SOME NOTES ON THE DELIMITATION OF GENERA
IN THE CAMPAÑULACEAE. I

BY

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INTRODUCTION

The delimitation of genera in the Campanulaceae, especially in the subtribe Campanulinae, meets with serious difficulties. LINNAEUS (1753, 1754) distinguished 3 genera: Campanula, Phyteuma, and Trachelium. In A. DE CANDOLLE’s (1830) monograph of the family 334 species were recognized, classed in 21 genera. Species of 12 of these genera had formerly been included in Campanula. Yet the genus Campanula still appears too inclusive, and the delimitation of some other genera is open to dispute.

Not only the delimitation of genera presents serious difficulties, there is also no common opinion on the arrangement of the genera in tribes. The more important systems are those of SCHÖNLAND (in ENGEL and PRANTL, 1894) and of FEDOROV (1957). Schönland arrived at the following subdivision of the Campanuloideae: Campanuleae, Pentaphragmeae, and Sphenocleae. In the present paper only the first of these tribes will be taken into consideration. The tribe Campanuleae was divided by Schönland into three subtribes: Campanulinæ (Adenophora, Canarina, Heterocodon, Mindium (= Michauxia), Ostrowskia, Symphyandra, Phyteuma, Trachelium, Legousia, Campanula, Perocarpa), Wahlenbergineae (Codonopsis, Edraianthus, Jasione, Wahlenbergia and 13 other genera), and Platycodineae (Platycodon, Microcodon, Muschia). Fedorov (l.c.) divided the subfamily Campanuloideae into 8 tribes: I. Campanuleae (Campanula, Symphyandra, Brachycodon, Adenophora, Popoviocodonia, Astrocodon), II. Peracarpeae (Peracarpa), III. Ostrowskiaeae (Ostrowskia), IV. Michauxieae (Michauxia), V. Phyteumateae (Phyteuma, Asyneuma, Sergia, Cryptocodon, Cylindrocarpa, Legousia), VI. Wahlenbergieae (Wahlenbergia, Codonopsis, Platycodon), VII. Edraiantheae (Edraianthus), VIII. Jasioneae (Jasione).

The first 5 groups of the tribe Campanuleae of Fedorov correspond with the subtribe Campanulinae sensu Schönland; as the subtribe Campanulinae was not subdivided, the systems of Fedorov and Schönland are only partly comparable. It should be noted that Fedorov placed Legousia in the Phyteumateae.
Since the publication of A. de Candolle's monograph many new genera have been erected, most of them segregates from existing genera, especially from *Campanula*. Dumortier (1822) transferred *Campanula erinus* L. and *Campanula drabifolia* Sibth. to the genus *Roucela*. Nuttall (1843) distinguished *Heterocodon*, a monotypic American genus, which seems to be closely related to *Campanula*. Rafinesque (1837) transferred *Specularia perfoliata* A.D.C. to *Triadanis*, and Grisebach (1852) segregated *Asyneuma* from *Phyteuma*. The same was done by Boissier (1875), but he called this segregate *Podanthum*. Petromarula, a section of *Phyteuma*, was raised to generic rank by de Candolle (1830). The genus *Phyteuma*, however, was still considered to be too inclusive; 2 of its sections were raised to generic rank by Regel (1877) and by Schulz (1904), viz. *Cylindrocarpa* and *Synotoma*, respectively. Feer (1890) removed some marginal species from *Campanula*, e.g. *Campanula zoysii* Wulf to *Favratia*, *Campanula vidalii* Wats. to *Azorina*, *Campanula macrostyla* Boiss. et Heldr. to *Sicyocodon*. *Campanula americana* L., an aberrant species from Michigan, was transferred by Small (1903) to his monotypic genus *Campanulastrum*. Buser (1894) revised the genus *Trachelium*. He segregated the genera *Diosphaera* and *Tracheliopsis* and included *Campanula petraea* L. in *Tracheliopsis*. According to Bornmüller (1921) and Rechinger and Schiman-Czeika (1965) the differential characters between *Diosphaera* and *Tracheliopsis* fluctuate and seem to be incompletely correlated. In the opinion of Rechinger and Schiman-Czeika (l.c.) there are two possibilities:

a. to include these small genera (together with *Asyneuma*) in *Campanula*
b. to maintain *Diosphaera* and *Tracheliopsis* as separate genera.

