
MORPHOLOGICAL STUDIES TOWARD AN IMPROVED CLASSIFICATION OF CAMPANULACEAE S. STR.¹

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ABSTRACT

Growth and seedling morphology of 144 species representing 30 genera of Campanulaceae s. str. were studied. Two types of seedlings were found: Group A, with an elongated epicotyl and elongated internodes, and Group B, with a shortened (not visible) epicotyl and usually shortened internodes. These two types appear to be correlated with other vegetative characters. Thus, plants from Group A have an opposite leaf arrangement (at least early in ontogenesis), rhythmic seasonal growth with a long dormant period, and sympodial branching. Plants from Group B have a spiral leaf arrangement, continuous growth (at least in the non-flowering period), and sympodial and monopodial branching. Taxa in Group A are distributed mostly in Asia, whereas representatives in Group B occur almost worldwide. The two groups do not coincide with current taxonomic classifications but correspond remarkably well with the distribution of other characters such as pollen-grain morphology and correlate with groups based on molecular analysis; therefore, these two groups may reflect two lineages. Growth and seedling morphology are of taxonomic significance in Campanulaceae and can be used for treatments in conjunction with other characters. Taxonomic changes, which are supported by molecular data, are proposed.

Key words: Campanulaceae, growth and seedling morphology and development, taxonomy.

Campanulaceae herein are treated in a narrow circumscription (without Lobeliaceae) as a monophyletic group with a distinct geographical distribution and with well-defined morphological characters. Campanulaceae s. str., despite their size and importance in temperate floras, remain unrevised. This family, with about 50 genera and 800 species distributed worldwide, is the largest and most primitive and basal one within the order Campanulales (Lammers, 1992; Takhtajan, 1997). Although representatives of the family occur on all continents except Antarctica, the vast majority of genera and species are found in temperate regions of the Old World. Raven and Axelrod (1974) considered the family to have a Laurasian–African origin. The centers of distribution and diversity include the Mediterranean, East Asia, and South Africa (Shulkina, 1978; Kolakovsky, 1995; Hong, 1995; Eddie, 1997).

De Candolle's (1830) comprehensive monograph on the Campanulaceae provided a solid basis for all subsequent works. He divided the family into two tribes and later added a third tribe to accom-

modate *Merciera* (De Candolle, 1839). Schönland (1889) also divided the tribe Campanuloideae (Campanulaceae s. str. here) into three groups, based on mode of dehiscence and ovary position, but these three groups differed in composition from those of De Candolle. These two classifications became the basis for all future treatments (Table 1). Although the current systems differ greatly from the old ones in number of genera, as many taxa have been added during the last century, it is easy to understand what classification each particular author is following. Schönland's treatment has been used often and remains a currently useful reference.

Fedorov (1957), on the contrary, followed in general De Candolle's position and published a detailed classification for Campanulaceae growing in the former Soviet Union (FSU). Fedorov proposed 8 tribes (6 new) based on capsule dehiscence, corolla shape, and presence and shape of appendages between the calyx lobes. Kolakovsky (1995) proposed a new system with 4 subfamilies and 22 tribes based on internal fruit structure. He

¹ We are indebted to Ihsan Al-Shehbaz, Peter Stevens, and Peter Hoch for reading the text and providing useful remarks. Many thanks to Victoria Hollowell for careful editing. T. Shulkina thanks the people who helped her obtain Campanulaceae seeds from different parts of the world: J. P. M. Brenan, A. Cronquist, A. Dolukhanov, R. Gagnidze, R. Kamelin, A. Kolakovsky, N. Morin, H. B. Rycroft, and P. Wendelbo.

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Table 1. Treatment of genera in Campanulaceae.

De Candolle (1830, 1839)	Schönland (1897)
Fam. Campanulaceae	Subfam. Campanuloideae
Tribe Campanuleae	Subtribe Campanulinae
<i>Adenophora</i>	<i>Adenophora</i>
<i>Campanula</i>	<i>Campanula</i>
<i>Musschia</i>	<i>Heterocodon</i>
<i>Michauxia</i>	<i>Michauxia</i>
<i>Petromarula</i>	<i>Ostrowskia</i>
<i>Phyteuma</i>	<i>Peracarpa</i>
<i>Symphyandra</i>	<i>Phyteuma</i>
<i>Trachelium</i>	<i>Legousia</i>
	<i>Symphyandra</i>
	<i>Trachelium</i>
Tribe Wahlenbergieae	Subtribe Wahlenberginae
<i>Campanumoea</i>	<i>Campanumoea</i>
<i>Canarina</i>	<i>Cephalostigma</i>
<i>Cephalostigma</i>	<i>Codonopsis</i>
<i>Codonopsis</i>	<i>Cyananthus</i>
<i>Edraianthus</i>	<i>Edraianthus</i>
<i>Jasione</i>	<i>Heterochaenia</i>
<i>Lightfootia</i>	<i>Jasione</i>
<i>Microcodon</i>	<i>Leptocodon</i>
<i>Platycodon</i>	<i>Merciera</i>
<i>Prismatocarpus</i>	<i>Prismatocarpus</i>
<i>Roella</i>	<i>Rhigiophyllum</i>
<i>Wahlenbergia</i>	<i>Roella</i>
	<i>Siphocodon</i>
	<i>Treichelia</i>
	<i>Wahlenbergia</i>
Tribe Merciereae	Subtribe Platycodinae
<i>Merciera</i>	<i>Microcodon</i>
	<i>Musschia</i>
	<i>Platycodon</i>

described 9 new genera within *Campanula*, which have not yet been included in the *Vascular Plants of Russia and Adjacent Countries* (Czerepanov, 1995) due to their contradictory descriptions. Takhtajan (1997) divided the family into 4 subfamilies and 16 tribes, taking into consideration not only the fruit structure but also pollen-grain structure, ovary position, as well as the presence or absence of appendages between the calyx lobes. Subfamily Cyananthoideae includes the genera *Cyananthus*, *Codonopsis*, *Campanumoea*, *Leptocodon*, and *Platycodon*; subfamilies Ostrowskioideae and Canarinoideae are monotypic. The last subfamily, Campanuloideae, consists of 12 tribes and includes all remaining genera. Genera described by Kolakovsky were not included in the system. Hong (1995) tentatively divided the genera into 6 unnamed groups based primarily on various morphological characters. Eddie (1997) divided the family into two major tribes, with the differences between them consid-

ered to not warrant subfamilial status. Eddie's Platycodoneae subdivided into the following subtribes: Ostrowskiinae, Cyananthinae, Echinocodinae, Codonopsinae, Platycodinae, Campanumoeinae, and Canarininae. His Campanuleae comprised the following: Wahlenberginae, Jasioneinae, Musschiinae, Azorininae, and Campanulinae.

There is considerable disagreement among all prior classifications of Campanulaceae. Furthermore, there is no common opinion about generic limits or higher relationships among the major subdivisions of the family. Taxonomic problems in this family can be explained by the fact that nearly all of these earlier classifications had a geographical rather than biological basis. Thus, floristic treatments differ considerably in the generic delimitation of the Campanulaceae for the former U.S.S.R. (Fedorov, 1957), Europe (Fedorov & Kovanda, 1976; Tutin, 1976), Turkey (Damboldt, 1976), and China (Hong, 1983).

Genera crossing diverse geographical regions need multidisciplinary study, including research on the development of vegetative organs, morphology and anatomy of fruits and seeds, pollen grain structure, as well as molecular and serological data. As stated by Takhtajan (1997: 6), "We cannot establish phyletic relationships and construct phyletic lineages using only floral characters. It is all the more impossible to reconstruct phyletic lineages on the basis of the characters of the vegetative organs only." The greater the number of characters from different correlation groups taken into consideration, the closer we can approximate the evolutionary phylogeny of the family.

