differs from the neighbouring ones.

All the plants examined were tetraploid (2n = 68).

3. *C. scheuchzeri* Vill.

The plants investigated originated from the Tatra from a classical habitat of this taxon — Czerwone Wierchy (peak) and also from the neighbouring Giewont. They occur on grass-overgrown passes and slopes (Fig. 5).

nos. 62, 64 — slope of Małołączniak (ca. 2000 m a.s.l.)
no. 75 — slope of pass between Małołączniak and Krzesanica towards Litworowa (ca. 2000 m a.s.l.)
nos. 110, 111 — Giewont (ca. 1800 m a.s.l.).

Shoots branched in their upper part form panicles with few flowers. Stems ciliated on edges. Sharply ending, rather long and wide stem leaves showing but slight differences in length between the upper and lower ones. Edges of lower leaves ciliated at least at base. Basal leaves dry up before florescence. Buds on pendent (more or less bent peduncles but not drooping). Flowers large, violet, with a distinct vein running from base of corolla to tip of lobe and weakly outlined parallel veins. Ovary large and elongated.

All the plants exhibit high pollen fertility and set seeds from free pollination, but only exceptionally after artificial selfpollination.

On the experimental plot in Warsaw *C. scheuchzeri* comes into flower simultaneously with the later blooming plants of *C. polymorpha*.

Certain traits indicate that not all the plants reared were pure forms. Evidence of this may be found in the nontypical length of the anthers in some specimens and the fact that the pollen is not always cream--coloured as reported in classical descriptions. Not all plants had buds on characteristically bent peduncles or this feature was not exhibited by all the buds on one plant. Some plants had more numerous flowers on the stem or bluntly ending leaves. Since there also occurred, in the nearest neighbourhood on the area where the plants were collected for investigation, plants representing other taxa, and the further reported experimental results prove that intercrosses occur easil, it is possible that the *C. scheuchzeri* plants may have had, owing to introgression, a certain admixture of other species.

RESULTS OF CROSSES

In order to elucidate the relationships between the tetraploid taxa occuring in Poland, all possible inter-crosses were made in a total number of 318, of which 280 set seeds. No hybrids were obtained only in the case of the cross *C. scheuchzeri* ♀ × *C. polymorpha* ♂. This, however, may have been due to an insufficient number of replications.

1. Crosses within *C. rotundifolia* s. str.

Within this taxon most interesting are no doubt the crosses between its lowland and montane representatives, however, for comparative purposes, also the lowland representatives accepted, as standard types in

Table 2

Comparison of some characters of parental forms and their hybrids in the crosses within *C. rotundifolia* s. str.

Cross	Parental forms and their hybrids	Height of stems cm	Coefficient of shape of stem leaves	No. of flowers per stem	Corolla length mm	Corolla coefficient of incision	Corolla coefficient of enlargement	Ratio of calyx teeth length to corolla length	Pollen fertility %
	P 4	29(24—32)	8,8	10,2	22,7	0,33	1,73	0,42	97,5
	13	72(55—81)	11,1	42,4	18,1	0,36	1,69	0,34	98,1
	14	40(35—50)	9,6	15,2	20,5	0,33	1,81	0,31	98,0
	17	44(29—63)		29,6	19,1	0,32	1,91	0,30	49,8
	46	35(24—40)	11,5	13,1	20,3	0,33	1,75	0,27	98,0
between lowland representatives	F_1 13×46	45(38—50)	10,6	20,4	19,4	0,35	1,85	0,40	92,2
	46×13	42(35—47)	9,7	15,4	19,4	0,34	1,98	0,41	94,6
	F_1 4×14	27(23—30)	11,1	7,6	21,1	0,29	2,17	0,36	98,3
		27(26—29)		20,5	18,5	0,34	1,66	0,40	97,6
		32(20—40)	12,7	8,6	23,7	0,35	1,86	0,43	97,1
		34(30—38)	8,5	9,4	23,4	0,35	1,88	0,44	97,7
		35	9,6	13,0	19,2	0,29	1,59	0,28	99,3
	14×4	29(20—35)	11,5	8,9	21,2	0,34	1,70	0,31	97,0
		37(30—45)	8,9	14,1	21,9	0,33	1,95	0,32	98,5
between lowland and montane representatives		38(17—55)	10,2	18,7	21,7	0,33	1,88	0,35	98,4
		38(35—45)	7,8	16,4	21,7	0,33	1,83	0,39	98,1
	F_2 4×14	13—41	4,8—23,6	1,8—51,5	14,2—25,7	0,24—0,38	1,38—2,81	0,15—0,54	59,7—100,0
	14×4	6—40	5,7—17,6	1,2—40,2	12,8—28,3	0,27—0,39	1,51—2,48	0,20—0,56	65,1—100,0
	F_1 4×13	41(34—48)	10,5	21,1	19,6	0,34	1,83	0,33	80,7
	13×4	33(22—45)	14,2	12,8	22,0	0,36	1,77	0,38	
	F_1 17×4	25[1]		±10[1]	20,8	0,32	1,88	0,40	35,3

[1] Values obtained in the first year of vegetation (so a little decreased).

combination with other taxa, were intercrossed. Table 2 allows to compare some characters of the parental forms with those of the hybrids within *C. rotundiforia* s. str.

Crossability

All crosses attempted between the lowland representatives of *C. rotundifolia* s. str. succeeded readily. Of 35 pollinations seeds were obtained in 30, and the percentage of germination was high. Seeds from the crosses between plants of *C. rotundifolia* s. str. from the lowland and individuals from the Tatra were also obtained without difficulty. In 45 crosses, 39 set seeds. However, the percentage of germination was higher when the maternal form was a lowland plant. As indicated by Table 3 which gives a comparison of the crosses within *C. rotundifolia* s. str., the results were not uniform even when the same individuals were used in replicating as parental forms. The mean number of seeds set per capsule varied from values equal to those set by the maternal forms in free pollination to barely several seeds. On the other hand, F_1 hybrids always set seeds after free pollination in the same amounts per capsule as did the representatives of pure taxa. The results of the particular replications of the given cross must, therefore, be dependent on the heterozygousness of the outset forms, and to a large extent, on some accessory nongenetic factors, thus physiological and environmental. The importance of these factors and the necessity of taking them into account in the interpretation of results is indicated by their equally strong influence on plants originating from similar life conditions, namely from the environs of Warsaw. Therefore their action on montane plants reared on an experimental plot under conditions different from natural may be stronger.

