

Syntaxonomical survey of Alpine meadows in the Great Caucasus

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ABSTRACT: The paper suggests a syntaxonomy for alpine communities with prevalence of perennial herbs and grasses and alpine lichen heaths, and documents their regional variation along the Great Caucasus Ridge. The syntaxonomic diversity of the Caucasian alpine meadows is comprised of eight associations, eight subassociations, and at least six variants. One of these associations *Anemone speciosae-Campanuletum tridentatae* with four subassociations and four variants, is widely spread along the Caucasus. Three associations and two subassociations are restricted to the Western Caucasus and two to the Central; three associations with two subassociations are met in the Eastern Caucasus. All these associations are grouped into the novel Caucasian alliance – *Alchemillo caucasicae-Campanulion tridentatae*, which is assigned to the European class *Juncetea trifidi* and the order *Caricetalia curvulae*.

KEY WORDS: Syntaxonomic diversity, regional variation, community description, Caucasus

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INTRODUCTION

Due to their wide distribution and undeniable importance in modern man-made high mountain landscapes, alpine meadows and heaths have attracted the attention of vegetation scientists and conservation biologists. The first phytosociological study in the Caucasus was carried out by Guinochet (1984). Later, some fragments of a syntaxonomic system for this vegetation type were elaborated for the Kazbegi and Lagodekhy regions in Georgia (Bedoshvili 1985, 1989) and the Teberda Biosphere State Reserve in Karachayevo-Cherkessia (Onipchenko 1994).

This paper suggests a syntaxonomy for alpine communities with prevalence of perennial herbs and grasses and alpine lichen heaths (with reindeer moss as the dominant species), and documents their ecological and regional variation along the Great Caucasus Ridge. A provisional version of the classification was described elsewhere (Korotkov 1994) as well as a complete relevé set for communities with restricted area and their syntaxonomy (Korotkov & Belonovskaya 2001).

STUDY AREA

There are three main natural regions traditionally recognized in the Great Ridge: the Western, Central and Eastern Caucasus. The Western and the most elevated Central Caucasus constitute the main morphostructural block of the ridge. Lithologically it consists mainly of crystalline granites of Palaeozoic and Proterozoic origin, with Palaeozoic and Mesozoic metamorphic and sedimentary rock impregnation. The high mountain zone of the Eastern Caucasus is formed by Jurassic metamorphic schist (Gerasimov & Galabov 1984).

The Great Caucasus has classical high mountain orography, with a more or less continuous main chain and numerous side branches. The recent morphogenesis of the high mountains is governed by nival-glacial processes, which results in the frequent occurrence of glacial relief forms, especially in the Western and Central Caucasus. The Eastern Caucasus is not so intensively affected by glacial processes and is characterized by smooth relief forms resulting from intensive weathering and erosion during the active contemporary uplift.

The climate along the ridge of the alpine belt is not subject to considerable variation: low annual mean temperature (-3°C), low sum of temperatures above 10°C (260°C), a very short vegetative period (1.5–2 months). The warmest month is August with a mean temperature of $7^{\circ}\text{--}8^{\circ}\text{C}$, but frost can occur throughout the whole summer. Precipitation decreases from 2330–3350 mm in the Western to 1890–2100 mm in the Central Caucasus, and to 1590 mm in the Eastern Caucasus. Snow cover remains for 250–300 days. Its accumulation depends on the relief forms, slope orientation against the wind, and its velocity: windward steep slopes and crest line have the least snow cover (Gerasimov & Galabov 1984; Onipchenko 1994). By removing snow and fine materials, the wind plays a key role in the morphogenesis of summit plateaus.

Mountain meadow soil is the predominant type in the alpine belt of the Caucasus. These soils are characterized by a shallow (10–15 cm) profile, sometimes with a well-developed turf horizon. They exhibit acid reaction, high gravel content (13%) and high humus content (20–30%) in the upper horizon (Gerasimov & Galabov 1984). The variant under ass. *Potentilletum crantzii* on Mt. Kerkray (Dagestan) can serve as an example. The soil profile is subdivided into three or four horizons. The upper dark brown turf horizon (0–8 cm) is abundantly pierced by roots. The humus horizon (8–20 cm) is represented by moderately skeletal (50%) brown loam. It can be sharply or continuously (with delimitation of a special transitional horizon) substituted by orchid-brown highly skeletal (80%) illuvial loam (up to 50 cm) on underlying bedrock.

The vegetation studied is most common in places where convex relief surfaces and plateaus modulated by frost weathering and wind deflation are formed. Such sites favor cryogenic activity because the soil can be free of snow during the winter. The cryogenic activity also occurs in critical periods during autumn and spring when the soil is generally uncovered or only temporarily covered by snow and frequently waterlogged.

METHODS

The survey employed individual phytosociological relevés of the vegetation of the highest part of the Greater Caucasus from the Laba River headwaters in the west to the middle course of the Samur River in the east, selected from the authors' collection as well as from pools of some other investigators. The study sites are located above the timberline, at elevations ranging from about 2400 to 3300 m a.s.l. close to the crest line.

Sample stands were chosen subjectively in order to document the variation in the vegetation in each area. The relevés were collected following the Braun-Blanquet approach (Becking 1957). The relevés varied in size from 4 to 10 m². The general database contained 177 relevés with 315 species; 168 relevés formed the basis of this paper. At every site elevation, the inclination, aspect and surface stoniness were estimated in the field. The stoniness values are given as percentage cover of stones, bare rock and gravel on the soil surface of each relevé.

Species nomenclature follows Czerepanov (1995), with some exceptions (Korotkov 1989). To standardize the species names from different sources, *Flora of Turkey* (Davis 1965–1978) was also used. The relevés were organized with the help of the Vegtab program (Dähler 1989). They were first classified using the MULVA program (Ver. 4.2; Wildi & Orloci 1988), with resemblance analysis based on the Ochiai index, principal component and correspondence analysis, and subsequent grid analyses. Direct application of cluster analysis was practically useless in classifying the Caucasian alpine meadows because it failed to transform the relevé set into more or less distinct groups. The scheme represented below corresponds to the principal results of the numerical classification. The concept of character species and differentiating species follows Becking (1956). Only about 5 relevés were extracted from the general set to illustrate each syntaxon.

