CYTOTAXONOMIC STUDIES IN THE GENUS CAMPANULA

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ABSTRACT

DE CANDOLLE (1830) divided the genus *Campanula* into two large sections on basis of the presence or absence of calyx-appendages between the calyx-lobes. BOISSIER (1875) attached great value to the mode of dehiscence of the capsule, and divided the genus into two sections. None of the existing classifications seems to be a natural one. As cytological investigations and crossing experiments might give valuable information for a natural classification, it was decided to investigate:

a. The classification of the species within the genus *Campanula* based on morphological, cytological, and genetic data.
b. The variability of a number of species, based on cytological investigations and growing experiments carried out under uniform conditions.

In Chapter I a survey is given of the most important literature on the classification of the genus *Campanula*.

The cytological data, hitherto published, are listed in Chapter II. 77 species were studied cytologically, the chromosome numbers of plants of 729 different localities were counted. At the end of Chapter II some drawings of the somatic chromosomes of a number of species are given.

The integration of cytological and morphological data is given in Chapter III. It appeared that, beside some rare chromosome numbers ($2n = 24, 26, 28, 36, 56, 58$), also some cytological series exist, each of which has its own basic number: $x = 8, 10, 15, 17$. Within each series the species usually show a great morphological resemblance. Also species studied by other authors show a combination of morphological and cytological characters corresponding with the correlations in the species which were studied by the present author. There are many reasons justifying the supposition that Sugiura, who reported many chromosome numbers, did not correctly identify the plants on which the chromosome count was based.

In Chapter IV a survey of the results of the crossing experiments is given. The features pointing to relationship (dealt with in Chapter III) were tested by the crossing experiments. Some species with basal and apical dehiscence of the fruit are crossable. Hybrids were obtained from crosses between some species with and without calyx-appendages. Species belonging to different subsections of Fedorov's system turned out to be crossable. In view of these facts the classifications given by de Candolle, Boissier and Fedorov cannot be regarded as natural. With the exception of species belonging to the $x = 15$– and the $x = 17$–series it was impossible to cross species belonging to different cytological series. From the self-pollination experiments the conclusion may be drawn that self-fertilization is a rarely occurring phenomenon in the genus *Campanula*. Most species investigated turned out to be self-sterile. Insect pollination is the rule, self-pollination the exception.

As only 40–50 % of the total number of species of the genus *Campanula* have been investigated cytologically as well as morphologically, only a provisional division of the genus *Campanula* into a number of groups was given (Chapter V).

These 7 groups are regarded as natural, but neither their interrelationship nor the relation of some of these groups to other genera of the family *Campanulaceae* is clear yet. At the end of Chapter V theories on the evolution of the chromosome numbers are discussed. The author gives an opinion differing from the one given by Böcher on the origin of some chromosome numbers.

In Chapter VI a survey is given of the results of experimental cultivations of a great number of plants of 9 polymorphic species.

INTRODUCTION

The genus *Campanula* includes approximately 300 species. Often great differences are observed among these species in vegetative respect, but the flower morphology is fairly uniform. The botanists, who studied this genus, met with considerable difficulties in making a natural subdivision into subgenera, sections and subsections.

In fact, after the excellent monograph by A. DE CANDOLLE (1830) no work has been done on the taxonomy of the genus as a whole. A. FEDOROV (1957), in his introduction to the study of the genus in the Flora U.S.S.R. XXIV, states rightly that this monograph still has not lost its great value. de Candolle attached great value to the presence of calyx appendages between the calyx lobes. On account of these characters he divided the genus into two large sections: *Medium* (calyx appendages present) and *Eucodon* (calyx appendages absent). It is possible that this character was useful in the classification of the species distinguished by de Candolle, but in several species described later this character was found to fluctuate. It is true that this character is still of importance, but in some groups of the genus it is not correlated with a number of other major characters. As, after 1830, no revision or monograph on this subject has appeared in print, the only new classifications existing are those published in local floras and in review articles.

The Flora Orientalis III gives a classification of the species in the genus *Campanula* according to BOISSIER (1875). Boissier considered the way in which the dehiscence of the capsule is carried out of fundamental importance. On account of this character he divided the genus into two sections, viz. *Rapunculus* (dehiscence: lateral-apical) and *Medium* (dehiscence: lateral-basal). Most local floras follow Boissier's system.

Like Boissier, Fedorov (l.c.) distinguishes two sections. Within these sections the latter author distinguishes a great number of subsections.

None of the existing classifications appears to be a natural one. Cytological investigations may give valuable indications for a natural classification as in the case of the genera *Nicotiana* (GOODSPEED, 1954), *Cornus* (DERMEN, 1932), *Calochortus* (BEAL, 1939), *Crepis* (BABCOCK, 1947), *Juncus* (SNOGERUP, 1963) and many other genera. The cytological data known up to the present (cf. MARCHAL, 1920; SUGIURA, 1942) are partly contradictory and partly showing the inadequacy of classifications on morphological basis only.

The possibility of the occurrence of intraspecific cytological variation in a number of species should not be excluded. This, namely, is the case in many species belonging to different systematic groups: *Cardamine pratensis* L. (LÖVKVIST, 1956; BERG, unpubl.); *Caltha palustris* L. (REESE, 1954); *Claytonia virginica* L. (ROTHWELL, 1954, 1959; LEWIS, 1959), and in other species. It is also possible, however, that cytological differences are due to an erroneous identification of the voucher material. Be this as it may, further cytological as well as morphological investigations in the genus seem necessary.

If intraspecific cytological variation occurs, it is of importance to know whether this phenomenon is correlated with the geographic distribution of the cytotypes considered. Therefore, it is also necessary to study living material collected in many different localities. These combined cytological and geographic studies, supplemented by growing-experiments carried out under uniform conditions, possibly give a much better insight in the variability of the species than mere herbarium studies can be expected to give us.

On account of the reasons stated above it was decided to investigate:

1. The classification of the species within the genus *Campanula*, based on morphological, cytological and genetic data.
2. The variability of a number of species, based on cytological investigations and growing-experiments carried out under uniform conditions.

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CHAPTER I

THE CLASSIFICATION OF THE GENUS CAMPANULA

In this chapter a brief survey will be given of the most important literature on the classification of the genus *Campanula*.

A. THE PLACE OF THE GENUS CAMPANULA IN THE FAMILY CAMPANULACEAE

A subdivision into tribes and genera of the family *Campanulaceae* has been given by BENTHAM in BENTHAM and HOOKER (1876) and by SCHÖNLAND (in ENGLER and PRANTL, 1894). The former author divided the family into 3 tribes: I. *Lobelieae*; II. *Cyphieae*; III. *Campanuleae*. Schönland distinguished 3 subfamilies: I. *Lobelioideae*; II. *Cyphioideae*; III. *Campanuloideae*. As the delimitation of these three groups is identical, there is no essential difference in both systems. Schönland, however, gives a more detailed subdivision of the 3 groups than Bentham. He divided the subfamily *Campanuloideae* into 3 tribes: 1. *Campanuleae*; 2. *Pentaphragmeae*; 3. *Sphenocleae*. The tribe *Campanuleae* is divided into 3 subtribes: a. *Campanulinae*; b. *Wahlenberginae* and c. *Platycodinae*. The subtribe *Campanulinae* is characterized by laterally dehiscent fruits and inferior ovaries built up of carpels which, in the case of isomery, are situated opposite the sepals and stamens. According to Schönland the following genera belong to this subtribe: 1. *Adenophora*, 2. *Canarina*, 3. *Michauxia*, 4. *Ostrowskia*, 5. *Symphyandra*, 6. *Phyteuma*, 7. *Trachelium*, 8. *Legousia* (= *Specularia*), 9. *Campanula*, 10. *Heterocodon*, and 11. *Peracarpa*. Some authors consider one of the sections of the genus *Phyteuma* as a separate genus, namely *Asyneuma*.

Bentham divided the tribe *Campanuleae* (i.e. Schönland's subfamily *Campanuloideae*) into 5 groups, based on the mode of dehiscence of the capsule. The fifth group distinguished by Bentham corresponds more or less with the subtribe *Campanulinae* sensu Schönland. The genera *Canarina* and *Peracarpa*, however, are placed in another group on account of the characters of their fruits, whereas the genus *Heterocodon* is included in the genus *Campanula*.

Many species, at present included in the genera *Specularia*, *Symphyandra*, *Adenophora*, and *Asyneuma* and in some genera of the subtribes *Wahlenberginae* and *Platycodinae*, were formerly often regarded as belonging to the genus *Campanula*. On the other hand, new species are still being added to the genus *Campanula*. The genus still includes approximately 300 species. The genus *Campanula* appears to be heterogeneous to a certain extent in the author's opinion. On the other hand, it is not always clear why certain species were excluded from the genus. When for instance the species *Campanula raddeana* Trautv. and *Symphyandra armena* (Stev.) DC. are closely compared it is not clear why they are classified in different genera, whereas the species *Campanula raddeana* Trautv. and *Campanula erinus* L. are included in the same genus.

In vegetative respect species belonging to different genera often show a great resemblance. Consequently, the differential characters must often be looked for in the flower. Table 1 shows the way in which some genera within the subtribe *Campanulinae* are delimited.

SUGIURA (1942) published several observations on the basic chromosome numbers. Many of his cytological observations are incorrect (Chapter III). Therefore, some doubt seems to be justified. From Table 1 it is clear that the section *Rapunculus* of the genus *Campanula* and the genus *Specularia* are closely related. In many respects the genera *Adenophora* and *Symphyandra* are related to *Campanula* section *Medium*. The differences between the genera *Asyneuma* and *Campanula* are restricted mainly to the shape of the corolla. The present author follows in the main de Candolle's delimitation. It may be said, however, that the genus has not yet been satisfactorily delimited.

TABLE 1

A comparison of some characters of 7 genera of the subtribe *Campanulinae*.

Genus	Basal number of chromosomes (x)	Shape of the corolla	Anthers free/connate	Disc enlarged, cylindrical (+); not enlarged (—)	Number of locules/ovary	Capsule: elongate (+); not elongate (—)	Mode of dehiscence of the capsule: apical; medial; basal
Legousia (= *Specularia*)	8 (?); 10	rotate	free	—	3	+	apical
Campanula Section I **Rapunculus**	8; 10; 17	campanulate, infundibular	free	—	3	— (sometimes ±)	apical
Campanula Section II **Medium**	12; 14; 17	campanulate, infundibular, tubular	free	—	3(5)	—	basal (medial)
Adenophora	17	campanulate	free	+	3	—	basal
Symphyandra	17	campanulate	connate	—	3	—	basal
Phyteuma	6; 7; 9	5-partite, petals apically connivent	free	—	2–3	—	medial
Asyneuma (= *Podanthum*)	12; 17(?)	5-partite, petals apically not connivent	free	—	3	—	apical medial basal
Trachelium	17	hypocrateriform	free	—	2–3	—	basal

Beside morphological investigations also cytological investigations and crossing-experiments will give valuable information on the delimitation of the genera in the subtribe *Campanulinae*.

B. THE SYSTEM OF A. DE CANDOLLE (1830)

The only monograph on the genus as a whole was published by A. de Candolle. He considered the presence of calyx appendages between the calyx lobes of primary importance:

section I *Medium*: calyx appendages present
section II *Eucodon*: calyx appendages absent

Table 2 gives the classification of the species according to the system of de Candolle.

Column 5 shows the species investigated cytologically by the present author, column 6 shows the species investigated by other authors only.

75 out of 137 species recognized by de Candolle are investigated cytologically, these being species from all groups of the genus.

TABLE 2

The classification of the species of the genus *Campanula*, according to the system of A. de Candolle (1830).

Section	Characters			Number of species	Species investigated cytologically by the present author	Species investigated only by other authors
MEDIUM 1) calyx appendages present 2) capsule 3-5-locular 3) capsule dehiscent with basal valves	§1. capsule 5-locular; stigmata 5; many-flowered; basal leaves with long petioles	basal leaves irregularly lyrate or laciniate; petioles marginate and lobate		9	C. celsii; C. rupestris	C. anchusiflora; C. andrewsii; C. laciniata; C. lyrata; C. rupestris; C. tomentosa; C. tubulosa
		basal leaves ovate or lanceolate; petioles not marginate		4	C. medium	C. betonicifolia; C. pelviformis
	§2. capsule 3-locular; stigmata 3; one- many-flowered	one-flowered; basal leaves rosulate		9		C. allionii; C. dasyantha; C. pallasiana; C. pilosa
		many- or few-flowered; flowers pedicellate, not capitate		22	C. alliariaefolia; C. alpina; C. barbata; C. dichotoma; C. punctata; C. sarmatica; C. sibirica; C. speciosa	C. calamenthifolia; C. caucasica; C. saxatilis
EUCODON 1) calyx appendages absent 2) capsule 3-locular 3) capsule dehiscent with basal or apical valves	§1. capsule dehiscent with basal valves, erect, sessile; flowers capitate or spicate; biennial or perennial	flowers capitate		2		C. lingulata
		style exserted; flowers glomerate, subpedicellate; stem ascendent, simple; lower leaves petiolate		2	C. petraea	
		style included; flowers glomerate; stem erect, simple; lower leaves petiolate		3	C. cervicaria; C. glomerata	
		style often included; flowers spicate; stem erect, simple; leaves sessile		3	C. multiflora; C. spicata; C. thyrsoidea	
	§2. capsule dehiscent with basal valves, nutant; calyx lobes entire; flowers sometimes sessile	flowers ± long, pedicellate basal leaves often cordate and petiolate mostly perennial	few- one-flowered; corolla mostly glabrous; capsule ovoid or spherical	22	C. caespitosa; C. carnica; C. collina; C. divaricata; C. excisa; C. pulla; C. rotundifolia; C. waldsteiniana	C. hostii; C. linifolia; C. rhomboidalis
			many-flowered; corolla glabrous; capsule ovoid	4	C. bononiensis; C. latifolia; C. rapunculoides; C. trachelium	
			few-flowered; corolla puberulous; capsule turbinate	6	C. colorata	
		flowers opposite the leaves, pedicellate; capsule turbinate; branches ± dichotomous; leaves small, sessile, oblong; annual		3	C. erinus	C. drabaefolia
	§3. capsule dehiscent with basal valves, erect; flowers pedicellate; basal leaves petiolate, always cordate; leaf base often persistent	corolla tubular, 5-lobed, pubescent or velutinous; basal leaves rosulate; few-flowered		3		
		corolla rotate, deeply 5-cleft, often pubescent outside; style exserted		3	C. garganica	C. elatinioides; C. elatines
		corolla infundibular, campanulate or tubular, 5-lobed, glabrous; roots thick		5	C. macrorhiza; C. portenschlagiana	C. morettiana; C. raineri
		corolla broadly campanulate-rotate, ± 5-cleft, glabrous; roots often thick		6	C. fragilis; C. isophylla; C. lactiflora; C. pyramidalis	
	§4. capsule dehiscent with apical valves, erect; calyx lobes often denticulate; basal leaves often obovate, short-petiolate, sometimes cordate; flowers pedicellate	valves of the capsule between the middle and the apex; not dichotomously branched		1		
		valves of the capsule near the apex; flowers often long-petioled; not dichotomously branched		30	C. americana; C. carpatica; C. loeflingii; C. patula; C. peregrina; C. persicifolia; C. primulaefolia; C. rapunculus; C. spathulata; C. steveni	C. cenisia; C. ramosissima C. uniflora
		valves of the capsule near the apex; flowers shortly pedicellate, opposite the leaves; branches ± dichotomous		1		

C. The system of Boissier (1875)

In part III of the Flora Orientalis Boissier gives a different classification, based on the mode of dehiscence of the capsule, namely lateral-apically (section *Rapunculus*) or lateral-basally (section *Medium*). (From now on the terms apical and basal dehiscence will be used for the sake of convenience.)

The section *Medium* sensu Boissier has considerable more species than the section *Medium* sensu de Candolle, as the species belonging to the first three groups (marked with §) of the section *Eucodon* de Candolle have been added. The section *Rapunculus* Boissier corresponds with group 4 (= § 4) of the section *Eucodon* de Candolle.

Although at first sight there is a great difference between the two systems, yet the resemblance is very great, only the order of magnitude of importance of the characters has been inverted. Table 3 gives the classification according to Boissier. One should, however, take into account the fact that only species from a limited part of the distribution area of the genus, namely Greece, Egypt and the Near East (West of the Indus) are treated here.

Out of the 125 species Boissier studied, 46 were cytologically investigated. These 46 species represented all groups.

In 1894 Boissier's classification is used by Schönland in vol. IV.5 of "Die natürlichen Pflanzenfamilien". He included a number of species occurring outside the distribution area mentioned above in Boissier's system.

In fact, Nymann's classification in his Conspectus Florae Europeae (1878–1882) also corresponds with Boissier's classification. He divided the genus into 3 groups, without mentioning whether these groups are sections or subgenera: I. *Media*; II. *Campanulastra*; III. *Rapunculi*. The group *Media* is the same as the subsection *Quinqueloculares* of Boissier's system, the group *Campanulastra* is the same as the *Triloculares* of Boissier's system and the group *Rapunculi* is the same as the section *Rapunculus*. An advantage of Nymann's classification is the fact that now most European species have been included in Boissier's system.

Most floras of later date like Parsa's (1948), Hayek's (1931), and Fedorov's (1957) refer back to Boissier to a certain extent. Fedorov (1957), however, occupies a special position among Boissier's followers. His system will be discussed separately.

D. The system of Fedorov (1957)

Fedorov accepts Boissier's two sections *Medium* and *Rapunculus*. His classification, however, differs in that the sections are subdivided into a great number of subsections and series. About this he remarks: "In the subsections and series some groups of species are united, which in a number of essential characters show a great resemblance and seem to be related phylogenetically. Therefore, in our system of subsections there is no rigid hierarchy of characters". In Table 4 a survey is given of the cytologically investigated species, arranged according to the system of Fedorov.

TABLE 3

The classification of the species of the genus *Campanula* according to the system of BOISSIER (1875).

Section						Number of species	Species investigated cytologically by the present author	Species investigated cytologically only by other authors
Medium capsule with basal dehiscence	Capsule 5-locular (Subsection QUINQUELOCULARES)					14	*C. incurva; C. lanata*	*C. anchusiflora; C. tubulosa;* *C. betonicifolia; C. lyrata;* *C. saxatilis; C. laciniata;* *C. tomentosa; C. pelviformis*
	capsule 3-locular (Subsection TRILOCULARES)	perennial or monocarpic	flowers ± long pedicellate; corymbose, paniculate, racemose or single	appendiculate	ELATAE: plants ± tall; inflorescence paniculate or racemose; capsule nutant	6	*C. sibirica; C. sclerotricha; C. alliariaefolia; C. sarmatica; C. collina*	—
					SCAPIFLORAE: stems erect, low, uniflorous; capsule nutant	8	*C. tridentata; C. aucheri*	—
					RUPESTRES: stems few-flowered; very often fragile, low or decumbent	21	*C. raddeana*	*C. caucasica; C. imeritina;* *C. calamenthifolia*
				exappendiculate	SAXICOLAE: stems few-flowered; low, often decumbent	18	*C. garganica; C. rotundifolia; C. sartorii*	—
					TRACHELIOIDEAE: stems tall; flowers racemose; capsule nutant	5	*C. latifolia; C. trachelium; C. rapunculoides; C. bononiensis*	—
			flowers sessile, spicate	appendiculate		1	—	—
				exappendiculate		5	*C. multiflora*	—
			flowers sessile, capitate	appendiculate		3	—	*C. lingulata*
				exappendiculate		1	*C. glomerata*	—
		annual	appendiculate			11	*C. dichotoma*	*C. propinqua; C. macrostyla*
			exappendiculate			9	*C. erinus*	*C. drabaefolia*
Rapunculus capsule with apical dehiscence	perennial					8	*C. lactiflora; C. persicifolia;* *C. latiloba; C. steveni;* *C. spruneriana;* *C. phyctidocalyx*	—
	biennial					6	*C. michauxioides; C. peregrina; C. rapunculus*	—
	annual					9	—	*C. ramosissima*

TABLE 4

A survey of the species examined cytologically, arranged according to the system of FEDOROV (1957).

Section	Subsection	Number of species	Species investigated cytologically by the present author	Species investigated cytologically only by other authors
Medium	QUINQUELOCULARES Boiss.	2	—	*C. lyrata*
	SPINULOSAE (Fom.) Fed.	1	—	*C. mirabilis*
	TRILOCULARES Boiss.	16	*C. hohenackeri; C. sibirica; C. longistyla*	*C. caucasica*
	PHASIDIANTHE Fed.	1	—	*C. imeritina*
	TULIPELLA Fed.	1	*C. punctata*	—
	DASYSTIGMA Fed.	1	*C. alpina*	—
	ANNUAE (Boiss.) Fed.	2	*C. erinus*	*C. propinqua*
	EUCODON (DC.) Fed.	8	*C. latifolia; C. rapunculoides; C. trachelium; C. bononiensis*	—
	INVOLUCRATAE (Fom.) Fed.	12	*C. glomerata; C. farinosa; C. oblongifolia; C. trautvetteri; C. multiflora; C. cervicaria*	—
	DICTYOCALYX Fed.	1	—	—
	CORDIFOLIAE (Fom.) Fed.	9	*C. sclerotricha; C. alliariaefolia; C. ochroleuca*	—
	LATILIMBUS Fed.	14	*C. collina; C. sarmatica*	—
	TRIGONOPHYLLUM Fed.	6	—	—
	SYMPHYANDRIFORMES (Fom.) Fed.	11	*C. raddeana; C. kemulariae*	—
	OREOCODON Fed.	7	—	—
	SCAPIFLORAE (Boiss.) Fed.	26	*C. tridentata; C. aucheri*	—
	RUPESTRIS (Boiss.) Fed.	6	—	—
	HYPOPOLION Fed.	1	—	*C. hypopolia*
	HETEROPHYLLA (Nym.) Fed.	6	*C. rotundifolia; C. kladniana; C. napuligera*	*C. gieseckiana*
Rapunculus	CAMPANULASTRUM (Small) Fed.	16	*C. lactiflora; C. rapunculus; C. persicifolia; C. patula; C. abietina; C. steveni*	—
	ROTULA Fed.	1	*C. carpatica*	—
	MELANOCALYX Fed.	1	—	*C. uniflora*
	ODONTOCALYX Fed.	1	*C. lasiocarpa*	—

Out of 150 species, 44 species representing the majority of the subsections, were investigated cytologically, thus showing a great deal of the total variability of the genus.

E. OTHER TAXONOMICAL WORK ON THE GENUS CAMPANULA

Several authors have tried to split off a number of "borderline" species from the genus and to transfer them to other, mostly monotypical, genera. FEER (1890, b) transferred the species *C. zoysii* Wulf. to the genus *Favratia*, *C. vidalii* Wats. to the genus *Azorina* and *C. macrostyla* Boiss. et Heldr. to the genus *Sicyocodon*. Although in the present author's opinion his arguments are well-founded, in most floras Feer's views are not accepted. SMALL (1903) transferred the species *Campanula americana* L. to the genus *Campanulastrum*. DUMORTIER (1822) transferred the species *C. erinus* L. and *C. drabaefolia* Sibth. et Sm. to the genus *Roucela*.

WITASEK (1901) and HRUBY (1930, 1950) made an elaborate study of the subsection *Heterophylla.* This is a very intricate complex of species, all of which have in common that the basal leaves differ in shape from the stem leaves.

QUÉZEL (1954) studied the North African species, FOMIN (1903–1907) the species of the Caucasus, HAYEK (1931) the species of the Balkan Peninsula, HAYEK (in HEGI, 1925) those of Central-Europe, and SHETLER (1963) the North American species.

H. CL. CROOK (1951) published a book for gardeners in which a great number of species is briefly described. This book has supplied the present author with some valuable information on the way in which a number of species should be grown.

What has been said in this chapter is not intended to give a complete survey of the taxonomic literature on the genus *Campanula,* but only a summary of the most prominent literature on the taxonomy of the genus.

The cytotaxonomic studies will be discussed in the following chapters.

CHAPTER II

THE CHROMOSOME NUMBERS OF THE INVESTIGATED SPECIES

A. INTRODUCTION

In this chapter a survey will be given of the cytological data of the genus *Campanula,* hitherto published. Table 5 gives a survey of the chromosome counts of the present author, in Table 6 a comparison between the data of Table 5 and those of other authors is given. The species not investigated before, or counted by other authors only, are also included in Table 6. At the end of this chapter some drawings of the somatic chromosomes of some species will be given.

B. MATERIAL AND METHODS

The plants investigated were partly transferred from their natural habitat to the experimental plot, partly grown from seeds. The seeds were obtained from wild (i.e., not cultivated) plants or from plants cultivated in botanical gardens. The plants were raised from seeds in the greenhouse, and 3 or 5 plants from each lot were established; (cultivated material: 3 plants; wild material: 5 plants). After having been grown in pots for some months, the plants, with the exception of the annual and biennial species, were transferred to the experimental plot, where they were grown under uniform conditions. It appeared that in this country some species are not hardy, viz.: *C. incurva, C. patula* ($2n = 40$), *C. peregrina, C. primulaefolia, C. thyrsoidea* and *C. vidalii.* Therefore, during the winter specimens of these species were grown in pots under glass.

The determination of the chromosome numbers was based on the study of roottip mitoses. The fixative Karpechenko gave better results than Carnoy in the squashing technique as well as in the section technique. The roottips, which were fixed without pre-treatment, were embedded in paraffin and sectioned in the usual way. Microtome sections of 15 μ were stained according to Heidenhain's haematoxylin method. Unlike the method of staining with orcein or carmine after squashing, good results were obtained with the method mentioned above, the contrast between the cytoplasm and the chromosomes being sharp. Also, the chromosomes turned out to be sufficiently spread in the metaphase-plates in the microtome sections. Mainly for this reason the squashing method was abandoned in an early stage.

In order to make a comparison of the lengths of the chromosomes possible, roottips of nearly all species were fixed in a fixative of the same concentration. This was done on the same day under weather conditions that did not vary perceptibly.

Voucher specimens have been deposited in the herbarium of the State University of Utrecht (U).

C. Results

A complete list of the species studied is given in Table 5, together with the collection number and the place of origin of the material. The plants, the origin of which is not known exactly, are regarded as cultivated and marked by an asterisk (*). The botanical gardens, from which the seeds of cultivated plants were obtained, are listed in column 4.

Table 5

The number of chromosomes of the species examined cytologically, with reference to the collection numbers and the origin of the material.

Species	Coll. no.	2n	Origin of the material
C. abietina Griseb. et Schenk	C 613	80	Poland: E. Carpathian Mts.
C. alliariaefolia Willd.	C 241	34	U.S.S.R. (Armenia): collected in nature
	C 752*	34	England: Alp. Gard. Soc., Ascot
	C 240*	34	E. Germany: Greifswald
	C 272*	34	Italy: Pallanza
	C 36*	34	Italy: Siena
	C 848*	34	Poland: Bydgoszcz
	C 359*	34	Scotland: St. Andrews
C. alpina Jacq.	C 328	34	Czecho-Slovakia: Vysoké-Tatry
	C 615	34	Poland: E. Carpathian Mts.
C. americana L.	C 408	58	U.S.A.: Michigan, collected in nature
	C 409	58	U.S.A.: idem
	C 636	58	U.S.A.: idem
	C 558*	58	U.S.A.: Lisle (Illinois)
	C 410*	58	U.S.A.: Minneapolis (Minnesota)

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. aucheri DC.	C 231*	34	Austria: Vienna
	C 134*	34	W. Germany: Frankfurt a. Main
	C 169*	34	W. Germany: Bonn
	C 311*	34	W. Germany: München
	C 344*	34	Sweden: Göteborg
	C 223*	34	Switzerland: Champex
	C 304*	34	Switzerland: Lausanne
C. barbata L.	C 544	34	Austria: Carnic Alps
	C 738	34	Austria: idem
	C 733	34	Austria: Cetic Alps
	C 236	34	Austria: Schneeberg, 2070 m (S. of Vienna)
	C 548	34	Austria: Strechau Oppenberg (Steiermark)
	C 284	34	Austria: Hohe Tauern
	C 482	34	Austria: N. Tirol
	C 657	34	Czecho-Slovakia: N. Moravia
	C 12	34	France: Col de Lautaret, 2000 m (Htes Alpes)
	C 95	34	France: idem
	C 522	34	France: Mont Cenis (Savoie)
	C 579	34	France: Col de Saisies, 1900 m (Savoie)
	C 832	34	France: idem
	C 816	34	France: Les Saix (Hte Savoie)
	C 591	34	Italy: Valtellina
	C 853	34	Italy: idem
	C 575	34	Switzerland: Val d'Arpette, 1700 m (Wallis)
	C 789	34	Switzerland: Gletsch, 1940 m (Wallis)
	C 561	34	Switzerland: Gabris (St. Gallen)
	C 584	34	Switzerland: Mont Noble (Wallis)
	C 865	34	Switzerland: collected in nature, precise locality unknown
	C 509*	34	England: Kew Bot. Gard.
	C 510*	34	England: idem
	C 870*	34	Hungary: Vácrátót
C. bononiensis L.	C 397	34	Bulgaria: seeds collected in nature, precise locality unknown
	C 649	34	Czecho-Slovakia: Cesky Kras (W. of Praha)
	C 609	34	Czecho-Slovakia: Tarbucka (E. Slovakia)
	C 822	34	Czecho-Slovakia: idem
	C 900	34	E. Germany: Ketzerbachtal b. Wahnitz (Saksen Anhalt)
	C 902	34	E. Germany: Wallhausen (Saksen Anhalt)
	C 403	34	Hungary: collected in nature
	C 499	34	Hungary: idem
	C 500	34	Hungary: idem
	C 889	34	Hungary: idem
	C 276	34	Romania: near Suatu (Raional Cluj.)
	C 670	34	U.S.S.R.: Carpathian Mts.
	C 625	34	U.S.S.R.: S. Crimea
	C 49	34	U.S.S.R.: Serpukhovskii (distr. Moskva)
	C 45*	34	U.S.S.R.: Moskva
	C 637*	34	U.S.S.R.: Rostov
C. caespitosa Scop.	C 798	34	Austria: collected in nature
C. carnica Schied.	C 858	34	Italy: Friuli

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. carpatica Jacq.	C 96	34	Czecho-Slovakia: seeds collected in nature, precise locality unknown
	C 254	34	Czecho-Slovakia: Dobinska (N. Slovakia)
	C 261	34	Czecho-Slovakia: Drevenik (N. Slovakia)
	C 603	34	Czecho-Slovakia: Lipovce (E. Slovakia)
	C 818	34	Czecho-Slovakia: Slovansky Kras-Zadiel
	C 668	34	Czecho-Slovakia: Tatry Mts.
	C 892	34	Czecho-Slovakia: idem
	C 841	34	Poland: collected in nature, precise locality unknown
	C 846	34	Poland: idem
	C 559	34	Poland: near Zakopane
	C 217*	34	Austria: Frohnleiten
	C 463*	34	Austria: Graz
	C 461*	34	Austria: idem
	C 225*	34	Austria: Vienna
	C 190*	34	Belgium: Antwerp
	C 230*	34	England: London
	C 232*	34	England: idem
	C 552*	34	England: Liverpool
	C 826*	34	Finland: Helsinki
	C 827*	34	Finland: idem
	C 191*	34	W. Germany: Essen
	C 205*	34	W. Germany: Göttingen
	C 150*	34	the Netherlands: Amsterdam
	C 151*	34	the Netherlands: idem
	C 75*	34	the Netherlands: Rotterdam
	C 262*	34	the Netherlands: coll. de Graaff
	C 277*	34	Romania: Cluj
	C 346*	34	Sweden: Göteborg
	C 300*	34	Switzerland: Lausanne
C. cashmiriana Royle	C 761*	28	England: Alp. Gard. Soc., Ascot
C. celsii DC.	C 711	34	Greece: Mt. Lycabettus
C. cervicaria L.	C 400	34	Bulgaria: collected in nature, precise locality unknown
	C 582	34	Romania: Cazanele Dunarii (raion Orsova)
	C 730*	34	Sweden: Uppsala
C. cochleariifolia Lam.	C 282	34	Austria: Carinthia
	C 663	34	Czecho-Slovakia: Belanské Tatry
	C 607	34	Czecho-Slovakia: Liptovske Tatry (N. Slovakia)
	C 800	34	France: Bramans, 1250 m (Savoie)
	C 23	34	France: Mont Cenis, 1900 m (Savoie)
	C 503A	37	France: idem
	C 503B	37	France: idem
	C 503C	34	France: idem
	C 503D	34	France: idem
	C 503E	37	France: idem
	C 503F	35	France: idem
	C 180	34	Switzerland: collected in nature, precise locality unknown
	C 10	34	Switzerland: Mt. Säntis (St. Gallen)

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. cochleariifolia Lam. (cont.)	C 526*	34	Austria: Frohnleiten
	C 464*	34	Austria: Graz
	C 505*	34	Canada: Vancouver
	C 871*	68	England: Alp. Gard. Soc., Ascot
	C 355*	34	W. Germany: Oldenburg
	C 220*	34	Switzerland: Champex
	C 569*	34	Switzerland: Geneva
	C 570*	34	Switzerland: idem
	C 868*	34	Switzerland: Neuchâtel
C. collina Bieb.	C 453	68	U.S.S.R.: Armenia, collected in nature
	C 919	68	U.S.S.R.: idem
	C 167*	68	W. Germany: Bonn
	C 369*	68	Sweden: Uppsala
	C 383*	68	U.S.S.R.: Moskva
C. colorata Wall. in Roxb.	C 368*	28	Denmark: Copenhagen
C. dichotoma L.	C 219*	24	Italy: Palermo
C. divaricata Michx.	C 310	34	U.S.A.: W. Virginia
C. erinus L.	C 306	28	Portugal: environment of Coimbra
	C 101	28	Portugal: prov. Estremadura
	C 119	28	Portugal: collected in nature, precise locality unknown
	C 57	28	Portugal: idem
	C 494	28	Portugal: idem
	C 554	28	Portugal: idem
	C 599	28	Portugal: idem
	C 725	28	Portugal: idem
	C 910	28	Portugal: idem
	C 211*	28	Portugal: Lisboa
C. excisa Schleich. ex Mur.	C 792	34	Switzerland: Col du Simplon, 2050 m (Wallis)
C. farinosa (Roch.) Andrz. ex Bess.	C 530	30	Hungary: collected in nature
	C 661*	30	U.S.S.R.: Moskva
C. fragilis Cyr.	C 764*	32	England: Alp. Gard. Soc., Ascot
	C 904*	32	U.S.A.: Moorestown N.J.
C. garganica Ten.	C 173*	34	Austria: Graz
	C 504*	34	Canada: Vancouver
	C 360*	34	Scotland: St. Andrews
	C 483*	34	Scotland: Edinburgh
	C 763*	34	England: Alp. Gard. Soc., Ascot
	C 146*	34	England: Chelsea Phys. Gard.
	C 209*	34	W. Germany: Göttingen
	C 183*	34	W. Germany: Hamburg
	C 60*	34	the Netherlands: Baarn
	C 61*	34	the Netherlands: idem
C. glomerata L.	C 474	30	Austria: S. of Vienna, Wienerwald
	C 665	30	Czecho-Slovakia: Belanské Tatry Mts.