Description of hybrids between lowland representatives

As example of hybrids between lowland *C. rotundifolia* s. str. may serve the reciprocal crosses between plants no. 13 (Fig. 1. in B i e l a w-s k a 1964) and no. 46 (Table 2). Of both F_1 each comprised 10 plants. Reciprocal F_1s are in many respects intermediate between the parental forms (height of plants, number of flowers per stem, length of corolla, coefficient of corolla incision) and have a similar coefficient of shape of the stem leaves. hey also exhibit the same type of branching as both the parental forms, i.e. on the whole length of the shoots and the same type of foliation — numerous stem leaves long, narrow with pointed endings. The stems both of the parent forms and the F_1 hybrids had a short pubescence. On the other hand, the hybrids hand longer calyx teeth and some of them had more recurved lobes as shown by the higher
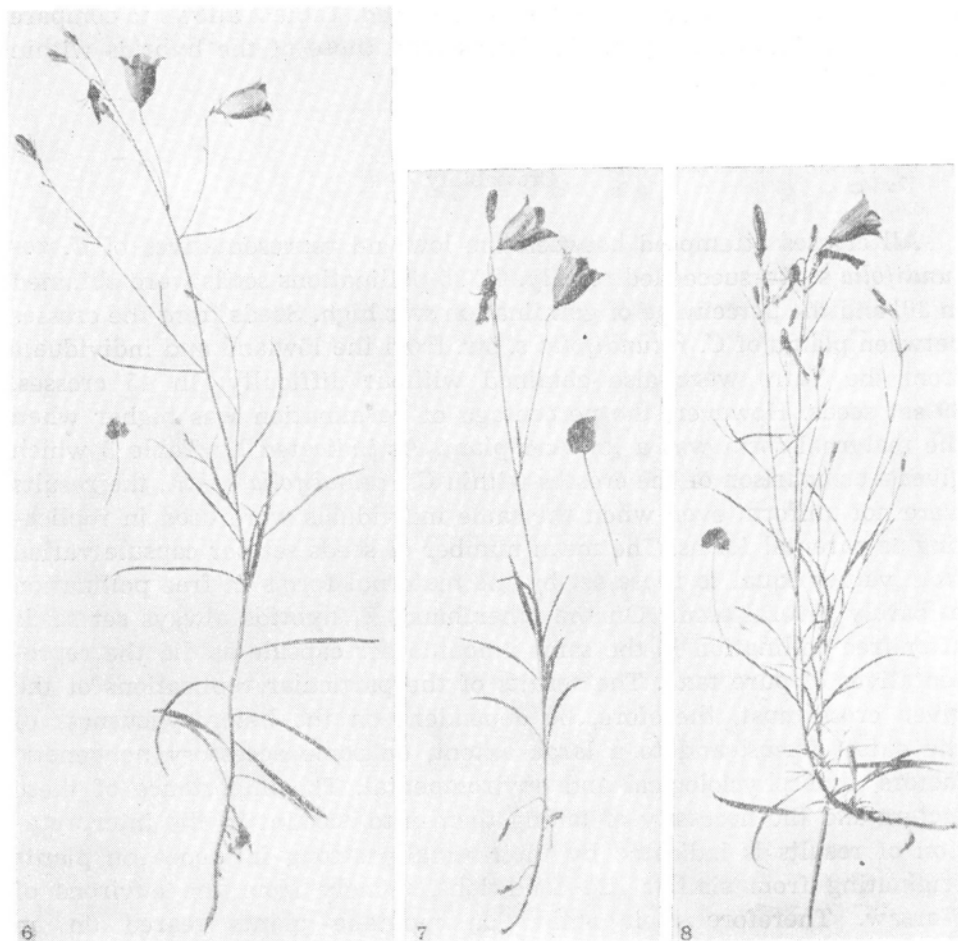
Fig. 6. F₁ hybrid of the lowland and montane representatives of *C. rotundifolia* L. s. str. (4×14)

Fig. 7. F₁ hybrid of *C. routndifolia* L. s. str. ♀ × *C. polymorpha* Witasek ♂ (14×10)

Fig8. F₁ hybroid of *C. polymorpha* Witasek ♀ × *C. rotundifolia* L. s. str. ♂ (2×14)

value of the coefficient of corolla enlargement. A certain influence of the maternal forms was visible. The reciprocal F₁s, when they differed by some character, were as a rule more similar to the corresponding female parental form.

All the F₁ hybrids had very fertile pollen and set seeds profusely from free pollination.

F₂ were also produced by selfpollination of both F₁ individuals. The plants, however, were not numerous and grew in somewhat different conditions than the F₁ ones, therefore the numerical data relative to the external morphology are not comparable. The pollen fertility of the F₂

Table 3

Seed fertility of maternal forms and F_1 hybrids in the crosses within *C. rotundifolia* s. str.

Cross		Mean number of seeds set per capsule			Percentage of hybrid seed germination
		by the maternal plant		by F_1 hybrid	
		from free pollination	from cross pollination	from free pollination	
between lowland representatives	13×14	138,8	118,6	75,8(58,0— 91,0)	96,0
			91,0	—	—
	13×46	138,8	40,1	97,5(43,0—207,0)	88,0
			118,7	—	—
	46×13	78,7	95,5	112,4(45,0—182,0)	82,0
			4,0	—	—
between lowland and montane representatives	14×4	92,1	116,0	122,9(51,5—217,4)	47,6
			29,5	141,9(59,0—209,6)	87,1
			23,0	86,3(70,6—103,0)	94,4
			114,0	—	—
	4×14	136,3	85,0	79,5(14,4—146,2)	44,4
			137,5	36,0	11,2
			41,0	—	20,0
			14,0	—	25,0
			21,5	—	80,0
	4×13		35,0	—	4,3
	13×4	138,8	144,0	—	33,3
	13×22		37,3	—	—
	14×22	92,1	4,0	—	—
	46×22	78,7	152,0	—	—
	17×4	71,2	64,0	—	68,0

segregants was high: F_2 13×46 — 86.2 (62.6—98,9)%; F_2 46×13 — 91.3 (88.6—95.1)%. In free pollination, however, some of them set seeds less profusely: F_2 13×46 — 73.9 (8.2—145.6) seeds per capsule and F_2 46×13 — — 76.7 (49.0—116.6) seeds per capsule.

F_1 and F_2 came into flower on the experimental plot simultaneously with the parental forms, i.e. in the end of May and first days of June.

Description of hybrids between lowland and montane representatives

The cytogenetic interrelationships between the montane and lowland representatives of *C. rotundifolia* s. str. were studied in more detail and on more extensive material. As example are shown the reciprocal crosses between plant no. 14 from the environs of Warsaw (Fig. 2) and plant no. 4 from Antałówka (Zakopane) (Fig. 3). Fig. 6 presents the hybrid F_1 4×14.

Table 3 lists certain characters of the parental forms and F_1 and F_2 individuals. Repeated crosses between the same individuals and in the

Table 4

Range of variation of the coefficient of corolla incision in parental forms and their hybrids in the crosses within *C. rotundifolia* s. str.

	N	0,24	0,25	0,26	0,27	0,28	0,29	0,30	0,31	0,32	0,33	0,34	0,35	0,36	0,37	0,38	0,39	0,40
F$_1$ 14×4	28				2	1		1	2	5	**5**	7	4	1				
4×14	16		1			1			1	1	**2**	4	1	4				1
F$_2$ 14×4	160	1	1		1	1	5	7	7	24	**24**	19	19	17	15	11	10	
4×14	109			2	3	3	7	7	17	10	**8**	21	11	8	4	6		

Note. Classes presented in bold-face correspond to parental forms.

same direction show a high variation. The situation in these crosses is similar to that observed in the case of crosses between the lowland representatives. As regards most characters, the F_1 considered jointly as two reciprocal crosses are intermediate between the parental forms and at the same time exhibit a more pronounced influence of the maternal form (heigh, coefficient of shape of stem leaves, length of corolla, ratio of calyx teeth length to length of corolla). Comparison of the range of variation of characters in both F_1 individuals and in their F_2 descendants is interesting. These ranges are practically identical. Although the ranges for F_2 are in all cases wider than those for the corresponding F_1, nevertheless the fact should be kept in mind that also the size of the F_2 population is several times larger. The range of variation of the corolla incision coefficient is listed here as example (table 4).

In both generations of F_1 of the reciprocal crosses all the individuals exhibited a pollen fertility similar to that of the parental forms. Within the F_2 population there were about 68 and 65 percent of individuals with good pollen, in one of the F_2 their number did not fall below 60 and in the other below 40 percent (table 5).

Table 5

Range of variation of the pollen fertility in parental forms and their hybrids in the crosses within *C. rotundifolia* s. str.

	N	100%	90%	80%	70%	60%	50%	40%
F_1 14× 4	37	**37**						
4×14	21	**21**						
F_2 14× 4	137	**94**	29	11	3			
4×14	98	**64**	23	6	3		1	1

Note. Classes presented in bold-face correspond to parental forms.

All the plants, both from F_1 and F_2 set seeds after free pollination, and it was also easy to obtain seeds by selfpollination of F_1 and F_2 plants.

The first generation of the hybrids came into flower on the experimental plot in Warsaw in the same period as did the parental forms, whereas the dates of efflorescence of the F_2 segregants were more extended in time: only very few plants flowered earlier than the parental forms and both the F_1 individuals, and the last came into flower with a delay of one month or more.