DESCRIPTION OF SYNTAXA

Syntaxonomic scheme

Juncetea trifidi Hadač in Klika & Hadač 1944 (*Caricetea curvulae* Br.-Bl. & Jenny 1926)

Caricetalia curvulae Br.-Bl. 1926

Alchemillo caucasicae-*Campanulion tridentatae* all. nov.

Nardo stricti-*Geranietum gymnocauli* Korotkov & Belonovskaya 2001

Nardo stricti-*Geranietum gymnocauli festucetosum variaae* Korotkov & Belonovskaya 2001

Nardo stricti-*Geranietum gymnocauli cerastietosum purpurascens* Korotkov & Belonovskaya 2001

Alopecuro dasyanthi-*Asteretum alpini* Korotkov & Belonovskaya 2001

Hedysaro hedysaroidis-*Campanuletum collinae* Korotkov & Belonovskaya 2001

Polygono vivipari-*Kobresietum bellardii* Korotkov & Belonovskaya 2001

Potentiletum crantzii Korotkov & Belonovskaya 2001

Potentiletum crantzii vacciniatosum myrtilli Korotkov & Belonovskaya 2001

Potentiletum crantzii kobresietosum simpliciusculae Korotkov & Belonovskaya 2001

Alchemillo sericeae-*Caricetum umbrosae* Korotkov & Belonovskaya 2001

Astragaletum incerti Korotkov & Belonovskaya 2001

Anemono speciosae-*Campanuletum tridentatae* Korotkov & Belonovskaya 2001

Anemono speciosae-*Campanuletum tridentatae eritrachietosum nanae* subass. nov.

Anemono speciosae-*Campanuletum tridentatae cetrarietosum cuculatae* subass. nov.

Anemono speciosae-*Campanuletum tridentatae fritillarietosum luteae* subass. nov.

Anemono speciosae-*Campanuletum tridentatae primulaetosum elatioris* subass. nov.

***Nardo stricti-Geranium gymnocauli* Korotkov & Belonovskaya 2001**

(Table 1, rel. 1–5)

These west Caucasian communities show transitional features towards the neighboring carpet-like meadows. Thus they have some atypical features such as poor cover of lichens and bryophytes, the tendency to develop on warm gentle slopes or almost horizontal surfaces with slightly skeletal soil, forming rather dense vascular plant cover (60–90%) and turf. Altitude range is 2400–3000 m a.s.l. Average species richness is lower than in all other meadow associations – 28 species per relevé. The total number of species in the relevés was 131.

The association is differentiated by *Nardus stricta*, *Geranium gymnocaulon*, *Gagea fistulosa*, *Leontodon hispidus*, and several affinity species of the Caucasian carpet-like meadows (the alliance *Colpodion variegatae*) – *Sibbaldia procumbens*, *Carex atrata*, *Corydalis alpestris*, *Matricaria caucasica*, or at least by their increased participation (*Colpodium variegatum*). The abundance of the group of typical alpine meadows species is weakened here. The specific and attractive physiognomy is determined by the high (50–70 cm) herb *Geranium gymnocaulon* – a very common dominant adding a nice red-violet color to the communities during the blossoming period in July–August.

This association can be subdivided into two units of subassociation rank. The first one (relevés 2–5) – *Nardo stricti-Geranium gymnocauli cerastietosum purpurascens* – resembles communities of the *Colpodion variegatae* and is indicated as typical. The second one to the common alpine meadows from the *Alchemillo caucasicae-Campanulion tridentatae*. Communities of the first subassociation prefer gentle slopes (1–2°, maximum 10°). They are characterized by rather high coverage of vascular plants (70–95%). Mosses and lichens are nearly absent. It is differentiated by *Cerastium purpurascens*, *Luzula multiflora*, *Anthoxanthum odoratum*, *Myosotis alpestris*, *Pedicularis rostrata*, *Ranunculus oreophylus*, *Fritillaria lutea* and *Corydalis alpestris*.

***Alopecuro dasyanthi-Asteretum alpini* Korotkov & Belonovskaya 2001**

(Table 1, rel. 6–10)

Communities of this association generally occupy gentle south- and west-facing slopes in the elevation range of 2800–2900 m a.s.l. It is characterized by impoverished plant cover (30–50% for phanerogams and 10–25% for lichens). The soil is highly skeletal (70–90%). Thus this vegetation type can be considered as transitional to scree communities. Average species richness is 35 species per relevé. The total number of species is 86. The association is characterized by the presence of the vascular plants *Aster alpinus*, *Alopecurus dasyanthus*, *Centaurea pulcherrima*, *Anthyllis vulneraria*, *Potentilla nivea*, *Trifolium polyphyllum*, *Oxytropis campestris* and *Campanula saxifraga*, and the lichens *Parmelia centrifuga*, *Placolecanora rubina*, *Dactylina madreporiformis*, *Umbilicaria cylindrica* and *Rhizocarpon viridiatrum*. *Campanula tridentata* and *Cetraria nivalis* often are more abundant than other species. Differentiating species in this association are *Chamaesciadium acaule* and *Gentiana verna*. Many species are dependent on the skeletal substrate. These communities are confined to the Western Caucasus.

Hedysaro hedysaroidis-Campanuletum collinae Korotkov & Belonovskaya 2001

(Table 1, rel. 11–15)

These communities without a definite preference occupy slopes covered with considerable gravel and bare rock (10–60%) in a broad altitudinal belt of 2650–3050 m a.s.l. Average cover of vascular plants is 40–60%, cover of lichens is variable at 1–25% (up to 55%), and cover of mosses is poor. Average species richness is 44 species per relevé, and the total number of species is 113. The association is characterized by *Campanula collina*, *Gentiana ciliata*, *Hedysarum hedysaroides*, *Scorzonera cana*, *Agrostis lazica*, *Minuartia verna*, *Cirsium acaule* and *Polytrichum juniperinum*. The relatively rare species *Chaerophyllum millefolium* seems to prefer these communities. The association is characterized by polydominant structure but *Antennaria dioica* obviously prefers these communities. The association's specific appearance is determined by red-lilac flowers of *Hedysarum hedysaroides* and *Campanula collina*. Features of *Juncetea trifidi*, *Caricetalia curvulae* and to some extent *Anemone-Campanulion* are developed here better than in other associations. The communities are widely distributed throughout the Western and Central Caucasus.

