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Diversity and Florogenesis of Subnival Flora of the Caucasus

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Abstract: This paper presents the results of systematic, ecopathological, and chorological studies of the diversity of the subnival belt (zone) flora of the Caucasus Mountains, peculiarity of altitudinal distribution, endemism and florogenesis. Comparative analysis of the diversity of the subnival flora on different types of stone and at different altitudes in various parts of the Caucasus has been made. It is based on field investigation and on literature research. 226 species, 96 genera and 35 families were recorded in the subnival belt of the Caucasus within a range of 2,800 (2,900)-4,000 m a.s.l. Among these 117 species or 51% are common endemics of the Greater Caucasus and Caucasus. It is proved that floristic elements of different origin (authochronic and aloctonic) and age (Miocene-Pliocene and Pleistocene) contributed to the florogenesis of the subnival belt of the Caucasus. The Caucasian, the Eu-Caucasian, the Eastern Asian, the Minor Asian, the Dagestan-Iranian, the Caucasia-European groups plaied an important role in the florogenesis. Criophilic evolution on the of the some plants was related to oreophytizacion during formation of the Caucasus mountains (in the second half of the Tertiary), as well as the glaciations scale. Species composition and coenotic role are different in various parts of the Caucasus and within each part. This is conditioned by the different hypsometry of various parts of the Caucasus, the character of glatiations, edaphic and climatic conditions, lythological diversity. Compared with the Greater Caucasus, the relative floristic poverty of the Lesser Caucasus is due to low elevations and extensive rather recent vulcanism.

Key words: Caucasus mountain, subnival flora, geographycal isolation, endemic, glatiation, volcanogenic rock-screes.

1. Introduction

Different data have been provided on the diversity of the subnival flora of different parts of the Caucasus. 80-230 plant species were recorded within the boundaries of the Greater Caucasus [1-9] and 60-100 species in the Lesser Caucasus [10-12]. In part these differences are caused by inclusion of species more comon in the subalpine and alpine belts in floristic lists of the subnival zone. For example, A. Dolukhanov [3] indicated 191 species for the volcanic plateau of the river mouth Didi Liakhvi (in the central Greater Caucasus) at 3,300 m a.s.l. This number seems unlikely high for the subnival zone and was increased due to inclusion of subalpine and alpine species (*Anemone fasciculata* L., *Geranium ibericum* Cav., *Delphinium speciosum* M. Bieb., *Inula orientalis* Lam., *Polygonum carneum* C. Koch (= *Bistorta carnea* (C. Koch) Kom.), *Cardamine uliginosa* Bieb., *Chaerophyllum roseum* Bieb., *Swertia iberica* Fisch. & C.A. Mey., *Macrotomia echinoides* (L.) Boiss. (= *Huynchia pulchra* (Roem. & Schult.) Greuter & Burdet), *Gentiana septemfida* Pall., *Betonica grandiflora* Willd. (= *B. macrantha* C. Koch), and *Centaurea cheiranthifolia* Willd., etc.). These plants are typical species of the meadows (subalpine and alpine) of the glacially formed Caucasian high mountains [6, 7] and create diverse phytocenoces. The studies conducted by A. Kharadze [1, 2], B. Zurebiani [4], and B. Prima [5] reflect better the diversity of typical subnival flora of the Caucasus. The subnival zone represents the upper level of the alpine belt,

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almost devoid of soil cover. Therefore, it seems unreasonable to include here the vegetation of the nival belt as it is given in some works [8, 9]. Only a few plants are found here and respectively only mono- or bidominant plant communities [2]. In the European Alps the upper limit of the closed vegetation distribution is mainly at 2,800 m a.s.l. [13-16]. At the same time, it is also worth noting that systematic and geographical diversity of the flora in the subnival belt, this inique, comparatively young climatic zone, fails to reflect its coenotic and landscape diversity fully i.e., the so-called beta and gamma diversity [17].

The reason for data differences is insufficient knowledge of high mountain areas, different definitions of the subnival zone, and more or less different high montane relief, climate, hypsometry and history of peri-glacial flora formation process in various parts of the Caucasus. In this context formation process of high mountain flora was influenced by a different extent of glaciation in the western, central and eastern parts of the Greater Caucasus, and the Lesser Caucasus in the Quaternary. It is known that during the Pleistocene glaciers descended to 1,000-1,200 m in the western Greater Caucasus, to 680-700 m in the central Greater Caucasus (Svaneti, gorges of the rivers Mulkhura, Dolra, Nenskra), to 1,700-1,800 m in the eastern Greater Caucasus (Tusheti, Pirikiti Khevsureti, gorges of the rivers Pirikiti Alazani, Asa and Arghuni) and to 2,200-2,300 m in the Lesser Caucasus [18-20]. At present the subnival belt in the Greater Caucasus covers altitudes of 2,900-3,800 (-4,000) m. Its lower boundary is a transition strip and “intersection” between upper alpine and subnival belts. Complex eco- and coenotones of these two belts frequently occur in this strip.

2. Description of the Study Area

2.1 Orography and Geology

The Great Caucasus stretches for about 1,500 km from the north-west to the south-east, between the Taman Peninsula to the Apsheron Peninsula. According to the absolute altitudes and other physico-geographical peculiarities it is traditionally divided into three parts: west, central and east Caucasus. The borders between these sections are Mt. Elbrus and Mt. Kazbeg. The highest peaks surpass an elevation of 5,000-5,600 m and are located in the Central Caucasus (Fig 1). Of these 15 summits are permanently covered by snow and glaciers, and exceed the Alps in altitude, among them Montblanc. The highest peaks, Elbrus (5,642 m) and Kazbegi (5,033 m), are situated on the lateral ridge and represent cones. The highest summit of the southern macroridges is Shkhara (5,624 m).