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
	C 589	30	Czecho-Slovakia: near Nitra (C. Slovakia)
	C 652	30	Czecho-Slovakia: near Praha
	C 604	30	Czecho-Slovakia: Lomnické (Vysoké Tatry Mts.)
	C 608	30	Czecho-Slovakia: Zdiar (Vysoké Tatry Mts.)
	C 434	30	Denmark: Agerup Roskilde (Sjaelland)
	C 447	30	Denmark: Logstor
	C 395	30	France: S. Cévennes
	C 374	30	France: near Obernai (Bas Rhin)
	C 638	30	France: idem
	C 520	30	France: Essarois (Côte d'Or)
	C 336	30	France: Fixin (Côte d'Or)
	C 828	30	Hungary: collected in nature, precise locality unknown
	C 729	30	Italy: Segusina Valley
	C 98	30	Romania: collected in nature, precise locality unknown
	C 583	30	Romania: Zau de Cimpie (raion Ludus)
	C 66	30	Scotland: St. Cyrus (Kincardine)
	C 126	30	Sweden: Skåne, Härslov
	C 457	30	U.S.S.R.: Armenia, collected in nature, precise locality unknown
	C 108	30	U.S.S.R.: Annemoïs near Tartu (Estonia)
	C 110	30	U.S.S.R.: Sörve (Estonia)
	C 614	30	U.S.S.R.: E. Carpathian Mts.
	C 903	30	U.S.S.R.: idem
	C 389	30	U.S.S.R.: near Pskov (S. of Leningrad)
	C 631	30	U.S.S.R.: idem
	C 116	30	U.S.S.R.: Pulkoro near Leningrad
	C 907	30	U.S.S.R.: environment of the river Smotricz
	C 177*	30	Austria: Graz
	C 178*	30	Austria: idem
	C 528*	30	Austria: Frohnleiten
	C 720*	30	Austria: idem
	C 398*	30	Bulgaria: Sofia
	C 402*	30	Czecho-Slovakia: Praha
	C 621*	30	Denmark: Copenhagen
	C 624*	30	Denmark: idem
	C 297*	30	England: Kew Bot. Gard.
	C 298*	30	England: idem
	C 365*	30	France: Toulouse
	C 158*	30	W. Germany: Berlin
	C 184*	30	W. Germany: Hamburg
	C 161*	30	W. Germany: Münster
	C 33*	30	Italy: Siena
	C 847*	30	Poland: Bydgoszcz
	C 222*	30	Switzerland: Champex
	C 519*	30	Switzerland: Bern
	C 612*	30	Yugoslavia: Serajewo
C. grossekii Heuff.	C 765*	34	England: Alp. Gard. Soc., Acsot
	C 248*	34	W. Germany: Marburg
	C 35*	34	Italy: Siena
	C 38*	34	Italy: idem
	C 266*	34	the Netherlands: coll. de Graaff

* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. hohenackeri Fisch. et Mey.	C 242	34	U.S.S.R.: Armenia, collected in nature, precise locality unknown
	C 455	34	U.S.S.R.: idem
	C 920	34	U.S.S.R.: idem
C. incurva Auch.	C 721*	32	Austria: Frohnleiten
	C 766*	32	England: Alp. Gard. Soc., Ascot
	C 140*	32	England: Chelsea Phys. Gard.
C. isophylla Mor.	C 767*	32	England: Alp. Gard. Soc., Ascot
	C 379*	32	the Netherlands: Baarn
	C 926*	32	the Netherlands: idem
	C 927*	32	the Netherlands: idem
	C 928*	32	the Netherlands: idem
C. kemulariae Fom.	C 324*	34	Austria: Linz
	C 228*	34	Austria: Vienna
	C 302*	34	Switzerland: Lausanne
C. kladniana (Schur) Wit.	C 782*	68	England: Alp. Gard. Soc., Ascot
C. lactiflora Bieb.	C 156*	36	Germany: Berlin
	C 170*	36	Germany: Bonn
	C 572*	36	Switzerland: Geneva
C. lanata Friv.	C 176*	34	Austria: Graz
	C 174*	34	Austria: idem
	C 770*	34	England: Alp. Gard. Soc., Ascot
	C 771*	34	England: idem
	C 728*	34	England: Chelsea Phys. Gard.
	C 843*	34	W. Germany: München
	C 149*	34	the Netherlands: Amsterdam
	C 744*	34	Scotland: Edinburgh
C. lasiocarpa Cham.	C 772*	34	England: Alp. Gard. Soc., Ascot
	C 923*	34	England: Cobham
C. latifolia L.	C 656	34	Czecho-Slovakia: Krkonose Mts. (N.E. Bohemia)
	C 317	34+5B	Sweden: collected in nature, precise locality unknown
	C 188*	34	Belgium: Antwerp
	C 577*	34	England: Alp. Gard. Soc., Ascot
	C 758*	34	England: idem
	C 781*	34	England: idem
	C 290*	34	E. Germany: Jena
	C 534*	34	E. Germany: Rostock
	C 153*	34	the Netherlands: Amsterdam
	C 745*	34	Scotland: Edinburgh
	C 740*	34+3B	Scotland: idem
	C 485*	34	Scotland: idem
	C 513*	34	Sweden: Göteborg
	C 340*	34	Switzerland: Geneva
	C 339*	34	Switzerland: idem
	C 48*	34	U.S.S.R.: Moskva
C. latiloba DC.	C 487*	16	England: Oxford

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. loeflingii Brot.	C 307	18	Portugal: environment of Coimbra
	C 556	18	Portugal: collected in nature, precise locality unknown
	C 597	18	Portugal: idem
	C 210*	18	Portugal: Lisboa
	C 296*	20	England: Kew Bot. Gard.
	C 727	20	Portugal: collected in nature, precise locality unknown
C. longistyla Fom.	C 338*	34	Switzerland: Geneva
C. macrorhiza Gay	C 683	34	France: Maritime Alps
C. medium L.	C 913	34	France: environment of Grenoble (Isère)
	C 166*	34	W. Germany: Bonn
	C 157*	34	W. Germany: Berlin
	C 56*	34	Portugal: Lisboa
	C 616*	34	Romania: Bucuresti
	C 28*	34	U.S.S.R.: Ashkabad
C. michauxioides Boiss.	C 486*	30	E. Germany: Jena
C. multiflora Waldst. & Kit.	C 168*	32	W. Germany: Bonn
C. napuligera Schur	C 512*	34	Sweden: Göteborg
C. oblongifolia (C. Koch) Char.	C 246	90	U.S.S.R.: Armenia, collected in nature
	C 918	90	U.S.S.R.: idem
C. ochroleuca Kem. Nath.	C 200*	34	E. Germany: Dresden
	C 289*	34	E. Germany: Jena
	C 385*	34	U.S.S.R.: Moskva
C. patula L.	C 541	20	Austria: near Klagenfurt
	C 421	20	Denmark: Pomlenakke (E. Falster)
	C 316	20	Sweden: collected in nature, precise locality unknown
	C 489	20	Sweden: idem
	C 805	20	Sweden: idem
	C 115	20	U.S.S.R.: Otradnoje, N. of Leningrad
	C 622*	20	Denmark: Copenhagen
	C 774*	20	England: Alp. Gard. Soc., Ascot
	C 546	40	Austria: Aigen/Ennstal, Steiermark
	C 611	40	Yugoslavia: collected in nature, precise locality unknown
	C 345*	40	Sweden: Göteborg
C. peregrina L.	C 776*	26	England: Alp. Gard. Soc., Ascot
	C 679*	26	England: Cobham
	C 165*	26	W. Germany: Bonn
C. persicifolia L.	C 281	16	Austria: near Klagenfurt
	C 542	16	Austria: idem
	C 654	16	Czecho-Slovakia: Centr. Bohemia, precise locality unknown
	C 590	16	Czecho-Slovakia: region of Ceské Stredohori (N.W. Bohemia)

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C persicifolia L. (cont.)	C 647	16	Czecho-Slovakia: W. Bohemia, precise locality unknown
	C 5	16	Czecho-Slovakia: near Bratislava
	C 606	16	Czecho-Slovakia: idem
	C 650	16	Czecho-Slovakia: near Praha
	C 669	16	Czecho-Slovakia: Tatry Mts.
	C 814	16	France: Auxey (Côte d'Or)
	C 124	16	Sweden: Ivetofta (Skåne)
	C 466	16	Sweden: Nydala, Bagghemmet (Småland)
	C 314	16	Sweden: collected in nature, precise locality unknown
	C 566	16	Sweden: idem
	C 567	16	Sweden: idem
	C 478	16	Switzerland: collected in nature, precise locality unknown
	C 585	16	Switzerland: Stravers, 1000 m (Wallis)
	C 114	16	U.S.S.R.: Otradnoje, N. of Leningrad
	C 113	16	U.S.S.R.: Isle of Saaremaa (Estonia)
	C 908	16	U.S.S.R.: near river Smotricz
	C 462*	16	Austria: Graz
	C 326*	16	Austria: Linz
	C 327*	16	Austria: idem
	C 186*	16	Belgium: Antwerp
	C 619*	16	Denmark: Copenhagen
	C 144*	16	England: Chelsea Phys. Gard.
	C 458*	16	England: idem
	C 506*	16	England: Kew Bot. Gard.
	C 507*	16	England: idem
	C 182*	16	Monaco: Bot. Gard.
	C 154*	16	the Netherlands: Amsterdam
	C 426*	16	the Netherlands: Baarn
	C 155*	16	the Netherlands: Leiden
	C 746*	16	Scotland: Edinburgh
	C 739*	16	Sweden: Göteborg
	C 313*	16	Sweden: Stockholm
	C 301*	16	Switzerland: Lausanne
	C 837*	16	U.S.S.R.: Minsk
	C 47*	16	U.S.S.R.: Moskva
C. petraea L.	C 682	34	France: Maritime Alps
	C 164*	34	Austria: Innsbruck
	C 560*	34	W. Germany: Marburg
C. portenschlagiana Roem. & Sch.	C 401	34	Italy: collected in nature, precise locality unknown
	C 295*	34	England: Kew Bot. Gard.
C. poscharskyana Degen.	C 145*	34	England: Chelsea Phys. Gard.
	C 459*	34	England: idem
	C 59*	34	the Netherlands: Baarn
	C 361*	34	Scotland: St. Andrews
	C 587*	34	Switzerland: Lausanne
	C 588*	34	Switzerland: idem
C. prenanthoides Dur.	C 106	34	U.S.A.: Redwoods, Mendouno County, S. of Richardson (California)

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. primulaefolia Brot.	C 54	36	Portugal: collected in nature, precise locality unknown
	C 911	36	Portugal: idem
	C 308*	36	Portugal: Coimbra
	C 600*	36	Portugal: idem
	C 553*	36	Portugal: Lisboa
C. pulla L.	C 14	34	Austria: Raxalpe
	C 517	34	Austria: Patscherkofel, 1900 m
	C 133*	34	W. Germany: Frankfurt a. Main
C. punctata Lam.	C 428	34	Japan: collected in nature, precise locality unknown
	C 226*	34	Austria: Vienna
	C 508*	34	England: Kew Bot. Gard.
	C 137*	34	W. Germany: Frankfurt
	C 844*	34	W. Germany: München
	C 347*	34	Sweden: Göteborg
	C 366*	34	Sweden: Uppsala
	C 514*	34	Sweden: idem
	C 387*	34	U.S.S.R.: Moskva
C. pyramidalis L.	C 76	34	Yugoslavia: Novi Vinodal
	C 215*	34	Austria: Frohnleiten
	C 899*	34	Czecho-Slovakia: Brno
	C 141*	34	England: Chelsea Phys. Gard.
	C 294*	34	England: Kew Bot. Gard.
	C 488*	34	England: Oxford
	C 249*	34	W. Germany: Freiburg
	C 118*	34	Poland: Warszawa
C. raddeana Trautv.	C 216*	34	Austria: Frohnleiten
	C 777*	34	England: Alp. Gard. Soc., Ascot
	C 877*	34	England: idem
	C 148*	34	England: Chelsea Phys. Gard.
	C 303*	34	Switzerland: Lausanne
C. rapunculoides L.	C 862	68	Romania: Muscel, reg. Ploiesti
	C 456	68	U.S.S.R.: Armenia, collected in nature, precise locality unknown
	C 547	102	Austria: Aigen Ennstal (Steiermark)
	C 732	102	Austria: Stub Alpe (Steiermark)
	C 672	102	Czecho-Slovakia: Carpathian Mts.
	C 895	102	Czecho-Slovakia: idem
	C 906	102	Czecho-Slovakia: N. Moravia
	C 433	102	Denmark: Roskilde (Sjaelland)
	C 396	102	France: S. Cévennes
	C 335	102	France: Cléry (Côte d'Or)
	C 673	102	France: Languedoc
	C 501	102	France: St. Michel de Maurienne, 900 m (Savoie)
	C 20	102	France: Termignon, 1400 m (Savoie)
	C 378	102	France: Collines de Sigolsheim (Ht. Rhin)
	C 643	102	France: Obernai (Bas Rhin)
	C 645	102	France: idem

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. rapunculoides L. (cont.)	C 87	102	W. Germany: environment of Münster, near Sihlense (Westphalia)
	C 197	102	Italy: Friuli
	C 854	102	Italy: Valtellina
	C 43	102	the Netherlands: Wrakelberg near Wylré (Limburg)
	C 404	102	the Netherlands: O. Voorne (Z. Holland)
	C 405	102	the Netherlands: idem
	C 406	102	the Netherlands: idem
	C 407	102	the Netherlands: idem
	C 674	102	the Netherlands: Schweiberger bos, near Mechelen (Limburg)
	C 675	102	the Netherlands: idem
	C 676	102	the Netherlands: idem
	C 715	102	Sweden: Andrarum Verkean Alunbruket (Skåne)
	C 468	102	Sweden: Ven Backafall (Skåne)
	C 26	102	Sweden: collected in nature, precise locality unknown
	C 318	102	Sweden: idem
	C 565	102	Sweden: idem
	C 806	102	Sweden: idem
	C 807	102	Sweden: idem
	C 107	102	U.S.S.R.: Annemoïs near Tartu (Estonia)
	C 109	102	U.S.S.R.: Tartu, Toomemägi (Estonia)
	C 243	102	U.S.S.R.: Armenia, collected in nature, precise locality unknown
	C 916	102	U.S.S.R.: idem
	C 630	102	U.S.S.R.: N. Caucasus
	C 394	102	U.S.S.R.: Latvia, collected in nature, precise locality unknown
	C 626	102	U.S.S.R.: idem
	C 325*	102	Austria: Linz
	C 233*	102	Austria: idem
	C 185*	102	Belgium: Antwerp
	C 189*	102	Belgium: idem
	C 320*	102	Belgium: Brussels
	C 321*	102	Belgium: idem
	C 399*	102	Bulgaria: Sofia
	C 915*	102	Canada: Ottawa
	C 255*	102	Czecho-Slovakia: Bratislava
	C 620*	102	Denmark: Copenhagen
	C 779*	102	England: Alp. Gard. Soc., Ascot
	C 162*	102	France: Verrieres le Buisson
	C 332*	102	Finland: Helsinki
	C 533*	102	E. Germany: Rostock
	C 251*	102	W. Germany: Freiburg
	C 869*	102	Hungary: Vácrátót
	C 632*/ C 634* C 890*/	102	Italy: Palermo
	C 891*	102	Italy: idem
	C 354*	102	Italy: Roma
	C 34*	102	Italy: Siena
	C 37*	102	Italy: idem
	C 181*	102	Italy: Torino

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
	C 63*	102	the Netherlands: Baarn
	C 267*	102	the Netherlands: coll. de Graaff
	C 849*	102	Poland: Bydgoszcz
	C 120*	102	Poland: Warszawa
	C 53*	102	Portugal: Lisboa
	C 212*	102	Portugal: idem
	C 535*/ C 537*	102	Spain: Valencia
	C 131*	102	Switzerland: Neuchâtel
	C 51*	102	U.S.S.R.: Alma Ata
	C 845*	102	U.S.S.R.: Riga
C. rapunculus L.	C 521	20	France: Cléry (Côte d'Or)
	C 829	20	France: Dennemont (S. et Oise)
	C 252	20	France: near Nantes (Loire Inf^{re})
	C 376	20	France: Obernai (B. Rhin)
	C 203	20	France: Grand Quevilly (S. Mar.)
	C 490	20	France: idem
	C 748	20	France: idem
	C 563	20	E. Germany: Rohrsen/Weser
	C 492	20	W. Germany: near Kassel
	C 598	20	Portugal: collected in nature, precise locality unknown
	C 726	20	Portugal: idem
	C 912	20	Portugal: idem
	C 618*	20	Denmark: Copenhagen
C. rotundifolia L.	C 896	34	Czecho-Slovakia: Carpathian Mts.
	C 737	34	Czecho-Slovakia: Krkonose Mts.
	C 651	34	Czecho-Slovakia: near Praha (N.E. Bohemia)
	C 77	34	W. Germany: Berlin-Tegel
	C 491	34	W. Germany: near Kassel
	C 78	34	W. Germany: Hazelbrünn, N. of Kottenstein, 450 m (Oberfranken)
	C 79	34	W. Germany: Putlarktal, E. of Kottenstein, 400 m (Oberfranken)
	C 74	34	Sweden: Herrestad Parish Granhogen
	C 271	34	Sweden: idem
	C 390	34	U.S.S.R.: near Pskov
	C 627	34	U.S.S.R.: Mt. Rais (N. Ural) 1)
	C 480	68+2B	Austria: N. Tirol
	C 7	68	Belgium: la Calamine (Neu-Moresnet)
	C 42	68	Belgium: idem
	C 414	68	Belgium: ruine Reinardstein near Robertville
	C 415	68	Belgium: idem
	C 549	68	Canada: E. Canada, precise locality unknown
	C 664	68	Czecho-Slovakia: Belanské Tatry Mts.
	C 820	68	Czecho-Slovakia: Bobrovec (N. Slovakia)
	C 671	68	Czecho-Slovakia: Carpathian Mts.
	C 260	68	Czecho-Slovakia: Drevenik (N. Slovakia)
	C 736	68	Czecho-Slovakia: Krkonose Mts. (N.E. Bohemia)
	C 201	68	Czecho-Slovakia: Simonov Cernochovom (E. Slovakia)
	C 259	68	Czecho-Slovakia: idem

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* = cult. material.

1) See Chapter VI.

Species	Coll. no.	2n	Origin of the material
C. rotundifolia L. (cont.)	C 86	68	Denmark: Egtved (W. Jutland)
	C 6	68	Denmark: Mellg (N. Sjaelland)
	C 99	68	Denmark: Milby Nordsfall
	C 84	68	Denmark: Tarm (W. Jutland)
	C 83	68	Denmark: Tømmerup (N. Fyn)
	C 85	68	Denmark: Ulfborg (N. Jutland)
	C 712	68	England: Ainsdale, N. of Liverpool (Lancashire)
	C 103	68+2B	England: near Carlisle (Cumberland)
	C 199	68+2B	England: near Hunstanton (Norfolk)
	C 836	68+3B	England: Lancashire, precise locality unknown
	C 909	68	England: Teesdale district (Durham)
	C 813	68+4B	France: la Clayette (Saone et Loire)
	C 334	68	France: Fixin (Côte d'Or)
	C 794	68	France: Region du Grenainon, 2100 m (Ht. Savoie)
	C 138	68+2B	France: Isneauville (S. Mar.)
	C 577	68	France: idem
	C 8	68	France: Col du Lautaret, 2000 m (Ht. Alpes)
	C 58	68	France: near Nancy
	C 377	68	France: between Niederbronn and Bitche, N. Vosges (Bas Rhin)
	C 640	68	France: idem
	C 639	68	France: Obernai (Bas Rhin)
	C 204	68	France: Orival (S. Mar.)
	C 24	68	France: environment of Paris
	C 749	68	France: Grand Quevilly (S. Mar.)
	C 22	68+4B	France: Termignon, 1400 m (Savoie) 1)
	C 67	68	W. Germany: near Lübeck
	C 41	68	W. Germany: between Schmidt and Heimbach (Eiffel)
	C 105	68	W. Germany: Selent, E. of Kiel (Holstein)
	C 94	68	Italy: Valtellina
	C 194	68+2B	Italy: idem
	C 852	68	Italy: idem
	C 857	68+2B	Italy: idem
	C 72	68	the Netherlands: Aldemirdum (Frielsand)
	C 73	68	the Netherlands: idem
	C 427	68	the Netherlands: near Gieten (Drenthe)
	C 71	68	the Netherlands: near Vledder (Drenthe)
	C 685	68	the Netherlands: near Emmen (Drenthe)
	C 422/ C 425	68	the Netherlands: between Almelo and Marienberg (Overijssel)
	C 380	68	the Netherlands: het Singraven near Denekamp (Overijssel)
	C 439	68	the Netherlands: near Otterlo (Gelderl.)
	C 39	68	the Netherlands: Maarn (Utrecht)
	C 40	68	the Netherlands: between Valkenswaard and Bergeyk (N. Brabant)
	C 677	68	the Netherlands: near Mook (Limburg)
	C 64	68	Poland: Puszcza Kampinoska
	C 65	68	Scotland: St. Cyrus (Kincardine)
	C 104	68	Scotland: near Edinburgh
	C 125	68	Sweden: Skåne, Maglarp Stavsten

* = cult. material.

1) See Chapter VI.

Species	Coll. no.	2n	Origin of the material
	C 717	68	Sweden: idem
	C 25	68	Sweden: Skåne, Veberöd
	C 213	68	Sweden: Anggården (Västergötland)
	C 315	68	Sweden: collected in nature, precise locality unknown
	C 568	68	Sweden: idem
	C 808	68	Sweden: idem
	C 793	68	Switzerland: Champex Lac, 1500 m (Wallis)
	C 117	68	U.S.S.R.: Pulkoro, N. of Leningrad
	C 50	68	U.S.S.R.: Serpukhovskii (distr. Moskva)
	C 111	68	U.S.S.R.: Sörve (Estonia)
	C 338	68	U.S.S.R.: near Leningrad
	C 628	68	U.S.S.R.: idem
	C 214*	68	Austria: Frohnleiten
	C 529*	68	Austria: idem
	C 286*	68	Austria: Klagenfurt
	C 17*	68+3B	Austria: Vienna
	C 229*	68	Austria: idem
	C 319*	68	Belgium: Brussels
	C 825*	68	Finland: Helsinki
	C 550*	68	France: Paris
	C 371*	68	France: Strasbourg
	C 363*	68	France: Toulouse
	C 163*	68	France: Verrieres-le-Buisson
	C 759*	68	England: Alp. Gard. Soc., Ascot
	C 769*	68+3B	England: idem
	C 787*	68	England: idem
	C 747*	68+2B	E. Germany: Rostock
	C 250*	68	W. Germany: Freiburg
	C 29*	68	Italy: Siena
	C 30*	68	Italy: idem
	C 32*	68	Italy: idem
	C 152*	68	the Netherlands: Amsterdam
	C 850*	68	Poland: Bydgoszcz
	C 119*	68	Poland: Warszawa
	C 393*	68	U.S.S.R.: Leningrad
	C 452*	68	U.S.S.R.: Low
	C 419*	68	Romania: Bucuresti
	C 420*	68	Romania: idem
	C 635*	68	Scotland: St. Andrews
	C 743*	68	Scotland: Edinburgh
	C 341*	68	Switzerland: Geneva
	C 342*	68	Switzerland: idem
	C 571*	68+2B	Switzerland: idem
	C 348*	68	Sweden: Göteborg
	C 716*	68	Sweden: Lund
	C 734*	68	Yugoslavia: Ljubljana
	C 731	102	Alaska 1)
	C 330	102	Czecho-Slovakia: near Nitra
	C 139	102	France: St. Adrien (S. Mar.)
	C 580	102	France: idem
	C 122	102	France: environment of Clermont-Ferrand (Puy de Dôme)
	C 523	102	France: St. Léger de Fourches (Côte d'Or)
	C 465*	102	England: Leeds

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* = cult. material.

1) See Chapter VI.

Species	Coll. no.	2n	Origin of the material
C. rupestris Sibth. & Sm.	C 755*	34	England: Alp. Gard. Soc., Ascot
	C 293*	34	England: Kew Bot. Gard.
	C 382*	34	U.S.S.R.: Moskva
C. sarmatica Ker-Gawl	C 722*	34	Austria: Frohnleiten
	C 545*	34	Austria: Klagenfurt
	C 783*	34	England: Alp. Gard. Soc., Ascot
	C 147*	34	England: Chelsea Phys. Gard.
	C 460*	34	England: idem
C. sartori Boiss. & Heldr.	C 760*	34	England: Alp. Gard. Soc., Ascot
	C 784*	34	England: idem
	C 312*	34	W. Germany: München
C. scheuchzeri Vill.	C 18	68	Austria: Raxalpe
	C 867	68	Switzerland: collected in nature, precise locality unknown
	C 768*	68	England: Alp. Gard. Soc., Ascot
C. sclerotricha Boiss. & Kotsch.	C 511*	34	England: Kew Bot. Gard.
C. sibirica L.	C 15	34	Austria: Hainburg
	C 235	34	Austria: idem
	C 473	34	Austria: idem
	C 601	34	Czecho-Slovakia: Slovensky Kras, Zadiel (E. Slovakia)
	C 605	34	Czecho-Slovakia: Hatfa
	C 667	34	Czecho-Slovakia: Carpathian Mts.
	C 897	34	Czecho-Slovakia: idem
	C 4	34	Czecho-Slovakia: Salka
	C 2	34	Czecho-Slovakia: Slovensky Kras (E. Slovakia)
	C 1	34	Czecho-Slovakia: Belanské Tatry Mts.
	C 160	34	Hungary: collected in nature, precise locality unknown
	C 496	34	Hungary: idem
	C 195	34	Italy: Friuli
	C 275	34	Romania: Borovici (Raion Borovici)
	C 581	34	Romania: Cazanale Dunarii (Raion Orsava)
	C 863	34	Romania: Reg. Cazane (Raion Orsova)
	C 417	34	Romania: Cheile Turzii (Reg. Cluj, Raion Turda)
	C 171*	34	Austria: Graz
	C 257*	34	Czecho-Slovakia: Bratislava
	C 136*	34	W. Germany: Frankfurt a. Main
	C 247*	34	W. Germany: Marburg
	C 221*	34	Switzerland: Champex
	C 384*	34	U.S.S.R.: Moskva
C. spathulata Sibth. & Sm.	C 337*	20	Switzerland: Geneva
C. speciosa Pourr.	C 833	34	France: St. Maurice d'Ibie (Ardèche)
	C 551*	34	France: Paris
C. spicata L.	C 285	34	Austria: near Villach (Carinthia)
	C 596	34	Italy: Valtellina
	C 11	34	France: Col du Lautaret, 1900 m (Ht. Alpes)

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
	C 21	34	France: Termignon, 1350 m (Savoie)
	C 362	34	France: idem
	C 129*	34	Switzerland: Neuchâtel
	C 479*-A	51	Switzerland: idem
	C 479*-B/F	34	Switzerland: idem
C. spruneriana Hampe	C 358*	20	Scotland: St. Andrews
C. steveni Bieb.	C 244	32	U.S.S.R.: Armenia, collected in nature
	C 917	32	U.S.S.R.: idem
	C 392*	32	U.S.S.R.: Leningrad
C. thyrsoidea L.	C 573	34	France: Col de Crozet, Montoisey, Jura (Ain)
	C 13	34	France: Col du Lautaret, 2000 m (Ht. Alpes)
	C 93	34	France: idem
	C 331	34	Switzerland: Churfirsten (St. Gallen)
	C 484*	34	Scotland: Edinburgh
	C 130*	34	Switzerland: Neuchâtel
	C 477*	34	Switzerland: idem
	C 577*	34	Yugoslavia: Zagreb
C. trachelium L.	C 283	34	Austria: Noric Alps
	C 543	34	Austria: idem
	C 224	34	Austria: Raxalpe
	C 472	34	Austria: idem
	C 172	34	Austria: Stub Alpe (Steiermark)
	C 481	34	Austria: N. Tirol
	C 655	34	Czecho-Slovakia: C. Bohemia
	C 648	34	Czecho-Slovakia: E. Bohemia
	C 666	34	Czecho-Slovakia: Carpathian Mts.
	C 735	34	Czecho-Slovakia: Krkonose Mts. (N.E. Bohemia)
	C 610	34	Czecho-Slovakia: Lehnice (C. Slovakia)
	C 658	34	Czecho-Slovakia: N. Moravia
	C 653	34	Czecho-Slovakia: near Praha
	C 821	34	Czecho-Slovakia: Zuberec (N. Slovakia)
	C 436	34	Denmark: Boguas (N.W. Sjaelland)
	C 288	34	England: Steyning (Lancashire)
	C 817	34	France: Agey, Orgeux (Côte d'Or)
	C 750	34	France: Aix les Bain, 500 m (Savoie)
	C 524	34	France: Moloy (Côte d'Or)
	C 253	34	France: near Nantes (Loire Inf.)
	C 495	34	France: idem
	C 372	34	France: Pentes du Champ du Feu, 600 m, Vosges (Bas Rhin)
	C 646	34	France: idem
	C 373	34	France: environment of Strasbourg (Bas Rhin)
	C 641/ C 642	34	France: idem
	C 375	34	France: Sundgau, Forêt de Fulleren (Ht. Rhin)
	C 901	34	E. Germany: near Dessau (Saksen Anhalt)
	C 562	34	E. Germany: near Hameln (Saksen Anhalt)
	C 497	34	Hungary: collected in nature, precise locality unknown
	C 498	34	Hungary: idem
	C 593	34	Italy: Valtellina

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
C. trachelium L. (cont.)	C 594	34	Italy: idem
	C 446	34	Italy: between Camogli and S. Rocco (peninsula of Portofino)
	C 82	34	Italy: between Portofino and S. Fruttuoso (peninsula of Portofino)
	C 443	34	Italy: idem
	C 444	34	Italy: idem
	C 442	34	Italy: near Rapallo (peninsula of Portofino)
	C 44	34	the Netherlands: Savelsbos near Rijckholt (Limburg)
	C 416	34	the Netherlands: Geerendal near Schin op Geul (Limburg)
	C 840	34; 51	Poland: Zakopane
	C 719	34	Sweden: Brunnby, Kullaberg (Skåne)
	C 123	34	Sweden: Ivetofta (Skåne)
	C 469	34	Sweden: Ven Backafall
	C 718	34	Sweden: idem
	C 564	34	Sweden: collected in nature, precise locality unknown
	C 810	34	Sweden: idem
	C 795	34	Switzerland: Binn, 1100 m (Wallis)
	C 187*	34	Belgium: Antwerp
	C 322*	34	Belgium: Brussels
	C 323*	34	Belgium: idem
	C 531*	34	Belgium: idem
	C 617*	34	Denmark: Copenhagen
	C 206*	34	W. Germany: Göttingen
	C 835*	34	W. Germany: Marburg
	C 265*	34	the Netherlands: coll. de Graaff
	C 269*	34	the Netherlands: idem
	C 279*	34	the Netherlands: idem
	C 851*	34	Poland: Bydgoszcz
	C 121*	34	Poland: Warszawa
	C 842*	34	Scotland: St. Andrews
	C 866*	34	Switzerland: Neuchâtel
	C 838*	34	U.S.S.R.: Minsk
	C 46*	34	U.S.S.R.: Moskva
C. trautvetteri Grossh.	C 91	90	U.S.S.R.: Armenia, collected in nature
	C 724*	90	Austria: Frohnleiten
	C 773*	90	England: Alp. Gard. Soc., Ascot
	C 785*	90	England: idem
	C 576*	90	the Netherlands: Rotterdam
	C 245*	90	U.S.S.R.: Erevan
C. tridentata Schreb.	C 132*	34	W. Germany: Frankfurt a. Main
	C 349*	34	Norway: Bergen
	C 305*	34	Switzerland: Lausanne
	C 629*	34	U.S.S.R.: Leningrad
	C 660*	34	U.S.S.R.: Moskva
C. verruculosa Hoffmgg. & Link	C 102	20	Portugal: Algueciras (prov. Estremadura)
	C 352	20	Portugal: collected in nature, precise locality unknown
	C 493	20	Portugal: idem
	C 555	20	Portugal: idem

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* = cult. material.