Polygono vivipari-Kobresietum bellardii Korotkov & Belonovskaya 2001

(Table 1, rel. 16–20)

These communities are confined to the elevation range of 2750–2950 (at most 3000) m in the Central Caucasus. They are found mainly on north- and west-facing slopes of varying steepness, but prefer slightly convex or flat aclinic surfaces. Vascular plant and lichen cover varies broadly – 20–95% and 1–80%, respectively. Average species richness is 38 species per relevé. The total number of species is 151. The association is characterized by *Kobresia bellardii*, *Polygonum viviparum*, *Androsace villosa*, *Salix arbuscula*, *Astragalus levieri*, *Carex obtusata*, *Cladonia pocillum* and *Dicranum fuscenscens*, and locally differentiated by *Thalictrum alpinum* and *Hypnum cupressiforme*. *Festuca ovina*, *Campanula tridentata*, *Carex sempervirens*, *Cetraria nivalis*, *Cetraria islandica*, *Thamnolia vermicularis*, *Alchemilla caucasica*, and *Carum caasicum* generally prevail, but most abundant are one of the following species – *Kobresia bellardii*, *Astragalus levieri*, or *Bromopsis variegata*.

The association exhibits signs of heterotony and can be split into two phytocoenoses with yet unclear syntaxonomic statuses, differentiated by *Pedicularis rostrata*, *Carex obtusata*, *Eritrichium nanum*, *Luzula spicata*, *Gentiana pyrenaica*, and *Arenaria lychnidea* (first set of relevés), and by *Campanula ciliata*, *Potentilla gelida*, *Parmelia centrifuga*, and *Dicranum fuscenscens*, (second set). Communities of the first type prefer north-facing slopes, while those of the second type tend to occupy warmer (predominantly west-facing) slopes.

Potentiletum crantzii Korotkov & Belonovskaya 2001

(Table 2, rel. 1–9)

Communities of this association are very common in the Eastern Caucasus and confined to cold north- and east-facing steep slopes in a broad altitude range – 2450–3300 m

Table 1. Alpine meadows restricted to the Western and Central Caucasus.

Relevé no.	1	2	3	4	5	Constancy (17 relevés)										6	7	8	9	10	Constancy (8 relevés)										11	12	13	14	15	Constancy (10 relevés)										16	17	18	19	20	Constancy (17 relevés)																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																												
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Table 1. Continued.

Relevé no.	1	2	3	4	5	C	6	7	8	9	10	C	11	12	13	14	15	C	16	17	18	19	20	C
<i>Carex sempervirens</i> V	+	·	·	2,2	·	II	1,2	1,2	1,2	+	+	V	+	+	·	1,2	+	IV	1,2	2,2	·	1,2	1,2	V
<i>Carum caucasicum</i> V	+	+	+	2,2	2,1	IV	·	·	+	·	·	II	1,3	1,2	·	1,2	1,2	V	1,1	1,2	1,1	·	1,1	IV
<i>Pedicularis verticillata</i> V, DAA	·	·	+	·	+	I	·	+	+	+	+	IV	·	·	·	·	1,2	I	·	·	1,2	·	·	I
<i>Gentiana pyrenaica</i> V	·	+	1,2	+	·	III	+	+	·	·	·	IV	·	+	·	·	·	II	·	·	·	·	·	III
<i>Minuartia imbricata</i> V	r	·	+	+	1,2	III	·	·	·	·	·	·	1,3	·	·	·	·	I	·	·	1,3	+	1,2	IV
<i>Euphrasia alboffii</i> V	·	·	·	·	·	I	·	·	·	·	·	·	+	+	·	+	·	V	+	+	·	·	+	IV
<i>Gentiana verna</i> V, DAA	·	·	+	·	·	I	+	+	+	+	+	IV	·	·	·	·	·	·	·	·	·	·	·	I
<i>Chamaecitadium acaule</i> V, DAA	·	·	·	·	·	I	+	+	·	·	·	V	·	·	·	·	·	·	I	·	·	·	·	I
<i>Viola calcarata</i> V	+	+	+	·	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
<i>Accompanying species</i>																								
<i>Veronica gentianoides</i>	1,2	+	+	+	+	V	·	+	+	+	+	IV	+	1,2	+	+	1,1	V	+	+	+	+	+	IV
<i>Anthemis marschalliana</i>	+	·	·	·	·	II	+	+	+	+	+	V	1,2	+	+	+	1,2	V	·	·	+	·	·	III
<i>Anemone speciosa</i>	+	1,1	1,1	·	·	III	+	+	+	+	+	V	+	2,2	1,1	1,1	1,2	V	·	·	+	+	1,1	III
<i>Minuartia circassica</i>	·	·	·	+	+	II	+	+	+	+	+	V	1,2	1,2	1,2	2,2	1,3	IV	·	·	+	·	·	I
<i>Cetraria cucullata</i>	·	·	·	·	·	·	+	1,2	1,2	·	1,2	IV	·	·	·	·	1,2	I	1,2	+	+	1,2	·	IV
<i>Primula elatior</i>	·	·	+	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	1,2	·	·	+	IV
<i>Cladonia macroceras</i>	·	·	·	·	·	II	·	·	·	·	·	·	+	+	·	·	+	·	·	+	+	+	+	IV
<i>Bromopsis variegata</i>	+	·	·	·	·	II	·	·	·	+	+	III	+	+	2,1	+	1,1	V	1,2	1,2	·	+	1,2	V
<i>Myosotis alpestris</i>	·	·	+	+	·	I	·	·	·	·	·	I	·	·	·	·	·	I	·	·	+	+	1,1	III
<i>Polygonum bistorta</i>	·	·	+	·	·	I	+	+	+	·	·	IV	·	·	·	·	·	·	+	+	+	+	+	III
<i>Eritrichium nanum</i>	·	·	·	·	·	·	+	·	·	·	+	IV	·	+	·	·	·	·	·	·	·	·	+	II
<i>Campanula ciliata</i>	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1,2	1,2	1,1	·	II
<i>Erigeron uniflorus</i>	·	·	·	·	·	I	·	+	·	·	·	III	+	·	·	1,1	+	IV	·	·	·	·	·	II
<i>Taraxacum crepidiforme</i>	·	·	+	1,2	·	II	·	·	·	·	·	·	+	+	+	+	+	IV	+	·	·	·	·	II
<i>Cladonia pyxidata</i>	·	·	·	·	·	I	+	+	·	·	·	·	·	+	+	+	+	IV	·	·	·	1,2	·	I
<i>Sedum tenellum</i>	+	r	·	·	+	III	·	·	·	·	+	II	·	+	·	·	·	II	·	·	·	+	·	I
<i>Parmelia saxatilis</i>	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I
<i>Potentilla crantzii</i>	1,2	r	·	1,2	+	IV	·	·	·	·	·	I	1,2	·	+	·	+	III	+	·	·	·	·	I
<i>Ranunculus oreophilus</i>	·	+	·	+	·	II	·	·	·	·	·	II	·	+	·	1,2	1,2	III	+	·	·	+	+	IV
<i>Vaccinium vitis-idaea</i>	·	·	·	·	·	I	·	·	·	·	·	II	·	1,2	·	+	·	II	·	·	·	·	+	III
<i>Bortramia ithyphylla</i>	·	·	·	+	·	I	+	·	·	·	·	I	+	+	·	·	·	II	·	·	·	·	·	I
<i>Desmatodon latifolius</i>	·	·	·	+	·	I	·	·	·	·	·	·	·	+	·	·	·	II	1,3	·	·	·	·	I
<i>Gentiana septemfida</i>	·	·	·	·	·	·	·	·	+	·	·	II	·	+	·	·	·	I	·	·	·	+	+	II

