

## SOME NOTES ON THE DELIMITATION OF GENERA IN THE CAMPANULACEAE. II

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### DISCUSSION

In this chapter some problems of classification of "borderline" species and of segregates from some genera are discussed. The position of *Triodanis* versus *Specularia* and the delimitation of the genera *Phyteuma* and *Campanula* is also taken into consideration.

### I. SEGREGATES FROM CAMPANULA

a. *the position of the species with the diploid chromosome number  $2n = 28$ .*

*Campanula erinus* L. and *Campanula drabifolia* Sibth. are closely related and differ from other annual species of *Campanula* by their glabrous filaments, which are gradually broadened towards the base, their dichotomously branched stems, and their sepals, which enlarge after the flowers wither and then become unequal (at least in *C. erinus*), thus simulating a zygomorphous condition. Dichotomous branching also occurs in the appendiculate species *Campanula dichotoma* L. (not as distinctly as in *C. erinus*), but its filaments are of the same shape as in most other species of the genus *Campanula*. Most *Campanula* species are characterized by the diploid chromosome number  $2n = 34$  (or by a polyploid level derived from the base number  $X = 17$ ). The number  $2n = 28$  occurs in the species mentioned before and in *Campanula colorata* Wall. in Roxb. (GADELLA, 1964; PODLECH and DAMBOLDT, 1964), *Campanula cashmeriana* Royle (GADELLA, 1964), *Campanula adsurgens* Ler. et Lev. (PODLECH and DAMBOLDT, 1964), and *Campanula arvatica* Lag. (PODLECH and DAMBOLDT, l.c.). These species have the following distribution: *C. erinus* and *C. drabifolia*: the Mediterranean region; *C. arvatica* and *C. adsurgens*: Spain; *C. cashmeriana* and *C. colorata*: the Himalayan region. In spite of their identical chromosome numbers these species are certainly not related to each other and seem to have developed from different stocks. All species lack calyx-appendages. The Spanish species have apically dehiscent fruits, the dehiscence in the other species is basal. Only *C. erinus* and *C. drabifolia* are dichotomously branched. *C. adsurgens* is placed in the *Garganica*-group by H. CL. CROOK (1951).

DAMBOLDT (1965, a) made an extensive study of the *Garganica* group and excluded *C. adsurgens* on the basis of the chromosome number and the mode of dehiscence of the capsule (in the *Garganica*-group the dehiscence is basal). The systematic position of the two Spanish species is doubtful, but they show a certain resemblance to the species of group 7 of my provisional system of classification of the genus *Campanula* (GADELLA, 1964, p. 79). In this group are placed all species with the chromosome number  $2n=34$ , having, with a very few exceptions, basally dehiscent fruits. The Spanish species lack the characters and habit of the other 6 groups of this tentative system. Therefore it seems justified to place them in group 7. To this group also belong species with the numbers  $2n=32$  (*Isophyllae*) and  $2n=30$  (species of the subsection *Involucratae* of Federov's system). The species of the *Involucratae* are certainly closely related to the species of the subsection *Eucodon* ( $2n=34$  in most species), as it proved to be possible to produce hybrids between *C. glomerata* L. and *C. trachelium* L., which are characterized by the chromosome numbers  $2n=30$  and  $2n=34$ , respectively. The hybrid has 32 chromosomes.

In my previous paper (GADELLA, 1964) I suggested that the number  $2n=32$  might have originated from the number  $2n=34$  by reduction. On the other hand, if not only the numbers  $2n=30$ ,  $2n=32$  and  $2n=34$  are somehow related to each other but also to the number  $2n=28$ , as suggested by a certain morphological resemblance, another hypothetical explanation of the origin and interrelationship of these chromosome numbers is possible. If  $X=8$  would be the primary base number of the genus, the number  $X=7$  could have been derived from this number by reduction (the number  $2n=28$  arose by polyploidization). The number  $2n=32$  may have its origin in the doubling of the number  $2n=16$ . The species *C. persicifolia* L. ( $2n=16$ ), *C. latiloba* A.DC. ( $2n=16$ ), and *C. stevensii* Bieb. ( $2n=32$ ) do not show a relationship to the species of group 7 and for that reason they have been placed in an entirely different group (group I, GADELLA, 1964).

