Cytogenetic relationships between lowland and montane species of *Campanula rotundifolia* L. group. I. *C. cochleariifolia* Lam. and *C. rotundifolia* L.

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INTRODUCTION

Campanula rotundifolia L. is, according to Szafer, Kulczyński and Pawłowski (1953), common in Poland on the lowlands and in the lower belt of Carpathian and Sudetic Mts. while *C. cochleariifolia* Lam. occurs on limestone rocks in the Tatra Mts. All studied individuals of the species of the *rotundifolia* group belong to the tetraploid complex, only *C. cochleariifolia* is diploid. The present investigation was undertaken to study the relationships between this diploid species and the tetraploid *C. rotundifolia*.

MATERIAL AND METHODS

All the plants studied (with the exception of two) were brought directly from natural habitats. They were planted on an experimental plot in Warsaw and all reared in similar conditions.

The individuals of *C. rotundifolia* L. used for crosses originated from the following sites:

no. 13 — Pyry near Warsaw,

no. 46 — environs of Warsaw (transplanted from the University Botanical Garden),

no. 4 — Zakopane, Antolówka.

The individuals of *C. cochleariifolia* Lam. were from:

nos 48 and 49 — Tatra Mts., the valley Dolina Sedmi Promenov,

no. 77 — Tatra Mts., above the gorge Wąwóz Kraków,

nos 82, 84 — Tatra Mts., upper part of the gorge Wąwóz Kraków,

no. 113 — Tatra Mts., the valley Dolina Strążyska,

no. 107 — from seeds received from the Botanical Garden in Geneva,

no. 108 — from seeds received from the Botanical Garden in Mainz (plants transplanted from the Botanical Garden of Warsaw University).

In order to obtain comparable results the plants representing pure species were measured for the first time in the next year after transplantation and the hybrids — in the second year of vegetation. All the

measurements were repeated at least twice. Thus the results reported are means from two or more years. Measurements were made on fresh plants.

As height of the individual was assumed the modal value and not the length of the tallest stem, since in the species examined there occurred single overgrown stems and taking them into consideration would obscure the true picture. Therefore in the tabulations as height of shoots the modal value is given and, in parentheses, the range of height variation.

The length of the corolla was measured along the central rib from the base to the end of the corolla lobe. The dimensions given are means calculated from measurements of at least five flowers. A smaller number was examined only in some parent forms of *C. cochleariifolia* which did not develop vigorously enough after transplantation to the lowland and did not flower profusely. It was very difficult to measure the width of the flowers. The majority of forms of the studied *Campanula* species has flowers with corolla lobes recurved to a varying extent. Also the depth of incision of the corolla lobes varies. In view of the foregoing, the ratio of the corolla length to the distance between the tips of the lobes, after cutting open and flattening the corolla, was determined. Further this value will be referred to as the coefficient of the corolla enlargement. Another coefficient used was the ratio of the corolla lobe length to that of the corolla, termed the coefficient of incision of the corolla. The mean value of these coefficients are always based on at least five flowers.

The comparison of leaves on the stems was also difficult in view of their great variability on one individual and also because the lower leaves on the stem of some forms dry up early and the upper leaves exhibit less distinct differences. On account of this the lower sessile leaves on young stems were measured and compared. The values reported are means calculated from measurements of at least three leaves on three stems.

As the beginning of flowering was assumed the moment when the first fully developed flower appeared.

The pollen fertility was determined after staining with 2% aceto-carmin with glycerine in a 1:1 ratio. The species investigated are highly protandrous and the pollen is shed on the style before the flower opens. It was, therefore collected from mature anthers or from the style of unopened buds. The pollen fertility was calculated on the basis of at least two flowers (2—3 anthers in each flower) during two vegetative seasons.

The crossing was effected under cellophane bags. In order to protect the flowers completely from selfpollination, the flowerbuds were castrated at least 48 hrs before pollination. The flowers were

pollinated on the day when the tripartite stigma opened and they were additionally pollinated every day for 4 — 5 days until the stigma wilted. The progeny from selfpollination was also obtained by daily artificial additional pollination of the flowers with their own pollen in the bags.

The material for cytological studies was partly fixed in Navashin's fixative and prepared by the paraffin method (section thickness 13 μ), stained with cristall violet. Part of the material was fixed in a mixture of alcohol and glacial acetic acid (3 : 1) and used for squash preparations which were stained with acetoorcein after Žuk (1963).

PARENTAL FORMS

A. Campanula cochleariifolia L a m.

C. cochleariifolia L a m. (*C. pusilla* H a e n k e) occurs exclusively in the mountains of central Europe, Greece and Great Britain beeing an exception, chiefly on limestone rocks. The species exhibits a smaller variability than *C. rotundifolia* and the individuals at hand were typical for the species.

C. cochleariifolia is a perennial with thin short rhizomes. Flower stems most frequently ascendant, sometimes erect. The height of the individuals examined varied from 5.5 to 14 cm, except those from Geneva which were up to 16 cm high.

The stems in their superior parts (below the inflorescence) or in the lower part are coloured by anthocyanin. The only exceptions were the forms with white flowers (no. 108) and with very pale flowers (no. 82). The stems, at least in their lower part, are hirsute, in the superior part generally glabrous.

Basal leaves on rather long petioles, obovate, coarsely serrate. They are not shed before flowering. The petioles hirsute in various degrees, in some cases the pubescence passes to the blade. The basal leaves gradually pass into stem leaves. The latter on the lower part of the stem are obovate-lanceolate, coarsely serrate, tapering into a short petiole. Towards the tip of the stem the leaves become smaller and narrower, they no more have serrate edges and pass to sessile ones. The top leaves are small, linear-lanceolate and entire. The petioles and sometimes the leaf bases are hirsute. The whole stems are foliated though not very densely.

In the population from the upper part of the gorge Wąwóz Kraków a ratio of 7.9 — 9.5 was established between the length of the lower sessile leaves on young stems and their width. In the individual from the valley Dolina Strążyska the ratio was 1.6.

C. cochleariifolia has drooping flower buds in unilateral racemes, sometimes in loose panicles. Branchings occur all along the stems. The average

number of flowers per stem was 2.3—6. Only plants reared from the seeds received from Geneva had more paniculate inflorescences in which the number of flowers varied from 6—15, mean 9.1, in plant no. 108 it varied from 4—9, mean 6.6.

Corolla funnel-shaped, sometimes slightly bulging at the base with five slightly incised lobes. These lobes in most cases are not recurved, only in some forms they are slightly bent. The lengths of the corolla varied from 12.5—17.8 mm. The coefficient of incision was 0.18—0.30 and the coefficient of enlargement — 1.88—2.39. *C. cochleariifolia* has pale violet or blue flowers. According to the Horticultural Colour Chart the individuals under study exhibited the following colours: Aster Violet 38/1, Veronica Violet 639/1, Hyacinth Blue 40/1, 40/2, Wistaria Blue 640/1, Flax Blue 642/1. One plant had pure white corollas.