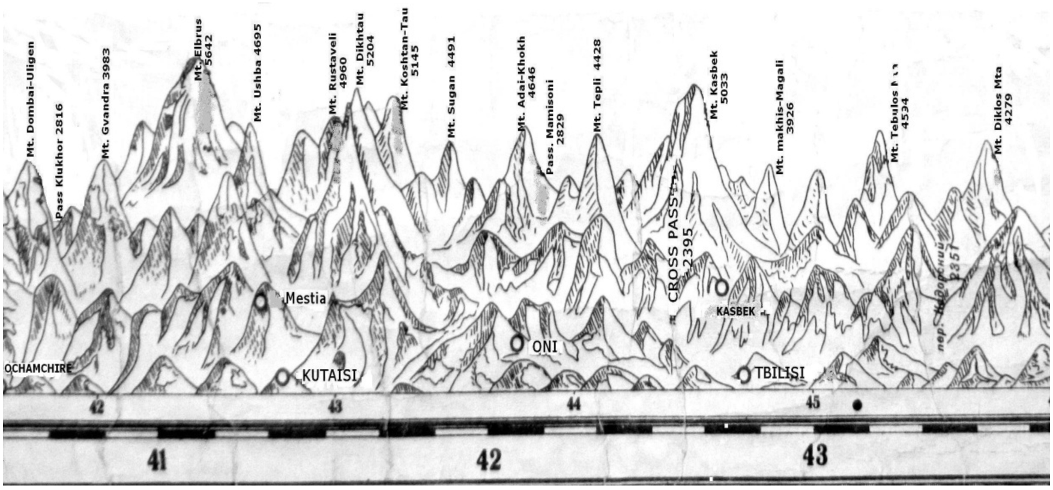

Fig. 1 Geographysical profile of Caucasus.

The Caucasus Mountains differ from the Alps by minor length and width, greater absolute and relative heights of the peaks, comparatively simple orographic height and existence of young (Pliocene-Quaternary) volcanoes.

Upper Proterozoic and Paleozoic crystal slates play a prominent role in the geological structure of the western region of the Caucasus. The main watershed ridge from the mouth of the Belaya River to the Mamisson Pass is built of granites, gneisses, metamorphic and crystal rocks. Jurassic slates of the Mesozoic period, sandstones and Cretaceous limestones are spread as stripes on both sides of this crystal axis.

In the geological structure of the East Caucasus intrusive and metamorphic rocks almost do not take part. An exception is the barren granite massif in the Dariali Canyon (gorge of the river Tergi). The eastern part of the Caucasus is mainly built with Jurassic sediments. Rocks of the Cretaceous are represented only sporadically (north-east Daghestan and north Azerbaijan). Unlike in the western part of the Caucasus, young effusive rocks of which the volcanic relief of the Tergi, Ksani-Aragvi (East Georgia) is built, are widespread in the east. They are of Quaternary origin, but in some places Pliocene volcanic remnants are preserved. The largest volcanic cones in the Greater Caucasus are Elbrus, Mkinvaltsveri (Kazbegi), Kabarjini, and the Keli Plateau.

Compared to the West Caucasus, due to the dry continental climate in the East Caucasus the lower limit of permanent glaciers is 150-200 m higher at 3,600-3,700 m a.s.l. [18-20]. These conditions cause differences in altitudinal distribution and partially in spatial distribution of plants between these two parts of the Caucasus.

2.2 Climate

The peculiarity of the complex mountain relief determines the climatic diversity of the Caucasus. The Caucasus range is located at the junction of the temperate and subtropical climatic zone. This border is caused by the Greater Caucasus mountain range which blocks the intrusion of cold air masses from the north to the south and warm masses from Transcaucasia to the north. The northern part of the Caucasus belongs to the temperate zone and Transcaucasia belongs to subtropical zone. A main difference between both is air temperature. The average annual temperature is 10 °C on the northern slopes and in the south—16 °C. The average January temperature in Transcaucasia is 5 °C, in west Transcaucasia—6 °C, and in the eastern Caucasus—3 °C. In summer there is minor difference between the north and south, but on the other hand remarkable contrast of temperatures between the west and east part exists. In the west Caucasus the average temperature in July is 23-24 °C and in the east—25-29 °C.

Climatic peculiarity of the Caucasus is also conditioned by the fact that it is subject of movements of Atlantic and Mediterranean humid air masses on the one hand and of dry Eurasian continental masses on the other hand. Stavropol Upland and Likhi Ridge play an important role for climate peculiarities of various parts of the Caucasus. Annual rainfall varies between 100 mm and 3,682 mm. Climatic conditions are subject of vertical zoning and at the same time, fluctuate in horizontal direction too. Atmospheric precipitations decrease from the west to the east.

2.3 Soils

Over 50 soil types which comprise more than one half of the soil diversity of the former Soviet Union, have been described on the territory of the Caucasus. This diversity is conditioned by lithological and geomorphological peculiarities, mountain rocks, age of relief and history [21, 22].

The main soil types of the Caucasus are: moderate belt steppe soils, forest soils, dry and humid subtropical soils, mountain meadow-steppe soils, mountain-meadow chernozem, meadow soils, swamp soils, grove soils and numerous other types of soils. The highest diversity of the Caucasus soils can be found in the lowlands, and it decreases in the mountains.

High-mountain soil types of the Caucasus change with the vertical belts. Brown forest soils predominate in the forest belt. On the north and northwest facing slopes, where subalpine crooked-stemmed birch forests and thickets of *Rhododendron caucasicum* Pall. are common, peat-humus soils are presented that frequently extend up to 2,500 m. Soil cover on the limestone territory of the Caucasus is made up by calcareous humus soils.