a.s.l. Vascular plant cover is 50–80%. Mosses are moderately represented here (10–25%), while heath features are suppressed (lichens cover only 5–10%). Gravel and bare rock participation is moderate (up to 20%). Average species diversity is 34 species per relevé, and the number of species in all records is 130.

The association is characterized by rather vague delimitation, based exclusively on the differentiating species *Potentilla crantzii*, *Colpodium variegatum*, *Antennaria dioica*, *Taraxacum crepidiforme*, *Sibbaldia procumbens* and *Stereocaulon paschale*. The first two species usually prevail in different combinations with *Festuca ovina*, *Campanula tridentata*, *Alchemilla caucasica*, *Carex sempervirens* and *Carum caasicum*. Syntaxonomically this unit does not demonstrate a high degree of individuality, and carries the name of one of the most common species, *Potentilla crantzii*. In accordance with its incoherent phytosociological structure, the association is split into two subassociations.

***Potentilletum crantzii vaccinetosum myrtilli* Korotkov & Belonovskaya 2001**

(Table 2, rel. 4–9)

It is the typical subassociation of the syntaxon (the nomenclatural type of the association and subassociation; relevé 6). The subassociation is characterized by typical meadow physiognomy, distinguished by *Carum caasicum*, *Minuartia imbricata*, *Anthemis marschalliana*, and pronounced representation of both *Vaccinium* species: *V. vitis-idaea* and *V. myrtillus*. The latter reaches dominant status only in these communities. In respect to geographical distribution and habitat they follow the association as a whole. The plant coverage is less dense than in the second subassociation: 35–70% vascular plants, 1–17% bryophytes (exceptionally 50%), and 1–15% lichens.

***Potentilletum crantzii kobresietosum simpliciusculae* Korotkov & Belonovskaya 2001**

(Table 2, rel. 1–3)

The communities exhibit more or less pronounced grassland-heath character, due to the dominance of *Kobresia simpliciuscula* and the more frequent presence of *Cetraria nivalis*, *C. cucullata* and *Thamnolia vermicularis*. The altitudinal range is 2900–3100 m a.s.l. This subassociation mostly develops on fresh and cold, north- and west-facing, relatively steep (10–25°) slopes. Coverage is 70–85% vascular plants, 5–25% mosses and 5–15% lichens.

***Alchemillo sericeae-Caricetum umbrosae* Korotkov & Belonovskaya 2001**

(Table 2, rel. 10–17)

Similarly to the *Anemono-Campanuletum*, this association unites communities with the most typical alpine meadow appearance in the eastern part of the Caucasian Main Range. It is found in all regions and occupies the belt between 2800 and 3200 m a.s.l., mainly cold north- and west-facing, relatively steep slopes (10°–25°). The character species are *Alchemilla sericea*, *Taraxacum confusum*, *Euphrasia brevipila*, *Empetrum nigrum*, *Distichium inclinatum*, and *Lecanora epibryon*. *Carex umbrosa* differentiates the association from other syntaxa in the Eastern Caucasus. Average diversity is 35 species

per relevé. The total number of species is 90. Vascular plants cover 30–80% of the surface. *Carex umbrosa*, *Festuca ovina* and *Arenaria lychnidea* impart a grassland appearance to the sites with *Alchemillo sericeae*-*Caricetum*. *Alchemilla caucasica*, *A. sericea* and *Carum caucasicum* are very common as well. Despite the lack of some ordinary components such as *Antennaria dioica* and *Gentiana verna* these alpine meadows well correspond to the phytosociological properties of *Caricetea curvulae*. Mosses and lichens are well represented and cover 10 and 15%, respectively. 10–15% each. Among them prevail *Distichium inclinatum* and *Cetraria islandica*. Gravel, bare rock and bare ground account for 10–30%. The skeletal character of the substrate coincides well with the presence of *Chamaesciadium acaule*, *Anthemis marschalliana* and *Arenaria lychnidea*.