Davis (1950) described the genus *Zeugandra*, which is characterized by connate filaments. *Zeugandra* is related most closely to *Campanula*, but differs more markedly from that genus than do *Symphyandra* or *Adenophora* (Davis, l.c.).

Fedorov (1957), in his excellent treatment of the family *Campanulaceae* in Flora U.S.S.R., distinguished 5 new genera in the *Campanulae*, namely *Brachycodon*, a genus to which he transferred *Campanula fastigiata* Duf., regarded by de Candolle as intermediate between *Specularia* and *Campanula*, *Popoviocodonia*, to which he transferred *Adenophora uyemurae* Kudo and *Campanula stenocarpa* Trautv. et Mey., *Astrocodon*, where he placed *Campanula crusheana* Fisch ex Rgl. et Til. and *Campanula expansa* Rud., *Sergia* with the species *Campanula severzovi* Rgl. and *Asyneuma regelii* Bornm., and, finally, *Cryptocodon*, containing *Campanula monocephala* Trautv.

Despite the fact that many (small) genera have been split off from *Campanula*, still some doubt is justified with regard to its homogeneity. Especially in the past few years much attention has been given to cytological studies in the genus: Böcher (1960, 1963, 1964), Contandrio-
poulos (1964), Damboldt (1965, a, b), Fernandes (1962), Gadella (1962, 1963, 1964), Hubac (1961, 1962), Kovanda (1966), Merxmüller and Damboldt (1962), Phitos (1963; 1964, a and b; 1965), Podlech and Damboldt (1964), Podlech (1962, 1965). Crossing experiments have also been used as an aid to taxonomy: Bielawska (1964), Damboldt (1965 a and b), Gadella (1963, 1964, 1966 in press), Podlech (1965). These studies demonstrated that Campanula is not homogeneous in cytological respect. Gadella (1964) attempted a provisional subdivision of the genus Campanula in 7 groups, each of which is characterized by a certain base number of chromosomes and by a certain combination of morphological characters. A new arrangement of the genus Campanula will be necessary, but it should be based on a thorough knowledge not only of the genus itself but also of other genera of the subtribe Campanulinae. Moreover, the delimitation of the genera should be based on a much larger number of characters, not only morphological but also cytological, supplemented by cytogenetic and chemotaxonomic evidence.

Cytological data, insofar as they are available, are still too incomplete to contribute much to the solution of the problem. Hitherto 57 species of the Campanulaceae (sensu Schönland), not including Campanula, have been studied cytologically, most of these by Rosen (1931), Sugiura (1942), Favarger (1953), Contandriopoulos (1962, 1964) and Podlech and Damboldt (1964). The available cytological information is partly confusing, sometimes many different chromosome numbers having been reported for the same species, partly very incomplete. Therefore it is necessary to fill as many gaps as possible. Unfortunately it is generally very difficult to collect plants in their native habitat. Only by collaboration of many botanists in various parts of the world a representative collection of taxa can be built up.

In this paper a contribution to the knowledge of the cytology of the Campanulaceae is given, and some problems pertaining to the delimitation of some of the genera in question are discussed. The author would highly appreciate to receive seeds of species of the above-cited genera, preferably collected in nature, but garden material would also be welcome.

**Material and methods**

The material was obtained in the form of seed samples distributed by various botanical gardens. The origin of these plants is not known exactly. Some plants, however, were collected in nature:


b. *Campanula aucheri* A.DC. and *Campanula stevenii* Bieb. (coll. no. C 962 resp. C 961). Seeds of these plants were kindly supplied by
Prof. Dr. A Fedorov; they had been collected in the Ahmaghan mountains in the Caucasus.

c. Seeds of *Campanula rapunculoides* L. (coll. no. C 958) and of *Campanula oblongifolia* (Koch) Char. (coll. no. C 960), collected in Armenia, were distributed by the botanical garden of Erevan.

d. Mr. E. Kliphuis kindly supplied me with some seeds of *Campanula patula* L., coll. no. C 932, and of *Campanula trachelium* L., coll. no. C 933, collected in Switzerland, in San Abondio (Tessin) and near Lugano, Novaggio, respectively.

e. Some plants of *Jasione montana* L., coll. no. 2446, were dug out in the Dutch National Park De Boschplaat (West-Frisian Isle of Ter-schelling) and grown in pots.

f. Seeds of the species *Legousia speculum-veneris* (L.) Fisch., coll. no. C 2124, were collected near Bouilland, France.