Mountain meadow soils are presented at the elevation from 1,800-2,100 m to 2,700-3,100 m a.s.l. The soils of the subalpine belt include forest brown soils, average depth skeletal forest brown soils, soddy mountain meadow soils, and so on. The soils of the alpine include soddy mountain-meadow soils, underdeveloped skeletal mountain meadow soils, soddy-skeletal and primitive soils of medium and small depth [21, 22] The mentioned soils are frequently located in a complex in the Greater Caucasus.

3. Materials and Methods

The present work summarizes long-term research results carried out by us on the Caucasus and literature study. The research is based on the analysis of systematic and geographical structure of the flora of the subnival zone, ecotopology, peculiarities of hypsometric distribution, coenosis diversity of various floristic complexes, endemism and florogenesis issues. Atypical plant species indicated for this zone by some researchers were excluded from the general list of flora. Aspects and inclination degrees of slopes were taken into account; botanical-geographical profiles and floristic lists compiled at every 100 (200) m a.s.l upwards.

Types of the distribution ranges of the high mountain plant species are given according to the typological system of the distribution ranges elaborated for the Caucasus by Gagnidze and Ivanishvili [23, 24]. The system of Grossheim [25] was also used with some amendments. The classification of distribution range types is based on the so-called “center of gravity” of species distribution, as well as their common distribution. Within each type of distribution range groups of distribution ranges that show local or comparatively wide distribution of taxa are singled out.

Plant taxonomy and nomenclature follows Ketskhoveli et al. [26], Czerepanov [27], Gagnidze [28], and Takhtajan et al. [29].

4. Results and Discussion

4.1 Systematical Structure

The subnival belt flora of the Greater Caucasus comprises 226 species, 96 genera and 35 families. It includes common plants typical only for the subnival zone as well as those spread on the limits between this zone and upper alpine belt.

The leading families are *Asteraceae* (25 species), *Caryophyllaceae* (25 species), *Brassicaceae* (23 species), *Poaceae* (14 species), *Fabaceae* (12 species), *Campanulaceae*, *Scrophulariaceae*, *Ranunculaceae*, *Rosaceae* (each 11 species), *Saxifragaceae* (10 species), *Primulaceae* (7 species), *Apiaceae* (6 species), *Lamiaceae* (5 species), *Crassulaceae*, *Gentianaceae*, *Cyperaceae*, *Liliaceae* (each 4 species). The remaining families are presented by 1-3 species. The leading genera are *Campanula* (11 species), *Saxifraga*, *Minuartia* (each 10 species), *Ranunculus* (9 species), *Draba* (8 species), *Cerastium* (7 species), *Alchemilla* (5 species), *Silene*, *Primula*, *Sedum*, *Anthemis*, *Gentiana*, *Alchemilla*, *Carex* (each 4 species). *Campanulaceae* and *Saxifragaceae* are represented only by a single genus in the subnival zone (Fig. 2).

Species composition and coenotic role are different both in various parts of the Caucasus and within each part. This is conditioned by the above mentioned

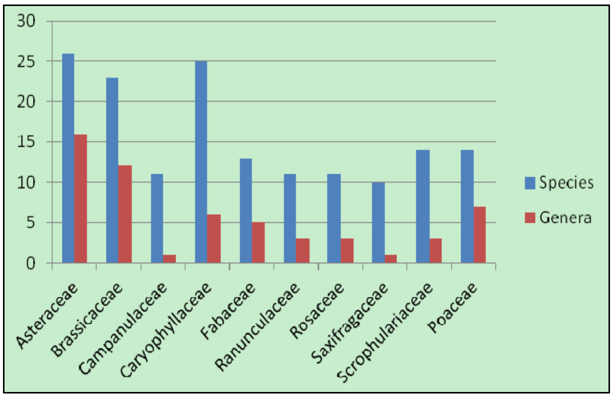

Fig. 2 The families with the largest number of taxa and genera.

circumstances—different hypsometry of various parts of the Caucasus, the character of glaciations, edaphic and climatic conditions, lithological diversity, history of flora formation, and so on.

In the massive mountain system of the Greater Caucasus the volcanic cones of the Elbrus and Kazbegi yield to other mountain parts by floristic diversity. This fact is conditioned by the juvenility of soil cover in this place which is formed by lavas of the Quarternary period and also strong Quarternary glaciations in the Central Caucasus [2]. For example, the petrophile flora of volcanic relief of the subnival belt in the Mount Kazbegi environs is rather species poor. At 3,200-3,400 m a.s.l. only *Saxifraga sibirica* L., *S. flagellaris* Willd., *S. moschata* Wulfen, *Delphinium caucasicum* C.A. Mey., *Omalotheca supina* (L.) Cass., *Ranunculus caucasicus* M.Bieb., *Myosotis alpestris* F.W. Schmidt, *Veronica gentianoides* Vahl, *Campanula tridentata* Schreb., *Cerastium polymorphum* Rupr., *Minuartia imbricata* Woron., *Sedum tenellum* M. Bieb., *Epilobium anagallidifolium* Lam., and *Senecio taraxacifolius* (M. Bieb.) DC., are found; *Senecio sosnovskyi* Sof., inhabits areas at glacier ends between skeleton substrates in silver carpets of mosses (*Racomitrium canescens*) and *Tephroseris karyaginii* (Sof.) Holub., grows up to 3,050 m. These species are widespread almost everywhere in the Greater Caucasus.