Calyx teeth short, rather wide, only slightly tapering to the tip, ending bluntly in most of the plants, straight, less frequently slightly bent. The length of the calyx teeth varied from 3.0—5.3 (7.0) mm and their ratio to the length of the corolla varied from 0.22 to 0.31 reaching in the case of the plant from the valley Dolina Strążyska 0.38.

Anthers more than twice the length of the filament, only in two individuals they were almost equal to it and in two others even somewhat longer.

Pollen in the unopened anthers is of various rose shades, after falling on the style take on a darker or lighter grey hue. Only the form with white flowers (no. 108) had cream-coloured pollen. The percentage of morphologically good pollen in the individuals investigated varied from 59.3 to 98.2, mean 84.7.

C. cochleariifolia plants flowered on the experimental plot in Warsaw between June 1 and 20.

In the given culture conditions *C. cochleariifolia* did not set seeds by self-pollination in the majority of cases, although it was artificially pollinated as has been described. Of the several seeds produced not one germinated. All the plants, however, set seeds after free pollination.

All the cytologically examined plants were diploid ($2n = 34$).

B. *Campanula rotundifolia* L.

Campanula rotundifolia L. is found in the temperate and subarctic zone of the northern Hemisphere.

The plant is a perennial with thin branching rhizomes. The species is highly variable and for this reason a list of the more prominent traits of the plants used as parent forms in crosses with *C. cochleariifolia* is given. The individuals differ widely.

For crosses with *C. cochleariifolia* two lowland forms of *C. rotundifolia* were used (no. 13 and 46) and a montane form (no. 4) (Table 1).

The flower stems of these plants are paniculate branched. No. 4 and 46 had flowers on long lateral shoots, all reared more or less the top of the stem. No. 13 had densely foliated side shoots of about equal length so that the flowers were distributed along the whole stem. All three forms contained anthocyanin in their stems.

Table 1
Comparison of parental forms of *C. rotundifolia* L.

	No. 13	No. 46	No. 4
Height of stems	72(55–81) cm	35(24–40)cm	29(24–32) cm
Pubescence on lower part of stems	hirsute	pubescent	glabrous
Ratio of length and width of stem leaves on young shoots	11.1	11.5	8.8
Stem leaves – ending	pointed	pointed	blunt
Basal leaves edges	serrate	dentate	dentate
No. of flowers per stem	42.4	13.1	10.2
Length of corolla	18.1 mm	20.3 mm	22.7 mm
Coefficient of corolla incision	0.36	0.33	0.33
Coefficient of corolla enlargement	1.69	1.75	1.73
Colour of corolla	38/1	38	38/1
Ratio of calyx teeth length to corolla length	0.34	0.27	0.42
Percentage of morphologically good pollen	98.1	98.0	97.5

The basal leaves of all these plants had reniform leaves with long glabrous petioles. They dried up before the time of flowering. Lower leaves on the stem with short petioles, lanceolate, glabrous, the lowest serrate; towards the top of the stem linear-lanceolate, sessile, entire, upper leaves linear. In nos 4 and 46 there were wide differences between the dimensions of the upper and lower leaves. Stem leaves occur almost exclusively on the lower part of the shoot. In no. 13 the stem leaves were more numerous, much longer, relatively narrow and did not diminish upward in such an extent.

The flower buds were always erect. The flowers in branched multi-lateral racemes. The corolla was rather wide, campanulate, with 5 recurved lobes rather deeply incised.

Calyx teeth shorter than half the length of the corolla, narrow, tapering gradually from the base, pointed at the tip. Only no. 46 had relatively short teeth not characteristic for the species. Nevertheless, in crosses with this individual, hybrids with relatively long calyx teeth were obtained, as if the plant had dimensions typical for *C. rotundifolia*.

Anthers distinctly more than twice as long as the filament, no. 4 had some shorter anthers. This plant showed a tendency to petaloidy. All intermediate stages from normally developed five anthers through

forms with a petal-shaped violet process on the filament, filaments transformed to a petal with a reduced anther at the tip, some of the stamens transformed to a part of the corolla — up to completely male sterile flowers with a double corolla were present. Pollen was cream coloured.

The forms just described flowered on the experimental plot in Warsaw between May 25 and June 8 generally in the following order: nos 46, 4, 13, *C. cochleariifolia*.

All the three forms were highly fertile after free pollination, they also produced a small number of seeds after artificial selfpollination — greater than *C. cochleariifolia*.

All the three forms were tetraploid ($2n=68$). In no. 46 in some PMC's an irregular course of meiosis was observed. Polyvalents, univalents and bridges could be seen.

DESCRIPTION OF HYBRIDS

The crosses of the *C. cochleariifolia* with *C. rotundifolia* plants were attempted in three successive vegetation periods in the years 1957, 1958, 1959. A total of 47 crosses *C. rotundifolia* ♀ × *C. cochleariifolia* ♂ and 18 reciprocal ones was made (Table 2).

Table 2
Results of crosses between *C. rotundifolia* and *C. cochleariifolia*

	<i>C. rotundifolia</i> ♀ × <i>C. cochleariifolia</i> ♂	<i>C. cochleariifolia</i> ♀ × <i>C. rotundifolia</i> ♂
I. No. of capsules with no seed setting	9 capsules	8 capsules
II. No. of capsules with seed setting		
1. Seeds did not germinate from	19 capsules (3—167 seeds per capsule, total ca. 800 seeds)	10 capsules (1—86 seeds per capsule, total ca. 300 seeds)
2. Seeds germinated from	19 capsules	0
sown	1243 seeds	0
germinated	19 seedlings	0
grown-up	16 plants	0
flowering plants	12	0

Cross 38/57 (*C. rotundifolia* no. 13 ♀ × *C. cochleariifolia* no. 48 ♂)

The cross gave 5 capsules with 217 seeds, four of which germinated. One seedling died early and the three others did not produce flower stems. They were hybrids since they exhibited traits characteristic of *C. cochleariifolia*. All the plants had the basal leaf petioles hirsute.

Cross 53/57 (*C. rotundifolia* no. 13 ♀ × *C. cochleariifolia* no. 49 ♂)

From 5 capsules 935 seeds were obtained but only one germinated. The plant was grown in the greenhouse for two vegetation seasons (Table 3).

The hybrid developed well and formed rhizomes in autumn. The flowers were rather narrow, ending sharply at the base, the corolla lobes were recurved, the dimensions of the corolla were intermediate between the two parent forms but closer to *C. cochleariifolia*. The shape and colour of the corolla resembled, however, *C. rotundifolia*. The large dimensions of the calyx teeth were probably due to the greenhouse conditions.

The anthers were more than twice the length of the filaments in both parental forms. The hybrid had a tendency of shortening of anther length characteristic for the *cochleariifolia* species. The plant was practically male-sterile since it produced extremely small amounts of pollen. In spite of repeated attempts of selfpollination no seeds were set.