Astragaletum incerti Korotkov & Belonovskaya 2001

(Table 2, rel. 18–21)

Only four very specific relevés are available from communities in the vicinity of the settlement Kuruš, southern Dagestan, between 2500 and 2850 m a.s.l. These communities occupy cold north-facing steep slopes (25°–30°) and have well-developed cover of vascular plants (60–80%) and mosses (10–15%) but poor cover of lichens. The association is extraordinarily rich in species (52 species per relevé and 89 species in total) but the participation of alien species is weak. *Astragalus incertus*, *Gentiana aquatica*, *Galium verum*, *Kobresia schoenoides*, *Minuartia aizoides*, *Trifolium ambiguum*, *Cerastium arvense* and *Solorina saccata* can be considered diagnostic. The most abundant species are *Astragalus incertus*, *Minuartia azoides*, *Festuca ovina*, *Alchemilla caucasica*, *Chamaesciadium acaule* and *Distichium capillaceum*. The phytocoenosis has some more controversial features: a high abundance of phanerogams instead of mosses on steep slopes and peat, and, unlike the other alpine communities, the lack of *Carum caucasicum*.

Anemone speciosae*-*Campanuletum tridentatae ass. nov. hoc loco (nom. type of the alliance *Alchemillo caucasicae*-*Campanulion tridentatae*)

(Table 3, rel. 1–22)

NOMENCLATURAL TYPE: Table 3, rel. 10 (field rel. 126).

More than 70 relevés were assigned to the association, occurring throughout the entire alpine belt and even outside its range at altitudes from 2450 to 3200 m a.s.l., on slopes with widely varying inclinations and aspects. The association includes the most typical Caucasian alpine meadows and heaths. Dominants – *Campanula tridentata* and *Anemone speciosa* impart to the sites fascinating blue-cream appearance from late June to early August. The high constancy and abundance of *Carex umbrosa*, *C. sempervirens*, the high mountain variety of *Festuca ovina*, and reindeer moss also contribute to specific physiognomy of the communities. Geographically the floristic composition does not vary greatly. This unit differs negatively from other associations of *Alchemillo*-*Campanulion* (i.e. it doesn't contain both its proper character species and diagnostic species of other associations) but expresses obvious heterogeneous symptoms, so that it can be subdivided into four subassociations and four variants. The unusually high number of

Ch. Juncetea trifidi (K); Caricetalia curvulae (O); Anemone speciosae-Campanulion tridentatae (V)																					
Festuca ovina K Luzula spicata K Cetraria islandica K Thamnolia vermicularis K, DAPK Cetraria nivalis K, DAPK Primula farinosa K Antennaria dioica K, DAP Helictotrichon versicolor O Campanula tridentata V Carex umbrosa V, DAS Alchemilla caucasica V Arenaria lychnidea V Carex sempervirens V Carum caucasicum BV, DAPV Pedicularis verticillata V Gentiana pyrenaica V Minuartia imbricata V, DAPV Euphrasia alboffii V, DAI Gentiana verna V Chamaecisadium acaule V Viola calcarata V	2,3	1,3	2,3	1,2	3,2	2,2	2,2	1,2	2,2	1,3	1,3	1,3	1,3	1,2	V	2,3	2,3	2,3	1,2	4	
	1,4	+	1,2	+	+	+	+	+	+	+	1,1	+	+	1,1	V	+	+	+	+	4	
	1,1	+	1,2	2,1	+	1,1	+	+	1,1	1,2	1,2	+	+	1,1	IV	+	+	+	+	4	
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	II	+	+	+	+	1	
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	II	+	+	+	+	2	
	1,2	+	1,2	1,1	+	1,1	1,1	1,1	+	1,2	1,1	+	1,2	+	V	1,1	+	+	+	4	
	1,2	1,1	1,2	1,1	1,1	+	+	+	1,1	1,2	1,2	+	+	1,1	V	+	+	+	1,2	3	
	2,2	2,1	1,1	2,1	1,1	2,2	2,2	1,1	2,2	2,1	2,1	2,2	1,1	1,1	V	+	+	+	1,1	2,1	3
	+	+	+	+	+	+	+	+	1,2	1,2	1,2	+	+	1,1	V	+	+	+	1	2,1	2
	2,1	1,2	2,1	3,2	2,2	2,1	2,1	2,1	1,2	1,2	1,2	1,2	1,2	1,2	2,2	V	2,2	3,2	3,2	2,2	4
	+	1,2	1,2	+	+	+	+	+	+	+	1,3	1,3	2,3	1,3	1,2	V	+	1,2	+	+	2
	1,1	1,2	2,2	2,2	1,2	2,2	3,2	1,1	+	2,2	2,2	+	+	1,1	+	V	1,2	1,2	+	+	4
	1,1	+	+	2,1	+	2,1	+	1,2	1,1	1,1	1,2	1,1	1,1	1,1	V	+	+	+	+	+	1
	+	1,1	1,2	+	+	+	+	+	+	+	+	+	+	+	I	+	+	+	+	+	1
+	+	+	+	+	+	+	1,2	1,1	2,2	+	+	+	+	+	II	+	+	+	+	+	1
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	II	+	+	+	+	+	1
+	+	+	1,1	1,1	1,1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	4
+	+	1,1	1,2	1,1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3
+	+	1,1	+	+	+	+	+	+	1,2	1,2	+	+	+	+	+	+	+	+	+	+	2
+	+	+	+	+	+	+	+	+	1,1	1,1	+	+	+	+	+	+	+	+	+	+	3
+	+	+	+	+	+	+	+	+	1,2	2,2	+	+	+	+	+	+	+	+	+	+	2
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1
Ch. Salicetea herbaceae, Salicetalia herbaceae, Colpodion variegati																					
Taraxacum crepidiforme	2,1	+	+	+	1,1	+	1,1	1,1	1,1	+	+	+	+	+	V	+	1,1	1,1	1,1	4	
Potentilla crantzii DAP	1,2	2,1	1,2	1,1	+	+	+	+	+	1,2	1,2	+	1,2	+	IV	+	+	1,2	+	4	
Sedum tenellum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	IV	+	+	+	+	3	
Sibbaldia procumbens DAP	+	+	+	+	+	+	+	+	+	1,2	1,2	+	+	+	III	+	+	+	+	2	
Omalotheca supina	+	+	1,1	+	+	+	+	+	+	1,1	1,1	+	+	+	III	+	+	+	+	3	
Plantago atrata	+	+	+	+	+	+	+	+	1,2	2,2	+	+	+	+	I	+	+	+	+	2	
Luzula multiflora	+	+	+	+	+	+	+	+	+	+	+	+	+	+	I	+	+	+	+	1	
Accompanying species																					
Veronica gentianoides	2,1	2,1	+	+	+	+	1,1	+	+	+	+	+	+	1,2	V	+	1,2	+	+	2	
Cladonia macroceras	+	+	+	1,2	1,2	1,2	+	+	1,2	+	+	+	+	+	V	+	+	+	+	1	
Anthemis marschalliana DAPV	+	+	+	+	+	+	1,1	1,1	+	+	1,2	1,1	+	+	IV	+	+	+	+	2	

