

Syntaxonomic classification of forb steppes and related vegetation of subalpine and alpine belts in the Pamir-Alai Mountains (Tajikistan, Middle Asia)

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Academic editor: Alireza Naqinezhad ♦ **Linguistic editor:** Jim Martin

Received 24 February 2023 ♦ **Accepted** 19 September 2023 ♦ **Published** 24 November 2023

Abstract

Aims: To complete the syntaxonomic scheme of subalpine forb steppes in the Pamir-Alai Mountains in Tajikistan with some remarks on its environmental predictors. **Study area:** Tajikistan. **Methods:** A total of 149 relevés were sampled in 2014 and 2021 using the seven-degree cover-abundance scale of the Braun-Blanquet scheme. These were classified with a modified TWINSPAN algorithm with pseudospecies cut-off levels of 0%, 2%, 5% and 25%, and total inertia as a measure of cluster heterogeneity. Diagnostic species were determined using the *phi* coefficient as a fidelity measure. Detrended Correspondence Analysis (DCA) was used to show compositional differences between the distinguished alpine and subalpine grassland units. **Results:** Our classification revealed 12 clusters of alpine and subalpine grassland vegetation in Middle Asia. A total of nine new associations and three communities were distinguished. New vegetation types at potential class rank for Irano-Turanian subalpine and alpine grasslands have been proposed: forb steppes with *Eremogone griffithii* and *Nepeta podostachys* in subalpine and alpine belts and alpine grasslands with *Festuca alaica* and *Festuca kryloviana* for mesic habitats in the alpine belt. The main factors differentiating the species composition were the mean diurnal temperature range, the sum of annual precipitation, precipitation seasonality and the minimum temperature of the coldest month. **Conclusions:** Our study sheds light on the open habitat vegetation in the Pamir-Alai Mountains and has contributed to the consistent hierarchical classification of the vegetation of the eastern Irano-Turanian region. Subalpine and alpine forb steppes are a very interesting and distinct grassland type in Middle Asia. The syntaxonomic position of some of the distinguished communities is still unclear and further research on this type of alpine and subalpine vegetation within the mountains of Middle Asia is needed.

Taxonomic references: The nomenclature of the vascular plants follows Plants of the World Online (POWO 2023) and problematic taxonomic issues were solved according to The World Flora Online (WFO 2023). Nomenclature of *Stipa* spp. follows Nobis et al. (2020, 2022) and of *Geranium* spp. Cherepanov (1995). The nomenclature of bryophytes follows Ignatov et al. (2006).

Abbreviations: DCA = Detrended Correspondence Analysis.

Keywords

alpine vegetation, forb, Middle Asia, Pamir-Alai, phytogeography, grassland, syntaxonomy

Introduction

Grasslands represent one of the most extensive and diverse formations of the world, yet they are undervalued and under-researched (García-Mijangos et al. 2021). Alpine meadows and pastures are known to be one of the most prominent and species-rich communities, particularly in mountainous landscapes (Kočí 2001). Semi-dry grasslands even hold the world records for vascular plant species richness at spatial scales between 10 and 50 m², exceeding 100 vascular plant species on plot sizes of 25 m² in some regions of Central and Eastern Europe (Wilson et al. 2012; Chytrý et al. 2015). In Middle Asia, semi-dry meadows (so called “ostepiennye luga”), are considered to be among the most species-rich phytocoenoses (Afanasjev 1956; Safarov 2018). This type of Middle Asian vegetation has not yet been described in a hierarchical system based on modern phytosociological studies (Nowak and Nowak 2022). In the Pamir-Alai steppe meadows are located on slopes in the vicinity of the lower-lying lush tall-forb vegetation which descends into the forest zone (deciduous or juniper stands). They can also be found adjacent to typical alpine meadows, or occur in a mosaic with cryophilous steppes and cushion-tragacanthic vegetation that are found on dry hill tops and scree (Nowak et al. 2016b, 2021a, 2021b, 2022a, 2022b). Zohary (1973) in his work devoted to the vegetation of Middle East, refers to this vegetation type as “malacophyllous subalpine and alpine steppes”, including both alpine and subnival grasslands, but without any proposal for a higher taxonomic rank. In Tajikistan, the first definition of the subalpine and alpine grasslands was provided by Koroleva (1940) that identified meadows dominated by *Aconogonon hissaricum*, *Dactylis glomerata*, *Geranium regelii*, and *Poa bucharica* (so-called *Herbetea dactylosa*). Additionally, Afanasjev (1940) proposed the group of *Herbetea graminosa subalpina* for the grasslands with *Alopecurus seravschanicus*, *Geranium regelii*, *Nepeta podostachys*, *Piptatherum alpestre* and *Poa bucharica*. In this work a clear distinction is made between these forb meadows and other grasslands like alpine swards with *Oxytropis* spp. (Nano-*Herbetea* or Nanoherbetea alpina), fens (*Caricetea*) and *Kobresia* mats (*Cobresietea*). To a large extent, subalpine meadows of the Pamir-Alai are structurally similar to the oromediterranean grasslands on calcareous substrates of the Iberian Peninsula, the Western Alps and the Apennines from the *Festuco hystricis-Ononideteta striatae* Rivas-Mart. et al. 2002 (Mucina et al. 2016). Some of these communities (e.g. with *Morina coulteriana*) resemble the oromediterranean xeric grasslands and cushion-tragacanthic scrubs on calcareous substrates of southern Greece (e.g. *Stipo pulcherrimae-Morinion persicae* Quezel 1964; Mucina et al. 2016). The communities of subalpine steppe meadows are natural herb-rich vegetation that dominate in the subalpine belt of the Pamir-Alai ranges with the Irano-Turanian climate characterised by a summer period with a strong drought (Djamali et al. 2012). This unfavourable period of relative dryness in the middle of the

growing season, combined with intensive grazing, results in low plant coverage in steppe meadows. High soil exposure is often observed in communities dominated by *Geranium regelii*, *Leucopoa karatavica*, *Ligularia thomsonii* and *Nepeta podostachys*, like in grasslands on shallow limestone soils and rocky habitats of the Balkans in SE Europe (Matevski et al. 2018). There are also notable similarities in physiognomy between steppe meadows in the subalpine belt of the Pamir-Alai, which occur within the transitional forest zone and just above the treeline, and meadow steppes found to the north of the forest-steppe zone in boreal regions, such as in the southern Urals (e.g. Klokov 1981; Didukh and Korotchenko 1996; Vasilevich and Bibikova 2008).

The vegetation of semi-dry alpine meadows in Middle Asia and Tajikistan in particular has been defined in different ways over the long history of vegetation studies in the region. Semi-dry alpine meadows have been described as the subalpine meadow of *Calamagrostis* spp., with *Geranium regelii* and *Nepeta podostachys* as co-dominants (*beynikovye luga*), reported from Hissar, Vahsh, Karateginian and Hazratishokh within an altitudinal range of 2,500–2,800 m a.s.l. (Safarov 2018). In the Peter the First and Darvaz ranges, semi-dry grasslands are described as the group of *Alopecurus seravschanicus-Hordeum turkestanicum* meadows. Both types were assigned to the so-called cryophytic meadows (*Megagrammion hol-articum*; Safarov 2018). However, this vegetation type, described by Ovchinnikov (1948, 1957) and Sanyukovich (1960), is included in tall-forb vegetation as “*krupnotravnye luga*” (supposedly *Prangetea ulopterae* in the current classification system). In our research we follow the concept of Sidorenko (1971) and Sanyukovich (1982), that distinguish the subalpine-alpine meadows as a separate type of grasslands occurring at elevations between 2,400 to 3,600 m a.s.l., have a total vegetation cover up to 70–95% and a height of up to 80–120 cm. In addition, it is worth noting that the *Piptatherum alpinum* community, which occurs mostly in the alpine belt of central Tajikistan (a frequent species in our dataset), is also classified in this type. Difficulties and misunderstandings in the classification systems of alpine and subalpine grasslands have often been caused by the misidentification of important dominants. For example, phytocenoses dominated by *Geranium regelii* in a separate type of grassland called “alpine lawns” (*gornye travniki* - *Mesocoryphion oreoasiaticum*) in the Russian-language literature (Safarov 2018) is the result of the misidentification of *Geranium collinum* and *G. regelii*. In our opinion, *Geranium collinum* is more often associated with wet meadows and anthropogenic grasslands in river valleys than with alpine grasslands. Typical “geranniki” dominated by *G. regelii* should be included in the steppe meadows of the subalpine belt.

Additionally, in the regions of Middle Asia with a Mediterranean-type climate and intensive grazing, a distinct formation of the so-called meadow-steppe “*lugostepy*” or “*ostepennye luga*” has also been distinguished. This vegetation type includes phytocenoses with a dominance

of *Adonis turkestanicus*, *Artemisia dracunculus* and *A. pamirica* (Afanasjev 1956; Safarov 2018), which is related to more humid habitats, although they are able to tolerate drought in the topsoil. However, these dominants are not adapted to extremely low temperatures. Communities of this formation are classified as Pliocene-post-Pleistocene vegetation remnants (Kamelin 1971).

In this paper we describe the subalpine and alpine grasslands of the Pamir-Alai ranges of Tajikistan, based on 149 relevés. In particular, we focus on the following questions: (1) Which plant communities can be distinguished in this region? (2) What is the species composition and structure of these communities and how can their compositional variation be reflected in a syntaxonomic classification? (3) What are the main ecological drivers of the species composition?

Study area

The study area covers the western part of Tajikistan, located in the central part of Middle Asia in a transition zone between two ecoregions: Hissaro-Alai open woodlands and Pamir alpine desert and tundra (Dinerstein et al. 2017). The study was conducted within the Pamir-Alai Mountain system including the Zaravshan (about 370 km long), Hissar (about 200 km long), and

Peter the First (about 200 km long) mountain ranges, each stretching in a W-E direction, and the smaller Vahsh range, which extends for about 80 km in a SW-NE direction (Figure 1). The study region encompasses an area of ca. 18,000 km². Sampling was carried out in the subalpine and alpine belts within the altitudinal range of ca. 2,400 to 3,700 m a.s.l. above the juniper woods upper line (Nowak et al. 2022a). The study area is under the influence of a warm and continental Irano-Turanian type of bioclimate, which is characterised by great spatial variation in winter versus summer precipitation, depending on elevation (Djamali et al. 2012). The Irano-Turanian type of bioclimate has generally low mean annual precipitation (ca. 280 mm). The highest precipitation occurs in winter, but spring rainfalls may occasionally be higher than in the winter. Evident seasonality in precipitation, hot summers with the highest temperature in July (mean = 23.9 °C), and cold winters with the lowest temperature in January (mean = 6.7 °C), together with high continentality distinguish this type of bioclimate from adjacent Euro-Siberian, Mediterranean, Saharo-Sindian, and Central-Asiatic bioclimatic types (Djamali et al. 2012). However, due to the high topographic heterogeneity of the Pamir-Alai Mountain system, bioclimatic variables considerably vary between the mountain ranges encompassed by this study, depending on altitude, aspect, and inclination of slopes.

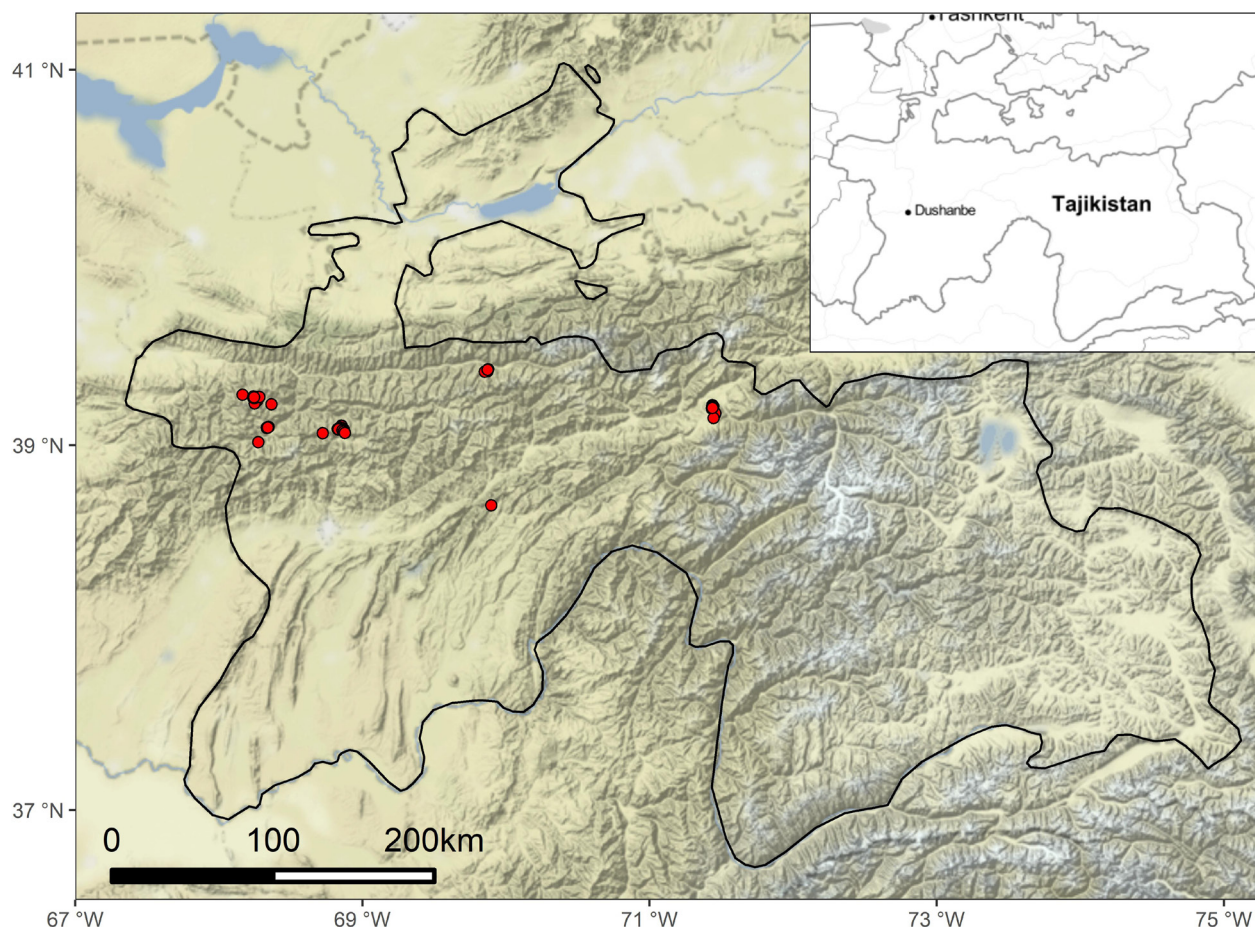


Figure 1. Study area and distribution of the relevés (n = 149).

Methods

Data sampling and data analyses

This study was conducted in the Irano-Turanian subalpine and alpine zone in Tajikistan. In total, 149 relevés were collected in 2014 and 2021 in subalpine and alpine grassland vegetation of the Peter the First, Vahsh, Zeravshan and Hissar Mountains. The size of each relevé was 10 m² following the recommendations of GrassPlot consortium regarding plot size (Dengler et al. 2018). In each plot, all vascular plant and bryophyte species were recorded using the seven-degree Braun-Blanquet cover-abundance scale (Westhoff and van der Maarel 1973), a commonly used method in vegetation classification (Nowak and Nowak 2022). The geographical coordinates were measured for each plot using a GPSMAP 60CSx device with an accuracy of ±10 m based on the WGS84 reference frame. Coordinates for each plot were given in decimal scale (Suppl. material 1).

