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Systematics of *Campanula* L. subgenus *Scapiflorae* (BOISS.) OGAN. and its ecogeographical differentiation in the mountains of Eurasia

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ABSTRACT**:** Synopsis of *Campanula* subg. *Scapiflorae* and maps of the areas of its species are given. The area of the group consists of 3 parts with large disjunctions: European (1 species), Caucasian and North-West Asian (16 species) and East Siberian – Far Eastern (3 species). In Caucasian and North-West Asian part 3 centers of development stand out: Central Caucasus, Northern Colchis and Armenian Highlands. The subgenus is represented by petrophytes growing almost exclusively in the alpine, subalpine and middle mountain belts in humid mountains and in accordance with boreal moisture regime. Hypothetical ancestor of the group is supposed to be a medium mountain belt petrophyte and evergreen mesophyte growing in a humid steady climate, in sunny shadeless places. The evolution was developing towards acquiring cryomorphic adaptations, and, in a number of cases, week xeromorphic ones. The subgenus must have been formed by the beginning of the possible migrations around the 3 parts of its area, i. e. by the beginning of Pliocene. The most possible primary center of the group is Armenian Highlands and the Great Caucasus.

KEYWORDS*: Campanula* subg. *Scapiflorae*, Systematics, Ecology, Distribution, Migrations, Centers of variability, Evolution, Mountains of Eurasia

Introduction

Working up the taxonomically complicated *Scapiflorae* group for the project "Critical checklist of Caucasian flora" (S-Petersburg) brought to its survey in the whole (OGANESIAN 1993, 1994), as only 4 species out of 20 grow away from Caucasian – North-West Asian part of the area. Naturally, Caucasian – North-West Asian species are studied better than the others (OGANESIAN 1995). It should be noted that *Scapiflorae* is a very compact group with a good isolation from other taxa of the family by the number of features [and especially by the structure of the seed surface, which has no analogues in other groups of *Campanulaceae* studied (THULIN 1975; BELYAYEV 1984a, 1984b, 1985, 1986; OGANESIAN 1985; SHETLER & MORIN 1986)], and has no subdivision into sections. The majority of the species (except those marked in the synopsis and in the text) are approximately equal in alliance to each other. The arrangement of the species in the synopsis also gives some idea of their affinity.

Only the main synonyms used in the basic Floras are cited in the synopsis, as the complete synonymy is published before (OGANESIAN 1993, 1995).

Material and Methods

Caucasian – North-West Asian species have been studied on materials of the Herbaria B (partially), E (partially), ERE, LE, LENUD, MW, SAV (partially), SUCH, TBI, TGM, as well as in nature during the expeditions to South Transcaucasia. All the factual data of this group of species are original. In some cases the dotted maps of the areas are expended with literature data (DAMBOLD 1979; ASSADI 1987). The information about the distribution and ecology of European, Siberian an Far-Eastern species are from literature in the main (HAYEK 1930; KRYLOV 1949; FEDOROV 1957; POPOV 1959; GREBENSČIKOV 1960; SHETLER 1963; VOROSCHILOV 1966; STOJANOV & al. 1967; MALYSČEV 1972; TOLMAČEV 1974; FEDOROV 1976; HEGI & MERXMÜLLER 1976; MALYSČEV & PESCHKOVA 1979; GREUTER & al. 1984; REVUSCHKIN 1988; KHOKHRJAKOV 1989), that is why dotted maps of the areas of these species are not given.

Synopsis

Genus *Campanula* L. 1753, Sp. Pl. 1: 163; idem, 1754, Gen. Pl. ed. 5: 77.

Subgen. *Scapiflorae* (BOISS.) OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 146. – Grex *Scapiflorae* BOISS. 1875, Fl. Or. 3: 894. – Ser. *Scapiflorae* (BOISS.) FOMIN 1904, Fl. Cauc. Crit. 4, 6: 45. – Sect. *Scapiflorae* (BOISS.) KHARADZE 1949, Not. Syst. Geogr. Tphilis. 15: 25. – Subsect. *Scapiflorae* (BOISS.) FED. 1957, Fl. URSS 24: 256. – Grex *Rupestres* BOISS. 1875, Fl. Or. 3: 894, p. p. – Ser. *Rupestres* (BOISS.) FOMIN 1905, Fl. Cauc. Crit. 4, 6: 68, p. p. – Sect. *Rupestres* (BOISS.) KHARADZE 1949, l. c.: 24, p. p., incl. typ. – Subsect. *Rupestres* (BOISS.)

FED. 1957, l. c.: 465, 282, p. p., incl. typ. – Subsect. *Dasystigma* FED. 1957, l. c.: 461, 186. – Gen. *Hemisphaera* KOLAK. 1984, Okhrana prirody Gruzii 12: 161.

Typus: *C. ciliata* STEVEN

1. *C. petrophila* RUPR. 1867, Bull. Acad. Sci. Pétersb. 11: 186.
Distribution: Central and eastern parts of the Great Caucasus. – Fig. 3.
Habitats: Rocks, moraines, screes, rare on the subalpine meadows and alpine carpets*. Middle mountain, subalpine and alpine belts, 1600-3300 m a. s. l.