(cont.)

intra-association units coincides with a considerably high degree of floristic differences between them, because about twenty species can be regarded as differentiating, but these differences are still weaker than those between associations.

The subassociations are split into two physiognomic groups – meadows and heaths.

***Anemono speciosae-Campanuletum tridentatae fritillarietosum luteae* subass. nov.**

hoc loco

(Table 3, rel. 11–16)

NOMENCLATURAL TYPE: Table 3, rel. 14 (field rel. 168).

These meadows prefer gentle slopes and are positively differentiated by *Fritillaria lutea*, *Myosotis alpestris*, *Bromopsis variegata*, *Cerastium purpurascens*, *Luzula multiflora*, *Anthoxanthum odoratum*, *Distichium inclinatum*, *Dicranum fuscescens* and *Abietinella abietina*, while *Pedicularis verticillata* and *Gentiana verna* fall out. It is the same species group that plays a differentiating role in the subassociations of *Nardo-Geranietum*. Probably this similarity depends on the similarity of variations in inclination.

***Anemono speciosae-Campanuletum tridentatae eritrichietosum nanae* subass. nov.**

hoc loco

(Table 3, rel. 1–5)

NOMENCLATURAL TYPE: Table 3, rel. 2 (field rel. 48).

These comparatively impoverished meadows generally occupy south-facing slopes and negatively differ from their predecessors. Two variants can be distinguished due to the asymmetric distribution of *Taraxacum crepidiforme*, *Primula elatior*, *Kobresia simpliciuscula*, *Ranunculus oreophilus*, *Anthemis marschalliana*, *Polygonum bistorta*, *Pedicularis comosa* and *Veronica gentianoides*. They are more often in the variant with *Anthemis marschalliana*.

***Anemono speciosae-Campanuletum tridentatae cetrarietosum cucullatae* subass. nov.**

hoc loco

(Table 3, rel. 6–10)

NOMENCLATURAL TYPE: Table 3, rel. 10 (field rel. 126) (the nomenclatural type of the association and subassociation).

The most common alpine heaths, they are differentiated by reindeer moss species – *Cetraria cucullata*, *Cetraria nivalis*, *Cetraria ericetorum*, *Cladonia rangiferina*, *Cladonia mitis* and *Cladonia macroceras*, their satellites *Cladonia digitata* and *Cladonia coniocraea*, as well as by the two vascular species *Trifolium polyphyllum* and *Oxytropis campestris*. Some epilithes occur more often here due to better development of suitable substrate – *Cladonia pyxidata*, *Umbilicaria cylindrica*, *Peltigera rufescens* and *Solorina crocea*.

***Anemono speciosae-Campanuletum tridentatae primulaetosum elatioris* subass. nov.**

hoc loco

(Table 3, rel. 17–22)

NOMENCLATURAL TYPE: Table 3, rel. 18 (field rel. 26).

In the eastern part of the range this subassociation includes the most species-poor (average species richness 18 species per relevé) closed communities of the Caucasian

Table 3. Ass. *Anemone speciosae*-*Campanuletum tridentatae*. (* – nomenclatural type of association, or subassociation).