Vegetation-plot data were stored in the Vegetation of Middle Asia database (GIVD ID: AS-00-003; Nowak et al. 2017), which are available in the Global Vegetation Database sPlot (Bruehlheide et al. 2019), and analysed in R version 4.0.5 (R Core Team 2022), and JUICE software (Tichý 2002). Modified TWINSpan (Hill 1979; Roleček et al. 2009) provided an initial understanding of the data structure and resolution. The cover-abundance scale was transformed using the three-step interval scale with cut-off levels at 0%, 2%, 5%, and 25%. Total inertia was used as a measure of cluster heterogeneity (Roleček et al. 2009). Taxa identified only at the genus level were excluded. Diagnostic species were determined using the *phi* coefficient as a fidelity measure (Tichý and Chytrý 2006). Group size was standardised and the Fisher exact test ($p < 0.05$) was applied for determination of diagnostic species. Species with a *phi* coefficient higher than 0.20 were considered diagnostic for a particular cluster. Diagnostic taxa for alliances were defined as those with a *phi* coefficient ≥ 0.20 in at least two clusters within this alliance. Species with frequency higher than 30% were considered constant species, and those with a maximum cover value exceeding 20% as the dominant species of an individual cluster (corresponding to a vegetation unit). The resulting TWINSpan clusters at the highest division corresponded to phytosociological units. TWINSpan yielded floristically well-characterised terminal clusters with their own diagnostic species (Dengler et al. 2005; Michl et al. 2010). These terminal clusters were considered as associations or plant communities, depending on certainty of taxonomic status of the diagnostic species, and recommendations of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). The habitat profile and authors' field experience were used for the interpretation of meaningful vegetation units.

To show compositional differences between the delimited units, Detrended Correspondence Analysis (DCA) was computed using the 'vegan' package version 2.5.4 (Oksanen et al. 2019). Species cover values of the

Braun-Blanquet scale were transformed to a percentage scale (+, 1, 2, 3, 4 to 1, 3, 13, 38, 63, respectively) and log-transformed [$\log(x+1)$] with down-weighting of rare species. For ecological interpretation of the ordination axes, altitude and climatic parameters were plotted onto a DCA ordination diagram as supplementary variables. Climatic data were extracted from the CHELSA database version 2.1 (<http://chelsa-climate.org>; Karger et al. 2017). Prior to the analysis, correlations between the 19 bioclimatic variables were calculated using the Spearman correlation coefficient to reduce the number of available variables. Variables indicating strong multicollinearity ($r > 0.75$ all pairwise comparisons) were removed, and we retained variables most clearly interpretable from an ecological point of view. The climatic variables used for analysis were: mean annual temperature (bio1), mean annual temperature range (bio2), minimum temperature of the coldest month (bio6), annual precipitation (bio12), and precipitation seasonality (bio15).

The synoptic table with the fidelity and frequency of all diagnostic species is presented in Table 1, and the analytic table including all plots analysed in this study in Suppl. material 1. Type relevés of newly described associations are presented in Appendix 1. Diagnostic species with *phi* coefficient ≥ 0.40 and constant species with frequency $\geq 30\%$ are shown in the main text.

The nomenclature of the vascular plants follows Plants of the World Online (POWO 2023), problematic taxonomic issues were based on The World Flora Online (WFO 2023), and bryophytes follows Ignatov et al. (2006). Nomenclature of *Stipa* spp. follows Nobis et al. (2020; 2022) and of *Geranium* spp. Cherepanov (1995). The plant material collected during field studies was deposited in the Herbarium of Middle Asia Mountains, hosted in OPUN (University of Opole, Poland) and KRA (Jagiellonian University, Poland).

Results

General floristic features and relations between plant communities

The total number of taxa recorded in the whole data set (149 relevés) was 336 with only 43 exceeding 5% of constancy. The taxa with the highest frequencies included plants typical of forb steppes such as *Geranium regelii* (86 occurrences), *Ligularia thomsonii* (72), *Nepeta podostachys* (69), *Poa bucharica* (60), *Eremogone griffithii* (55), *Cousinia franchetii* (51), *Helictotrichon hookeri* (39), *Euphorbia sarawshanica* (37) and *Aulacospermum roseum* (37). In addition, one of the most common species was *Aconogonon coriarium* (52), which has its ecological centre in the tall-forb vegetation from the class *Prangetea ulopterae* Klein 1987. Also *Ferula kokanica*, *F. kuhistanica*, *F. karategina* and *F. ovina*, associated with tall-forb vegetation, were identified in the analysed dataset. The wide ecological amplitude within the Pamir-Alai is demonstrated

Table 1. Synoptic table of Irano-Turanian subalpine and alpine forb steppe and alpine grasslands in the Pamir-Alai Mountains. The *phi* coefficient values (in superscript) in the table are multiplied by 100. Main values are species frequencies (in percentages). Diagnostic species (*phi* ≥ 0.2) are shaded and sorted according to decreasing *phi*. Cluster No.: 1 – *Morinetum coulterianae*; 2 – *Cousinia outichaschensis*-*Lepechiniella sarawschanica* community; 3 – *Smelowskio calycinae*-*Dracocephalum scrobiculati*; 4 – *Phlomoidetum sarawschanicae*; 5 – *Onobrychidetum echidnae*; 6 – *Alopecuro himalaici*-*Veronictetum gorbunovii*; 7 – *Dracocephalum formosum* community; 8 – *Allium giganteum* community; 9 – *Erigeronto seravschanici*-*Eremuretum hissarici*; 10 – *Poa alpinae*-*Swertietum graciliflorae*; 11 – *Astragalo alpini*-*Linnetum olgae*; 12 – *Ligulario alpigenae*-*Solenantheum karategini*.

Cluster No.	1	2	3	4	5	6	7	8	9	10	11	12
No. of relevés	7	4	19	13	6	22	2	2	16	7	26	25
Ass. <i>Morinetum coulterianae</i>												
<i>Morina coulteriana</i>	100 ⁸³	.	.	8	33	.	.	.	.	.	.	.
<i>Veronica capillipes</i>	57 ⁷⁴	.	.	.	.	.	.	.	.	.	.	.
<i>Hyssopus seravschanicus</i>	43 ⁶⁴	.	.	.	.	.	.	.	.	.	.	.
<i>Scorzonera inconspicua</i>	43 ⁶⁴	.	.	.	.	.	.	.	.	.	.	.
<i>Papaver pavoninum</i>	43 ⁶⁴	.	.	.	.	.	.	.	.	.	.	.
<i>Galium spurium</i>	57 ⁶¹	.	.	.	.	.	.	.	13	.	12	.
<i>Eremopoa persica</i>	57 ⁶⁰	.	.	15	.	.	.	.	6	.	.	4
<i>Cousinia mulgediifolia</i>	29 ⁵²	.	.	.	.	.	.	.	.	.	.	.
<i>Trigonella gontscharovii</i>	29 ⁵²	.	.	.	.	.	.	.	.	.	.	.
<i>Lipskya insignis</i>	29 ⁵²	.	.	.	.	.	.	.	.	.	.	.
<i>Bromus oxyodon</i>	29 ⁵²	.	.	.	.	.	.	.	.	.	.	.
<i>Erigeron umbrosus</i>	29 ⁵²	.	.	.	.	.	.	.	.	.	.	.
<i>Dianthus darvazicus</i>	29 ⁴⁸	.	.	.	.	.	.	.	.	.	4	.
<i>Angelica ternata</i>	29 ⁴⁷	.	5	.	.	.	.	.	.	.	.	.
<i>Artemisia rutifolia</i>	29 ⁴⁶	.	.	.	.	.	.	.	6	.	.	.
<i>Melica jacquemontii</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Scrophularia pamiro-alaica</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Astragalus saratagius</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Astragalus pteroccephalus</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Bromus lanceolatus</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Cicer macroanthum</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Draba lanceolata</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Pachypterygium brevipes</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Glaucium elegans</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Lagochilus seravschanicus</i>	14 ³⁶	.	.	.	.	.	.	.	.	.	.	.
<i>Lappula squarrosa</i>	29 ³⁵	25	.	.	.	.	.	.	.	.	.	.
Comm. <i>Cousinia outichaschensis</i>-<i>Lepechiniella sarawschanica</i>												
<i>Cousinia outichaschensis</i>	.	75 ⁸⁶	.	.	.	.	.	.	.	.	.	.
<i>Lepechiniella sarawschanica</i>	.	50 ⁶⁹	.	.	.	.	.	.	.	.	.	.
<i>Potentilla pamiroalaica</i>	.	50 ⁶⁶	.	.	.	.	.	.	.	.	.	4
<i>Oxytropis lehmannii</i>	.	100 ⁶²	32	23	33	.	.	.	.	.	23	20
<i>Juniperus polycarpus</i> var. <i>seravschanica</i> (sl)	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Gypsophila fedtschenkoana</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Bunium persicum</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Ephedra minuta</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Rochelia leiocarpa</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Semenovia furcata</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Androsace caduca</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
<i>Potentilla orientalis</i>	.	25 ⁴⁸	.	.	.	.	.	.	.	.	.	.
Ass. <i>Smelowskio calycinae</i>-<i>Dracocephalum scrobiculati</i>												
<i>Taraxacum minutilobum</i>	.	.	74 ⁷⁶	15	.	.	.	.	.	.	.	.
<i>Dracocephalum scrobiculatum</i>	.	.	68 ⁷³	15	.	.	.	.	.	.	.	.
<i>Poa hissarica</i>	.	.	68 ⁶⁹	23	.	.	.	.	.	.	.	.
<i>Oxytropis savellanica</i>	.	.	63 ⁶⁸	.	17	.	.	.	.	.	.	.
<i>Draba alticola</i>	.	.	26 ⁵⁰	.	.	.	.	.	.	.	.	.
<i>Richeria pyrethroides</i>	.	.	26 ⁴³	.	.	.	.	.	.	.	8	.
<i>Dichodon cerastoides</i>	.	.	37 ⁴²	8	17	5	.	.	.	.	.	.
<i>Lomatocarpa albomarginata</i>	.	25	37 ³⁹	.	.	.	.	.	.	.	.	12
<i>Rhodiola coccinea</i>	.	.	16 ³⁸	.	.	.	.	.	.	.	.	.
<i>Smelowskia calycina</i>	.	.	11 ³¹	.	.	.	.	.	.	.	.	.
<i>Trisetum spicatum</i>	.	.	11 ³¹	.	.	.	.	.	.	.	.	.
<i>Potentilla evestita</i>	.	.	11 ³¹	.	.	.	.	.	.	.	.	.
<i>Carex orbicularis</i>	.	.	11 ³¹	.	.	.	.	.	.	.	.	.
<i>Oxytropis microsphaera</i>	14	.	32 ³¹	15	17	.	.	.	.	.	.	.
<i>Omalotheca supina</i>	.	.	26 ²⁵	.	17	18	.	.	13	.	.	.
<i>Gagea capillifolia</i>	.	.	11 ²⁵	.	.	5	.	.	.	.	.	.
<i>Holosteum glutinosum</i>	.	.	11 ²²	8	.	.	.	.	.	.	.	.
Ass. <i>Phlomoidetum sarawschanicae</i>												
<i>Astragalus bornmuellerianus</i>	.	.	5	38 ⁵⁶	.	.	.	.	.	.	.	.
<i>Phlomoides sarawschanica</i>	.	.	5	46 ⁵¹	17	5	.	.	.	.	.	.
<i>Artemisia korovinii</i>	.	.	16	38 ⁴⁹	.	.	.	.	.	.	.	.

Cluster No.	1	2	3	4	5	6	7	8	9	10	11	12
No. of relevés	7	4	19	13	6	22	2	2	16	7	26	25
<i>Scorzonera acanthoclada</i>	.	.	5	38 ⁴⁵	.	.	.	.	6	.	.	12
<i>Leucopoa karatavica</i>	.	.	.	23 ³⁹	.	.	.	.	.	.	8	.
<i>Arenaria rotundifolia</i>	.	.	.	15 ³⁸	.	.	.	.	.	.	.	.
<i>Astragalus bactrianus</i>	.	.	.	15 ³⁸	.	.	.	.	.	.	.	.
<i>Veronica rubrifolia</i>	.	.	5	46 ³⁶	.	.	50	.	6	.	.	16
<i>Euphorbia sarawtschanica</i>	43	.	5	69 ³⁴	33	5	.	.	44	14	35	16
<i>Artemisia lehmanniana</i>	.	.	.	15 ³³	.	.	.	.	.	.	4	.
<i>Carduus nutans</i>	.	.	.	15 ³¹	.	.	.	.	6	.	.	.
<i>Artemisia glanduligera</i>	.	.	.	15 ³¹	.	.	.	.	6	.	.	.
<i>Festuca valesiaca</i>	14	.	.	31 ³⁰	.	.	.	.	.	.	15	16
<i>Polygonum fibrilliferum</i>	.	.	11	15 ²⁷	.	.	.	.	.	.	.	.
<i>Polygonum aviculare</i>	.	.	.	15 ²⁶	.	.	.	.	13	.	.	.
Ass. Onobrychidetum echidnae												
<i>Onobrychis echidna</i>	.	.	.	.	50 ⁶⁹	.	.	.	.	.	.	.
<i>Lomatocarpa steineri</i>	.	.	11	.	50 ⁶²	.	.	.	.	.	.	.
<i>Scrophularia griffithii</i>	.	.	.	.	33 ⁴⁶	.	.	.	6	.	4	4
<i>Potentilla virgata</i>	.	.	.	.	17 ³⁹	.	.	.	.	.	.	.
<i>Geranium linearilobum</i>	.	.	.	.	17 ³⁹	.	.	.	.	.	.	.
<i>Draba alajica</i>	.	.	.	.	17 ³⁹	.	.	.	.	.	.	.
<i>Crepis pulchra</i>	14	.	5	15	50 ³⁹	.	.	.	6	.	27 ¹⁶	8
Ass. Alopecuro himalaici-Veronicetum gorbunovii												
<i>Oxytropis michelsonii</i>	.	.	.	8	.	73 ⁷⁰	.	.	.	.	19	.
<i>Alopecurus himalaicus</i>	.	.	.	.	.	45 ⁶⁶	.	.	.	.	.	.
<i>Ranunculus rufosepalus</i>	.	.	.	.	.	32 ⁵⁵	.	.	.	.	.	.
<i>Phlomoideis oreophila</i>	.	.	.	.	.	41 ⁵⁴	.	.	.	.	12	.
<i>Veronica gorbunovii</i>	.	.	.	.	.	41 ⁵⁰	.	.	.	.	12	8
<i>Aulacospermum roseum</i>	14	.	11	.	.	73 ⁴⁶	.	.	.	43	38	20
<i>Primula kaufmanniana</i>	.	.	.	.	.	23 ⁴²	.	.	.	.	4	.
<i>Draba rosularis</i>	.	.	.	.	.	18 ⁴¹	.	.	.	.	.	.
<i>Ferula karategina</i>	.	.	.	.	.	18 ⁴¹	.	.	.	.	.	.
<i>Potentilla tephroleuca</i>	.	50	21	.	.	45 ³⁶	.	.	.	.	.	.
<i>Piptatherum microcarpum</i>	.	.	.	.	.	18 ³³	.	.	.	.	8	.
<i>Psathyrostachys kronenburgii</i>	.	.	.	.	.	18 ³³	.	.	.	.	.	8
<i>Paraquilegia caespitosa</i>	.	.	.	.	.	14 ³¹	.	.	.	.	4	.
<i>Lindelofia olgae</i>	.	.	.	.	.	14 ³¹	.	.	.	.	.	4
<i>Oxytropis kuhistanica</i>	.	.	.	.	.	9 ²⁹	.	.	.	.	.	.
<i>Erigeron sogdianus</i>	.	.	.	.	.	9 ²⁹	.	.	.	.	.	.
<i>Trigonella iskanderi</i>	.	.	.	.	.	9 ²⁹	.	.	.	.	.	.
<i>Carex regeliana</i>	.	.	.	.	.	9 ²⁹	.	.	.	.	.	.
<i>Koeleria pyramidata</i>	.	.	.	.	17	41 ²⁷	50	.	.	.	15	20
Comm. Dracocephalum formosum												
<i>Dracocephalum formosum</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Galium turkestanicum</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Alchemilla hissarica</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Convolvulus lineatus</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Euphrasia pectinata</i>	.	.	.	.	.	.	100 ⁹⁸	.	.	.	4	.
<i>Hordeum turkestanicum</i>	.	.	.	.	.	.	100 ⁹⁶	.	.	.	.	8
<i>Carex stenophylla</i> subsp. <i>stenophylloides</i>	.	.	.	15	.	.	100 ⁹¹	.	.	.	.	4
<i>Pedicularis verae</i>	.	.	.	15	.	18	100 ⁷²	.	.	.	8	36 ¹⁸
<i>Cirsium esculentum</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Medicago lupulina</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Astragalus tibetanus</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Myosotis cespitosa</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Allium weschniakowii</i>	.	.	.	.	.	5	50 ⁶⁶	.	.	.	.	.
<i>Seseli schrenkianum</i>	.	.	.	.	.	.	50 ⁶⁵	.	6	.	.	.
<i>Inula rhizocephala</i>	.	.	.	15 ¹³	.	.	50 ⁵⁹	.	.	.	.	.
Comm. Allium giganteum												
<i>Rosa ecae</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Allium giganteum</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Solenanthus circinnatus</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Thermopsis alpina</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Polygonatum sewerzowii</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Corydalis darvasica</i>	.	.	.	.	.	.	100 ¹⁰⁰	.	.	.	.	.
<i>Ferula kuhistanica</i>	.	.	.	.	.	.	100 ⁹⁸	.	.	.	.	4
<i>Origanum vulgare</i> subsp. <i>gracile</i>	.	.	.	.	.	.	100 ⁹⁷	6	.	.	.	.
<i>Elaeosticta hirtula</i>	.	.	.	8	.	.	100 ⁹⁶	.	.	.	.	.
<i>Phlomoideis lehmanniana</i>	.	.	.	.	.	.	100 ⁹⁴	.	.	.	8	4
<i>Potentilla kulabensis</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Silene vulgaris</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Tulipa praestans</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Barbarea vulgaris</i> subsp. <i>arcuata</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Microthlaspi perfoliatum</i>	.	.	.	.	.	.	50 ⁶⁹	.	.	.	.	.
<i>Lamium album</i>	.	.	.	.	.	.	50 ⁶⁵	6	.	.	.	.