In the F_1 hybrids of both reciprocal crosses meiosis occurred without disturbances as in the parental taxa.

The data relative to the described cross of *C. rotundifolia* s. str. no. 14 with the montane plant no. 4 find confirmation in the results of other

Table 6

Seed fertility of maternal forms and F_1 hybrids in the crosses between *C. rotundifolia* s. str. and *C. polymorpha*

Cross	Mean number of seeds set per capsule			Percentage of hybrid seed germination
	by the maternal plant		by F_1 hybrid	
	from free pollination	from cross pollination	from free pollination	
46×10	78,7	15,7	166,8(103,2—317,4)	57,0
		51,0	137,6 (66,2—216,8)	48,0
14×10	92,1	73,0	207,7(112,2—282,8)	54,0
13×10	138,8	261,0	117,6	71,3
14×2	92,1	108,0		—
2×14	200,0	179,5	116,6 (92,2—137,8)	3,3
		91,0		32,5
		73,0		60,0
14×7	92,1	70,0	234,0(118,0—303,6)	62,5
		177,0	181,9(104,6—229,2)	88,3
7×14	148,0	256,0		0,0
7×13		190,0		0,0
		145,0		73,3
		43,0		63,3
		34,0		55,0
13×7	138,8	34,0	170,1(101,8—198,0)	92,0
46×25	78,7	95,0	109,4	32,0
25×46	67,0	1,0	82,6	100,0
25×13		143,0	180,6	92,0
13×25	138,8	25,0	85,8	80,0
46×28	78,7	62,0	121,4	72,0
28×46	55,6	262,0	80,8	92,0
28×13		254,0	150,0	100,0
13×28	138,8	191,6	101,2	100,0
14×31	92,1	121,0	72,3	52,0
31×14		192,0	115,4	60,0
31×46		60,0		0,0
31×13		190,0		40,0
13×31	138,8	142,6		0,0
14×34	92,1	5,0		0,0
46×34	78,7	93,0	152,8	36,0
34×46		221,2		4,0
34×13		133,3		0,0
13×34	138,8	91,3	149,0	84,0

crosses of the same montane plant with other lowland ones (tables 2 and 5). In the cross 17×4, plant no. 17 exhibited a greatly reduced fertility and transmitted this trait to its progeny.

The lowland and montane plants of *C. rotundifolia* s. str., though differing somewhat morphologically behave in the crosses similarly as do the intercrossed lowland representatives. No genetic barriers between them limiting crossing or causing reduced pollen or seed fertility could be observed.

2. Crosses between *C. rotundifolia* s. str. and *C. polymorpha*

Crossability

C. polymorpha (26 individuals) originating from various stands in the Tatra was crossed with lowland plants of *C. rotundifolia* s. str. Seeds were obtained from 161 crosses, whereas 16 crosses failed to yield progeny. Analogously as in the previously described crosses within *C. rotundifolia* s. str., the mean number of seeds set per capsule varied widely, from several seeds to numbers largely exceeding the seeds set by the maternal form in free pollination. This refers both to the successive replications of the crosses between the same parental individuals and between different plants (table 6). The seeds germinated well, however, generally better when *C. rotundifolia* s. str. was the maternal plant.

The first generation of the hybrids also set seeds profusely from free pollination similarly as the representatives of both the pure taxa. All the F_2 segregants also set seeds after free pollination.

Interesting supplementary data on the interrelationships between *C. polymorpha* and *C. rotundifolia* s. str. might be obtained from the crosses of *C. polymorpha* with montane representatives of *C. rotundifolia* s. str. However, such crosses were performed only sporadically and do not allow fully comparable conclusions, although no indications of differences were observed.

The mean number of seeds set by F_1 per capsule reached 340, and a high percentage of the seeds from F_1 germinated. F_1 showed a high fertility of seeds. As seen the results obtained agree with the previously obtained ones.

Description of hybrids

Certain characteristics of the parental forms and of the hybrids from crosses between the lowland forms of *C. rotundifolia* s. str. and the alpine representative of *C. polymorpha* are listed in table 7. The reciprocal crosses between *C. rotundifolia* s. str. no. 14 and *C. polymorpha* nos. 10 and 2 from ca. 2000 and 1800 m a.s.l. respectively, (Fig. 7 — F_1 14×10,

Comparison of some characters of parental forms and their hybrids

	Height of stems cm	Coefficient of shape of stem leaves	No. of flowers per stem
P 4	29(24—32)	8,8	10,2
13	72(55—81)	11,1	42,4
14	40(35—50)	9,6	15,2
46	35(26—40)	11,5	13,1
2	17(12—19)	14,0	10,0
10	15	12,0	3,0
25	25(20—30)	11,8	10,8
28	26(21—31)	16,2	13,6
34	14(11—16)	9,2	5,0
80	6 (5— 7)	5,5	1,8
F_1 2×14	24(20—30)	14,8	6,7
	23(16—40)	9,7	8,3
	30(25—40)	10,3	7,1
F_2 2×14	17—43	8,6—19,4	3,5—21,6
F_1 14×10	32(25—45)	8,6	13,8
	35(25—52)	9,1	10,4
	30(20—50)	10,6	6,4
F_2 14×10	5—50	4,0—18,4	1,0—58,5
F_1 25×13	24(19—27)	13,7	11,2
13×25	23(15—35)	6,1	9,8
25×46	16(12—20)	11,9	3,8
46×25	25(20—33)	12,3	11,6
F_1 28×13	46(38—50)	11,2	16,0
13×28	50(46—58)	10,3	19,8
28×46	33(28—35)	12,5	14,4
46×28	29(26—34)	10,6	7,8
F_1 13×34	37(35—39)	7,4	20,2
34×46	19(17—21)	9,8	8,8
46×34	25(19—37)	10,5	6,5
F_1 4×10	23(20—26)		18,2
F_1 80× 4	17(11—20)	7,5	7,1

le 7

in the crosses between *C. rotundifolia* s. str. and *C. polymorpha*

Corolla			Ratio of calyx teeth length to corolla length	Pollen fertility %
length mm	coefficient of incision	coefficient of enlargement		
22,7	0,33	1,73	0,42	97,5
18,1	0,36	1,69	0,34	98,1
20,5	0,33	1,81	0,31	98,0
20,3	0,33	1,75	0,27	98,9
24,7	0,33	2,15	0,40	98,9
22,3	0,29	1,69	0,34	97,7
21,8	0,26	2,02	0,40	98,1
23,3	0,29	2,03	0,34	99,0
23,1	0,31	1,98	0,32	99,5
21,8	0,29	2,05	0,32	96,6
21,8	0,31	2,11	0,42	98,2
20,0	0,34	2,05	0,48	97,7
18,3	0,34	1,91	0,42	98,6
18,0—24,1	0,25—0,37	1,73—2,55	0,22—0,56	65,2—100,0
22,7	0,32	1,82	0,37	98,2
22,6	0,32	1,84	0,40	98,6
19,2	0,31	1,90	0,43	96,5
12,5—25,0	0,23—0,46	1,38—2,53	0,18—0,57	23,7—100,0
18,3	0,31	1,89	0,36	99,0
19,1	0,29	2,03	0,36	98,4
20,3	0,32	2,05	0,28	98,9
20,0	0,31	1,92	0,35	97,2
21,3	0,27	2,06	0,32	97,5
20,5	0,33	1,96	0,40	99,0
22,9	0,29	1,96	0,37	96,8
22,3	0,30	2,02	0,42	97,2
19,8	0,36	1,78	0,34	98,3
20,8	0,32	1,94	0,40	95,9
21,7	0,34	1,84	0,39	99,0
17,6	0,32	1,63	0,43	
17,7	0,31	2,23	0,39	98,5

Fig. 8 — F_1 2×14) have been studied in more detail. Table 7 also includes the corresponding variation ranges of the characters of F_2.