Species	Coll. no.	2n	Origin of the material
	C 684	20	Portugal: idem
	C 914	20	Portugal: idem
	C 52*	20	Portugal: Lisboa
C. vidalii Wats.	C 27	56	Can. Isles: Tenerife (Cult. ?)
	C 202*	56	England: Oxford
	C 55*	56	Portugal: Lisboa
C. waldsteiniana Roem. & Sch.	C 135*	34	Austria: Graz
	C 137*	34	Austria: idem
	C 786*	34	England: Alp. Gard. Soc., Ascot
	C 878*	34	England: idem
	C 179*	34	W. Germany: Frankfurt a. Main
	C 208*	34	W. Germany: Göttingen

* = cult. material.

Table 6 gives a survey of the cytological data of the species of the genus *Campanula*, known up to the present. In the second column chromosome numbers pertaining to the present investigations are given; the data derived from literature are mentioned in the other columns [1]).

The somatic chromosomes of a number of species were drawn with the aid of an Abbé Camera Lucida.

The data, mentioned in this chapter, will be discussed further in Chapter III, in connection with morphological data.

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[1]) After the manuscript had gone to press, a paper by D. PODLECH and J. DAMBOLDT (Ber. d. Deutsch. Bot. Ges. 76: 360–369. 1963) has appeared, in which the chromosome numbers of 39 species of the family *Campanulaceae* are reported.

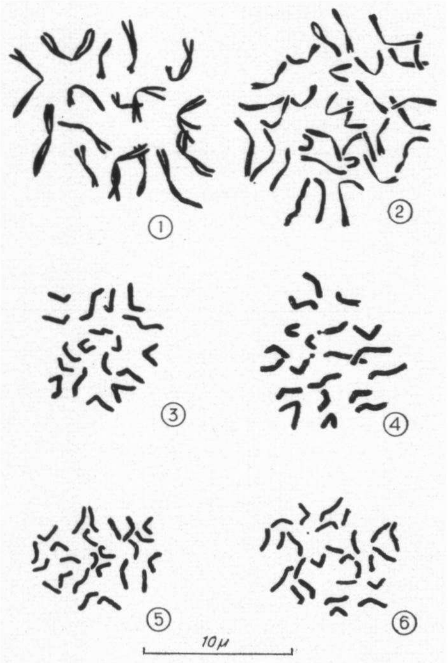

Fig. 1A.

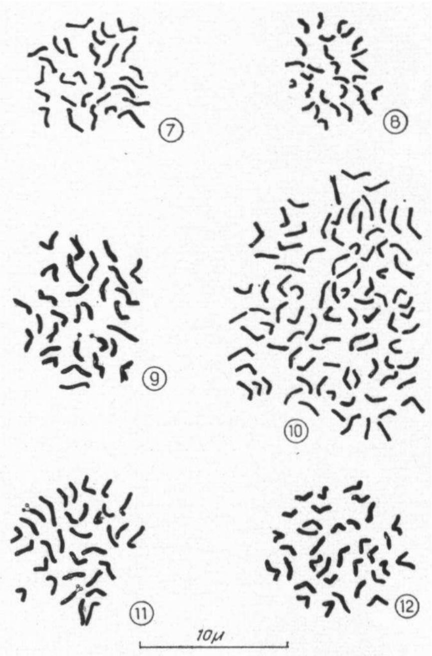

Fig. 1B.

Fig. 1A. Somatic chromosomes of *Campanula*, camera lucida drawings. 1. *C. persicifolia* L., 2n = 16, (C 113); 2. *C. steveni* Bieb., 2n = 32, (C 917); 3. *C. loeflingii* Brot., 2n = 18, (C 210); 4. *C. loeflingii* Brot., 2n = 20, (C 296); 5. *C. dichotoma* L., 2n = 24, (C 219); 6. *C. peregrina* L., 2n = 26, (C 776).

Fig. 1B. Somatic chromosomes of *Campanula*, camera lucida drawings. 7. *C. erinus* L., 2n = 28, (C 554); 8. *C. colorata* Wall. in Roxb., 2n = 28, (C 368); 9. *C. glomerata* L., 2n = 30, (C 389); 10. *C. trautvetteri* Grossh., 2n = 90, (C 576); 11. *C. fragilis* Cyr., 2n = 32, (C 764); 12. *C. carpatica* Jacq., 2n = 34, (C 463).

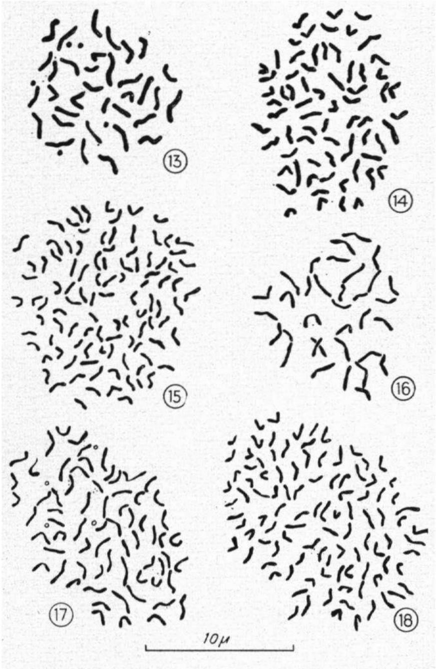

Fig. 1C.

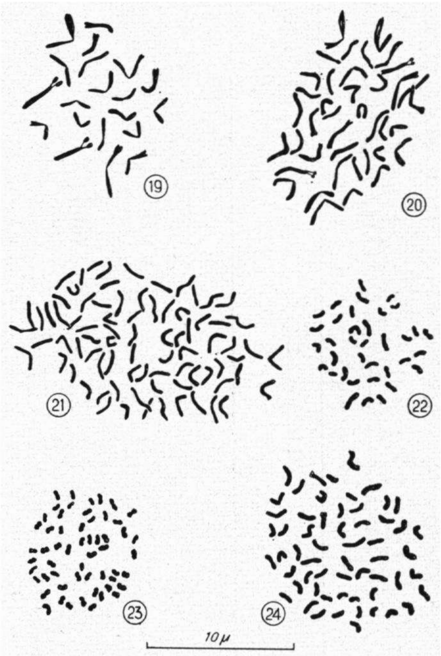

Fig. 1D.

Fig. 1C. Somatic chromosomes of *Campanula*, camera lucida drawings. 13. *C. latifolia* L., 2n = 34 + 5B, (C 317); 14. *C. rapunculoides* L., 2n = 68, (C 456); 15. *C. rapunculoides* L., 2n = 102, (C 212); 16. *C. rotundifolia* L., 2n = 34, (C 737); 17. *C. rotundifolia* L., 2n = 68 + 4B, (C 22); 18. *C. rotundifolia* L., 2n = 102, (C 330).

Fig. 1D. Somatic chromosomes of *Campanula*, camera lucida drawings. 19. *C. patula* L., 2n = 20, (C 316); 20. *C. patula* L., 2n = 40, (C 345); 21. *C. abietina* Griseb. et Sch., 2n = 80, (C 613); 22. *C. lactiflora* Bieb., 2n = 36, (C 572); 23. *C. vidalii* Wats., 2n = 56, (C 55); 24. *C. americana* L., 2n = 58, (C 636).

TABLE 6

A survey of the cytological investigations carried out up to the present in the genus *Campanula*. The second column refers to the present investigations, the other columns to investigations carried out by other authors.

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. abietina Griseb. et Schenk	80	Sugiura (1938, 1942)	unknown	68
C. alaskana Leichtl. ex Bedd. (synonymous with *C. rotundifolia*)	—	Sugiura (1940, 1942)	Alaska	34
C. alliariaefolia Willd.	34	Marchal (1920)	unknown	34
		Matsuura and Suto (1935)	unknown	96
		Sugiura (1938)	unknown	68
		Sugiura (1942)	unknown	34
C. allionii Vill.	—	La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	34
C. alpina Jacq.	34	Skalinska *et al.* (1959)	Poland: High Tatra	34
C. americana L.	58	Sugiura (1938, 1942)	unknown	102
C. anchusiflora Sibth. & Sm.	—	Phitos (1963)	Greece: Isle of Hydra	34
C. andrewsii DC.	—	Phitos (1963)	Greece: Volos	34
C. aucheri DC.	34	—	—	—
C. barbata L.	34	Marchal (1920)	unknown	34
		Löve and Löve (1944)	cult. mat.	34
		Mattick (in Tischler, 1950)	Austria	34
C. barbeyi Feer	—	Merxmüller and Damboldt (1962)	Italy: Gargano	34
C. barrelieri Presl	—	Merxmüller and Damboldt (1962)	Italy: Gragnano near Castellamare di Stabia	32
C. baumgarteni Beck.	—	Gutermann (in Löve and Löve, 1961)	Germany: Pfälzer Wald	68
		Podlech (1962)	France: Weissenburg	68

C. beckiana Hayek	—	*Sugiura (1941)*	*unknown*	*68*
		Gutermann (in Löve and Löve, 1961)	Austria: W. of Vienna	68
C. betonicifolia Sibth. & Sm.	—	Marchal (1920)	unknown	34
		Sugiura (1940, 1942)	unknown	34
C. bocconei Vill.	—	Podlech (1962)	France: Briançon	68
C. bononiensis L.	34	Marchal (1920)	unknown	34
		Rosen (1931)	unknown	34
		Sugiura (1938, 1942)	unknown	34
C. caespitosa Scop.	34	Sugiura (1942)	unknown	68
		Gutermann (in Löve and Löve, 1961)	Austria: Wiener Schneeberg	34
C. calamenthifolia Lam.	—	Sugiura (1942)	unknown	34
C. carnica Schied.	34	Sugiura (1940)	unknown	34
		Böcher (1960)	cult. mat.	34
		Gutermann (in Löve and Löve, 1961)	Italy: M. Pasabio, Judicarian Alps	34
C. carpatica Jacq.	34	Marchal (1920)	unknown	34
		Sugiura (1938, 1942)	unknown	34
		Koller (in Darlington & Janaki-Ammal, 1945)	unknown	32
C. cashmiriana Royle	28	—	—	—
C. caucasica Bieb.	—	Sugiura (1938, 1942)	unknown	102
C. cavolinii Ten.	—	Merxmüller and Damboldt (1962)	Italy: Abruzzen near Roccaraso	32
C. celsii DC.	34	Phitos (1963)	Greece: Mt. Lycabettos	34
C. celtidifolia Boiss. (syn. with *C. lactiflora* Bieb.)	—	Sugiura (1942)	unknown	34
C. cenisia L.	—	Favarger (1957)	Switzerland	ca. 34
C. cervicaria L.	34	Sugiura (1940)	unknown	24
		Sugiura (1942)	unknown	26

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. cochleariifolia Lam.	34	Sugiura (1940, 1942)	unknown	68
	68	Marchal (1920)	unknown	34
		Mattick (in Tischler, 1950)	Austria	34
		Böcher (1960)	France: Gorge du Dard	34
		Gutermann (in Löve and Löve, 1961)	Alps of France and Germany	34
C. collina Bieb.	68	Sugiura (1938, 1942)	unknown	68
C. colorata Wall. in Roxb.	28	Kishore (1951)	India: Environment of Simla	24
C. constantinii Beauv. & Top.	—	Phitos (1963)	Greece: Dirphys	34
C. dasyantha Bieb.	—	Sakai (1935)	unknown	34
C. davurica Siev. (syn. with *C. glomerata*)	—	Sugiura (1940, 1942)	unknown	30
C. dichotoma L.	24	—	—	—
C. divaricata Michx.	34	La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	40
C. drabaefolia Sibth. & Sm.	—	Sugiura (1938, 1942)	unknown	34
C. dubia DC. (syn. with *C. gieseckiana* Vest ssp. *groenlandica* (Berl.) Böch.)	—	Gutermann (in Löve and Löve, 1961)	Sweden: Abisko (Lappland)	68
C. elatines L.	—	Merxmüller and Damboldt (1962)	Italy: Cottian Alps, Crissolo	34
C. elatinioides Moretti	—	Merxmüller and Damboldt (1962)	Italy: Lago d'Iseo, Marone	34, 35
C. elegans Roem. & Sch.	—	Sugiura (1938, 1942)	unknown	102
C. erinus L.	28	Koller (in Darlington and Janaki-Ammal, 1945)	unknown	28
		Larsen (1956)	Italy: Minuto	28

C. excisa Schleich. ex Mur.	34	Podlech (1962)	Switzerland: Simplon	34
C. farinosa (Roch.) Andrz. ex Bess.	30	—	—	—
C. farinulenta Kern. & Wettst.	—	Podlech (1962)	Yugoslavia: Dalmatia, Biokovo	68
C. fenestrellata Feer	—	Merxmüller and Damboldt (1962)	Yugoslavia: Dalmatia, Karlobag	34
C. filicaulis Dur.				
var. *reboudiana* (Pomel) Maire	—	Quézel (1957)	N. Africa: Outat el Hajj	16
var. *filicaulis*	—	Quézel (1957)	N. Africa: Seksaouas	48
var. *pseudoradicosa* Lit. et Maire	—	Quézel (1957)	N. Africa: m'Goun	48
C. fragilis Cyr.	32	Marchal (1920)	unknown	34
		Merxmüller and Damboldt (1962)	Italy: Gragnano near Castellammare di Stabia (Campania)	32
			Italy: Mt. Montea (Calabria)	32
C. fritschii Wit.	—	Podlech (1962)	France: Vallée du Var	68
C. garganica Ten.	34	Marchal (1920)	unknown	34
		Sugiura (1938, 1942)	unknown	34
		Merxmüller and Damboldt (1962)	Italy: Gargano	34
C. gieseckiana Vest				
ssp. *gieseckiana*	—	Böcher (1936, 1960)	Greenland	34
		Böcher and Larsen (1950)	Greenland	34
ssp. *groenlandica* (Berl.) Böch.	—	Böcher (1936, 1938, 1960)	Greenland	68
		Böcher and Larsen (1950)	Greenland	68
		Löve and Löve (1950)	Iceland	68
C. glomerata L.	30	Marchal (1920)	unknown	34
		Griesinger (1937)	Austria: N. Tirol, Trins	30
		Sugiura (1938, 1942)	unknown	68
C. grossekii Heuff.	34	Sugiura (1938, 1942)	unknown	34
C. guinochetii Quéz.	—	Quézel (1957)	N. Africa: m'Goun	28 or 32
C. hellenica (Hay.) Podl.	—	Podlech (1962)	Greece: Mt. Tymphi	34
C. hispanica Willk.	—	Böcher (1960)	Spain: Montes de Vittoria	68

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. hohenackeri Fisch. et Mey.	34	—	—	—
C. hostii Baumg. (syn. with *C. beckiana* Hay.)	—	Sugiura (1942)	unknown	68
C. hypopolia Trautv.	—	La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	34
C. imeritina Rupr.	—	Sugiura (1940, 1942)	unknown	34
C. incurva Auch.	32	—	—	—
C. isophylla Mor.	32	de Vilmorin and Simonet (1927) Merxmüller and Damboldt (1962)	unknown Italy: Promontorio di Noli	32 32
C. istriaca Feer	—	Merxmüller and Damboldt (1962)	Yugoslavia: Istria, Plomin	34
C. justiniana Wit.	—	Podlech (1962)	Yugoslavia: Divača Austria: Krainer Schneeberg	34 34
C. kemulariae Fom.	34	—	—	—
C. kladniana (Schur) Wit.	68	Sugiura (1940, 1942) Böcher (1960)	unknown Carpathian Mts. (probably)	68 68
C. laciniata L.	—	Sugiura (1942)	unknown	102
C. lactiflora Bieb.	36	Sugiura (1938, 1942)	unknown	34
C. lanata Friv.	34	Sugiura (1942)	unknown	34
C. lasiocarpa Cham.	34	—	—	—
C. latifolia L.	34	Marchal (1920) de Vilmorin and Simonet (1927) Sugiura (1938, 1942) Löve and Löve (1944)	unknown unknown unknown Sweden: Lund	34 34 34 34

C. latiloba DC.	*16*	*Overton (1905)*	*unknown*	*16*
		Marchal (1920)	*unknown*	*16*
		Sugiura *(1938, 1942)*	unknown	16
C. lepida Feer	—	Merxmüller and Damboldt (1962)	Yugoslavia: Velebit	34
C. lingulata Waldst. & Kit.	—	Sugiura (1940, 1942)	unknown	34
C. linifolia Scop. (syn. with *C. carnica* Schied.)	34	Sugiura (1942)	unknown	34
C. loeflingii Brot.	18	Larsen (1954)	Portugal: Coimbra	18
	20	A. Fernandes (1962)	Portugal: Serra da Lousa	18
		Böcher (1963)	Portugal: Coimbra	18
C. longistyla Fom.	34	de Vilmorin and Simonet (1927)	unknown	34
		Sugiura (1938, 1942)	unknown	34
C. loretiana Wit.	—	Podlech (1962)	Andorra	34
C. lyrata Lam.	—	Phitos (1963)	Greece: Isle of Mytilene	34
C. macrantha Fisch. in DC. (syn. with *C. latifolia* L.)	34	Sugiura (1940, 1942)	unknown	34
C. macrorhiza Gay				
var. *macrorhiza*	34	Guinochet (1942)	Monaco	34
var. *pubescens* DC.	—	Guinochet (1942)	France: Maritime Alps	55, 56
var. *angustiflora* Tanf. ex Parl.	—	Guinochet (1942)	France: Maritime Alps	68
var. *jurjurensis* Chab.	—	Quézel (1957)	N. Africa: Mt. Djurdjura	102
C. macrostyla Boiss. & Heldr.	—	Marchal (1920)	unknown	20
C. marchesetii Wit.	—	Sugiura (1938, 1942)	unknown	34
		Podlech (1962)	Yugoslavia: Ajdovscina	68
C. mairei Pau	—	Quézel (1953)	N. Africa	16
C. medium L.	34	Marchal (1920)	unknown	34
		Sugiura (1938, 1942)	unknown	34
		La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	34

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. michauxioides Boiss.	30	Sugiura (1940, 1942)	unknown	24
C. mirabilis Alb.	—	Sugiura (1940, 1942)	unknown	102
C. moesiaca Vel.	—	Sugiura (1938, 1942)	unknown	34
C. morettiana Reich.	—	Sugiura (1940, 1942)	unknown	68
C. multiflora Waldst. & Kit.	32	Sugiura (1940, 1942)	unknown	16
		Baksay (1958)	Hungary: Szentendre	18
C. napuligera Schur	34	—	—	—
C. oblongifolia (C. Koch) Char.	90	—	—	—
C. ochroleuca Kem. Nath.	34	—	—	—
C. pallasiana Roem. & Sch.	—	Sugiura (1940, 1942)	unknown	34
C. patula L.	20	Rutland (1941)	England	20
	40	Vaarama (in Löve and Löve, 1948)	unknown	20
		Mattick (in Tischler, 1950)	Austria	± 50
		Löve and Löve (1956)	Iceland	20
C. pelviformis Lam.	—	Sugiura (1938, 1942)	unknown	34
C. peregrina L.	26	—	—	—
C. persicifolia L.	16	Marchal (1920)	unknown	16
		Gairdner (1926)	unknown	16
		de Souza Violante (1929)	unknown	16
		Gairdner and Darlington (1930, 1932)	Austria: Gmunden	16
			Austria: Innsbrück	16
			Bulgaria: Varna	16
			France: Auvergne, Murols	16

			Sweden: Mälar	*16*
		Straub (1936, 1937)	unknown	16
		Sugiura (1938, 1940)	unknown	16
cult. var. "Telham Beauty"	—	Darlington and Gairdner (1930, 1932)	unknown	32
C. petraea L.	34	—	—	—
C. phyctidocalyx Boiss. & Noé (syn. with *C. persicifolia* L.)	16	Sugiura (1942)	unknown	112
C. pilosa Pall. ex Roem. & Sch.	—	Sugiura (1938, 1942)	unknown	34
C. piperi Howell	—	La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	34
C. portenschlagiana Roem. & Sch.	34	Marchal (1920) Sugiura (1938, 1942) Merxmüller and Damboldt (1962)	unknown unknown Yugoslavia: Biokovo; Makarska	34 102 34
C. poscharskyana Degen.	34	Sugiura (1940, 1942) Merxmüller and Damboldt (1962)	unknown Yugoslavia: Gruda, S.E. of Dubrovnik	34 34
C. praesignis Beck	—	Podlech (1962)	Austria: Höllental	34
C. prenanthoides Dur.	34	—	—	—
C. primulaefolia Brot.	36	Marchal (1920)	unknown	26
C. propinqua Fisch. et Mey. var. *grandiflora* Milne-Redhead	—	Sugiura (1940, 1942)	unknown	20
C. pseudostenocodon Lac.	—	Podlech (1962)	Italy: Gran Sasso	102
C. psilostachya Boiss. & Kotsch.	—	Sugiura (1942)	unknown	34
C. pulcherrima Schrank & Zeyh. ex Steud. (syn. with *C. rapunculoides* L.)	—	Sugiura (1938, 1942)	unknown	102
C. pulla L.	34	Sugiura (1938, 1942) Gutermann (in Löve and Löve, 1961)	unknown Austria, Germany	68 34

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. punctata Lam.	34	MARCHAL (1920)	unknown	34
		DE VILMORIN and SIMONET (1927)	unknown	34
		SUGIURA (1938, 1942)	unknown	34
C. pyramidalis L.	34	MARCHAL (1920)	unknown	34
		SUGIURA (1938, 1942)	unknown	34
C. raddeana Trautv.	34	ROSÉN (1931)	unknown	34
		SUGIURA (1940)	unknown	102
		SUGIURA (1942)	unknown	34
C. raineri Perp.	—	SUGIURA (1938, 1942)	unknown	34
C. ramosissima Sibth.	—	MARCHAL (1920)	unknown	20
C. rapunculoides L.	68, 102	MARCHAL (1920	unknown	102
		DE VILMORIN and SIMONET (1927)	unknown	102
		BELLING (in TISCHLER, 1931)	unknown	102
		SUGIURA (1938, 1942)	unknown	102
		LÖVE and LÖVE (1944)	Sweden: Lund	102
C. rapunculus L.	20	ARMAND (1912)	unknown	20
		MARCHAL (1920)	unknown	20
		LARSEN (1956)	France: Meun sur Loire; Roque Houte	20
			Italy: Campidoglio	20
C. reiseri Hal.	—	PHITOS (1963)	Greece: N. Sporades, Jura	34
C. reuteriana Boiss. & Bal.	—	SUGIURA (1938, 1942)	unknown	34
C. rhomboidalis L.	—	SUGIURA (1938, 1942)	unknown	34
		FAVARGER (1949)	Switzerland: Mt. Arpille	34
		GUTERMANN (in LÖVE and LÖVE, 1961)	France: Alps of Dauphiné	34

C. rotundifolia L.	34	ARMAND (1912)	unknown	40
	68	BÖCHER (1936, 1960)	Greenland	34
	102	BÖCHER (1960)	France, Sweden, Denmark, U.S.S.R.	34
		BÖCHER and LARSEN (1950)	Greenland	34
		GUTERMANN (in LÖVE and LÖVE, 1961)	Italy	34
		MARCHAL (1920)	unknown	68
		BÖCHER (1936, 1938)	Greenland	68
		SUGIURA (1942)	unknown	68
		BÖCHER (1960); GUINOCHET (1942)	France	68
		BÖCHER (1938, 1960)	Norway	68
		BÖCHER and LARSEN (1950)	Norway	68
		BÖCHER (1936, 1960)	Denmark	68
		BÖCHER (1960)	England; the Netherl.; U.S.S.R.; Germany; Sweden; Eire; Norway; Finland; Faroes; Yugoslavia	68
		BÖCHER and LARSEN (1950)	Iceland	68
		GUTERMANN (in LÖVE and LÖVE, 1961)	Austria, Germany	68
		LÖVE and LÖVE (1956)	Iceland	68
		BÖCHER (1963)	France	72 + 4B
		HUBAC (1961)	France	102
		GADELLA (1962)	France, Czecho-Slovakia	102
		GADELLA (1963)	France	102
ssp. *litardierei* Guin.		PODLECH (1962)	France	68
ssp. *xylorrhiza* Schwarz		PODLECH (1962)	Austria	102
C. rupestris Sibth. & Sm.	34	PHITOS (1963)	Greece: Mega Spilaeon	34
C. sabatia De Not	—	PODLECH (1962)	Italy: Promontorio di Noli	34
			Italy: Mt. Bignone	34
			Italy: Borghetto Santo Spirito	34
C. sardoa Lev. ex Nym.	—	PODLECH (1962)	Italy: Mt. di Oliena	34
C. sarmatica Ker-Gawl	34	MARCHAL (1920)	unknown	34
		SUGIURA (1938, 1942)	unknown	34
C. sarmentosa Hochst. ex Rich.	—	SUGIURA (1942)	unknown	34
C. sartori Boiss. & Heldr.	34	—	—	—

Species	New Count 2n	References		
		Author	Origin of the material	2n
C. saxatilis L.	—	Sugiura (1940, 1942) Phitos (1963)	unknown Greece: between Sellia and Myrthios	34 34
C. saxifragioides Doum.	—	Quézel (1957)	N. Africa: Ayachi	14 or 16
C. scheuchzeri Vill.	68	Böcher (1936) Sugiura (1940, 1942) Böcher (1960) Gutermann (in Löve and Löve, 1961)	unknown unknown Switzerland: Brienzer Rothorn Austria, Germany, France, Italy	68 68 ca. 68 68
C. sclerotricha Boiss. & Kotsch.	34	—	—	—
C. sibirica L.	34	Sugiura (1942) Baksay (1956)	unknown Hungary: Mt. Nagyszenas	102 34
var. *divergentiformis* Jav.		Baksay (1956)	Hungary: Mt. Szarvaskö, Belkö, Ablakoskö, and Tarkö of Mts. Bükk	34
C. spathulata Sibth. & Sm.	20	—	—	—
C. speciosa Pourr.	34	Sugiura (1940, 1942)	unknown	68
C. spicata L.	34	Larsen (1960)	Italy: Cortina	34
C. spruneriana Hampe	20	—	—	—
C. stenocodon Boiss. & Reut	—	Podlech (1962)	France: Maritime Alps, Col di Larche	34
C. steveni Bieb.	32	Koller (in Darlington and Janaki-Ammal, 1945)	unknown	40
C. subpyrenaica Timb. (syn. with *C. persicifolia* L.)	—	Sugiura (1942)	unknown	16
C. thyrsoidea L.	34	Rosen (1931)	unknown	34

		Sugiura (1938, 1942)	*unknown*	*48*
		Larsen (1954)	*Switzerland: Schynige Platte*	*34*
C. tomentosa Vent. (syn. with *C. celsii* DC.)	—	Sugiura (1942)	unknown	34
C. tommasiniana Koch	—	Merxmüller and Damboldt (1962)	Yugoslavia: Istria, Lovran	34
C. trachelium L.	34	Marchal (1920)	unknown	34
		Sugiura (1938, 1942)	unknown	34
		Löve and Löve (1944)	Sweden: Lund	34
C. transtagana R. Fernandes	—	A. Fernandes (1962)	Portugal: Near Vila Velha de Rodao	20
C. trautvetteri Grossh.	90	—	—	—
C. tridentata Schreb.	34	—	—	—
C. tubulosa Lam.	—	La Cour (in Darlington and Janaki-Ammal, 1945)	unknown	34
		Phitos (1963)	Greece: Isle of Creta	34
C. turbinata Schott, Nym. et Kotsch.	34	Sugiura (1940, 1942)	unknown	34
(syn. with *C. carpatica* Jacq.)				
C. uniflora L.	—	Löve and Löve (1956)	Iceland	34
		Jörgensen, Sörensen and Westergaard (1958)	Greenland: Clavering Island	34
C. vaillantii Quéz.	—	Quézel (1957)	N. Africa: M'Korn	14
C. verruculosa Hoffmgg. & Link	20	—	—	—
C. vidalii Wats.	56	de Mesquita Rodriguez (1954)	unknown	56
C. waldsteiniana Roem. & Sch.	34	Gadella (1962)	unknown	34
		Merxmüller and Damboldt (1962)	Yugoslavia: Dalmatia, Mali Halan	34
C. witasekiana Vierh.	—	Gutermann (in Löve and Löve, 1961)	Austria: Wienerwald	34
			Italy: M. Pasubio	34
		Podlech (1962)	: Soboth	34

CHAPTER III

THE RELATION BETWEEN MORPHOLOGICAL AND CYTOLOGICAL CHARACTERS

A. INTRODUCTION

The main object of the present investigations is to integrate morphological, cytological, and genetical data. A classification, based on morphological and geographic studies only, may be less objective than a classification based on the integration of data derived from a great variety of disciplines, such as: morphology, physiology, ecology, cytology, genetics and transplant studies.

Units, morphologically identical, but not identical in other respects, will not be classified differently in general. On the other hand, the use of morphological data only, may give rise to an unsatisfactory classification. Morphological characters are most important, but the classification should not be based on them only.

The family *Campanulaceae* presents a clear example: On basis of the connate anthers of a number of species de Candolle placed these species in the genus *Symphyandra*, whereas the species with free anthers are placed in the genus *Campanula*. At first sight, however, it is not clear why de Candolle based his classification in the first place on this character, and not, for example, on the mode of dehiscence of the fruit. As this last character is correlated with several other characters in the genus *Campanula* as well as in the genus *Symphyandra*, de Candolle's decision was not an obvious one. The result of his decision was a useful system, but is his classification also the most objective one? This decision, based on morphological data only, might be checked by a correlation of data derived from a great variety of disciplines.

It is the author's intention to give an evaluation of the objectivity of some classifications of the genus *Campanula* which were based on morphological characters by other authors. In the first place, morphological and cytological data will be correlated. Secondly, the conclusion based on these studies, will be tested by crossing experiments (see Chapter IV).

B. THE CYTOLOGICAL OBSERVATIONS OF SUGIURA

Table 6 gives a survey of the species, the chromosome numbers of which are known up to the present. 144 out of approximately 300 species were investigated cytologically, which is about 50 %, a rather high percentage for a genus of this size. 77 species were investigated by the present author; 58 of these have been investigated by other authors before. The chromosome numbers of 20 of these 58 species differ from those reported by other authors. 16 species of this category were also investigated by SUGIURA (1938, 1940, 1941, 1942). It is very unlikely that in all these species intraspecific cyto-

TABLE 7

Some important morphological and cytological characters of 77 species of the genus *Campanula*.