Table 3
Comparison of the parental forms with the hybrid (cross 53/57)

	<i>C. rotundifolia</i> no. 13 ♀	<i>C. cochleariifolia</i> no. 49 ♂	F ₁
Height of stems	72(55–81)cm	10 cm	40(27–45)cm
Pubescence on lower part of stems	pubescent	hirsute	hirsute
Basal leaves edges	serrate	serrate	serrate
Ratio of length and width of stem leaves on young shoots	11.1	*	7.4
Foliation of stems	abundant	abundant	scanty
Stem leaves — width	narrow	wide	intermediate
— ending	pointed	blunt	pointed
— ribs and petioles	glabrous	pubescent	pubescent
Flower buds	erect	drooping	in 1st year of vegetation — erect, in the second — drooping
No. of flowers per stem	42.4	2.6	11.8
Length of corolla	18.1 mm	13.7 mm	14.2 mm
Coefficient of corolla incision	0.36	0.30	0.30
Coefficient of corolla enlargement	1.69	1.88	2.04
Ratio of calyx teeth length to corolla length	0.34	0.29	0.57

* In *C. cochleariifolia* the range is 1.6–9.8.

In the second year of vegetation the hybrid came into flower 12 days after the parental *C. rotundifolia* plants in the period when *C. cochleariifolia* flowers.

The hybrid was not examined cytologically. On the basis of its morphological features it may be considered as being triploid.

Table 4

Comparison of the parental forms with the hybrids (cross 77/59)

	<i>C. rotundifolia</i> no. 13 ♀	<i>C. cochleariifolia</i> no. 77 ♂	F ₁								
	Mean	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8		
Height of stems	72(55—81) cm	7(5—9)cm	17.5 cm	13(11—15) cm	11(9—13) cm	25(20—30) cm	18(15—21) cm	16(13—19) cm	21(17—24) cm	18(16—20) cm	18(15—20) cm
Ratio of length and width of stem leaves on young shoots	11.1	*	6.58	5.2	—	7.5	9.4	—	6.3	5.2	5.9
Steam leaves — length	long	short		narrow	short	long	long	long	long	long	long
— width	narrow	wide		blunt	narrow	narrow	narrow	narrow	narrow	narrow	narrow
— ending	pointed	blunt		erect	erect	pointed	pointed	pointed	pointed	pointed	pointed
Flower buds	erect	drooping	erect			erect	erect	erect	erect	erect	erect
No. of flowers per stem	42.4	4.0	4.3	1.9	4.6	12	4.2	3.1	2.0	2.6	3.7
Length of corolla	18.1 mm	16.3 mm	18.5 mm	16.2 mm		19.3 mm	19.9 mm	17.6 mm	20.5 mm	20.3 mm	17.2 mm
Coefficient of corolla incision	0.36	0.26	0.34	0.37		0.33	0.33	0.36	0.35	0.30	0.34
Coefficient of corolla enlargement	1.69	2.26	1.84	1.92		2.03	1.91	1.68	1.93	1.99	1.54
Colour of corolla	38/1	640/1		38		39/1	38	38	39	38	38
Ratio of calyx teeth length to corolla length	0.34	0.23	0.34	0.30		0.41	0.32	0.32	0.37	0.35	0.35
Ratio of anther to the filament length	> 2	< 2		> 2	> 2	> 2	> 2	< 2	> 2	< 2	< 2
Percentage of morphologically good pollen	98.3	97.6	87.5	45.4**	92.0	86.1	95.3	98.4	96.1	92.6	94.4

* In *C. cochleariifolia* the range is 1.6—9.8.

** In the 1st year of vegetation 4.2%, in the second — 86.5%.

Cross 77/59 (*C. rotundifolia* no. 13 ♀ × *C. cochleariifolia* no. 77 ♂)

Of the 50 seeds, not too well developed, 11 germinated. Three were white albinos and died soon, 8 plants flowered (Table 4).

From these no. 1 was most similar in habit to *C. cochleariifolia*.

The inflorescences of all the individuals were composed of few flowers like the paternal form but their shape and colour resembled those of the maternal plant.

In two individuals disturbances characteristic for hybrids were noted: scant production of pollen and hypotrophy of the pollen sacs in their top part.

All the hybrids set seeds from free pollination and also small quantities after artificial selfpollination. Six individuals were backcrossed both with the maternal and paternal form. All these crosses gave seeds (Table 11).

The course of meiosis was studied in nos 4 and 5. A tetraploid number of chromosomes was found and disturbances in meiosis were observed. The lack of proper's fixed material did not allow an exact cytological analysis.

Cross 135/58 (*C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 48 ♂)

The majority of seeds were not well developed, only few looked normal. Of the 25 seeds sown 3 germinated and one seedling subsisted, the plant died after two vegetation periods (Table 5).

The stem leaves were broad and their dimensions changed but slightly upwards as it happens in *C. cochleariifolia*. The flower shape resembled that of the maternal form, although the length of the corolla and its hue were similar to the paternal *C. cochleariifolia* plant.

In the first vegetation period the hybrid produced no seeds after selfpollination, in the second period it yielded one capsule with 117 poorly developed seeds none of which germinated.

Cytological examination proved that the hybrid was triploid ($2n=51$).

It was established that in the course of the first meiotic division bivalents are dominant in number (15—21), univalents (3—9) as well as polyvalents are present. It was not possible to determine definitively in each case if they were trivalents or tetravalents. Thus conjugation between at least some chromosomes of *C. rotundifolia* and *C. cochleariifolia* is possible. In anaphase I unsynchronized separation of chromosomes was observed, a single chromosome mostly taking so great an advance on the others that it was already on the spindle pole while the others still formed a plate. Bridges could also be seen in the anaphase. In the plasma rejected chromosome bodies, mostly bivalents were found.

Table 5

Comparison of the parental forms with the hybrid (cross 135/58)

	<i>C. rotundifolia</i> no. 46♀	<i>C. cochleariifolia</i> no. 84♂	F ₁
Height of stems	35(24–40)cm	12(10–14)cm	19–21 cm
Stems in lower part	slight ascendant	ascendant	slight ascendant
Pubescence on lower part of stems	pubescent	glabrous	pubescent
Branching of stems	in upper part	on whole stem	in upper part
Basal leaves — edges	dentate	serrate	serrate
—petioles	glabrous	pubescent	pubescent
Ratio of length and width of stem leaves on young shoots	11.5	8.7	6.1
Stem leaves — length	long	short	long
— ending	pointed	blunt	blunt
Flower buds	erect	drooping	erect
No. of flowers per stem	13.1	2.3	3.0
Length of corolla	20.3 mm	15.8 mm	16.5 mm
Coefficient of corolla incision	0.33	0.20	0.31
Coefficient of corolla enlargement	1.75	2.5	1.84
Colour of corolla	38	40/1	38/1
Ratio of calyx teeth length to corolla length	0.27	0.29	0.35
Ratio of anther to the filament length	> 2	≥ 2	> 2
Colour of pollen	cream	rose	rose
Percentage of morphologically good pollen	98.9	92.4	55.9

Cross 27/58 (*C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 82 ♂)

Three well developed seeds were obtained two of which germinated. One plant gave no flower stems and died in the first winter, the second (no. 27/58-1) is still alive after 4 years and flowers every year (Table 6).