As regards several of the features taken into account (height of plant, number of flowers per stem, coefficient of shape of stem leaves), the first two hybrid generations are intermediate between the parental forms, though they exhibit a high variation. The variation range of the characters in F_2 is much wider than in F_1 as compared with the difference in crosses within *C. rotundifolia* s. str., thus *C. polymorpha* is a somewhat further removed taxon. The coefficient of corolla incision (table 8) may serve as example of the differences in the range of variation. These data prove the quantitative character of the inheritance of traits involving the dimensions of the plants and the conditioning of these characteristics by many genes, the number of which cannot be established on the basis of the material examined. The type of foliation: the distribution of the stem leaves and the character of their endings, are also polygenically inherited. In F_2 segregants with stems foliated in their lower part predominate quantitatively. On the other hand, plants with pointed and blunt leaves occured in more or less similar numbers. In view of the insufficient number of F_2 segregants obtained it was also impossible to establish the number of gene pairs influencing both these characteristics.

The author, however, succeeded in demonstrating that the occurrence of pubescence on the stems is a dominant trait. The *C. polymorpha* plants used in the crosses had glabrous stems. The first generation of the hybrids with *C. rotundifolia* s. str. with hirsute stems had in all replications stems covered with pubescence and in F_2 segregation occurred in the following proportions: 187 plants with hirsute and 63 with glabrous stems and in the second generation of the reciprocal cross which yielded but few individuals, the respective values were 19 and 2.

This ratio in tetraploids is understandable if we assume either a disomic type of heredity or heterozygousness of the hirsute form. For this ratio both assumptions are plausible. The progeny of plant no. 14 produced by artificial selfpollination, namely, was not uniform and consisted both of individuals with hirsute and glabrous stems.

Several crosses of other representatives of *C. polymorpha* with lowland forms of *C. rotundifolia* s. str. and several replications of the same crosses yielded, as regards most of the traits investigated, also intermediates between the parental forms, although this cannot be considered a rule valid in all cases (e.g. the crosses with *C. polymorpha* no. 25). In the case of *C. polymorpha* plants with glabrous stem crossed with *C. rotundifolia* s. str. F_1 always had hirsute shoots, this confirming the dominant character of this gene as established in the cross *C. rotundifolia* s. str. no. 14 ♀ × *C. polymorpha* no. 10 ♂.

All the F_1 generation had pollen as fertile as in the parental forms. In the F_2 14×10 and 2×14 investigated only few segregants exhibited

Table 8

Range of variation of the coefficient of corolla incision in parental forms and their hybrids in the crosses between C. *rotundifolia* s. str. and C. *polymorpha*

	N	0,23	0,24	0,25	0,26	0,27	0,28	0,29	0,30	0,31	0,32	0,33	0,34	0,35	0,36	0,37	0,38	0,39	0,40	0,41	0,42	0,43	0,44	0,45	0,46
F_1 14×10	29						**2**	8	1	2	**3**	7	1	1	1	1	1	1							
F_2 14×10	266	1	1	2	3	15	**9**	23	29	36	**38**	25	29	26	12	6	5	2	2						1
F_1 2×14	5								1	1	**1**	1	1												
F_2 2×14	28					1	3	6	1	2	**5**	4	1	2	1	1									

Note. Classes presented in bold-face correspond to parental forms.

Table 9

Range of variation of the pollen fertility in parental forms and their hybrids in the crosses between
C. rotundifolia s. str. and *C. polymorpha*

	N	100%	90%	80%	70%	60%	50%	40%	30%	20%
F$_1$ 14×10		X								
F$_2$ 14×10	247	**140**	71	22	9	3	1		1	
F$_1$ 2×14		X								
F$_2$ 2×14	29	**24**	4		1					

Note. Classes presented in bold-face correspond to parental forms.

a lowered fertility (table 9), about 94 percent of the individuals had more than 70 percent of morphologically good pollen.

The F$_1$ hybrids came into flower on the experimental plot in the last days of May or at the very beginning of June at the period of efflorescence of the parental rotundifolia plant and earlier than the parental polymorpha. The dates of efflorescence of F$_2$ extended rather beyond those of the parental *C. polymorpha* and only few flowered before F$_1$ and *C. rotundifolia*.

Data for the replications of the crosses between the same individuals carried out in the same direction and those concerning the reciprocal crosses frequently also show rather wide differences in the crosses *C. polymorpha* × *C. rotundifolia* s. str., analogous to the results of crosses within *C. rotundifolia* s. str.

The results listed in tables 6 and 7 demonstrate the absence of genetic barriers which would make intercrossing of the taxa examined difficult.

Cytological examination of the 14×10 F$_1$ hybrids showed that meiosis occurs in them without disturbances. In metaphase I 34 bivalents were observed on each plate, and only sporadically earlier splitting of one pair of chromosomes. Division II also occurred without disturbances.

3. Crosses between *C. scheuchzeri* and *C. rotundifolia* s. str. and between *C. scheuchzeri* and *C. polymorpha*

Crossability

The crosses between *C. scheuchzeri* and *C. rotundifolia* s. str. involved 14 representatives of *C. scheuchzeri* and standard lowland *C. rotundifolia* s. str. plants nos. 13, 14 and 46 as well as the montane plant no. 4. Hybrids were easily obtained, although, as compared with the foregoing crosses, the percentage of pollinated flowers which did not set seeds was higher. Seeds were obtained from 44 crosses, nine yielded no seeds. About one half of the seeds germinated, similarly as in the previously described crosses (table 10). In contrast, however, to the foregoing data,

Table 10

Seed fertility of maternal forms and F_1 hybrids in the crosses between *C. scheuchzeri* and *C. rotundifolia* s. str. as well as between *C. scheuchzeri* and *C. połymorpha*

Cross	Mean number of seeds set per capsule			Percentage of hybrid seed germination
	by the maternal plant		by F_1 hybrid	
	from free pollination	from cross pollination	from free pollination	
14× 64	92,1	110,6	97,4 (47,2—137,2)	100,0
13× 64	138,8	107,0	112,3 (81,6—164,7)	92,0
14× 62	92,1	187,5	126,0(100,0—160,0)	40,0
62× 14		101,0	84,0 (42,4—106,0)	68,0
62× 13		25,0		0,0
14×110	92,1	87,5	67,2 (22,6—107,8)	48,0
110× 46		120,0		—
		129,0		—
		132,0		—
110× 13		319,0		—
111× 46		248,0		—
75× 46		120,0	96,4 (83,0—114,0)	32,0
46× 75	78,7	114,0	171,0(168,4—173,6)	68,0
4×111	136,3	45,0		—
		165,0		—
34×110		191,6		0,0
109×111		163,0		—
75× 78		>55,0		68,0

the differences between the replications and reciprocal crosses were less pronounced. Seeds from crosses of *C. scheuchzeri* with the montane *C. rotundifolia* s. str. were not sown.

The F_1 hybrids obtained set seeds profusely from free pollination, whereas the F_2 yielded but few seeds after artificial self pollination. Several plants belonging to three different F_1 were backcrossed in both directions with the parental form *C. rotundifolia* s. str. In all cases a profusion of seeds was obtained.

Crosses between *C. scheuchzeri* and *C. polymorpha* yielded hybrid seeds in quantities similar to those set by the parental forms after free pollination. The seeds germinated only in one case. All the F_2 segregants set seeds after free pollination. In F_2 14×64 the number of seeds varied from 14.4 to 130.0 per capsule, and in F_2 13×64 from 23.2 to 218.5 (cf. table 10).