The courtesy of directors of Botanical Gardens who supplied me with seeds for these investigations, is gratefully acknowledged.

The chromosome counts are based on the study of roottip-mitoses (metaphase-plates). For this purpose roottips were fixed in Karpechenko, embedded in paraffin and sectioned at 15 micron. The sections were stained according to Heidenhain's haematoxylin method. The voucher specimens as well as the microscopical preparations are deposited or preserved in the Utrecht Museum and Herbarium.

**RESULTS**

The results of the cytological investigations are listed in the table, together with a survey of previous investigations of the same species. The following remarks may be added to this list: (See Table I).

I. **ADENOPHORA**

The genus *Adenophora* is undoubtedly characterized by the base number $X = 17$. This number was found by all authors working on the cytology of this (unsufficiently) known genus: Matsuura and Suto (1935); Modilewski (1934); Rosen (1931); Sugiura (1942). Polyploidy in the genus was observed by Matsuura and Suto (l.c.) in the species *Adenophora hakusanensis* Nakai ($2n = 51$) and by Sugiura (l.c.) who counted $2n = 102$ in four species. In some species chromosome numbers deviating from the euploid level were observed by Matsuura and Suto (l.c.): *Adenophora remotiflora* Miq. and *Adenophora thunbergiana* Kudo, $2n = 37$, and *Adenophora lamarckii* Fisch., $2n = 104$.