The stem leaves did not exhibit so wide differences in the dimensions between the upper and lower ones as observed in *C. rotundifolia*. The basal leaves subsist after flowering which may be due to the greenhouse conditions. The shape of the flowers is nearly identical to *C. rotundifolia*, the corolla lobes however are less developed and their colour is lighter.

Pollen fertility was very high, much more so than in the paternal form in which, beside flowers with highly fertile pollen, others with fertility reduced to 41.6% or with degenerated anthers were found.

The hybrid set numerous seeds after free pollination as well as when pollinated artificially with its own pollen. In the second year of vegetation 120 seeds were obtained (Table 11).

Cytological examination showed that the hybrid is tetraploid ($2n=68$) and meiosis runs in it regularly. On the plates of metaphase I bivalents

Table 6

Comparison of the parental forms with the hybrids (cross 27/58-1)

	<i>C. rotundifolia</i> no. 46 ♀	<i>C. cochleariifolia</i> no. 82 ♂	F ₁	F ₂ range of variation
Height of stems	35(26-40) cm	7(5-9) cm	13(12-15) cm	13-30 cm
Stems in lower part	slight ascendant	ascendant	slight ascendant	
Pubescence of lower part of stems	pubescent	hirsute	pubescent	
Branching of stems	in upper part	on whole stem	in upper part	3 individuals - on whole stem, 2 individuals - in upper part
Anthocyanin in stems	very abund- ant	absent	less abund- ant	1 individual - very abund- ant, 1 individual - less abund- ant, 3 individuals - absent
Basal leaves - petioles	glabrous	hirsute	hirsute	
Ratio of length and width of stem leaves on young shoots	11.5	*	7.7	7.4-10.3
Stem leaves	in lower part	on whole stem	on whole stem	on whole stem
— length	long	short	long	short
— ending	pointed	blunt	pointed	pointed
— petioles	glabrous	hirsute	hirsute	
Flower buds	erect	drooping	erect	erect
No. of flowers per stem	13.1	3.4	3.0	2-10.7
Length of corolla	20.3 mm	12.5 mm	19.1 mm	20.3-21.4 mm
Coefficient of corolla incision	0.33	0.18	0.35	0.31-0.34
Coefficient of corolla enlargement	1.75	2.01	1.97	1.82-2.2
Colour of corolla	38	40/2	38/1	38,38/1,40/1, white
Ratio of calyx teeth length to corolla length	0.27	0.29	0.41	0.29-0.36
Ratio of anther to the filament length	>2	<2	>2	2 individuals >2 3 individuals <2
Colour of pollen	cream	cream with rose hue	roseate	
Percentage of morphologically good pollen	98.9	70.7**	98.5	82.5-87.0

* In the population of *C. cochleariifolia* including individual no. 82 the range was 3.4-9.5.

** The mean calculated on the basis of flowers with filled anthers.

prevails and also trivalents (2—7) as well as univalents were present. This seems to indicate an at least partial conjugation between the chromosomes of *C. rotundifolia* and *C. cochleariifolia*. In anaphase I the chromosomes separated unregularly and on the plates of metaphase II uneven numbers of chromosomes occurred. It is noteworthy that the maternal individual shows some disturbances in the course of meiosis also but smaller than the hybrid.

F₂ hybrids of the cross 27/58-1 (*C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 82 ♂)

One hundred seeds were sown of which 7 germinated and 5 seedlings survived. One plant died after the first year and two after the second (Table 6).

The majority of the F₂ individuals were not much taller than those of F₁ and had lateral shoots on whole stem. One plant almost attained the height of *C. rotundifolia* no. 46 and exhibited similar branching of the upper part of the stem and anthocyanin coloured stems in contrast to the other individuals.

The number of flowers per stem was similar as in *C. cochleariifolia* with exception of one plant (F₂ 27/58-1 no. 5). The coefficient of corolla enlargement for two individuals was intermediate and for two others closer to that for *C. cochleariifolia* no. 82. The coefficient of incision of the corolla was the same as for *C. rotundifolia* no. 46 and F₁.

The pollen of all the individuals with one exception was cream coloured.

All these plants set seeds after free pollination. Three plants were pollinated with their own pollen artificially and they all produced small quantities of seeds.

F₃ hybrids of the cross 27/58-1 (*C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 82 ♂)

In spring 1962 seeds of the selfpollinated F₂ plants were sown. The result was the following:

F ₂ individual	Seeds sown	Seeds germinated	Plants grown-up
2	9	5	4
3	33	11	9
5	12	0	0

After one year only the floral traits can be compared (Table 7).

The flower buds of all F₃ individuals were erect as in *C. rotundifolia*. The flowers of F₃ 27/58-1/2 and 27/58-1/3 were similar to that of *C. rotun-*

difolia. As compared with the parent forms their coefficient of corolla incision was similar to that of *C. rotundifolia* no. 46, F_1 and parental F_2 individuals. The value of the coefficient of corolla enlargement was lower, that is changed in the direction characteristic for *C. rotundifolia*.

Table 7

Comparison of F_3 hybrids with their initial forms (cross 27/58-1)

	27/58-1/2		27/58-1/3	
	F_2	F_3 range of variation	F_2	F_3 range of variation
Length of corolla	21.4 mm	16.2— —17.7 mm	21.0 mm	17.0— —19.7 mm
Coefficient of corolla incision	0.31	0.30—0.39	0.34	0.32—0.40
Coefficient of corolla enlargement	2.17	1.76—2.01	1.93	1.61—2.03
Colour of corolla	white	38,39,39/1	38	38,39/1,738/3
Ratio of calyx teeth length to corolla length	0.35	0.22—0.41	0.29	0.30—0.43
Percentage of morphologically good pollen	87.1	67.5 —97.3	86.7	(26.4)61.5— —97.0

Both F_3 generations, though composed of few individuals showed a much wider range of variation in the ratio: length of calyx teeth — length of corolla than in F_2 . In the case of F_3 27/58-1/2 it exceeds both parental forms, F_1 and F_2 and, in the case of F_3 27/58-1/3 — F_1 and F_2 attaining almost the value for the parental individuals of the initial cross. The mean values are shifted in the direction characteristic for *C. cochleariifolia*.

Pollen fertility in both groups was high, 60—100 per cent, only one individual in F_3 27/58-1/3 had a greatly lowered fertility (26.4%) similarly as in F_3 40/57.

Cross 40/57 (*C. rotundifolia* no. 4 ♀ × *C. cochleariifolia* no. 48 ♂)

From two capsules 13 seeds were obtained. Only one germinated. The plant survived in the greenhouse over two vegetation periods (Table 8).

The hybrid resembled *C. cochleariifolia*. The stems were coloured with anthocyanin. Stem leaves were of intermediate size, rather short and wide with blunt endings.

The shape of the flowers approximated that of *C. cochleariifolia*, they were however somewhat larger and the lobes more recurved. The anthers of the hybrid were less than twice the length of the filaments and showed a tendency to petaloidy.