2. *C. saxifraga* M. BIEB. 1808, Fl. Taur.-Cauc. 1:155.
2a. Subsp. *saxifraga*.
Distribution: Western and central parts of the Great Caucasus (to the west of the Terek river). – Fig. 4.
Habitats: Rocks, moraines, screes, rare on the subalpine and alpine meadows. Middle mountain, subalpine and alpine belts, (1400) 1600-3200 m a. s. l.
2b. Subsp. *argunensis* (RUPR.) OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 148. - .*C. argunensis* Rupr. 1867, Bull. Acad. Sci. Pétersb. 11: 181. – *C. doluchanovii* KHARADZE 1947, Not. Syst. Geogr. Tphilis. 13: 54.
Distribution: Eastern part of the Great Caucasus (to the east of the Terek river). – Fig. 4.
Habitats: Rocks, moraines, screes, rare on the alpine meadows. Middle mountain, subalpine and alpine belts, (1200) 1600-3300 (4000) m a. s. l.
2c. Subsp. *meyerana* (RUPR.) OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 148. – *C. meyerana* RUPR. 1867, Bull. Acad. Sci. Pétersb. 11: 178. – *C. fominii* GROSSH. 1933, Trudy Azerb. Fil. Acad. Nauk SSSR 1: 56.
Distribution: Narrow endemic of the Schakhdagh mountain and basin of Kusarčay river (Eastern Caucasus). – Fig. 4.
Habitats: Limestone rocks. Middle mountain, subalpine and alpine belts, 1800-2800 m a. s. l.
2d. Subsp. *aucheri* (A. DC.) OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 149. – *C. aucheri* A. DC. 1839, in DC., Prodr. 7, 2: 460. – *C. alpigena* K. KOCH 1850, Linnaea 23: 638. – *C. ruprechtii* BOISS. 1875, Fl. Or. 3: 905. – *C. armazica* KHARADZE 1947, Not. Syst. Geogr. Tphilis. 13: 51. – *C. froedinii* RECH. fil. 1950, Öst. Acad. Wiss. Math.-Nath. Kl. Anz. 87: 195.
Distribution: Minor Caucasus, Pontic ridge, Armenian Highlands (North-West), Elburs ridge. – Fig. 4.
Habitats: Rocks, moraines, screes, sceleton soils, stony alpine meadows, rare on the alpine carpets. Middle mountain, subalpine and alpine belts, (1000) 1700-3500 (4000) m a. s. l.

3. *C. besenginica* FOMIN 1902, Trav. Jard. Bot. Tiflis 6, 2: 8, descr. emend. OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 150.

* In the sense of Caucasian authors (NARINIAN 1962)

Distribution: Central Caucasus. - Fig. 1.
Habitats: Rocks and moraines, mainly at the glaciers. Middle mountan, subalpine and alpine belts, 1700-2700 m a. s. l.

4. *C. kryophila* RUPR. 1867, Bull. Acad. Sci. Pétersb. 11: 184.
Distribution: Narrow endemic of Ardon river in its upper flow (Central Caucasus). – Fig. 2.
Habitats: Rocks at the glaciers. Alpine belt, 2100-3000 m a. s. l.
Affinity: Close related to *C. zeyensis* and *C. kadargavanica*.

5. *C. zeyensis* AMIRKH. & TAVASIEV 1974, Bull. Mosk. Obsč. Ispit. Prir., Otd. Biol. 84, 6: 119.
Distribution: Upper flow of the Zeydon river (Central Caucasus). Known only from the type gathering. – Fig. 3.
Habitats: Granite screes. Alpine belt, 2000 m a. s. l.
Affinity: Close related to *C. kryophila* and *C. kadargavanica*.

6. *C. kadargavanica* AMIRKH. & KOMZHA 1984, Botaničeskije issledovanija v zapovednikakh RSFSR: 138.
Distribution: Narrow endemic of the mountain massifs Tbaukhokh, Karunkhokh and Kionkhokh (Central Caucasus). – Fig. 2.
Habitats: Limestone rocks. Forest belt, 1000 m a. s. l.
Affinity: Close related to *C. kryophila* and *C. zeyensis*.

7. *C. ardonensis* RUPR. 1867, Bull. Acad. Sci. Pétersb. 11:185.
Distribution: Narrow endemic of Ardon river in its upper flow (Central Caucasus). – Fig. 4.
Habitats: Rocks. Lower and middle mountain, subalpine and alpine belts, 1200-2300 m a. s. l.

8. *C. bellidifolia* ADAMS 1805, in F. WEBER & D. MOHR., Beitr. Naturk. 1: 47. – *C.adami* M. BIEB. 1808, Fl. Taur.-Cauc. 1: 155. – *C. sosnowskyi* KHARADZE 1949, Not. Syst. Geogr. Tphilis. 13: 109.
Distribution: Upper flows of rivers Terek, Fiagdon and Ardon and some adjacent mountain ridges (Central Caucasus). – Fig. 1.
Habitats: Rocks. Middle mountain, subalpine and alpine belts, (1000) 1500-3000 (3400) m a. s. l.

9. *C. circassica* FOMIN 1905, Fl. Cauc. Crit. 4, 6: 52, descr. emend. OGAN. 1993, Bot. Žurn. (Leningrad) 78, 3: 151. – *C. anomala* FOMIN 1905, l. c.: 53.
Distribution: Northern Colchis (Northern part of Western Transcaucasia).– Fig. 1.
Habitats: Rocks, moraines, stony alpine and subalpine meadows (substrata mainly limestone). Middle mountain, subalpine and alpine belts, (800) 1800-3200 m a. s. l.
Affinity: Allied to *C. radchensis* and *C. songutica*.