II. **ASYNEUMA**

In this genus the following chromosome numbers have been found:
<table>
<thead>
<tr>
<th>Species</th>
<th>Collection number</th>
<th>2n</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. trachelioides Maxim.</td>
<td>C 2121</td>
<td>34</td>
<td></td>
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<tr>
<td>A. lobeloides (Willd.) Hand.-Mazz.</td>
<td>C 2063</td>
<td>24</td>
<td><strong>Asyneuma</strong> SUGIURA (1942): 2n = 34.</td>
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<tr>
<td>A. canescens (W. et K.) Griseb. et Sch.</td>
<td>C 775; C 2012</td>
<td>30</td>
<td></td>
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<tr>
<td>C. elliottii DC.</td>
<td>C 2080; C 2137</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. oblongifolia (C. Koch) Charadz.</td>
<td>C 938</td>
<td>34</td>
<td><strong>Campanula</strong> LA COUR (in DARLINGTON and JANAKI-AMMAL, 1945): 2n = 3</td>
</tr>
<tr>
<td>C. aukeri A. DC.</td>
<td>C 962</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>C. panarinii (C. Koch) Charadz.</td>
<td>C 960</td>
<td>90</td>
<td><strong>Campánula</strong> GADELLA (1964): 2n = 90; PODLECH and DAMBOLDT (1964) 2n = 90 + 2B</td>
</tr>
<tr>
<td>C. patula L.</td>
<td>C 932</td>
<td>20</td>
<td>see GADELLA, 1964: 2n = 20, 2n = 40.</td>
</tr>
<tr>
<td>C. rapunculoides L.</td>
<td>C 958</td>
<td>102</td>
<td>see GADELLA, 1964: 2n = 68, 2n = 102.</td>
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<tr>
<td>C. rhomboidea L.</td>
<td>C 831</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>C. trachellum L.</td>
<td>C 933</td>
<td>34</td>
<td>see GADELLA, 1964: 2n = 34 (51).</td>
</tr>
<tr>
<td>C. rotundifolia Royd. var. angustifolia Nannf.</td>
<td>C 2085; C 2153</td>
<td>16</td>
<td><strong>Codonopsis</strong></td>
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<tr>
<td>C. ovata Benth.</td>
<td>C 2003; C 2004</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>C. tenuifolium L.</td>
<td>C 2036; C 2037</td>
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<td></td>
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<tr>
<td>C. davallianum T.</td>
<td>C 2067; C 2099</td>
<td></td>
<td></td>
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<tr>
<td>C. dianthiflorum DC.</td>
<td>C 2147; C 2154</td>
<td></td>
<td></td>
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<tr>
<td>C. pilosa (Franch.) Nannf.</td>
<td>C 2008; C 2101</td>
<td>16</td>
<td></td>
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<tr>
<td>J. montana L.</td>
<td>2446</td>
<td>12</td>
<td><strong>Jasiona</strong> ROSEN (1931): 2n = 12; WULFF (1937): 2n = 12, 14; PODLECH and DAMBOLDT (1964): 2n = 12.</td>
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<tr>
<td>L. speciosum-veneris (L.) Fisch.</td>
<td>C 775; C 2006;</td>
<td>20</td>
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<tr>
<td>L. pentagona (L.) Thell.</td>
<td>C 2124</td>
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<tr>
<td>P. hemisphaericum L.</td>
<td>C 2022; C 2025</td>
<td>28</td>
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<tr>
<td>P. nudum Schmidt</td>
<td>C 2134</td>
<td>22</td>
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<tr>
<td>P. orbiculare L.</td>
<td>C 2081</td>
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<td></td>
</tr>
<tr>
<td>P. scaposum Schulz</td>
<td>C 2041; C 2042</td>
<td>26</td>
<td><strong>Phyteuma</strong> SUGIURA (1940): 2n = 26; MATTECK (in TICHLER, 1950): 2n = 24.</td>
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<tr>
<td>P. spicatum L.</td>
<td>C 2043; C 2044</td>
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<tr>
<td>P. sibiricum L.</td>
<td>C 2095; C 2096</td>
<td></td>
<td></td>
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<tr>
<td>P. siboubruckneri Vest</td>
<td>C 2102; C 2104</td>
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<tr>
<td>P. salicifolium L.</td>
<td>C 2115; C 2116</td>
<td></td>
<td></td>
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<tr>
<td>P. sieboldii (Jacq.) A. DC.</td>
<td>C 2127</td>
<td></td>
<td></td>
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<tr>
<td>P. grandiflorum (Jacq.) A. DC.</td>
<td>C 2024</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>P. glutinosum (Jacq.) A. DC.</td>
<td>C 2028; C 2083</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>P. zhuzilinense Z.</td>
<td>C 2013; C 2149</td>
<td>24</td>
<td>ARMAND (1912): 2n = 36; CONTANDRIOPoulos (1962): 2n = 24; SKALINSKA (1964): 2n = 22 + 0-3B.</td>
</tr>
<tr>
<td>S. armena (Stev.) A. DC.</td>
<td>C 351; C 2020</td>
<td>34</td>
<td><strong>Symphysandria</strong> SUZUKI and KOBIRA (1949): 2n = 18.</td>
</tr>
<tr>
<td>S. hofmannii Pant.</td>
<td>C 2112; C 2113</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. wanneri (Roch.) Heuff</td>
<td>C 2014; C 2027</td>
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<td></td>
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<tr>
<td>S. cretica A. DC.</td>
<td>C 809</td>
<td>34</td>
<td><strong>Triadanis</strong> DR VILMORIN and SIMONET (1927): 2n = 34.</td>
</tr>
<tr>
<td>T. falcata (Ten.) McVaugh</td>
<td>C 2093</td>
<td>26</td>
<td></td>
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<tr>
<td>T. perfollata (L.) Nieuwl.</td>
<td>C 2030; C 2091</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>W. hederacea (L.) Rochb.</td>
<td>C 2095; C 2076</td>
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<td></td>
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<tr>
<td>W. marginata (Thunb.) A. DC.</td>
<td>C 2136; C 2148</td>
<td>72</td>
<td><strong>Wahlenbergia</strong> BORGOMANN (1964): 2n = 54, ca. 90.</td>
</tr>
</tbody>
</table>
A. limoniifolium (L.) Bornm. 2n = 24 ROSEN (1931);
CONTANDRIOPOULOS (1964).