In the first vegetation period the hybrid did not set seeds after self-

Table 8

Comparison of the parental forms with the hybrids (cross 40/57)

	<i>C. rotundifolia</i> no. 4 ♀	<i>C. cochlearii-</i> <i>folia</i> no. 48 ♂	F ₁	F ₂ range of variation
Height of stems	29(24–32) cm	10 cm	20(15–34) cm	10–35 cm
Stems in lower part	slight ascendant	ascendant	ascendant	ascendant
Pubescence on lower part of stems	glabrous	pubescent	pubescent	pubescent
Branching of stems	on whole stem	on whole stem	in upper part	13 individuals – on whole stem 2 individuals – in upper part
Basal leaves edges	dentate	serrate	serrate	
Ratio of length and width of stem leaves on young shoots	8.8	*	4.7	3.6–9.4
Stem leaves —	in lower part	on whole stem	on whole stem	
— length	long	short	intermediate	
— petiole pubescence	glabrous	hirsute	hirsute	
Flower buds	erect	drooping	erect	erect
No. of flowers per stem	16.4	2.6	2.2	2.5– –26(36)**
Length of corolla	22.7 mm	13.7 mm	17.1 mm	14.3– –22.4mm
Coefficient of corolla incision	0.33	0.30	0.29	0.30–0.39
Coefficient of corolla enlargement	1.73	1.88	1.93	1.53–2.15
Colour of corolla	38/1	642/1	637	38,38/1, 39,39/1
Calyx teeth — width	wide	narrow	wide	5 individuals – wide, 9 individuals – narrow
— ending	blunt	pointed	pointed	1 individual – blunt, 14 individuals – pointed
Ratio of calyx teeth length to corolla length	0.42	0.29	0.33	0.29–0.49
Colour of pollen	cream	rose	cream	9 individuals – cream, 6 individuals – rose
Percentage of morphologically good pollen	97.7		19.4	(48.7)69.4– –98.1***

* In *C. cochlearitifolia* the range is 1.6–9.8.

** In parentheses the number of flowers on the single stem of the individual no. 8.

*** In parentheses the percentage of morphologically good pollen of the aberrant individual no. 11.

pollination, in the second season from three of the flowers pollinated only one yielded 31 seeds.

In the second vegetation period the hybrid came into flower one day later than the maternal plant and earlier than any *C. cochleariifolia* individual.

Cytological examination showed the hybrid to be triploid ($2n=51$).

Conjugation in meiosis was abnormal. In the first division 5—6 polyvalents (probably trivalents) appeared, as well as bivalents and univalents. In anaphase I unsynchronized separation of the chromosomes was observed. Several bridges regularly occurred in each cell. Rejected chromosomes could also be seen at the edge of the spindle or in the cytoplasm. In consequence of the abnormal separation at A I, there occurred at M II 20 to 41 chromosomes. Disturbed separation of chromosomes at A II caused lagging of them and their loss in the cytoplasm.

F_2 hybrids of the cross 40/57 (*C. rotundifolia* no. 4 ♀ × *C. cochleariifolia* no. 48 ♂)

Of the 25 seeds 16 germinated and 15 plants survived (Table 8).

The F_2 hybrids were of intermediate height as compared to the parental forms of the initial cross and their mean height was equal to the modal height of F_1 .

Table 9

Seed setting in F_2 hybrids (cross 40/57) after free pollination, artificial selfpollination and crossing with *C. rotundifolia*

F_2 individual	Free pollination	Artificial selfpollination	F_2 ♀ × <i>C. rotundifolia</i> no. 13 ♂	<i>C. rotundifolia</i> no. 13 ♀ × F_2 ♂
1		1961 ±		
	±	1962 —	—	+
3		1961 ±		
	+	1962 —	+	+
4		1961 ±		
	±	1962 +	—	+
5	+	1961 ±	+	+
6	+	1961 +	+	±
9	+	1961 —	+	+
10	+	1962 +	+	±
11		1961 +		
	+	1962 ±	±	+
14		1961 ±		
	+	1962 —	+	+
15		1961 —		
	+	1962 ±	+	+

+ Good seed setting.

± Slight seed setting.

— No seeds.

The number of flowers per stem showed wide variation, its range included both parental forms and by far exceeded the range of variation of this trait in *C. rotundifolia* no. 4. The range of variation of the corolla length extended from the dimensions in one parental form in the initial cross to those in the other and the range of the coefficient of corolla enlargement exceeded in both directions the values of the same index for the parental forms. The corollas of the majority of the F_2 segregants had a coefficient of incision close to the parental *C. rotundifolia*. In three cases it exceeds this value and only in two was equal to that of the parental form of *C. cochleariifolia*.

The range of variation of the ratio: calyx teeth — corolla length exceeds the values for both parental forms and F_1 .

In this F_2 family aberrant plants, typical for triploid's progeny, occurred. In plant no. 8 all young buds dried up. The second aberrant plant, no. 15, did not flower in the first year and in the second year was only late in flowering. Individuals with disturbances in pollen production were found. These were manifested by the appearance of flowers with empty anthers or with only some of the pollen sacs filled. Many individuals produced few pollen grains per anther. The tabulated values of pollen fertility refer to the anthers containing pollen.

The seeds setting of these F_2 plants (Table 9) was rather high both after selfpollination and after backcrossing to *C. rotundifolia* no. 13.

Meiosis was studied in eight F_2 individuals. They all proved to be aneuploid with a number of chromosomes close to $4x$ and showed disturbances in the course of meiosis such as bridges in anaphase I and abnormal separation of chromosomes. Less frequently chromosomes in advance and more frequently — lagging ones, or sometimes rejected chromosomes in the cytoplasm were also observed.

F_3 hybrids of the cross 40/57 (*C. rotundifolia* no. 4 ♀ × *C. cochleariifolia* no. 48 ♂)

In spring 1962 seeds obtained by selfpollination of F_2 segregants were sown. The following result was obtained:

F_2 individual	Seeds sown	Seeds germinated	Plants grown-up
1	17	0	0
3	6	0	0
4	10	1	0
5	12	0	0
6	80	3	1
11	83	31	31
14	20	5	5

Table 10

Comparison of F₃ hybrids with their initial forms (cross 40/57)

	40/57-11		40/57-14	
	F ₂	F ₃ range of variation	F ₂	F ₃ range of variation
Length of corolla	16.3 mm	12.3— — 18.7 mm	18.4 mm	14—20.2 mm
Coefficient of corolla incision	0.39	0.32—0.44	0.33	0.36—0.39
Coefficient of corolla enlargement	1.54	1.36—2.09	1.64	1.63—1.98
Colour of corolla	38	38,38/1, 39,39/1	38/1	38,39,39/1
Ratio of calyx teeth length to corolla length	0.42	0.35—0.54	0.34	0.36—0.48
Percentage of morphologically good pollen	46.1	0 — 92.6	89.5	4.7 — 93.6

After one vegetation period only the floral characteristics can be compared (Table 10).