Vegetative characters in higher plants are accorded only a limited place in classification, despite the angiosperms being first divided into two great subclasses according to the number of cotyledons as early as the 13th century by Albertus Magnus. Publications in which the importance of vegetative characters is supported are not numerous (e.g., Stebbins, 1974; Tomlinson, 1984). However, life forms and growth patterns, ultimately influencing the structure of the mature plant, are often ignored or little emphasized because of the common opinion that all these characters are adaptive. However, life forms include many distinctive vegetative characters that can be taxonomically valuable if they are stable.

The goals of this study are (1) to study vegetative organs and development of life forms in representative species across Campanulaceae; (2) to select characters that are common to species groups that may have taxonomic value; (3) to compare the groups suggested by these characters with formal

classifications for congruence with other morphological and molecular data.

We examined seedling morphology, growth patterns, leaf arrangement, seasonal development and behavior, and branching patterns before and after first flowering in studied plants. Special attention was paid to genera whose placement varies in current systems: *Azorina*, *Campanulastrum*, *Canarina*, *Edraianthus*, *Musschia*, *Ostrowskia*, and *Platycodon*. Also included were representatives of recently segregated genera: *Annaea* (= *Campanula*), *Gadellia* (= *Campanula*), *Hemisphaera* (= *Campanula*, subsect. *Scapiflorae*), *Neocodon* (= *Campanula*, sect. *Rapunculus*), and *Theodorovia* (= *Campanula*).

MATERIAL AND METHODS

Plants of 144 species in 30 genera were examined (Table 2). The studied genera represent taxa from 2 tribes of De Candolle (1830), 3 subtribes of Schönland (1889), 8 subtribes of Fedorov (1957), 17 tribes of Kolakovsky (1995), and 14 tribes of Takhtajan (1997), and they provide a representative sample of the Campanulaceae. Almost half of the studied taxa were formed by the species of *Campanula* (65) and other genera (13) of the flora of the FSU. All new genera described by Kolakovsky were split from *Campanula* as well. As the most complete classification for this group was made by Fedorov (1957), the list of studied species was mainly arranged according to the system published in the *Flora of the U.S.S.R.* All plants were grown at the Komarov Botanical Institute (St. Petersburg, Russia) and a few (*Azorina vidalii*, *Campanulastrum americanum*, *Campanula kemulariae*, *C. punctata*, *Canarina canariensis*) also at the Missouri Botanical Garden (St. Louis, Missouri, U.S.A.). The taxonomic identity of all plants was confirmed when flowering. Vouchers are partly deposited in the general herbarium at the Komarov Botanical Institute (LE) (e.g., *Canarina canariensis*, Shulkina, 1978; with no numbers as is typical in Russian herbaria), and partly in the herbarium at the Department of Living Plants collections at the Komarov Botanical Institute.

Plants were grown outdoors or in greenhouses, depending on the plant's requirements. Seeds were collected in nature throughout the former Soviet Union and the midwestern United States by the senior author. They were also obtained from other collectors undertaking field trips on the islands of Macaronesia, or in the Middle East or South Africa, as well as from different botanical gardens. Seeds were sown in the greenhouses at the Komarov Bo-

tanical Institute in early spring (March) during 1973–1990. Observations were made every other day during germination and early stages of seedling growth and once a week for maturing plants. Sample size per collection (species investigated) was 20 to 50 plants whenever possible, but in some cases fewer seedlings were available. The period of germination and cotyledon size and shape were noted, and the first leaves were examined. Seedlings were illustrated when they had first leaves and fully developed cotyledons, approximately one, rarely two, months after first appearance. At this time seedlings were transplanted into larger pots.

Most plants were planted in summer in an experimental plot in the open air, but some (*Azorina*, *Canarina*, *Diosphaera*, *Musschia*, *Roella*) were kept in greenhouses. Some portions of outside plants were brought back into greenhouses in late autumn to study the presence and length of their dormant period. Leaf arrangement and branching patterns were examined throughout the year as were the presence of green leaves or renewal buds during the winter months. The timing and position of new growth were recorded in early spring. Plants were dug out, and the development of their underground organs was checked in the first year and while flowering. Life forms of some species (above- and underground organs) were also studied in nature by the senior author in the Caucasus, southern Siberia, Central Asia, the Russian Far East, the Carpathians, the Mediterranean, and the midwestern United States.

RESULTS AND DISCUSSION

GROSS MORPHOLOGY

The Campanulaceae include plants with varied life forms. As shown in previous studies (Shulkina, 1978) most species, including members of about 30 genera, are perennial herbs, and these are found throughout the range of the family. Annuals, mainly in the Mediterranean region and the New World, rarely in East Africa and Australia, also very rarely in East Asia, are present in 11 genera. Some African annuals are relatively long-lived plants (e.g., *Wahlenbergia undulata* lives 10–12 months), whereas the Mediterranean annuals are usually short-lived (e.g., *Brachycodonia fastigiata*, 1–2.5 months). Thirteen genera consist completely or partly of arborescent and semi-arborescent plants. These dwarf trees and shrubs occur in the Azores, Madeira, the Mascarenes, Reunion, and South Africa (e.g., *Azorina*, *Musschia*, *Heterochaenia*, *Berernice*, *Prismatocarpus*). Three genera include her-

Table 2. List and location of taxa studied, number of species used/general number of species in each genus. All vouchers are at the Komarov Botanical Institute, St. Petersburg, Russia (LE). Type species are in bold.

<i>Adenophora</i> 8/40, Eurasia		
<i>A. stenanthina</i> (Ledeb.) Kitag.	Perennial	Altay
<i>A. kurilensis</i> Nakai	Perennial	Korea*
<i>A. liliifolia</i> (L.) A. DC.	Perennial	E Europe
<i>A. nikoensis</i> Franch. & Sav.	Perennial	Korea*
<i>A. pereskiiifolia</i> (Fisch. ex Roem. & Schult.) G. Don	Perennial	Siberia
<i>A. tetraphylla</i> (Thunb.) Fisch.	Perennial	Sakhalin
<i>A. trachelioides</i> Maxim.	Perennial	Far East
<i>A. triphylla</i> (Thunb.) A. DC.	Perennial	China*
<i>Azyneuma</i> 4/50, Disjunct, Europe & E Asia		
<i>A. japonicum</i> (Miq.) Briq.	Perennial	Far East
<i>A. otites</i> (Boiss.) Bornm.	Biennial	France*
<i>A. pulchellum</i> (Fisch. & Mey.) Bornm.	Biennial	E Caucasus
<i>A. salignum</i> (Waldst. & Kit. ex Besser) Fed.	Perennial	E Caucasus
<i>Azorina</i> 1/1, Azores		
<i>A. vidalii</i> (Wats.) Feer	Dwarf tree	Portugal*
<i>Brachycodonia</i> 1/1, Mediterranean, E Caucasus, C Asia		
<i>B. fastigiata</i> (Dufour ex A. DC.) Fed.	Annual	C Asia
<i>Campanula</i> L. 70/300, Northern Hemisphere		
section <i>Campanula</i>		
subsection <i>Quinqueloculares</i> Boiss.		
<i>C. medium</i> L.	Biennial	France*
<i>C. crispa</i> Lam.	Biennial	Caucasus
subsection <i>Spinulosae</i> (Fomin) Fed.		
<i>C. mirabilis</i> Albov	Perennial	W Caucasus
subsection <i>Triloculares</i> Boiss.		
<i>C. sibirica</i> L.	Perennial	Siberia
<i>C. caucasica</i> Bieb.	Perennial	E Caucasus
<i>C. hohenackeri</i> Fisch. & C. A. Mey.	Perennial	Caucasus
<i>C. komarovii</i> Maleev	Perennial	W Caucasus
<i>C. longistyla</i> Fomin	Perennial	W Caucasus
subsection <i>Phasidianthe</i> Fed.		
<i>C. imeretina</i> Rupr.	Perennial	W Caucasus
subsection <i>Tulipella</i> Fed.		
<i>C. punctata</i> Lam.	Perennial	Far East
subsection <i>Dasystigma</i> Fed.		
<i>C. alpina</i> Jacq.	Perennial	Carpathians
subsection <i>Annuae</i> (Boiss.) Fed. = <i>Roucella</i> Dumort.		
<i>C. erinus</i> L.	Annual	France*
<i>C. propinqua</i> Fisch. & C. A. Mey.	Annual	Armenia
subsection <i>Campanula</i>		
<i>C. latifolia</i> L.	Perennial	Caucasus
<i>C. bononiensis</i> L.	Perennial	N Caucasus
<i>C. cordifolia</i> C. Koch	Perennial	W Caucasus
<i>C. megrelica</i> Manden. & Kuth.	Perennial	W Caucasus
<i>C. odontosepala</i> Boiss.	Perennial	E Caucasus
<i>C. rapunculoides</i> L.	Perennial	E Europe
<i>C. trachelium</i> L.	Perennial	E Europe
subsection <i>Involucratae</i> (Fomin) Fed.		
<i>C. glomerata</i> L.	Perennial	E Europe

Table 2. Continued.