Species	Diploid number of chromosomes																	Length of the chromosomes				Duration of life			Shape of the basal leaves		Calyx appendages		Ratio length of the stigma : length of the style		Style		Capsule						
																																	Number of locules		Mode of dehiscence			Position	
	16	18	20	24	26	28	30	32	34	36	40	56	58	68	80	90	102	< 2 μ	2-(3) μ	3-(4) μ	4-6 μ	annual	biennial	perennial	not cordate	cordate	present	absent	1 : 1 or 2 : 1	1 : 5 (10)	glabrous	not glabrous	3	5	apical	medial	basal	erect	not erect
C. abietina															×				×					×	×			×		×		×	×		×				×	
C. alliariaefolia									×										×					×		×	×			×		×	×				×		×
C. alpina									×										×				×		×		×			×		×	×				×		×
C. americana													×						×				×		×			×		×		×	×				×	×	
C. aucheri									×										×					×	×		×			×		×	×				×		×
C. barbata									×										×				×		×		×			×		×	×				×		×
C. bononiensis									×										×					×		×		×		×		×	×				×		×
C. caespitosa									×										×					×		×		×		×		×	×				×		×
C. carnica									×										×					×		×		×		×		×	×				×		×
C. carpatica									×										×					×		×		×	×		×		×		×			×	
C. cashmiriana						×												×						×	×			×		×		×	×				×		×
C. celsii									×										×				×		×		×			×		×		×			×	×	
C. cervicaria									×										×				×		×			×		×		×	×				×	×	
C. cochleariifolia									×					×					×					×		×		×		×		×	×				×		×
C. collina														×					×					×		×		×		×		×	×				×		×
C. colorata						×												×				×			×			×		×		×	×				×		×
C. dichotoma				×															×			×			×		×			×		×	×				×		×
C. divaricata									×										×					×	×			×		×		×	×				×		×
C. erinus						×													×			×			×			×		×		×	×				×		×
C. excisa									×										×					×		×		×		×		×	×				×		×
C. farinosa							×												×					×		×		×		×		×	×				×	×	
C. fragilis								×											×					×		×		×		×		×	×				×	×	
C. garganica									×										×					×		×		×		×		×	×				×	×	
C. glomerata							×												×					×		×		×		×		×	×				×	×	
C. grossekii									×										×					×		×	×			×		×	×				×		×
C. hohenackeri									×										×				×		×		×			×		×	×				×		×
C. incurva								×											×				×			×	×			×		×	×				×	×	
C. isophylla								×											×					×		×		×		×		×	×				×	×	
C. kemulariae									×										×					×		×	×			×		×	×				×	×	
C. kladniana														×					×					×		×		×		×		×	×				×		×
C. lactiflora										×								×						×	×			×	×		×		×		×			×	
C. lanata									×										×				×			×	×			×		×	×				×	×	
C. lasiocarpa									×										×					×	×			×		×		×	×		×			×	
C. latifolia									×										×					×		×		×		×		×	×				×		×
C. latiloba	×																				×			×	×			×	×		×		×		×			×	
C. loeflingii		×	×																	×		×			×			×		×		×	×		×			×	
C. longistyla									×										×				×		×		×			×		×	×				×		×
C. macrorhiza									×										×					×		×		×		×		×	×				×	×	
C. medium									×										×				×		×		×			×		×		×			×		×
C. michauxioides							×												×				×		×			×	×		×		×				×		×
C. multiflora								×											×				×		×			×		×		×	×				×	×	
C. napuligera									×										×					×		×		×		×		×	×				×		×
C. oblongifolia																×			×					×		×		×		×		×	×				×	×	
C. ochroleuca									×										×					×		×	×			×		×	×				×		×
C. patula			×								×									×			×		×			×		×		×	×		×			×	
C. peregrina					×														×				×		×			×	×		×		×		×			×	
C. persicifolia	×																				×			×	×			×	×		×		×		×			×	
C. petraea									×										×					×	×			×		×		×	×				×	×	
C. portenschlagiana									×										×					×		×		×		×		×	×				×	×	
C. poscharskyana									×										×					×		×		×		×		×	×				×	×	
C. prenanthoides									×										×					×	×			×		×		×	×				×		×
C. primulaefolia										×								×						×	×			×	×		×		×		×			×	
C. pulla									×										×					×		×		×		×		×	×				×		×
C. punctata									×										×					×		×	×			×		×	×				×		×
C. pyramidalis									×										×				×			×		×		×		×	×			×		×	
C. raddeana									×										×					×		×	×			×		×	×				×	×	
C. rapunculoides														×			×		×					×		×		×		×		×	×				×		×
C. rapunculus			×																	×			×		×			×		×		×	×		×			×	
C. rotundifolia									×					×			×		×					×		×		×		×		×	×				×		×
C. rupestris									×										×				×		×		×			×		×		×			×	×	
C. sarmatica									×										×					×		×	×			×		×	×				×		×
C. sartori									×										×				×			×		×		×		×	×				×	×	
C. scheuchzeri														×					×					×		×		×		×		×	×				×		×
C. sclerotricha									×										×					×		×	×			×		×	×				×		×
C. sibirica									×										×				×		×		×			×		×	×				×		×
C. spathulata			×																	×				×	×			×		×		×	×		×			×	
C. speciosa									×										×				×		×		×			×		×	×				×		×
C. spicata									×										×				×		×			×		×		×	×				×	×	
C. spruneriana			×																	×				×	×			×		×		×	×		×			×	
C. steveni								×													×			×	×			×	×		×		×		×			×	
C. thyrsoidea									×										×				×		×			×		×		×	×				×	×	
C. trachelium									×										×					×		×		×		×		×	×				×		×
C. trautvetteri																×			×					×		×		×		×		×	×				×	×	
C. tridentata									×										×					×	×		×			×		×	×				×		×
C. verruculosa			×																	×			×		×			×		×		×	×		×			×	
C. vidalii												×						×						×	×			×		×		×	×				×		×
C. waldsteiniana									×										×					×	×			×		×		×	×				×		×

logical variation should play an important rôle, because this phenomenon is not very common in the genus *Campanula* (see Table 5). On the other hand, these differences might be due to the following facts:

1. the material, on which the count is based, is incorrectly identified.
2. the chromosome numbers are inaccurately determined.
3. the material, on which the count is based, is of cultivated origin.

MERXMÜLLER and DAMBOLDT (1962) suggested that the difference in chromosome number might be due to the use of: "in Kultur entstandene Formen". This however, does not seem likely as may be concluded from Table 5. As the present author found the same chromosome numbers as Sugiura (with the exception of the numbers $2n = 48$ and $2n = 112$), the possibility stated under 2 cannot be the right one. In all probability, however, Sugiura did not correctly identify the plants on which the count was based. This is supported by the report of the chromosome numbers of the species *C. cervaria* ($2n = 30$) and *C. cervicaria* ($2n = 26$). The first species does not exist, the name probably finds it origin in an error in the writing of the name. For this reason, it seems justified to doubt those chromosome numbers reported by Sugiura which were not checked by the present author.

If a correlation between the number of chromosomes and a certain combination of morphological characters should exist in the species investigated, it might be possible to check the chromosome numbers of the species not studied by the present author.

Consequently, the correlation of these characters was studied in the 77 species mentioned in Table 5.

C. THE RELATION BETWEEN THE MORPHOLOGICAL AND CYTOLOGICAL CHARACTERS OF THE SPECIES INVESTIGATED BY THE PRESENT AUTHOR

The following morphological characters were studied: calyx appendages (de Candolle); position of the capsule (de Candolle); the mode of dehiscence of the capsule (Boissier); the number of locules of the fruit (Boissier, de Candolle); duration of life (Boissier); shape of the basal leaves (Sugiura), and other characters. In general, these characters were considered to be of fundamental importance, judging from the systems of the authors concerned.

The following cytological characters were studied: the number of chromosomes, their size and their shape. According to LÖVE (1963) these characters are of considerable importance in the delimitation of genera.

The species were divided into 4 classes on basis of the chromosome length:

1. chromosomes very short, $< 2\ \mu$.
2. chromosomes short, generally these chromosomes are approximately $2\ \mu$ long; the longest chromosomes, however, may have a length of $3\ \mu$.

3. chromosomes medium-sized, their length varying from 3–4 μ.
4. chromosomes long, 4–6 μ.

Generally, the somatic chromosomes of the same species do not vary considerably with respect to their length. Usually, the position of the centromere is clearly visible in the medium-sized and long chromosomes only. Table 7 gives a survey of some cytological and morphological characters of the species investigated.

The data of Table 7 are summarized in Table 8.

TABLE 8 – The relation between some

Diploid number of chromosomes	16	32				34													
Size of the chromosomes																			
very short																			
short			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
medium-sized																			
long	x	x																	
Duration of life																			
annuals																			
biennials			x	x		x	x			x	x				x	x			
perennials	x	x			x			x	x			x	x	x			x	x	x
Shape of the basal leaves																			
cordate			x		x			x		x		x	x		x		x		x
not cordate	x	x		x		x	x		x		x			x		x		x	
Calyx appendages																			
present (section *Medium* sensu de Cand.)			x			x	x								x	x	x	x	x
absent (section *Eucodon*)	x	x		x	x			x	x	x	x	x	x	x					
Ratio length of the style length of the stigma																			
10-5:1			x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
1:1 (2)	x	x						x											
Indument of the style																			
glabrous	x	x						x											
not glabrous			x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Capsule																			
3-locular	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x
5-locular						x	x												
dehiscence apical (section *Rapunculus*)	x	x						x	x										
dehiscence basal (section *Medium* sensu Boiss.)			x	x	x	x	x			x	x	x	x	x	x	x	x	x	x
erect	x	x	x	x	x	x		x	x	x	x	x			x		x		
not erect							x						x	x		x		x	x
Number of species having the combination of characters concerned	2	1	1	1	2	2	1	1	1	1	4	1	11	4	1	6	2	2	6

The following conclusions may be drawn from this table:

1. The section *Medium* sensu de Candolle is more or less homogeneous in cytological respect. 19 out of 21 appendiculate species have the chromosome number 2n = 34, 1 species 2n = 24, and 1 species 2n = 32. Apparently, polyploidy does not occur within the group of appendiculate species. (The term "appendiculate species" is used for "species with calyx-appendages between the calyx-lobes").

morphological and cytological characters

34 68	34 68 102	68	68 102	30		90	24	26	28		36	56	58	18 20	20		20 40	80
				x					x	x	x	x						
x	x	x	x		x	x	x	x					x					
														x	x	x	x	±x
							x			x				x				
				x				x					x		x		x	
x	x	x	x		x	x			x		x	x				x		x
x	x	x	x	x	x	x							±x					
							x	x	x	x	x	x		x	x	x	x	x
							x											
x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
x	x	x	x		x	x	x		x	x		x	x	x	x	x	x	x
				x				x			x							
				x				x			x							
x	x	x	x		x	x	x		x	x		x	x	x	x	x	x	x
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
				x				x			x		x	x	x	x	x	x
x	x	x	x		x	x	x		x	x		x						
					x	x		x			x	x	x	x	x	x	x	x
x	x	x	x	x			x		x	x								
1	1	3	1	1	2	2	1	1	1	2	2	1	1	1	2	2	1	1

2. The section *Eucodon* DC. is cytologically very heterogeneous.
3. The section *Rapunculus* and *Medium* sensu Bossier are in cytological respect heterogeneous.
4. Species with linear or lanceolate leaves (in general: not cordate leaves) may have different chromosome numbers. Therefore, a classification based on this character alone, is not a natural one.
5. The species with the chromosome number 2n = 32 are heterogeneous in morphological respect as well as in the shape of the chromosomes. One of the species, having this number, is closely related to the species with the number 2n = 16. In view of this fact, *C. steveni* is considered to be tetraploid within the x = 8-series.
6. The remaining species with the chromosome number 2n = 32 are more or less closely related to those with the number 2n = 34. It may be possible that these species are derived from species with the number 2n = 34.
7. Many species have 34 chromosomes. These species are morphologically very heterogenous.
8. The species with the chromosome numbers 2n = 34, 2n = 68, and 2n = 102 are morphologically related. This points in the direction of the existence of an x = 17-series, consisting of diploids, tetraploids and hexaploids.
9. Neither the size and shape of the chromosomes, nor the morphological characters of the species of the x = 8-series support the view that these species are related to those of the x = 17-series.
10. The species with the number 2n = 30 are morphologically heterogeneous. One of these species, however, differs not only from the species with the number 2n = 30, but also from all other species of the genus *Campanula*. This species (*C. michauxioides*) has a combination of characters not occurring in any other species, viz.: a flat deeply cleft corolla, a glabrous style, a different shape of the inflorescence, and the fact that the length of the style and the length of the stigmata are the same. Consequently, it is doubtful that the species concerned should be included in the genus *Campanula*.

    On the other hand, two species with the number 2n = 30 are very closely related to the species having the number 2n = 90. Fedorov included these species in the subsection *Involucratae*, series *Glomeratae*. It is very likely that a series with the basic number x = 15 does exist, notwithstanding the fact that no species were found with the number 2n = 60 up to the present.
11. The species of the x = 15-series agree more or less with a number of species of the x = 17-series in their external morphology. It is not impossible that the species of these 2 series are closely related.
12. The species with the numbers 2n = 20, 40, 80 are closely related in morphological respect. These species belong to a

series with the basic number x = 10. (It should be noted that the species with the number 2n = 30 and 2n = 90 belong to the x = 15-series.)

13. The chromosome number 2n = 18 (*C. loeflingii*) was possibly derived from the number 2n = 20. This theory is supported by the morphological resemblance of this species to species of the x = 10-series, as well as by the fact that in the species concerned also the number 2n = 20 was counted. Moreover, R. FERNANDES (1962) discovered the species *C. transtagana* (2n = 20) which is very closely related to *C. loeflingii.*
14. There is a theory that the basic number x = 17 was the result of a cross between a species with the number 2n = 16 and 2n = 18. The correlations between the morphological and cytological characters, shown in Table 8, do not support this theory.
15. The following species do not belong to any of the series mentioned before: *C. dichotoma* (2n = 24); *C. peregrina* (2n = 26); *C. erinus, C. colorata, C. cashmiriana* (2n = 28); *C. primulaefolia, C. lactiflora* (2n = 36); *C. vidalii* (2n = 56); *C. americana* (2n = 58). They are not related and in the combination of characters they show a more or less marked difference from the species of the x = 17-series. Probably, some of these species should be excluded from the genus *Campanula.*
16. The species *C. vidalii* (2n = 56) differs in many characters from, and cannot be confused with any other species of the genus. For this reason, the origin of the number 2n = 56 cannot be explained by the doubling of the number 2n = 28.
17. Notwithstanding the fact that the species with the numbers 2n = 18 and 2n = 36 have some characters in common (see Table 8), they differ in many respects, namely in the shape of the leaves, the mode of branching of the stems, the duration of life and the shape of the flower and the style. Consequently, these species are not related to each other. The origin of the number 2n = 36 cannot be explained by doubling the number 2n = 18.
18. In the author's opinion it is unlikely that a species with the number 2n = 34 gave rise to a species with the number 2n = 36.

The conclusion may be drawn that there is a correlation between a certain combination of morphological characters and the number of chromosomes of the species concerned. On basis of these correlations, the chromosome numbers reported by other authors will be discussed. The species discussed below were investigated by the present author as well as by other authors.

No uniform opinion exists on the number of chromosomes of the following species listed in Table 6:

1. **C. abietina** Grieseb. et Sch.

This species is closely related to *C. patula.* Hayek regarded *C. abietina* as a variety of *C. patula.* There are, however, some characters justifying the treatment as seperate species. *C. abietina* has very thin, weak and glabrous stems, whereas those of *C. patula* are thicker, firmer and sometimes not glabrous. Moreover, *C. abietina* has stolons at the basis of the stems, a character which is absent in *C. patula*. The leaves of *C. abietina* are thin and more or less transparant when dry, whereas those of *C. patula* are thicker. The calyx lobes of *C. patula* are sometimes dentate, those of *C. abietina* are never dentate. *C. abietina* is a perennial plant which flowers earlier when cultivated (and during a longer period) than *C. patula*. In cytological respect, the species form a series: *C. patula*: 2n = 20, 40; *C. abietina* 2n = 80. On these facts the present author bases his opinion that Sugiura's count (2n = 68) is incorrect.

2. **C. alliariaefolia** Willd.

Nearly all species with calyx appendages have the chromosome number 2n = 34. The diploid level was never exceeded within the group of appendiculate species, so the count of SUGIURA (1942), 2n = 68, is probably incorrect. Also the number 2n = 96, reported by MATSUURA and SUTO (1935) should be regarded as incorrect.

3. **C. americana** L.

The chromosome number of *C. americana* (2n = 102) was previously reported by SUGIURA (1942). The species differs in many respects from other species of the genus *Campanula*. LÖVE (1954) was of the opinion that *C. americana* and *C. rapunculoides* are vicarious species with an atlantic disjunction. These species are not related to each other, neither in morphological nor in cytological respect. *C. americana* differs from the other species of the genus *Campanula* in its 5-partite flat corolla, its style, which is bent upwards, and by the shape of its leaves. For this reason, SMALL (1903) transferred the species to a new genus: *Campanulastrum*, which is supported by cytological observations of the present author (2n = 58). On the other hand, the relation between this species and those of the genus *Asyneuma* should also be investigated. (In Chapter IV the results of some crossing experiments between *C. americana* and some other species of the genus *Campanula* are dealt with.)

4. **C. caespitosa** Scop.

SUGIURA (1942) was the only one who reported the chromosome number 2n = 68, which number differs from that found by Gutermann and the present author (2n = 34). On morphological basis, however, it is impossible to check whether Sugiura's report is correct.

5. **C. carpatica** Jacq.

SUGIURA (1938, 1942), MARCHAL (1920), and the present author (studying 30 strains of this species) counted the chromosome number 2n = 34. Koller found the number 2n = 32. The numbers 2n = 32 and 2n = 34, being found within the same species, might suggest that a transition between the x = 8- and the x = 17-series exists. Koller's observation, however, is not beyond doubt, as *C. carpatica* differs from the species of the x = 8-series, not only in morphological respect, but also in the shape of the chromosomes.

6. **C. cervicaria** L.

SUGIURA (1940, 1942) reported the numbers 2n = 24 and 2n = 26. The species is allied to *C. spicata* (2n = 34) and *C. multiflora* (2n = 32), but not allied to *C. dichotoma* (2n = 24) and *C. peregrina* (2n = 26). This relation shows that the number 2n = 34, found by the present author, is correct.

7. **C. colorata** Wall. in Roxb.

C. colorata and *C. cashmiriana* (2n = 28) belong to the "Himalayan-group" (cf. CL. CROOK, 1951). Consequently, the number 2n = 24, reported by KISHORE (1951) does not seem to be correct.

8. **C. fragilis** Cyr.

As this species shows a great resemblance to some other species with the chromosome number 2n = 32 (*C. barrelieri* Presl, *C. cavolinii* Ten., *C. isophylla* Morett.), the number 2n = 34, reported by MARCHAL (1920) is probably incorrect.

9. **C. glomerata** L.

The numbers 2n = 34 and 2n = 68, published by MARCHAL (1920) and SUGIURA (1942) respectively, were not confirmed by the observations of GRIESINGER (1937) and by those of the present author, who studied plants from many different localities. In view of the fact that the species *C. farinosa* (2n = 30), *C. oblongifolia* (2n = 90) and *C. trautvetteri* (2n = 90) are closely allied to *C. glomerata*, the observations of Marchal and Sugiura are likely to be incorrect.

10. **C. lactiflora** Bieb.

This species differs from the species of the genus which have the number 2n = 34. The counts of the present author, based on 10 plants, showed the number 2n = 36 in all cases, whereas Sugiura counted the number 2n = 34. In view of the many characters in which this species differs from other species of the genus *Campanula*, Sugiura's observation is incorrect.

11. **C. michauxioides** Boiss.

This species has nothing in common with the species of the x = 15-series [*C. glomerata* (2n = 30) and *C. farinosa* (2n = 30)]. Moreover, in the author's opinion the species differs too much from the other species of the genus *Campanula* to be classified in it.

Probably the species belongs to the genus *Asyneuma*, but further investigations are necessary to corroborate this supposition.

12. **C. multiflora** Waldst. et Kit.

This species is related to *C. cervicaria* (2n = 34) and *C. spicata* (2n = 34). The chromosome number is intermediate (2n = 32) between those of *C. glomerata* (2n = 30) and *C. spicata* (2n = 34). In morphological respect, the species has more in common with *C. spicata* and *C. cervicaria* than with *C. glomerata*. The chromosome numbers 2n = 16 and 2n = 18, reported by SUGIURA (1940, 1942) and BAKSAY (1958), respectively, could not be confirmed. It crosses one's mind that these authors may have reported the haploid number.

13. **C. phyctidocalyx** Boiss. & Noë.

C. phyctidocalyx is a nomenclatural synonym of *C. persifolia* (2n = 16). It seems rather strange that SUGIURA (1942) reported the number 2n = 112. It is very unlikely that Sugiura's observation should be correct.

14. **C. portenschlagiana** Roem. et Sch.

In some morphological respects there is a relation between the species *C. portenschlagiana*, *C. poscharskyana* and *C. waldsteiniana*, all having the diploid number 2n = 34. Therefore, Sugiura's count (2n = 102) should be regarded as incorrect.

15. **C. primulaefolia** Brot.

Notwithstanding the fact that the species *C. primulaefolia* (2n = 36) and *C. peregrina* (2n = 26) are very distinct (cf. CL. CROOK, 1951), they resemble each other in certain respects. Marchal's report (2n = 26) on this species is probably due to the fact that he confused these two species.

16. **C. raddeana** Trautv.

The present investigations showed the number 2n = 34 for the two species *C. raddeana* and *C. kemulariae*. Previous counts on the first species by SUGIURA (1940, 1942) were 2n = 102 and 2n = 34, respectively. For the same reason as indicated under 2, the number 2n = 102 might be regarded as incorrect.

17. **C. sibirica L.**

SUGIURA's count (1942), 2n = 102, could not be confirmed by the present author. For the same reason as indicated under 2, the number 2n = 102 is not correct.

18. **C. speciosa L.**

SUGIURA's report (1940, 1942), 2n = 68, may be incorrect for reasons stated before [cf. *C. alliariaefolia* (2), *C. raddeana* (16), *C. sibirica* (17)].

19. **C. steveni** Bieb.

KOLLER's report (1945), 2n = 40, might suggest that this species belongs to the x = 10-series. In fact, this species has some characters in common with the species of the x = 10-series, but still more characters with those of the x = 8-series. 11 plants were cytologically investigated, all clearly showing the number 2n = 32. For this reason, Koller's count is seriously doubted.

20. **C. thyrsoidea** L.

This species is closely allied to *C. spicata*. ROSÉN (1931), LARSEN (1954), as well as the present author found the number 2n = 34. Based on this, SUGIURA's count (1938, 1942), 2n = 48, might be regarded as incorrect.

D. A DISCUSSION ON THE CHROMOSOME NUMBERS OF SOME SPECIES NOT INVESTIGATED BY THE PRESENT AUTHOR

67 Species of the genus belong to this category. Some authors studied groups of morphologically related species. A discussion on the chromosome number of these species will be given below, using the data given in Table 8. The following groups are distinguished:

a. 7 species investigated by PHITOS (1963): *Rupestris*-group.
b. 14 species investigated by PODLECH (1962): Subsection *Heterophylla*.
c. 9 species studied by MERXMÜLLER and DAMBOLDT (1962): *Garganica*-group; "*Fragilis*-complex"; and 1 species more or less related to these groups.
d. 5 species studied by QUÉZEL (1957): N. African species.
e. 32 species studied by other authors.

a, b, c: In the observations of PHITOS (1963), PODLECH (1962), and MERXMÜLLER and DAMBOLDT (1962) the present author finds a corroboration of his conclusions regarding the correlation of cytological and morphological characters. The species, studied by the authors mentioned, show a combination of morphological and cytological characters corresponding with the correlations in other species which were studied by the present author (cf. Table 8).

d: The observations of QUÉZEL (1953, 1957). QUÉZEL (1953) investigated the species *C. mairei* (n = 8) and in 1957 he studied the following species: *C. filicaulis* Dur. (n = 8, 24); *C. guinochetii* Quéz. (n = 14 or 16); *C. rotundifolia* L. ssp. *macrorhiza* (Gay) Guin. var. *jurjurensis* Chab. (n = 61); *C. saxifragioides* Doum. (n = 7 or 8); *C. vaillantii* Quéz. (n = 7). The species concerned belong to different groups of the genus.

1. *C. mairei* Pau (n = 8). This species is closely related to *C. persicifolia* (2n = 16). For this reason, the chromosome number reported by Quézel was to be expected.
2. *C. rotundifolia* L. ssp. *macrorhiza* (Gay) Guin. var. *jurjurensis* Chab. (n = 61).

At an earlier date the subspecies *macrorhiza* of *C. rotundifolia* was studied by GUINOCHET (1942) a.o. In his opinion 2 varieties are met with: a diploid type (var. *eumacrorhiza*, n = 17) and a tetraploid type (var. *angustifolia*, n = 34). Quézel regarded the forms of the Djurjura mountains (N. Africa) as hexaploid, and reported the number n = 61 for the variety *jurjurensis*. If this variety is hexaploid, the correct chromosome number should be n = 51 and not n = 61. Probably the number reported by him is due to a printer's error.

These forms, which differ in many respects from *C. rotundifolia*, are sometimes regarded as varieties of the species *C. macrorhiza* Gay: var. *macrorhiza* (2n = 34), var. *angustiflora* Tanf. ex Parl. (2n = 68), and var. *jurjurensis* Chab. (2n = 102). It is remarkable that the same cytological differentiation occurs within this S. European–N. African complex as well as in the collective species *C. rotundifolia*.

3. In his publication of 1953 Quézel discusses the species *C. mairei*: "Notons que chez *C. rapunculus* n = 10, alors que dans le groupe de rotundifolia n'est très élevé (34); il en est de même pour les diverses espèces nord africaines appartenant à la section *Medium*".

The other species reported by Quézel in 1957 belong to the section *Medium*. In view of these facts it is rather surprising that these appendiculate species should not have the basic number x = 17, but the numbers mentioned above. Moreover, Quézel observed intraspecific cytological variation in three out of four appendiculate species. 9 % (i.e. 5 out of 57 species) of the European species investigated, from various localities, show intraspecific cytological variation. However, of the North African species investigated, 50 % is characterized by this phenomenon. On the other hand, it may be possible that Quézel could not establish the chromosome number of these species with certainty (cf. the word "ou" between the counts given by him). Therefore, the species *C. saxifragioides* (n = 7 or 8) and *C. guinochetii* (n = 14 or 16) are not discussed further.

Most of the appendiculate species have the chromosome number 2n = 34. Of 30 species, investigated by the present author, 28 have the number 2n = 34, 1 species has the number 2n = 32, and 1 the number 2n = 24.

These facts, together with the reports of Quézel, suggest that beside the x = 17-series, also a series with the basic number x = 8 should exist. The following chromosome numbers might occur within this x = 8-series: 2n = 16, 24, 32, 48 (the first and last number of this series refer to North African species).

The numbers 2n = 24 (*C. dichotoma*) and 2n = 32 (*C. incurva*) will be discussed first. In many respects *C. incurva* is closely related to the species *C. lanata* (2n = 34) and *C. medium* (2n = 34), not to one of the species studied by Quézel. It may be possible that the number 2n = 32 was a result of reduction of the number 2n = 34 and not of doubling of the number 2n = 16. The other species, *C. dichotoma* (2n = 24) has many characters in common with *C. imeritina*, a perennial Caucasian species, placed by Fedorov in the subsection *Phasidianthe*. *C. dichotoma* differs from the appendiculate species, investigated by the present author, in having dichotomous branches and axillary flowers.

Though not related to *C. dichotoma* (2n = 24), *C. filicaulis* (2n = 16, 48) differs from other appendiculate species in the absence of an inflorescence, the flowers being more or less axillary. In the author's opinion, it is not impossible that the appendiculate species partly belong to the series with the basic number x = 17, partly to the series with the basic number x = 8. A reinvestigation of the North African species is desirable, however.

According to BÖCHER's hypothesis (1960), the number 2n = 34 may have arisen from the doubling of a trisomic diploid: [2 × (8 + 8 + 1)]. Undoubtedly, the species *C. persicifolia* (2n = 16) or *C. latiloba* (2n = 16), or their ancestors, are not involved in the formation of such trisomic diploids, as their chromosomes are very long and differ in shape from those of the species belonging to other cytological series within the genus. On the other hand, if Böcher's hypothesis is right, appendiculate species with the chromosome number 2n = 16, such as *C. filicaulis* or its ancestors, may have played an important rôle in this process. From the geographic point of view, however, this would be rather strange. In N. Africa only 7 % of the species of the genus occur (22 out of approximately 300 species). In the Caucasus and some adjacent regions more than 50 % of the total number of species of the genus is found. This part of the area may rightly be called the main variation centre of the genus. All subsections of the genus *Campanula* are represented here. Many species are restricted to the Caucasian region; they are endemics. All these facts point to the conclusion that the genus *Campanula* originated in the present main variation-centre and not in North-Africa. These facts may be of vital importance for the study of the evolution of the genus.

C. vaillantii Quéz., an appendiculate species having the diploid number 2n = 14, is not related to the exappendiculate species *C. colorata* (2n = 28) and *C. cashmiriana* (2n = 28). If Quézel's observation should be right, this number may be a result of reduction of the number 2n = 16 of one of the North-African appendiculate species. A reinvestigation of this species is also desirable.

e. There remain 32 species to be discussed of which 22 have a combination of morphological and cytological characters corresponding with that in the species studied by the present author. The following species belong to this category: *C. allionii* (2n = 34); *C. beckiana* (2n = 68); *C. betonicifolia* (2n = 34); *C. calamenthifolia* (2n = 34); *C. cenisia* (2n = ± 34); *C. dasyantha* (2n = 34); *C. gieseckiana* (2n = 34, 68); *C. hispanica* (2n = 68); *C. hypopolia* (2n = 34); *C. lingulata* (2n = 34); *C. moesiaca* (2n = 34); *C. morettiana* (2n = 68); *C. pallasiana* (2n = 34); *C. pelviformis* (2n = 34); *C. pilosa* (2n = 34); *C. piperi* (2n = 34); *C. raineri* (2n = 34); *C. ramosissima* (2n = 20); *C. rhomboidalis* (2n = 34); *C. sarmentosa* (2n = 34); *C. transtagana* (2n = 20); *C. uniflora* (2n = 34).

These observations confirm the conclusions derived from Table 8. These species will not be discussed any further.

The remaining 10 species are characterized by a combination of cytological and morphological characters not corresponding with that in the species studied by the present author. These species will be discussed briefly.

1, 2. **C. caucasica** Bieb. (2n = 102), **C. laciniata** L. (2n = 102).

Sugiura's counts (1942), 2n = 102, are seriously doubted in view of the fact that the appendiculate species, investigated by the present author, are never tetraploid or hexaploid. Moreover, according to Phitos (1963) some species that are closely related to *C. laciniata*, have the diploid chromosome number 2n = 34. A reinvestigation of these species is desirable.

3. **C. drabaefolia** Sibth. & Sm. (2n = 34).

This species is very closely related to *C. erinus* (2n = 28). For this reason, the chromosome number reported by Sugiura (1942) is undoubtedly incorrect.

4. **C. elegans** R. et Sch. (2n = 102).

Sugiura's count (1942), 2n = 102, is seriously doubted by the present author.

5. **C. imeritina** Rupr. (2n = 34).

In view of the fact that the species *C. dichotoma* (2n = 24) and *C. imeritina* are closely allied, the report of the chromosome number of *C. imeritina* (2n = 34) by Sugiura (1942) should be checked.

6. **C. macrostyla** Boiss. et Heldr. (2n = 20).

This species has a rather isolated position within the genus *Campanula*. According to Boissier, this species belongs to the group of appendiculate species of the subsection *Triloculares*, but Feer (1890, b) transferred the species to the new genus *Sicyocodon*. Though Feer's opinion seems to be well-founded, most authors did not agree with him, as in most floras the species is still referred to the genus *Campanula*. If Marchal's count (2n = 20) is correct, the chromosome number presents a new argument in favour of the splitting off of this species from the genus *Campanula*. The species *C. macrostyla* has nothing in common with the diploid species of the x = 10-series.

7. **C. mirabilis** Alb. (2n = 102).

As was pointed out in the discussion of the species *C. caucasica* and *C. laciniata*, the appendiculate species investigated by the present author turned out to be diploid. Therefore, Sugiura's counts (1940, 1942) are presumably incorrect.

8, 9. **C. propinqua** Fisch. et Mey (2n = 20); **C. reuteriana** Boiss. et Bal. (2n = 34).

These appendiculate annual species show a great resemblance to the species *C. dichotoma* (2n = 24). Therefore, the chromosome numbers of these species should be checked.

10. **C. psilostachya** Boiss. et Kotsch. (2n = 34).

At first, Boissier referred this species to the genus *Campanula*, later he transferred it to the genus *Podanthum* (this genus is also regarded as a subgenus of the genus *Phyteuma*). Morphological data support Boissier's opinion. SUGIURA (1942) counted the chromosome number of this species: 2n = 34.