Description of hybrids

Some of the characters of the parental forms and the hybrids are given in Table 11. The crosses of plant no. 64 (*C. scheuchzeri*) with two

Table 11

Comparison of some characters of parental forms and their hybrids in the crosses between *C. scheuchzeri* and *C. rotundifolia* s. str. as well as between *C. scheuchzeri* and *C. polymorpha*

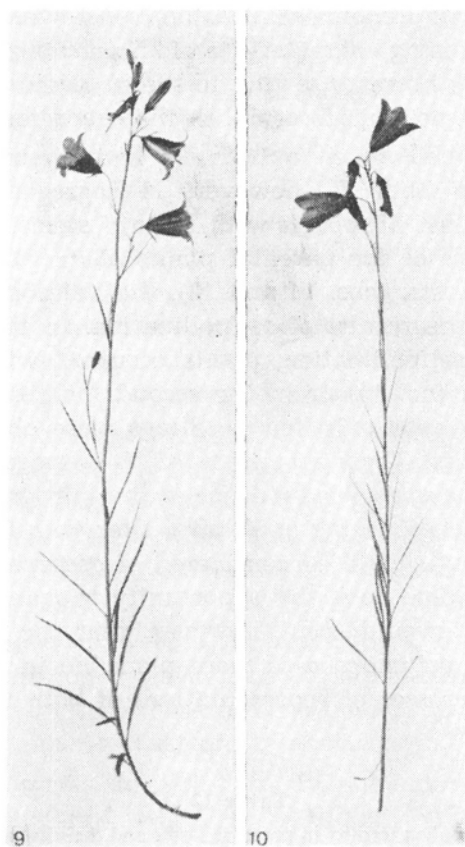|	Height of stems cm	Coefficient of shape of stem leaves	No. of flowers per stem	Corolla length mm	Corolla coefficient of incision	Corolla coefficient of enlargement	Ratio of calyx teeth length to corolla length	Pollen fertility %
P								
62	16(13—20)	10,8	6,2	23,6	0,28	2,33	0,31	95,6
64	25(19—30)		5,8	18,7	0,26	2,11	0,44	89,2
75	21(18—25)		1,3	21,1	0,34	1,78	0,32	83,2
110	16(10—21)	9,3	3,5	19,0	0,31	2,21	0,28	
13	72(55—81)	11,1	42,4	18,1	0,36	1,69	0,34	98,1
14	40(35—50)	9,6	15,2	20,5	0,33	1,81	0,31	98,0
46	35(24—40)	11,5	13,1	20,3	0,33	1,75	0,27	98,0
78	9 (8—10)		3,6	24,3	0,28	2,17	0,32	94,2
F_1 13 × 64	29(25—36)	10,0	14,8	19,6	0,37	1,99	0,31	85,8
F_2 13 × 64	6—40	3,6—21,4	2,3—35,2	14,3—22,8	0,28—0,40	1,73—2,67	0,23—0,46	16,6—98,0
F_1 14 × 64	27(22—35)	8,0	9,3	22,1	0,31	2,17	0,27	97,1
F_2 14 × 64	14—27	5,4—12,2	3,8—19,2	15,2—22,3	0,26—0,37	1,79—2,56	0,28—0,49	20,8—96,4
F_1 62 × 14	24(21—25)	7,4	13,6	20,2	0,31	2,09	0,32	97,3
14 × 62	25(23—26)	7,6	10,9	19,6	0,29	2,21	0,35	97,5
F_1 14 ×110	25(17—35)	6,8	15,9	17,2	0,35	1,72	0,23	99,5
F_1 75 × 46	30(25—38)	5,9	18,1	19,1	0,34	1,70	0,28	97,2
46 × 75	30(24—45)	8,1	16,1	19,9	0,33	1,84	0,32	96,6
F_1 75 × 78	15(12—20)	12,1	4,7	21,6	0,30	2,03	0,27	94,8

Fig. 9. F_1 hybrid of *C. rotundifolia* L.s.str. ♀ × *C. scheuchzeri* Vill. ♂ (14×64)

Fig. 10. F_1 hybrid of *C. scheuchzeri* Vill. ♀ × *C. rotundifolia* L.s.str. ♂ (62×14)

plants of *C. rotundifolia* s. str. nos 13 and 14 were studied in more detail. Each of these crosses is described separately on account of the low number of F_2 segregants reared. The results cannot be given jointly in view of the wide differences between the plants nos. 13 and 14. Fig. 9 shows the hybrids F_1 14×64. Both F_1 (13×64 and 14×64) were intermediate as regards the height of the plants and number of flowers per stem. The length of the corolla and the coefficients of the corolla dimensions behaved as if *C. scheuchzeri* no. 64 cultivated on the lowland had some-what smaller flowers, this being quite probable. The range of variation of the plant height in F_2 was shifted towards lower values, thus towards *C. scheuchzeri*. On the other hand, the ranges of variation of the coef-ficient of shape of the stem leaves and of the characters of the flowers only slightly exceeded the values characteristic for the parental plants or remained within the range of variation of these values.

In all F_1 plants a vein running from the base of the corolla to the tip

of the lobe and less pronounced parallel veins were distinctly visible in the flowers, this being characteristic of C. scheuchzeri. In F_2 this trait was also manifested, however, owing to the small number of individuals available it was not possible to establish the character of its inheritance.

All the plants belonging to both F_1 had hirsute shoots like the parental plants. In both F_2, however, 11 segregants occurred with glabrous stems against 48 plants with hirsute stems. This would prove the heterozygousness of the parental plants. As regards the individuals of C. rotundifolia s. str. (nos. 14 and 13), the heterozygousness assumed was confirmed by the results of selfpollination. In the progeny of both these plants from selfpollination, plants occurred with glabrous shoots already in the first (no. 14) or in the second (no. 13) generation. After many attempts this year only few seedlings were obtained from selfed C. scheuchzeri plants. The appearance of F_2 segregants with glabrous shoots may in this case be also evidence of the introgression of the genes of C. polymorpha neighbouring on natural sites with C. scheuchzeri. The theoretical possibility should be considered of occurrence of spontaneous mutations which seldom have the opportunity to manifest themselves in tetraploid plants. It would seem, however, that the assumption of the introgression of C. polymorpha is more plausible in view of the ready occurrence of intercrosses of representatives of both these taxa.

Table 12

Range of variation of the pollen fertility in parental forms and their hybrids in the crosses between C. rotundifolia s. str. and C. scheuchzeri

	N	100%	90%	80%	70%	60%	50%	40%	30%	20%	10%
F_1 13×64				X							
F_2 13×64	35	14(2)	13(5)	2(1)	1		4(2)			1(1)	
F_1 14×64		X									
F_2 14×64	19	10(2)	3(1)	2				2	1	1	

Note. In parenthesis a number of plants producing a limited quantity of pollen is given.
Classes presented in bold-face correspond to parental forms.

Stem leaves of the first generation hybrids grew high up on the stem up to the inflorescence in a pattern characteristic for C. scheuchzeri, they exhibited, however, larger differences between the length of the lower and higher leaves than those observed in the wild representatives of this taxon. In F_2 most individuals had a type of foliation similar to C. scheuchzeri.

The trait of erect buds proved to be dominant since all the F_1 individuals exhibited it like C. rotundifolia s. str. In F_2 segregation occurred. Of the 46 plants 39 had erect buds, and seven buds on bent peduncles.

These data should be verified quantitatively on a more extensive material in order to estimate the number of gene pairs conditioning this trait.

F_1 had highly fertile pollen. In F_2 segregation occurred. About 80 percent of the segregants in both crosses had more than 70 percent of good pollen (table 12). There also appeared plants with lowered fertility and others in which quantitative limitation of pollen occurred, not associated with reduction of fertility. Individuals with a limited quantity of pollen are put in parentheses in table 18 after the column, showing the size of the given class.

F_1 hybrids came into flower in the experimental plot in the beginning of June at a date intermediate between the blooming of the parental forms, and F_2 segregants flowered throughout June and up to mid July.

The results of other crosses between the representatives of the taxa discussed conformed with the here described results. Fig. 10 presents the hybrid F_1 62×14 belonging to the reciprocal cross in respect to those previously discussed. Comparative data also point to the intermediate position of the first hybrid generation as regards almost all the traits examined.