I agree with BÖCHER (1964) that it is very difficult to imagine that 17 is a primary base number in the genus. On the other hand, it does not seem likely that the species of group I and II ( $X=8$  and  $X=10$ , respectively) have developed from the same stock as the species of group 7.

In figure I an attempt is made to arrange the chromosome numbers of the species of group 7 according to their hypothetical origin. (The figure partly corresponds with that of BÖCHER, 1960.) The subsections of Federov's system have been incorporated in this figure. Some data are derived from the studies of PODLECH (1965), DAMBOLDT (1965, a and b), PODLECH and DAMBOLDT (1964), CONTANDRIOPOULOS (1964). Especially in the subsection *Involucratae* the possibility exists that the numbers  $2n=32$  and  $2n=30$  are the result of reduction of the number  $2n=34$ . The same holds true for the group *Isophyllae* versus *Garganicae*. Further investiga-

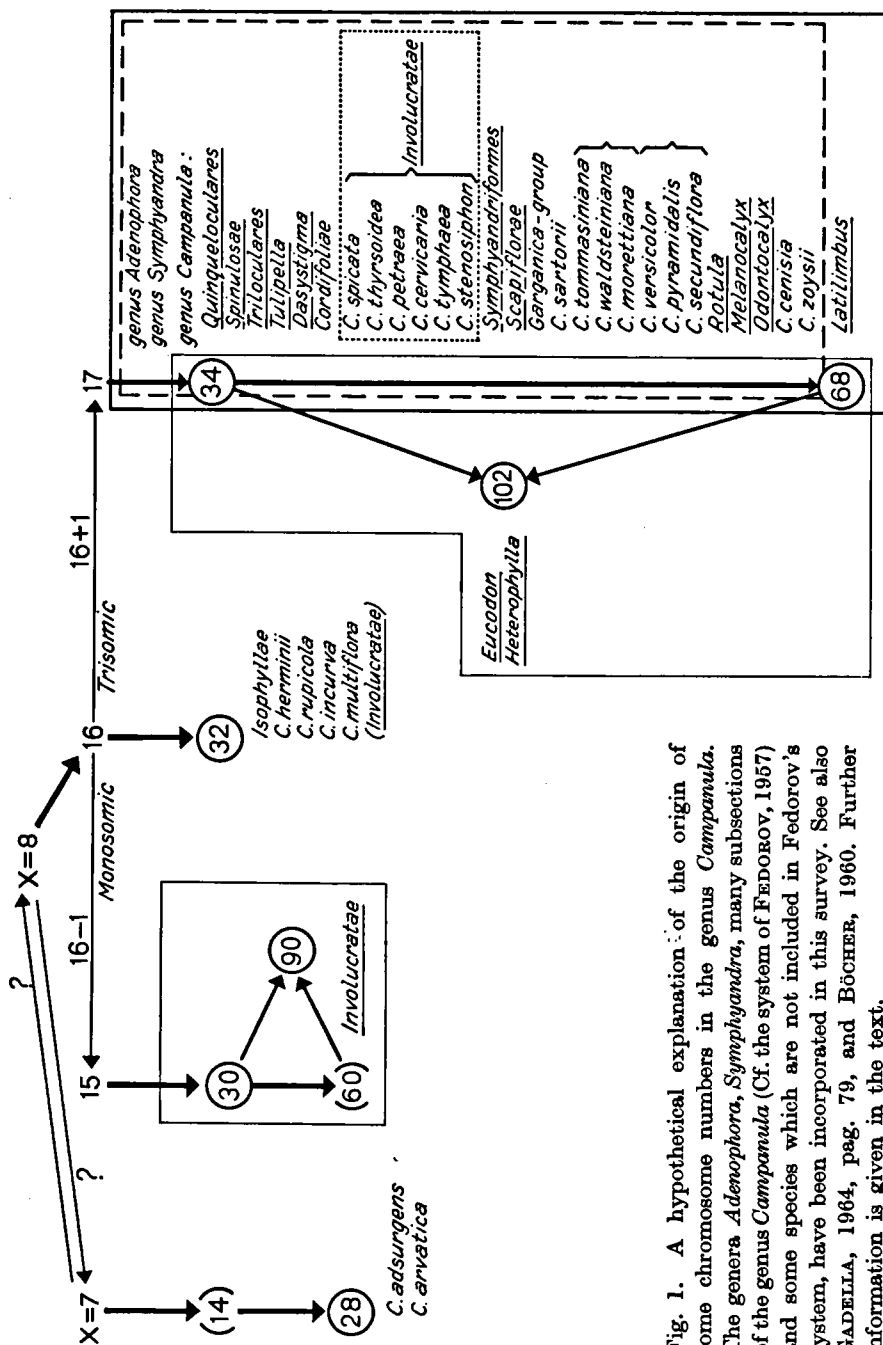


Fig. 1. A hypothetical explanation of the origin of some chromosome numbers in the genus *Campanula*. The genera *Adenophora*, *Symphyandra*, many subsections of the genus *Campanula* (Cf. the system of FEDOROV, 1957) and some species which are not included in Fedorov's system, have been incorporated in this survey. See also GADELLA, 1964, pag. 79, and BÖCHER, 1960. Further information is given in the text.

tions are needed in order to arrive at more definite conclusions with regard to the question which of the two hypotheses is more likely.

The species of the Himalaya group ( $2n=28$ ) are not dichotomously branched and have normal filaments, ciliate at the base and not abruptly dilated. Fedorov placed some morphologically related species in his series *Canescentes* of the subsection *Oreocodon*. They form a more or less natural group, occupying a distinct part of the area of the genus. I could not find any floral characteristics which might have lent support to generic separation of the subsection *Oreocodon* from *Campanula*. Yet the general appearance of these species, their habit to produce frequently cleistogamous flowers (by which characteristic they all differ from other species of the genus) and their number of chromosomes may justify the elevation of the subsection to at least subgeneric rank.