Few cytological data are available of the genus *Podanthum*. ROSÉN (1931) counted the number 2n = 24 in 2 species, whereas SUGIURA (1940, 1941), who studied 4 species, counted: 2n = 24, 2n = 34, 2n = 102 in 2, 1, 1 species, respectively. In view of the many misidentifications made by Sugiura, a reinvestigation of the chromosome number of the species *C. psilostachya*, as well as an investigation of the relation between the genera *Campanula* and *Podanthum* are desirable.

E. A CORRELATION OF THE NUMBER OF CHROMOSOMES AND THE SIZE OF THE POLLENGRAINS

In his book "Variation and evolution in Plants", pag. 302, STEBBINS (1950) remarks:

"An increase in size of the individual cells is perhaps the most widespread effect of polyploidy. It often makes possible the use of measurements of certain cells of the plant, particularly the guard cells of the stomata and the mature pollengrains, to suggest the diploid or the polyploid condition of plants represented only by herbarium material, or in which for other reasons actual counting is not practicable".

From this, the conclusion may be drawn that much time can be saved by measuring the pollengrains. Stebbins, however, adds the restriction that the chromosomes of the species concerned should be of equal size.

BÖCHER (1960) measured pollengrains of a number of strains of the collective species *C. rotundifolia* L. He observed that in general the pollengrains of the tetraploid strains are larger than those of the diploid ones.

It seemed appropriate to check Böcher's observations and to compare the size of the pollengrains of the diploid and tetraploid strains with the size of hexaploid ones.

The method of preparation was the following: ripe, fresh pollengrains were dispersed in a solution of iodine in potassium iodide. By this method it was possible to distinguish the empty, the shriveled pollengrains, and the micropollengrains from the good ones. 100 pollengrains were measured in each plant. The pollengrains of fresh plants did not differ in size from the pollengrains of dried specimens.

Figure 2 gives a survey of the size of the pollengrains of 49 species.

The vertical lines represent the variation of the diameter of 75–100 % of the pollengrains of the species concerned.

From the figure the following conclusions may be drawn:

1. The diameter of the pollengrains of the species with long

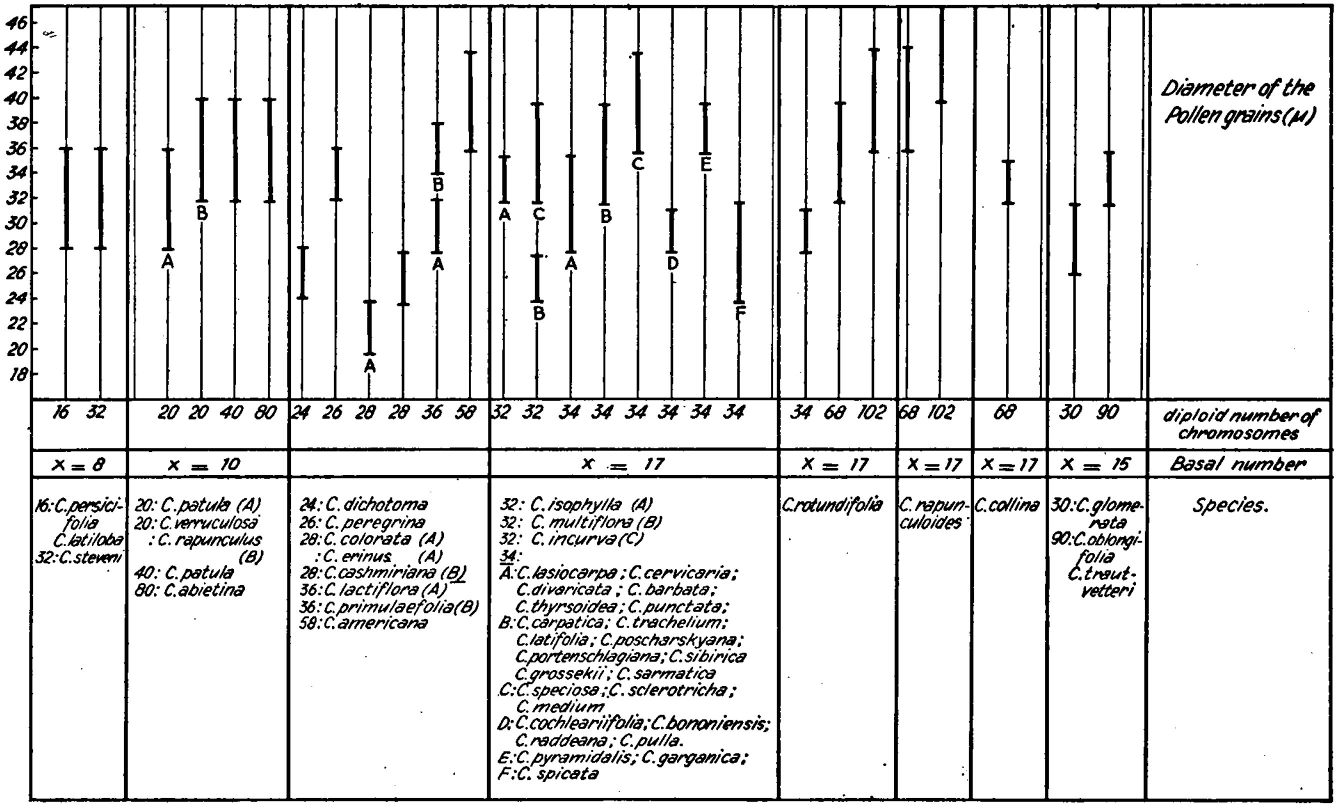

Fig. 2. The diameter of the pollengrains and the chromosome number of some species of the genus *Campanula*. Each vertical line represents the diameter of 75–100 % of the pollengrains of the species concerned.

chromosomes (x = 8-series) is not correlated with the degree of polyploidy.

2. Within the x = 10-series only the diploid and tetraploid strains of *C. patula* showed a correlation between the degree of polyploidy and the size of the pollengrains (Table 9). This correlation, however, could not be demonstrated in the octoploid species *C. abietina*, its pollen-size being more or less equal to that of the diploid species *C. verruculosa.*
3. Species with the chromosome number 2n = 28 have small pollengrains.
4. The species with the number 2n = 36 are heterogeneous with respect to the size of the pollengrains.
5. The species with the number 2n = 34 are heterogeneous with respect to the size of the pollengrains (cf. the size of the pollengrains of *C. medium* and *C. spicata*).
6. Within the collective species *C. rotundifolia*, the number of chromosomes is clearly correlated with the size of the pollengrains (Table 10a + b). Also some related diploid species: *C. excisa*, *C. cochleariifolia* and *C. pulla* have small pollengrains.
7. The pollengrains of some diploid species are larger than those of the tetraploid species *C. collina.*

Table 9

The relation between the size of the pollengrains and the degree of polyploidy of some species of the x = 10-series.

Species	Coll. no.	2n	Diameter (μ)				
			24–28	28–32	32–36	36–40	40–44
C. loeflingii Brot.	C 296	20	12	88			
	C 727	20	97	3			
C. rapunculus L.	C 252	20		36	64		
	C 376	20		1	93	6	
	C 490	20		3	79	18	
	C 492	20			94	6	
	C 521	20			58	42	
	C 563	20			49	51	
	C 618	20			27	69	4
C. verruculosa Hoffmgg. & Link	C 52	20			69	31	
	C 684	20			2	73	25
C. spruneriana Hampe	C 358	20			14	80	6
C. patula L.	C 115	20	10	88	2		
	C 316	20	4	83	13		
	C 541	20		2	62	33	3
	C 345	40		2	23	69	6
	C 611	40		1	59	30	10
C. abietina Griseb. & Sch.	C 613	80			64	33	3

8. Within the series *Rapunculoideae* Char. the degree of polyploidy is correlated with the size of the pollengrains (Table 11).
9. Within the series *Glomeratae* Char. the degree of polyploidy is also correlated with the size of the pollengrains.

TABLE 10A

The relation between the size of the pollengrains and the degree of polyploidy of 3 cytotypes of *C. rotundifolia* L. From each plant 100 pollengrains were measured. The origin of the material is indicated in Table 5.

Coll. no.	2n	Diameter (μ)					
		24–28	28–32	32–36	36–40	40–44	44–48
C 74	34	21	78	1			
C 77	34	26	70	4			
C 78	34	8	65	27			
C 79	34		75	25			
C 216	34	14	86				
C 390	34		58	42			
C 491	34	5	86	9			
C 6	68		15	82	3		
C 40	68		2	90	8		
C 41	68		2	20	76	2	
C 42	68		2	78	20		
C 111	68		2	81	17		
C 117	68			90	10		
C 125	68		4	92	4		
C 199	68		4	63	33		
C 237	68			94	6		
C 250	68		2	34	62	2	
C 341	68		48	50	2		
C 342	68	8	32	58	2		
C 420	68			13	87		
C 122	102			3	59	38	
C 330	102			11	76	13	
C 465	102				12	72	16
C 523	102				17	36	47
C 580	102			1	52	42	5

TABLE 10B

The relation between the size of the pollengrains and the degree of polyploidy of 3 cytotypes of *C. rotundifolia* L. (summary).

2n	Number of pollengrains measured	Diameter (μ)						
		24–28	28–32	32–36	36–40	40–44	44–48	48–52
34	700	74 =10½%	518 =*74* %	108 =15½%				
68	1300	8 = ½%	113 = 9 %	845 =*65* %	330 =25 %	4 = ½ %		
102	500			15 = 3 %	216 =*43* %	201 =40 %	64 =13 %	4 =1 %

TABLE 11

The relation between the degree of polyploidy and the size of the pollengrains of some species of the series *Rapunculoideae* Char.

Species	Coll. no.	2n	Diameter (μ)						
			24–28	28–32	32–36	36–40	40–44	44–48	48–52
C. bononiensis L.	C 276	34	2	92	6				
	C 403	34		38	62				
	C 649	34	6	92	2				
C. rapunculoides L.	C 456	68				41	59		
	C 862	68			1	35	50	12	2
	C 197	102				16	62	22	
	C 243	102				2	72	26	
	C 378	102				17	41	38	4
	C 399	102				4	35	59	2
	C 335	102					20	70	10
	C 405	102						80	20

The following conclusions may be drawn:

Only in a few instances the size of the chromosomes is correlated with the degree of polyploidy. This correlation could be demonstrated only in very closely related species, but there are exceptions. The results available show that in some groups valuable indications may be obtained from the simple method of measuring the pollengrains of herbarium material, for instance in the series *Glomeratae*, the series *Rapunculoideae*, and in the collective species *C. rotundifolia.*

CHAPTER IV

CROSSING EXPERIMENTS

A. INTRODUCTION

C. CROOK (1951) gives a survey of the hybrids of natural or garden origin known up to the present. He correctly remarks that hybrids of both categories are rare. According to him, the natural diversity of the genus may have fully satisfied horticulturists. In floras also, few hybrids have been recorded.

In some cases only one of the parent species of garden hybrids is known. Sometimes, species that are remotely related in taxonomical respect, are regarded as the parent species. It is not clear why closely related species hardly ever produce hybrids in nature, whereas in taxonomical respect the parent species of a number of garden hybrids may be related only remotely. For this reason, it will be necessary to check the identification of the parental species of some garden hybrids by crossing experiments. It was not the author's intention, however, to produce new garden hybrids or to identify the parent species of putative hybrids by these crossing experiments, but to test the features pointing to relationship, which were described in Chapter III.

As to the problem of self-sterility, there is no uniform opinion. Before turning to crossing experiments, it seemed appropriate to study this problem first.

B. SELF-POLLINATION EXPERIMENTS

According to KERNER (1891) and KIRCHNER (1897) self-fertilization may occur when there is no pollination by insects. This opinion is maintained in Hegi's Illustrierte Flora von Mittel-Europa (VI. 1) and in the Flora of the British Isles by Clapham, Tutin and Warburg.

On the other hand, WITASEK (1902) observed that a plant of the species *C. rotundifolia* failed to produce seeds after isolation. The present author never observed the production of ripe fruits and seeds in isolated individuals of the well-known indoor plant *C. isophylla*.

As the shape of the flower is generally closely related with the possibility of self-fertilization, some details of it will be given first. SPRENGEL (1793) describes the mode of pollination of 4 species, viz. of *C. latifolia, C. rotundifolia, C. patula, C. glomerata.* The flowers of these species are strongly proterandrous, and pass from the male into the female phase. Consequently, in the male phase self-fertilization is impossible. Sprengel distinguished the following phases in the development of the flower:

I. male phase:

1. flower closed; nectar absent; anthers closed and pressed closely against the hair collectors of the style.
2. flower closed; pollen is shed on the hair collectors of the style; the filaments are bent backwards now.
3. the flower opens; the style elongates, the stigmata forming an elongation of the style, not being spread; nectar present; insects visiting the flower for their nectar, pick up the pollen from the hair collectors on their legs; the filaments shrivel.

II. female phase:

1. the stigmata are spread, their receptive part being exposed now; pollination is completed by insects still visiting the flowers for their nectar.

Consequently, old flowers are pollinated (and fertilized) by young ones.

Notwithstanding the fact that Sprengel describes the above mentioned facts correctly, his observations do not give a satisfactory solution on the problem of self-sterility, because self-pollination may occur when the visit of insects fails to occur or is prohibited. Neither does de Candolle give a satisfactory explanation of this problem.

Besides extensive descriptions of the position of the hairs on the style, de Candolle draws attention to the mode of fertilization in the genus *Campanula*.

According to him, there are three explanations possible:

1. Insect-pollination (Sprengel).
2. Seeds formed without preceding pollination.
3. Self-fertilization.
   a. via the hair collectors before the flowers open.
   b. during the time in which the hair collectors are dropped the stigmata bend backwards, become more or less recurvate, and touch the pollengrains of the same flower.

In the opinion of de Candolle only few insects visit the flowers of *Campanula*, so that Sprengel's opinion may be wrong. In the opinion of the present author, this is not supported by the facts.

The fact that emasculated flowers produce seeds after isolation may be in favour of the second explanation. De Candolle emasculated some flowers before any pollen was shed, and observed that the artificially opened flowers did not develop themselves any further. This observation cannot be supported by the experiments of the present author. The development of the style was exactly the same in emasculated and in intact flowers, but emasculated flowers never produced seeds after isolation.

If explanation 3a should be right, the stigmata would be superfluous. A more detailed study on the morphology and function of the hair collectors was published by WILSON (1842) and BRONGNIART (1839). Brongniart observed that the hairs are retractile and invaginate when the flowers are open during a certain period. This is in contradiction with de Candolle's opinion that the hair collectors are caducous. The hairs are not massive and have a small aperture at the apex. A basal cavity of the hairs enables the invagination. During the invagination pollengrains are sometimes conveyed to the interior of the style. As there is no connection between the style-canal and the cavity of the hair collectors, it is impossible that pollentubes, which might be formed, should reach the ovules. Moreover, it appeared that the pollengrains germinated only on the papillae of the stigmata. Wilson confirms Brongniart's observation of the retraction by invagination of the hair collectors, but in his opinion germination of the pollengrains in the cavity of the hair collectors might result in the fertilization of the ovules, as, hardly ever, he observed pollengrains on the branches of the stigmata. Wilson, however, did not carry out experiments for the solution of the problem. The present author never observed that seeds were formed after dissection of the branches of the stigmata before anthesis. It would be rather strange if the stigmata were functionless.

The production of seeds in the ovaries of pendent flowers, enveloped in bags before anthesis, would be in favour of the last explanation (3b) given by de Candolle. But if this were true, erect flowers, enveloped in bags before anthesis, would never produce seeds. To investigate this, pendent as well as erect flowers of several species were enveloped in bags before anthesis. The results of these experiments are dealt with in Table 12.

TABLE 12

The position of the flower and the possibility of obtaining seeds after enveloping the flower bud.

Species	Position of the flower			Number of flowers enveloped	Number of capsules containing seeds
	erect	horizontal	pendulous		
C. alliariaefolia			x	4	0
C. barbata			x	7	0
C. bononiensis		x		7	0
C. carpatica	x			20	0
C. cochleariifolia (2n = 34)	x	x		16	0
C. glomerata (2n = 30)	x			42	0
C. grossekii		x		14	0
C. isophylla	x			10	0
C. lactiflora	x			2	0
C. latifolia	x			6	0
C. loeflingii (2n = 18)	x			7	0
C. medium		x		6	0
C. patula (2n = 20)	x			11	0
C. patula (2n = 40)	x			9	9
C. persicifolia		x		28	6
C. poscharskyana	x			13	0
C. pulla			x	7	0
C. rapunculoides (2n = 102)			x	18	0
C. rotundifolia (2n = 68)	x	x		45	0
C. rotundifolia (2n = 102)	x	x		8	0
C. sarmatica			x	16	0
C. sibirica		x		18	0
C. trachelium		x		18	0

From these results the following conclusions may be drawn:

1. The pollengrains of the same plant are hardly ever capable to fertilize the ovules.
2. The position of the flowers is not important with regard to the problem of self-fertilization.
3. In only one population of *C. persicifolia* and in plants of a tetraploid strain of *C. patula* self-fertilization occurred.
4. The pollen tubes do not reach the ovules via the hair collectors.

As no seeds were produced after enveloping the flower buds, a new experiment was carried out: with the aid of a pair of tweezers pollengrains were transferred to the stigmata of the same flower or to other flowers of the same plant. In this way the following species were pollinated—the numbers in parentheses indicating the number of self-pollinated flowers—: *C. aucheri* (3); *C. barbata* (7); *C. glomerata* (12); *C. grossekii* (16); *C. latifolia* (8); *C. latiloba* (5); *C. multiflora* (24); *C. oblongifolia* (7); *C. patula* (28); *C. persicifolia* (50); *C. punctata* (5); *C. rapunculoides* (7); *C. rapunculus* (25); *C. rotundifolia*, 2n = 34 (19); *C. rotundifolia*, 2n = 68 (13); *C. rotundifolia*, 2n = 102 (8); *C. sibirica* (18); *C. steveni* (3); *C. trautvetteri* (30); *C. tridentata* (13); only the self-pollinated flowers of *C. steveni* produced fruits with ripe seeds. In the remaining 290 flowers of other species no seeds were formed.

From these experiments the conclusion may be drawn that self-fertilization is a rare phenomenon and that the hair collectors play only a secondary rôle. The very frequent visits of insects clearly show that fertilization happens after cross-pollination, indeed.

C. INTERSPECIFIC CROSSES

1. *Introduction*

By crossing experiments between the species available an answer may be given to the following questions:

a. Is the x = 8-series isolated and homogeneous?
   Is the x = 8-series related to the x = 17-series?
b. Is the x = 8-series related to the x = 10-series?
   Is the x = 10-series homogeneous?
c. Is it possible to obtain hybrids from crosses between species with and without calyx appendages? Is it possible to intercross appendiculate species?
d. Is it possible to produce hybrids by crossing species with basal and apical dehiscence of the fruit?
e. Are the species of the x = 15-series related to or derived from the species of the x = 17-series?
f. Is it possible to intercross species of the series *Latifoliae* and *Rapunculoideae*?
   Are the two cytotypes of *C. rapunculoides* crossable?
g. Is it possible to produce hybrids by crossing the 3 cytotypes of *C. rotundifolia*?
   Can hybrids be obtained by crossing *C. rotundifolia* and some related diploid species?
h. Is it possible to make artificial hybrids between *C. americana* and some other species of the genus *Campanula*?
i. Is the species *C. lactiflora* crossable with some other species of the genus?

2. *Material and methods*

Before any pollen was shed (4–5 days before anthesis, depending on the weather-conditions), the flowers were emasculated by means of a pair of tweezers (care was taken to cause as little damage as possible). Access of insects was prevented by bags enveloping the flowers. At the time of anthesis the ripe pollen was placed on the fully developed branches of the stigma. Contamination by pollen of other species was prevented by the enveloping bags.

These interspecific crossing experiments were carried out with a number of strains. The following plants of *C. carpatica* (♀) and *C. persicifolia* (♂) were crossed: C 478 × C 559 (3 flowers); C 654 × C 150 (1); C 507 × C 150 (2); C 542 × C 261 (5); C 542 × C 559 (5); C 301 × C 261 (3); C 301 × C 559 (4); C 314 × C 603 (3); C 281 × C 603 (3); C 542 × C 603 (4); C 154 × C 150 (4). It was not possible, however, to cross the same number of strains in all cases.

After 6–8 weeks the seeds formed were harvested.

Morphological description as well as cytological investigations of the produced hybrids will be published at a later date[1]).

Intraspecific cross-pollination, carried out in this way, always resulted in the production of viable seeds. The method was, however, not checked in all species.

3. *Results*

The results of the crossing experiments are arranged in the same order as the questions were put.

a. The results of some interspecific crosses, the maternal plants being of the x = 8-series.

In morphological and cytological respect the x = 8-series is clearly distinct. Unfortunately, seasonal isolation prevented (at least under garden conditions) the crossing of *C. persicifolia* and *C. steveni*. *C. steveni* flowers in May, the other species in June and July.

Table 13 gives a survey of the interspecific crosses, the maternal plants being of the x = 8-series.

The following conclusions may be drawn:

> The species of the x = 8-series, as far as investigated, can intercross. No hybrids were obtained from crosses between the species *C. persicifolia* (2n = 16) with *C. isophylla* (2n = 32) and *C. persicifolia* (2n = 16) with *C. incurva* (2n = 32).
>
> The species *C. persicifolia* (2n = 16) and *C. carpatica* (2n = 34) are not crossable, although both species have the same mode of dehiscence of the capsule [the same is true for the cross between *C. latiloba* (2n = 16) and *C. carpatica* (2n = 34)].
>
> It was impossible to produce hybrids as a result of crossing *C. persicifolia* with appendiculate or exappendiculate species both with basal dehiscence of the fruit.

These experiments show that the x = 8-series, as far as investigated by the present author, has an isolated position in the genus. These facts confirm the conclusions based on cytological and morphological studies described in Chapter III.

b. The results of interspecific crosses, the maternal plants being of the x = 10-series.

Table 14 gives a survey of crosses between species, the maternal plants of which have the basic number x = 10.

4 diploid species of the x = 10-series are intercrossable (Table 14). No hybrids were obtained as a result of crosses between species of the x = 8- and x = 10-series.

c. Crosses between species with and without calyx-appendages.

The experiments demonstrated that sometimes hybrids were

---

[1]) The following hybrids died in a very early stage: *C. pyramidalis* × *C. carpatica; C. pyramidalis* × *C. isophylla; C. carpatica* × *C. pulla; C. spicata* × *C. thyrsoidea; C. spicata* × *C. multiflora; C. latifolia* × *C. trachelium; C. rotundifolia* (2n = 34 × 2n = 68); (2n = 34 × 2n = 102).

TABLE 13

The results of some interspecific pollinations; the maternal plants belong to the x = 8-series. +: hybrids obtained; —: no progeny. The numbers in parentheses indicate the number of pollinated flowers.

♂ → ♀ ↓	*C. persicifolia* (2n = 16)	*C. latiloba* (2n = 16)	*C. steveni* (2n = 32)	*C. verruculosa* (2n = 20)	*C. rapunculus* (2n = 20)	*C. abietina* (2n = 80)	*C. pyramidalis* (2n = 34)	*C. carpatica* (2n = 34)	*C. lactiflora* (2n = 36)	*C. isophylla* (2n = 32)	*C. incurva* (2n = 32)	*C. punctata* (2n = 34)	*C. grossekii* (2n = 34)	*C. trachelium* (2n = 34)	*C. rapunculoides* (2n = 102)
C. persicifolia (2n = 16)	+(5) —(78) (selfed)	+(7)		—(6)	—(12)		—(11)	—(40)	—(8)	—(7)	—(3)	—(8)	—(6)	—(4)	—(7)
C. latiloba (2n = 16)	+(3)	—(5) (selfed)						—(5)							
C. steveni (2n = 32)			+(3) (selfed)			—(3)									

TABLE 14

The results of some interspecific pollinations; the maternal plants belong to the x = 10-series. +: hybrids obtained; —: no progeny.

♂ → / ♀ ↓	*C. loeflingii* (2n = 18)	*C. verruculosa* (2n = 20)	*C. patula* (2n = 20)	*C. rapunculus* (2n = 20)	*C. patula* (2n = 40)	*C. abietina* (2n = 80)	*C. persicifolia* (2n = 16)	*C. steveni* (2n = 32)	*C. carpatica* (2n = 34)
C. loeflingii (2n = 18)	—(7)								
C. loeflingii (2n = 20)									—(11)
C. verruculosa (2n = 20)				+(5)			—(3)		
C. patula (2n = 20)		+(3)	—(31) selfed	+(3)					
C. rapunculus (2n = 20)			+(3)	—(25) selfed	—(4)				
C. patula (2n = 40)					+(9) selfed				
C. abietina (2n = 80)								—(2)	

TABLE 15

The results of interspecific pollinations between appendiculate and exappendiculate species. +: hybrids obtained; —: no progeny.

	Appendiculatae				Exappendiculatae				
♂ → / ♀ ↓	*C. alliariaefolia* (2n = 34)	*C. grossekii* (2n = 34)	*C. punctata* (2n = 34)	*C. sclerotricha* (2n = 34)	*C. trachelium* (2n = 34)	*C. bononiensis* (2n = 34)	*C. rapunculoides* (2n = 68)	*C. rapunculoides* (2n = 102)	*C. pyramidalis* (2n = 34)
Appendiculatae									
C. alliariaefolia (2n = 34)					+(10)				
C. grossekii (2n = 34)					+(8)	—(6)	+(6)		—(11)
Exappendiculatae									
C. trachelium (2n = 34)			—(14)	—(5)					
C. bononiensis (2n = 34)		—(26)							
C. rapunculoides (2n = 102)		—(14)	—(13)						
C. glomerata (2n = 30)		(+8)			+(4)			—(9)	

obtained by crossing appendiculate and exappendiculate species (Table 15).

C. grossekii could be crossed with *C. trachelium* and *C. grossekii* with *C. rapunculoides* (2n = 68). Even the species *C. alliariaefolia* and *C. trachelium* are crossable, but the hybrids show some yellowness in the leaves and remain small. After some months these hybrids died. Hybrids between *C. glomerata* and *C. grossekii,* and between *C. glomerata* and *C. trachelium* will be discussed under e.

The crosses between a number of appendiculate species are dealt with in Table 16.

Only in some cases hybrids were obtained.

d. Crosses between species with basal and apical dehiscence of the fruit.

As maternal plants were used: *C. lactiflora, C. pyramidalis, C. isophylla, C. persicifolia,* and *C. carpatica.* With respect to the dehiscence of the capsule these species form a morphological series. All species have erect fruits. The fruits of *C. persicifolia* and *C. carpatica* dehisc with apical pores, those of *C. lactiflora* with apical valves. The fruits of *C. pyramidalis* dehisc with medio-lateral pores and those of *C. isophylla* with basal valves. The results of the crosses of this category are shown in Table 17.

From the results mentioned in Table 17 the following conclusions may be drawn:

C. persicifolia (x = 8-series) is not crossable with any other species with apical, medial or basal dehiscence of the fruit.
C. carpatica (x = 17-series) is crossable with *C. pyramidalis* (erect, medio-lateral dehiscing fruits) and with *C. pulla* (pendent fruits with basal dehiscence).
C. isophylla (2n = 32) is crossable with *C. pyramidalis* (2n = 34).
C. lactiflora is not crossable with the other species with apical dehiscence of the fruit, investigated by the present author.

These conclusions are summarized in Figure 3.

This figure shows that a classification of the species of the genus *Campanula,* based on the mode of dehiscence of the capsule, is not natural. On account of this character *C. carpatica* has been classified in a group (section *Rapunculus,* dehiscence of the capsule apical) which is only distantly related to the group to which it should belong on account of the characters: cordate basal leaves, short chromosomes. Much more important is a classification on basis of *combinations* of characters. A classification of species with basal or apical dehiscence of the fruit on basis of the following combinations of characters seems justified:

- the combination short chromosomes, basic number x = 17, cordate basal leaves, apical or basal dehiscence of the fruit.
- the combination long chromosomes, basic number x = 8, lanceolate basal leaves, apically dehiscent fruits.

The relationship indicated by the combination of morphological

TABLE 16

The results of interspecific pollinations of appendiculate species among each other. +: hybrids obtained; —: no progeny.

♂ → / ♀ ↓	*C. medium* (2n = 34)	*C. sibirica* (2n = 34)	*C. alliariaefolia* (2n = 34)	*C. grossekii* (2n = 34)	*C. barbata* (2n = 34)	*C. aucheri* (2n = 34)	*C. tridentata* (2n = 34)	*C. sarmatica* (2n = 34)	*C. punctata* (2n = 34)	*C. ochroleuca* (2n = 34)	*C. lanata* (2n = 34)	*C. dichotoma* (2n = 24)
C. medium (2n = 34)	—(6) selfed	—(7)		—(5)	—(3)							
C. sibirica (2n = 34)		—(43) selfed	—(8)									—(2)
C. alliariaefolia (2n = 34)			—(4) selfed					+(2) —(3)		+(7)	—(5)	
C. grossekii (2n = 34)		—(10)	—(3)	—(30) selfed								
C. barbata (2n = 34)					—(14) selfed							
C. aucheri (2n = 34)						—(5) selfed						
C. tridentata (2n = 34)							—(13) selfed					
C. sarmatica (2n = 34)			—(7)	—(4)				—(16) selfed				
C. punctata (2n = 34)									—(5) selfed			

TABLE 17

The results of interspecific pollinations between species with apical, medial and basal dehiscence of the fruit. +: hybrids obtained; —: no progeny.

♂ → / ♀ ↓	Dehisc.: apical					Dehisc.: medial	Dehisc.: basal									
	C. persicifolia (2n = 16)	*C. carpatica* (2n = 34)	*C. lactiflora* (2n = 36)	*C. verruculosa* (2n = 20)	*C. peregrina* (2n = 26)	*C. pyramidalis* (2n = 34)	*C. isophylla* (2n = 32)	*C. pulla* (2n = 34)	*C. cochleariifolia* (2n = 34)	*C. rotundifolia* (2n = 68)	*C. waldsteiniana* (2n = 34)	*C. poscharskyana* (2n = 34)	*C. glomerata* (2n = 30)	*C. oblongifolia* (2n = 90)	*C. latifolia* (2n = 34)	*C. incurva* (2n = 32)
Dehisc.: apical																
C. persicifolia . . . . (2n = 16)	+(5) —(78) selfed	—(40)	—(8)	—(6)		—(11)	—(7)									—(3)
C. carpatica . . . . (2n = 34)		—(20) selfed	—(13)				—(25)	+(6)	—(11)	—(6)	—(3)	—(6)	—(8)	—(6)		—(4)
C. lactiflora . . . . (2n = 36)	—(6)	—(3)	—(2) selfed		—(3)	—(10)	—(8)								—(6)	
Dehisc.: medial																
C. pyramidalis . . . (2n = 34)		+(29)	—(7)	—(7)			+(14)									
Dehisc.: basal																
C. isophylla . . . . (2n = 32)		—(3)					—(10) selfed									

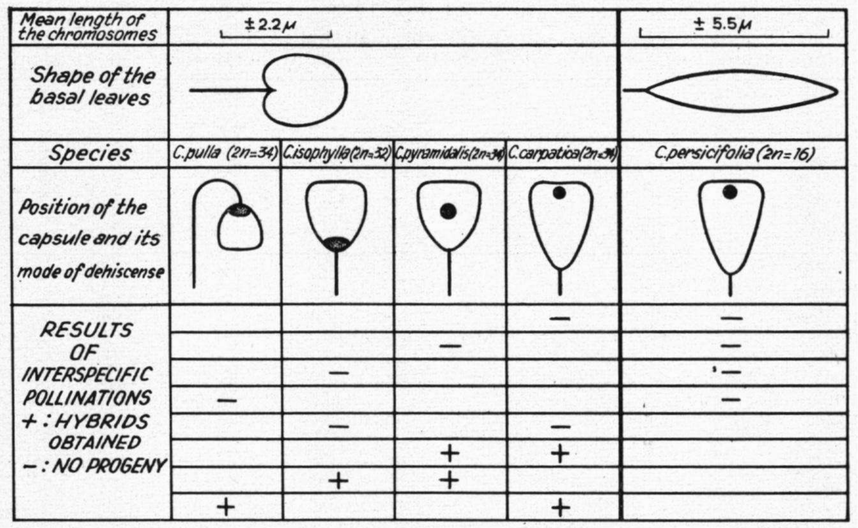

Fig. 3. The relation between some morphological and cytological characters on one side and the possibility of obtaining hybrids on the other side of some species of the genus *Campanula*.

and cytological characters (described in Chapter III) is confirmed by crossing experiments.

e. The relation between the x = 15- and the x = 17-series.