The scarce crosses between *C. scheuchzeri and C. polymorpha* had hirsute shoots, blunt-ended leaves like *C. polymorpha*, distributed on the stem characteristically like those to *C. scheuchzeri*. The structure of the flower was also similar to that of *C. scheuchzeri*. The buds were erect.

Thus nothing seems to point to fundamental differences in the relations of *C. scheuchzeri* with *C. rotundifolia* s. str. and *C. polymorpha*, as far as such conclusions may be based on comparison with a single cross.

4. Comparison of crosses between tetraploid taxa

Comparison of crosses between representatives of tetraploid taxa of the *C. rotundifolia* L. group allows to characterize in some extent the interrelation of these systematic units. From the results presented in table 13 and the data given in the text it is evident that, as regards the ability of intercrossing, there are no essential differences between the representatives of *C. rotundifolia* s. str. from the lowland and those from montane habitats, nothing reveals any genetic barriers between them. A large majority of pollinations is effective and the seeds germinate well. The exuberant F_1 plants had a highly fertile pollen and set seeds after free pollination as well as after artificial selfpollination. All the F_2 plants were also fertile. The results were better when the lowland plant was the maternal form, maybe this was due to the fact that the plants were reared in lowland conditions.

The results obtained point to a similar absence of genetic barriers between *C. rotundifolia* s. str. and *C. polymorpha*. Analogously as in the

Table 13

Crossability of tetraploid taxa and the pollen fertility of F_1 and F_2 hybrids

	No. of flowers pollinated		Percentage of hybrid seed germination	Pollen fertility %	
	+	—		F_1	F_2
C. rotundifolia s. str. — lowland representatives	30	5	81,0	85—100	80—100
C. rotundifolia s. str. — lowland and montane representatatives	39	6	35,9	80—100	45—100
♀ — lowland representative	18	—	47,0		
♀ — montane representative	21	6	21,9		
C. rotundifolia s. str. lowland representatives — C. polymorpha	151	16	45,3	90—100	24—100
♀ — lowland rotundifolia s. str.	81	7	64,0		
♀ — polymorpha	70	9	29,6		
C. rotundifolia s. str. montane representatives — C. polymorpha	10	—	59,0		
♀ — montane rotundifolia s. str.	4	—	50,0		
♀ — polymorpha	6	—	68,0	98	
C. rotundifolia s. str. — C. scheuchzeri	44	9	52,7	80—100	20— 99*
♀ — rotundifolia s. str.	33	5	59,5		
♀ — scheuchzeri	11	4	46,0		
C. scheuchzeri — C. polymorpha	6	2			
♀ — scheuchzeri	1	1	34,0	95	
♀ — polymorpha	5	1	0,0		

* Some plants producing a limited amound of pollen.

previous crosses, only 10 percent of the pollinated flowers did not set seeds, and this as in the former cases, may be ascribed to accidental factors. The mean percentage of germinating seeds in F_1 is in this combination even higher than in the preceding group, and similarly, the hybrids with a lowland plant as maternal form germinate better, the reason for this being probably the same. Pollen fertility both in F_1 and F_2 was high. The scarce hybrids of montane plants of C. rotundifolia s. str. and C. polymorpha set without exception seeds which germinated well.

Thus we see that these taxa differ almost exclusively in certain morphological features and in their geographical distribution. Some of the distinguishing characters may be conditioned by one gene as has been established for the pubescence on the stems, whereas the inheritance of others is polygenic. The differences in the traits polygenically conditioned find their reflection in the ranges of variation of the F_1 and F_2 hybrids. If we compare the variation ranges of the coefficient of

corolla incision quoted as examples (tables 4 and 8), it may be seen that in the case of crosses within *C. rotundifolia* s. str. the variation ranges for F_1 and F_2 show smaller differences than in the case of crosses between *C. rotundifolia* s. str. and *C. polymorpha* where the range for F_2 is much wider than for F_1. The differences between these taxa occur also in the distribution of leaves on the stems, the endings of the stem leaves and the structure of the flower; shape of corolla, of ovary, endings and length of calyx teeth, however, the inheritance of these traits was not closer studied.

On the basis of the data discussed one could assume that both these taxa are not distinct species but rather different ecotypes which have undergone selection in different habitat conditions.

The possibility of crosses of *C. polymorpha* with other exclusively montane taxa is not without meaning for the arising of morphological differences between this species and *C. rotundifolia*. Evidence to the fact that such possibilities of crossing exist is brought by the results of crosses between *C. polymorpha* and another montane tetraploid, *C. scheuchzeri*. The crosses of *C. polymorpha* and *C. rotundifolia* s. str. with *C. schuchzeri* are almost as easy and successful as those between the former two taxa. The F_1 seeds germinate as well as those from crosses of *C. rotundifolia* with *C. polymorpha*, the F_1 hybrids have a high pollen fertility and set seeds profusely. In F_2 segregation occurs as regards pollen fertility. Individuals with lowered pollen fertility appear as well as others producing good pollen in limited quantities. *C. scheuchzeri* is no doubt a taxon further removed in relationship with the other two, although its relationship is still fairly close. There is reason to believe (F_2 plants with glabrous stems) that introgression of genes may occur from *C. polymorpha* to *C. scheuchzeri*. The data available so far are not sufficient for drawing fargoing conclusions.

DISCUSSION

The complex *Campanula rotundifolia* s.l. has a very intricate structure. Böcher (1966) says that it "may resemble a dense jungle", in which on the basis of up-to-date data it is difficult to distinguish the primary diploid "trunks". The contemporary diploids have, namely, not lost their ability of intercrossing, and the lack of natural intermediate forms between them may be ascribed to the existence of a disjunction between their ranges or an ecological separation. On the other hand, introgression between the species occurs on a wide scale at the tetraploid level similarly as it does in other polyploid complexes. The tetraploid taxa with overlapping ranges are connected by a number of intermediate forms. They exhibit a very high variability and, at least on the mid-

-European lowland, constitute a swarm of poorly delineated small systematic entities (B ö c h e r 1959, 1960, 1961, 1963a). It has been experimentally demonstrated that representatives of taxa at different polyploid levels are able to cross (G a d e l l a 1964, B ö c h e r 1966).

The finding that hybridization is easier at the tetraploid level as compared to the diploid has been confirmed in most studies (A v e r s 1953, B e r n s t r ö m 1953), although exceptions are also known (N o r d e n s k i ö l d 1956), in tetraploid hybrids a certain degree of dysharmony between the chromosomes being admissible. Products of irregular segregation, particularly polysomes, may survive and then stabilize regaining normal fertility.

Interesting data on the evolution occurring at the tetraploid level have been reported by K i h a r a (1963), Z o h a r y and F e l d m a n (1962) and F e l d m a n (1965a, b, c), for the genus *Aegilops*. The authors stress the important role played in this process by crossing and recombination which is the consequence of conjugation of homoeologous chromosomes and of the resulting translocations. B ö c h e r (1936, 1960) observed multivalents both in diploid and tetraploid *Campanula* occurring with varying frequency. The very scarce polyvalents were also observed in the course of this work. The multivalents of *Campanula rotundifolia* — in view of the obscure evolutional origin of this group — may be also considered as evidence of the existence of translocation or else as a proof of autopolyploidization at some evolutional step. As indicated by the presently obtained data, it is doubtless that there are no obstacles to the crossing of tetraploid taxa. This is probably one of the reasons owing to which the development of barriers of genetic isolation between them is difficult. According to taxonomic standards the complex *Campanula rotundifolia* might be treated as one huge species with a certain number of subspecies. However, according to B ö c h e r (1966) in the case of a group exhibiting such polymorphism, these units should be assigned the rank of species, attention should also be paid to the role of geographic isolation, and entities which as a result of this isolation behave as "good species", should be treated as species. The notion of species in the case should be modified to correspond to this peculiar complex. On the other hand, the ploidy level may serve as criterion for distinguishing subspecies. B ö c h e r (1960, 1961, 1966) distinguishes on this basis a diploid and a tetraploid subspecies within *C. gieseckiana*. In his opinion, however, so far no sufficient grounds exist for establishing an analogous division within the mid-European *C. rotundifolia* s. str.