In my opinion the species with the number  $2n=28$  may be grouped as follows: *Campanula erinus* and *Campanula drabifolia* should be transferred to the genus *Roucela* Dumortier as *Roucela erinus* (L.) Dumort. and *Roucela drabifolia* (Sibth.) Dumort., respectively; *Campanula adsurgens* and *Campanula arvatica* should be maintained in the genus *Campanula*. *Campanula colorata* and *Campanula cashmeriana* are to be placed in the subsection *Oreocodon*, but this subsection should be raised to much higher rank. This will be done in the framework of a new classification of the genus *Campanula*.

*b. Campanula vidalii* Wats.

For reasons stated by FEER (1890) and supported by cytological evidence (MESQUITA RODRIGUEZ, 1954; GADELLA, 1964) this species has to be placed in the (monotypic) genus *Azorina* Feer as *Azorina vidalii* (Wats.) Feer.

*c. Campanula zoysii* Wulf.

PODLECH and DAMBOLDT (1964) determined the chromosome number of this species:  $2n=34$ . Despite the morphological peculiarities of this species they are of the opinion that it should remain in the genus *Campanula* where it may be placed in a special section. In the present author's opinion FEER (1890) goes too far in transferring this species to *Favratia*. Podlech and Damboldt's opinion is supported by cytological evidence.

*d. Campanula macrostyla* Boiss. et Heldr.

FEER (1890) transferred this species to *Sicyocodon*. MARCHAL (1920) determined its chromosome number:  $2n=20$ . However, it does not show any relationship to the species of group 2 ( $X=10$ ). On the other hand, *C. macrostyla*, which belongs according to Boissier to the section *Medium* sensu Boissier, subsection *Triloculares*, *Appendiculatae*, *Annuae*, is rather distinct from other species of the genus *Campanula*. In the present author's opinion it seems worthwhile to reinvestigate the number of chromosomes

of this remarkable species before making further taxonomic decisions. Moreover, the group of appendiculate annual *Campanula* species, of which 11 species occur in the region covered by the Flora Orientalis should be investigated more in detail in order to arrive at further conclusions with regard to their place in the genus. In my opinion it seems preferable to maintain the species for the present in the genus *Campanula*.

e. *Campanula americana* L.

In my previous paper (GADELLA, 1964) I suggested that *Campanula americana* should be removed, both on cytological and morphological evidence, from the genus and placed in the monotypic genus *Campanulastrum* Small.

f. *Campanula fastigiata* Duf. ex DC.

A. DE CANDOLLE (1830) remarked that this species is intermediate between *Specularia* and *Campanula*; in his opinion it might be included with equal justification in the one genus or in the other.