In the Kazbegi region (east part of the Central Caucasus) the floristically most interesting part are the watershed between the Aragvi and Tergi rivers (in mt. Chaukhebi massif) and surrounding shale screes. At 3,349 m a.s.l. all the above listed plants and also *Lamium tomentosum* Willd., *Jurinella subacaulis* Iljin, *Chaerophyllum humile* Stev., *Cerastium kasbek* Parrot, *Symphyoloma graveolens* C.A. Mey., *Primula bayernii* Rupr., *Cruciata coronata* (Sibth. & Sm.) Ehrend., *Scrophularia minima* M. Bieb., and *Viola minuta* M. Bieb., are found. Of interest is also Kuro massif and especially Khde shale gorge (gorge of the Kistinka River).

Volcanogenic rock-screes of the Mt. Fidar in the eastern part of the Central Caucasus are floristically richer. In spite of the fact that there the subnival zone is only fragmented and lower (3,000-3,200 m), rare species like *Dentaria microphylla* Willd., *Corydalis alpestris* C.A. Mey., *Cerastium polymorphum* Rupr., *Jurinella subacaulis* Iljin, *Ranunculus lojkae* Sommier & Levier, *Veronica schistosa* E.A. Busch, *V. telephiifolia* Vahl, *Apterigia pumila* Galushko, *Eunomia rotundifolia* C.A. Mey., *Oxytropis cyanea* M. Bieb., *Pedicularis armena* Boiss. and Huet, *Polygonum viviparum* L., etc. are found. The mentioned species diversity is caused by the fact that due to the comparatively low altitude the Keli volcanic plateau was less affected by glaciation than other parts of the Central Caucasus. Floristically the eastern part of the Keli volcanic plateau—Arkhi ridge (the mouth of the Ksani River) is similar to Mt. Fidar although *Eunomia rotundifolia* C.A. Mey. is absent.

Floristically, the East Caucasus, especially its NE part, is rather different. For example, in the Atsunta-Kvakhidi massif at 2,999-3,200 m a.s.l. (ca. 42º N; ca. 45º E), both local endemics of the East Caucasus—*Ranunculus tebulossicus* Prima, *Vicia larissae* Prima, *Erisimum subnivale* Prima, *Alopecurus tuscheticus* Trautv., *Silene caucasica* (Bunge) Boiss., *Veronica petraea* Steven, *Arabis farinacea* Rupr., *Podospermum grigoraschvili* Sosn., *Pyrethrum aromaticum* Tzvelev, and common endemics of the Central and East Caucasus like

Campanula petrophila Rupr., *Cerastium multiflorum* C.A. Mey., *Silene humilis* C.A. Mey., *Primula bayernii* Rupr., *Saxifraga ruprechtiana* Manden., *Campanula argunensis* Rupr., and *Jurinea filicifolia* Boiss. are present. Autochthonous development of the high mountain flora of the East Caucasus in the first place is associated with other parts of the Caucasus on its long-term isolation. At present this isolation is caused by the depression between Cross pass and the Bezhtin ridge [17]. In general the vegetation of the Kazbegi region reveals similarities with the vegetation of the East Caucasus but the spectrum of Caucasian endemic species of the subnival zone is rather different between both regions.

The major reason for this difference is the fact that in the East Caucasus, due to dry continental climate, the lower border of everlasting snowcaps and glaciers is elevated to 3,700 (3,800) m. On the relief released from the glaciers, closed phytocenoses are relevantly lifted up with edificators are *Festuca woronowii* Hack., and other grasses of the so-called “antagonistic” communities (*Poa alpina* L., *Colpodium variegatum* (Boiss.) Griseb., *Alopecurus dasyanthus* Trautv., *Festuca supina* Schur). In this high-altitude areas of cryogenic relief the occurrence of *Sibbaldia parviflora* Willd., *Chamaesciadum acaule* (M. Bieb.) Boiss., *Campanula tridentata* Schreb., *Minuartia inamoena* Woron., and *Cerastium polymorphum* Rupr., is also important.

If we take global climate models into account altitudinal distribution of the high mountain and among them subnival belt plants will probably significantly change in the nearest future. These models indicate striking changes for the Caucasus region caused by a rise of the yearly global mean temperature by about 3 degrees until the end of this century (2071-2100) compared to 1961-1990 (Fig. 3) Due to this the upper distribution border of some plant species is supposed to shift upwards approximately by 100-150 m. At the same time mesophilous communities will be replaced by xeromesophylic communities. The tendencies of such changes are already more or less observable in the East Caucasus. An example of this can be the rise of alpine belt plants *(Aconitum tuscheticum* N. Busch, *Heracleum osseticum* Manden., *Pseudomuscari pallens* (M. Bieb.) Garbari, *Aster alpinus* L. etc.) in the East Caucasus up to the lower border of the subnival belt [30].

4.2 Geographycal Analysis and Florogenesis

The subnival belt flora of the Caucasus includes 7 types and 16 subgroups of the distribution range (Table 1, Fig. 4). The Eucaucasian type (EUCAUC) includes 84 species. Subgroups are: proper Caucasian

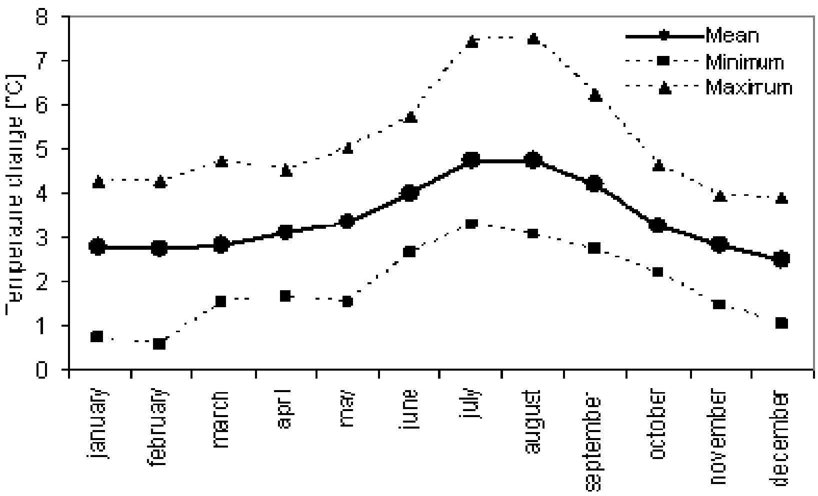

Fig. 3 Temperature projection 2071-2100 vs. 1961-1990 Ensemble-range of 20 global climate models, Scenario A1B (www.cenn.org. Newsletter, November, 2011).