The situation is still more complicated by the fact that the taxa treated at present as diploid ($n = 17$) should rather be considered as allotetraploids descending from taxa with $n = 8$ and 9. F e r n a n d e s (1962) believes that the occurrence of polysomics and translocations played an essential role in their evolution. This hypothesis, however, is not

borne out by investigations on the chromosome morphology. If the plants with $2n = 34$ are assumed as tetraploids, the contemporary tetraploids should be considered as octoploids formed owing to the doubling of this genome. It would seem, however, that any attempt at assuming some single mechanism of polyploidization in *Campanula rotundifolia* would not be justified. The evolution of the rotundifolia group has no doubt passed through several different phases and the present taxa may have arisen both as the result of allo- as of autoploidy (B ö c h e r 1960, 1961 a; G a d e l l a 1964). The course of this process still remains obscure. The possibility of a polytopic origin of the tetraploid forms of *C. rotundifolia* has been postulated by G u i n o c h e t (1942b) and H u b a c (1962) on the basis of the distribution of the contemporary diploid taxa. The diploid forms belonging to the *C. rotundifolia* group occur on the northern and southern border of the range and several stands have been found on the mid-European lowland. No evidence is available which would indicate that these diploids ever intercrossed directly. On the other hand, the tetraploid forms, morphologically very similar to the corresponding diploids occur at present in Greenland (*C. gieseckiana* — B ö c h e r 1960, 1961) and in southern France (*C. macrorhiza* — G u i n o c h e t 1942a, b). G u i n o c h e t (1942b) advanced the hypothesis that the tetraploid forms spreading from the north met on the northern border of the Mediterranean region either directly with the endemic diploids from the south, or rather with tetraploid descendants from these southern forms. The same author believes that there exist between the contemporary tetraploids of North America and the Eurasian ones sufficiently wide morphological differences which would allow to assume that they formed independently. Experimental data are, however, lacking on the cytogenetic relationships between them. The tetraploid *C. gieseckiana* ssp. *groenlandica* exhibits, on the other hand, introgression from the north-American tetraploids to which its representatives are in various degrees more similar than to the mid-European tetraploids (B ö c h e r 1966), whereas some mountain Scandinavian populations resemble the Greenland plants. This may also be ascribed to introgression (B ö c h e r 1966).

The same author also suggests the possibility of occurrence of transitional forms between the tetraploid *C. rotundifolia* s. str. and *C. polymorpha* or *C. scheuchzeri*. This assumption found confirmation in the experimental results described in the present paper.

In the *C. rotundifolia* s.l. group, the greatest variation of the habitus is observed among the tetraploids in mountain regions, thus in the most differentiated environment creating, consequently, conditions in which natural selection of biotypes most suitable for various kinds of habitats may occur. T u r e s s o n (1930—1931) quoted examples of various forms of *C. rotundifolia* arising owing to selection in various climatic conditions both montane and lowland. Increased variability on some areas may also

be an indication of introgression of genes originating from other species occuring on the given territory.

In the crosses performed, hybrid seeds were obtained from all possible combinations in the taxa, although sometimes breeding of the hybrids failed or gave only few individuals.

Most cross-pollinations between the representatives of C. *rotundifolia* s. str. and C. *polymorpha* yielded seeds germinating well, the hybrids in the first and second generation had a high pollen and seed fertility, behaving like intraspecific hybrids. The most characteristic feature of interspecific hybrids is generally sterile pollen and irregular meiotic division (S t e b b i n s 1945), whereas in the crosses examined they occurred without disturbances. Certain differences were observed in the ranges of variation as regards external morphology. As compared with the crosses within the lowland C. *routndifolia* s. str., wider variation ranges and more pronounced transgression in respect to the values characteristic of the parental forms occurred in the crosses between C. *rotundifolia* s. str. and C. *polymorpha,* and in a smaller degree between the lowland and montane C. *rotundifolia* s. str. According to C l a u s e n's opinion (1953) this proves a greater genotypic distinctness of C. *polymorpha* and C. *rotundifolia* s. str. and of the montane and lowland forms of C. *rotundifolia* s. str. than between the lowland C. *rotundifolia* s. str. The habitus of C. *polymorpha* is not uniform as indicated by the name assigned to it. In some traits it resembles C. *rotundifolia* s. str. but at the same time it exhibits features characteristic for alpine flora. Among other features it differs from the lowland C. *rotundifolia* s. str. plants by its lower height, larger flowers and frequently by stems bearing only one flower. However, the same individuals when grown on the lowland were higher and formed inflorescences with scarce flowers. This is no doubt a symptom of incomplete stabilization of the genetic differences between C. *polymorpha* and C. *rotundifolia* s. str. and of a wide phenotypic variability. Some differences between these taxa may be due to mutation of one gene as for instance in the case of lack of pubescence on the stems.

The traits characteristic of C. *polymorpha* are in some extent exhibited by C. *rotundifolia* s. str. plants from montane habitats. This might be considered as due to introgression of the C. *polymorpha* genes, or one might assume that by natural selection closely related genotypes are chosen in similar habitat conditions and that we are dealing here with convergence. Habitus convergence in various plant species in similar environmental conditions is well known. Sufficient information is lacking at the present moment for establishing whether clinal variation interrelates on the territory of Poland the lowland C. *rotundifolia* s. str. with C. *polymorpha* via the montane C. *rotundifolia* s. str. plants. The process of biotype selection and of individuation of ecotypes in various

environmental conditions counteracts in this case the opposed action of outbreeding and the consequent easy intercrossing (B ö c h e r, L a r s e n and R a h n 1955). Introgression from *C. polymorpha* may explain the occurrence of plants with glabrous stems and a habitus identical to that of *C. polymorpha* among the progeny of montane representatives of *C. rotundifolia* s. str. originating from artificial selfpollination.

Confrontation of these data allows to advance the hypothesis that *C. polymorpha* is not a distinct species, at any rate as far as biosystematic criteria are concerned (C l a u s e n, K e c k and H i e s e y 1939; L e w i s 1959). It might be considered as an ecotype differentiated in mountain conditions, while leaving to it the rank of species for systematic purposes. According to V a l e n t i n e and L ö v e's opinion (1958) the form of a plant represents its response to its environment, and the same population may be considered as two species on the basis of taxonomic criteria, and as two ecotypes from the biosystematic aspect.

Neither was a sharp delimitation found in the case of the last tetraploid taxon investigated, *C. scheuchzeri*, although it exhibits wider differences as regards a number of traits such as in the first place the characteristic bending of the buds, ciliation on the edges of the stems in their lower part and the prominent vein running from the base of the corolla to the tip of the lobe. The F_1 hybrids between *C. scheuchzeri* and *C. rotundifolia* s. str. were viable and fertile plants and the variation ranges of many characters in the F_2 hybrids largely exceeded the values characteristic for the parental forms. The genetic isolation is, however, still weak and is not manifest sooner than in F_2. Some of the F_2 segregants are weak plants and, besides their low viability, exhibit a lowered fertility due above all to a limitation of the amount of pollen. Thus, although the first generations of crosses between *C. rotundifolia* s. str. and *C. scheuchzeri* could be obtained as easily as in the crosses with the previously discussed tetraploids, nevertheless the reduced viability of F_2 points to the formation of some genetic barriers.