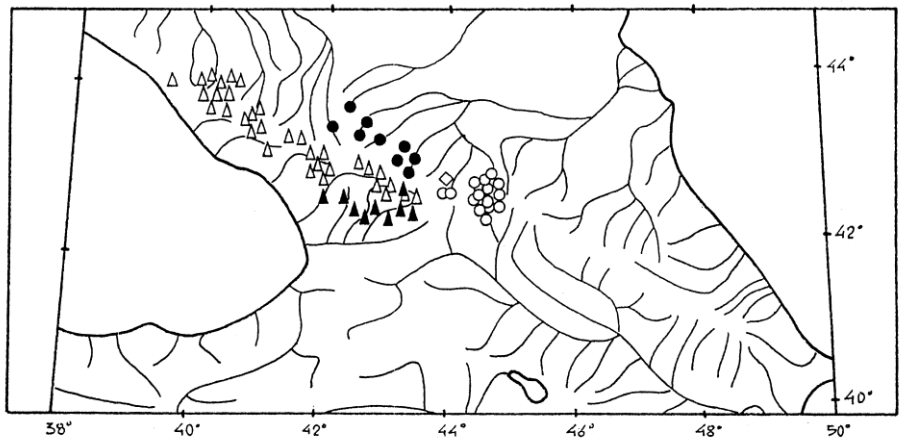

Fig. 1. Distribution of the species
△ ***C. circassica;*** ▲ ***C. radchensis;*** ◇ ***C. songutica;*** O ***C. bellidifolia;***
● ***C. besenginica.***

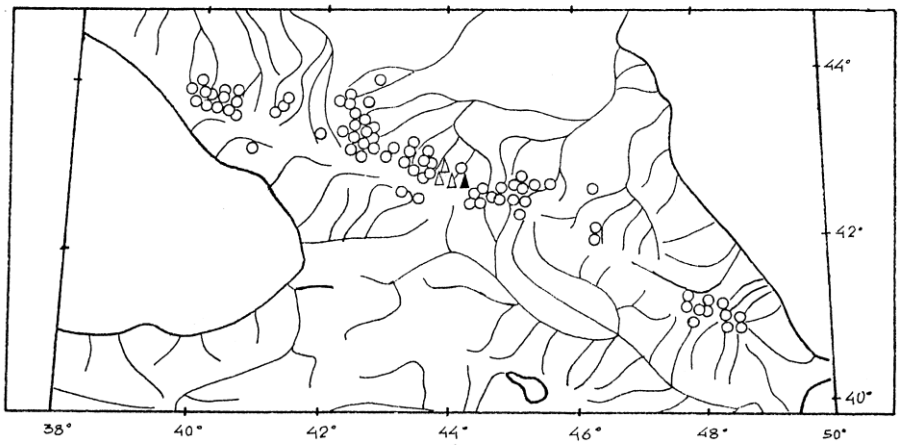

Fig. 2. Distribution of the species
O ***C. ciliata;*** △ ***C. kryophila;*** ▲ ***C. kadargavanica.***

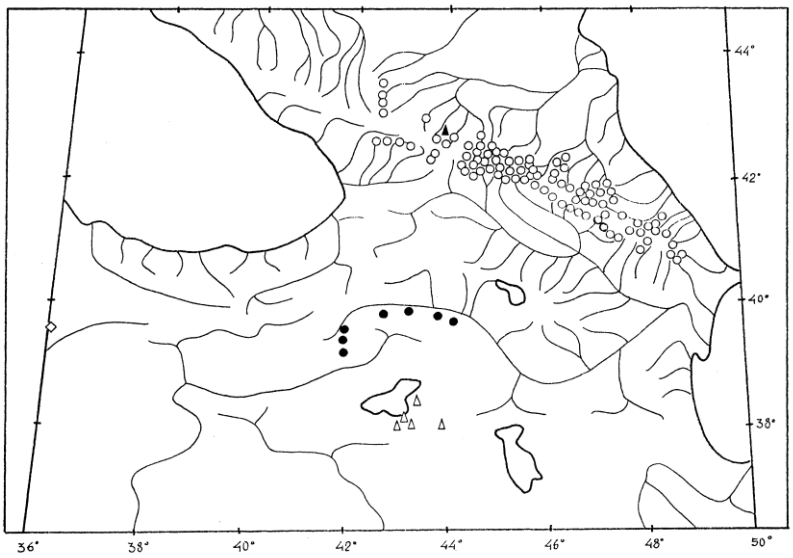

Fig. 3. Distribution of the species
○ *C. petrophila*; ▲ *C. zeyensis*; ● *C. ledebouriana*; △ *C. bornmuelleri*;
◇ *C. pulvinaris*