Table 1 Chorological and ecotopological spectrum of the subnival flora.

Types	Groups	Ecotopes					Species
		var.r	var.s-sts	lr	ls-sts	alp.car	
Eucauc	eucauc	10	13	-	-	2	25
	eucauc: w. gr. cauc.	2	2	5	2	4	15
	eucauc: centr. gr. cauc.	2	2	-	-	-	4
	eucauc: o. gr. cauc.	6	13	-	-	3	22
	eucauc: w. centr. gr. cauc.	1	2	-	-	1	4
	eucauc: centr. o gr. cauc.	6	4	-	-	-	10
	eucauc-cauc. min.	-	3	1	-	-	4
Cauc	cauc: lat. cauc	10	18	-	-	5	33
	cauc.- as. min	5	20	-	-	14	39
	cauc- as. anter	7	17	-	-	8	32
	cauc-europ	-	1	-	-	-	1
	cauc- medit	1	-	-	-	-	1
Europ-Medit	europ-medit.	1	1	-	-	1	3
Medit-As. min	medit-as. min.	-	1	-	-	1	2
Palearkt	palearkt.	8	2	-	-	4	14
Holarkt	holarkt.	6	5	-	-	5	16
Pancont	pancont.	-	-	-	-	1	1
Total: 7	17	75	94	6	2	49	226

Abbreviations and symbols used:

Cauc	Caucasian	lat. Cauc	Common Caucasian
Eucauc	Eucaucasian or Greater Caucasian	centr. gr.cauc	Central and Eastern Greater Caucasian
o. gr. cauc	Eastern Greater Caucasian	centr et o.gr. cauc	Central and Eastern Greater Caucasian
w. gr. cauc.	Western Caucasian group	w.centr.gr.cauc	Western Central Caucasian
As Min	Asia Minor	West Asian	Asia Anterior
Medit	Mediteranian	Europ	European
Holarkt	Holarktic	Paleark	Palearktic
Pancont	Pancontinetal	var. r	Various rock
Lr	Limestone rock	ls-sts	Limestone screes and stone sceletion substrate
alp.car	Alpine carpet	var.s-sts	Various lithological screes and stone sceletion substrate

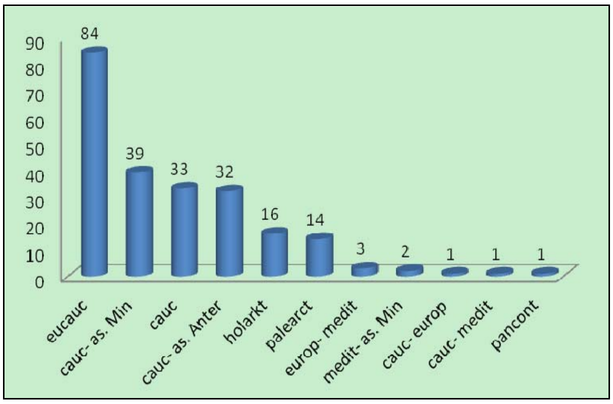

Fig. 4 Distribution of the species to phytogeographic region.

(EUCAUC) like *Campanula circassica* Fomin, *Valeriana saxicola* C.A. Mey., *Pseudobetckea caucasica* (Boiss.) Lincz., *Scrophularia minima* M. Bieb., *Delphinium caucasicum* C.A. Mey., *Saxifraga pseudolaevis* Oetting., *Anthemis sosnovskyana* Fed., and *Cerastium polymorphum* Rupr., West Caucasian (w.gr.cauc) like *Campanula circassica* Fomin., *Ranunculus lojkae* Sommier & Levier, *Minuartia trautvetteriana* Sosn. & Charadze, and *Saxifraga pontica* Albov, East Caucasian (o.gr.cauc) like *Trigonocaryum involucratum* Kusn., and *Valeriana daghestanica* Rupr. ex Boiss., West and Central Caucasian (w.gr.cauc.) like *Barbarea ketzkhoveli* Mardalejschvili, *Charesia akinfievii* (Scmalh.) E.A. Busch, and *Cerastium undulatifolium* Sommier & Levier, and Central and East Caucasian (centr.w.gr.cauc.) like *Tripleurospermum caucasicum* Hayek, *Teprhoseris karjaginii* Holub, *Primula bayernii* Rupr., *Draba siliquosa* M. Bieb., *Cerastium kasbek* Parrot, and *Minuartia inamoena* Woron. It should be mentioned that the above listed species are endemic species of the Greater Caucasus and their distribution is restricted to the Greater Caucasus or parts of it. This fact indicates once more that the Caucasus is a mountain system of distinct geographical isolation for the origination and distribution of endemic species [1-5, 7, 10, 12, 31-34].

The Caucasian type (CAUC) includes 106 species. Among these, 33 species, like *Eunomia rotundifolia* C.A. Mey., *Pseudovesicaria digitata* Rupr., *Scrophularia ruprechti* Boiss., *Carex meinshauseniana* V.I. Krecz., and *C. medwedewii* Leskov belong to the common Caucasia group. These species are endemic or subendemic to the Caucasus.