Cluster No.	1	2	3	4	5	6	7	8	9	10	11	12
No. of relevés	7	4	19	13	5	22	2	2	16	7	26	25
Ass. Erigeronto seravschanici-Eremuretum hissarici												
Astragalus corydalinus	.	.	.	.	.	.	.	.	56 ⁷⁴	.	.	.
Eremurus hissaricus	.	.	.	.	.	.	.	.	50 ⁶⁹	.	.	.
Hypericum scabrum	.	.	.	.	.	.	.	.	38 ⁶⁰	.	.	.
Iris hoogiana	.	.	.	.	.	.	.	.	25 ⁴⁸	.	.	.
Rumex paulsenianus	.	.	.	.	.	.	.	50	50 ⁴²	.	8	4
Campanula glomerata	.	.	.	.	.	.	.	.	19 ⁴²	.	.	.
Agrostis canina	.	.	.	.	.	.	.	.	25 ⁴¹	.	.	8
Bromus popovii	.	.	.	.	.	.	.	.	13 ³⁴	.	.	.
Festuca rubra	.	.	.	.	.	.	.	.	13 ³⁴	.	.	.
Dactylis glomerata	.	.	.	.	.	.	.	.	19 ³¹	.	8	4
Erigeron seravschanicus	.	.	.	.	33	.	.	.	31 ²⁸	14	.	8
Ass. Poo alpinae-Swertietum graciliflorae												
Poa alpina	.	.	.	.	.	23 ¹⁴	.	.	.	86 ⁷⁹	4	.
Swertia graciliflora	.	.	5	.	.	14	.	.	.	71 ⁷³	.	.
Anemonastrum protractum	.	.	.	.	17	14	.	.	.	86 ⁷²	.	16
Androsace darvasica	.	.	.	.	17	9	.	.	.	71 ⁶⁵	.	12
Parrya pinnatifida	.	.	.	.	.	.	.	.	.	43 ⁶⁴	.	.
Polygonum vvedenskyi	.	.	.	.	.	14	.	.	6	57 ⁶²	.	.
Klasea algida	.	.	.	.	.	9	.	.	.	57 ⁶⁰	.	16
Potentilla vvedenskyi	.	.	.	.	.	9	.	.	19	57 ⁵⁹	.	.
Oxytropis immersa	.	.	.	.	.	9	.	.	.	43 ⁵⁷	.	.
Erigeron vicarius	.	.	.	.	.	9	.	.	.	43 ⁵¹	4	8
Minuartia litwinowii	.	.	.	.	.	5	.	.	.	29 ⁴⁸	.	.
Potentilla crantzii	.	.	5	.	.	.	.	.	.	29 ⁴⁷	.	.
Gagea vegeta	.	.	.	.	.	.	.	.	.	14 ³⁶	.	.
Astragalus kokandensis	.	.	.	15	.	18	.	.	13	43 ³⁶	8	12
Draba olgae	.	.	.	.	17	.	.	.	.	29 ³⁵	4	4
Ass. Astragalo alpini-Linetum olgae												
Linum olgae	.	.	.	.	.	.	.	.	.	.	81 ⁸⁹	.
Leymus secalinus	.	.	.	.	.	.	.	.	.	.	46 ⁶¹	8
Myosotis stricta	.	.	.	.	.	.	.	.	.	.	38 ⁶⁰	.
Thymus minutus	.	.	.	.	.	.	.	.	.	.	35 ⁵⁷	.
Potentilla pedata	.	.	.	.	.	.	.	.	.	.	42 ⁵⁵	12
Phleum phleoides	.	.	.	.	.	.	.	.	25	.	54 ⁵⁴	8
Crepis darvasica	.	.	.	.	.	.	.	.	.	.	27 ⁵⁰	.
Silene tachtensis	.	.	.	.	.	9	.	.	6	.	38 ⁵⁰	.
Bupleurum exaltatum	.	.	.	.	.	.	.	.	13	.	35 ⁴⁸	.
Dracocephalum integrifolium	.	.	.	.	.	.	.	.	.	.	23 ⁴⁶	.
Asyneuma argutum	14	.	.	.	17	.	.	50	25	.	73 ⁴⁶	16
Hedysarum tenuifolium	.	.	.	.	.	.	.	.	.	.	27 ⁴⁶	4
Tragopogon turkestanicus	.	.	.	.	.	14	.	.	6	.	42 ⁴⁵	12
Thesium alatavicum	.	.	.	.	.	.	.	.	13	.	31 ⁴⁴	.
Erysimum odoratum	.	.	.	.	.	.	.	.	25	.	38 ⁴¹	8
Gypsophila cephalotes	.	.	.	.	.	.	.	.	.	29	38 ³⁹	12
Astragalus alpinus	.	.	.	.	.	.	.	.	.	.	15 ³⁸	.
Astragalus macropterus	.	.	.	.	.	.	.	.	.	.	15 ³⁸	.
Solidago kuhistanica	.	.	.	.	.	.	.	.	.	.	15 ³⁸	.
Epilobium angustifolium	.	.	.	.	.	.	.	.	.	.	15 ³⁸	.
Dictamnus albus	.	.	.	.	.	.	.	.	.	.	15 ³⁸	.
Hieracium virosum	.	.	.	.	17	.	.	.	.	.	27 ³⁸	.
Astragalus aksuensis	.	.	.	.	.	.	.	.	.	.	19 ³⁴	8
Rosa nanothamnus	.	.	.	.	.	.	.	.	.	.	12 ³³	.
Scrophularia gontscharovii	.	.	.	.	.	.	.	.	.	.	12 ³³	.
Rosa ovczinnikovii (sl)	.	.	.	.	.	.	.	.	.	.	12 ³³	.
Thalictrum minus subsp. maxwellii	.	.	.	.	.	5	.	.	.	.	15 ²⁹	4
Hedysarum flavescens	.	.	.	.	17	.	.	.	.	.	19 ²⁷	4
Klasea sogdiana	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Eremurus robustus	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Helichrysum mussae	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Stipa caucasica	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Phlomoides arctifolia	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Silene longicalycina	.	.	.	.	.	.	.	.	.	.	8 ²⁷	.
Bromus paulsenii	.	.	5	8	.	5	.	.	.	.	15 ²³	.
Acantholimon komarovii	.	.	5	.	.	5	.	.	.	.	12 ²²	.
Lomelosia alpestris	.	.	.	.	.	.	.	.	6	.	12 ²²	4
Potentilla hololeuca	.	.	.	.	17	.	.	.	.	.	15 ²²	4
Ass. Ligulario alpinae-Solenanthesetum karategini												
Alopecurus apiatus	.	.	.	.	.	.	.	.	.	.	.	48 ⁶⁸
Ligularia alpigena	.	.	.	.	17	.	.	.	.	.	19	64 ⁶¹
Helictotrichon tianschanicum	.	.	.	.	17	.	.	.	.	.	.	48 ⁵⁷
Solenanthus karateginus	.	.	.	.	.	.	.	.	.	.	.	32 ⁵⁵
Bistorta elliptica	.	.	.	.	.	.	.	.	.	.	.	28

Cluster No.	1	2	3	4	5	6	7	8	9	10	11	12
No. of relevés	7	4	19	13	6	22	2	2	16	7	26	25
<i>Phleum alpinum</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Gentianella turkestanorum</i>	.	.	.	.	.	.	.	.	6	.	.	4
<i>Picris nuristanica</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Cirsium incanum</i>	43 ⁶⁴	.	.	.	.	.	.	.	.	.	.	.
<i>Chesneya crassipes</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Euphrasia regelii</i>	.	.	.	.	17	.	.	.	.	.	.	4
<i>Ephedra intermedia</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Rochelia cardiosepala</i>	.	.	.	8	.	.	.	.	.	.	.	.
<i>Cotoneaster zeravschanicus</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Rosa fedtschenkoana</i>	14	.	.	.	.	.	.	.	6	.	.	.
<i>Juniperus pseudosabina</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Ferula ovina</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Calamagrostis pseudophragmites</i>	.	.	.	.	.	.	.	.	.	.	8	4
<i>Lophanthus subnivalis</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Ranunculus turkestanicus</i>	.	.	5	.	.	9	.	.	.	.	.	.
<i>Jurinea baldschuanica</i>	.	.	.	.	.	.	.	.	6	.	4	.
<i>Ranunculus sewerzowii</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Thymus seravschanicus</i>	.	.	.	.	17	.	.	.	.	.	.	4
<i>Oxytropis guntensis</i>	.	.	5	.	.	.	.	.	.	.	.	.
<i>Ranunculus rubrocalyx</i>	.	.	.	.	17	.	.	.	.	14	.	.
<i>Astragalus coluteocarpus</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Euphrasia cyclophylla</i>	.	.	.	.	.	.	.	.	19	.	12	16
<i>Polygonum paronychioides</i>	14	25	.	.	.	.	.	.	.	.	.	.
<i>Parrya turkestanica</i>	.	.	.	.	.	5	.	.	.	.	.	.
<i>Elymus fedtschenkoi</i>	.	.	.	.	.	.	.	.	6	14	.	.
<i>Prangos pabularia</i>	.	.	.	.	.	.	.	50	19 ¹⁶	.	4	.
<i>Achillea millefolium</i>	.	.	.	.	.	.	.	.	6	.	12	8
<i>Galagania fragrantissima</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Lathyrus pratensis</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Chorispora sabulosa</i>	.	.	5	.	.	9	.	.	.	.	.	.
<i>Onobrychis grandis</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Piptatherum purpurascens</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Stellaria brachypetala</i>	.	.	5	.	.	.	.	.	.	.	.	.
<i>Mertensia dshagastanica</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Phleum pratense</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Phlomis speciosa</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Gastrolychnis uralensis</i>	.	.	5	.	17	.	.	.	.	.	.	.
<i>Erigeron oreades</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Thalictrum kuhistanicum</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Tulipa turkestanica</i>	.	.	.	.	17	.	.	.	6	.	.	.
<i>Cousinia pannosa</i>	.	.	.	8	.	.	.	.	.	.	.	.
<i>Linum macrorrhizum</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Oxyria digyna</i>	.	.	.	.	.	5	.	.	.	.	.	.
<i>Pseudosedum condensatum</i>	.	.	.	.	.	.	.	.	6	.	.	4
<i>Onosma gmelinii</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Valeriana ficariifolia</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Cousinia radians</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Kobresia persica</i>	.	25	5	.	.	.	.	.	.	.	.	.
<i>Tanacetum pseudachillea</i>	.	.	.	.	.	.	.	.	.	.	8	4
<i>Crataegus turkestanica</i> (sl)	.	.	.	.	.	.	.	.	6	.	.	.
<i>Potentilla flabellata</i>	.	.	5	.	.	.	.	.	.	.	.	.
<i>Onobrychis viciifolia</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Astragalus rubescens</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Artemisia santolinifolia</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Carex diluta</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Valeriana fedtschenkoi</i>	.	.	5	.	.	.	.	.	.	.	.	.
<i>Allium hexaceras</i>	.	.	5	.	.	.	.	.	.	.	.	.
<i>Carex pachystylis</i>	.	.	.	8	.	.	.	.	.	.	.	.
<i>Astragalus adpreseipilosus</i>	.	.	.	8	.	9	.	.	.	.	.	12
<i>Rosa kokanica</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Jurinea bipinnatifida</i>	.	.	.	.	.	5	.	.	.	.	4	.
<i>Trifolium repens</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Oxytropis tachtensis</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Mentha longifolia</i> var. <i>asiatica</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Vicia tenuifolia</i>	.	.	.	.	.	.	.	.	.	.	4	.
<i>Kudrjashevya jacubi</i>	.	.	.	.	.	.	.	.	6	.	.	.
<i>Gagea vvedenskyi</i>	.	.	5	8	.	.	.	.	.	14	.	.
<i>Astragalus mucidus</i>	.	.	.	.	.	.	.	.	.	.	.	4
<i>Galium pamiroalaicum</i>	.	.	.	.	17	.	.	.	.	.	8	.
<i>Leontopodium ochroleucum</i>	.	.	5	.	17	.	.	.	.	.	.	.
<i>Adonis turkestanica</i>	14	.	.	15	.	.	.	.	13	.	4	8
<i>Eriqeron bellidiformis</i>	.	.	5	.	.	.	.	.	.	.	.	.

by *Carex turkestanica* (33 occurrences in the dataset), which has the highest constancy and abundance in steppe vegetation (Nowak et al. 2016a; 2018). Alpine grassland plants like *Myosotis alpina* (50), *Oxytropis lehmannii* (26), *Festuca alaica* (22), and *Ligularia alpigena* (22) were also included in the group of most frequent species. Despite the close contact of the forb steppe with typical cryophilous steppes, the latter group contributed only a few and uncommon taxa in the dataset, such as *Festuca valesiaca*, *Myosotis stricta*, *Poa bulbosa*, and *Stipa kirghisorum*. However, we noted more species associated with scree vegetation, including *Artemisia rutifolia*, *Eremopoa persica*, *Galium spurium*, *Papaver pavonicum* and *Veronica capillipes*. We also noted species originating from woods and xeric scrubs, such as *Cotoneaster zeravschanicus*, *Crataegus turkestanica*, *Juniperus pseudosabina*, *J. polycarpus* var. *seravschanica*, *Rosa ecae*, *R. fedtschenkoana* and *R. kokanica*. In contrast, the subalpine forb steppe of the Pamir-Alai included a low number of species of open and ruderal habitats (e.g. *Cirsium incanum*).