The species *C. glomerata* (2n = 30), *C. grossekii* (2n = 34), and *C. trachelium* (2n = 34) are intercrossable. Their hybrids have the chromosome number 2n = 32. Consequently, a close relationship between these species, and therefore also between the x = 15- and x = 17-series can be shown. The crossability of appendiculate and exappendiculate species has been demonstrated again (appendiculate: *C. grossekii*; exappendiculate: *C. glomerata* and *C. trachelium*).

Beside these crosses also some species of the subsection *Involucratae* (Fom.) Fed. were crossed: *C. glomerata* (2n = 30), *C. oblongifolia* (2n = 90), and *C. trautvetteri* (2n = 90), all belonging to the series *Glomeratae* Char. and *C. multiflora* (2n = 32) belonging to the series *Cervicariae* Fed. 2 species with spicate inflorescences were added to the above mentioned group of species, viz. *C. spicata* (2n = 34) and *C. thyrsoidea* (2n = 34). Both species belong to the group with sessile flowers (group 1 of the section *Eucodon* de Candolle). Table 18 gives a survey of the results of these crosses.

C. multiflora (2n = 32) is crossable with *C. spicata* (2n = 34), whereas the latter species is crossable with *C. thyrsoidea* (2n = 34). The hexaploid species *C. trautvetteri* and *C. oblongifolia* are also crossable.

Table 19 shows the crossability of some species in connection with their morphological and cytological characters.

This table clearly demonstrates that *C. multiflora* is more related

TABLE 18

The results of some interspecific pollinations, the maternal plants being of the x = 15-series (supplemented by *C. multiflora* and *C. spicata*). +: hybrids obtained; —: no progeny.

♂ → / ♀ ↓	*C. glomerata* (2n = 30)	*C. oblongifolia* (2n = 90)	*C. trautvetteri* (2n = 90)	*C. multiflora* (2n = 32)	*C. spicata* (2n = 34)	*C. thyrsoidea* (2n = 34)	*C. trachelium* (2n = 34)	*C. bononiensis* (2n = 34)	*C. rapunculoides* (2n = 102)	*C. grossekii* (2n = 34)
C. glomerata . . . . (2n = 30)	—(54)	—(6)	—(7)	—(9)	—(4)	—(4)	+(4)	—(3)	—(9)	+(8)
C. oblongifolia . . . (2n = 90)	—(20)	—(7)	+(11)							
C. trautvetteri . . . (2n = 90)			—(30)				—(9)			
C. multiflora . . . . (2n = 32)				—(24)						
C. spicata . . . . . (2n = 34)				+(9)		+(9)				

TABLE 19

The relation between some morphological and cytological characters on one side and the possibility of obtaining hybrids on the other side of some species with capitate and spicate inflorescences.

Species 2n	*C. glomerata* 30	*C. multiflora* 32	*C. spicata* 34	*C. thyrsoidea* 34
basal leaves: rosulate: + not rosulate: —	—	+	+	+
shape of the leaf	ovate-oblong, cordate at the base	lanceolate	linear-lanceolate	lanceolate
inflorescence	flowers in terminal or axillary glomerules	glomerules forming a discontinuous terminal spike	glomerules forming a more or less discontinuous terminal spike	glomerules forming a continuous terminal spike
duration of life	perennial	biennial	biennial	biennial
intraspecific pollinations: +: hybrids obtained —: no progeny	— — —	— +	— + +	— +

to the "spicate" species *C. thyrsoidea* and *C. spicata* than to *C. glomerata*, although the number of chromosomes of *C. multiflora* is intermediate.

f. Interspecific crosses between species of the series *Latifoliae* Char. and *Rapunculoideae* Char.

Although some seeds were obtained by crossing the species, it proved impossible to germinate them. Only *C. latifolia* and *C. trachelium* were successfully crossed, as well as the two cytotypes of *C. rapunculoides*. Table 20 gives the results of the interspecific crosses between the species of the subsection *Eucodon* (DC.) Fed.

TABLE 20

The results of interspecific pollinations within the group *Trachelioideae* [=subsection *Eucodon* (Boiss.) Fed.]. + = hybrids obtained; — = no progeny.

♂ → / ♀ ↓	*C. latifolia* (2n = 34)	*C. trachelium* (2n = 34)	*C. bononiensis* (2n = 34)	*C. rapunculoides* (2n = 68)	*C. rapunculoides* (2n = 102)
C. latifolia (2n = 34)	—(6) +(8)	—(8) +(8)			
C. trachelium (2n = 34)	—(18)	—(18)	—(11)		—(15)
C. bononiensis (2n = 34)		—(22)	—(7)	—(36)	—(51)
C. rapunculoides (2n = 68)		—(6)	—(22)		+(4)
C. rapunculoides (2n = 102)	—(5)	—(11)	—(36)	+(18)	—(25)

g. Crosses between the 3 cytotypes of the species *C. rotundifolia* L.

TABLE 21

The results of some intraspecific pollinations between diploid, tetraploid and hexaploid plants of *C. rotundifolia*. +: hybrids obtained; —: no progeny.

♂ → / ♀ ↓	*C. rotundifolia* (2n = 34)	*C. rotundifolia* (2n = 68)	*C. rotundifolia* (2n = 102)
C. rotundifolia (2n = 34)	—(19) selfed	+(11)	+(13)
C. rotundifolia (2n = 68)	+(8) —(5)	—(58) selfed	+(18)
C. rotundifolia (2n = 102)	—(6)	+(14)	—(16) selfed

Table 21 shows that hybrids were obtained from all crosses between the three cytotypes of this collective species.

Cytological investigations of the hybrids from the cross between tetraploid and hexaploid plants showed the number 2n = 85. These plants did not produce pollengrains, whereas seed-formation was not

TABLE 22

The results of some intraspecific pollinations between diploid, tetraploid and hexaploid plants of *C. rotundifolia*. Above broken line: intraspecific pollinations. Below broken line: self-pollinations.

♀		♂		Number of polli-nated flowers	Number of formed fruits with ripe seeds	Obtained hybrids viable or not
Coll. no. and origin of the material	2n	Coll. no. and origin of the material	2n			
C 79 W. Germany: Putlarktal	34	C 67 W. Germany: Lübeck	68	7	7	—
C 78 W. Germany: Hazelbrünn	34	C 480 Austria: N. Tirol	68	4	4	—
C 79 W. Germany: Putlarktal	34	C 523 France: St. Léger de Fourches	102	7	7	—
C 78 W. Germany: Hazelbrünn	34	C 122 France: Clermont-Ferrand	102	6	6	—
C 671 Carpathian Mts.	68	C 79 W. Germany: Putlarktal	34	7	7	—
C 138 France: Isneauville	68	C 79 W. Germany: Putlarktal	34	5	0	
C 813 France: la Clayette	68	C 651 Czecho-Slovakia: Praha	34	1	1	—
C 229 cult. mat.	68	C 122 France: Clermont-Ferrand	102	13	13	+
C 259 Czecho-Slovakia: Simonov	68	C 523 France: St. Léger de Fourches	102	5	5	+
C 523 France: St. Léger de Fourches	102	C 79 W. Germany: Putlarktal	34	6	0	
C 122 France: Clermont-Ferrand	102	C 32 cult. mat.	68	9	9	+
C 523 France: St. Léger de Fourches	102	C 422 the Netherlands: Marienberg	68	5	5	+
- - -	- - -	- - -	- - -	- - -	- - -	- - -
C 79 W. Germany: Putlarktal	34	C 79 idem	34	17	0	
C 8 France: Col du Lautaret	68	C 8 idem	68	6	0	
C 194 Italy: Valtellina	68	C 194 idem	68	14	0	
C 635 cult. mat.	68	C 635 idem	68	4	0	
C 480 Austria: N. Tirol	68	C 480 idem	68	9	0	
C 671 Carpathian Mts.	68	C 671 idem	68	13	0	
C 122 France: Clermont-Ferrand	102	C 122 idem	102	8	0	
C 523 France: St. Léger de Fourches	102	C 523 idem	102	8	0	

observed. Detailed morphological descriptions of these hybrids, as well as a study of the meiosis will be given in a later publication.

In Table 22 the places of origin of the plants, used in these intraspecific crosses, are given.

Table 23 shows that the species *C. cochleariifolia* (2n = 34) and *C. pulla* (2n = 34), related in some respects to *C. rotundifolia*, are not crossable with the cytotypes of *C. rotundifolia*.

TABLE 23

The results of some interspecific pollinations between *C. rotundifolia* and some morphologically related diploid species.

♂ → ♀ ↓	*C. pulla* (2n = 34)	*C. cochleariifolia* (2n = 34)	*C. rotundifolia* (2n = 34)	*C. rotundifolia* (2n = 68)	*C. rotundifolia* (2n = 102)
C. pulla . . . . (2n = 34)	—(7) selfed			—(3)	
C. cochleariifolia . . . (2n = 34)		—(16) selfed	—(6)	—(7)	—(9)
C. rotundifolia . . . . (2n = 68)		—(6)			
C. rotundifolia . . . . (2n = 102)		—(10)			

h. The results of some interspecific crosses, the maternal plants belonging to *C. lactiflora* Bieb.

The Tables 13 and 17 show that the species *C. lactiflora* Bieb. cannot be crossed with the other investigated species with apical or basal dehiscence of the fruit.

i. The results of some interspecific crosses, the maternal plant belonging to *C. americana* L.

C. americana L. differs from the other species of the genus *Campanula* in morphological and cytological respect. Crosses between this species and *C. lactiflora*, *C. isophylla*, and *C. carpatica* (7 pollinations in each case) did not result in the formation of seeds.

D. GENERAL CONCLUSIONS

1. Self-fertilization is the exception, cross-fertilization the rule.
2. The diploid species of the x = 10-series are intercrossable.
3. The species of the x = 8-series are not crossable with those of the x = 10- and the x = 17-series. The diploid species of the x = 8-series are crossable.
4. The x = 15-series is morphologically and genetically related to the x = 17-series. The species of the x = 15-series may have arisen through reduction from the x = 17-series.

5. It is impossible to give a natural classification of the species of the genus *Campanula* based on a single character. Therefore, the classification given by de Candolle and Boissier should not be regarded as natural. A classification that seems more natural is suggested in Chapter V.
6. Hybrids were produced between tetraploid and hexaploid plants of the species *C. rapunculoides*.
7. Hybrids were produced between the diploid, tetraploid and hexaploid strains of *C. rotundifolia*.
8. The species *C. lactiflora* and *C. americana*, which differ in morphological and cytological respect from the other species of the genus, are not crossable with other species of the genus as far as investigated up till now.

CHAPTER V

SOME GENERAL REMARKS ON THE CLASSIFICATION AND EVOLUTION OF CAMPANULA

A. Introduction

As Löve (1963) pointed out, cytological studies may give valuable information on the delimitation of genera. In his opinion morphological characters are the main criteria for the identification of a genus, but also the following cytological characters are of the greatest importance:

basic number of chromosomes;
size of the chromosomes;
shape of the chromosomes;

The data dealt with in the former chapters clearly showed that the genus *Campanula* is very heterogeneous in morphological and cytological respect. Therefore, the genus seems to be a collective genus. Although a splitting up of the genus is pointless, the delimitation should be considered in connection with other genera of the family *Campanulaceae*. It is the author's intention to continue his investigations in this direction. Such investigations may contribute to a better insight of the relation between and the delimitation of the genera *Campanula*, *Symphyandra*, *Legousia*, *Asyneuma*, and *Adenophora*.

For the time being, a provisional division of the genus into a number of groups can be given. In the author's opinion these groups can be regarded as natural groups. The decision to give only this provisional division is based on the following points:

Only 40–50 % of the species of the genus have been investigated morphologically as well as cytologically.
The interrelationship of the 7 groups is not clear, although some light has been thrown on this problem by crossing experiments.
The relationship of some groups of species to some other genera of the family *Campanulaceae* is not clear.

TABLE 24

The cytological and morphological characters of 7 groups of species considered to be natural.

Group	Cytological characters		Morphological characters							
								capsule		
	basic number of chromosomes	size of the chromosomes	basal leaves: cordate: + not cordate: —	duration of life	calyx appendages +: present —: absent	ratio length of the style length of the stigma	style: glabrous; not glabrous	number of locules	position: erect; not erect	apical, basal (medial) dehiscence
I	8	long	—	perennial	—	1:1(2)	glabrous	3	erect	apical
II	10	medium-sized	—	annual biennial perennial	—	8–5:1	not glabrous	3	erect	apical
III	13	short/ medium-sized	—	biennial	—	1:1	glabrous	3	erect	apical
IV	18(?)	very short	—	perennial	—	1:1	glabrous	3	erect	apical
V	12(?)	short	—	annual	+	7:1	not glabrous	3	not erect	basal
VI	14(?)	very short	—	annual perennial	—	10–6:1	not glabrous	3	not erect	basal
VII	17*) 15	short	+, —	biennial perennial	+, —	10–5:1	not glabrous (except for 1 species)	3(5)	erect/ not erect	mostly basal; sometimes apical or medial

*) Some species with the chromosome number $2n = 32$ are placed here.

B. SOME TAXONOMIC SUGGESTIONS

As was pointed out in the preceding chapters, the sections distinguished by de Candolle and Boissier cannot be regarded as natural. For this reason, the raising of the subsections of Fedorov's system to sectional rank suggested itself to the author. Although many subsections and series of his system seem to be natural, the crossing experiments showed that some of these subsections cannot be regarded as natural. In fact, species belonging to different subsections turned out to be crossable: e.g., *C. glomerata* (subsection *Involucratae*) × *C. trachelium* (subsection *Eucodon*), and *C. alliariaefolia* (subsection *Latilimbus*) × *C. trachelium* (subsection *Eucodon*). Therefore, the original plan of raising Fedorov's subsections to sectional rank has been abandoned and only a provisional subdivision of the genus is given (Table 24). A brief survey will be given, in which an attempt is made to show which species or groups of species (corresponding to Fedorov's subsections or not) belong to the groups distinguished by the present author. Future investigations will possibly reveal the real nature and interrelationship of these groups.

Group I: x = 8, 2n = 16, 32.

4 Species belong to this group: *C. persicifolia* (2n = 16); *C. latiloba* (2n = 16); *C. mairei* (2n = 16); *C. steveni* (2n = 32).

FEDOROV (1957) included *C. persicifolia* and *C. steveni* in the subsection *Campanulastrum* (Small) Fed. As the species *C. americana* L. is regarded as belonging to a separate genus for which SMALL (1903) used the name *Campanulastrum*, it is not clear why Fedorov used the name *Campanulastrum* for one of the subsections of his system. As was stated before, the opinion of Small is supported by cytological data and by the results of crossing experiments.

Both the subsection *Campanulastrum* and some of its series distinguished by Fedorov are to a great extent heterogeneous. A division of the series *Rapunculiformes* into 2 groups seems more natural: one group to which the greater number of the species belongs, all having the chromosome number 2n = 20 (or polyploids within the x = 10-series), and another, small, group to which the species of the x = 8-series belong. The last group should be placed in the series *Stevenianae* Fed., which probably is quite natural. The remaining species of this series should be investigated further.

Those plants of the species *C. steveni*, investigated by the present author, belong to the variety *sibirica* DC. Some authors regard this variety as a separate species: *C. altaica* Ldb.

Group II: x = 10; 2n = 18, 20, 40, 80.

To this group belongs the greater part of the species of the series *Rapunculiformes* Fed., as well as the annual species of the section *Rapunculus* of Boissier's system.

Group III: x = 13; 2n = 26.

The species *C. peregrina* L. belongs to this group. This species differs from practically all other species of the genus; only *C. primulaefolia* resembles *C. peregrina* in some respects. As *C. primulaefolia* has 36 very small chromosomes, a real relationship between this species and *C. peregrina* does not seem likely.

Group IV: x = 18 (?); 2n = 36.

To this group belong *C. lactiflora* Bieb. and *C. primulaefolia* Brot. The former species is characterized by the absence of "Saftdecken", i.e., the broadened basal part of the filament [this character is also absent in the species *C. erinus* (2n = 28) and *C. drabaefolia*]. In the other species of the genus *Campanula* "Saftdecken" are present. Owing to the absence of "Saftdecken" the annular nectar producing disc is visible between the short, stiff filaments. In view of this, group IV does not seem to be homogeneous.

From Figure 7 in de Candolle's monograph might be concluded that the fruits of *C. lactiflora* dehisc basally. This, however, is wrong, as the fruits always open by apical valves.

Probably the species *C. hieracioides* Kol. and *C. pontica* Alb. (both belonging to the series *Lactiflorae*) also belong to Group IV.

Group V: x = 12 (?); 2n = 24.

To this group belongs *C. dichotoma*. This species is closely related to *C. imeritina* (subsection *Phasidianthe* Fed.). It seems highly probable that beside *C. dichotoma* also the greater part of the group, consisting of annual appendiculate species of the section *Medium* sensu Boissier, belongs to this subsection, and, therefore, to group V.

Group VI: x = 14 (?); 2n = 28.

This group includes: *C. erinus*, *C. colorata*, *C. cashmiriana*. The classification in the genus *Campanula* of the first species mentioned, however, is subject to serious doubt, as the species differs in many characters from most other species of the genus. *C. erinus* is characterized by a very small tubular corolla, which is glabrous outside, by the absence of "Saftdecken", by glabrous filaments and by the dichotomously branched stems.

DUMORTIER (1822) placed the species *C. drabaefolia* and *C. erinus* in the genus *Roucela*. The present author agrees with Dumortier in this respect.

The characters of the other species show a strong resemblance. The broad foliaceous calyx lobes and the corolla, which is shortly pubescent outside, are conspicuous. The relation of these species to the other species of the "Himalayan-group" (cf. CL. CROOK, 1951) has to be clarified still. From the biosystematic point of view this group as a whole could be a very interesting object for study.

Some species of the subsection *Oreocodon* Fed., resembling the species mentioned above, may also belong to Group VI.

C. vidalii (2n = 56) should not be included in Group VI. There are many arguments in favour of Feer's view that the species should be transferred to the genus *Azorina* Feer. His arguments, based on morphological studies, are corroborated by cytological evidence (cf. number and size of the chromosomes).

Group VII: $x = 15$; $x = 17$; $2n = 30, 90$; $2n = 34, 68, 102$; $2n = 32$.

This group includes the greater number of species of the genus *Campanula*. The group is not homogeneous, but no clear discontinuities are seen. In the opinion of the present author, the following subsections of Fedorov's system belong to this group: *Quinqueloculares*; *Spinulosae*; *Triloculares*; *Dasystigma* (including *C. barbata* and *C. speciosa*); *Eucodon*; *Involucratae*; *Dictyocalyx*; *Cordifoliae*; *Latilimbus*; *Scapiflorae*; *Hypopolion*; *Heterophylla*; Also 3 subsections of the section *Rapunculus* belong to Group VII: *Rotula*; *Melanocalyx*; *Odontocalyx*. The species *C. zoysii* and *C. cenisia* may belong to this group, but further investigations are necessary to corroborate this statement. The delimitation of some subsections of Fedorov's system is subject to dispute as some hybrids were obtained from crosses between species belonging to different subsections.

The species *C. thyrsoidea* and *C. spicata* are closely allied to the species of the series *Cervicariae* (subsection *Involucratae*). The spicate inflorescence of these species consists of a number of congested glomerules. In fact, the capitate and spicate inflorescences do not differ essentially, both consisting of compact glomerules. Therefore, the species concerned should be classified in the subsection *Involucratae* and not in separate groups as was done in the classification of de Candolle and Boissier.

There is a striking resemblance between the species of the subsection *Symphyandriformes* and a number of species of the genus *Symphyandra*. Further investigations are necessary to determine whether it is correct to keep these groups apart or not.

The subsection *Scapiflorae*, consisting of 32 species, is well delimited. This subsection is extremely suitable for future biosystematic investigations.

C. THEORIES ON THE EVOLUTION OF THE CHROMOSOME NUMBERS

Many authors, following TISCHLER (1950), are of the opinion that the basic chromosome number $x = 17$ was the result of amphiploidy: a cross between species with chromosome numbers $2n = 16$ and $2n = 18$ ($8 + 9 \rightarrow 17$). Tischler, however, adds the following remark to this hypothesis: "Trotzdem der Nachweis bis jetzt nicht erbracht wurde". LARSEN (1954) and A. FERNANDES (1962) follow Tischler's hypothesis. BÖCHER (1960) assumed that the number $2n = 34$ was the result of the doubling of a trisomic diploid: $(8 + 8 + 1) \times 2$.

Neither Tischler's hypothesis nor that of Böcher can be supported by the facts mentioned in Chapter III and IV. At any rate, it is impossible to derive the chromosome number of the species of the $x = 17$-series from such species as *C. persicifolia* ($2n = 16$) and *C. loeflingii* ($2n = 18$) or their direct ancestors. Only species with short chromosomes (having the number $2n = 16$ and $2n = 18$) would give a satisfactory explanation of Tischler's hypothesis. Also Böcher's hypothesis would be supported by the existence of species (with short chromosomes) having the number 2n = 16. According to QUÉZEL (1957), species with the number 2n = 16 occur in the Atlas Mountains (N. Africa). A reinvestigation of the North African species is desirable, however.

A. FERNANDES (1962) regards x = 6 as the primary basic number of the genus. According to him polysomic evolution, combined with translocations, might have given rise to the remaining basic numbers: $x = 6 \rightarrow x = 7 \rightarrow x = 8 \rightarrow x = 9 \rightarrow x = 10$. If this hypothesis would be right, species with small chromosomes (x = 6) gave rise to species with very small chromosomes (x = 7) which in turn gave rise to species with very long chromosomes (x = 8). In the opinion of the present author, Fernandes' hypothesis does not seem plausible.

BÖCHER (1960) arranged the hypothetical origin of some chromosome numbers in a diagram (Fig. 4).

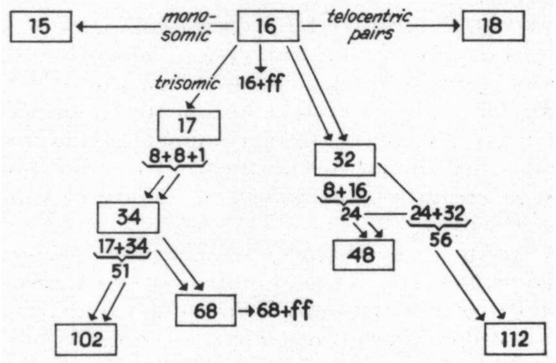

Fig. 4. Diagram showing a theory of the evolution of the chromosome numbers in the genus *Campanula* (taken from the paper by BÖCHER, 1960). Double arrows: doubling of the chromosome number; the somatic chromosome numbers are framed.

On Böcher's diagram the following remarks can be made:

Böcher's view on the origin of the numbers 2n = 68 and 2n = 102 corresponds with the present author's view.

Only *C. steveni* (2n = 32) originated from the diploid stock of the x = 8-series by chromosome doubling. The chromosome number 2n = 32 is probably derived by reduction from the number 2n = 34.

The explanation of the origin of the numbers 2n = 24 (16 + 8) and 2n = 48 (2 × 24) seems doubtful, unless QUÉZEL's (1957) counts are corroborated by later investigations. The numbers 2n = 56 and 2n = 112 (2 × 56) should be left out of the diagram.

The chromosome number 2n = 18 is possibly derived by reduction from the number 2n = 20, and did not originate by tetrasomic evolution from 2n = 16.

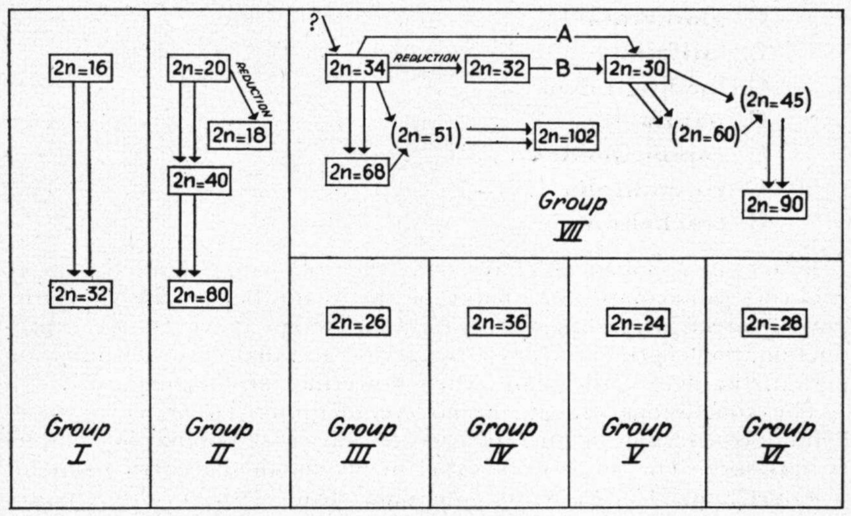

Fig. 5. The seven groups, considered to be natural by the present author. Within some groups the chromosome numbers are arranged according to their hypothetical origin. The origin of the number 2n = 30 might be explained by reduction of 2n = 34 directly (A) or via 2n = 32 (B). Double arrows: doubling of the chromosome number; the somatic chromosome numbers are framed.

The relation between the 7 groups, which the present authors regards as natural, is not known. Therefore, it is impossible yet to give a complete diagram of the origin of the chromosome numbers of the genus *Campanula*. Consequently, in Fig. 5 the hypothetical origin of the chromosome numbers is given only within a few groups. Further research is necessary to arrive at more definite conclusions concerning the origin of the chromosome numbers of the remaining groups.

CHAPTER VI

SOME POLYMORPHIC SPECIES

A. INTRODUCTION

Beside the correlation of morphological and cytological characters and the results of crossing experiments of a number of species and groups of species, also the intraspecific variability of a number of polymorphic species was studied. The species were grown under uniform conditions.

The following species will be discussed:

1. **C. cochleariifolia** Lam.
2. **C. garganica** Ten.

3. **C. glomerata** L.
4. **C. latifolia** L.
5. **C. loeflingii** Brot.
6. **C. patula** L.
7. **C. rapunculoides** L.
8. **C. rotundifolia** L.
9. **C. trachelium** L.

Beside morphological characters, the following characters were studied: winter-hardiness, habit of the plant before the flowering period (erect, ascending, prostrate), the extent of vegetative reproduction, the length of the flowering period and that of the germination period, the age of the plant when flowering for the first time.

The conclusions drawn are not yet definite. To arrive at more definite conclusions, a study of a greater variety of population-samples is necessary. The cultivation experiments should be carried out for a longer time. Consequently, the data dealt with in this chapter should be regarded as basis for further investigations. Thorough investigations on a broader basis are planned.

B. Experimental cultivations

The results of the experimental cultivations will be discussed separately for each species studied.

1. **C. cochleariifolia** Lam.

Although *C. cochleariifolia* is a polymorphic species (cf. Hruby, 1930, 1950), it appeared that the plants studied were fairly uniform. In the group "*Pusillae*" the chromosome number 2n = 68 was counted in plants of one strain (C 871) of garden origin. These plants show the characters regarded as typical for *C. cochleariifolia*: the shape of the basal leaves (cordate, almost circular leaves with usually three prominent teeth), the presence of the basal leaves during the flowering period, low stems and nutant flower buds, short, adpressed or more or less patent calyx-lobes of which the length is shorter than 1/3 of the length of the corolla, a short campanulate corolla, pink colour of the pollengrains. The only difference between strain C 871 and the typical *C. cochleariifolia* is the entirely glabrous stem (the stiff hairs are confined to the petioles). Alpine races with glabrous stems were described by Hruby (l.c.) under the name *C. cochleariifolia*Lam. subsp. *cochleariifolia* forma *umbrosa* Hoffm. subforma *notata* (Schott) Hr. The plants of strain C 871 have the same characters as those described by Hruby, therefore, these plants cannot be regarded as small plants of the species *C. rotundifolia*.

The other plants investigated differ mainly in the colour of the pollengrains (yellow in C 505 — C 526 — C 569; pink in all other plants) and in the length of the style (included in some plants, exserted in others).

TABLE 25

A survey of the differential characters of 5 species of the "*garganica*-group". The characters of the plants investigated by the present author are compared with those of the species distinguished by Feer.

Characters (according to Feer, 1890[8])		Species					Coll. no.							
		C. garganica Ten. p.p.	C. barbeyi Feer	C. istriaca Feer	C. fenestrellata Feer	C. lepida Feer	C 61	C 146	C 173	C 183	C 209	C 360	C 483	C 504
Indument	plant glabrous		×		×	×	×	×	×	×	×	×	×	
	plant not glabrous	×		×										×
Plant branched from the base		×	×				×	×	×	×	×		×	×
Plant branched from the middle				×	×	×						×		
Ratio depth : diameter of the corolla (mm)	10 : 15	×												
	10 : 12-14		×											
	10 : 12-20			×			×	×	×	×	×	×	×	×
	6 : 12-15				×									
	6 : 10					×								
Ratio length of pedicel : depth of flower	3-5 : 1	×					×		×		×		×	×
	1 : 1		×											
	2-4 : 1					×								
	2 : 1			×				×		×		×		
Capsule semi-ellipsoid; green longitudinal bands alternating with white ones					×		×	×	×	×	×	×	×	×
Capsule semi-ellipsoid; cyathiform or obconical; green		×	×	×		×								
Calyx-lobe lanceolate, narrowed towards the base					×		×	×	×	×	×	×	×	×
Calyx-lobe lanceolate, not narrowed at the base		×	×	×										
Ratio length of calyx-lobe : length of corolla-lobe	1 : 2	×								×				
	1 : 3		×	×	×	×	×	×	×		×	×	×	×
Corolla glabrous within		×	×			×								
Corolla very short pilose within				×	×		×	×	×	×	×	×	×	×
Shape of the basal part of the filament	cordate	×	×		×		×	×	×	×	×	×	×	
	deltoid			×		×								×
Colour of the pollengrains	sulphureous	×	×											
	blue				×		×	×	×	×	×	×	×	×
Ratio length of stigma : length of style	1 - 4			×										
	1 - 5					×								
	1 - 6				×		×	×	×	×	×	×		
	1 - 8	×	×										×	×
Seeds flat		×		×										
Seeds not flat			×			×	×	×	×	×	×	×	×	×
Seeds brown		×	×		×	×	×	×	×	×	×	×	×	×
Seeds yellow				×										
Seeds shiny			×			×	×	×	×	×	×	×	×	×
Seeds dull		×		×	×									
Flowering period	May					×								
	June	×	×	×	×		×	×	×	×		×		
	July				×		×	×	×	×	×	×	×	×
	August							×	×	×	×	×	×	×
	September							×			×	×		

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2. C. garganica Ten.

FEER (1890a) described 4 species which are closely related to, and often confounded with, *C. garganica*: *C. barbeyi*, *C. istriaca*, *C. fenestrellata*, and *C. lepida*. Table 25 gives a survey of the differential characters of these 4 species (and of *C. garganica*) and of the characters of the strains studied by the present author. The characters of the plants studied remained constant under uniform garden conditions.

From this survey the conclusion may be drawn that the plants investigated agree in many respects with the species *C. fenestrellata*, but differ from this species in some other respects. None of the plants studied agreed with *C. fenestrellata* in more than 9 out of 14 characters. In the author's opinion, there are two possible explanations to account for this discrepancy:

The plants investigated are interspecific hybrids.
Feer wrongly raised some forms to specific rank.

As only plants of garden origin were studied, it is not impossible that introgressive hybridization gave rise to the plants concerned.

Extensive investigations of plants in their natural habitat are necessary to determine whether the pure forms, described by Feer, occur in nature. Investigations on this problem are carried out by Merxmüller and Damboldt in Münich. For the time being, the plants studied are regarded as belonging to *C. garganica* Ten. (s.l.).

3. C. glomerata L.

C. glomerata is a highly polymorphic species. The chromosome number of all strains turned out to be 2n = 30.

C. farinosa (Roch.) Andrz. ex Bess. is often regarded as a variety of *C. glomerata*. In the author's opinion, however, *C. farinosa* should be regarded as a separate species:

a. Morphological criteria are: unbranched, long, densely greyish-tomentose stems (type A, Fig. 6); the leaves being very densely greyish-tomentose below (Fedorov correctly draws attention to the resemblance of the leaves of *C. farinosa* and *C. bononiensis*); the narrow elongate inflorescence, consisting of many dark-purple flowers. These characters remained constant under uniform garden conditions.

b. The flowering period begins late: in the experimental garden the plants begin to flower in the third week of July.

c. The geographic distribution shows marked differences: *C. farinosa* inhabits the Balkan Peninsula, Bessarabia, the Southern parts of the U.S.S.R., Asia Minor (except Turkey), whereas *C. glomerata* inhabits the Northern part of Europe and (partly) the same regions as *C. farinosa*. The species are ecologically isolated in the overlapping regions of the distribution area: *C. farinosa* occurs in the steppe-zone, *C. glomerata* in the wood-zone.