32 species belong to the Caucasus-Anterior Asian type (CAUC-AS.ANTER): *Minuartia aizoides* Bornm., *Didimophysa aucheri* Boiss., *Draba hispida* Willd., *Sedum tenellum* M. Bieb., *Alchemilla sericea* Willd., *A. retinervis* Buser, *Pedicularis crassirostris* Bunge, *Veronica gentianoides* Vahl, *V. minuta* C.A. Mey., *V. telephiifolia* Vahl., *Senecio taraxacifolius* (M. Bieb.) DC., *Poa caucasica* Trin., etc. This group also includes the monotypic genus *Vavilovia* Fed., which rarely occurs in the Caucasus and is mainly distributed in Anterior Asia and also in Armenia.

39 species belong to the Caucasus-Minor Asian type (CAUC-AS.MIN): *Carum caucasicum* Boiss., *Nepeta supina* Stev., *Thlaspi huetii* Boiss., *Minuartia colchica* Charadze, *Rhododendron caucasicum* Pall., *Vavilovia formosa* Fed., *Geranium gymnocaulon* DC., *Epilobium algidum* M. Bieb., *Pedicularis nordmanniana* Bunge, *Luzula pseudosudetica* V.I. Krecz., *Alopecurus glacialis* C. Koch, *A. dasyanthus* Trautv., etc., 1 species to the Caucasus-European type (CAUC-EUROP) (*Saxifraga exarata* Vill., *S. moschata* Wulfen); 3 species to the Euro-Mediterranean type (EUROP-MEDIT) (*Festuca* woronowii Hack., *Gentiana pyrenaica* L., *Plantago saxatilis* M. Bieb.); 12 species to the Palearctic type (PALEARKT) 14 species (*Erigeron uniflorus* L., *Taraxacum porphyranthum* Boiss., *Lloydia serotina* (L.) Salisb. ex Rchb., *Potentilla crantzii* (Crantz) Beck ex Fritsch, *P. gelida* C.A. Mey., *Poa alpina* L., *Oxyria elatior* R. Br. ex Meissn., etc.), and 16 species to the holarctic type (HOLARKT) (*Myosotis alpestris* F. W. Schmidt, *Cerastium cerastioides* (L.) Britton, *C. polymorphum* Rupr., *Epilobium anagallidifolium* Lam., *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Trisetum spicatum* (L.) K. Richt., etc.).

Of the total number of subnival belt flora 117 species or 51% are endemic. Among these, 80 species are endemics of various parts of the Greater Caucasus and 33 species are common endemics of the Caucasus. In the subnival belt of lateral ridges of the East Caucasus local steno-endemic species occur like *Ranunculus tebulossicus* Prima, *Veronica bogosensis* Tumadzhanov, *Pyrethrum aromaticum* Tzvelev, *Didymophysa aucheri* Boiss., *Silene humilis* C.A. Mey., *Saxifraga ruprechtiana* Manden.. *Vicia larissae* Prima, *Pseudobeckea caucasica* (Boiss.) Lincz., and *Alopecurus tuscheticus* Trautv. Very sporadic distribution is characteristic for the Caucasus-Anterior Asian oligotypic genus *Vavilovia* Fed. (*V. formosa* (Steven) Fed.). This plant, with *Silene humilis* C.A. Mey., *Pseudobetckea caucasica* (Boiss.) Lincz., *Veronica bogosensis* Tumadzhanov, and *Ranunculus tebulossicus* Prima, is among the higher plants within the Greater Caucasus. Floristically, slate screes and rocky habitats are most diverse (Fig. 4).

In the subnival belt 5 endemic genera of the Caucasus are widespread. As a result of morphological and geographical study it has been established that *Symphyoloma* C.A. Mey., is the oldest endemic genus; it is a diploid plant (2n = 22) [35]. Its origin is connected with adaptation to cold environments which resulted in a specialized life form [33, 36, 37]. The monotypic *Pseudobetckea* (Hock.) Lincz. of the subnival belt is also considered to be one an old species. It is related to *Valerianella* Hill and the Andean *Betckea* DC. As a result of high altitude adaptation, probably during the orogenesis of the Caucasus, its fruits and flowers has been reducing. The formation of this plant as high montane life form must have happened also as a result of cryophilization by means of oreophitization due to orogenesis of the

Caucasus [33, 37].

The endemic genus *Pseudovesicaria* (C.A. Mey.) Rupr., of the Great (Central and East Caucasus) and Lesser Caucasus, is also restricted to the subnival belt. It is an orophyte with rosette habit and is characterized by succulent leaves. This plant is also characterized by Anterior-Asian-Mediterranean related links. It is related with the old xerophytic, Anterior-Asian monotypic *Elburzia* Hedge (*E. fenestrata* (Boiss.) Hedge) and *Coluteocarpus* Boiss., and with the Anterior -Asian-Central Asian genus *Didymophysa* Boiss.

An endemic monotypic genus of the Central Caucasus (N Ossetia, Svanetia) is *Charesia* E.A. Busch (*Ch. akinfievii* (Schmalh.) E.A. Busch.). It is related to *Silene* L., especially to some of its Anterior Asian species but sharply differs from it by box structure, as well as pollen morphology [33]. An endemic genus of the NE part of the Caucasus is *Trigonocaryum* Trautv. (*T. involucratum* Kusn.). It is related to *Myosotis* L., differing from it in chromosome number (2n = 14). Their main ranges are the subalpine and alpine belts, and it reaches the subnival belt only in Daghestan.

In spite of a significant number of apomictic and clonally expanded species in the highlands genetic diversity is rather high [38-41]. However, an exception are the so-called refugium species [41]. In the Caucasus subnival belt some of the above listed plants can be considered as refugium species, like *Delphinium caucasicum* C.A. Mey., *Symphyolma graveolens* C.A. Mey., *Ranunculus helenae* Albov, and *Pseudobetckea caucasica* (Boiss.) Lincz.