<i>C. cephalotes</i> Nakai	Perennial	China*
<i>C. oblongifolia</i> (C. Koch) Charadze	Perennial	S Caucasus
<i>C. trautvetteri</i> Grossh. & Fed.	Perennial	S Caucasus
subsection <i>Cordifolia</i> (Fomin) Fed.		
<i>C. alliariifolia</i> Willd.	Perennial	Caucasus
<i>C. dolomitica</i> E. Busch	Perennial	Caucasus
<i>C. makaschvilii</i> E. Busch	Perennial	W Caucasus
subsection <i>Latilimbus</i> Fed.		
<i>C. collina</i> Bieb.	Perennial	Caucasus
<i>C. albovii</i> Kolak.	Perennial	W Caucasus
<i>C. irinae</i> Kuth.	Perennial	W Caucasus
<i>C. sarmatica</i> Ker-Gawl.	Perennial	C Caucasus
<i>C. sommieri</i> Charadze	Perennial	N Caucasus
subsection <i>Trigonophyllon</i> Fed.		
<i>C. dzychrica</i> Kolak.	Perennial	W Caucasus
<i>C. autraniana</i> Albov	Perennial	W Caucasus
subsection <i>Symphyandriiformes</i> (Fomin) Fed.		
<i>C. kolenatiana</i> C. A. Mey. ex Rupr.	Perennial	Tbilisi*
<i>C. bayerniana</i> Rupr.	Perennial	S Caucasus
<i>C. choziatowskyi</i> Fomin	Perennial	S Caucasus
<i>C. kemulariae</i> Fomin	Perennial	W Caucasus
<i>C. ossetica</i> Bieb.	Perennial	Tbilisi*
<i>C. raddeana</i> Trautv.	Perennial	Caucasus
subsection <i>Oreocodon</i> Fed.		
<i>C. incanescens</i> Boiss.	Perennial	C Asia
<i>C. kachetica</i> Kantsch.	Perennial	Caucasus
<i>C. kantschavelii</i> Zagareli	Perennial	Caucasus
subsection <i>Scapiflorae</i> (Boiss.) Fed. = <i>Hemisphaera</i> Kolak		
<i>C. anomala</i> Fomin	Perennial	N Caucasus
<i>C. aucheri</i> A. DC.	Perennial	Caucasus
<i>C. bellidifolia</i> Adams	Perennial	Caucasus
<i>C. biebersteiniana</i> Roem. & Schult.	Perennial	Caucasus
<i>C. chamissonis</i> Fed.	Perennial	Far East
<i>C. ciliata</i> Steven	Perennial	E Caucasus
<i>C. saxifraga</i> Bieb.	Perennial	N Caucasus
<i>C. tridentata</i> Schreb.	Perennial	Caucasus
subsection <i>Rupestris</i> (Boiss.) Fed.		
<i>C. karakuschensis</i> Grossh. = <i>Theodorovia</i> Kolak.	Perennial	S Caucasus
<i>C. lehmanniana</i> Bunge = <i>Hyssaria</i> Kolak.	Perennial	C Asia
subsection <i>Hypopolion</i> Fed.		
<i>C. hypopolia</i> Trautv.	Perennial	Caucasus
subsect. <i>Heterophylla</i> (Nym.) Fed.		
<i>C. rotundifolia</i> L.	Perennial	E Europe
<i>C. polymorpha</i> Witasek	Perennial	Carpathians
section <i>Rapunculus</i> (Fourr.) Boiss.		
subsection <i>Campanulastrum</i> Fed.		
<i>C. rapunculus</i> L. = <i>Neocodon</i> Kolak.	Perennial	N Caucasus
<i>C. abietina</i> Griseb. & Schenk = <i>Neocodon</i> Kolak.	Perennial	Carpathians
<i>C. alberti</i> Trautv. = <i>Neocodon</i> Kolak.	Perennial	C Asia
<i>C. altaica</i> Ledeb. = <i>Neocodon</i> Kolak.	Perennial	S Siberia
<i>C. beauverdiana</i> Fomin = <i>Neocodon</i> Kolak.	Perennial	S Caucasus
<i>C. hemchinica</i> C. Koch = <i>Neocodon</i> Kolak.	Perennial	W Caucasus

Table 2. Continued.

<i>C. hieracioides</i> Kolak. = <i>Annaea</i> Kolak.	Perennial	W Caucasus
<i>C. lambertiana</i> A. DC. = <i>Neocodon</i> Kolak.	Perennial	N Caucasus
<i>C. patula</i> L. = <i>Neocodon</i> Kolak.	Perennial	E Europe
<i>C. persicifolia</i> L. = <i>Neocodon</i> Kolak.	Perennial	E Europe
<i>C. pontica</i> Albov = <i>Neocodon</i> Kolak	Perennial	W Caucasus
<i>C. stevenii</i> Bieb. = <i>Neocodon</i> Kolak.	Perennial	S Caucasus
<i>C. turzcaninovii</i> Fed.	Perennial	S Siberia
subsection <i>Rotula</i> Fed.		
<i>C. carpatica</i> Jacq.	Perennial	Carpathians
subsection <i>Melanocalyx</i> Fed.		
<i>C. uniflora</i> L.	Perennial	N Siberia
subsection <i>Odontocalyx</i> Fed.		
<i>C. lasiocarpa</i> Cham.	Perennial	Far East
<i>Campanulastrum</i> 1/1, North America		
<i>C. americanum</i> (L.) Small	Biennial	MO, U.S.A.
<i>Canarina</i> 2/3, Canary Islands, disjunct E Africa		
<i>C. canariensis</i> (L.) Vatke	Perennial	Spain*
<i>C. eminii</i> Aschers.	Perennial	France*
<i>Codonopsis</i> 6/30, E and C Asia		
<i>C. clematidea</i> (Schenk) C. B. Clarke	Perennial	C Asia
<i>C. ovata</i> Benth.	Perennial	China*
<i>C. pilosa</i> Chipp	Perennial	England*
<i>C. pilosula</i> (Franch.) Nannf.	Perennial	Far East
<i>C. ussuriensis</i> (Rupr. & Maxim.) Hemsl.	Perennial	Far East
<i>C. vincifolia</i> Kom.	Perennial	Japan
<i>Cyananthus</i> 4/23, E Asia		
<i>C. lobatus</i> Wall. ex Benth.	Perennial	Great Britain*
<i>C. inflatus</i> Hook.f. & Thomson	Perennial	Great Britain*
<i>C. integer</i> Wall. ex Benth.	Perennial	Austria*
<i>C. microphyllus</i> Edgew.	Perennial	Great Britain*
<i>Diosphaera</i> 1/3, Middle East		
<i>D. hysteraantha</i> Rech.f. & Schiman-Czeika	Perennial	Spain*
<i>Edraianthus</i> 4/24, E Mediterranean		
<i>E. graminifolius</i> (L.) A. DC.	Perennial	Italy*
<i>E. horvatii</i> Lakusic	Perennial	Yugoslavia*
<i>E. pumilio</i> (Portenschlag) A. DC.	Perennial	Yugoslavia*
<i>E. sutjeskae</i> Lakusic	Perennial	France*
<i>E. tenuifolius</i> (Waldst. & Kit.) A. DC.	Perennial	France*
<i>Gadellia</i> 1/1, Caucasus		
<i>G. lactiflora</i> (Boiss.) Schulkina	Perennial	Caucasus
<i>Githopsis</i> 3/4, W North America		
<i>G. calycina</i> Benth.	Annual	W North America
<i>G. diffusa</i> A. Gray	Annual	W North America
<i>G. pulchella</i> Vatke	Annual	W North America
<i>G. specularioides</i> Nutt.	Annual	W North America
<i>Jasione</i> 3/20, Europe, N Africa		
<i>J. heldreichii</i> Boiss. & Orph.	Biennial	France*
<i>J. laevis</i> Lam.	Ann., bien.	France*
<i>J. montana</i> L.	Biennial	Switzerland*
<i>Legousia</i> 3/20, Europe, N Africa, Americas		
<i>L. falcata</i> (Ten.) Fritsch	Annual	Spain*

Table 2. Continued.