Relevé no.	1	2*	3	4	5	Constancy (12 relevés)					Constancy (30 relevés)					Constancy (11 relevés)					Constancy (18 relevés)								
Field relevé no.	64	48*	111	104	116	67	68	69	118	126*	57	98	170	168*	100	102	43	26*	27	28	30	33	300	310	320	320	290	290	
Altitude (×10 m)	300	275	280	270	300	270	270	260	260	270	265	240	270	260	245	260	300	310	320	320	290	290	300	310	320	320	290	290	
Aspect	NE	SE	S	S	S	00	S	S	S	SW	E	W	SW	W	W	NW	N	W	W	W	SW	W	N	W	W	W	SW	W	
Slope (degrees)	02	20	25	20	15	00	02	12	12	02	01	05	01	05	05	05	15	10	25	20	05	25	15	10	25	20	05	25	
Cover: vascular plants (%)	15	60	70	50	50	70	65	75	65	50	75	40	75	65	50	60	45	35	35	30	20	60	45	35	35	30	20	60	
Cover: mosses (%)	01	15	01	00	00	00	00	00	01	00	00	05	05	01	01	05	00	03	01	01	05	01	00	03	01	01	05	01	
Cover: lichens (%)	15	15	40	15	03	54	65	45	35	45	00	10	10	15	10	25	25	50	45	45	20	20	25	50	45	45	20	20	
Gravel & bare rock (%)	70	.	01	03	20	02	03	00	00	01	25	10	10	01	35	10	25	00	05	05	01	02	25	00	05	05	01	02	
Ch. <i>Juncetea trifidi</i> , K ; <i>Caricetalia curvulae</i> , O ; <i>Anemone speciosae</i> - <i>Campanulion tridentatae</i> , V																													
<i>Festuca ovina</i> K	1,2	2,2	2,2	1,2	1,2	V	2,2	2,2	2,1	2,2	1,2	2,3	1,2	1,3	1,2	1,2	V	2,3	2,1	2,2	2,2	2,2	V	2,3	2,1	2,2	2,2	2,2	2,2
<i>Luzula spicata</i> K	+	1,1	+	.	+	V	+	+	1,1	+	2,1	V	.	1,1	.	+	IV	.	+	+	+	+	IV	.	+	+	+	+	+
<i>Cetraria islandica</i> K	1,2	2,2	2,2	1,2	+	IV	2,2	2,2	3,2	2,2	2,2	V	.	1,2	1,2	1,2	IV	2,2	3,2	2,2	3,2	2,2	IV	2,2	3,2	2,2	2,2	2,2	2,2
<i>Thamnolia vermicularis</i> K	.	1,1	2,1	+	+	II	2,1	1	2,2	2,1	1,1	V	.	+	.	+	III	.	2,1	3,1	2,1	.	III	.	2,1	3,1	2,1	.	1,1
<i>Cetraria nivalis</i> K	1,1	.	.	+	.	II	2,2	2,2	1,2	1,2	+	III	.	.	.	+	I	+	2,1	1,2	2,1	+	IV	+	2,1	1,2	2,1	+	1,1
<i>Primula farinosa</i> K , D _{ACP}	+	+	+	.	.	II	+	+	.	+	.	II	.	.	.	+	I	.	+	+	+	+	IV	.	+	+	+	+	+
<i>Helictotrichon versicolor</i> O	.	+	.	+	.	IV	2,1	2,1	.	1,1	+	1,2	+	.	.	+	III	1,2	1,1	+	+	1,1	V	1,2	1,1	+	+	1,1	1,1
<i>Antennaria dioica</i> K	+	+	.	.	.	II	+	+	1,1	1,2	+	IV	+	+	.	+	II	1,2	+	.	.	.	II	1,2	+	.	.	1,1	1,1
<i>Campanula tridentata</i> V	1,2	2,2	1,2	1,2	3,2	V	3,2	2,2	2,2	1,2	2,2	V	1,3	2,2	2,2	3,2	V	1,3	2,2	2,1	2,1	3,1	V	2,1	2,1	2,1	2,1	3,1	2,1
<i>Anemone speciosa</i>	1,1	3,2	2,2	+	+	V	1,2	1,2	1,2	2,2	1,1	V	+	1,2	1,2	2,1	IV	+	1,2	+	+	+	IV	2,1	+	+	.	.	.
<i>Carex umbrosa</i> V	2,2	.	+	1,2	1,2	III	.	1,1	1	+	2,2	V	1,2	1,2	1,3	1,2	V	1,2	2,2	2,2	2,2	2,2	V	1,2	2,2	2,2	2,2	3,2	
<i>Alchemilla caucasica</i> V	1,2	.	+	+	+	IV	+	+	+	+	+	III	+	+	1,1	1,1	V	1,1	1,1	1,1	1,1	.	IV	1,1	1,1	1,1	.	+	
<i>Arenaria lychnidea</i> V	.	.	+	+	+	III	.	.	+	+	+	III	.	.	.	.	II	.	+	.	.	+	II	.	+	.	.	+	+
<i>Carex sempervirens</i> V	+	2,2	.	1,2	3,2	V	2,2	2,2	2,2	2,2	+	V	.	.	.	+	II	.	1,2	2,2	1,2	.	III	.	1,2	2,2	1,2	.	.
<i>Carum caucasicum</i> V	.	+	.	.	+	IV	1,2	+	+	+	+	IV	+	1,1	+	+	V	1,1	+	1,1	1,1	+	IV	1,1	+	1,1	1,1	+	1,1
<i>Pedicularis verticillata</i> V	+	+	.	.	+	III	+	+	+	+	+	II	.	.	.	.	IV	+	+	+	+	+	IV	+	+	+	+	+	+
<i>Gentiana pyrenaica</i> V	+	+	+	+	+	V	+	+	+	+	1,1	V	+	+	1,1	+	IV	+	+	+	+	+	III	+	+	+	+	+	+
<i>Minuartia imbricata</i> V , D _{ACP}	.	.	.	.	.	I	+	+	+	+	+	II	r	.	.	.	I	+	+	+	+	+	IV	+	+	+	+	+	+
<i>Gentiana verna</i> V	.	+	.	.	.	II	+	+	+	+	.	II	.	.	.	.	II	+	+	+	+	+	II	+	+	+	+	+	+
<i>Chamaecadietum acaule</i> V	.	.	+	+	.	I	.	+	.	.	.	I	.	.	.	.	I	.	+	+	+	.	II	.	+	+	+	+	+
<i>Viola calcarata</i> V	+	.	+	.	.	I	.	.	.	.	+	II	1,1	+	+	.	III	+	+	+	+	+	III	+	+	+	+	+	+
D. <i>Anemone speciosae</i> - <i>Campanuletum tridentatae</i> cetrarietosum cucullatae																													
<i>Cladonia macroceras</i>	.	.	.	.	.	I	+	+	+	+	+	V	.	+	.	.	I	.	.	.	.	.	I	.	.	.	.	.	.
<i>Cetraria ericetorum</i>	.	.	+	.	+	II	+	1,2	1,2	+	+	IV	.	.	.	.	IV	.	.	.	.	.	I	.	.	.	.	.	.

(cont.)

Table 3. Continued.