Caucasian and Anterior Asian species distributed in the subnival belt are *Eunomia rotundifolia* C.A. Mey., *Saxifraga cartilaginea* Willd., *Chaerophyllum humile* (M. Bieb.) Boiss., *Valeriana saxicola* C.A. Mey., *Senecio taraxacifolius* (M. Bieb.) DC., *Draba bryoides* DC., *Pedicularis crassirostris* Bunge, *Lamium tomentosum* Willd., *Primula amoena* M. Bieb., etc. [1, 3, 11].

Species belonging to the Daghestan-Iranian are *Didymophysa aucheri* Boiss., *Cicer minutum* Boiss. & Hohen., and *Dracocephalum botryoides* Steven. These are rare species occurring only in Daghestan and north Iran [42, 43]. It should be noted that Didymophysa aucheri is also distributed in NE Iraq and N Anatolia. This species and *D. fedchenkoana* Regel (from Afghanistan) are characterized by limited distribution. They are typical petrophytes, sometimes reaching as high as 4,000 m a.s.l. [44]. Narrowly limited distribution within the Greater Caucasus is characteristic to *Cicer minutum* Boiss. & Hohen. (NE Caucasus, Bazar-Diuzi mountain system) which was collected there by Prima for the first time. The distribution of the mentioned plant proves once more that floristic links (“intermontane links”) existed between the Caucasus and Minor Asia in Pliocene and Pleistocene [44].

In the subnival belt a rather small number of Arctic mountain species (*Poa alpina* L., *Trisetum spicatum* (L.) K. Richt., *Lloydia serotina* (L.) Salisb. ex Rchb., *Cerastium cerastioides* (L.) Britton, *Minuartia verna* (L.) Hiern, *Saxifraga flagellaris* Willd., *Omalotheca supina* (L.) DC., *Potentilla crantzii* (Crantz) Beck ex Fritsch, *Thalictrum alpinum* L.), Caucasian-European (*Corydalis alpestris* C.A. Mey., *Myosotis alpestris* F. W. Schmidt, *Saxifraga moschata* Wulfen, *S. exarata* Vill.), and Caucasian-Central Asian (*Primula algida* Adams, *Herniaria caucasica* Rupr., *Oxyria elatior* R. Br. ex Meissn., *Potentilla gelida* C.A. Mey) are present.

Different data have been obtained as a result of karyosystematic study of species of the alpine and subnival belts. Karyological studies have established that in the Caucasus subnival belt diploid species [35, 45] but in the Swiss Alps and Arctic polyploid species dominate [46-49]. The question arises again as to what stimulates polyploidy in plants. Are there severe climatic conditions, assimilation of new territories by plants or both of them? This question is again disputable. To solve the orogenesis within the compared regions and peculiarities of glaciations and floristic history should be considered. The important features chaping the complex evolutionary history of alpine plants include narow ecological adaptation to severe habitats, abrubt altitudinal gradients of well-difined ecological riches [50, 51]. In high mountains each florocoenosic complex (high mountain meadows, tall herbaceous, alpine carpets, petrophytes, and so on.) represents the community of ecologically and coenotically different species formed during long period. This opinion is also supported by the fact that species of meadows and rocks are karyologically remarkably different. The latter is characterized by rich endemism and accordingly, a major number of diploid species. We totally agree with Sokolovskaya and Strelkova [45] who explained the low percentage of polyploids in the Caucasus by a great number of endemic species which origin is connected with the Caucasian orogenesis. The distribution success of polyploid cytotipes is probably more due to the benefits of apomictic reproduction than to genetic consequences of polyploidization [52]. In the same way, the small number of polyploid species in the subnival belt can be explained by the high number of old authochronic oreophites [35]. Although there is evidence that plant ploidy does not always depend on the altitude we consider that this factor plays a determining role in the Caucasus as an isolated mountain system. This opinion is also supported by the fact that in the Caucasus despite decrease of species number with altitude, the relative number of endemic species increases [1-7, 31-33]. This especially concerns the subnival belt with dominating rock-scree and skeletal substrate ecotopes. Compared with these the alpine carpets and comparatively “closed” coenoses are characterized with realtively low endemism.

There are different points of view on the origin and age of the high mountain flora of the Caucasus. Such disagreement always focused on the alpine (subnival) belt. As Korner [15] indicated, the origin of present-day high mountain taxa is a heredy mainly of Tertiary elements, consisting of a mixture of immigrants from various initial floras and new evolutionary lines [53-56].

Some authors consider that formation of the core of the Caucasus alpine flora is connected with the Tertiary [57-61]. Other botanists believe a considerable role is played by processes within the Quaternary [25, 37, 62-64]. Migration processes also played important role in this process. Aspects of florogenesis of the subnival belt are especially concerned by Kharadze [1, 2, 35, 37], who states that the species of early as well as comparatively recent origin played an important role in the formation of the core of the subnival belt flora. To the first belong Caucasus-Anterior Asian species which root back to more low-altitude plants of the Tertiary. Due to gradual adaptation towards existing ecological conditions they started to inhabit cooler areas. This view is evidenced by links between species of some genera (*Campanula* L., *Cerastium* L., *Silene* L., *Saxifraga* L., *Scrophularia* L., *Erysimum* L., *Pedicularis* L., *Delphinium* L., *Jurinea* Cass.) of the middle and subnival zones of the Caucasus mountains, geographical and hypsometric vicariance. Another group developed as a result of oreophytization of the Caucasian-Anterior Asian or authochtonously from Caucasian ancestor species (*Cerastium kasbek* Parrot., *Saxifraga scleropoda* Sommier & Levier).