The flower buds of all F₃ individuals were erect as in *C. rotundifolia*. Both in F₃ 40/57-11 and F₃ 40/57-14 the flowers resembled those of *C. rotundifolia*. This was manifest in the fact that the ranges of variation of the coefficient of corolla incision were shifted in the direction characteristic of this species. The range of variation of corolla enlargement coefficient in the case of F₃ 40/57-14 was contained in such range in F₂ and in the case of F₃ 40/57-11 was slightly shifted in the direction characteristic for *C. rotundifolia*. The ratio of the calyx teeth length to the corolla length also showed a shift in the same direction.

Pollen fertility in both F₃ families exhibited a very characteristic distribution of values. In F₃ 40/57-11 24 plants showed a fertility of 40—80 per cent and one plant produced no fertile pollen at all. In F₃ 40/57-14 three plants had 85—93 per cent of fertile pollen and one 4.7 per cent only.

COMPARISON OF THE HYBRIDS OBTAINED

To cross *Campanula rotundifolia* L. with *C. cochleariifolia* L. presents serious difficulties. After many pollinations only few hybrids were obtained. Sixteen individuals survived that is nearly 1 per thousand of the seeds potentially set. They fall into two groups: triploids (3 plants) and tetraploids (9 plants). In three combinations the hybrids produced no flower stems. Both groups of F₁ hybrids show distinct differences and certain common traits.

The majority of the F₁ hybrids resembled the *C. rotundifolia* plants as regards the shape of flowers, the kind of stem branching and the

stem leaves. But the leaves were relatively broader and they never showed the distinctly reduced dimensions towards the top of the stem characteristic of *C. rotundifolia*. The shape of the flowers in both groups of hybrids was almost identical as in *C. rotundifolia*. This is most visibly shown by the high values of the coefficient of the corolla incision and the corolla lobes always recurved. The hybrids had also characteristic long calyx teeth and consequently high values of the ratio: length of teeth — corolla length. The trait of erect buds exhibited by *C. rotundifolia* appeared in 11 of the 12 F_1 individuals. One of them, 53/57, had drooping buds. This trait appeared only in the second vegetation period and was found neither in the segregants in other crosses nor in F_2 and F_3 .

The influence of *C. cochleariifolia* was evident in the height of the hybrids and number of flowers per stem. All F_1 hybrids were nearly intermediate in height between the parental forms, approximating, however, in a larger or smaller degree the paternal form. The influence of *C. cochleariifolia* parent was still more pronounced in number of flowers per stem. The group of tetraploid hybrids showed closer resemblance to the paternal form as regards certain morphological features. These plants were much lower than the triploids descending from the same maternal form. They also had usually a smaller number of flowers per stem.

Table 11

Seed setting and their germinating in F_1 hybrids and backcrosses

F_1	Selfpollination				Free pollination	$F_1 \varnothing \times$ <i>C. rotundifolia</i> no. 13 ♂	<i>C. rotundifolia</i> no. 13 ♀ $\times F_1 \sigma$
	seed setting	seed sown	seedlings germinated	plants grown-up			
Triploids							
53/57	—						
135/58	++	117	0				
40/57	+	25	16	15			
Tetraploids							
77/59 no. 1	+	30	2	2		+	+
3	+	27	0		+++		
4	++	14	2	2	++	+	+
5	++	20	3	2	++	++	++
6	+	10	2	2	+++	++	+
7	+	24	14	14	+++	++	++
8	++	5	3	2	+++	+	++
27/58—1	++	100	7	5	++	++	++

+++ Normal seed setting (of the same order as the maternal plant after free pollination).

++ Reduced seed setting.

+ Few seeds obtained.

— No seeds.

As was to expect a distinct difference in pollen fertility and seed setting was observed between the triploid and tetraploid hybrids. The triploids were either male-sterile (53/57) or had a greatly reduced percentage of morphologically good pollen (19.4% in 40/57, 55.9% in 135/58). Of the three triploid individuals one produced no seeds after selfpollination and the remaining two yielded but a small number in the second vegetation period after the unsuccessful trials. Quite a high percentage of germinating seeds was obtained from plant 40/57 only (Table 11).

All the tetraploid hybrids had a high percentage of morphologically good pollen (86.1—98.5%) and set seeds both after free and selfpollination. The seeds obtained in the latter way, however, had a low germination power. Six of the tetraploids set seeds after crossing with the *C. rotundifolia* which was their maternal form (Table 11). The number of seeds produced by free pollination was in the hybrids 77/59 of the same order as in the maternal *C. rotundifolia* no. 13.

Differences also occurred between the progeny of the triploid and tetraploid plants. The descendants of the triploid exhibited a wider range of variation of the height and number of flowers per stem and also of other traits. Some individuals showed distinct developmental disturbances (e.g. F₂ 40/57 nos 8 and 15). Only the shape of the flowers was similar in the groups originating from triploids and tetraploids showing the dominant influence of *C. rotundifolia* manifested by the shift of some coefficients towards values characteristic of this species. This tendency was still more prominent in F₃ generations.

The eight F₂ individuals examined, descending from the triploid, are aneuploids in which the chromosome number approximates 4x. Thus more viable proved the combinations with a chromosome number close to that in *C. rotundifolia*.

Pollen fertility in the F₂ progenies both of tetraploid and triploid hybrids was rather high amounting to 82.5—87.0 per cent and 69.4—98.1 per cent respectively. In the progeny of the triploid, however, the range of variation was wider. In the third generations descending from both groups a characteristic segregation of values occurred: high fertility of most individuals and large deviations of single plants with a greatly reduced fertility.

The F₂ progenies of both triploid and tetraploid hybrids set seeds after free pollination and aneuploid triploid's progeny in reciprocal crosses with *C. rotundifolia* (Table 9).

DISCUSSION

The crosses between the tetraploid *C. rotundifolia* L. and diploid *C. cochleariifolia* L. am. demonstrated the possibility of hybridization in natural conditions. According to Crook (1951) both natural and

artificial hybrids are rare in the genus *Campanula*. He mentions a hybrid of *C. cochleariifolia* and *C. rotundifolia* with the remark that it was indistinguishable from *C. rotundifolia*. He also mentions two probable artificially produced hybrids between these two species. No data, however, of the morphology of these plants and their chromosome number are given.

Positive results of crosses were obtained by the present author only in the case, if the tetraploid species *C. rotundifolia* was the maternal form. Also Gairdner (1926) obtained only hybrids when pollinating the tetraploid garden variety *C. persicifolia* — Telham Beauty ($2n=32$) with diploid *C. persicifolia* ($2n=16$). Seeds from the reciprocal cross did not germinate. Positive results were also obtained exclusively in crosses of the type $4x \text{♀} \times 2x \text{♂}$ by Müntzing (1930) in *Galeopsis*, Levan (1936) in *Allium*, Mehlquist (1945) in *Dianthus*, Nygren (1957) in *Melandrium*.