The species *C. glomerata* (2n = 30), *C. farinosa* (2n = 30), *C. oblongifolia* (2n = 90), and *C. trautvetteri* (2n = 90) resemble each other in many respects, but experimental cultivation under uniform conditions clearly showed that the differential characters are hereditary. Species with the number 2n = 60 have not yet been found, but it would be interesting to know if such species do occur. For this reason, it is desirable to determine the chromosome numbers of the following species: *C. cephalotes* Nak. (N.E. China and Japan), *C. subcapitata* Pop. (Carpathian Mountains), *C. symphytifolia* (Alb.) Kol. (Abchasia), *C. maleevii* Fed. (W. Transcaucasian region), and *C. panjutinii* Kol. (Abchasia).

Various modes of branching of the plants investigated are met with (Fig. 6). The mode of branching remained constant under uniform garden conditions (only in some cases plants showed branching type A in 1961 and type B in 1962 and 1963). The following branch-systems are distinguished:

type A: main stem of the plant unbranched [C 33 — C 126 — C 158 — C 184 — C 222 — C 298 — C 365 — C 457 — C 519 — C 604 — C 608 — C 612 — C 621 — C 665]. The plants of this type flower early (from the end of May and the beginning of June) and attain a height of 50 cm.

type B: main stem branched, lateral stems with terminal glomerules only (total "inflorescence" elongate) [C 177 — C 178 — C 389 — C 395 — C 398 — C 528 — 638]. The plants showing this branch-system are partly early-flowering, partly late-flowering. They vary in length from 40–110 cm.

type C: the same as type B, but the total "inflorescence" is corymbose [C 336]. This strain is early flowering, the plants are low.

type D: main stems branched, the lateral stems unbranched. Lateral stems with terminal and lateral glomerules. Total "inflorescence" elongate [C 66 — C 108 — C 110]. The plants showing this type of branching, flower late (after the first week of July) and attain a height of 70–120 cm.

type E: the same as type D, the total "inflorescence", however, is paniculate [C 116 — C 161 — C 297 — C 434 — C 614 — C 652]. The plants flower late and attain a height of ca. 100 cm.

type F: main and lateral stems branched, total "inflorescence" paniculate [C 402 — C 631]. The plants flower late and attain a height of 80–110 cm.

type G: the same as type F, total "inflorescence" corymbose [C 624]. The plants flower early and are moderately high (ca. 70 cm).

Most of the other characters studied are distributed at random among the plants showing the branching-types described before. The subtending leaves of the glomerules, however, are larger than the glomerules in plants showing branching type A. In other plants, showing other branching-systems, this character is variable. The

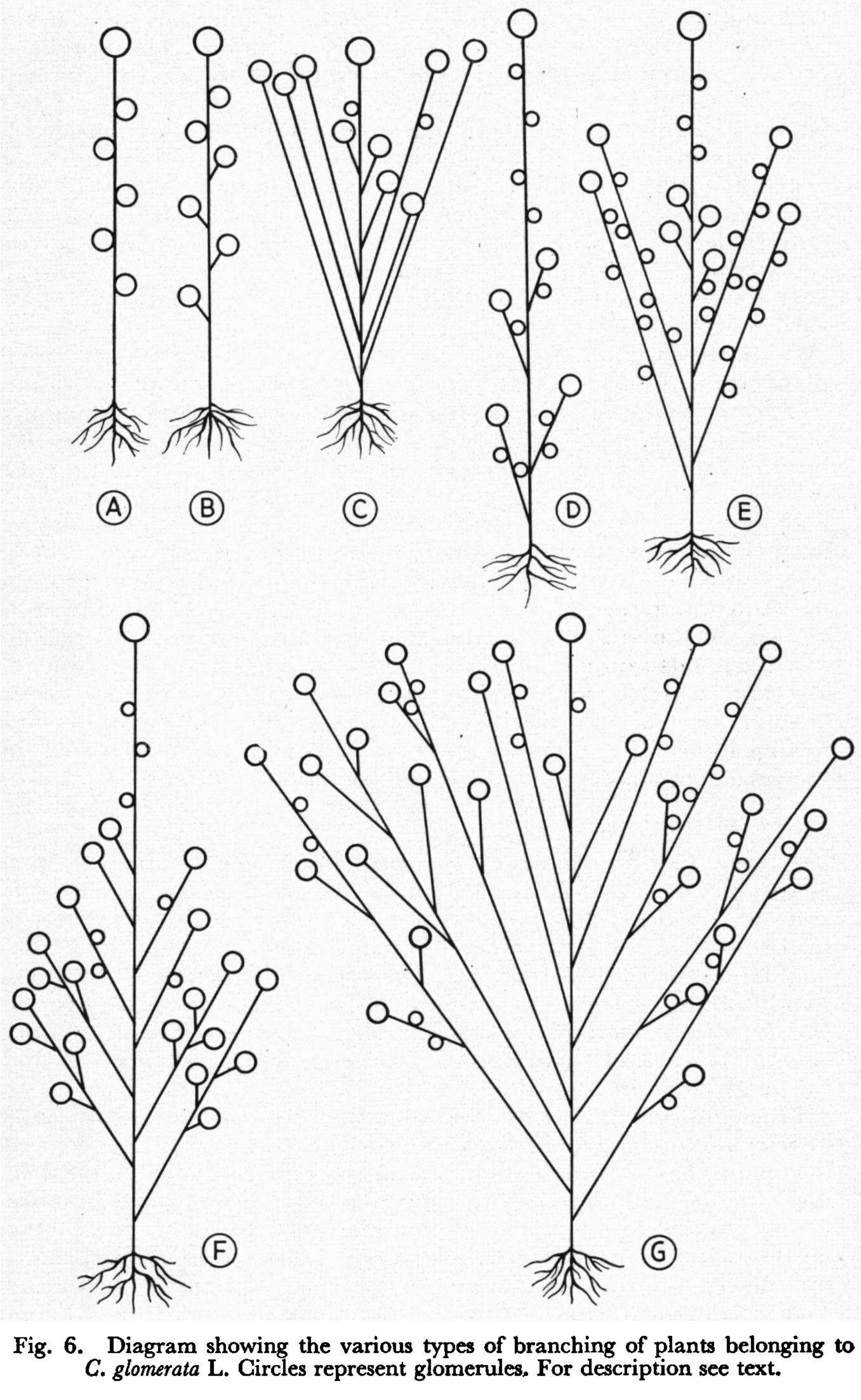

Fig. 6. Diagram showing the various types of branching of plants belonging to *C. glomerata* L. Circles represent glomerules. For description see text.

length of the corolla usually varies from 15–20 mm, but some strains are characterized by large corollas (25–27 mm). The corolla is usually glabrous outside, with the exception of those of plants with coll. no.: C 184 — C 222 — C 298 — C 624 — C 474 — C 589 — C 652. In these plants the corolla is more or less puberulous outside. In *C. farinosa* the corolla is also puberulous outside, but other characters generally suffice to distinguish this species from *C. glomerata*. The indument of the calyx is different in a number of strains: a. only outside densely hirsute; b. stiff hairs present on the margins of the calyx-lobes; c. a combination of a. and b.

It was not possible to refer the plants investigated to one of the varieties distinguished within the species *C. glomerata* L.: var. *aggregata* (Willd.) Koch, var. *elliptica* (Kit.) Koch, var. *serotina* Wettst. As all plants studied have a great number of glomerules, the plants cannot be referred to the varieties *elliptica* and *serotina* which show a maximum of 3 glomerules. Some strains may be referred to the variety *aggregata*, but in general they lack some characters regarded as typical for this variety.

Only a few of the investigated plants were dug out in nature, most of the plants were grown from seeds. For this reason, only in some instances the relation between the shape of the plant growing in nature and the shape of the plant under garden conditions, is known. In the author's opinion, it is desirable to study this relation first (in plants sampled throughout the distribution area) in order to ascertain whether the varieties described in literature are modifications or real intraspecific entities. The effect of environmental modification of a number of characters will be investigated by growing experiments under various conditions.

4. C. latifolia L.

A. de Candolle regards *C. macrantha* Fisch. and *C. eriocarpa* Bieb. as varieties of *C. latifolia* L.: *C. latifolia* L. var. *macrantha* (Fisch.) DC. and var. *eriocarpa* (Bieb.) DC. The variety *macrantha* is characterized by pilose stems and strigose acuminate leaves, glabrous calyx-tubes and large corollas; the variety *eriocarpa* is characterized by pilose stems, obtuse leaves and densely hispid calyx-tubes; the variety *latifolia* is characterized by glabrous stems, glabrous calyx-tubes and acuminate leaves. In Table 26 the characters of the plants investigated by the author are shown.

From this survey may be concluded that it is difficult or impossible to refer the investigated plants to one of the three varieties. None of the plants has a combination of characters regarded as typical for the varieties mentioned before. This may have been caused by intraspecific hybridization, as most plants are of garden origin. Neither do the plants of strain C 317 and C 656, collected in nature, match the description of the varieties concerned. Extensive herbarium studies, combined with transplant experiments of plants from different parts of the distribution area are necessary to arrive at a better delimitation of the intraspecific taxa.

TABLE 26

The variability of some strains of *C. latifolia* L.

Coll. no.	Height of the plant		Length of the leaves		Indument of the dorsal side of the leaves					Indument of the stem			Number of flowers/stem			Length of the corolla (mm)			Indument of the calyx tube	
	< 50 cm	> 80 cm	5–6 cm (not acuminate)	9–16 cm (acuminate)	glabrous	scarcely strigose	densely strigose	hairs adpressed	hairs erect	glabrous	scarcely pilose	densely pilose	1	5–9	14–16	30–35	35–45	45–50	glabrous	densely hispid
C 317	x		x				x	x				x		x			x			x
C 656	x		x			x		x		x			x					x	x	
C 48*		x		x	x					x					x		x		x	
C 153*	x		x				x	x			x			x		x				x
C 188*	x		x				x	x			x			x			x		x	
C 290*		x		x		x		x				x			x		x			x
C 339*	x		x				x	x				x			x		x		x	
C 485*	x		x				x	x				x	x			x				x
C 513*	x		x			x		x			x			x		x				x
C 534*	x		x				x		x			x		x				x		x

5. **C. loeflingii** Brot.

In 1962 R. Fernandes described the species *C. transtagana* and pointed out the characters in which this species differs from *C.loeflingii*. *C. loeflingii* has the chromosome number 2n = 18, *C. transtagana* 2n = 20. The plants investigated by the present author partly showed the number 2n = 18, partly the number 2n = 20. For this reason, it was supposed that some plants belong to *C. transtagana*. In morphological respect, however, the plants with the chromosome number 2n = 20 show a combination of characters regarded as typical for *C. loeflingii* by R. Fernandes (table 27).

Consequently, *C. loeflingii* may have 2 chromosome numbers, 2n = 18 and 2n = 20. The number 2n = 18 may be the result of reduction of the number 2n = 20, but further investigations are necessary to corroborate this supposition. In plants of two strains (C 296, C 727; 2n = 20) one pair of satellite bearing chromosomes is met with, whereas in the plants with the number 2n = 18 satellites could not be observed. The colour of the pollengrains was not described by Fernandes; de Candolle described the pollengrains of *C. loeflingii* as yellow. This, however, could not be confirmed, most plants having blue pollengrains. [except strain C 296 in which the pollengrains are yellow.] In Fig. 7 (A, B, C) plants having the number 2n = 18 are drawn, the plants with the number 2n = 20 are drawn in Fig. 8 (A, B, C). (See p. 88-91).

6. **C. patula** L.

Hitherto, only plants with the chromosome number 2n = 20 were found. It is true that Mattick (in Tischler, 1950) reported the number n = 25, counted in Austrian material, but this count could not be confirmed by Löve and Löve (1956) and by the present author. But in a number of plants, originating from Austria and Yugoslavia, the number 2n = 40 was counted. The pollengrains of the diploid plants are smaller than those of the tetraploid plants. It was impossible to distinguish the diploid and tetraploid plants morphologically (Table 28).

Diploid as well as tetraploid plants may have glabrous or hairy stems and leaves, large or small corollas and calyx-lobes, yellow pollengrains, and may or may not be winter-hardy. The flowering period of both types overlaps. The distribution area of both types is not known. Pollen-measurements may give valuable information on this problem.

7. **C. rapunculoides** L.

The chromosome number was determined in plants originating from 68 different localities [2n = 68 (2 ×); 2n = 102 (66 ×)]. The distribution of the tetraploid and hexaploid plants is shown in Figure 9. (See pag. 93).

Notwithstanding the close relationship of the tetraploid plants with the hexaploid West-European plants, it was supposed that the tetra-

TABLE 27

A comparison of the characters of the species *C. loeflingii* Brot. and *C. transtagana* R. Fernandes, and of the plants investigated by the present author.

Character	*C. loeflingii* Brot.	*C. transtagana* R. Fernandes	Collection number					
			C 210	C 307	C 556	C 597	C 296	C 727
height of the plant (cm)	–	–	25	30	30	35	35	40
plant strongly branched		x				x		x
plant less branched	x		x	x	x		x	
stem decumbent		x						
stem erect	x		x	x	x	x	x	x
cauline leaves attenuate towards the base		x			x			x
cauline leaves rotundate towards the base	x		x	x		x	x	
calyx tubes rounded at the base		x						
calyx tubes obconical	x		x	x	x	x	x	x
length of the corolla ≤ 13 mm		x						
length of the corolla > 13 mm	x		x (23 mm)	x (23 mm)	x (20 mm)	x (17 mm)	x (15 mm)	x (16 mm)
calyx lobes 3–5 mm long		x						
calyx lobes $>$ 3–5 mm long	x		x	x	x	x	x	x
stigmata very short		x						
stigmata long	x		x	x	x	x	x	x
pollen blue	–	–	x	x	x	x		x
pollen yellow	–	–					x	
capsule rounded at the base		x						
capsule not rounded at the base	x		x	x	x	x	x	x
$2n = 18$	x		x	x	x	x		
$2n = 20$		x					x	x

TABLE 28

A comparison of some diploid and tetraploid plants of *C. patula* L.

Character		Collection number						
		C 115	C 316	C 421	C 541	C 622	C 611	C 345
basal leaves	glabrous	x			x		x	
	hairy		x	x		x		x
stem	glabrous	x	x		x		x	x
	hairy			x		x		
mean height of the stem (cm)		55	50	55	45	45	50	70
mean length of the corolla (mm)		18	25	18	15	17	16	25
mean length of the calyx-teeth (mm)		7	8	5	6	6	4	8
colour of the pollengrains		purple	yellow	yellow	yellow	yellow	yellow	yellow
hardiness of the plant	hardy			x	x	x		x
	not hardy	x	x				x	
flowering period (1963)		7/6–20/8	1/6–16/7	7/6–17/7	27/5–27/7	1/6–17/7	16/6–20/7	15/6–30/7
2n = 20		x	x	x	x	x		
2n = 40							x	x

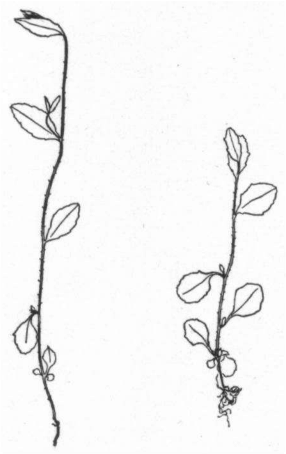

Fig. 7A. *C. loeflingii* Brot., 2n = 18; Coll. no. C 556.
A young plant of 7 weeks old.

Fig. 7B. *C. loeflingii* Brot., 2n = 18; Coll. no. C 556.
A plant of 10 weeks old.

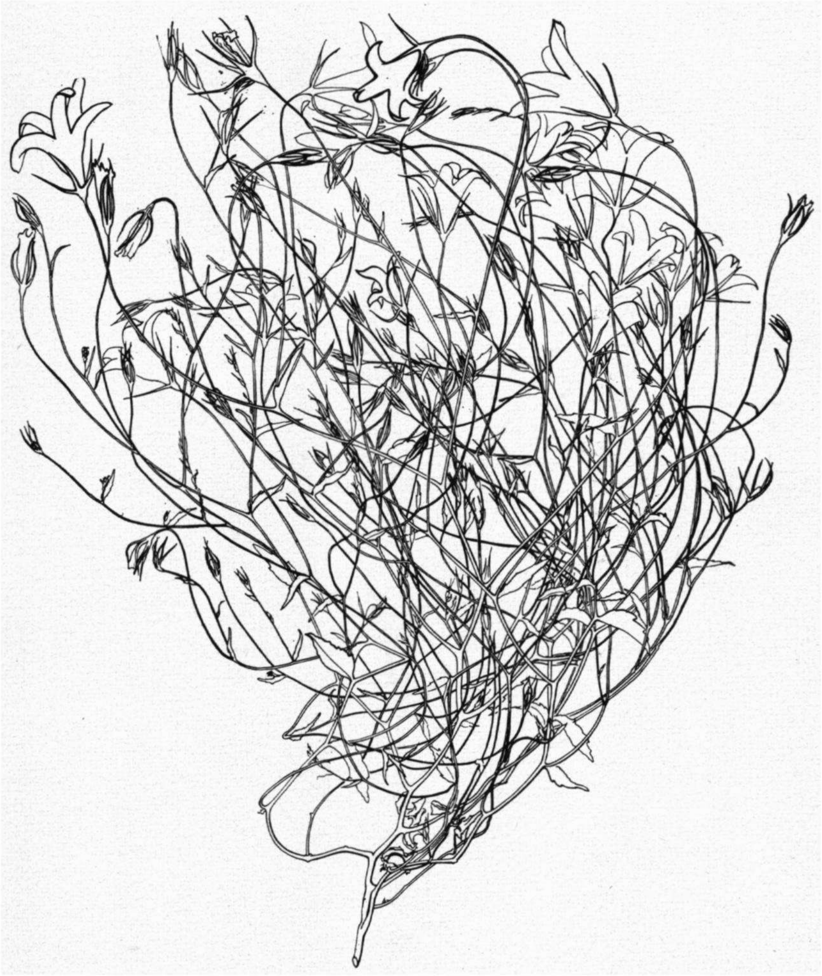

Fig. 7C. *C. loeflingii* Brot., 2n = 18; Coll. no. C 556.
A plant of 14 weeks old.

ploid plants might be referred to the East-European species *C. grossheimii* Char. or *C. cordifolia* Koch. (Table 29).

From the table, however, it is clear that this supposition is not correct; the tetraploid plants show a great resemblance to *C. rapunculoides*. Also, the results of the crossing experiments are in favour of the fact that the tetraploid plants should be referred to *C. rapunculoides*.

The plants (tetraploids as well as hexaploids), grown by the present author, did not match Fedorov's description in quantitative respect, for it appeared that hexaploid plants attained a height of 1.90 m in the experimental plot [C 332, C 267]. The base of the basal leaves is in most cases cordate, but also truncate and obtuse leaf-bases are

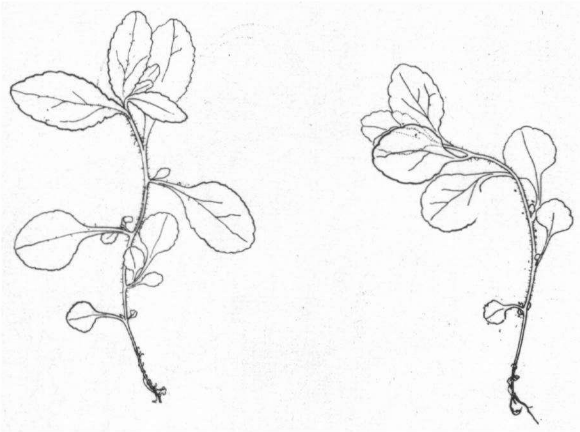

Fig. 8A. *C. loeflingii* Brot., 2n = 20; Coll. no. C 727. A young plant of 7 weeks old.

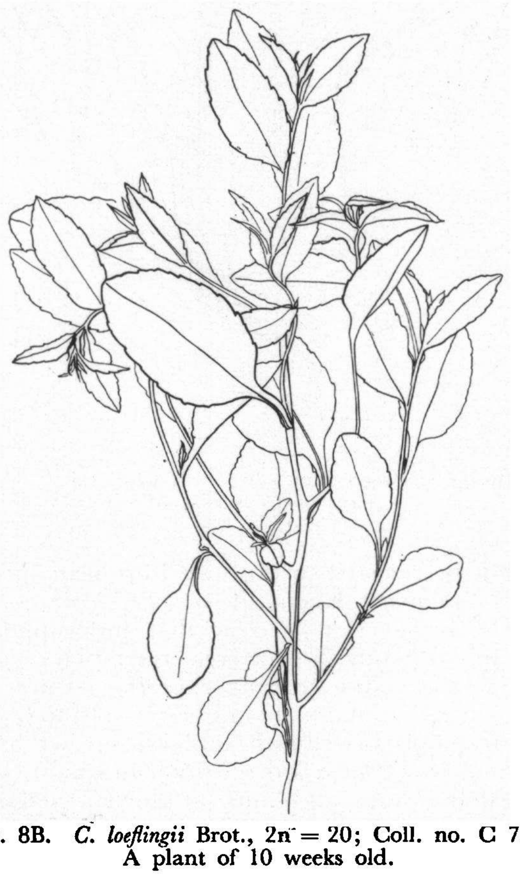

Fig. 8B. *C. loeflingii* Brot., 2n = 20; Coll. no. C 727. A plant of 10 weeks old.

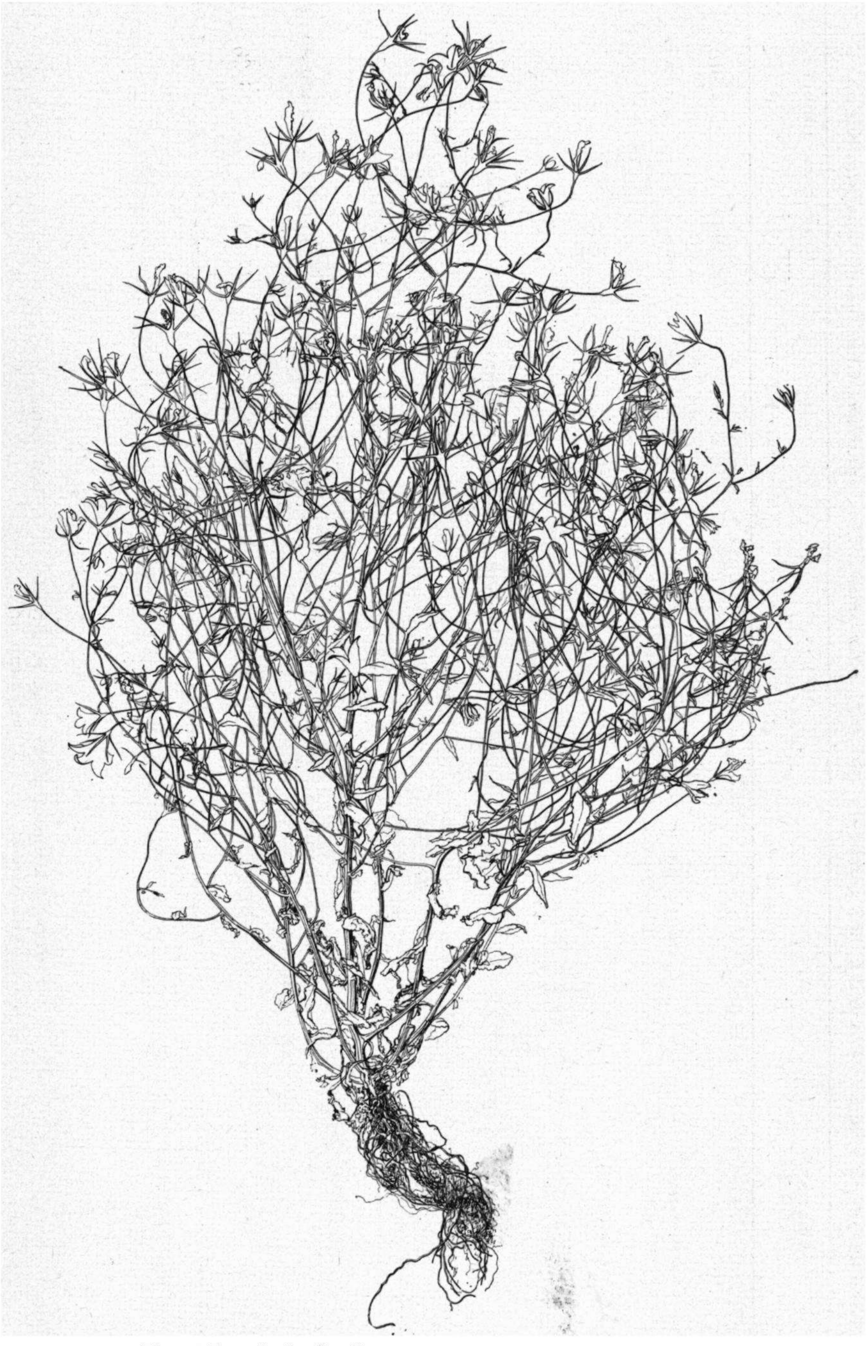

Fig. 8C. *C. loeflingii* Brot., 2n = 20; Coll. no. C 727.
A plant of 14 weeks old.

TABLE 29

The characters of the strains C 456 and C 862 and of the species *C. rapunculoides* L., *C. grossheimii* Char. and *C. cordifolia* Koch.

Character (according to FEDOROV, 1957)		Species			Collection number	
		C. rapunculoides L.	*C. grossheimii* Char.	*C. cordifolia* Koch	C 456	C 862
height of the stem (cm)		30–100	50–100	< 100	85–90	50
indument of the stem		shortly pilose (glabrous)	glabrous or pilose	glabrous (rarely pilose)	pilose	glabrous
base of the basal stem leaves cordate		x		x	x	
base of the basal stem leaves obtuse or truncate			x			x
indument of the leaves	upper surface	adpressed pilose	adpressed pubescent	hispid on the veins	adpressed pilose	glabrous
	lower surface	long hairs on the veins	long hairs on the veins		long hairs on the veins	glabrous
length of the basal stem leaves (cm)		5–15 (acc. to de Candolle)	ca. 10	small (length?)	4–5	6–7
indument of the calyx tube		densely puberulous (sometimes glabrous)	more or less hirsute	glabrous	long white-haired	glabrous
length of the corolla (mm)		20–25	30–40	10–23	27–29	26–28
shape of the corolla		campanulate or infundibuliform	campanulate	campanulate/ infundibuliform	infundibuliform	infundibuliform
colour of the flower	purple	x	x		x	x
	bluish			x		
distribution area		Europe, Caucasus, Asia Minor	W. and E. Transcaucasian area	Asia minor	—	—
diploid chromosome number		102	—	—	68	68

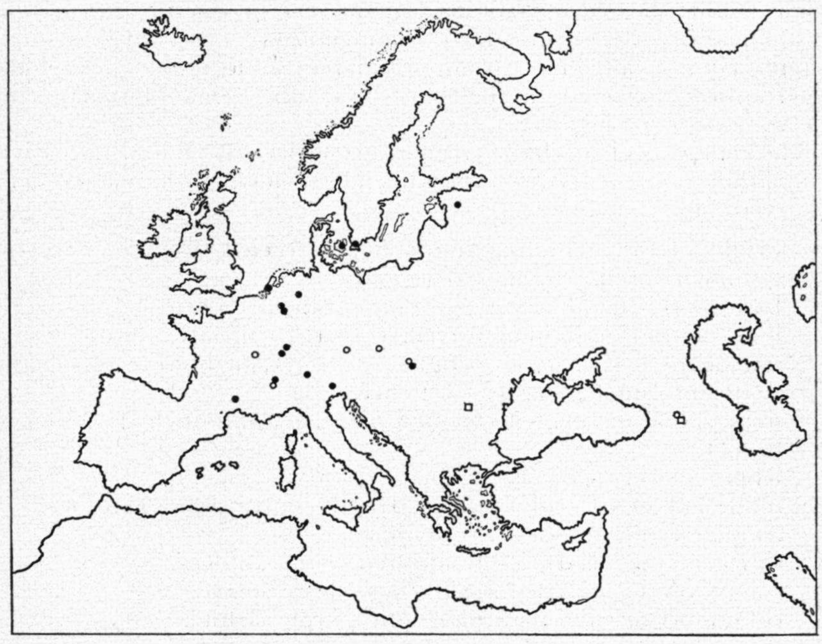

Fig. 9. The distribution of the investigated tetraploid and hexaploid plants of *C. rapunculoides* L.; Circles: hexaploid plants; Squares: tetraploid plants; Open circles and squares: flowering in the first year; Solid circles: flowering in the second year.

found, e.g., in C 251, C 433, C 501, C 537, C 547, C 620, C 621, C 632, C 644, C 645, C 672, C 673, C 674. In most cases, the basal stem leaves are truncate or obtuse at the base, and rarely cordate as was described by Fedorov. The calyx-tube of *C. rapunculoides* is puberulous, sometimes glabrous [C 53, C 212, C 354]. The corolla is often longer than 30 mm [C 243, C 335, C 468, C 536, C 537, C 626, C 632, C 644, C 672, C 674]. The shape of the corolla is campanulate in a number of strains and infundibular in others. All hexaploid and tetraploid plants have dark or light purple corollas (never bluish!). It seems not right to compare the characters of plants grown in an experimental garden with the descriptions given in floras, which are usually based on plants collected in nature.

Within the *Rapunculoideae* Char. an euploid series exists: $2n = 34$ (*C. bononiensis*); $2n = 68$ (*C. rapunculoides*); $2n = 102$ (*C. rapunculoides*). The number $2n = 102$ may have arisen by chromosome doubling of a triploid: $17 \times 34 \rightarrow 51$; $2 \times 51 \rightarrow 102$. It would be interesting to find out if diploid plants of *C. rapunculoides* occur in E. Europe, especially in the Caucasus. Also, chromosome counts in the species *C. grossheimii* and *C. cordifolia* are necessary to arrive at more definite conclusions concerning the origin of the number $2n = 102$.

All plants appeared to be hardy, the flowering period beginning in the period 25 June–7 July and ending in the last week of August.

Some strains showed a vigorous vegetative reproduction (formation of stolons), in other strains this phenomenon was observed to a small extent or not at all. Plants from 16 different localities (14 hexaploid, 2 tetraploid) flowered in their first year, the remaining plants in the second year (Fig. 9).

The morphological characters vary considerably, but within each strain they remained fairly constant. The following characters were observed (and remain constant):

height of the stem: maximum length varied from 50–195 cm
indument of the stem: hairy, glabrous.
base of the basal leaves: cordate, truncate, obtuse.
base of the basal stem leaves: cordate, truncate, obtuse.
size of the leaves: large, length > 10 cm; medium-sized, length 5–10 cm; small, length < 5 cm.
mode of branching of the inflorescence: unbranched; strongly branched.
length of the pedicels of open flowers: 2–17 mm.
indument of the calyx-tubes: densely puberulous, glabrous.
length of the corolla: 15–38 mm.
shape of the corolla: infundibular, campanulate.
colour of the pollengrains: yellow, grey, pink.
colour of the style: purple, light purple, white.
shape of the fruit: spherical, ovoid.

Various combinations of characters occurred in the strains studied. In fact, it appeared that the same combination of characters was not observed in any of the plants investigated. Some combinations of characters are rare: yellow pollengrains and a strongly branched inflorescence; vigorous vegetative reproduction and flowering in the first year of life; long pedicels and branched inflorescences; long (> 30 mm) and campanulate corollas; white styles and yellow pollengrains. Although there is a considerable intraspecific variability, it was impossible to divide the material into subspecies or varieties. In Fig. 10 the Armenian [C 456] plants are shown, in Fig. 11 the Romanian [C 862] plants.

8. **C. rotundifolia** L.

C. rotundifolia is a very complex species. The species is treated here in the sense of J. Hruby (1950). The following species, studied by the present author, are not regarded as belonging to this collective species: *C. caespitosa* Scop.; *C. carnica* Schied.; *C. cochleariifolia* Lam.; *C. excisa* Schleich. ex Murr.; *C. kladniana* (Schur) Wit.; *C. macrorhiza* Gay; *C. napuligera* Schur; *C. scheuchzeri* Vill. Plants originating from 128 different localities were cytologically investigated, the chromosome number being: 2n = 34 (11 ×); 2n = 68 (110 ×); 2n = 102 (7 ×). The distribution of these cytotypes is shown on the map (Fig. 12).

It was impossible to identify the plants of 3 strains:

a. C 627; 2n = 34 — seeds collected in 1961 by V. A. Gavriljuk in the polar regions of the Ural mountains (near Mt. Rais).

Fig. 10. A tetraploid plant of *C. rapunculoides* L., originating from Armenia (C 456). Below at right: a basal leaf.