<i>L. hybrida</i> (L.) Delarbe	Annual	Greece*
<i>L. pentagonia</i> (L.) Druce	Annual	France*
<i>Leptocodon</i> 1/2, E Asia		
<i>L. gracilis</i> (Hook.f.) Lem.	Perennial	Great Britain*
<i>Michauxia</i> 1/7, E Mediterranean		
<i>M. laevigata</i> Vent.	Perennial	Caucasus
<i>Musschia</i> 2/2, Madeira Islands		
<i>M. aurea</i> (L.) Dum.	Shrublet	Great Britain*
<i>M. wollastonii</i> Lowe	Dwarf tree	Great Britain*
<i>Ostrowskia</i> 1/1, C Asia, Afghanistan		
<i>O. magnifica</i> Regel	Perennial	Central Asia
<i>Peracarpa</i> 1/1, E Asia		
<i>P. circaeoides</i> (F. Schmidt) Feer	Perennial	Russian Far East
<i>Physoplexis</i> 1/1, Europe (Alps)		
<i>P. comosa</i> (L.) Schur	Perennial	Switzerland*
<i>Phyteuma</i> 7/40, Europe		
<i>P. betonicifolium</i> Vill.	Perennial	France*
<i>P. globulariifolium</i> Sternb. & Hoppe	Perennial	France*
<i>P. orbiculare</i> L.	Perennial	E Europe
<i>P. spicatum</i> L.	Perennial	E Europe*
<i>P. vagneri</i> A. Kern.	Perennial	E Europe*
<i>Platycodon</i> 1/1, E Asia		
<i>P. grandiflorus</i> (Jacq.) A. DC.	Perennial	Russian Far East
<i>Popoviocodonia</i> 1/1, Russian Far East		
<i>P. uyemurae</i> (Kudo) Fed.	Perennial	Russian Far East
<i>Roella</i> 1/25, South Africa		
<i>R. ciliata</i> L.	Perennial	South Africa
<i>Sergia</i> 1/2, C Asia		
<i>S. sewerzovii</i> (Regel) Fed.	Perennial	C Asia
<i>Symphyandra</i> 4/12, E Mediterranean		
<i>S. armena</i> (Steven) A. DC.	Perennial	Caucasus
<i>S. cretica</i> A. DC.	Perennial	Greece*
<i>S. hofmannii</i> Pant.	Biennial	France*
<i>S. pendula</i> (Bieb.) A. DC.	Perennial	Switzerland*
<i>Trachelium</i> 2/7, Mediterranean		
<i>T. caeruleum</i> L.	Shrublet	Italy*
<i>T. rumelianum</i> Hampe	Shrublet	Italy*
<i>Wahlenbergia</i> 6/150, Southern Hemisphere, Europe, SE Asia		
<i>W. albomarginata</i> Hook. f.	Ann., per.	Great Britain*
<i>W. gracilis</i> (Forst.) A. DC.	Ann., per.	Great Britain*
<i>W. hederacea</i> (L.) Reichenb.	Ann., per.	Great Britain*
<i>W. procumbens</i> A. DC.	Ann., per.	Great Britain*
<i>W. undulata</i> (L. f.) A. DC.	Ann., per.	South Africa
<i>Zeugandra</i> 1/2, Middle East (Iran)		
<i>Z. iranica</i> P. H. Davis	Perennial	Iran

Number of species follows Mabberley (1997), except *Cyananthus* (Shrestha, 1992) and *Edraianthus* (Lakušić, 1974). Taxonomic division within *Campanula* follows Fedorov (1957).
 * Species of cultivated origin.

baceous vines (*Campanumoea*, *Canarina*, *Codonopsis*).

The different life forms in the Campanulaceae have been accommodated within several commonly used gross morphological systems (Du Rietz, 1931; Raunkiaer, 1934; Serebrjakov, 1962). Comparison between these gross morphological groups and taxonomic classifications shows no agreement. The same life form may be present in different tribes, and individual tribes may include more than one life form. A single genus can include life forms with different life spans (e.g., *Campanula* includes perennials, biennials, and annuals). Closely related species sometimes have different types of adaptation (e.g., *C. hohenackeri* has a well-developed primary root system, whereas mature plants of *C. caucasica* have rhizomes, and both species belong to the same subsection *Triloculares*). Therefore, the life form groups arranged according to existing morphological systems do not correlate with Campanulaceae taxonomic classifications, and perhaps the current taxonomic systems do not reflect natural groups within the family.

SEEDLING MORPHOLOGY

The initial and early stages of plant growth are significant to the survival of seedlings in various kinds of environments (Stebbins, 1971, 1974). Seedling morphology (along with other characters) has been useful for the delimitation of taxa above the generic level in some families such as Crasulaceae (Ohba, 1978), Gesneriaceae (Burt, 1977), and Sapotaceae (Bokdam, 1977), at the generic level within the tribe Cynometreae of the Fabaceae (Léonard, 1957), and species level in the genus *Calophyllum* (Stevens, 1980).

All species studied in Campanulaceae have epigeal (aboveground) germination (Fig. 1), with cotyledons usually oval in shape with an apical notch. Cotyledons may be as large as 6.3×8.3 mm (*Canarina canariensis*) and as small as 1.5×1.0 mm (*Gadellia lactiflora*). The primary leaves emerge in two or three weeks, and cotyledons persist during the first two months of development. The position of the primary leaves varies, and as a result there are two different types of seedlings within the family (see Table 3).

The first seedling group, "Group A," has an elongated epicotyl (1–11 cm long) and elongated first internodes. The length of the epicotyl and internodes may vary even in one species under different conditions. Young plants of some species can produce shorter internodes when occurring in unfavorable habitats. Thus, *Ostrowskia magnifica* grown

in the open air in St. Petersburg might have internodes 2–3 cm long, whereas in greenhouses and in its native habitat in Central Asia the internodes are 10 cm or more. Although the length of the epicotyl and internodes may vary, they are always present.

A second group, "Group B," has no visible epicotyl, and the first internodes are practically absent. Leaves appear immediately above cotyledons and form a rosette.

Seedling morphology in each genus is relatively uniform. It is true not only with oligotypic genera such as *Canarina*, *Musschia*, *Sergia*, and *Trachelium*, but also with rich genera such as *Campanula* and *Phyteuma*. Species of *Campanula* studied here belong mostly to the flora of the FSU and include representatives of both sections and the 24 subsections of Fedorov's (1957) classification. *Campanula* is morphologically heterogeneous, and seedlings differ markedly in size, first leaf shapes, and development patterns. However, they all form rosettes at the beginning of growth. All examined species do not have an epicotyl and the first internodes are very short. On the basis of seedlings, *Annaea*, *Hemisphaera*, *Neocodon*, *Theodorovia*—genera described by Kolakovsky—do not stand apart noticeably from the other *Campanula* species. The only *Campanula* that has an elongated seedling is *C. lactiflora*, which is now segregated in *Gadellia*.