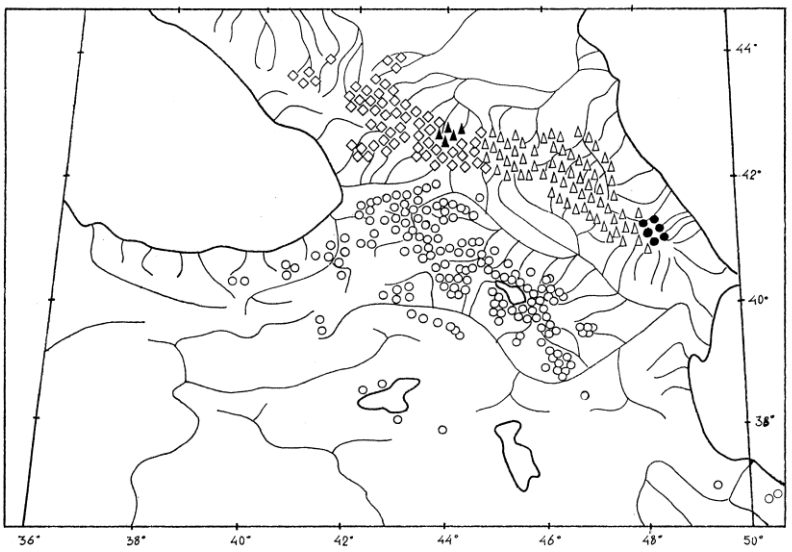

Fig. 4. Distribution of the species
◇ *C. saxifraga* subsp. *saxifraga*; △ *C. saxifraga* subsp. *argunensis*;
● *C. saxifraga* subsp. *meyerana*; ○ *C. saxifraga* subsp. *aucheri*; ▲ *C. ardonensis*

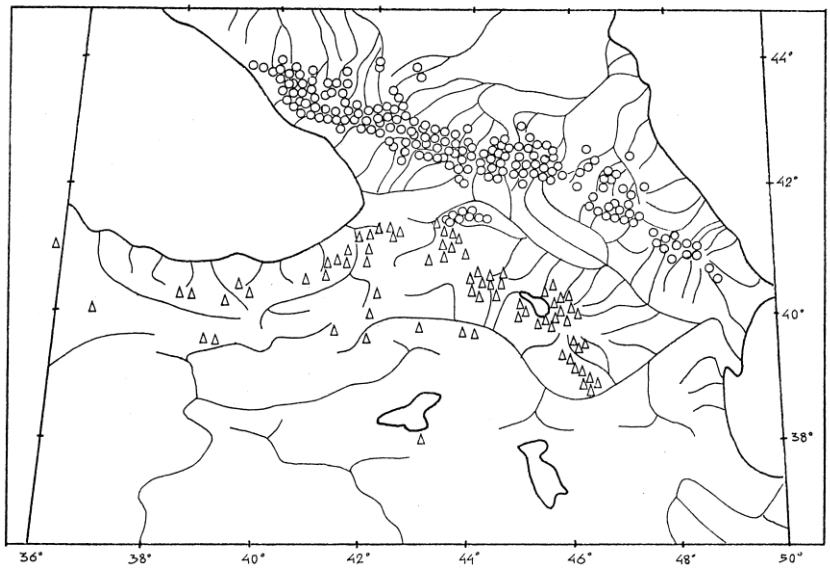

Fig. 5. Distribution of the species
△ *C. tridentata* subsp. *tridentata* (isn't marked locality: Antalya Çubuk Boğasi, 3 km S of Hafispaşa, 860 m, Huber-Morath 15720 (South Anatolia);
○ *C. tridentata* subsp. *biebersteiniana*

10. *C. radchensis* KHARADZE 1947, Not. Syst. Geogr. Tphilis. 13: 53.
Distribution: Northern Colchis (North-West Georgia). – Fig. 1.
Habitats: Limestone rocks, screes, stony places. Subalpine and alpine belts, 1900-2800 m a. s. l.
Affinity: Allied to *C.circassica* and *C. songutica*.

11. *C. songutica* AMIRKH. 1984, Botaničeskije issledovanija v zapovednikakh RSFSR: 136.
Distribution: Upper flow of Urukh river, Zey ridge (Central Caucasus). Known only from the type gathering. – Fig. 1.
Habitats: Moraines at the glacier. Alpine belt, 3100 m a. s. l.
Affnity: Allied to *C. circassica* and *C. songutica*.

12. *C. tridentata* SCHREB. 1766, Icon. Descr. Pl. Dec. 1: 3, Tab. 2.
12a. Subsp. *tridentata.* – *C. bithynica* A. DC. 1839, in DC., Prodr. 7, 2:460.
Distribution: Minor Caucasus, Pontic ridge, Armenian Highlands (North and West), South Anatolia (Antalya, near Hafispasa). – Fig. 5.
Habitats: Alpine carpets, rare subalpine meadows, stony places and rocks. Subalpine and alpine belts, (1600) 2500-3900 m a. s. l.

12b. Subsp. *biebersteiniana* (ROEM. & SCHULT.) OGAN. 1981, Bot. Žurn. (Leningrad) 66, 3: 403. – *C. biebersteiniana* ROEM. & SCHULT. 1819, Syst. Veg. 5: 147. – *C. rupestris* M. BIEB. 1808, Fl. Taur.-Cauc. 1: 154, non SMITH 1806. – *C. tridens* RUPR. 1867, Bull. Acad. Sci. Petersb. 11:175. – *C. akuschensis* GUSSEJNOV 1970, Bot. Žurn. (Leningrad) 55: 1500.
Distribution: Great Caucasus and Trialeti ridge (Minor Caucasus). – Fig. 5.
Habitats: Alpine carpets, stony alpine meadows, subalpine meadows. Subalpine and alpine belts, (1200) 2200-3100 m a. s. l.