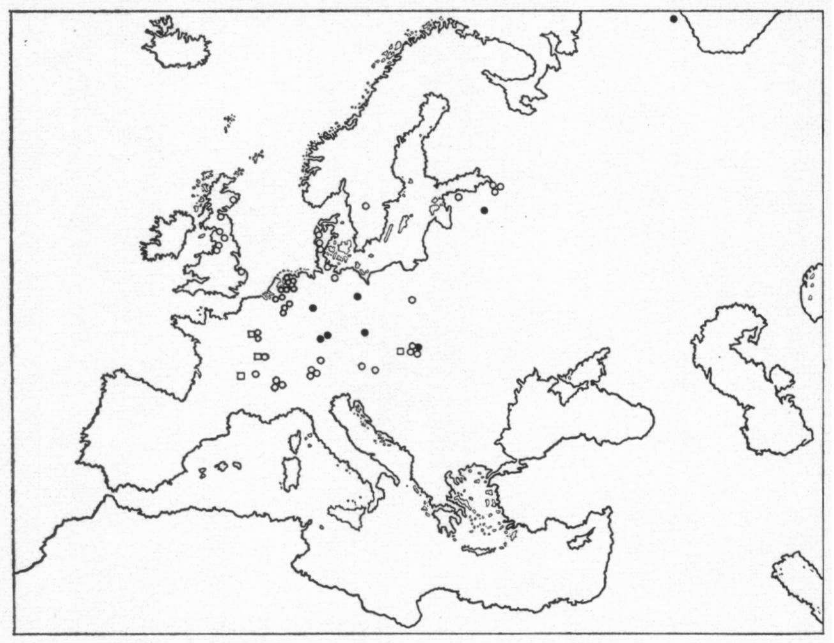

Fig. 12. The distribution of the investigated diploid, tetraploid and hexaploid plants of *C. rotundifolia* L.; Solid circles: diploid plants; Open circles: tetraploid plants; Squares: hexaploid plants.

b. C 22; 2n = 68 + 4 B — seeds supplied by the Botanical Garden of Toulouse, collected in nature at Termignon, French Alps, 1400 m.

c. C 731; 2n = 102 — seeds obtained from the Botanical Garden of Uppsala, collected in nature in Alaska.

These strains will be discussed first:

a. C 627 In 1962 the seeds germinated within 10 days, but the young plants remained small and prostrate. Contrary to the other strains of *C. rotundifolia* [with the exception of C 731], these plants did not flower in the first year. Also in 1963 the plants remained small and prostrate and did not flower. Probably the plants should be referred to the diploid subspecies *gieseckiana* of *C. gieseckiana* Vest in R. & Sch.

b. C 22. BÖCHER (1963) investigated plants from the same locality. He found the deviating number 2n = 72 + 4 B. On the other hand, the present author found the number 2n = 68 + 4 B, without any doubt, in various metaphase-plates of 2 plants. Apparently, the Termignon-population is heterogeneous in cytological respect. In many tetraploid plants B-chromosomes were counted by BÖCHER (1960). The present author, too, observed B-chromosomes in the following plants:

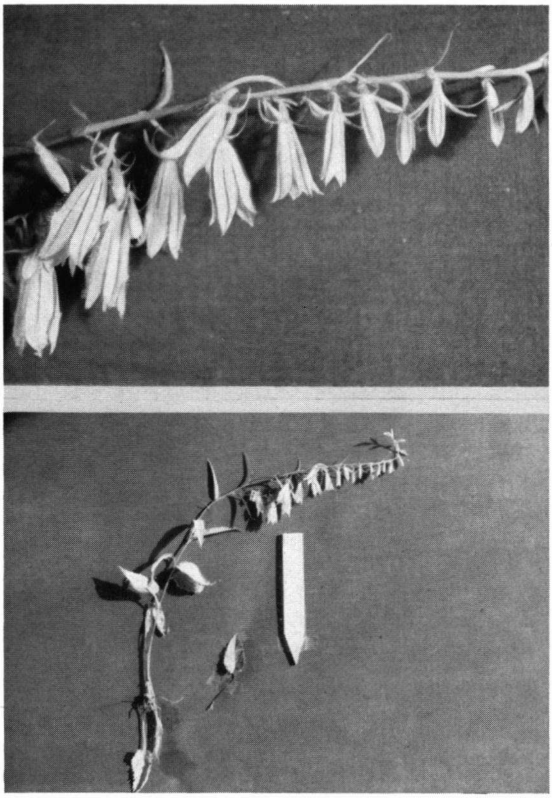

Fig. 11. Photographs showing a tetraploid plant of *C. rapunculoides* L., originating from Romania (C 862).

Fig. 17. The habit of 3 hexaploid strains of *C. rotundifolia* L., photographed in the last week of May, before the flowering period.
C 523: prostrate; C 580: ascending-erect; C 122: erect, very compact.

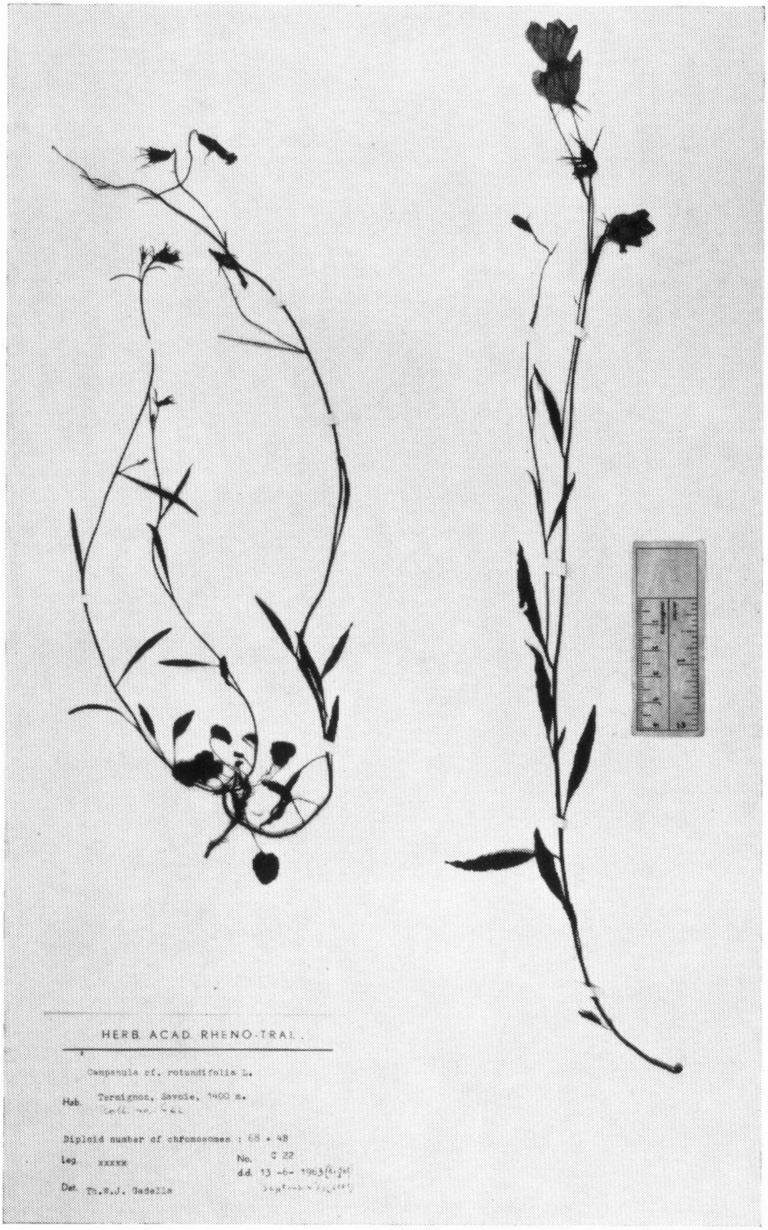

Fig. 13. The plants originating from Termignon, French Alps. (*C.* cf. *rotundifolia* L.; Coll. no. C (22).

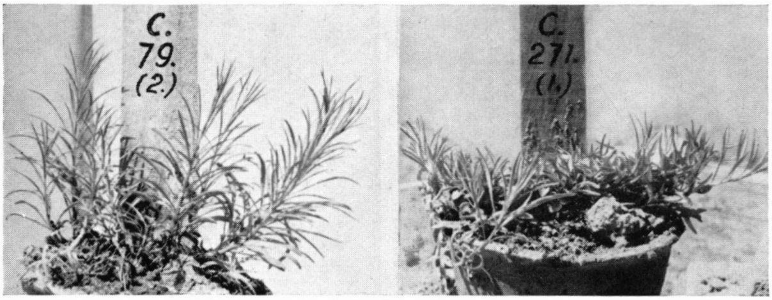

Fig. 15. The habit of 2 diploid strains of *C. rotundifolia* L., photographed in the last week of May, before the flowering period.
C 271: prostrate;
C 79: erect.

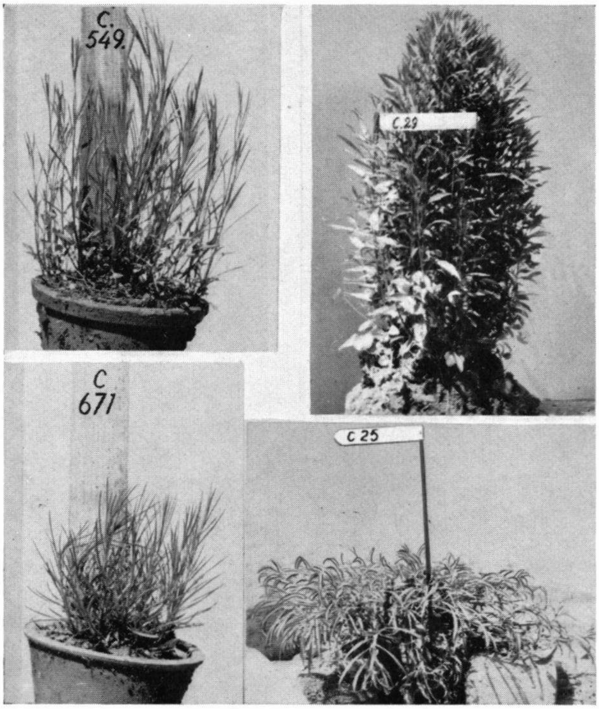

Fig. 16. The habit of 4 tetraploid strains of *C. rotundifolia* L., photographed in the last week of May, before the flowering period.
C 25: prostrate; C 549, C 671: erect, lax; C 29: erect, compact.

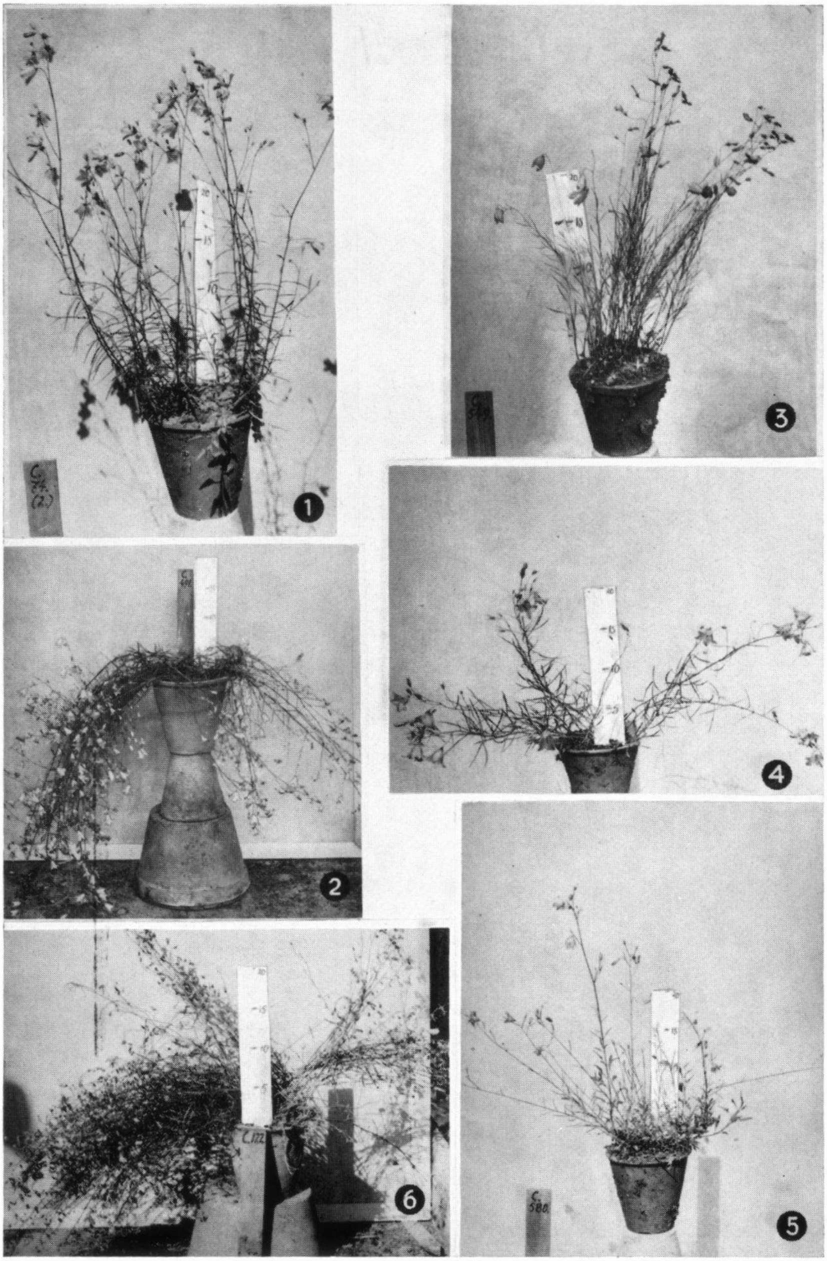

Fig. 18. The habit of a number of diploid, tetraploid and hexaploid plants of *C. rotundifolia* L., in the first week of August, during the flowering period. 1. C 74, 2n = 34, erect; 2. C 491, 2n = 34, pendulous; 3. C 549, 2n = 68, erect; 4. C 259, 2n = 68, patent-erect; 5. C 580, 2n = 102, erect-patent; 6. C 122, 2n = 102, erect at first, but becoming pendulous later on.

68 + 2 B : C 103; C 138; C 194; C 199; C 480; C 571; C 747; C 857.
68 + 3 B : C 17; C 769; C 836.
68 + 4 B : C 22; C 813.

The plants from Termignon show the same morphological characters as were described by Böcher [cf. Figs. 3 and 4 of Böcher's (1963) paper and Fig. 13 of this paper].

The plants are early flowering (from the last week of May). Böcher (1963) remarks (p. 117): "According to Merxmüller the plants are not identical with either *C. rotundifolia* or *C. scheuchzeri*, but might be interpreted as belonging to a hybrid between these species". According to Böcher, the plants may be of hybrid origin, but the following points do not support this view:

a. The chromosome number of the hybrid is 2n = 72 + 4 B, whereas the supposed parents (*C. rotundifolia* and *C. scheuchzeri*) have the number 2n = 68.
b. The pollenfertility is high.
c. No seeds were obtained after crossing plants of *C. rotundifolia* (2n = 68) and the Termignon-plants.

The first objection cannot refer to the plants investigated by the present author. The second and third objections are not in favour of a hybrid origin of the Termignon-plants. Böcher (1963) continues (p. 120): "At the present stage of knowledge the conclusion may be drawn that the plant from Termignon cannot be a primary hybrid between species with 2n = 68. However, it may have evolved from such a hybrid by subsequent chromosome repatterning and increase in chromosome number". The plants investigated by the present author might be regarded as primary hybrids, Böcher's plants as secondary hybrids within the same population.

c. C 731. The seeds germinated after 17 days, but the (hexaploid) plants remained small and did not flower in 1963 contrary to the plants of *C. rotundifolia* grown from seeds sown at the same time. As the plants did not flower, it was not possible to identify them, but the shape of the leaves justifies the placing of these plants in the collective species *C. rotundifolia* or in a related species.

The chromosome number 2n = 102 is a rarely occurring number in the "*Vulgares*-group":

C. rotundifolia L.: France; Czecho-Slovakia.

C. macrorhiza Gay var. *jurjurensis* Chab.: Djurjura Mountains (N. Africa).

C. pseudostenocodon Lac.: Italy.

C. rotundifolia L. ssp. *xylorhiza* Schwarz: Austria.

In Arctic regions only diploid and tetraploid plants are known up to the present [*C. gieseckiana* Vest in R. & Sch.: subsp.

gieseckiana 2n = 34; subsp. *groenlandica* (Berl.) Böch. 2n = 68]. Hexaploid plants were probably the result of chromosome doubling of a hybrid between diploid and tetraploid plants. In view of this, the 2 subspecies of *C. gieseckiana* might be involved in the formation of these arctic hexaploid plants. Further investigations, however, are necessary to arrive at more definite conclusions on this subject.

The other strains are highly polymorphic. The 3 cytotypes turned out to be indistinguishable in morphological respect. The diploid plants do not show a combination of morphological characters by which it might be possible to distinguish them from tetraploid and hexaploid plants. The size of the pollengrains is usually a "safe" indicator for the degree of polyploidy of the plants concerned.

A survey of the flowering period of diploid, tetraploid and hexaploid plants is given in Figure 14.

The following conclusions may be drawn:

Diploid plants flower late;
Tetraploid plants flower early or late;

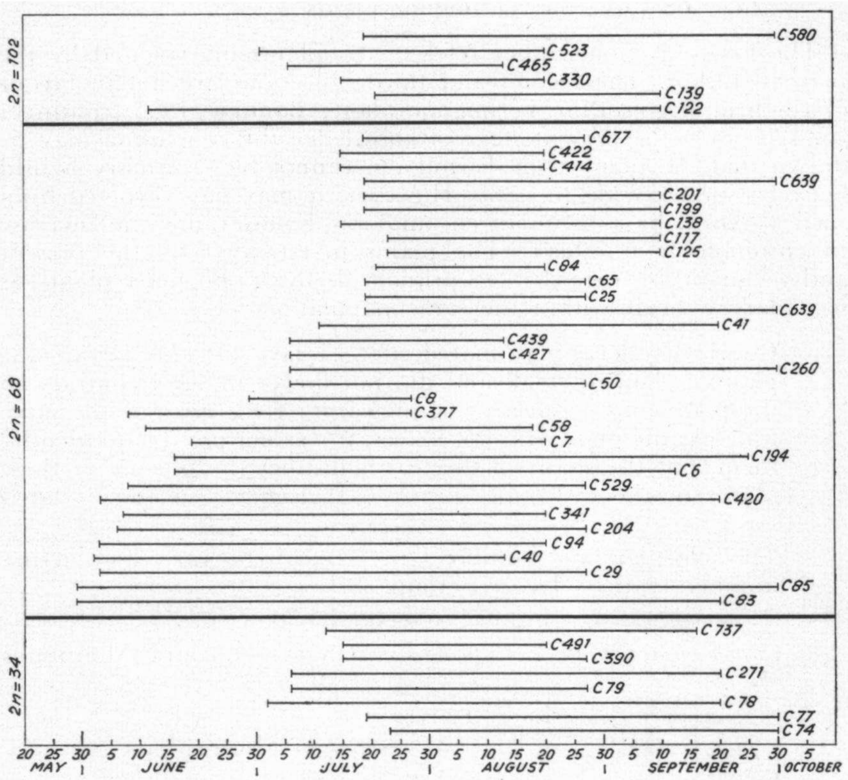

Fig. 14. The length of the flowering period of diploid, tetraploid and hexaploid plants of *C. rotundifolia* L., originating from different localities in Europe.

Table 30

Physiological and morphological characters of 7 diploid strains of *C. rotundifolia* L.

Coll. no.	Flowering period (1963)	Germination period (days)	Mean length of the stem (cm)	Cauline leaves gathered at the base (+ or —)	Transitional leaves: present + absent —	Shape of the cauline leaves	General habit before the flowering period	Number of flowers per stem				Mean length of the calyx teeth (mm)	Direction of the calyx teeth (adpressed; spreading; recurvate)	Mean length of the corolla (mm)	Mean width of the corolla (mm)	Shape of the corolla campanulate; infundibuliform	Colour of the corolla	Colour of the pollengrains	Style exserted or included	Colour of the style
								1–4	4–10	10–20	> 40									
C 77	19/7–30/9	16	45	—	+	linear	loose; prostr.	x	x			4	adpressed	13	8	camp.	light blue	pale grey	incl.	dark blue
C 78	2/7–20/9	18	35	—	+	linear	loose; prostr.	x	x			4	adpressed	14	8	camp.	blue	pale yellow	incl.	dark blue
C 79	6/7–27/8	12	35	—	+	linear	loose; erect		x	x		6	spreading	10	8	camp./inf.	dark blue	pale grey	exs.	dark blue
C 271	6/7–20/9	11	25	—	—	lin./lanc.	loose; prostr.			x		5	spread./recurv.	11	9	camp.	blue	pale grey	incl.	dark blue
C 390	15/7–27/8	10	60	+	—	lin./lanc.	compact; ascend.				x	6	adpressed	10	8	infund.	blue	purple	exs.	dark blue
C 491	15/7–20/8	23	80	—	+	lanceolate	loose; prostr.				x	4	spreading	8	8	camp.	dark blue	pink-purple	exs.	blue
C 737	12/7–16/9	18	40	—	+	lanceolate	loose; prostr.			x		6	spreading	15	15	camp.	blue	pale yellow	incl.	dark blue

Table 31

Physiological and morphological characters of 30 tetraploid plants of *C. rotundifolia* L.

Coll. no.	Flowering period (1963)	Germination period (days)	Mean length of the stem (cm)	Cauline leaves gathered at the base (+ or —)	Transitional leaves: present + absent —	Shape of the cauline leaves: linear; lanceolate; setaceous	General habit before the flowering period: loose; compact; erect; ascending; prostrate	Number of flowers per stem					Mean length of the calyx teeth (mm)	Direction of the calyx teeth (adpressed; spreading; recurvate)	Mean length of the corolla (mm)	Mean width of the corolla-opening (mm)	Shape of the corolla campanulate or infundibuliform	Colour of the corolla	Colour of the pollengrains	Style exserted or included	Colour of the style
								1–4	4–10	10–20	20–40	> 40									
C 420	3/6–27/9	9	50	—	—	lanceolate	loose; erect	x					6	spread./recurv.	18	15	infund.	dark blue	pale yellow	incl.	dark blue
C 549	2/7–23/9	29	—	—	—	lin./lanc.	loose; erect	x					5	adpressed	14	15	camp.	blue	pale grey	incl.	blue
C 138	15/7–10/9	13	80	—	—	lin. lanc.	loose; ascend.				x		3	adpressed	13	10	infund.	blue	purple	exs.	dark blue
C 348	24/6–13/8	15	45	—	—	lanceolate	loose; prostr.		x				4	spread./recurv.	13	11	camp.	dark blue	pale yellow	incl.	dark blue
C 671	6/7– 4/8	23	30	—	—	setaceous	loose; erect		x				3	spread./recurv.	15	15	camp.	blue	pale grey	incl.	blue
C 480	24/6– 4/8	19	45	+	—	lin./lanc.	compact; prostr.		x				4	adpressed	12	13	camp.	light blue	pale yellow	exs.	dark blue
C 29	3/6–27/8	13	25	+	—	lanceolate	compact; erect		x				5	adpressed	15	14	camp.	blue	pale yellow	exs.	dark blue
C 41	11/7–20/9	—	45	—	—	linear	compact; ascend.			x	x		4	adpressed	15	11	infund.	blue	pale grey	exs.	dark blue
C 58	12/6–13/8	—	25	+	+	lanceolate	loose; ascend.			x			4	spreading	12	12	camp.	blue	pale grey	incl.	blue
C 85	16/6–23/9	16	54	—	+	lin./lanc.	compact; prostr.					x	7	spread./recurv.	15	11	camp.	blue	pink-purple	incl.	blue
C 105	15/7–26/9	13	60	—	+	linear	compact; prostr.					x	6	adpressed	13	11	camp.	light blue	pale grey	incl.	dark blue
C 199	19/7–10/9	14	35	—	—	linear	compact; prostr.				x		3	adpressed	10	9	camp.	blue	pale grey	incl.	light blue
C 259	11/7–10/9	10	45	—	—	lin./lanc.	compact; erect		x	x	x		8	spreading	13	12	infund.	dark blue	purple	incl.	dark blue
C 73	15/7–10/9	—	50	—	—	lin./lanc.	compact; prostr.			x	x		6	spreading	11	10	camp.	light blue	pale grey	incl.	light blue
C 25	17/7–27/8	17	55	±	—	lin./lanc.	compact; prostr.					x	5	adpressed	12	9	camp.	blue	pale grey	exs.	dark blue
C 32	19/6–13/9	13	65	—	—	lin./lanc.	compact; erect			x			5	adpressed	17	16	camp.	blue	pale yellow	incl.	blue
C 6	16/6–12/9	18	55	—	—	linear	compact; prostr.				x	x	5	spread./recurv.	15	13	camp.	blue	pale yellow	incl.	blue
C 7	19/6–20/8	16	40	—	—	linear	compact; prostr.			x	x	x	4	spreading	14	11	camp.	dark blue	pale yellow	incl.	dark blue
C 152	2/7–13/8	13	60	—	—	lanceolate	compact; erect				x		3	adpressed	17	14	camp.	light blue	pale yellow	incl.	dark blue
C 201	19/7–10/9	14	50	—	—	linear	loose; erect			x			8	spreading	16	13	camp.	light blue	pale grey	exs.	dark blue
C 341	7/6–20/8	10	45	—	—	lanceolate	compact; erect			x			4	spreading	18	15	camp.	light blue	pale grey	incl.	dark blue
C 117	23/7–10/9	11	70	—	—	lin./lanc.	loose; prostr.			x			7	adpressed	15	12	camp.	blue	pale yellow	exs.	dark blue
C 260	6/7–27/9	13	50	—	—	linear	loose; erect			x	x		4	adpressed	13	9	infund.	dark blue	pink-purple	exs.	dark blue
C 99	19/7–20/8	—	40	±	—	setaceous	loose; prostr.			x			4	adpressed	13	10	infund.	light blue	pale yellow	exs.	light blue
C 423	15/7–20/8	—	45	—	—	linear	compact; prostr.				x		4	spread./recurv.	10	8	infund.	blue	pale grey	incl.	light blue
C 388	15/7–10/9	11	60	—	—	lin./lanc.	compact; prostr.					x	4	adpressed	12	11	camp.	blue	pink-purple	incl.	dark blue
C 577	6/7–20/8	17	80	—	—	lin./lanc.	loose; erect			x			5	adpressed	15	13	camp.	blue	purple	incl.	blue
C 83	19/7–20/9	13	80	—	—	lanceolate	compact; prostr.				x		5	adpressed	12	10	camp.	light blue	pale grey	exs.	dark blue
C 8	24/6–27/7	21	25	—	—	linear	loose; erect		x				3	adpressed	15	13	camp.	blue	pale yellow	incl.	dark blue
C 42	12/7–13/8	—	40	—	—	linear	compact; erect			x	x		8	spreading	8	7	camp.	blue	pale grey	exs.	dark blue

Table 32

Physiological and morphological characters of 5 hexaploid strains of *C. rotundifolia* L.

Coll. no.	Flowering period (1963)	Germination period (days)	Mean length of the stem (cm)	Cauline leaves gathered at the base (+ or —)	Transitional leaves: present + absent —	Shape of the cauline leaves	General habit before the flowering period	Number of flowers per stem			Mean length of the calyx teeth (mm)	Direction of the calyx teeth (adpressed; spreading; recurvate)	Mean length of the corolla (mm)	Mean width of the corolla (mm)	Shape of the corolla campanulate; infundibuliform	Colour of the corolla	Colour of the pollengrains	Style exserted or included	Colour of the style
								10–20	20–40	> 40									
C 122	12/6–10/9	27	45	—	—	linear	compact; erect		x		4	spread./recurv.	12	11	camp.	dark blue	pale grey	incl.	dark blue
C 330	15/7–20/8	13	45	—	—	linear	compact; erect	x			4	adpressed	12	10	infund.	dark blue	pale grey	exs.	dark blue
C 465	6/7–13/8	25	60	+	—	lanceolate	loose; ascending	x			5	spreading	15	14	camp.	blue	pale grey	incl.	dark blue
C 523	2/7–20/8	13	75	—	—	lin./lanc.	loose; prostr.			x	6	adpressed	16	12	camp.	light blue	pale grey	incl.	light blue
C 580	19/7–30/9	18	50	—	—	lanceolate	compact; ascend.			x	4	adpressed	10	8	camp.	light blue	pale grey	exs.	light blue

f. p. 100.

Hexaploid plants flower sometimes early [C 122], mostly late;
Generally, the early flowering tetraploid plants flower during a longer period than the late flowering tetraploids;
The beginning and duration of the flowering period is not correlated with the geographic latitude of the place of origin of the material.

Böcher (1960, p. 58 and 59) worked out a key as a summary of the description of the plants studied by him. He remarks: "The key is not intended to make all determinations possible of plants from nature and may therefore be most useful for future experimental work and for taxonomical considerations and treatments". In order to permit a comparison between Böcher's results and those of the present author, the characters listed in Böcher's key were studied.

Tables 30, 31, 32 show the characters of a number of diploid, tetraploid, and hexaploid plants.

Figures 15, 16, and 17 show the habit of diploid, tetraploid, and hexaploid plants before the flowering period. The habit of some plants during the flowering period is given in Figure 18.

From these figures and tables the following conclusions may be drawn:

a. *Diploid plants*

The diploid plants investigated by the present author have many (> 6) and small (sensu Böcher) flowers. In the plants investigated by Böcher these characters were correlated with the absence of transitional leaves and with cauline leaves that are more or less evenly distributed (group 9_I, Böcher, 1960). Only in plants of strain C 271 this combination of characters occurs. In the plants of strain C 390 the stem leaves are gathered towards the base. Therefore, the diploid plants studied by the present author cannot be incorporated in the key worked out by Böcher.

With regard to the size-classes of the flowers, the following remark can be made: the length of the corolla of the plants studied by the present author never exceeded a length of 19 mm. Generally, the corolla has a length of 12–15 mm. Böcher, on the other hand, considers flowers of 16–19 mm as small, and of 19–20 mm as medium-sized. He included the large-flowering species *C. gieseckiana* subsp. *groenlandica* in his key. This species was not studied by the present author, who regards flowers of 8–10 mm as small, of 11–15 mm as medium-sized, and of 16–18 mm as large.

b. *Tetraploid plants*

The tetraploid plants are extremely polymorphic. The plants of 2 strains [C 420 — C 549] are few-flowered (a maximum of 4 flowers per stem). This character is correlated in the plants studied by Böcher with stem-leaves gathered at the stem-base, the presence of transitional leaves, large flowers and arctic distribution. None of the strains investigated have transitional leaves and gathered stem-leaves. With regard to the number of flowers per stem these strains should be included in Böcher's group 5_{II}, with regard to the leaf-characters in group 9_{II}.

The plants of the strains C 671 and C 99 belong to Böcher's group 8_{I}.

The remaining tetraploid plants belong to Böcher's group 9_{II}. This group is very heterogeneous.

c. *Hexaploid plants*

The hexaploid plants have grey pollen grains. In most other respects they agree with the plants of Böcher's group 9_{II}. The pollen-grains of the hexaploid plants, however, are larger than those of the tetraploid plants of group 9_{II}.

As it was impossible to distinguish diploid, tetraploid and hexaploid plants by a certain combination of morphological characters, the 3 cytotypes might be regarded as intraspecific units. This view is supported by the fact that the cytotypes are intercrossable. The population samples, taken at random, probably represent only a small amount of the total variability of *C. rotundifolia*. The delimitation of the species *C. rotundifolia* and some other diploid and tetraploid species is not satisfactory. Extensive studies on this subject are necessary. The plasticity of a great number of characters and the crossability of a number of strains ought to be studied too.

9. **C. trachelium** L.

Although Hayek (in Hegi, 1925) does not regard this species as polymorphic, great (constant) differences were found between the plants studied. Beside physiological differences (beginning of the flowering period, length of the germination period and winterhardiness), constant morphological differences were found. Some plants began to flower in the first week of June, whereas others began to flower in the first week of August (most plants began to flower between 25 June and 7 July). The flowers of the early-flowering strains [C 123; C 416; C 481; C 610; C 666] are whithered when the late-flowering strains [C 82; C 373; C 375; C 442; C 443; C 444; C 446; C 642; C 646] begin to flower. The germination period varied considerably in length: 10–53 days. Some strains were not hardy, for, during the severe winter 1962/1963 many plants died.

The following characters vary considerably:

Height of the plants (varying from 50–130 cm).
Length of the largest leaf (varying from 5–18 cm).
Indument of the stem (glabrous; scattered or densely pilose).
Flower bearing stems (lax or compact).
Mean length of the calyx-lobes (varying from 7–17 mm).
Mean length of the corolla (varying from 18–42 mm).
Indument of the calyx-tube (glabrous; scattered or densely pilose).

Many combinations of the characters occur. It was impossible to divide the plants into varieties or subspecies. The early-flowering strains could not be distinguished from the late-flowering strains by a certain combination of characters.

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