Other consistent characters of vegetative and reproductive organs are common to species of each seedling group. In Group A, the plant is sympodial and its leaves are opposite (*Campanumoea*, *Canarina*, *Codonopsis*, *Cyananthus*, *Leptocodon*, *Ostrowskia*, *Platycodon*), at least in ontogenesis. In such mature plants the leaf arrangement may remain opposite or become whorled (*Canarina*, *Ostrowskia*) or spiral (some species of *Cyananthus*). These species are perennials; only *Legousia* and some *Cyananthus* species are annuals (Shrestha, 1992). All have sympodial growth patterns, and shoots die every year even if they do not terminate in a flower, and the next year's shoots come from axillary buds. Following the first year's growth, the plants are dormant during the unfavorable season, be it cold or dry. Thus, *Codonopsis*, *Leptocodon*, and *Platycodon*, which occur in eastern Asian regions without snow cover, have a deep dormant period in winter. *Canarina* (Canary Islands and East Africa) and *Ostrowskia* (Central Asia) are both geophytes growing in a climate with a long dry period (spring and summer for *Canarina* and summer for *Ostrowskia*), during which they are dormant. Even in the greenhouses with constant warmth and humidity these plants have a deep dormant period.

In seedling Group B, all plants have a rosette of

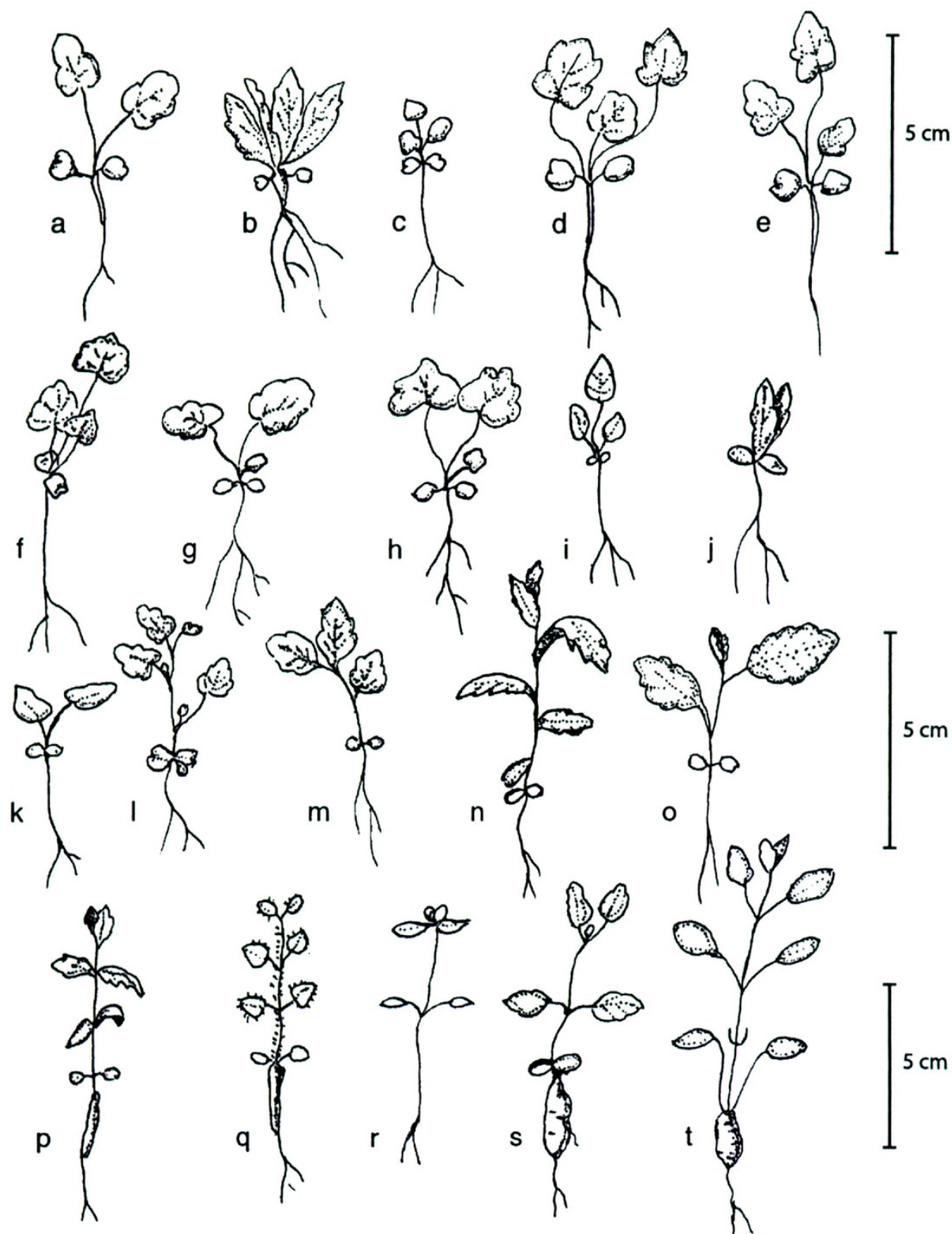


Figure 1. Seedling morphology. Examples of plants with shortened epicotyl (a to l). First row: —a. *Campanula latifolia*. —b. *Symphyandra armena*. —c. *Brachycodonia fastigiata*. —d. *Adenophora liliifolia*. —e. *Popoviocodonia uyemurae*. Second row (scale as above): —f. *Michauxia laevigata*. —g. *Phyteuma spicatum*. —h. *Asyneuma salignum*. —i. *Sergia sewerzowii*. —j. *Edraianthus graminifolius*. Third row: —k. *Campanulastrum americanum*. —l. *Peracarpa circaeoides*. Examples of plants with an elongated epicotyl (m to t). —m. *Gadellia lactiflora*. —n. *Azorina vidalii*. —o. *Musschia aurea*. Fourth row: —p. *Platycodon grandiflorus*. —q. *Codonopsis pilosula*. —r. *Cyananthus microphyllus*. —s. *Canarina canariensis*. —t. *Ostrowskia magnifica*, with cotyledons in the first year and primary stem the next year. All plants taken from collections at LE.

Table 3. Seedling grouping in Campanulaceae.

Group A (elongated epicotyl)	Group B (reduced epicotyl, rosette-formers)
<i>Azorina</i>	<i>Adenophora</i>
<i>Campanumoea</i>	<i>Asyneuma</i>
<i>Canarina</i>	<i>Brachycodonia</i>
<i>Codonopsis</i>	<i>Campanula</i>
<i>Cyananthus</i>	<i>Campanulastrum</i>
<i>Gadellia</i>	<i>Cryptocodon</i>
<i>Legousia</i>	<i>Cylindrocarpa</i>
<i>Leptocodon</i>	<i>Diosphaera</i>
<i>Musschia</i>	<i>Githopsis</i>
<i>Ostrowskia</i>	<i>Edraianthus</i>
<i>Platycodon</i>	<i>Jasione</i>
	<i>Michauxia</i>
	<i>Peracarpa</i>
	<i>Physoplexis</i>
	<i>Popoviocodonia</i>
	<i>Roella</i>
	<i>Sergia</i>
	<i>Symphyandra</i>
	<i>Trachelium</i>
	<i>Zeugandra</i>

leaves or at least the first internodes are shortened in early ontogenesis. Plants have spirally arranged leaves. The group includes annuals, biennials, perennials, and semi-arborescent forms with various types of seasonal development and branching. Annuals can have 2 to 4 leaves in a rosette, and the epicotyl axis terminates in a flower. All subsequent reproductive branches usually arise from the meristems in the upper leaf axils just beneath the terminal flower, e.g., *Campanula erinus*, *Githopsis calycina*.

In biennials an epicotyl axis produces a rosette of leaves during the first year (up to 100 leaves in *Campanula medium*) and elongated internodes the next year that terminate in a flower or in thyrsoid inflorescences, e.g., *Asyneuma pulchellum*, *Campanula barbata*, *C. crispa*, *C. medium*, *Michauxia laevigata*.