FEDOROV (1957) placed it in his monotypic genus *Brachycodon* (tribe *Campanuleae*). The genus *Legousia*, on the other hand, was placed by Fedorov in his tribe *Phyteumateae*, where he put the genera *Asyneuma* and *Phyteuma*. Unfortunately *C. fastigiata* could not be investigated by the present author. As A. de Candolle attached great value to the mode of dehiscence of the capsule (which is apical in this species), he placed *C. fastigiata* in another section than *C. erinus*, which shows a certain resemblance to *C. fastigiata* (dichotomously branched stems, glabrous, not widened filaments, annual life cycle). If the species is to be removed from the genus *Campanula*, which is highly probable, the relation between it and *Roucela erinus* and *Roucela drabifolia* should also be investigated.

g. *Campanula petraea* L.

This species was placed by BUSER (1894) in his new genus *Tracheliopsis*, section *Codonosphaera*. He paid special attention to the differences between the inflorescences of *C. glomerata* L. and *C. petraea* L. Despite the morphological peculiarities of *C. petraea* both ENGLER (1897) and BORNMÜLLER (1921) are of the opinion that it should remain in *Campanula*. The present author agrees with Engler and Bornmüller and places *Campanula petraea* in the subsection *Involucratae* of Fedorov's system. Further cytological and morphological studies are necessary in order to arrive at more definite conclusions regarding the generic status of *Tracheliopsis* and *Diosphaera*.

h. the genera *Popoviocodonia*, *Sergia*, *Astrocodon* and *Cryptocodon*

The removal of some species of *Campanula* to the above mentioned genera will not be discussed here for lack of cytological data, which are badly needed for clearing up their taxonomical position.

## II. HETEROCODON RARIFLORUM Nutt.

The systematic position of the genus *Heterocodon* as well as that of some endemic North-American species of *Campanula* should be studied in detail before it becomes possible to ascertain their place in the subtribe *Campanulinae*.

## III. THE POSITION OF SPECULARIA

DURANDE (1782) described the genus *Legousia*, an obscure genus name according to de Candolle. DE CANDOLLE (1830) described 7 species in his genus *Specularia*, a name that should be reduced to synonymy. The differences between some species of *Campanula* and of *Legousia* are small. According to McVAUGH (1945, a) the traditional features of the type species, the rotate corolla and the much elongated capsule disappear entirely or partly in the other species. He correctly remarked that some species of the genus *Campanula* (he mentioned *Campanula ramosissima* Sibth. et Sm.) are also provided with a rotate corolla, whereas the American species of *Specularia* have rather short capsules. McVaugh divided the genus *Specularia* into the following homogeneous biological units: a. *Specularia hybrida* A. DC. and *Specularia speculum* A. DC. (European species); b. *Specularia pentagonia* (L.) A. DC., to be removed to *Campanula* (where it was originally placed by Linnaeus); c. *Specularia falcata* A. DC. (a European species) and the American species were removed by him to the genus *Triodanis* Rafinesque. FERNALD (1946) did not agree with him in this respect and objected to the status of *Triodanis* as a separate genus. McVAUGH (1948) reopened the discussion because he regarded *Triodanis* as a good genus, equally well founded as most other genera of the *Campanulaceae*. The present cytological investigations support his opinion. The species *Legousia speculum-veneris*, *L. hybrida*, and *L. pentagonia* have the chromosome number  $2n=20$ , *Legousia falcata*  $2n=26$ , *Triodanis biflora* and *Triodanis perfoliata*  $2n=56$ .

In *Campanula* there are also species with the number  $2n=20$  in the subsection *Campanulastrum*, series *Rapunculiformes* of the system of Fedorov. Especially some annual species of this group, like *Campanula ramosissima* ( $2n=20$ ), with a rotate corolla, are closely related to *Legousia pentagonia*. Many species of the series *Rapunculiformes* show much resemblance to the European species of the genus *Legousia*, with the exception of *Legousia falcata*. The European species of *Specularia* have glabrous filaments (figure 2), which are gradually broadened towards the base. *Legousia pentagonia*, on the other hand has ciliate filaments widened towards the base. Therefore the transfer of *Legousia pentagonia* to *Campanula* seems justified, both on cytological and morphological evidence; on the other hand, the species of the  $X=10$ -group of *Campanula* hold a rather isolated position in this genus. Their morphological characters as well as the shape of their chromosomes show only some relation to the