Nepeta podostachys (potential class rank) and the order of *Nepetetalia podostachyos*. Alpine grasslands in our scheme (*Poo alpinae-Bistortion ellipticae* alliance) should be separated at potential class level as alpine grasslands with *Festuca alaica* and *F. kryloviana* and a potential order of alpine grasslands with *Geranium saxatile* and *Festuca alaica*.

The first group of open canopy forb steppe and pasture communities of the eastern Irano-Turanian region in the subalpine belt of the Pamir-Alai Mountains, corresponding to the alliance *Ligulario thomsonii-Geranion regelii*, is represented by clusters 1–6. Species with the highest frequency in this group are *Cousinia franchetii* (58%), *Eremogone griffithii* (58%), and *Aconogonon hissaricum* (40%). The second group including clusters 7–9 was assigned to the alliance *Artemision dracunculi* and represented steppe pastures of the subalpine belt in the Pamir-Alai Mountains. The most frequent species within this group were *Artemisia dracunculus* (80%), *Poa fragilis* (50%), *Astragalus corydalinus* (45%), and *Rumex paulsenianus* (45%). The third group, including clusters 10–12, was assigned to the

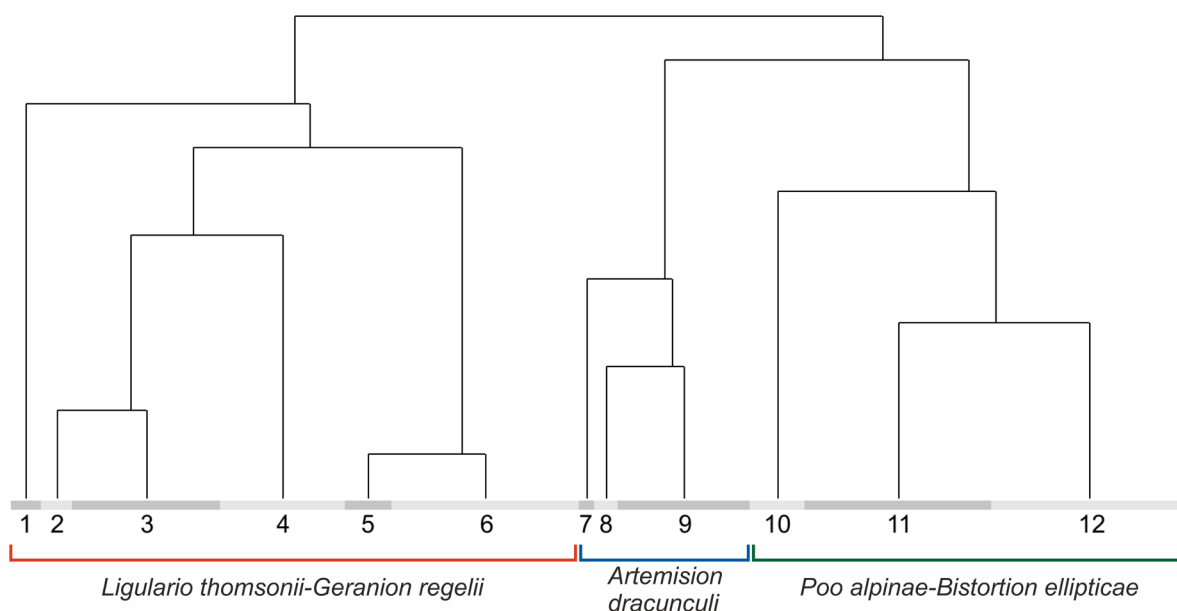


Figure 2. Dendrogram illustrating the assignment of relevé groups identified by TWINSpan to particular syntaxonomic units 1 – *Morinetum coulterianae*; 2 – *Cousinia outichaschensis-Lepechiniella sarawvschanica* community; 3 – *Smelowskio calycinae-Draconocephaletum scrobiculati*; 4 – *Phlomoideum sarawvschanicae*; 5 – *Onobrychidetum echidnae*; 6 – *Alopecuro himalaici-Veronicetum gorbunovii*; 7 – *Draconocephalum formosum* community; 8 – *Allium giganteum* community; 9 – *Erigeronto seravschanici-Eremuretum hissarici*; 10 – *Poo alpinae-Swertietum graciliflorae*; 11 – *Astragalo alpini-Linetum olgae*; 12 – *Ligulario alpigenae-Solenantheum karategini*.

Classification of the vegetation units

TWINSpan classification resulted in the delimitation of 12 clusters (Figure 2). Based on expert knowledge, three relevés with dominance of *Morina coulteriana* were relocated from cluster 4 to cluster 1, and two relevés with dominance of *Linum olgae* were moved from cluster 6 to cluster 11. The resulting clusters represent three major groups corresponding to three different alliances. We propose to classify subalpine forb steppes (*Ligulario thomsonii-Geranion regelii* and *Artemision dracunculi* alliances) as grassland vegetation with *Eremogone griffithii* and

alliance *Poo alpinae-Bistortion ellipticae*, which represented mesophilous grasslands in the alpine belt of the Pamir-Alai Mountains. Species with the highest relative frequency in this group were *Cousinia stephanophora* (55%), *Stachyopsis oblongata* (55%), *Carex turkestanica* (53%), *Helictotrichon hookeri* (48%) and *Gentiana olivieri* (47%).

The plant communities obtained by TWINSpan are presented on the first and second axis of the DCA ordination diagram (Figure 3). The first axis is linked with mean diurnal temperature range (bio2) and the sum of annual precipitation (bio12), which differentiate the alliances *Ligulario thomsonii-Geranion regelii* and *Poo alpinae-Bistortion*

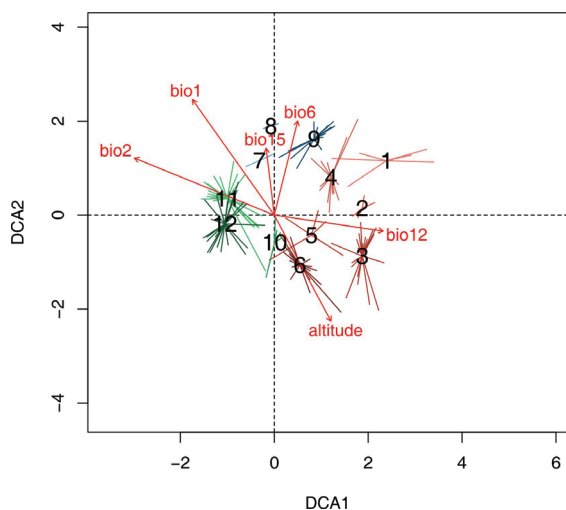


Figure 3. DCA ordination of forb steppe communities in the Pamir-Alai Mountains. The different colors refer to alliances: red – *Ligulario thomsonii-Geranion regelii*, blue – *Artemision dracunculi* and green – *Poa alpinae-Bistortion ellipticae*. Numbers on the ordination refer to centroids of clusters (see Figure 2 and Syntaxonomic synopsis).

ellipticae (especially clusters 11 and 12). Alpine grasslands included in the alliance *Ligulario thomsonii-Geranion regelii* were associated with higher precipitation (Figures 3 and 4f), while assemblages included in the alliance *Poa alpinae-Bistortion ellipticae* (clusters 11 and 12) were correlated with higher mean diurnal temperature range (Figures 3 and 4d). The second axis corresponded to gradients of precipitation seasonality (bio15) and minimum temperature of the coldest month (bio6), which seem to be an important factor distinguishing cluster 9 belonging to the alliance *Artemision dracunculi* from other alliances (Figures 3, 4e and 4g).

Syntaxonomic synopsis

Irano-Turanian subalpine and alpine forb steppe

Forb steppes with *Eremogone griffithii* and *Nepeta podostachys* (potential class rank)

Order: *Nepetetalia podostachyos* A. Nowak et al. ord. nov.

Subalpine and alpine forb steppe of the eastern Irano-Turanian origin of the Pamir-Alai Mountains and closely related vegetation

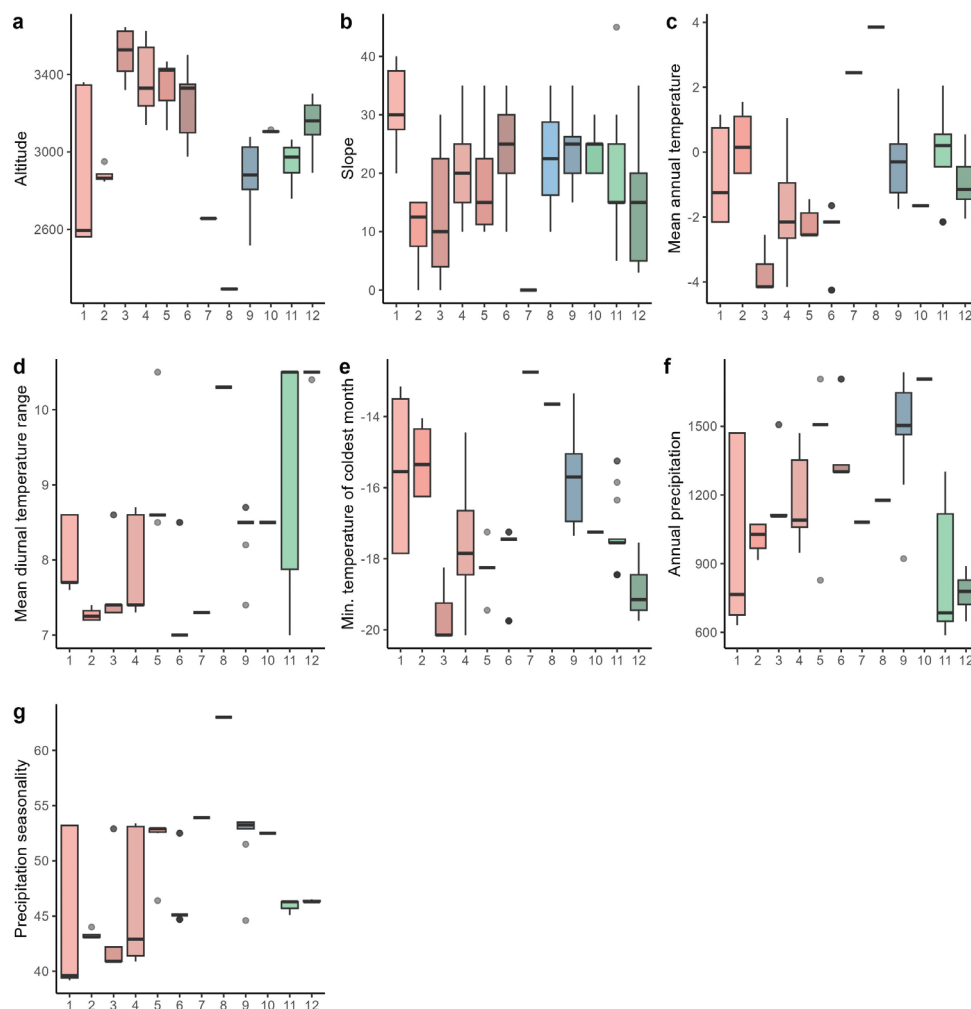


Figure 4. Boxplots showing median (line), quartiles, outliers and the range of (a) elevation, (b) slope, (c) mean annual temperature, (d) mean diurnal temperature range, (e) minimum temperature of the coldest month, (f) sum of annual precipitation and (g) precipitation seasonality. The different colours of the boxes represent alliances: red – *Ligulario thomsonii-Geranion regelii*, blue – *Artemision dracunculi* and green – *Poa alpinae-Bistortion ellipticae*. The abbreviations of the syntaxonomic units are explained in the Figure 2 and Syntaxonomic synopsis.

1.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. 2021a

- 1.1.1. *Morinetum coulterianae* A. Nowak et al. ass. nov. (cluster 1)
- 1.1.2. *Cousinia outichaschensis-Lepechiniella sarawschanica* comm. (cluster 2)
- 1.1.3. *Smelowskio calycinae-Draconocephaletum scrobiculati* A. Nowak et al. ass. nov. (cluster 3)
- 1.1.4.a. *Phlomoidetum sarawschanicae* A. Nowak et al. ass. nov. (cluster 4)
- 1.1.4.b. *Phlomoidetum sarawschanicae scorzoneretosum acanthocladae* A. Nowak et al. subass. nov.
- 1.1.5. *Alopecuro himalaici-Veronicetum gorbunovii* A. Nowak et al. ass. nov. (cluster 6)

Tragacanthic vegetation

- 1.1.6. *Onobrychidetum echidnae* A. Nowak et al. ass. nov. (cluster 5)

Mesophilous steppic pastures of the subalpine belt in the Pamir-Alai Mountains

1.2. Alliance: *Artemision dracunculi* A. Nowak et al. all. nov.

- 1.2.1. Community of *Dracocephalum formosum* (cluster 7)
- 1.2.2. Community of *Allium giganteum* (cluster 8)
- 1.2.3. *Erigeronto seravschanici-Eremuretum hissarici* A. Nowak et al. ass. nov. (cluster 9)

Mesic grasslands of the alpine belt of Middle Asia

Alpine grasslands with *Festuca alaica* and *Festuca kryloviana* (potential class rank)

Alpine grasslands with *Geranium saxatile* and *Festuca alaica* (potential order rank)

2.1. Alliance: *Poo alpinae-Bistortion ellipticae* S. Świerszcz et al. all. nov.

- 2.1.1. *Poo alpinae-Swertietum graciliflorae* S. Świerszcz et al. ass. nov. (cluster 10)
- 2.1.2. *Astragalo alpini-Linetum olgae* S. Świerszcz et al. ass. nov. (cluster 11)
- 2.1.3. *Ligulario alpigenae-Solenanthesetum karategini* S. Świerszcz et al. ass. nov. (cluster 12)

Forb steppes with *Eremogone griffithii* and *Nepeta podostachys* (potential class rank)

For the eastern territories of the Irano-Turanian region, a distinct class of subalpine steppes with a high abundance of forb species should be defined. This type of vegetation occurs throughout the Pamir-Alai, western and southern Tian Shan and Hindu-Kush and Kopet-Dagh Mountains. It develops on stony slopes with fertile soil. This forb steppe vegetation is used extensively as pastures and is often found in areas where juniper forests have been clearfelled.