In many perennials, e.g., *Adenophora liliifolia*, *Asyneuma japonicum*, *Campanula latifolia*, *C. glomerata*, *C. alliariifolia*, the main stem comes into flower after the production of short nodes over 2–4 years of growth. Further stem growth occurs from axillary buds after a dormant period. In some species mature plants do not have aboveground rosettes of leaves, but two or three pairs of scale leaves, below ground, e.g., all examined species of *Adenophora*. In the Mediterranean region, some plants retain green leaves not only in a basal rosette, but also at the mid-fertile nodes, and subsequent branches derive from axillary buds. Their

perennial stems are lignified, forming arborescent semi-shrubs, e.g., *Trachelium caeruleum*.

There are also many species of Group B with an indeterminate apical meristem. Many of these Campanulaceae develop a basal rosette that can overwinter under the snow. Reproductive branches are axillary, often leafless. In this case the branching pattern is clearly monopodial, e.g., *Campanula anomala*, *Edraianthus graminifolius*. The main rosette can persist or be replaced by axillary ones that also grow monopodially and bear second-order reproductive leafless stems. In some cases plants are monopodial but reproductive stems are leafy, e.g., species from subsection *Trigonophyllum*, such as *Campanula autraniana*. The other extreme is *Campanula karakushensis*, where the main rosette produces cataphylls only, and it is the axillary stems that are leafy and bear an inflorescence. In *Campanula polymorpha*, *C. rotundifolia*, and *C. uniflora* the apical meristem does not participate in formation of the plant body. The epicotyl axis produces a rosette of two or three leaves, after which the apical meristem diminishes. Axillary elongated stems are produced by basitonic (sympodial) branching terminating in inflorescences. Successive branches are produced from lower leaf axils on these second-order reproductive stems, and the branching pattern becomes basically sympodial. All examined species of each subsection of *Campanula* have a similar branching pattern, and this character is of taxonomic value within this genus.

Perennials of *Adenophora*, *Astrocodon*, *Asyneuma*, many species of *Campanula*, *Cryptocodon*, some *Phyteuma*, and *Popoviocodonia* enter dormancy after their initial anthesis. Also, perennial *Cylindrocarpa*, *Diosphaera*, *Edraianthus*, *Jasione*, *Physoplexis*, *Sergia*, *Symphyandra*, *Trachelium*, and some *Campanula* remain evergreen, but some have a short, easily interrupted dormant period. Although life form and seasonal rhythm vary widely within Group B, all plants of this group, including biennials and annuals, start as rosette plants.

An interesting correlation was found between seedling types and pollen grains. Dunbar (1973) and especially Avetisjan (1986, 1988) studied pollen within the family, the latter describing four groupings divided into nine types. These roughly sort into two assemblages corresponding to or coincident with seedling Groups A and B (see Fig. 2). The first pollen assemblage includes meridional-zonocolpate, equatorial-colporate, and colporidate pollen grains and includes *Cyananthus*, *Codonopsis*, *Leptocodon*, *Ostrowskia*, *Platycodon*, and *Canarina*. The second pollen assemblage has porate grains and includes *Asyneuma*, *Azorina*, *Bra-*

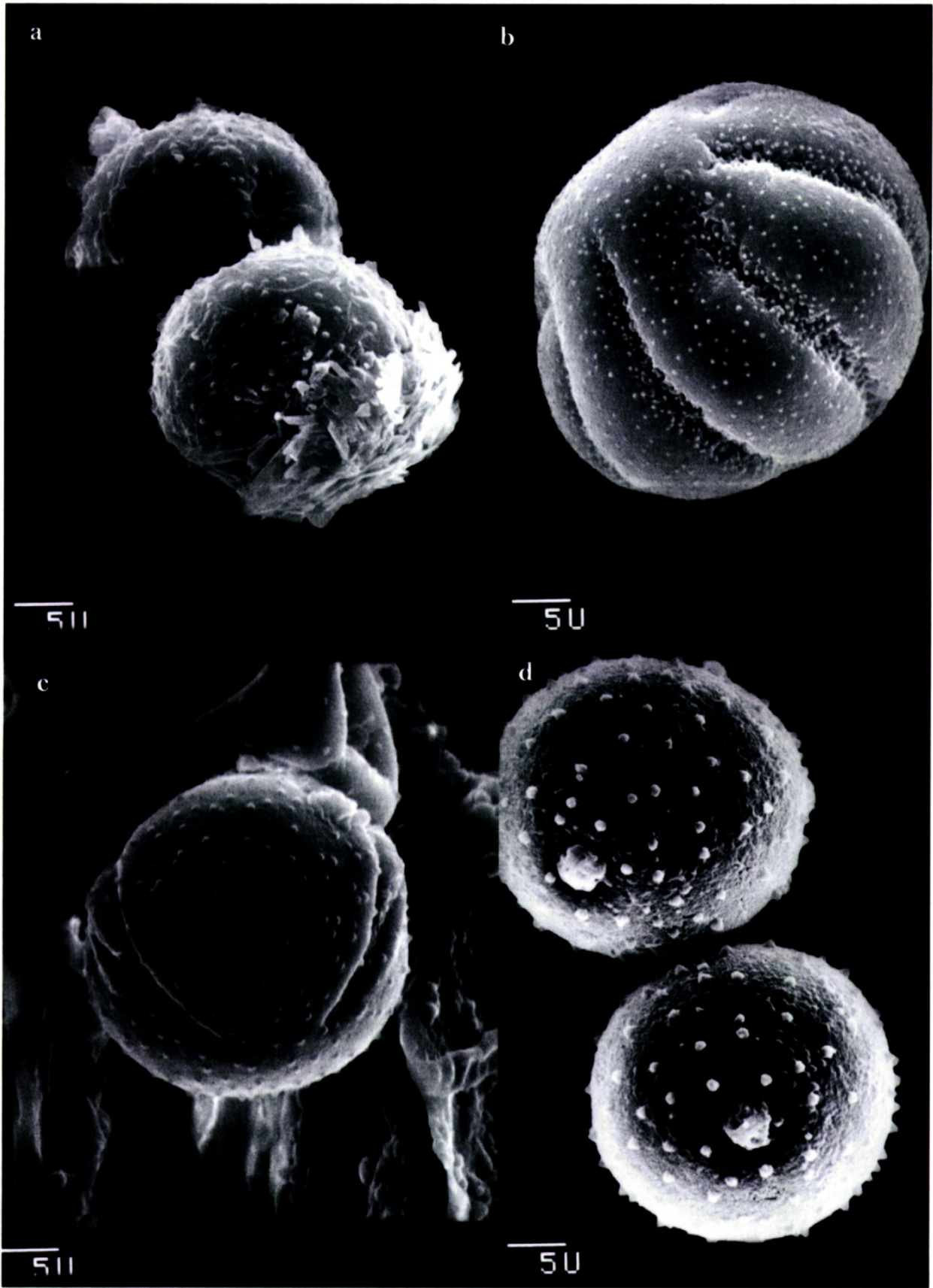


Figure 2. Pollen grains: —a. *Musschia aurea*, porate, *Lowe 161283* (MO). —b. *Codonopsis clematidea*, colpate, Central Asia, Turkestan Range, *Shulkina s.n.* (LE). —c. *Canarina canariensis*, colporate, *Crosby 11425* (MO). —d. *Gadellia lactiflora*, porate, Caucasus, Teberda, *Shulkina s.n.* (LE).