13. *C. ciliata* STEVEN 1812, Mém. Soc. Nat. Moscou 3: 256.
Distribution: Great Caucasus, mainly the nortern slope. – Fig. 2.
Habitats: Rocks, screes, stony alpine meadows, rare subalpine meadows and alpine carpets. Middle mountain, subalpine and alpine belts, (1400) 2000-3400 (3800) m a. s. l.

14. *C. ledebouriana* TRAUTV. 1873, Acta Horti Petropol. 2, 2: 477.
Distribution: Aghri ridge and upper flow of Araks river (Armenian Highlands). – Fig. 3.
Habitats: Basalt and limestone rocks, screes. Middle mountain and subalpine belts, 1700-2250 m a. s. l.
Affinity: Allied to *C. bornmuelleri* and *C. pulvinaris*.

15. *C. bornmuelleri* NÁBĚL. 1926, Publ. Fac. Sci. Univ. (Brno) 70: 3.
Distribution: South-eastern shore of the Van lake (Armenian Highlands). – Fig. 3.
Habitats: Granite and limestone rocks, screes. Subalpine and alpine belts, 2350-3500 m a. s. l.
Affinity: Allied to *C. ledebouriana* and *C. pulvinaris*.

16. *C. pulvinaris* HAUSSKN. & BORNM. 1905, Mitt. Thüring. Bot. Ver. N. F. 20: 29.
Distribution: Narrow endemic of the Karababa mountain (Taurus ridge). – Fig. 3.
Habitats: Rocks. Subalpine belt, 2000-2350 m a. s. l.
Affinity: Allied to *C. ledebouriana* and *C. bornmuelleri.*

17. *C. alpina* JACQ. 1762, Enum. Stirp. Vindob.: 36.
17a. Subsp. *alpina*.
Distribution: Eastern Alps, Carpatian mountains.
Habitats: Alpine and subalpine meadows and rocks in tne alpine and subalpine belts.
17b. Subsp. *orbelica* (PANČIĆ) URUM. 1923, Spis. Balg. Acad. Nauk 28: 147. – *C. orbelica* PANČIĆ 1886, Nov. Elem. Fl. Bulg.: 30.
Distribution: Mountains of the central part of the Balkan peninsula (Middle and West Stara Planina, Rila Planina, Vitosha, Ostrovskata Planina, Pirin Planina, West and Middle Rodopi Planina, Macedonia).
Habitats: Alpine meadows and rocks.

18. *C. dasyantha* M. BIEB. 1819, Fl. Taur.-Cauc. 3: 147. – *C. pallasiana* VEST. 1819, in ROEM. & SCHULT., Syst. Veg. 5: 138. – *C. pilosa* PALLAS ex ROEM. & SCHULT. 1819, l. c.: 148. – *C. altaica* A. DC. 1830, Monogr. Camp.: 229, non LEDEB. 1824. – *C. redowskyi* FISCH. 1873, Acta Horti Petropol. 1: 288, non *C. redowskiana* CHAM. & SCHLECHT. 1829.
Distribution: South-West Siberia (the Altai, Mongolian Altai, Sayany mountains, North Baikal, Stanovoy and Kolyma uplands, the Baykal, Bargusin and Yablonovy ridges), Okhotsk coast (Jug-Jur ridge).
Habitats: Mountain tundra, rocks, screes, sceleton soils, subalpine meadows, light larch forests. Subalpine and alpine belts.
Affinity. Allied to *C. aldanensis* and *C. chamissonis*.

19. *C. aldanensis* FED. & KARAV. 1957, in FED., Fl. URSS 24:466.
Distribution: Basins of the Lena river and its tribularies the Aldan and the Olekma (Jakutia).
Habitats: Limestone rocks in the wood-belt.
Affinity: Allied to *C. dasyantha* and *C. chamissonis*.

20. *C. chamissonis* FED. 1957, Fl. URSS 24: 279. – *C. dasyantha* auct. non M. BIEB.: CHAM. 1829, Linnaea 4: 37. – *C. dasyantha* auct. mult. p. p., non M. BIEB. – *C. pilosa dasyantha* HERDER 1872, Acta Horti Petropol. 1, 2: 288.
Distribution: Kamčatka Peninsula, Sakhalin Island (South), Aleutian, Kuril and Japanese (Khokkaido and Khondo- North) Islands.
Habitats: Rocks, sceleton soils and sandy slopes of the alpine belt, but can also reach the sea shore.
Affinity: Allied to *C. dasyantha* and *C. aldanensis*.

Discussion

Habitats

All the species are obligate or primary petrophytes. The only exception is the edificator of the formation of Caucasian alpine carpets (not the same as the “Alpenmatten” of European authors, NARINIAN 1962), *C. tridentata*, which is often met also in petrophyte habitats. On alpine carpets or alpine stony meadows are often met such species as *C. petrophila*, *C. circassica*, *C. ciliata*, *C. saxifraga*, *C. dasyantha* and *C. alpina*. It is easy to see that these species in particular are most wide-spread. Strictly saxiculous species usually grow in a small area, which can be accounted for the slow rate of their expansion (FOMIN 1903-1907).