Morphological isolation of the high mountain endemic genera *Pseudobetckea* (Hock.) Lincz., *Symphyoloma* C.A. Mey., and *Pseudovesicaria* Rupr., disjunct ranges and geographic variability evidence their early origin [35, 36]. Geographic isolation, tectonic movement, climatic changes, glaciation, high mountain habitat differentiation and variation in history of migration lead to high taxonomic richness [1-17, 31-37, 44-56, 65, 74]. Cold-climate evolution of the genera was related to oreophytization during formation of the Caucasus Mountains (in the second half of the Tertiary) as well as the glaciation scale. In Pleistocene their ranges must have been fragmented resulting in ecological differentiation of different populations [35, 36]. During the Pleistocene glacial periods between the Himalaya and Central Asia with the Iranian, Caucasian and some European mountains facilitated a long-distance migration of several cryophilic species [43]. As Elenevskii [75] indicated, also the high mountain flora of the Lesser Caucasus has different origins and correspondingly different plant species. Alpine carpets are settled by allochthonous species that invaded during the Pleistocene period and High Mountain rock communities by autochthonous species from the Miocene-Pliocene authochtone group. Botanical investigations conducted on the Mt. Aragaz and Javakheti Plateau (Lesser Caucasus) also evidenced different origins and age of the species of the subnival belt [10, 12].

The floristic composition of the subnival belt in the Lesser Caucasus, i.e. Didi Abuli (ca. 60 species), is similar to that of the subnival belt flora of the Greater Caucasus. In the massif of Didi Abuli (Lesser Caucasus) the subnival belt is situated above 2,920 m a.s.l., with small populations of *Pedicularis armena* Boiss. & A. Huet., *Draba hispida* Willd., *Erysimum krynitzkii* Bordz., *Senecio taraxacifolius* (M. Bieb.) DC., *Potentilla gelida* C.A. Mey., *Aster alpinus* L., *Plantago saxatilis* M. Bieb., *Murbeckiella huetii* (Boiss.) Rothm., *Myosotis alpestris* F.W. Schmidt, and *Luzula pseudosudetica* V.I. Krecz., Near the summit (above 3,250 m) only several ultra-oreophytes occur, like *Chamaesciadum acaule* (M. Bieb.) Boiss., *Cerastium pseudokasbek* Vysokoostr., *Tripleurospermum caucasicum* Hayek, *Jurinella subacaulis* Iljin, *Eunomia rotundifolia* C.A. Mey., *Minuartia woronowii* Schischk., *Pedicularis armena* Boiss. & A. Huet, *Erysimum krynitzkii* Bordz., *Astragalus vavilovi* Fedorov & Tamamsch., *Crepis wildenowii* Czerep., and the grasses *Poa alpina* L., *Festuca supina* Schur, and *Alopecurus dasyanthus* Trautv. During florogenesis of the Lesser Caucasus subnival belt a decisive role was played by the floristic centre of Anterior Asia (*Chamaesciadum acaule* (M. Bieb.) Boiss., *Veronica gentianoides* Vahl, *Carum caucasicum* (M. Bieb.) Boiss., *Saxifraga sibirica* L., *Pedicularis crassirostris* Bunge, *Draba hispida* Willd., *Luzula pseudosudetica* V.I. Krecz.), and a minor role by the floristic center of the Greater Caucasus (*Eunomia rotundifolia* C.A. Mey., *Tripleurospermum caucasicum* (Hayek.) and arcto-alpine floristic centers (*Myosotis alpestris* F.W. Schmidt) [10-12, 76].

A floristic link of the Greater and Lesser Caucasus is also provided by several ultra-oreophytes vicariant species in these two mountain systems differing in altitude and petrology. Compared with the Greater Caucasus, the relative floristic poverty of the Lesser Caucasus is due to low elevations and extensive rather recent vulcanism. Volcanic rocks (andesites, basalts) are less inhabited by plants than clay, slaty, and marl soils. The low level of endemism is also conditioned by weak geographical isolation.

5. Conclusions

An in-depth botanicalgeographic analysis of subnival flora of the Greater Caucasus proves that both autochthonous and allochthonous plant groups participated simultaneously in the florogenesis of the high mountains. To the first group belong *Scrophularia minima* M. Bieb., *Delphinium caucasicum* C.A. Mey., and the monotypic endemic genera *Symphyoloma* C.A. Mey., *Pseudovesicaria* (C.A. Mey.) Rupr., and *Pseudobetckaea* (Hock) Lincz. For cold climate adaptation of these plants oreophytization processes have more importance than glaciation phases. Their actual distribution and polymorphism took place rather recently in the Pleistocene [37, 63]. Plants of the second group are *Pedicularis crassirostris* Bunge, *Veronica gentianoides* Vahl, *V. minuta* C.A. Mey., *V. telephiifolia* Vahl, and *Senecio taraxacifolius* (M. Bieb.) DC. It should be noted that in the formation of the subnival belt species a significant role was played by orogenesis processes of the Caucasus, which is caused extinction of ancestral species at lower altitudes and resulted in their geographical isolation. This is proved by geographical and hypsometric vicarism of some species of *Campanula* L., *Cerastium* L., *Silene* L., *Erysimum* L., *Pedicularis* L., *Delphinium* L., and *Jurinea* Cass. Not only are the western, central and eastern parts of the Caucasus floristically different from each other, but also from neighboring mountain massifs. The above mentioned is conditioned by distinct geographic isolation pronounced in the mountain system of the Caucasus, different altitudes, petrology, and glaciogenic relief. Floristically, slate screes and rocky habitats are most diverse.

Along with elevation the proportion of autochthonous species is increased. In the subnival belt the role of arcto-alpine elements is relatively insignificant. Floristic similarity between the Great and Lesser Caucasus is mainly by allochthonous species.

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