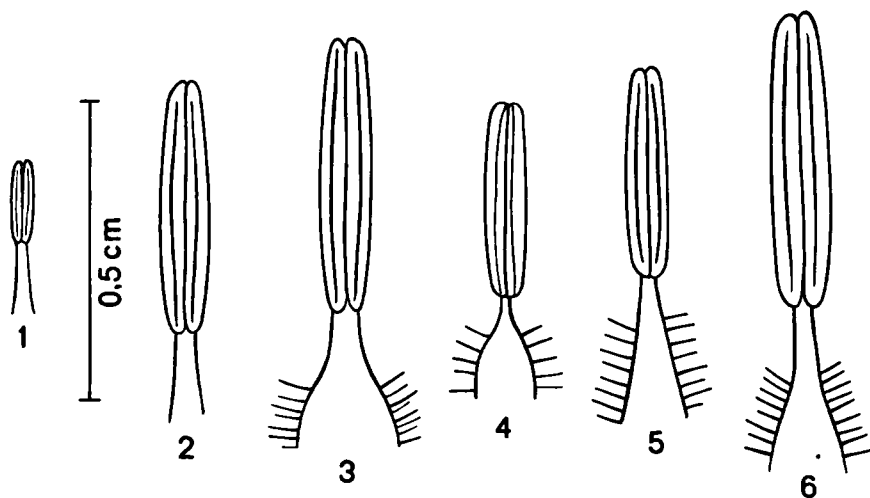


Fig. 2. Stamens of 6 species of the subtribe *Campanulinae*:  
 1. *Legousia hybrida* (L.) Delarb. - 2. *Legousia speculum-veneris* (L.) Fisch. - 3. *Campanula pentagonia* L. (= *Specularia pentagonia* (L.) A. DC.) - 4. *Triodanis perfoliata* (L.) Nieuwl. - 5. *Triodanis falcata* (Ten.) McVaugh - 6. *Campanula patula* L.

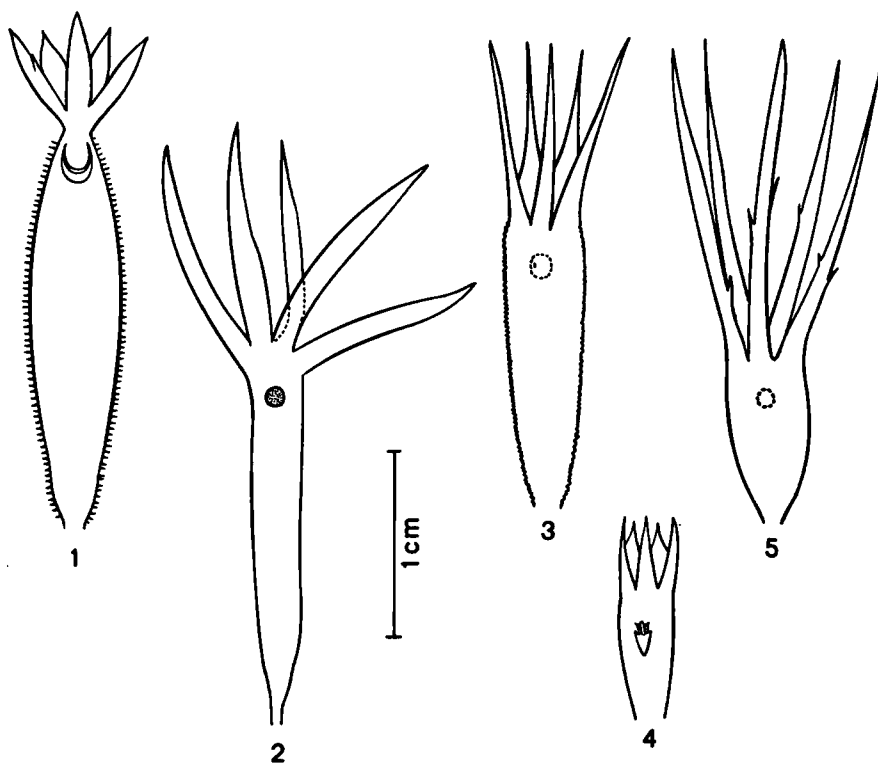


Fig. 3. Capsules of 5 species of the subtribe *Campanulinae*:  
 1. *Legousia hybrida* (L.) Delarb. - 2. *Campanula pentagonia* L. - 3. *Triodanis falcata* (Ten.) McVaugh - 4. *Triodanis perfoliata* (L.) Nieuwl. - 5. *Campanula patula* L.