Order: *Nepetetalia podostachyos* A. Nowak, S. Świerszcz, M. Nobis, G. Swacha et S. Nowak ord. nov. hoc loco

Typus: *Ligulario thomsonii-Geranion regelii* Nowak et al. 2021a (p. 192)

Diagnostic species: *Calamagrostis anthoxanthoides*, *Cousinia franchetii*, *Delphinium oreophilum*, *Eremogone griffithii*, *Gentiana olivieri*, *Geranium collinum*, *G. regelii*, *Geum kokanicum*, *Leymus alaicus*, *Ligularia thomsonii*, *Nepeta podostachys*, *Pedicularis krylovii*, *Poa bucharica*, *P. fragilis*, *P. pratensis*, *P. zaprjagajevii*, *Potentilla grisea*, *Rhodiola heterodonta*, *Semenovia dasycarpa*

Geographical range: Eastern Irano-Turanian phytogeographical region (Iran, Afghanistan, Uzbekistan, Kyrgyzstan and Tajikistan). Particularly the subalpine belts of the Pamir-Alai, Tian Shan and Hindu-Kush Mountains

Habitat characteristics: This order includes subalpine forb steppes dominated by species of Irano-Turanian distribution range. Plant communities of this order are part of the forest-steppe vegetation and occur in a mosaic with the juniper tree-stands. They are in close contact with typical alpine grasslands, cryophilic steppes, as well as high areas of juniper clearfell. The vegetation is characterised by a high proportion of forbs and develops mainly on fertile to moderately fertile soils in subhumid climates. As with other open vegetation in the region, the abundance and frequency of its undergrowth is strongly influenced by grazing.

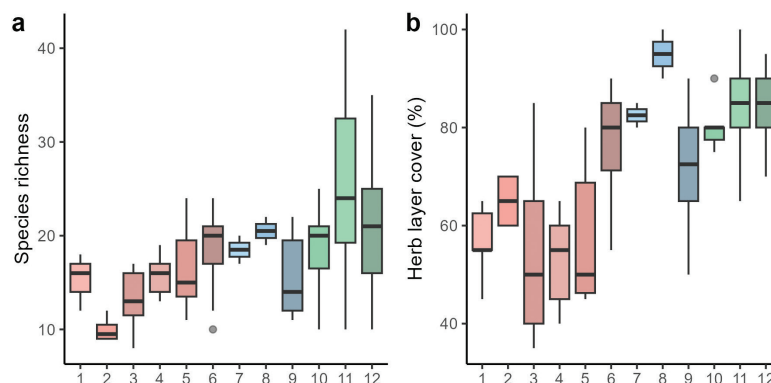


Figure 5. Boxplots showing median (line), quartiles, outliers and the range of (a) species richness and (b) cover of the herb layer, for particular syntaxonomic units. The different colours of the boxes represent alliances: red – *Ligulario thomsonii-Geranion regelii*, blue – *Artemision dracunculi* and green – *Poo alpinae-Bistortion ellipticae*. The abbreviations of the syntaxonomic units are explained in the Figure 2 and Syntaxonomic synopsis.

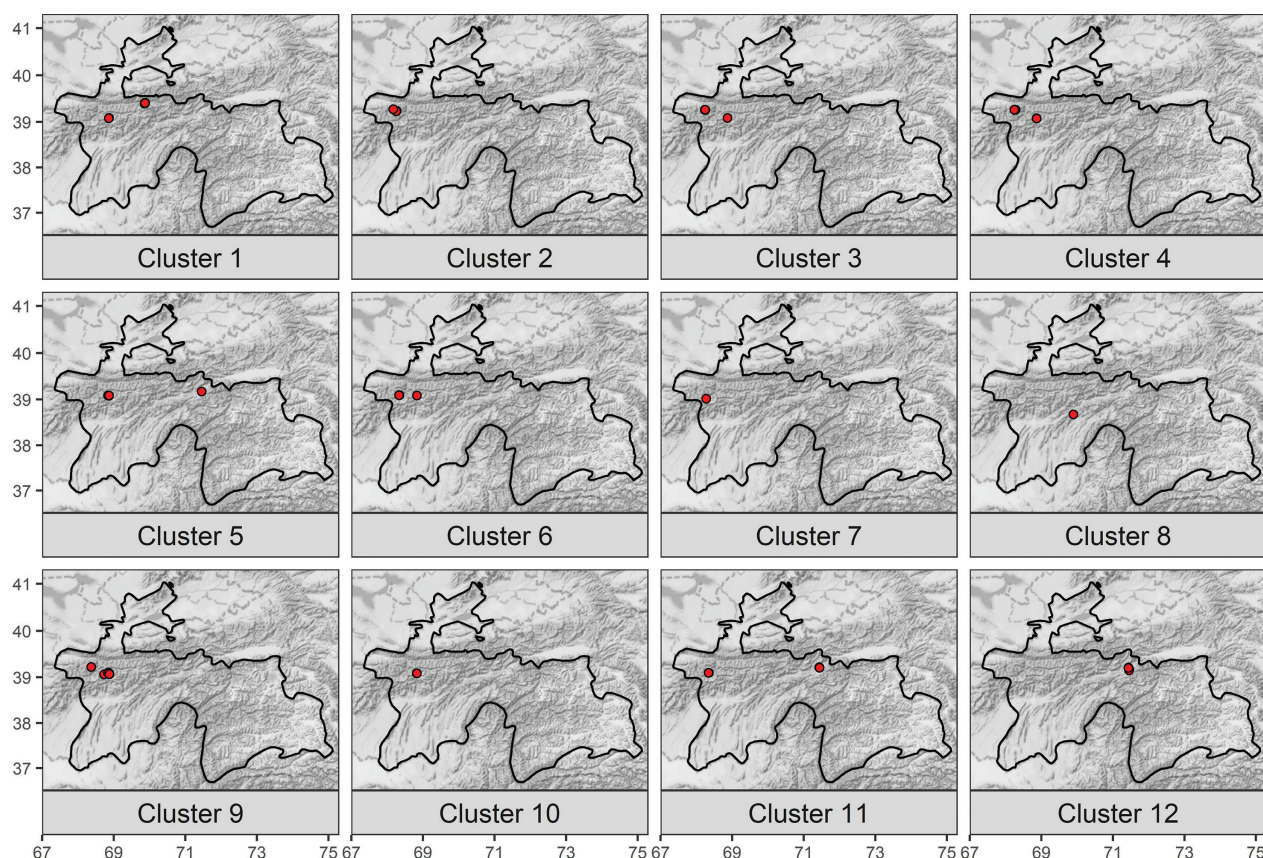


Figure 6. Distribution of relevés assigned to the particular vegetation units ($n = 149$). The name of syntaxa (1–12) are written in the Figure 2 and Syntaxonomic synopsis.

Subalpine and alpine forb steppe communities of the eastern Irano-Turanian region of the Pamir-Alai Mountains and closely related vegetation

1.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. 2021a

This alliance includes forb steppes of the western part of the Pamir-Alai, as well as the vegetation of the warmest slopes of the southwestern Tian Shan. Plant communities of this alliance develop in the gaps of sparse juniper woods in their upper zone and in subalpine pastures. The characteristic features of these habitats include a high proportion of stone and gravel debris, and a relatively high seasonality manifested by a decreased biomass production in mid-summer (dry period). This alliance includes typically pastoral, intensively grazed vegetation characterised by spiny plants (e.g. *Morina coulteriana* and *Scorzonera acanthoclada*).

The thorn cushion vegetation of *Onobrichidetum echidnae* was also provisionally assigned to this alliance. However, this association is clearly distinct as it inhabits wind-swept slopes and mountain passes at high elevations. Further studies on its syntaxonomic position are needed as it is widespread and more diverse in Central Asia (*Acantholimon* spp., *Astracantha* spp., *Astragalus lasiosemius* communities).

Probably the vegetation of the alliance *Ligulario thomsonii-Geranion regelii* is analogous to the subalpine grasslands of the western Himalayas (vegetation dominated

by *Geranium himalayense*) or grasslands with *Geranium albiflorum* in the Altay-Sayan ranges. The vegetation of this alliance develops in the subalpine zone (Figure 4a) and is characterised by a relatively lower herbaceous cover and is species poorer (Figure 5) when compared to the vegetation of the other two alliances. It was identified and described by Nowak et al. (2020) as the vegetation closely related to typical tall-forb vegetation of the class *Prangetea ulopterae* in the Pamir-Alai and western Tian Shan Mountains (Nowak et al. 2020, 2021a).

1.1.1. *Morinetum coulterianae* A. Nowak, S. Świerszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (Cluster 1; Figure 7a)

Typus: Appendix 1, rel. 1.1.1, holotypus hoc loco.

Diagnostic species: *Angelica ternata*, *Artemisia rutifolia*, *Cousinia mulgediifolia*, *Dianthus darvazicus*, *Eremopoa persica*, *Erigeron umbrosus*, *Galium spurium*, *Hyssopus seravschanicus*, *Lipskya insignis*, *Morina coulteriana*, *Papaver pavoninum*, *Scorzonera inconspicua*, *Trigonella gontscharovii*, *Veronica capillipes*

Constant species: *Artemisia dracuncululus*, *Cirsium incanum*, *Eremopoa persica*, *Euphorbia sarawschanica*, *Festuca olgae*, *Galium spurium*, *Hyssopus seravschanicus*, *Ligularia thomsonii*, *Morina coulteriana*, *Nepeta podostachys*, *Papaver pavoninum*, *Poa relaxa*, *Scorzonera inconspicua*, *Taraxacum raikoviae*, *Veronica capillipes*, *Ziziphora pamirolaica*

Dominant species: *Morina coulteriana*

Floristic and habitat characteristics: The range of the main diagnostic taxon, *Morina coulteriana*, covers Afghanistan, Middle Asia and the western Himalayas (POWO 2023). *Morina coulteriana* is a perennial plant inhabiting mostly the subalpine, alpine and subnival belts. In Tajikistan, it occurs mainly in the upper zone of thermophilous juniper forests, subalpine grasslands, tall-forbs, tragacanthic and cryophilous vegetation. The species was recorded on stony slopes but with fertile soil, at elevations from 2,000 to 3,800 m a.s.l. (Kinzikaeva 1988; Nowak and Nobis 2020). During the current research, plots of *Morinetum coulterianae* were found at the alpine elevations on the southern and south-eastern slopes around the Anzob Pass in the Hissar Mountains in western Tajikistan and on the western and north-western slopes of the Turkestan Mountains (Figure 6). *Morinetum coulterianae* is an alpine pasture in slightly rupicolous habitats, used for sheep grazing, noted between 2,595 and 3,360 m a.s.l. (mean ca. 2,904 m; Figure 4a), mainly at western and south-eastern aspects with an inclination of 20° to 40° (mean approximately 30°; Figure 4b). The number of vascular plant species ranges from 12 to 18 with a mean of 16 (Figure 5a). The mean cover value of the herb layer cover is about 55% ranging from 45% to 65% (Figure 5b). The vegetation is single-layered with no mosses found.

1.1.2. *Cousinia outichaschensis-Lepechiniella sarawschanica* comm. (cluster 2)

Diagnostic species: *Juniperus polycarpus* var. *seravschanica*, *Androsace caduca*, *Bunium persicum*, *Cousinia outichaschensis*, *Ephedra minuta*, *Gypsophila fedtschenkoana*, *Lepechiniella sarawschanica*, *Oxytropis lehmannii*, *Potentilla orientalis*, *P. pamiroalaica*, *Rochelia leiocarpa*, *Semenovia furcata*

Constant species: *Cousinia outichaschensis*, *Euphorbia cyrtophylla*, *Geranium regelii*, *Lepechiniella sarawschanica*, *Oxytropis lehmannii*, *Poa relaxa*, *Potentilla pamiroalaica*, *P. tephroleuca*

Dominant species: *Oxytropis lehmannii*

Floristic and habitat characteristics: The native range of *Cousinia outichaschensis* is Middle Asia, mainly mountainous areas of Tajikistan, Kyrgyzstan, Uzbekistan and Turkmenistan. This species occurs in Pamir-Alai on stony slopes and screes at an altitude of 1,700–3,600 m a.s.l. (Rasulova 1991; POWO 2023). *Lepechiniella sarawschanica* is endemic to north-western Tajikistan, reported from subalpine grasslands, juniper forests, steppes and cryophilous vegetation inhabiting stony, fine-grained slopes, at altitudes ranging from 2,500 to 4,200 m a.s.l. (Chukavina 1984). The community was recorded on rupicolous alpine habitats used as pastures mainly for sheep, located on gentle slopes of the Zeravshan Mountains (Figure 6), at altitudes of 2,850 to 2,950 m a.s.l. (Figure 4a). This vegetation prefers northern aspects with a low inclination of up to 15° (average approximately 10°, Figure 4b) or on flat ground. The total cover of herbs is approximately 65% (ranging from 60% to 70%; Figure 5b) and the species richness is low with 9 to 12 species per plot (average 10; Figure 5a).

1.1.3. *Smelowskio calycinae-Dracocephaletum scrobiculati* A. Nowak, S. Świerszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (cluster 3, Figure 7b)

Typus: Appendix 1, rel. 1.1.3, holotypus hoc loco.

Diagnostic species: *Dichodon cerastoides*, *Draba alticola*, *Dracocephalum scrobiculatum*, *Oxytropis savellanica*, *Poa hissarica*, *Richteria pyrethroides*, *Smelowskia calycina*, *Taraxacum minutilobum*

Constant species: *Aconogonon hissaricum*, *Cousinia franchetii*, *Dichodon cerastoides*, *Dracocephalum scrobiculatum*, *Eremogone griffithii*, *Erigeron cabulicus*, *Geranium regelii*, *Ligularia thomsonii*, *Lomatocarpa albomarginata*, *Nepeta podostachys*, *Oxytropis lehmannii*, *O. microsphaera*, *O. savellanica*, *Poa hissarica*, *Potentilla grisea*, *Taraxacum minutilobum*

Dominant species: *Dracocephalum scrobiculatum*, *Oxytropis savellanica*

Floristic and habitat characteristics: *Smelowskia calycina* is a relatively widespread species throughout the Pamir-Alai and Tian Shan ranges, as well as the Dzungarian Alatau, Tarbagatai, Hindu-Kush, growing mainly in subalpine to subnival belts (POWO 2023). In Tajikistan, it has been recorded in alpine grasslands, high alpine steppe and cryophilous subnival vegetation, on glacial moraines and scree, at altitudes of 2,500–4,900 m a.s.l. (Ovchinnikov 1978; Nowak and Nobis 2020). The range of *Dracocephalum scrobiculatum* is more restricted compared to the previous species and includes Tajikistan, Kyrgyzstan and Uzbekistan, with sites distributed across the Pamir-Alai and the western Tian Shan, inhabiting mainly gravelly slopes at altitudes of 2,900–3,800 m a.s.l. (Kochkareva 1986; POWO 2023). *Smelowskio calycinae-Dracocephaletum scrobiculati* forms rupicolous alpine swards that serve as pastures at the highest elevations of the Zeravshan and Hissar Mountains (Figure 6) at elevations of 3,320–3,640 m a.s.l. (mean approximately 3,500 m; Figure 4a). It covers gentle slopes with an average inclination of approximately 13° (Figure 4b), most often with a north-eastern and northern aspect. The number of vascular plant species ranges from 8 to 17 with a mean of 13 (Figure 5a). The cover of the herb layer ranges from 35 to 85%, the average is approximately 53% (Figure 5b).