These results do not exclude the possibility of obtaining hybrids from reciprocal crosses with the investigated *Campanula* species. The transfer to lowland conditions is most unfavourable to montane plants. *C. cochleariifolia* could be kept alive but a short time on the experimental plot in Warsaw and grew poorly. It is possible that it was the lowered vitality of the plant that made all crosses unsuccessful when this species was used as maternal form. Similar difficulties are mentioned by Gregor (1931) in the case of *Phleum*.

Nordenskiöld (1945) crossed reciprocally diploid and tetraploid species of *Phleum*. The crosses were quite successful and yielded triploid hybrids, morphologically intermediate but completely sterile. Söllner (1953, 1954) studied octoploid ($2n = 72$) and tetraploid ($2n = 36$) forms of *Cerastium arvense*, which, according to him do not produce hybrids in natural conditions. He succeeded, however, in producing artificially progeny in reciprocal crosses which behaved like triploids and not like hexaploids. Artificially produced hybrids from reciprocal crosses between polyploids of various degrees were also obtained by Steere (1932) in *Petunia* and Bernström (1944) in *Lamium*.

Hybrids between polyploids of different degree were obtained by Gregor and Sansome (1930) in *Phleum* and Nygren (1948) in *Calamagrostis*, even if the plant with a lower number of chromosomes was used as the maternal form.

The studied hybrids *C. rotundifolia* $\times$ *C. cochleariifolia* were not morphologically homogenous, as was to be expected, in view of the heterosigosity of the crossed species. The quite unexpected difference was in the number of chromosomes. Two groups were found: triploids and tetraploids. The expected triploids were even in minority. Among the twelve flowering plants there were only three of them. Their weak

vitality, low pollen fertility, poor seed setting and the disturbances in meiosis are associated with their triploid level. The same was shown by Sax (1922) in *Triticum*, Lesley (1928) in *Solanum*, Gairdner (1926) in *Campanula persicifolia*, Kostoff (1931) in *Nicotiana*, Müntzing (1933) in *Solanum*, Webber (1935) in *Gossypium*, Satina and Blakeslee (1937a, b) in *Datura*, Nordenskiöld (1941, 1945) in *Phleum*, Håkansson and Ellerström (1950) in *Secale*, Söllner (1954) in *Cerastium*, Nygren (1957) in *Melandrium*, Grant (1959) in *Amaranthus*, Tanaka and Kamemoto (1960) in *Vanda*, Sen and Vidyabhushan (1960) in *Cyamopsis*.

Triploids which do not exhibit such disturbances are also known, e.g. in *Hyacinthus* (Belling 1921, 1925) or *Lycoris* (Inariyama 1931).

The most interesting fact was, however, the appearance of tetraploid hybrids in F_1 . To check their hybrid origin following tests were performed. 200 flowers were left under isolating cellophane bags without additional pollination and from potential 20,000 seeds only four shrunken seeds developed which did not germinate. This experiment excluded the possibility of spontaneous selfpollination as Hegi (1909—1931) believed. It also made improbable the supposition of parthenogenetic descent of tetraploid hybrids. Gairdner and Darlington (1931) described diploid parthenogenetic plants originating from crosses of the type $4x \times 2x$ within the *C. persicifolia* species. The haploid pollen tube penetrated to the embryo sac but did not fertilize the egg cell.

Also Gadella (1963) did not obtain seeds from *C. rotundifolia* by way of selfpollination, after leaving the flowers under isolating bags without additional artificial pollination. Gadella's opinion that *C. rotundifolia* is selfsterile species is not true because this species sets seeds after artificial pollination with its own pollen, although not as abundantly as in crosspollination. The possibility of the origin of tetraploid plants as a result of accidental pollination seems nearly excluded. All hybridizations were done with the greatest possible care.

After artificial selfpollination *C. rotundifolia* sets seeds with great difficulty. Such plants, however, were obtained from both the maternal forms of *C. rotundifolia* which at the same time were used in crosses with *C. cochleariifolia*. Since the flowers of the hybrids *C. rotundifolia* $\times$ *C. cochleariifolia* resemble closely those of *C. rotundifolia*, differences between the hybrids and the selfs of their maternal forms could be expected only in the height of the plants and the number of flowers per stem. These differences were actually pronounced (Fig. 1—5, 6—11). One self of *C. rotundifolia* no. 13 had even more flowers per stem than the maternal form and was higher than the tetraploid and even triploid hybrids from the cross *C. rotundifolia* no. 13 ♀ $\times$ *C. cochleariifolia* ♂ . Eight selfs of *C. rotundifolia* no. 46 were distinctly taller than the tetraploid hybrid and had more flowers per stem, both

Fig. 1. *Campanula rotundifolia* no. 13.
(Phot. R. Bielawski)

Fig. 2. Self of *C. rotundifolia* no. 13.
(Phot. R. Bielawski)

in comparison with the just mentioned plant and with the triploid descending from the cross *C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* ♂. It should be borne in mind that the tetraploid hybrid progeny exhibited also a number of paternal traits, even more pronounced than

Fig. 3. Triploid hybrid of *C. rotundifolia* no. 13 ♀ × *C. cochleariifolia* no. 49 ♂ (53/57) (herbarium specimen).
(Phot. R. Bielawski)

Fig. 4. Tetraploid hybrid of *C. rotundifolia* no. 13 ♀ × *C. cochleariifolia* no. 77 ♂ (77/59 no. 4).
(Phot. R. Bielawski)

Fig. 5. *C. cochleariifolia*.
(Phot. R. Bielawski)

in the triploids which contained only one genome of *C. cochleariifolia* to two of *C. rotundifolia*.

The appearance of tetraploid progeny in crosses between a tetra- and diploid species is well known and found in various plants. Such cases have been described by Lawrence (1936) in *Delphinium*, Prywer (1936) in *Prunus*, Nordenskiöld (1937) in *Phleum*, Clausen, Keck and Hiesey (1941) in *Layia*, Mehlquist (1945) in *Dianthus*, Bains and Howard (1950) in *Solanum*, Simonet (1952) in *Iris Pogocyclus*, Avers (1953) in *Aster*, Söllner (1954) in *Cerastium*, Tsuchiya (1958) in *Hordeum*.

Fig. 6. *C. rotundifolia* no. 46.
(Phot. R. Bielawski)

Fig. 7. Self of *C. rotundifolia* no. 46.
(Phot. R. Bielawski)

Our fragmentary observations on meiosis in different *C. cochleariifolia* plants did not dissolve any disturbances that could lead to the formation of unreduced gametes. But in some plants an abortion of pollen grains was observed and in one plant (no. 84) triads and rare monads were found. The pollen grains of this individual were measured. The mean diameter of the pollen grains was 44.4μ ($36.9 - 45.1\mu$). Among about 14 000 of such grains two were 49.2μ large, two — 53.3μ and two — 61.5μ . Probably only the last two were the true unreduced grains because their dimensions were of the same order of size as the pollen grains of the tetraploid *C. rotundifolia* ($56 - 67\mu$) and of the tetraploid F_1 hybrids.