species of the  $X=8$ -series. These two series may be closely related (*Campanula loeflingii* Brot. holds an intermediate position in this respect, its diploid chromosome number being  $2n=18$ ). At any rate, it seems very unlikely that the species of the  $X=17$ -group are derived from the same stock as those with long chromosomes of the  $X=8$  and  $X=10$ -group of *Campanula*. The two remaining species of *Legousia*, *L. hybrida* and *L. speculum-veneris*, have some characters in common with some species of the  $X=10$ -group of *Campanula*, viz. the apically dehiscent erect fruit, chasmogamous flowers, annual life-span, but also some differences should be noted: the filaments of *Legousia* are not ciliate at the base and are gradually widened towards the base, and the corolla is usually rather deeply divided. The fruits of *Legousia* are more or less constricted at the apex (figure 3). For these reasons it seems justified to place *L. speculum-veneris* and *L. hybrida* in a separate genus.

On the position of the American species of the genus *Specularia* some light has been shed by cytological studies. *Triodanis* is a well-defined genus. Only the position of *Specularia falcata* needs some further consideration. Its chromosome number ( $2n=26$ ) deviates from the other species of *Triodanis* as well as of *Specularia*. Morphologically it fits the genus *Triodanis*. The occurrence of cleistogamous flowers, the spiciform inflorescence and the not abruptly contracted capsule are characters which *Specularia falcata* shares with *Triodanis*. In the American species the base chromosome number is  $X=14$ . The base number in *S. falcata* is  $X=13$ . The relation between these base numbers has yet to be clarified. For the moment it is justified to maintain *L. falcata* in *Triodanis*.

#### IV. SEGREGATES FROM PHYTEUMA

Of the five sections of *Phyteuma* distinguished by Schönland only one (section *Hedranthum*) remained in the genus *Phyteuma*, the other 4 were raised to generic rank (see page 503):

1. *Synotoma*: 1 species:  $2n=34$  (FAVARGER and HUYNH, in LÖVE and SOLBRIG, 1965).
2. *Petromarula*: 1 species:  $2n=30$  (PODLECH and DAMBOLDT, 1964).
3. *Asyneuma*:  $2n=24, 30, 56$ .
4. *Cylindrocarpa*: no cytological data available.

The species *Phyteuma comosum* L. (= *Synotoma comosum* (L.) Schulz) was placed by de Candolle in his first section of the genus, comprising only one species. Morphologically it does not fit in *Phyteuma*. The inflorescence of *Synotoma* is an umbel, the filaments are linear, the lobes of the corolla are connivent at the base and at the top at anthesis, whereas in *Phyteuma* (section *Hedranthum*) the inflorescences are capitate or spicate, the filaments are widened towards the base, the lobes of the



corolla are connivent when the flower opens but later become free, and the lobes are distinctly connate at the base. In my opinion, this remarkable species was correctly placed by Schulz in a separate genus; morphological and cytological data support his opinion. The segregation of *Petromarula* seems also to be supported by cytological evidence.

The genus *Asyneuma*, with many species, has so far been investigated very insufficiently, both from the morphological and from the cytological point of view. McVAUGH (1945, b) transferred the Californian species *Campanula prenanthoides* Dur. to *Asyneuma*. It shows indeed a great resemblance to this genus, but cytological studies (GADELLA, 1964) revealed the number  $2n = 34$ , a number which fits quite well in *Campanula*. The number, however, was based on the study of roottip-mitoses of a single plant. In 1965 some new counts were made that yielded the diploid number  $2n = 32$  without any doubt in 4 different plants, which, however, all originated from the same locality. It should very probably also be placed in *Asyneuma*, but cytological information is too scanty to be used as an argument.

*Asyneuma* seems a well-founded genus, but it is apparently not closely related to *Phyteuma* with which it was formerly united. Actually it shows some affinity to *Campanula*, but only little cytological evidence is available. Within the subfamily *Campanuloideae* it should perhaps better be placed in Fedorov's *Campanuleae* instead of in the *Phyteumateae*.