The present observations allow to suppose that an exchange of genes between *C. scheuchzeri* and *C. polymorpha* might occur when they are sympatric in nature. Hybrid seed, namely, was obtained in quantities similar to those set by the parental form after free pollination. The occurrence of F_2 segregants with glabrous stems in the crosses between *C. scheuchzeri* and *C. rotundifolia* s. str. might perhaps also be interpreted as the result of earlier introgression from *C. polymorpha*, particularly since we are dealing here with tetraploid plants in which the manifestation of eventual mutations is difficult. T u r e s s o n (1925) considered *C. scheuchzeri* as an alpine modification of the subalpine ecotype of *C. rotundifolia* analogously to *C.gieseckiana* which he believed to be a Scandinavian modification of this ecotype. A natural hybrid has

also been described hypothetically descending from *C. scheuchzeri* and *C. rotundifolia*. M e r x m ü l l e r asked by B ö c h e r to determine this plant found in the Alps at Termignon (France) declared on the basis of its habitus indicating traits intermediate between the presumable parental forms, that it probably is a hybrid of *C. rotundifolia* and *C. scheuchzeri*. B ö c h e r, however, (1963b) who also carried out cyto- logical examinations considers that this plant is not an F_1 hybrid but may evolve from the latter. It has, namely, firstly $2n = 72$, besides, it did not yield seeds in the cross with *C. rotundifolia* $(2n = 68)$ and in many respects it behaved like a representative of an already stabilized taxonomic entity. Only one of B ö c h e r's counterarguments does not seem justified in the light of the present results, that is the high pollen fertility of the presumable hybrid. Namely, no artificially bred F_1 hybrids between *C. scheuchzeri* and *C. rotundifolia* s. str. exhibited a lowered fertility. This is, however, not sufficient a basis to put in doubt the correctness of classification of the plant in question as a de- scendant of an hybrid and not as F_1 and it does not contradict the view of B ö c h e r as regards the systematic position of this plant.

The isolation of the *C. scheuchzeri* is probably more advanced than in the case of *C. polymorpha*. The former may probably be already considered as a distinct entity. On the basis of the criteria of C l a u- s e n, K e c k and H i e s e y (1939) and of L e w i s (1959) this taxon should, maybe, not be assigned a specific name but be considered as an ecotype in the hierarchy of biosystematic entities, with a weakened viability and fertility in its further generations leading to the formation of a new ecospecies.

Experimental investigations on plants from the territory of Poland established that the tetraploid taxa of *C. rotundifolia* s.l. are in an early phase of differentiation. According to B ö c h e r (1961, 1963a), the dif- ferences concern mainly quantitative characters which are most sus- ceptible to the influence of the environment and are an indication of such a stage of evolution. Besides, the tetraploids may intercross giving fertile hybrids. The reason of the difficulties in the formation of barriers of genetic isolation indispensable for the differentiation of distinct species in the *C. rotundifolia* group lies in the fact that the tetraploids belonging to this group, as outbreeding plants, intercross all the more readily. The different hybrids occurring as the result of recombination contribute to the increase of variation and the abolition of discontinuity (S t e b b i n s 1942, 1958; B a k e r 1953; C l a u s e n and H i e s e y 1958a, b).

In order to establish more generalized regularities, however, the data here reported would have to be compared with those obtained in crosses between plants from other parts of the range of this group.

CONCLUSIONS

1. The crosses between the lowland representatives of *C. rotundifolia* s. str. succeded readily as well as between the lowland and montane plants. No genetic barriers limiting crossing or causing reduced pollen or seed fertility could be observed.

2. The similar absence of genetic barriers between *C. rotundifolia* s. str. and *C. polymorpha* was observed. Pollen fertility in F_1 and F_2 was high. F_1s were intermediate as regards morphological characters. *C. rotundifolia* s. str. and *C. polymorpha* differ almost exclusively in certain morphological features and in the geographical distribution. Some of the distinguishing characters are conditioned by one gene as has been established for the pubescence on the stems. The inheritance of other is polygenic. In the case of crosses within *C. rotundifolia* s. str. smaller differences in variation range in F_1 and F_2 were observed than in the case of crosses between *C. rotundifolia* s. str. and *C. polymorpha*.

3. It is proposed to consider both these taxa not to be distinct species but rather different ecotypes selected in different habitat conditions.

4. The crosses of *C. polymorpha* and *C. rotundifolia* s. str. with *C. scheuchzeri* were almost as easy and successful as those between the former two taxa. F_1 hybrids had the high pollen and seed fertility, segregation in F_2 occured and individuals with lowered pollen fertility appeared as well as others producing good pollen in limited quantities. F_1 hybrids were intermediate as regards morphological characters in general. The feature of erect buds proved to be dominant. *C. scheuchzeri* is no doubt a taxon further removed from *C. rotundifolia* s. str. and *C. polymorpha*.

5. The differences between *C. polymorpha* and *C. rotundifolia* s. str. could also be due to the introgression of genes from *C. scheuchzeri* to *C. polymorpha*.

6. The tetraploid taxa of *C. rotundifolia* s.l. are in an early phase of differentiation. The fact that these tetraploids intercross readily contributes to the existence of difficulties in the formation fo barriers of genetic isolation. The introgression of genes occurs frequently.

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Stosunki cytogenetyczne pomiędzy niżowymi i górskimi gatunkami grupy *Campanula rotundifolia* L.

II. Tetraploidalne formy *C. rotundifolia* L. s. str. oraz *C. polymorpha* Witasek i *C. scheuchzeri* Vill. z terenu Polski

Streszczenie

Praca stanowi dalszą część badań nad stosunkami cytogenetycznymi w obrębie kompleksu *C. rotundifolia* L.s.l. i dotyczy trzech taksonów tetraploidalnych występujących w Polsce: *C. rotundifolia* L.s.str., *C. polymorpha* Witasek i *C. scheuchzeri* Vill. Wykonano 318 krzyżówek we wszystkich możliwych kombinacjach, z 280 krzyżówek otrzymano nasiona.

Otrzymane wyniki wskazują na brak barier genetycznych pomiędzy przedstawicielami *C. rotundifolia* s.str., pochodzącymi z niżu i ze stanowisk górskich, jak również pomiędzy *C. rotundifolia* s.str. i *C. polymorpha*. Mieszańce F_1 były w obu przypadkach bujne i wykazywały normalną płodność. *C. rotundifolia* s.str. i *C. polymorpha* różnią się prawie wyłącznie cechami morfologicznymi i rozmieszczeniem geograficznym. Niektóre różnice mogą być warunkowane jednogenowo, jak to stwierdzono dla owłosienia łodyg. W wyniku badań wysunięto hipotezę, że *C. polymorpha* w oparciu o kryteria biosystematyczne można uważać nie za odrębny gatunek, lecz ekotyp wyróżnicowany w odmiennych warunkach siedliskowych, pozostawiając jej rangę gatunkową dla potrzeb systematyki.

Otrzymanie mieszańców pomiędzy *C. polymorpha* i *C. scheuchzeri* dowodzi możliwości ewentualnego wpływu przekrzyżowywania z innymi taksonami górskimi na proces wyodrębniania się *C. polymorpha*.

C. scheuchzeri jest taksonem nieco dalej spokrewnionym z *C. rotundifolia* s.str. i *C. polymorpha*, lecz wzajemna izolacja genetyczna jest jeszcze słaba. W krzyżówkach pomiędzy *C. rotundifolia* s.str. i *C. scheuchzeri* występuje w F_2 osłabienie żywotności i ograniczenie płodności u niektórych segregantów. Cecha wzniesionych pąków okazała się dominująca. Istnieją również podstawy pozwalające przypuszczać, że występuje introgresja genów od *C. polymorpha* do *C. scheuchzeri*.

Otrzymane wyniki pozwalają stwierdzić, że tetraploidalne taksony grupy *C. rotundifolia* L.s.l. znajdują się we wczesnym stadium różnicowania. Różnice pomiędzy nimi polegają głównie na cechach ilościowych, a łatwość przekrzyżowywania się i zjawisko introgresji utrudniają powstawanie barier izolacji genetycznej.