Relevé no.	1	2*	3	4	5	C	6	7	8	9	10*	C	11	12	13	14*	15	16	C	17	18*	19	20	21	22	C	
<i>Cladonia mitis</i>	.	.	1,2	.	+	II	+	1,2	1,2	1,2	+	IV	.	.	.	.	.	1,2	I	.	.	.	.	.	.	.	
<i>Trifolium polyphyllum</i>	.	.	.	.	.	II	1,2	+	1,1	+	+	IV	.	.	.	.	.	.	II	.	.	.	.	.	.	.	
<i>Cladonia pyxidata</i>	.	.	.	.	+	II	+	+	+	.	+	IV	.	.	+	+	.	.	II	.	.	.	.	.	.	.	
<i>Cetraria cucullata</i>	.	.	.	+	.	I	2,2	2,2	1,2	1,2	+	III	.	+	.	.	.	.	I	.	.	.	.	.	.	.	
<i>Umbilicaria cylindrica</i>	.	.	.	.	.	.	+	+	+	+	+	III	.	.	.	.	.	.	I	.	.	.	.	.	.	.	
<i>Cladonia rangiferina</i>	.	.	.	.	.	.	+	1,2	.	+	1,2	III	.	.	.	.	.	.	I	.	.	.	.	.	.	.	
<i>Oxytropis campestris</i>	.	.	.	.	.	.	.	r	+	+	.	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cladonia digitata</i>	.	.	.	.	.	.	.	.	.	+	+	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cladonia coniocrea</i>	.	.	.	.	.	.	.	.	.	+	.	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Solorina crocea</i>	.	.	.	.	.	.	.	+	.	.	.	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>D. Anemone speciosae-Campanuletum tridentatae fritillarietosum luteae</i>																											
<i>Fritillaria lutea</i>	.	.	.	.	.	I	+	.	+	.	.	II	+	+	1,1	+	+	+	V	.	.	.	.	.	.	.	
<i>Myosotis alpestris</i>	.	.	.	.	.	I	.	.	.	.	.	I	+	+	+	+	+	+	V	.	.	.	.	.	.	.	
<i>Bromopsis variegata</i>	.	.	+	.	.	II	1,2	2,3	2,2	.	1,2	II	3,2	2,2	.	r	+	+	IV	.	.	.	.	.	.	.	
<i>Cerastium purpurascens</i>	+	.	.	.	.	I	.	.	.	.	.	I	+	+	+	+	+	+	IV	.	.	.	.	.	.	.	
<i>Luzula multiflora</i>	.	.	.	.	.	.	.	.	.	.	.	I	+	+	+	+	+	+	IV	.	.	.	.	.	.	.	
<i>Anthoxanthum odoratum</i>	.	.	+	.	.	I	.	.	.	.	.	I	.	.	+	+	+	+	III	.	.	.	.	.	.	.	
<i>Distichium inclinatum</i>	.	.	+	.	.	I	.	.	.	.	.	I	.	.	+	+	+	+	III	.	.	.	.	.	.	I	
<i>Dicranum fuscescens</i>	.	.	.	.	.	.	.	.	.	.	.	I	.	+	+	.	+	+	III	.	.	.	.	.	.	.	
<i>Abietinella abietina</i>	.	.	.	.	.	I	.	.	.	.	+	I	.	+	+	.	+	+	III	.	.	.	.	.	.	.	
<i>D. Anemone speciosae-Campanuletum tridentatae primulaetosum elatioris (ACP)</i>																											
<i>Primula elatior</i>	+	.	1,1	.	.	I	.	.	.	.	+	III	.	+	.	.	.	+	II	1,1	+	+	+	.	+	IV	
<i>Potentilla crantzii</i>	+	.	.	.	.	I	.	.	.	.	.	I	.	+	.	.	+	+	I	+	+	+	.	.	.	II	
<i>Taraxacum crepidiforme</i>	.	.	+	+	.	II	+	.	+	.	1,2	III	2,2	+	+	.	+	+	IV	.	1,1	1,1	+	.	.	II	
<i>Kobresia simpliciuscula</i>	+	.	.	.	.	I	.	.	1,2	.	.	II	+	.	.	.	.	.	I	.	.	.	.	1,3	1,3	II	
<i>Ranunculus oreophilus</i>	.	.	+	.	.	I	.	.	.	+	+	II	+	+	+	.	+	.	III	+	.	.	+	.	.	I	
<i>Anthemis marschalliana</i>	.	+	1,2	.	.	II	.	.	.	+	.	III	+	+	.	.	.	.	I	+	.	.	.	.	.	I	
<i>Polygonum bistorta</i>	+	+	+	.	.	II	+	+	+	+	.	IV	+	1,1	.	+	.	.	III	+	.	.	.	.	.	II	
<i>Accompanying species</i>																											
<i>Vaccinium vitis-idaea</i>	+	.	1,2	+	.	IV	.	.	.	.	+	IV	+	+	+	1,2	+	+	V	1,2	2,2	+	+	1,2	1,2	III	
<i>Veronica gentianoides</i>	1,2	.	+	.	.	III	1,2	1,2	+	+	+	V	+	+	+	.	+	+	V	.	.	.	.	.	.	III	
<i>Eritrichium nanum</i>	.	+	1,2	+	+	IV	1,1	1,2	+	1,1	+	IV	.	.	.	.	.	+	I	.	.	.	.	.	.	.	
<i>Minuartia circassica</i> D _{ACP}	.	+	.	+	+	III	+	.	.	.	+	III	.	+	+	+	+	+	III	.	.	.	.	.	.	.	

alpine belt. They are confined to its upper limit – usually higher than 3000 m a.s.l. – and are characterized by comparably low cover of vascular plants (30–60%) but high cover of lichens (20–45%, max. 70%). Thus they manifest heath features. Though *Primula farinosa*, *Potentilla crantzii*, *Minuartia circassica* and *Minuartia imbricata* are common components of all typical alpine meadows and heaths, they are definitely centered in this subassociation. On the other hand, *Pedicularis comosa*, *Potentilla gelida* and *Campanula collina* keep out of this type of community. One of the most intriguing phytosociological features of this subassociation is the extremely high content of diagnostic species. All but two of them play a differentiating role in at least one syntaxonomic rank.

Two variants are distinguished in this subassociation: the first, typical, with the differentiating species *Kobresia simpliciuscula*, *Ranunculus oreophilus*, *Anthemis marschalliana*, *Polygonum bistorta* and *Primula elatior* (the last one differentiates it by its high abundance); and the second with *Taraxacum crepidiforme*, where *Arenaria lychnidea*, *Viola calcarata*, *Chamaesciadium acaule*, *Primula farinosa*, *Potentilla crantzii*, *Omalotheca supina*, *Minuartia circassica* and *Carex sempervirens* are differentiating species (the last one differentiates it by its high abundance).

This subassociation is somewhat apart from other divisions of the association. The communities of this subassociation are spread through a broad geographical range in the Western and Central Caucasus and are differentiated by *Pedicularis comosa*, *Eritrichium nanum*, *Potentilla gelida*, *Cladonia rangiferina*, *Lloydia serotina*, *Anemone speciosa*, *Minuartia circassica*, *Cetraria cucullata* and *Cladonia mitis*.

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