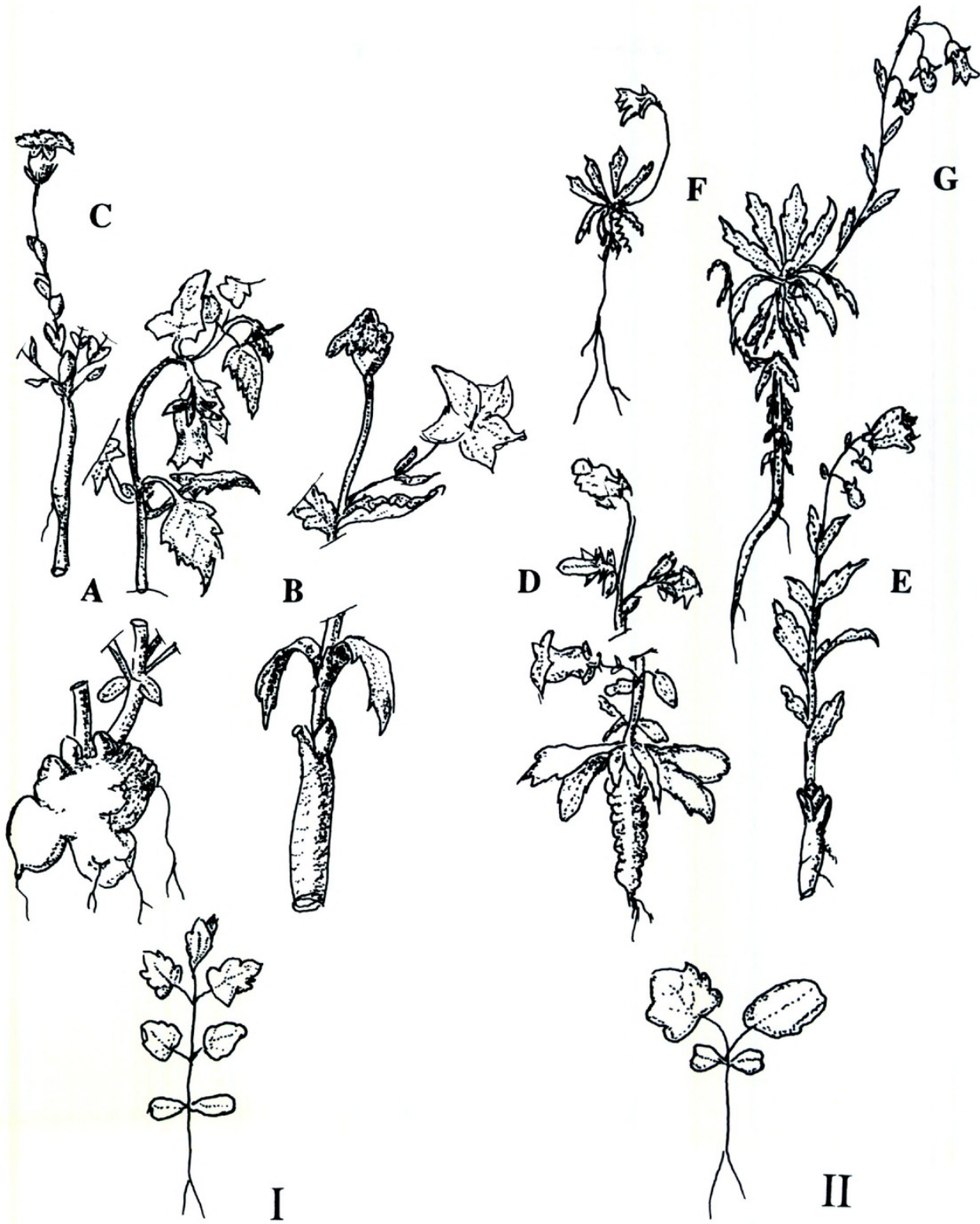


Figure 3. Two groups of plants within the Campanulaceae family. I. Plants with elongated seedlings: *Canarina canarioides* (A), *Platycodon grandiflorus* (B), *Cyananthus integer* (C). II. Plants with rosette seedlings: *Campanula mirabilis* (D), *Adenophora tetraphylla* (E), *Campanula tridentata* (F), *Azorina vidalii* (G).

chycodonia, *Campanula*, *Campanulastrum*, *Edraianthus*, *Gadellia*, *Jasione*, *Legousia*, *Michauxia*, *Musschia*, *Peracarpa*, *Popoviocodonia*, *Roella*, *Sergia*, *Symphyandra*, and *Trachelium*, covering those species of *Campanula* that were segregated into *Annaea*, *Hemisphaera*, *Neocodon*, and *Theodorovia*.

Almost all species of seedling Group A have colpate, colporate, and colpoidate pollen grains, whereas species of seedling Group B have only porate pollen grains (Fig. 3). There are some exceptions: species of *Azorina*, *Gadellia*, *Musschia*, and *Legousia* develop an elongated epicotyl (seedling

Group A), though their pollen grains are porate, as in seedling Group B. Three of these genera, *Azorina*, *Gadellia*, and *Musschia*, have spiral leaves in the earliest seedling stages. *Azorina* and *Musschia* both occur in a warm unseasonable climate and have continuing monopodial growth throughout the year, exceptional within Group A. The only character that associates *Azorina* and *Musschia* with group A is their elongated stem in the first year, which is pronounced to as long as 50–70 cm. Species of these two genera have arborescent life forms unusual within Campanulaceae. *Azorina vidalii*, which grows in the Azores Islands, is a dwarf tree or shrub to 1.5 m high (Feer, 1890; Vasilevskaya & Shulkina, 1976). During the first year it develops an elongated epicotyl and stem with elongated internodes. Subsequently, the internodes become shortened, but the main stem remains vegetative, and the axillary branches, all with elongated nodes, produce inflorescences in 2 to 3 years and die after fruiting. Two species of *Musschia* occur on the Madeira Archipelago. *Musschia wollastonii* is a monocarpic, unbranched dwarf tree to 1.5 m tall when flowering, with a rosette of large leaves (to 70 cm long) elevated above ground. The stems produce elongated internodes during the first year and shortened ones in following years. It comes to flower in 2 to 5 years and the flowering period lasts 4 to 6 months. The stems are crowned by long inflorescences (70–90 cm), and plants die after fruiting. *Musschia aurea* is a dwarf shrub 0.4–0.7 m high. The main stem has elongated internodes in the first year and rather shortened ones in the following years. All axillary branches are equivalent in length to the main one. The plant grows 2 to 5 years before flowering and inflorescences are terminal on the reproductive branches, which are monocarpic and die after fruiting. Molecular data from ITS sequences also support the position of *Azorina* (Shulkina & Gaskin, 1999) and *Musschia* (Eddie, 1984; Eddie et al., 2003 this issue) within Group B.

Endemic to the Caucasus, *Gadellia lactiflora* (seedling Group A herein) was segregated from *Campanula* (Shulkina, 1979). *Gadellia* has elongated seedlings, an unusual growth pattern with a dormant period and sympodial growth after the first year; an unusual chromosome number ($2n = 36$) and morphology (Gadella, 1964); some peculiarity in flowers such as narrow filaments; pollen grains with two pores (Shulkina, 1979); and an unusual septicidal fruit, which is dehiscent by pores and regularly cracks along the septa up to the axis column (Kolakovsky, 1986). Molecular (Eddie et al., 2003), serological (Gudkova & Borschenko, 1986), and seed morphology (Belyayev, 1984, 1985) data

also support its segregation from *Campanula*. At the same time, it has many characters in common with *Campanula*, including its spiral leaf arrangement, which proves that its elongated stem is of secondary origin.

One last exception in seedling Group A is the genus *Legousia*, the taxonomic position of which has been controversial (McVaugh, 1948; Fedorov, 1957) within Campanulaceae. The prismatic capsules and almost rotate corollas distinguish it from all other related taxa, sensu Phyteumateae (Fedorov, 1957). Shetler and Morin (1986), who investigated the seed structure of the North American Campanulaceae, also concluded that the taxonomic position of *Legousia* is unclear and more study is needed. Serological studies revealed differences separating *Legousia* from other genera within Phyteumateae (Gudkova & Borshchenko, 1991), and its elongated seedling is also a character that suggests reconsideration of its taxonomic position. Molecular studies (Eddie et al., 2003) show *Legousia* is nearer to *Campanulastrum* than *Phyteuma*.