The overwhelming majority of species of this subgenus grows in the high (alpine and subalpine) and medium mountain belts, and only some of them step down to the lower belt. Usually a high amplitude of altitudes correlates with wide area. A very peculiar xeromorphic species *C. ardonensis* is met in the lower and medium mountain belts, *C. kadargavanica* – only in lower belt.

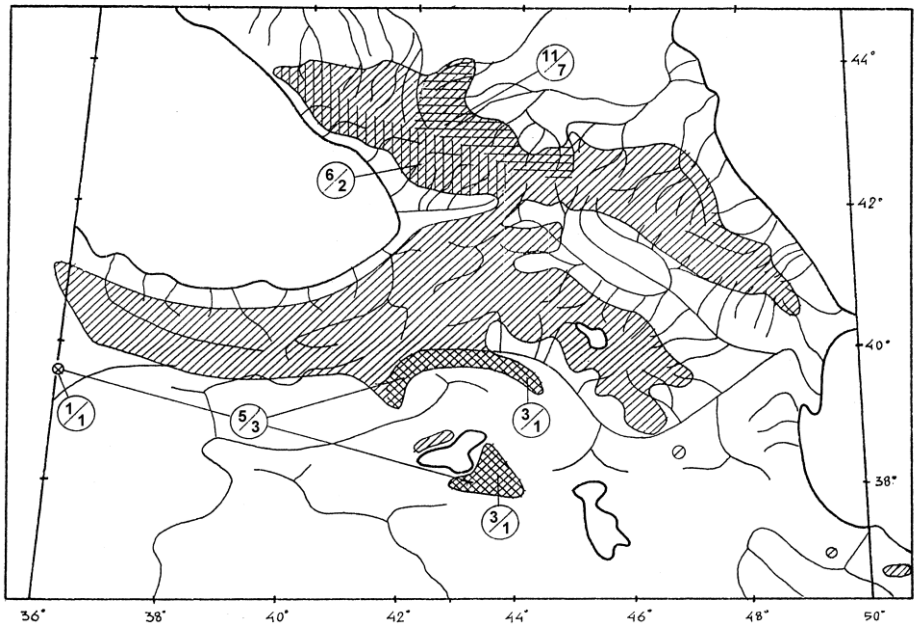

Fig. 6. Area of *Campanula* subg. *Scapiflorae* in the Caucasus and Armenian Highlands

Number of the species 1-4, no endemic species

The centers of autochtonous development are marked:

Central Caucasus;

Northern Colchis;

Armenian Highlands.

The numerator of the fraction shows general number of the species and the denominator – the number of endemic species in these centers.

Distribution and centers of development

The area of the subgenus is divided into 3 parts with large disjunctions: 1) European; 2) Caucasian and North-West Asian; 3) East Siberian and Far Eastern (Fig. 7). There is not a single common species in these 3 parts of the area.

In Europe the subgenus is represented by *C. alpina* with 2 subspecies. In East Siberian and Far Eastern parts of the area – by 3 vicarious species: *C. dasyantha*, *C. aldanensis* and *C. chamissonis*.

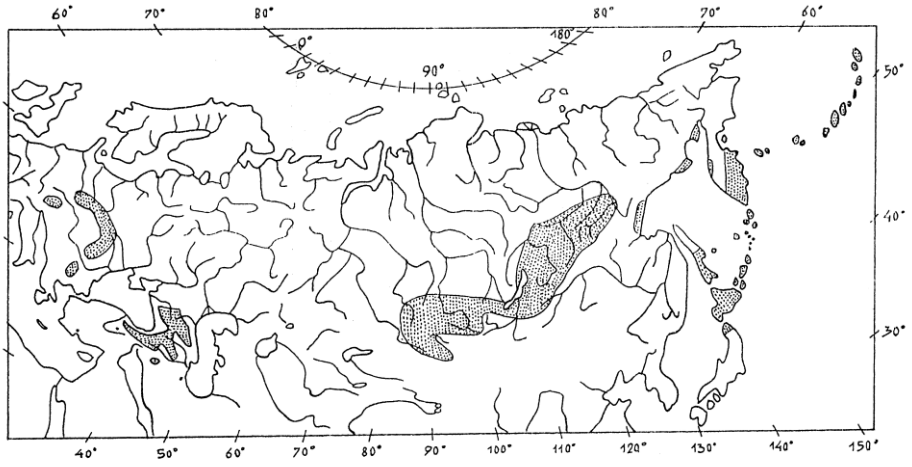

Fig. 7. Area of *Campanula* subg. *Scapiflorae*

The main number of the species (16 of 20) is centered in the area of the Caucasus and North-West Asia, or, if only to ignore some irradiations: in the Great Caucasus and Armenian Highlands with its flank ridges Taurus, Pontic and Minor Caucasus (geographical dividing of West Asia by ARMAND & al. 1956). On the Great Caucasus 13 species (15 taxa with subspecies) can be met, 11 species (15 taxa with subspecies) are endemics. In the Armenian Highlands with its flank ridges 5 species grow, 3 of which are rather narrow endemics growing at a considerably distance from each other. These 3 species (*C. ledebouriana*, *C. bornmuelleri* and *C. pulvinaris*) are taxonomically close, have some primitive features in common, and are definitely autochtonic and ancient, as distinct from two other yonger migrants *C. tridentata* subsp. *tridentata* and *C. saxifraga* subsp. *aucheri.*