## V. THE GENERA SYMPHYANDRA AND ADENOPHORA

At present *Campanula* contains groups of species which are only remotely related to each other, and some of its species or species-groups are undoubtedly closely related to the genera *Adenophora* and *Symphyandra*. NANNFELDT (1929) regarded *Adenophora* as closely connected with the group of *Campanula rotundifolia* (subsection *Heterophylla*). In my opinion, however, many species of *Adenophora* are related to some species of the subsection *Eucodon* (DC.) Fed. of *Campanula*. *Symphyandra armena* (Stev.) DC. differs from some species of the section *Symphyandriiformes* of *Campanula* only in its connivent anthers. *Symphyandra hojmannii* has much in common with some appendiculate biennial species of the section *Medium* sensu Boissier.

Since *Symphyandra* ( $X = 17$ ) and *Adenophora* ( $X = 17$ ) are probably derived from the same stock as many groups of species ( $X = 17$ ) of *Campanula*, it is not clear why species like *C. persicifolia* L. ( $2n = 16$ ), *C. loeflingii* Brot. ( $2n = 18$ ), *C. patula* L. ( $2n = 20$ ), *C. peregrina* L. ( $2n = 26$ ), *C. dichotoma* L. ( $2n = 24$ ) and *C. lactiflora* Bieb. ( $2n = 36$ ) still should be included in *Campanula*, whereas *Symphyandra* and *Adenophora* have been segregated as genera. It seems desirable in the present author's opinion to reunite the genera *Symphyandra* and *Campanula*.

*Adenophora* is characterized by the presence of a disc, long styles in

many species and by a mainly Asiatic distribution. Therefore the treatment as separate genera seems justified. But the distinction between them is weak. In figure I a survey of the chromosome numbers of group 7 of my provisional system is given. In this system the genera *Symphyandra* and *Adenophora* have also been included. They are probably derived from the same stock as the species of group 7 of *Campanula*; it does not seem plausible that the number  $2n=34$  would have originated independently in the genera *Campanula*, *Adenophora*, and *Symphyandra*.

## VI. THE GENERA PLATYCODON, CODONOPSIS, AND WAHLENBERGIA

These genera are placed by FEDOROV (1957) in the tribe WAHLENBERGIEAE. At present only few cytological data are available. The following base numbers occur in these genera: *Codonopsis* ( $X=8$ ); *Wahlenbergia* ( $X=9$ ); *Platycodon* ( $X=9$ ). It seems premature to attach much value to the scarce data available at this time.

*Wahlenbergia marginata* (Thunb.) A. DC. belongs to the section *Aikinia* and is characterized by a 3-locular capsule and 5 stamens. *Wahlenbergia lobelioides* A. DC., which belongs to the section *Lobelioides*, has a 2-locular capsule and 3 stamens. It is remarkable that the species with the lowest chromosome number, *W. lobelioides*:  $2n=18$ , has a more reduced flower than the species with the highest number: *W. marginata*,  $2n=72$ .

The section *Edraianthus* was removed from *Wahlenbergia* by A. de Candolle. CONTANDRIOPOULOS (1964) counted the number  $2n=32$  in 2 species of *Edraianthus*. These data support the segregation of *Edraianthus* from *Wahlenbergia*.

## SUMMARY

1. The chromosome numbers of 38 species belonging to 11 genera of the tribe *Campanuleae* of Schönland's system were determined. 13 of these species had not yet been investigated before.

2. A discussion is given of the differences between the present author's results and those of other authors.

3. The systematic position of the species of *Campanula* with the diploid chromosome number  $2n=28$  is reviewed. Some arguments are presented in favour of transferring *Campanula erinus* L. and *Campanula drabifolia* Sibth. to Dumortier's genus *Roucela*.

4. A hypothetical explanation of the origin of the chromosome numbers  $2n=28$ , 30, 32 and 34 of the genus *Campanula* is given.

5. The inclusion of *Specularia perfoliata* A. DC. and *Specularia biflora* Fisch. et Mey. in *Triodanis* is supported by cytological evidence.

6. *Campanula vidalii* Wats. and *Campanula americana* L. should be placed in the genera *Azorina* and *Campanulastrum*, respectively, both on morphological and cytological grounds.

7. The segregation of the genera *Asyneuma*, *Synotoma*, and *Petromarula* from *Phyteuma* is supported by cytological evidence.

8. The relation between the genera *Campanula*, *Symphyandra*, and *Adenophora* is discussed.

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