1.1.4.a. *Phlomoidetum sarawschanicae* A. Nowak, S. Świerszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (cluster 4, Figure 7c)

Typus: Appendix 1, rel. 1.1.4a, holotypus hoc loco.

Diagnostic species: *Artemisia korovinii*, *Astragalus bornmuellerianus*, *Phlomoides sarawschanica*, *Scorzonera acanthoclada*

Constant species: *Artemisia dracunculus*, *A. korovinii*, *Astragalus bornmuellerianus*, *Cousinia franchetii*, *Eremogone griffithii*, *Euphorbia sarawschanica*, *Festuca valesiaca*, *Geranium regelii*, *Ligularia thomsonii*, *Nepeta podostachys*, *Phlomoides sarawschanica*, *Poa bucharica*, *P. litvinoviana*, *Taraxacum raikoviae*, *Veronica rubrifolia*, *Ziziphora pamiroalaica*

Dominant species: *Artemisia dracunculus*, *A. lehmanniana*, *Leucopoa karatavica*, *Ligularia thomsonii*, *Nepeta podostachys*

Floristic and habitat characteristics: This newly distinguished association, with the main diagnostic species *Phlomoidea sarawschanica* endemic to Tajikistan, occurs mainly in the Zeravshan Mountain range (Kochkareva 1986). It creates rupicolous alpine grasslands at an elevation of approximately 3,300–3,600 m a.s.l. (Figure 4a). They are poor pastures for sheep and goats. *Phlomoidea sarawschanicae* inhabits south-eastern and eastern slopes with an inclination of about 15°–25°. The cover of the herb layer ranges from 40 to 60%. Plots include from 13 to 19 species, with an average of approximately 15 (Figure 5).

1.1.4.b. *Phlomoidea sarawschanicae scorzoneretosum acanthocladae* A. Nowak, S. Świeraszcz, M. Nobis, G. Swacha et S. Nowak subass. nov. hoc loco (Figure 7d)
Typus: Appendix 1, rel. 1.1.4b, holotypus hoc loco.

Diagnostic species: *Scorzonera acanthoclada*

Constant species: *Scorzonera acanthoclada*

Dominant species: *Scorzonera acanthoclada*

Floristic and habitat characteristics: Within the typical association we observed patches dominated by *Scorzonera acanthoclada*, which characterise intensively grazed subalpine and alpine pastures. The presence of this species differentiates the subassociation *Phlomoidea sarawschanicae scorzoneretosum acanthocladae*, which inhabits the southern slopes of the Anzob Pass in the Hissar Mountains and the south-eastern slopes of the Zeravshan Mountains, at elevations between 3,140 and 3,240 m a.s.l. (Figure 4a). The inclination of slopes ranged from 10° to 35° (mean approximately 20°). The total cover of the herb layer reached values from 40 to 65%, with a mean of approximately 50% and the plots consisted of 14 to 18 species per plot (mean approximately 16 species) (Figure 5).

1.1.5. *Alopecuro himalaici-Veronicetum gorbunovii* A. Nowak, S. Świeraszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (cluster 6, Figure 7f)

Typus: Appendix 1, rel. 1.1.5, holotypus hoc loco.

Diagnostic species: *Alopecurus himalaicus*, *Aulacospermum roseum*, *Draba rosularis*, *Ferula karategina*, *Oxytropis michelsonii*, *Phlomoidea oreophila*, *Primula kaufmanniana*, *Ranunculus rufosepalus*, *Veronica gorbunovii*

Constant species: *Aconogonon hissaricum*, *Allium hymenorhizum*, *Alopecurus himalaicus*, *Aulacospermum roseum*, *Calamagrostis anthoxanthoides*, *Cousinia franchetii*, *Delphinium oreophilum*, *Eremogone griffithii*, *Festuca alaica*, *Geranium regelii*, *Helictotrichon hookeri*, *Koeleria pyramidata*, *Ligularia thomsonii*, *Myosotis alpina*, *Nepeta podostachys*, *Oxytropis michelsonii*, *Phlomoidea oreophila*, *Poa bucharica*, *P. bulbosa*, *Potentilla algida*, *P. tephroleuca*, *Veronica gorbunovii*

Dominant species: *Festuca alaica*, *Helictotrichon hookeri*, *Myosotis alpina*, *Potentilla algida*

Floristic and habitat characteristics: The range of *Veronica gorbunovii* is limited to Pamir-Alai in Tajikistan, while *Alopecurus himalaicus* has a wider distribution extending from Bulgaria eastwards through Iran and Afghanistan to Kashmir and southern Middle Asia (Ovchin-

nikov 1957; Kochkareva 1986; POWO 2023). *Alopecuro himalaici-Veronicetum gorbunovii* is an alpine grassland inhabiting the subalpine and alpine belts of Hissar and Zeravshan Mountains (Figure 6), at altitudes from 2,979 to 3,500 m a.s.l. (mean approximately 3,250 m; Figure 4a). Patches of this vegetation grow on the northern and north-eastern slopes with a moderate inclination of about 10°–35° (average approximately 25°, Figure 4b). The total cover of the herb layer is high and ranges between 55 and 90% (average approximately 78%; Figure 5b). The richness of vascular plant species is moderate, ranging from 10 to 24 taxa per plot (average 19; Figure 5a). The cover of the moss layer is scarce, reaching from 2 to 3%.

Tragacanthic vegetation

1.1.6. *Onobrychidetum echidnae* A. Nowak, S. Świeraszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (cluster 5, Figure 7e)

Typus: Appendix 1, rel. 1.1.6, holotypus hoc loco.

Diagnostic species: *Lomatocarpa steineri*, *Onobrychis echidna*, *Scrophularia griffithii*

Constant species: *Calamagrostis anthoxanthoides*, *Cousinia franchetii*, *Crepis pulchra*, *Eremogone griffithii*, *Erigeron cabulicus*, *E. seravschanicus*, *Euphorbia sarawschanica*, *Festuca alaica*, *F. olgae*, *Gastrolychnis longicarphora*, *Geranium regelii*, *Ligularia thomsonii*, *Lomatocarpa steineri*, *Morina coulteriana*, *Onobrychis echidna*, *Oxytropis lehmannii*, *Pedicularis krylovii*, *Poa bucharica*, *P. fragilis*, *Potentilla algida*, *Rhodiola heterodonta*, *Scrophularia griffithii*, *Taraxacum raikoviae*

Dominant species: *Helictotrichon hookeri*, *Onobrychis echidna*

Floristic and habitat characteristics: The range of *Onobrychis echidna*, the main diagnostic species, is limited to Middle Asia and Afghanistan (POWO 2023). The plant occurs in the Pamir-Alai and Tian Shan Mountains growing in the cryophilous steppe and cushion-tragacanth zones, on stony, rupicolous slopes, at altitudes of 2,400–3,900 m a.s.l. (Ovchinnikov 1978). *Onobrychidetum echidnae* develops on wind-swept passes and mountain tops in Middle Asia. It forms a sparse vegetation with a typical alpine cushion-tragacanthic physiognomy. This association was mainly recorded on the western slopes of the Anzob Pass, and one plot was found on the northern slope of the Peter the First Mountains (Figure 6) at heights ranging from 3,112 to 3,466 m a.s.l. (average approximately 3,345 m; Figure 4a) with varying inclinations from 10° to 35° (average approximately 18°; Figure 4b). The cover of the herb layer (including *O. echidna*) ranges from 45 to 80%, with a mean of 57% (Figure 5b). The species richness is moderate with 11 to 24 species per plot (average 16; Figure 5a).

Mesophilous steppic pastures of the subalpine belt in the Pamir-Alai Mountains

1.2. Alliance: *Artemision dracunculi* A. Nowak, S. Świeraszcz, M. Nobis, G. Swacha et S. Nowak all. nov. hoc loco

Typus: *Erigeronto seravschanici-Eremuretum hissarici* A. Nowak et al. ass. nov.

This alliance includes typical pasture vegetation of the subalpine belt of the western part of Middle Asia. The communities of this group develop in relatively moist habitats with a well-developed soil profile, most often in river and stream valley bottoms. Less frequently (e.g. the community of *Dracocephalum formosum*) they occupy terraces and flat places on mountain slopes. This alliance includes vegetation with fairly high productivity, especially in spring and early summer. However, the individual vegetation patches vary considerably in terms of density and species richness, with grazing as controlling factor. Phytocoenoses of *Artemisia dracunculifolia* inhabit lower-lying sites in relation to the vegetation of the other two alliances.

Diagnostic species: *Artemisia dracunculus*, *Poa bulbosa*

1.2.1. Community of *Dracocephalum formosum* (cluster 7, Figure 8a)

Diagnostic species: *Alchemilla hissarica*, *Allium weschniakowii*, *Astragalus tibetanus*, *Carex stenophylla* subsp. *stenophylloides*, *Cirsium esculentum*, *Convolvulus lineatus*, *Dracocephalum formosum*, *Euphrasia pectinata*, *Galium turkestanicum*, *Hordeum turkestanicum*, *Inula rhizocephala*, *Medicago lupulina*, *Myosotis cespitosa*, *Pedicularis verna*, *Seseli schrenkianum*

Constant species: *Alchemilla hissarica*, *Allium weschniakowii*, *Artemisia dracunculus*, *Astragalus tibetanus*, *Carex stenophylla* subsp. *stenophylloides*, *Cirsium esculentum*, *Convolvulus lineatus*, *Dracocephalum formosum*, *Euphrasia pectinata*, *Galium turkestanicum*, *Gentiana olivieri*, *Geranium collinum*, *Hordeum turkestanicum*, *Inula rhizocephala*, *Koeleria pyramidata*, *Ligularia thomsonii*, *Medicago lupulina*, *Myosotis cespitosa*, *Pedicularis verna*, *Petrorhagia alpina*, *Poa bulbosa*, *P. pratensis*, *Potentilla asiae-mediae*, *Seseli schrenkianum*, *Veronica rubrifolia*

Dominant species: *Dracocephalum formosum*

Floristic and habitat characteristics: This community was rarely recorded in the Fann Mountains in the vicinity of Sarytag at an elevation of 2,656 to 2,657 m a.s.l. (Figure 4a), within the range of the main diagnostic species *Dracocephalum formosum*, a Middle Asian narrow endemic plant limited to western Tajikistan (Kochkareva 1986; POWO 2023). It grows in gaps of juniper shrubland (Figure 6). The herb layer of this community ranges from 80 to 85% (Figure 5b). Between 17 and 20 species were recorded per relevé (Figure 5a). These areas are used as subalpine pastures for cows, goats and sheep.

1.2.2. Community of *Allium giganteum* (cluster 8, Figure 8b)

Diagnostic species: *Allium giganteum*, *Barbarea vulgaris* subsp. *arcuata*, *Corydalis darwasica*, *Elaeosticta hirtula*, *Ferula kuhistanica*, *Lamium album*, *Microthlaspi perfoliatum*, *Origanum vulgare* subsp. *gracile*, *Phlomis lehmannaiana*, *Polygonatum sewerzowii*, *Potentilla kulabensis*, *Rosa ecae*, *Silene vulgaris*, *Solenanthus circinnatus*, *Thermopsis alpina*, *Tulipa praestans*

Constant species: *Aconogonon coriarium*, *Allium giganteum*, *Asyneuma argutum*, *Barbarea vulgaris* subsp.

arcuata, *Corydalis darwasica*, *Delphinium oreophilum*, *Elaeosticta hirtula*, *Ferula kuhistanica*, *Lamium album*, *Microthlaspi perfoliatum*, *Nepeta podostachys*, *Origanum vulgare* subsp. *gracile*, *Pedicularis krylovii*, *Phlomis lehmannaiana*, *Poa bulbosa*, *P. pratensis*, *Polygonatum sewerzowii*, *Potentilla kulabensis*, *Prangos pabularia*, *Rosa ecae*, *Rumex paulsenianus*, *Silene vulgaris*, *Solenanthus circinnatus*, *Thermopsis alpina*, *Tulipa praestans*

Dominant species: *Allium giganteum*

Floristic and habitat characteristics: Apart from the community with *Dracocephalum formosum*, the group of subalpine pastures included patches of the community dominated by *Allium giganteum*, a species native to Tajikistan, Turkmenistan, Uzbekistan, Afghanistan and Iran, recorded in the south-western Pamir-Alai, and Kopet-Dagh (Ovchinnikov 1963; POWO 2023). They form relatively homogeneous stands dominated by *Allium giganteum* preferring humid and fertile habitats, occurring on the well-watered slopes near Kosh-Ob village (Figure 6). The final classification and assignment of this community requires more data about the *Allium giganteum* range.

1.2.3. *Erigeronto seravschanici-Eremuretum hissarici* A. Nowak, S. Świerszcz, M. Nobis, G. Swacha et S. Nowak ass. nov. hoc loco (cluster 9, Figure 8c)

Typus: Appendix 1, rel. 1.2.3, holotypus hoc loco.

Diagnostic species: *Agrostis canina*, *Astragalus corydalinus*, *Campanula glomerata*, *Eremurus hissaricus*, *Hypericum scabrum*, *Iris hoogiana*, *Rumex paulsenianus*

Constant species: *Aconogonon coriarium*, *Artemisia dracunculus*, *Astragalus corydalinus*, *Eremurus hissaricus*, *Erigeron seravschanicus*, *Euphorbia sarawschanica*, *Geranium regelii*, *Hypericum scabrum*, *Ligularia thomsonii*, *Nepeta podostachys*, *Pedicularis krylovii*, *Petrorhagia alpina*, *Poa bucharica*, *P. fragilis*, *Rumex paulsenianus*, *Semenovia dasycarpa*

Dominant species: *Artemisia dracunculus*, *Ligularia thomsonii*

Floristic and habitat characteristics: *Eremurus hissaricus* is an endemic plant of Tajikistan occurring in the western Pamir-Alai. It inhabits rupicolous and mesic slopes, at altitudes of 2,000–3,000 m a.s.l. (Ovchinnikov 1963). *Erigeron seravschanicus* has a wider range compared to the previous species, covering Middle Asian countries and Xinjiang (Kinzikaeva 1988; POWO 2023). The majority of the plots of *Erigeronto seravschanici-Eremuretum hissarici* were found on slopes around the Anzob Pass in the Hissar Mountains (Figure 6). Additionally, the association was recorded in the Fann Mountains on the slopes of the Imat Valley and near Sarytag at elevations between 2,518 and 3,078 m a.s.l. (Figure 4a). It appears indifferent to exposure, but often occurs on south-western, north and north-eastern aspects. The inclination of slopes ranged from 15° to 35° (mean approximately 24°; Figure 4b). The mean value of the herb cover is about 73% ranging from 50% to 90% (Figure 5b). The cover of the moss layer is low reaching up to 5%. The vegetation is moderately rich in species and composed of 11 to 22 taxa, approximately 15 per plot (Figure 5a).