According to floristic regions within the Great Caucasus the species are distributed in the following way: 11 species in the Central Caucasus including the Upper Kuban (GALUSHKO 1976, 1980), 7 of them are endemic ones. There are 6 species, 2 of them endemics, in Northern Colchis, including Fisht and Oshten mountain massifs (MALEEV 1939; KOLAKOVSKY 1958). There are in 4 species each and no endemics in the Western Caucasus (up to the Teberdin-Dout ridge), in the Eastern Caucasus (excluding Fiagdon-Assin region according to GALUSHKO 1976), and on the central and eastern parts of the southern macroslope of Great Caucasus (Fig. 6).

Such a distribution shows that the center of autochtonous development for the majority of species is the central part of Great Caucasus, particularly its northern macroslope (and especially Northern Ossetia). It is confirmed by high variability of such widely spread species as *C. saxifraga*, *C. tridentata* and *C. petrophila*

here as well as in floristic region of Khevsureti-Pshavi-Tusheti (KETSKHOVELI 1975). Two closely related endemics of Northern Colchis – *C. circassica* and *C. radchensis* have a vicarious species *C. songutica* in the basin of Ardon river in the Central Caucasus. *C. tridentata* subsp. *biebersteiniana* and *C. ciliata* of Northern Colchis are somewhat different and are represented correspondingly by var. *barbata* FOMIN and var. *pontica* ALBOV. Consequently, Northern Colchis as well may be considered a center of formation of species in its own right, though less important than the Central Caucasus, but certainly combined with it. The more isolated area of development of the species is Armenian Highlands (including the bordering Taurus ridge), the endemic species of which have preserved some primitive features (such as few-flowered scapes) and exhibit weak affinity to the species of the Great Caucasus. But there is some resemblance between these species and *C. besenginica* (Central Caucasus). All this allows us to consider Armenian Highlands an independent and rather ancient center of development of subgenus *Scapiflorae*.

Ecological origin and adaptations

While considering the area of the subgenus as a whole (Fig. 7), it strikes the eye that the representatives of the group cover mainly humid mountains and very rarely semi-arid – Daghestan, Zangezur ridge, some parts of Armenian Highlands, medium flow of the Lena river (AGHAKHANIANTS 1981; AKMAN & KETENOĞLU 1986). On the other hand, a good correlation with the boreal regime of moisture is noted. There is Mediterranean regime only in Armenian Highlands including bordering ridges (AGHAKHANIANTS 1981; AKMAN & KETENOĞLU 1986) and monsoon one in the Far East (SUSLOV 1954).

Nevertheless studied by us leaves of *C. tridentata* subsp. *tridentata* and *C. saxifraga* subsp. *aucheri* from Armenia – almost the most arid area of their growth – have mesomorphic structute: dorsiventral leaves with 2 layer palisade tissue and 4-5 layer spongy one, the epidermis with not too thick outer walls. According to SHULKINA'S (1977, 1984, 1988) data the representatives of this group have a nude central bud, no dormant period and the leaves haven't got an abscission layer. In this case these features do not reflect the modern ecological conditions but the history of the group mesomorphic by the origin (ALEKSANDROV & TSKHAKAJA 1926; VASILEVSKAJA & ANTONOVA 1978; VASILEVSKAJA 1979). All this makes it possible to presume that the hypothetical ancestor of *Scapiflorae* subgenus was a medium (or low) mountain belt petrophyte, evergreen mesophyte growing in steady humid climate without drought period, in sunny shadeless places. The representatives of the group managed to adapt themselves to high insolation and fluctuations of temperature under highland conditions, but their distribution nowadays is limited by their need of sufficient precipitation during the short summer period of vegetation.

For the ancestral forms it is possible to recostruct few-flowered scapes (SHULKINA 1984; OGANESIAN 1991) and semi-immersed caudexes. The evolution was developing towards acquiring cryomorphic adaptations, and, in a number of cases, weak xeromorphic ones. Many species acquired overground caudexes

and cushion-shaped life-form which at the same time is an adjustment against the drought and low temperatures. An additional heat isolation and protection from transpiration of the plant as a whole may be created by the remains of the leaves left on the caudexes. The plants of this type are obligate petrophytes and may be able to use the moisture condenced in the cracks of the rocks. The species that are included in the formation of Caucasian alpine carpets to the contrary, thanks to the contractility of the roots, developed subground caudexes and overground rosettes of leaves. This ensured additional moisturising and heat insulation due to the structure of the tuft of the alpine carpet (NARINIAN 1966) and wintering under a snow layer. According to NARINIAN'S (1966, 1974) data plants with such life-forms have to.a certain extent, cryoxerophytic structure, adapted to a drought in the second half of summer. A. better wintering of a dormant bud of *C. tridentata* due to the pecularities of vernation is facilitated by its having 3 teeth at the tip of the leaf and pubescence of its margins (MIRZOEVA & AKHVERDOV 1967).

