SOME NOTES ON THE DELIMITATION OF GENERA IN THE CAMPANULACEAE. 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 ENGLER 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: *Campanulinae* (*Adenophora*, *Canarina*, *Heterocodon*, *Mindium* (= *Michauxia*), *Ostrowskia*, *Symphyandra*, *Phyteuma*, *Trachelium*, *Legousia*, *Campanula*, *Perocarpa*), *Wahlenberginae* (*Codonopsis*, *Edraianthus*, *Jasione*, *Wahlenbergia* and 13 other genera), and *Platycodinae* (*Platycodon*, *Microcodon*, *Musschia*). Fedorov (l.c.) divided the subfamily *Campanuloideae* into 8 tribes: I. *Campanuleae* (*Campanula*, *Symphyandra*, *Brachycodon*, *Adenophora*, *Popoviocodonia*, *Astrocodon*), II. *Peracarpeae* (*Peracarpa*), III. *Ostrowskieae* (*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.DC. to *Triodanis*, 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 *Campanuleae*, 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 sewerzowii* 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 *Campanuleae* (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 *Campanuleae* 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:

a. *Campanula allionii* Vill., coll. no. C 938, sent by the Jardin Botanique de Genève, seeds 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 Terschelling) 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 I.

A survey of the chromosome numbers of the investigated species, with reference to the collection numbers and to the investigations carried out by other authors

Species	Collection number	2n	References
Adenophora			
A. liliifolia (L.) Bess.	C 2084	34	MODILEWSKI (1934): 2n = 34; SUGIURA (1942): 2n = 102.
A. trachelioides Maxim.	C 2121	34	———
Asyneuma			
A. lobelioides (Willd.) Hand.-Maz.	C 2063	24	———
A. canescens (W. et K.) Griseb. et Sch.	C 775; C 2012 C 2090; C 2137	30	SUGIURA (1942): 2n = 34.
Campanula			
C. allionii Vill.	C 938	34	LA COUR (in DARLINGTON and JANAKI-AMMAL, 1945): 2n=3
C. aucheri A. DC.	C 962	34	GADELLA (1964): 2n = 34.
C. oblongifolia (C. Koch) Charadz.	C 960	90	GADELLA (1964): 2n = 90; PODLECH and DAMBOLDT (1964 2n = 90 + 2B.
C. patula L.	C 932	20	see GADELLA, 1964: 2n = 20, 2n = 40.
C. prenanthoides Dur.	C 106	32	GADELLA, 1964: 2n = 34 (see text).
C. rapunculoides L.	C 958	102	see GADELLA, 1964: 2n = 68, 2n = 102.
C. rhomboidalis L.	C 831	34	SUGIURA (1942): 2n = 34; FAVARGER (1949): 2n = 34; GUTE MANN (in LÖVE and LÖVE, 1961): 2n = 34; PODLECH (1965 2n = 34.
C. stevenii Bieb.	C 961	32	GADELLA (1964): 2n = 32.
C. trachelium L.	C 933	34	see GADELLA, 1964: 2n = 34 (51).
Codonopsis			
C. rotundifolia Royl. var. *angustifolia* Nannf.	C 2085; C 2153	16	———
C. ovata Benth.	C 2003; C 2004 C 2036; C 2037 C 2067; C 2099 C 2147; C 2154	16	———
C. pilosula (Franch.) Nannf.	C 2008; C 2101	16	———
Jasione			
J. montana L.	2446	12	ROSEN (1931): 2n = 12; WULFF (1937): 2n = 12, 14; PODLE and DAMBOLDT (1964): 2n = 12.
Legousia			
L. hybrida (L.) Delarb.	C 2009; C 2100	20	SUGIURA (1942): 2n = 20.
L. speculum-veneris (L.) Fisch.	C 778; C 2006; C 2124	20	SUGIURA (1942): 2n = 20; KOLLER (in DARLINGTON a JANAKI AMMAL, 1945): 2n = 14.
L. pentagonia (L.) Thell.	C 2007; C 2031 C 2092	20	SUGIURA (1942): 2n = 20.
Phyteuma			
P. betonicifolium Vill.	C 2056	24	FAVARGER (1953): 2n = 24; CONTANDRIOPOULOS (1962): 2n = 2
P. hemisphaericum L.	C 2022; C 2025 C 2134	28	FAVARGER (1953): 2n = 28; CONTANDRIOPOULOS (1962 2n = 28; MATTICK (in TISCHLER, 1950): 2n = 24.
P. nigrum Schmidt	C 2081	22	SUGIURA (1940): 2n = 26.
P. orbiculare L.	C 2088; C 2089	24	SUGIURA (1940): 2n = 26; MATTICK (in TISCHLER, 1950 2n = 24; FAVARGER (1953): 2n = 24; CONTANDRIOPOUL (1962): 2n = 24; BAKSAY (1956): 2n = 24.
P. scheuchzeri All.	C 2041; C 2042 C 2043; C 2044 C 2059; C 2074 C 2102; C 2104 C 2115; C 2116 C 2127	26	MARCHAL (1920): 2n=26; ROSEN (1931): 2n=36; CONTA DRIOPOULOS (1962): 2n = 26.
P. scaposum Schulz	C 2024	24	———
P. spicatum L.	C 2058; C 2083	22	ARMAND (1912): 2n = 36; CONTANDRIOPOULOS (1962): 2n = 24; SKALINSKA (1964): 2n = 22 + 0—3B.
P. zahlbruckneri Vest	C 2013; C 2149	24	———
Platycodon			
P. grandiflorum (Jacq.) A. DC.	C 2005; C 2010 C 2045; C 2046 C 2061; C 2073 C 2098; C 2101	18	KIHARA *et al.* (1931): 2n = 28; SUGIURA (1942): 2n = 1 SUZUKA and KORIBA (1949): 2n = 18.
Symphyandra			
S. armena (Stev.) A. DC.	C 351; C 2020 C 2112; C 2113	34	———
S. hofmannii Pant.	C 2014; C 2027	34	DE VILMORIN and SIMONET (1927): 2n = 34.
S. wanneri (Roch.) Heuff	C 809	34	———
S. cretica A. DC.	C 2077	34	———
Triodanis			
T. falcata (Ten.) McVaugh	C 2032; C 2139 C 2093	26	———
T. perfoliata (L.) Nieuwl.	C 2030; C 2091 C 2140	56	———
Wahlenbergia			
W. hederacea (L.) Rchb.	C 2017	36	———
W. lobelioides A. DC.	C 2018; C 2028 C 2029; C 2076	18	LARSEN (1960): 2n = 18.
W. marginata (Thunb.) A. DC.	C 2136; C 2148	72	BORGMANN (1964): 2n = 54, ca. 90.

A. limoniifolium (L.) Bornm.	2n = 24	ROSEN (1931); CONTANDRIOPOULOS (1964).
A. sibthorpianum (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 = 26). 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.