Mesic grasslands of the alpine belt of Middle Asia

Alpine grasslands with *Festuca alaiica* and *Festuca kryloviana* (potential class rank)

Alpine grasslands with *Geranium saxatile* and *Festuca alaiica* (potential order rank)

Based on floristic composition, we propose a separate vegetation type at potential class rank for alpine grasslands with *Festuca alaiica* and *F. kryloviana*, and a potential order of alpine grasslands with *Geranium saxatile* and *Festuca alaiica*. The proposed syntaxonomic units are distributed in the alpine belt of continental Asia, centred in Middle and Central Asia, mainly the Pamir-Alai, Tian Shan and Altai.

2.1. Alliance: *Poo alpinae-Bistortion ellipticae* S. Świerszcz, M. Nobis, G. Swacha, S. Nowak et A. Nowak all. nov. hoc. loco

Typus: *Ligulario alpigenae-Solenanthesetum karategini* S. Świerszcz et al. ass. nov.

Poo alpinae-Bistortion ellipticae includes short alpine grassland vegetation that is a vicariant of the western Asian and European vegetation of the *Poion alpinae*. Communities of this alliance develop in relatively moist and fertile habitats of the alpine belt of many mountain ranges of Middle Asia, excluding the East Pamir. They are used as summer pastures for sheep and goats, less frequently for horses and yaks. Phytocoenoses of this alliance are characterised by the highest species richness and the highest cover of herb and moss layers, when compared to the vegetation of the other two alliances.

Diagnostic species: *Aconitum seravschanicum*, *Aconogonon coriarium*, *Aster alpinus* var. *serpentimontanus*, *Carex turkestanica*, *Cousinia stephanophora*, *Eremurus kaufmannii*, *Erigeron pseudoseravschanicus*, *Festuca amblyodes*, *Saussurea sordida*, *Stachyopsis oblongata*, *Stipa kirghisorum*

2.1.1. *Poo alpinae-Swertietum graciliflorae* S. Świerszcz, M. Nobis, G. Swacha, S. Nowak et A. Nowak ass. nov. hoc. loco (cluster 10, Figure 8d)

Typus: Appendix 1, rel. 2.1.1, holotypus hoc loco.

Diagnostic species: *Androsace darvasica*, *Anemonastrum protractum*, *Erigeron vicarius*, *Klasea algida*, *Minuartia litwinowii*, *Oxytropis immersa*, *Parrya pinnatifida*, *Poa alpina*, *Polygonum vvedenskyi*, *Potentilla crantzii*, *P. vvedenskyi*, *Swertia graciliflora*

Constant species: *Androsace darvasica*, *Anemonastrum protractum*, *Astragalus kokandensis*, *Aulacospermum roseum*, *Calamagrostis anthoxanthoides*, *Cousinia franchetii*, *Eremogone griffithii*, *Erigeron vicarius*, *Geranium regelii*, *Helictotrichon hookeri*, *Klasea algida*, *Ligularia thomsonii*, *Myosotis alpinus*, *Oxytropis immersa*, *Parrya pinnatifida*, *Pedicularis krylovii*, *Poa alpina*, *P. bucharica*, *Polygonum vvedenskyi*, *Potentilla grisea*, *P. vvedenskyi*, *Rhodiola heterodonta*, *Swertia graciliflora*

Dominant species: *Aconitum seravschanicum*, *Anemonastrum protractum*, *Ligularia thomsonii*

Floristic and habitat characteristics: *Poa alpina* is a widespread species, recorded in the Arctic zone and in

the mountains of Eurasia and North America (Ovchinnikov 1957; POWO 2023). In Tajikistan, it grows in alpine grasslands, fens and mires, and pastures at an altitude of 2,700–3,700 m a.s.l. (Nowak and Nobis 2020). The range of the second, main diagnostic species *Swertia graciliflora* is limited to Middle Asia and includes the Pamir-Alai and Tian Shan Mountains in Tajikistan, Kyrgyzstan, Uzbekistan and Xinjiang. It inhabits grasslands, fens and mires, moraines and snow-beds in the alpine belt at an altitude of 2,300–3,800 m a.s.l. (Chukavina 1984; Nowak and Nobis 2020; POWO 2023). *Poo alpinae-Swertietum graciliflorae* is a sward on moist habitats that was found on the slopes around the Anzob Pass in the Hissar Mountains (Figure 6) with an inclination of 20° to 30° (mean approximately 23.5°; Figure 4b). It grows at altitudes from 3,100 to 3,108 m a.s.l. (average approximately 3,105 m; Figure 4a) with varying slope exposures. The number of vascular plant species ranges from 10 to 25 with a mean of approximately 19 (Figure 5a). The total cover of the herb layer is high, ranging from 75 to 90% with a mean of 80% (Figure 5b). Noteworthy is the presence of mosses with cover ranging from 2 to 8% (about 3% on average).

2.1.2. *Astragalo alpini-Linetum olgae* S. Świerszcz, M. Nobis, G. Swacha, S. Nowak et A. Nowak ass. nov. hoc. loco (cluster 11, Figure 8e)

Typus: Appendix 1, rel. 2.1.2, holotypus hoc loco.

Diagnostic species: *Astragalus alpinus*, *Asyneuma argutum*, *Bupleurum exaltatum*, *Crepis darvasica*, *Dracocephalum integrifolium*, *Erysimum odoratum*, *Hedysarum tenuifolium*, *Leymus secalinus*, *Linum olgae*, *Myosotis stricta*, *Phleum phleoides*, *Potentilla pedata*, *Silene tachtensis*, *Thesium alatavicum*, *Thymus diminutus*, *Tragopogon turkestanicus*

Constant species: *Aconogonon coriarium*, *Allium hymenorhizum*, *Asyneuma argutum*, *Aulacospermum roseum*, *Bupleurum exaltatum*, *Carex turkestanica*, *Cousinia stephanophora*, *Eremurus kaufmannii*, *Erigeron pseudoseravschanicus*, *Erysimum odoratum*, *Euphorbia sarawshanica*, *Gentiana olivieri*, *Geranium regelii*, *Gypsophila cephalotes*, *Helictotrichon hookeri*, *Leymus secalinus*, *Ligularia thomsonii*, *Linum olgae*, *Myosotis stricta*, *Petrorhagia alpina*, *Phleum phleoides*, *Poa pratensis*, *Potentilla pedata*, *Saussurea sordida*, *Semenovia dasycarpa*, *Silene tachtensis*, *Stachyopsis oblongata*, *Stipa kirghisorum*, *Thesium alatavicum*, *Thymus diminutus*, *Tragopogon turkestanicus*

Dominant species: *Linum olgae*

Floristic and habitat characteristics: The native range of *Linum olgae* covers Tajikistan, Kyrgyzstan, Uzbekistan and Kazakhstan. It inhabits subalpine and alpine belts and grows on slopes with mesic to stony-rupicolous topsoils at the altitudes of 2,000–3,200 m a.s.l. (Ovchinnikov 1981; POWO 2023). *Astragalus alpinus* is more widely distributed, expanding throughout the mountain ranges of the northern hemisphere. In Middle and Central Asia it was recorded in the Pamir-Alai, Tian Shan, Dzungarian Alatau (Ovchinnikov 1981; POWO 2023). *Astragalo alpini-Linetum olgae* is a typical alpine mesic forb grassland found in the slopes of the Fann Mountains, Hissar

Mountains and the Peter the First Mountains (Figure 6). This association develops on slopes with an inclination of 5° to 45° (average approximately 19°; Figure 4b), most often with a north-eastern exposure, at altitudes from 2,759 to 3,063 m a.s.l. (average approximately 2,950 m; Figure 4a). Both the species richness of the plots of this association and the cover of the herbaceous layer are the highest among all phytocoenoses of the alpine grasslands. There are between 10 and 42 species per plot (average approximately 25; Figure 5a). The cover of the herb layer is from 65 to 100% (average about 84%; Figure 5b).

2.1.3. *Ligulario alpigenae-Solenanthesetum karategini* S. Świerszcz, M. Nobis, G. Swacha, S. Nowak et A. Nowak ass. nov. hoc. loco (cluster 12, Figure 8f)

Typus: Appendix 1, rel. 2.1.3, holotypus hoc loco.

Diagnostic species: *Alopecurus apiatus*, *Artemisia leucotricha*, *Astragalus lasiosemius*, *Bistorta elliptica*, *Helictotrichon tianschanicum*, *Ligularia alpigena*, *Pulsatilla campanella*, *Solenanthus karateginus*, *Taraxacum kovaevskiae*

Constant species: *Aconitum seravschanicum*, *Aconogonon coriarium*, *Alopecurus apiatus*, *Carex turkestanica*, *Cousinia stephanophora*, *Erigeron pseudoseravschanicus*,

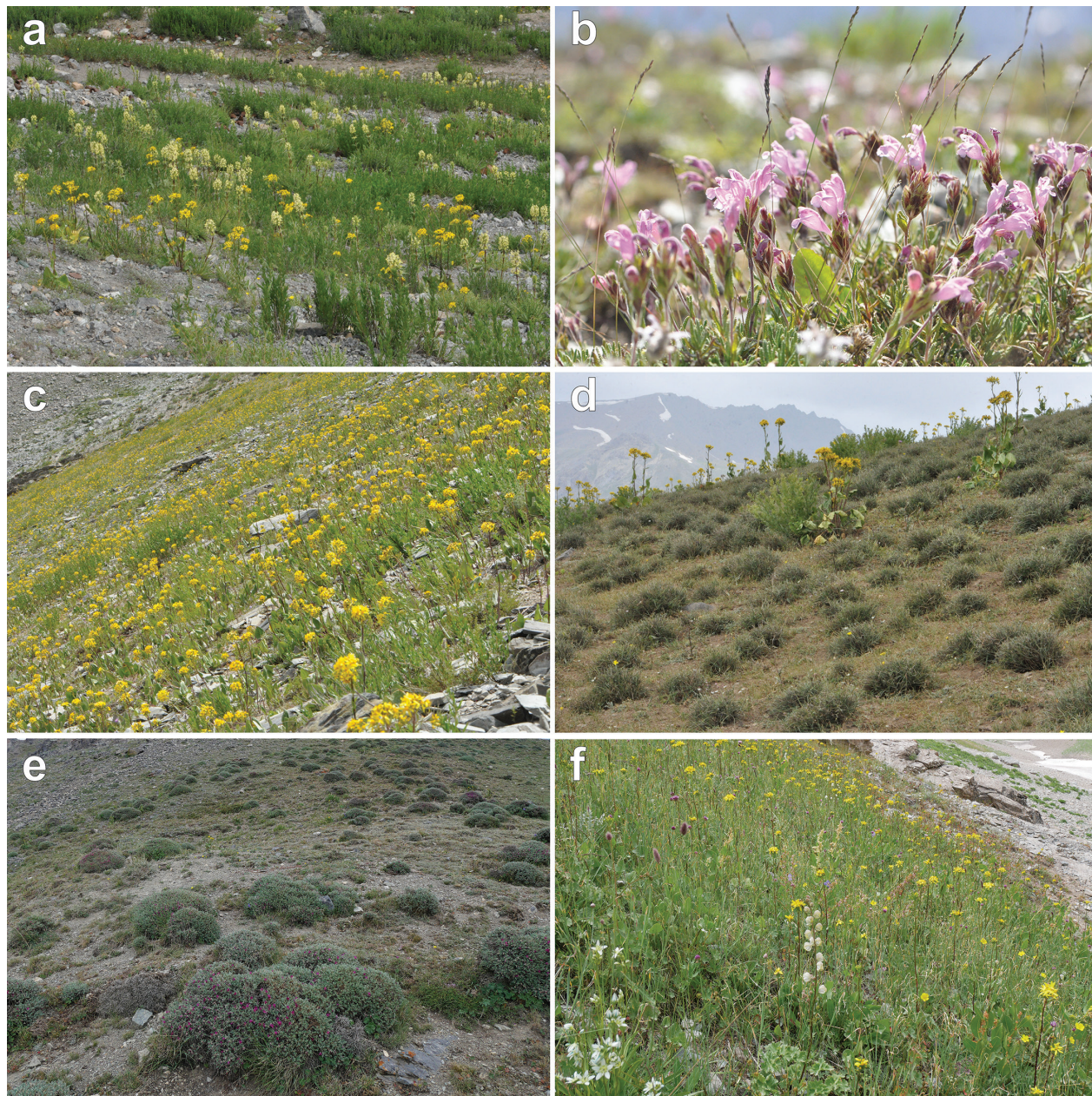


Figure 7. Photographs of the forb steppe and tragacanthic vegetation belonging to: a – *Morinetum coulterianae* in the Anzob Pass, Hissar Mountains; b – *Smelowskio calycinae-Dracocephaletum scrobiculati* in the Zeravshan Mountains, Kulikalon Plateau; c – *Phlomoidetum sarawschanicae* in the Zeravshan Mountains, near Anzob Pass; d – *Phlomoidetum sarawschanicae scorzoneretosum acanthocladae* in the Maychura Valley; e – *Onobrychidetum echidnae* in the Anzob Pass, Hissar Mountains; f – *Alopecuro himalaici-Veronicetum gorbunovii* in the Anzob Pass, Hissar Mountains (pictures a-d were taken by A. Nowak and e-f by S. Świerszcz).



Figure 8. Photographs of mesophilous steppic pastures of the subalpine belt and mesic grasslands of the alpine belt belonging to: a – community of *Dracocephalum formosum* in the Zeravshan Mountains; b – community of *Allium giganteum* near the Kosh-Ob village in Vakhsh Mountains; c – *Erigeronto seravschanici*-*Eremuretum hissarici* near the Anzob Pass, Hissar Mts; d – *Poo alpinae*-*Swertietum graciliflorae* near the Anzob Pass, Hissar Mts; e – *Astragalo alpini*-*Linetum olgae* in the Fann Mountains; f – *Ligularia alpigenae*-*Solenanthes karategini* near the Koshtegirmen village, the Peter the First Mountains (pictures a, b, d, e, f were taken by A. Nowak and c by S. Świerszcz).

Gentiana olivieri, *Geranium collinum*, *G. regelii*, *Helictotrichon tianschanicum*, *Leymus alaicus*, *Ligularia alpigena*, *Myosotis alpina*, *Nepeta podostachys*, *Pedicularis verae*, *Poa bucharica*, *P. litvinoviana*, *Potentilla asiae-mediae*, *Pulsatilla campanella*, *Rhodiola heterodonta*, *Saussurea sordida*, *Solenanthus karateginus*, *Stachyopsis oblongata*

Dominant species: *Aconogonon coriarium*, *Anthriscus glacialis*, *Artemisia leucotricha*, *Eremurus kaufmannii*, *Geranium collinum*, *G. regelii*, *Helictotrichon tianschanicum*, *Ligularia alpigena*, *Stachyopsis oblongata*, *Stipa kirghisorum*

Floristic and habitat characteristics: *Ligularia alpigena* is a perennial plant native to the mountain ranges of Afghanistan, Kazakhstan, Kyrgyzstan, Pakistan, Tajikistan, Uzbekistan and Xinjiang (Kinzikaeva 1988; POWO 2023). It grows on mesic soils on slopes at altitudes of 2,800–4,250 m a.s.l. (Kinzikaeva 1988). In Tajikistan it is a co-dominant species in mesic or wet alpine swards and pastures (Nowak and Nobis 2020). *Solenanthus karateginus* has a similar range, however limited to alpine habitats of south-eastern Kazakhstan, Kyrgyzstan, Tajikistan and Uzbekistan (Chukavina 1984; Nowak and Nobis 2020;

POWO 2023). The *Ligulario alpigenae-Solenanthes karategini* association is a typical alpine mesic grassland, denser and more productive than the *Astragalo alpini-Linetum olgae*. Plots of this phytocoenosis were found in the Peter the First Mountains, in the vicinity of the village of Koshtegirmen (Figure 6). They occupy mostly north-eastern slopes with an inclination of 3° to 35° (on average about 14°; Figure 4b), at altitudes from 2,893 m to 3,301 m a.s.l. (average ca. 3,160 m; Figure 4a). The species richness varies between 10 and 35 species (mean ca. 21; Figure 5a). The cover of the herb layer is relatively high and ranges from 70 to 95% (average about 85%; Figure 5b).