This division within Campanulaceae based on seedling type almost completely coincides with De Candolle's (1830, 1839) system. De Candolle's work included only half the genera now known, but the comparison is potentially useful. De Candolle recognized two major groups: Wahlenbergieae and Campanuleae (a third tribe, Merciereae, includes a single South African genus, *Merciera*, with 3 species, which was unfortunately unavailable for this study). The tribe Wahlenbergieae includes genera with "capsula apice dehiscens," whereas the tribe Campanuleae has plants with "capsula lateraliter dehiscens" (De Candolle, 1830). Almost all plants from his tribe Wahlenbergieae have "elongated" seedlings (Group A), whereas plants from Campanuleae have a "rosette" type of seedling (Group B).

A few exceptions need further discussion. De Candolle's division was based on external fruit structure. He placed *Edraianthus* and *Jasione* in the tribe Wahlenbergieae because both have apically dehiscent capsules. Kolakovsky (1982, 1995), who studied internal fruit structure, showed that fruits of many genera in Campanulaceae have a special organ (special tissue) that helps to open a capsule. The list of genera with an axicorn (as it was named by Kolakovsky) includes *Adenophora*, *Asyneuma*, *Campanula*, *Michauxia*, *Phyteuma*, *Popoviocodonia*, *Sergia*, and also *Edraianthus* and some other genera of Group B. This axicorn opens a pore on the lateral wall of the fruit in *Campanula* and other mentioned genera, while in *Edraianthus* it irregularly tears apart the membranous top of the capsule. Thus, capsules in *Edraianthus* and *Cam-*

panula open in different places but by the same mechanism. An explanation probably lies in a type of inflorescence of *Edraianthus*. All species of this genus have capitate inflorescences surrounded by bracts (Lakušić, 1973), and the apical opening of the fruit facilitates seed dispersal more readily than a basal or lateral opening. Therefore, the capsule of *Edraianthus* differs in its dehiscence mechanism from those of other genera with apical valves. Indeed, *Edraianthus* is related to our seedling group with basal rosettes, and this relationship is supported by molecular data (Eddie et al., 2003).

On the other hand, the groups in Shönland's system are very heterogeneous in growth and seedling characters. Thus, according to morphological division *Canarina* should be excluded from the *Campanula* alliance. *Edraianthus* is closely related to *Campanula* and not to genera with apical capsule dehiscence and should be excluded from the subtribe Wahlenberginae. *Musschia* should be excluded from subtribe Platycodinae. The taxonomic position of *Legousia* should be reconsidered.

There is greater similarity between our morphological groups and Takhtajan's (1997) system. His first three subfamilies (Cyanthoideae, Ostrowskioidae, Canarinoideae) include genera with an elongated epicotyl, our Group A. All studied species within our Group B, with a shortened epicotyl, belong to his subfamily Campanuloideae. Anomalous taxa (*Azorina*, *Musschia*) in which the elongated epicotyl may be of secondary origin are also in this subfamily, but isolated in separate tribes.

Data from molecular biology, such as chloroplast DNA structural changes, can contribute to Campanulaceae classification and have already been used in phylogenetic reconstruction of the Lobeliaceae (Knox et al., 1993). Recent molecular analyses of the Campanulaceae based on *rbcL* sequences (Cosner et al., 1994) and nuclear ribosomal DNA ITS sequence data of 93 taxa (Eddie et al., 2001, 2003) support two major lineages within the family (Shulkina & Gaskin, 1999).

CONCLUSIONS

Seedling morphology appears to be a useful character for the classification of Campanulaceae, with two major groups evident. The first one, seedling Group A (*Campanumoea*, *Canarina*, *Codonopsis*, *Leptocodon*, *Ostrowskia*, *Platycodon*, and *Cyananthus*) share elongated seedlings, opposite leaves (at least in the early stage), sympodial branching, and dormancy after the first year. Flowers are mostly in cymose inflorescences (*Platycodon*, *Canarina*, *Ostrowskia*), rarely solitary in the high mountain spe-

cies (*Cyananthus*). The ovary is superior, half-inferior, or inferior. The pollen grains range from 6- to 10-colpate (*Cyananthus*), colporate (*Canarina*, *Platycodon*), or colpoidate (*Campanumoea*), seen as primitive types within the Campanulaceae (Avetisjan, 1988). Capsule dehiscence is mostly apical by valves (*Codonopsis*, *Leptocodon*, *Platycodon*, *Cyananthus*), or lateral by cracks (*Ostrowskia*); there is no axicorn. Almost all taxa are diploid, with $2n = 14, 16, 18$ (Arano & Saito, 1979). Vessels with scalariform perforation plates are found in *Cyananthus*, *Platycodon*, and *Canarina* (Shulkina & Zikov, 1980). Genera of this group occur mostly in East Asia, and only *Canarina* has a disjunct distribution (Macaronesia and eastern Africa). Most genera are monotypic or oligotypic (*Canarina*, *Leptocodon*, *Ostrowskia*, *Platycodon*, *Campanumoea*), and many are considered paleorelicts with unclear relationships (Hedberg, 1961; Popov, 1963); their taxonomic positions vary in different systems.

"Group B" in Campanulaceae includes genera with rosette seedlings, spiral leaf arrangement, and different branching patterns (sympodial, monopodial). Immature plants of this group show no fixed dormancy; mature plants have various seasonal growth patterns and different life forms. The flowers are usually in cymose inflorescences modified into umbel-like, spike-like, and solitary forms. The ovary is inferior. All studied species have porate (including zonoporate and pantoporate) pollen grains. Fruit dehiscence varies, but the capsules never have apical valves; an axicorn is sometimes present. The chromosome numbers vary greatly, with numerous polyploid lines, but $x = 17$ in many (Gadella, 1964). The representatives of this group are widely distributed. Taxonomically the group includes the tribes Campanuleae (6 genera) and Phyteumateae (6 genera), among them large genera such as *Campanula* (300 spp.), *Asyneuma* (50 spp.), *Adenophora* (40 spp.), and *Phyteuma* (40 spp.). The numerous smaller genera with restricted ranges are *Githopsis* (western North America), *Edraianthus* (Apennines and Balkan Peninsula), and *Michauxia* (Turkey, the southern Transcaucasus, Iran). There are also monotypic and oligotypic genera: *Azorina* (Azores), *Cryptocodon* (Pamiro-Alay Mountains), *Cylindrocarpa* (Karatau, Tien Shan), *Musschia* (Madeira Islands), *Physoplexis* (southern Alps), *Popoviocodonia* (Russian Far East), *Sergia* (Tien Shan), and *Zeugandra* (northern Iran), etc. These habitats and environmental conditions obviously vary greatly, and the plants of the group have numerous life forms. All data lead us to conclude that the basal rosette and a shortened type of seedling represent morphological apomorphies. There is

strong evidence that the “elongated” type of seedling is plesiomorphic and characterizes more primitive Campanulaceae forms.

Therefore, two evolutionary directions, two lineages, can be traced within the family which correspond to the above two groups and probably reflect differences in the environments occupied by ancestral types. The recently recognized genus *Gadellia* (Shulkina, 1979) and the critical *Campanulastrum* (Small, 1903) are supported by morphological and molecular data, and both fall outside of *Campanula* s. str. The sister taxa to *Gadellia* in the ITS study (Eddie et al., 2003) is *Musschia aurea*, and this supports *Gadellia* as a genus distinct from *Campanula*. *Campanulastrum americanum* (*Campanula americana*) of the “rosette Group B” is not close to the *Campanula* alliance. Studies of pollen grain (Avetisjan, 1988), chromosome number and morphology (Gadella, 1964), seed-coat morphology (Shetler & Morin, 1986), and molecular data (Eddie et al., 2003) support segregation of *Campanulastrum*. The genus *Campanula* is highly heterogeneous and should be studied carefully. Further morphological and molecular investigations are needed to increase our understanding of monophyletic groups within this family. In Campanulaceae similarities due to convergent and parallel evolution occur both in reproductive and vegetative structures. All characters should be used in conjunction with others.

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Shulkina, Tatyana V, Gaskin, John F, and Eddie, W M M. 2003. "Morphological Studies toward an Improved Classification of Campanulaceae s. str." *Annals of the Missouri Botanical Garden* 90, 576–591. <https://doi.org/10.2307/3298543>.

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