The few tetraploid hybrids from our crosses were obtained from a large number of seeds sown. It seems that when *C. rotundifolia* is pollinated by *C. cochleariifolia* most of the ovules are reached by haploid

Fig. 8. Triploid hybrid of *C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 84 ♂ (135/58) (herbarium specimen).
(Phot. R. Bielawski)

Fig. 9. Tetraploid hybrid of *C. rotundifolia* no. 46 ♀ × *C. cochleariifolia* no. 82 ♂ (27/58).
(Phot. R. Bielawski)

Fig. 10. *C. cochleariifolia* no. 84. (herbarium specimen).
(Phot. R. Bielawski)

Fig. 11. *C. cochleariifolia* no. 82 (herbarium specimen).
(Phot. R. Bielawski)

pollen tubes and are fertilized. The triploid embryos originating from this fertilization are evidently highly unbalanced and most of them die in a young stage, sometimes producing shrunken or empty seeds. Only few of them are able to grow and to produce triploid hybrids. It seems that the fertilization and initial growth of embryos provide a stimulus for the development of the capsules. In these conditions the rare unreduced pollen grains of *C. cochleariifolia* have full opportunity to produce rare tetraploid hybrid embryos. Lewis and Lewis (1955) observed also symptoms of fertilization in interspecific crosses in *Clarkia*, after which no seeds were produced or only poorly developed ones. The inhibition of seeds development at various stages has been described and compared by Valentine and Woodell (1960) and Valentine (1961) in hybrids between nine diploid species of *Primula* belonging to the *Vernales* section as well as after crossing diploid and autotetraploid forms within *Primula veris*, *vulgaris* and *elatior*.

In this situation, if we assume that the development of seeds with tetraploid embryos due to fertilization with unreduced diploid pollen of *C. cochleariifolia*, is more normal and leads to the formation of good seeds and viable hybrids, then the frequency of the tetraploid hybrids

will be much higher in relation to triploids than that anticipated on the basis of frequency of unreduced pollen in *C. cochleariifolia* (1 to 7000).

Thus this might be an efficient system of selection of the unreduced pollen grains which at the same time reduces the barriers of incompatibility and sterility of F_1 hybrids between the species investigated. The tetraploid hybrids were fertile and could easily be crossed with *C. rotundifolia*. This opens new and much wider possibilities, than in the case of triploid hybrids, for introgression of *C. cochleariifolia* genes into the genome of *C. rotundifolia*. Triploid F_1 hybrids may also play a certain role in the flow of genes between the species under study. The F_2 progeny obtained from such a hybrid consisted of aneuploid plants with chromosome number close to $4x$. A similar observation was made by Levan (1936) in *Allium Schoenoprasum* and Valentine (1950) in *Viola*. The aneuploid hybrid swarms do not stabilize, however, as was shown by the studies of Lövkvist (1962) in *Cochlearia* and do not give balanced populations capable to compete successfully with those already present on the given habitat. If such hybrids occur, they are intermediate and can transmit certain hereditary traits in crosses with the parental species. Aneuploid *Campanula* hybrids which were the progeny of a triploid could readily be crossed with *C. rotundifolia*. They set good germinating seeds.

It is, however, unknown if the introgressive types would be found in the Tatra Mts appropriate conditions for eventual stabilization. According to Stebbins (1958) this process occurs most readily and most frequently in new habitats. Confirmation of this may be found in the investigations of Heiser (1947, 1949) in *Helianthus*. Some cases are known, in which introgressive types stabilized also in undisturbed habitats (Epling 1947a, investigations on *Arctostaphylos* and 1947b, on *Salvia*).

The crossability and the introgression of *C. cochleariifolia* genes may extend the already wide range of variation of the traits exhibited by *C. rotundifolia*.

CONCLUSIONS

1. The hybridization between the tetraploid *C. rotundifolia* and the diploid *C. cochleariifolia* is very limited. F_1 hybrids were only obtained in crosses of the $4x \text{♀} \times 2x \text{♂}$ type.

2. The hybrids obtained are either triploid or tetraploid.

3. The triploid hybrids exhibit many disturbances in meiosis and are highly sterile. The F_2 generation, small in number, originating from one triploid F_1 hybrid was aneuploid with chromosome numbers close to $4x$ and with a markedly increased fertility.

4. Tetraploid hybrids morphologically closer to *C. cochleariifolia*

than the triploid ones, have an almost normal fertility and disturbances in meiosis of the nearly same level as in *C. rotundifolia*. The F_2 obtained was also fertile.

5. Tetraploid hybrids arose probably owing to the fertilization by unreduced pollen grains of *C. cochleariifolia*. Since the majority of the zygotes formed by fertilization with the haploid pollen of *C. cochleariifolia* are inviable, the frequency of these tetraploid hybrids is relatively high.

6. The compatibility of the tetraploid hybrids with *C. rotundifolia* increases, in natural conditions, the possibility of eventual introgression between *C. rotundifolia* and *C. cochleariifolia*. This process, if it occurs at all, would to occur chiefly in the direction from *C. cochleariifolia* to *C. rotundifolia*.

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Stosunki cytogenetyczne między niżowymi i górskimi gatunkami grupy *Campanula rotundifolia* L. I. *C. cochleariifolia* Lam. i *C. rotundifolia* L.

Streszczenie

Celem pracy było zbadanie wzajemnych stosunków cytogenetycznych pomiędzy diploidalną *C. cochleariifolia* Lam. a tetraploidalną *C. rotundifolia* L.

Stwierdzono, że zdolność krzyżowania się *C. rotundifolia* i *C. cochleariifolia* jest silnie ograniczona. Mieszańce F_1 otrzymano tylko w wypadku krzyżówek typu $4x \text{♀} \times 2x \text{♂}$. Otrzymane mieszańce są bądź triploidalne, bądź tetraploidalne. Mieszańce triploidalne wykazują duże zaburzenia w mejozie i są w wysokim

stopniu sterylne. Nieliczne pokolenie F_2 , pochodzące od jednego triploidalnego F_1 , było aneuploidalne, o liczbach chromosomów zbliżonych do $4x$ i o wyraźnie podwyższonej płodności. Mieszańce tetraploidalne są morfologicznie bardziej zbliżone do *C. cochleariifolia* niż mieszańce triploidalne, wykazują prawie normalną płodność i zaburzenia w mejozie prawie na poziomie *C. rotundifolia*. Otrzymane F_2 jest również płodne. Mieszańce tetraploidalne powstają prawdopodobnie w wyniku funkcjonowania nie zredukowanych gamet *C. cochleariifolia*. Ilość mieszańców tetraploidalnych jest stosunkowo wyższa niż należałoby się spodziewać na podstawie częstości występowania nie zredukowanego pyłku. Występowanie mieszańców tetraploidalnych zwiększa w naturze możliwość ewentualnej introgresji pomiędzy *C. rotundifolia* i *C. cochleariifolia*. Introgresja zachodziłaby głównie w kierunku od *C. cochleariifolia* do *C. rotundifolia*.