A. sibthorpiianum (Roem. et Sch.) Bornm. 2n = 24 ROSEN (1931)
A. canescens (W. et K.) Griseb. et Schenk. 2n = 34 SUGIURA (1942)
A. campanuloides (Bieb.) Bornm. . . . . 2n = 102 SUGIURA (1942).
A. salicifolium (DC.) D. Sosn. . . . . . . 2n = 56 PODLECH and DAMBOLDT (1964)

In A. canescens the number 2n = 30 could be clearly demonstrated in plants originating from various sources. Therefore Sugiura's count should in all probability be regarded as incorrect. Serious doubt seems also justified with regard to Sugiura's observation of the number 2n = 102 in A. campanuloides. These facts permit the conclusion that the following numbers occur in Asyneuma: 2n = 24, 2n = 30, 2n = 56. As these numbers do not form an euploid series, it seems likely that several base numbers occur within the genus.

III. Codonopsis

ROSEN (1931) counted the number 2n = 16 in C. clematidea (Schrenk) Clarke and C. subsimplex Hook. f. et T. The species C. ovata Benth., C. pilosula (Franch.) Nannf. and C. rotundifolia Royle, counted by the present author, all showed the number 2n = 16, too.

IV. Jasione

The genus Jasione is characterized by the base number X = 6, as may be concluded from the data published by ROSEN (1931), WULFF (1937), PODLECH and DAMBOLDT (1964), and by FAVARGER and Huynh (in LÖVE and SOLBRIG, 1964). The counts made by Rosen, Wulff, Podlech and Damboldt in J. montana L. could be confirmed.

V. Phyteuma

Two new counts could be added to the list of chromosome numbers of Phyteuma species: P. scaposum Schulz (2n = 24) and P. orbiculare L. (2n = 24). The following counts could be confirmed by the present author: P. betonicifolium Vill. (2n = 24); P. hemisphaericum L. (2n = 28); P. orbiculare L. (2n = 24); P. scheuchzeri A.DC. (2n = 28). The closely related species Phyteuma nigrum Schmidt and P. spicatum L. showed the number 2n = 22. CONTANDRIOPOULOS (1962) counted 2n = 24 in P. spicatum, whereas SKALINSKA et al. (1964) observed the number 2n = 22 + 3B. The material used in the study of Contandriopoulos (originating from the Swiss Jura and Haute-Savoie) may also be characterized by the number 2n = 22 + 2B, as supposed by Skalinska.

Some previous counts of other authors could not be confirmed (cf. table). From the data available it is clear that the genus Phyteuma has more than one base number: 2n = 22, 2n = 24, 2n = 26, 2n = 28 (X = 11, 12, 13, 14).
VI. **Platycodon**

The number $2n = 18$ was counted in many plants from 8 different places of origin. This is in accordance with the observations of Sugiura (1942) and of Suzuka and Koriba (1949), but deviates from the observation of Kihara *et al.* (1931) who counted the number $2n = 28$. The number $2n = 28$ is probably erroneous.

VII. **Symphyandra**

The species of this genus are characterized by the base number $X = 17$.

VIII. **Triodanis**

Three species of this genus have been investigated cytologically: *Triodanis perfoliata* (L.) Nieuwl. ($2n = 56$); *Triodanis biflora* (R. et P.) Greene ($2n = 56$, Favarger and Huynh in Löve and Solbrig, 1965), and *Triodanis falcata* (Ten.) McVaugh ($2n = 26$). These species, as well as those of the genus *Legousia* (*Specularia*) are discussed in the next chapter.

IX. **Wahlenbergia**

The base number of this genus is undoubtedly $X = 9$. Gulline (in Darlington and Wylie, 1950) counted 5 species: $2n = 18$, $2n = 36$, $2n = 54$, $2n = 72$. In the species *Wahlenbergia marginata* (Thunb.) A.DC. intraspecific cytological variation occurs. The following numbers were counted in this species: $2n = 54$, $2n = ca. 90$, in plants collected in the Bismarck Mountains, E. New Guinea, Borgmann, (1964), and $2n = 72$ in garden material of different sources. The species *Wahlenbergia hederacea* (L.) Rchb. clearly showed the number $2n = 36$. 