Migrations

The isolated position of subgenus *Scapiflorae* by a number of features (OGANESIAN 1993) with vast area and great disjunctions speaks of its antiquity. TOLMAČEV (1958) consideres Oligocene to be the beginning of formation of petrophytes in the surroundings of hemihygrophyllous flora in the Great Caucasus. The majority of authors consider Miocene the time of formation of alpine petrophytes in the Caucasus (TAKHTAJAN 1946; FEDOROV 1952) or Miocene – Pliocene (ELENEVSKY 1964). CHARADZE (1970) accepts Miocene – Pliocene age for many species of this group.

Pre-glacial migrations. The contacts between the Great and Minor Caucasus were established since the end of Miocene (Sarmat – Meotis) (GROSSHEIM 1948) and since that time the Great Caucasus and Armenian Highlands may be considered a united center of development for *Scapiflorae* subgenus. Migrations from here to the Balkan Peninsula both climatically and orographically via Asia Minor and Aegeida were possible throughout the whole Pliocene (DOBRYNIN 1948) but in the given case there were carried out through the North (WULFF 1944). Migrations between Siberia and the Great Caucasus – Armenian Highlands via mountain systems of North Iran and Middle Asia were orographically possible since the beginning of Pliocene (SINITSIN 1962; AGAKHANIANTZ 1981), but climatically there were two possibilities: the first – in lower or medium Pliocene when monsoon regime of precipitation reigned in Middle Asia and not Mediterranean one (AGHAKHANIANTZ 1981); and the second – during the Pleistocene glaciations when the climate was cold, humid and steady and altitudional belts lower. But at low rate of dispersal of saxicolous species (FOMIN 1903-1907) the second possibility is rather doubtful.

Glacial migrations. The migrants of the glacial period, such as *C. saxifraga* and *C. tridentata* succeed in expansion from the Great Caucasus only within the precincts of Armenian Highlands. They should have had a considerable speed

rate of dispersal, as they disseminated on the newly-formed lava substrata, where the former vegetation was destroyed, along with formation of alpine carpets or stony alpine meadows (FEDOROV 1952).

A very interesting is fact of discovery of *C. tridentata* subsp. *tridentata* by Huber-Morath in South Anatolia in the vicinity of Antalya at an altitude of 860 m a. s. l. (DAMBOLDT 1979). This locality, being so far from the main part of the area, and not a very high altitude in conditions of hot Mediterranean climate can be only a glacial relic. It is worthy of note that here, near Antalya in a quaternary travertines lying at an altitude of 40 m a. s. l. were found the fossils of Siberian species *Salix caprea* L. and *S. cinerea* L. These fossils point to rather severe, even for this altitude, and sea-shore, climatic conditions during the Wurm Ice Age (FÜRON 1955). Another interesting isolated site than can also be considered a glacial relic is the site of *C. saxifraga* subsp. *aucheri* on the Elburs ridge. This locality confirms the opinion of the Elburs glaciation and spread of cold-resistent types in glacial period up to the northern slope of the Elburs (SINITSIN 1962).

Wide distribution of *C. alpina* in the Eastern Alps and the Carpatian mountains speaks in favour of the species quickly expansing in the sites just cleared of the glacial ice from the Balkan Peninsula. Just as wide distribution of the species of *Scapiflorae* subgenus in the mountains of Siberia and Far East also seems to be connected with fast expansion of them on the territories where repeated glaciations destroyed Tertiary flora (SUSLOV 1954; SINITSIN 1962). The absence of these species in Amursk – Primorsk region where there was no glaciation testifies in favour of it. All the ties between Aleutian Islands and Kamčatka were cut before the glacial period or at its very beginning (WULFF 1944). Japanese Islands together with Sakhalin had connection with the continent during maximal glaciations at the latitude of Sakhalin and made an unbroken land massif experiencing small-scale glaciations (SUSLOV 1954; ARMAND & al. 1956; SINITSIN 1962). The ties of Kuril Islands with Japanese and Kamčatka Peninsula were preserved even during the Pleistocene (SINITSIN 1962).

So, great disjunctions among European, Caucasian – North-West Asian and East Siberian – Far Eastern parts of the area of subgenus *Scapiflorae* as well as the fact that the subgenus is represented by different species in these 3 locations speaks of early migrations: one between the Caucasus – North-West Asia and Balkan Peninsula – from the beginning and to the end of Pliocene; the other – between the Caucasus – North-West Asia and Eastern Siberia – in the first half of Pliocene. The *Scapiflorae* subgenus must have been formed by the beginning of migrations among the 3 parts of the area, i. e. by the beginning of Pliocene, and is mesomorphic by the origin. Its representatives underwent the evolution in weakly competing and very ancient saxicolous and mound habitats which had preservative qualities and facilitated active speciation (FEDOROV & Fedorov 1929; KOLAKOVSKY 1961, 1991, 1995), which continues now as well, especially in the Great Caucasus.

It is impossible to state definitely the primary center of formation of subgenus *Scapiflorae* but the concentration of the species – counting those, which have

more primitive features, the presence of more or less close groups [*Campanula karakuschensis* GROSSH. = *Theodorovia karakuschensis* (GROSSH.) KOLAK.; *Campanula dzaaku* ALBOV = *Pseudocampanula dzaaku* (ALBOV)KOLAK.], and also the fact that the Great Caucasus and Armenian Highlands are one of the large centers of autochtonous development for the *Campanulaceae* family speak in favour of it.

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