Discussion

The distinction of forb steppe (semi-dry subalpine grasslands) vegetation in Middle Asia

Transitional vegetation types between steppes and meadows are often reported from continental Asia. Meadow steppes of the southern Urals have been included in the class *Festuco-Brometea* and the suballiance *Phlomenion pungentis* Saitov et Mirkin 1991 (Demina 2014; Yamalov et al. 2014). This vegetation is characterised by species from *Salvia*, *Phlomis*, *Seseli*, *Stachys*, *Veronica* and *Erysimum* genera. The north China meadow steppe is distributed in the ecotone of forest-steppe and classified as ‘cool temperate-subhumid grasslands managed by grazing’ (Ren et al. 2008; Wang and Ba 2008). It is divided into three subtypes: bunch grass, rhizome grass and forb meadow steppes. Steppe meadows of the Pamir-Alai are physiognomically and structurally mostly similar to Chinese forb meadow steppes. Forb meadow steppes in China are distributed on the Hunlunbair plateau and to the east and west of the Great Xing’an Mountains. They are dominated by perennial plants, especially *Filifolium sibiricum*. Moreover, this vegetation is species-rich (18–27 species per 1 m²), and has moderately sparse vegetation cover (55–65%). Vegetation height is from 10 to 70 cm depending on environmental conditions. This steppe has a short growing season from early May to late September. The forb meadow steppe is traditionally used for sheep and goat grazing (Wang and Ba 2008). The transitional character of meadow steppe vegetation is determined by the subhumid and warm-temperate climatic conditions (Ren et al. 2008). These conditions are typical for the subalpine belt of the Pamir-Alai Mountains as well. In China, depending on the local climatic conditions, the alpine meadow steppe, the subhumid montane meadow steppe and the cool temperate-subhumid meadow steppe were distinguished (Ren et al. 2008). They are all treated as natural vegetation. However, they are closely related to the forest-steppe belt (warm temperate-subhumid forest steppe). In the Pamir-Alai, the upper limit of the juniper tree-stand to some extent resembles the forest-steppe physiognomy, and after tree removal and subsequent grazing forb steppe vegetation develops. This type of vegetation is found adjacent to typical alpine meadows, cryophilous steppes,

as well as tall-forb vegetation that develop in the juniper woodland belt; in its lower part mainly thermophilous communities of *Prangetea ulopterae*, and in the upper part other communities with a high proportion of *Eremurus* spp. and *Phlomoidea* spp. (Nowak et al. 2020, 2022a). The substitution of species within the same genera demonstrates this proximity to other habitats, like *Poa bulbosa* (steppe) – *P. bucharica* (meadow steppe), *Festuca valesiaca* (steppe) – *F. alaica* (forb steppe), *Phlomis bucharica* (steppe) – *P. oreophila* (forb steppe), *Geranium collinum* (meadow) – *G. regelii* (forb steppe), *Ligularia alpigena* (alpine meadow) – *L. thomsonii* (meadow steppe), *Scabiosa songorica* (forb steppe) – *S. alpestre* (alpine meadow), etc.

It is difficult to decide whether this type of vegetation should be called ‘steppe meadow’ or ‘meadow steppe’. It certainly depends on the local ratio of forbs to graminoids, if it is surrounded more by meadows or by steppes and also by the usage, more pastoral or hay making. In the case of the subalpine grasslands of the Pamir-Alai, most of these parameters and proportions are variable. Due to the fact that most of the territory of these mountains is intensively grazed and very rarely mown (Golovkova 1959), we think that the most appropriate name would be forb steppe, compared to steppe meadows and meadow steppes, in which mowing plays a major role. Attention should also be drawn to the fact that grasslands of Middle Asia are to a large extent arid, particularly in the upper and lower limits of their occurrence. They develop adjacent to cryophilous steppes in higher elevations and thermophilous steppes in lower elevations (Golovkova 1959). This is reflected in the composition of subalpine meadow steppes of the Pamir-Alai by the frequent and sometimes quite abundant occurrence of steppe plants like *Bromus* spp., *Festuca valesiaca* and *Stipa kirghisorum*.

Of course, it is difficult to floristically compare grasslands of the Pamir-Alai Mountains with the steppes of NE China or the southern Urals. The Pamir-Alai vegetation is clearly dominated by species with an Irano-Turanian range of distribution. This makes the subalpine forb steppes of Tajikistan similar to the so-called “montane steppes” of the Middle East and Armenia (Ambarlı et al. 2020). This montane steppe is considered a natural vegetation of wind-swept slopes from the timberline to subalpine zone (1800–3500 m a.s.l.; Kürschner 1986). According to the majority of authors this vegetation is dominated either by tragacanthic (thorny cushion-forming dwarf shrub form) or soft-leaved plant species (Zohary 1973; Djamali et al. 2011). This division is also clear in our dataset. The majority of species are soft-leaved, but several, particularly *Acantholimon* ssp., *Astracantha* spp., *Astragalus* ssp., *Morina* ssp. are typical for thorn-cushion vegetation. An example of this type, developing on wind-swept habitats on mountain tops, passes and steep slopes is *Onobrychidetum echidnae*. Such tragacanthic shrubby vegetation is one of the most important features of high mountain zones throughout the Middle East, SW and Middle Asia (Zohary 1973; Frey and Probst 1986). The most common genera within this vegetation are *Acantholimon*, *Acanthophyllum*, *Astracantha*, *Astragalus*, *Arenaria*, *Gypsophila*,

Minuartia, *Onobrychis*, and *Ononis*. However, the majority of our plant communities are forb-rich and dominated by soft-leaved species from the genera *Aconogonon*, *Campanula*, *Geranium*, *Ligularia*, *Nepeta* and others. In the landscape of these forb steppes, solitary trees of junipers, or some patches of juniper shrubs (*Juniperus polycarpus*) are still present. These are remnants of the former sparse juniper forests and krummholz vegetation that declined after the introduction of intensive grazing and steppe nomadic culture in the region in 5000 BP (Tolstov et al. 1963; Frachetti 2012; Wagner et al. 2020).

Subalpine and alpine forb steppes of the Pamir-Alai can also be compared to some extent to the Mongolian montane meadow steppes that cover a large area of hilly lands between alpine mountain meadows and typical dry steppes (Pfeiffer et al. 2020). This vegetation is also related to forests and the forest-steppe ecotone. The generic composition of the diagnostic species (*Carex pediformis*, *Festuca sibirica*, *Helictotrichon schellianum*, *Koeleria macrantha*, *Stipa sibirica*, *S. grandis*, and *Thalictrum petaloideum*) is quite similar to the Middle Asian forb steppe vegetation.

Subalpine and alpine forb steppe varies according to habitat moisture, air humidity and grazing intensity. The aridity coefficient (the ratio of precipitation to evapotranspiration) can vary over quite a wide range and therefore this vegetation type will resemble more typical meadows in the wetter Hissar or Darwaz Mountains, while in the drier Zeravshan or Turkestan Mountains it will be more like mountain steppes. Additional data from the other mountainous regions of the Irano-Turanian province, in particular the Kopet-Dagh, Hindu-Kush, Zagros and Alborz, would provide insight into the diversity of this type of vegetation. However, there is no doubt that it is a very distinct syntaxon, resembling to some extent meadows and tall-forbs of the *Mulgedio-Aconitetea* in Europe (associated with montane forests with a high proportion of forbs) and remaining in a close dynamic and floristic relationships with juniper forests, as well as with mountain steppes and alpine meadows of Middle Asia.

Comparisons of the forb steppes of Tajikistan to the surrounding areas

North of Tajikistan, in western Tian Shan, subalpine forb steppes are found mainly in the upper montane and subalpine belts of Fergana, Talas, Pskem, Chatkal and Alai Mountains. Although our analyses, performed on a dataset of about 800 relevés (unpubl.), showed that they differ quite significantly in terms of floristic composition (high endemism of floras), they are very similar regarding structure and physiognomy. Towards the north, they become increasingly similar to the Euro-Siberian grasslands and they are dominated by *Bromus inermis*, *Dactylis glomerata*, *Galium verum*, *Poa angustifolia* and *Veronica spuria* (Wagner 2009). In the subhumid southern slopes of the northern and western Tian Shan, mesic montane and subalpine meadows can thrive at approximately 1,400–3,000 m a.s.l. on deep loamy soils (Korovin 1962; Wagner 2009; Wagner

et al. 2020). In some higher areas, they form parkland with *Juniperus polycarpus* var. *seravschanica*, *J. semiglobosa* or *Picea schrenkiana* showing the close relationship with forest and krummholz vegetation, as has been recorded from the Pamir-Alai (Korovin 1962). Montane meadows are a secondary vegetation of forests that were removed in favor of pastures (Wagner 2009). Since the last century, these meadows have been used mostly for hay making (Korovin 1962; Karmysheva 1982).

Additional data on mountain meadows are available for more humid areas in SE Kazakhstan in the Ala-Tau Mountains (Dimeyeva et al. 2016). Generally these data represent the alpine grasslands which are composed mainly of *Alopecurus pubescens*, *Dracocephalum imberbe*, *Geranium saxatile*, *Helictotrichon pubescens*, *Pedicularis kryloviana* and *Phlomis oreophila*. Their structure is not as open as the Pamir-Alaian meadow steppes and the proportion of Euro-Siberian species is much higher. However, from the lower montane belt, on chernozem and kastanozem soils, the steppe meadow is reportedly composed of xerophilic steppe bunch grasses (*Festuca valesiaca*, *Poa stepposa*, *Stipa capillata*), and mesophilic, xeromesophilic and mesoxerophilic species like *Achillea millefolium*, *Alfredia nivea*, *Bromus inermis*, *Elytrigia repens*, *Fragaria viridis*, *Nepeta pannonica*, *Salvia deserta*, *Thymus marschallianus* and *Verbascum orientale*. Despite a lower proportion of Irano-Turanian taxa, this type of vegetation should be considered as very similar to the subalpine forb steppes of Pamir-Alai and probably included in the same order. It is not as species rich, having 7 to 26 species per plot, in comparison to our data (8–45, 35 on average). The inclusion of this Ala-Tau Mountains vegetation into *Nepetetalia podostachyos* requires further research.

From the Fergana Mountains, there are data on two vegetation types similar to the subalpine Irano-Turanian forb steppe. The first vegetation type corresponds to subalpine pastures in Arslanbob county formed by a number of tall perennial herbs like *Aconogonon coriarium*, *Ligularia thomsonii* or *Prangos pabularia*. The second one exhibits a more alpine character with *Aster alpinus*, *Aulacospermum simplex*, *Heracleum dissectum* and *Phlomis oreophila* as diagnostic taxa (Borchardt et al. 2011). Despite the fact that the first community is to some extent related to tall-forbs, and the second to alpine meadows, both share a number of common species with Tajik forb steppes, including *Asyneuma argutum*, *Campanula glomerata*, *Lamium album* and *Stachyopsis oblongata*. Unfortunately, both vegetation types have a rather anthropogenic character, as the whole area is subjected to very significant human impacts (Borchardt et al. 2011). That is why the average species richness per plot and the total species pool are lower within the Arslanbob area.

Unfortunately, additional studies from neighbouring regions that could be used for comparisons are extremely scarce. From Kopet-Dagh, the meadows or meadow steppes are even not mentioned (e.g. Memariani et al. 2016). Memariani et al. (2016) only discuss mountain steppe from the middle montane belt, with thorn-cushion communities usually composed of *Onobrychis cornuta*,

Acantholimon spp., *Acanthophyllum* spp. and tragacanthic *Astragalus*. It is worth noting that in Kopet-Dagh the endemism rate is high, including many *Allium*, *Alyssum*, *Astragalus*, *Cousinia*, *Euphorbia* and *Silene* species, and comparable to the Pamir-Alai.

Due to the high degree of Irano-Turanian endemism, it is difficult to compare our results with vegetation data from Iran. Apart from the fact that phytosociological studies of alpine and subalpine grasslands have not been completed for Iran, differences in the floristic composition of the communities recorded in both areas are significant. Comparing, for example, the data from the subalpine and upper montane grasslands of Mount Tushal, only *Arenaria serpyllifolia*, *Bupleurum exaltatum*, *Cerastium inflatum*, *Dactylis glomerata* and *Lappula sinaica* are common to the Pamiro-Alaian grassland steppe (Akhani et al. 2013).

It is equally difficult to compare the forb steppe vegetation of the subalpine belt of the Pamir-Alai with the Anatolian vegetation of the class *Astragalo microcephali-Brometea tomentelli* Quézel 1973 - thorn-cushion communities, dwarf-shrublands and gappy subalpine limestone swards (Parolly 2004). This vegetation type has obvious habitat and structural similarities, although a completely different floristic composition. Perhaps both groups are geographic vicariants, the former with a Middle Asian, the latter with an Eastern Mediterranean distribution.

Unfortunately, no phytosociological data are currently available from the Hindu-Kush and western Himalayan ranges and therefore no detailed comparisons are possible at present. The occurrence of *Geranium himalayense* (which is treated by some sources as a synonym of *G. regelii*) over a large area of this region shows that forb-rich subalpine grasslands in the upper forest zone do occur in these areas. In addition, it is important to note the ambiguities in taxonomic treatment in the genus *Geranium*, section *Recurvata* (Troshkina 2021). *Geranium regelii*, which is one of the main diagnostic species of the forb steppe of the Pamir-Alai, is treated as a synonym of *G. himalayense* by POWO (2023), WFO (2023), and the eFlora of China (http://www.efloras.org/flora_page.aspx?flora_id=2; accessed 27 January 2023). According to other sources, for example Cherepanov (1995), which we follow here, it is an accepted species. An additional complication is that the identification of *Geranium collinum* is unclear in relation to *G. regelii* and *G. saxatile*.

Towards establishing a new class for the subalpine forb steppe in Middle Asia

One of the most important features of a distinct vegetation class is its evolutionary history and having its own exclusive endemics. It should also have a well-defined ecology and sufficient biological content (Pignatti et al. 1995). The subalpine and alpine forb steppe in Pamir-Alai is characterised by a quite rich floristic composition per plot as well as a large species pool. In our dataset from Tajikistan we recorded 336 species in 149 relevés. Although this type of vegetation has not been distinguished before, studies

of the flora of Tajikistan (Ovchinnikov 1957, 1963, 1968, 1975, 1978, 1981; Chukavina 1984; Kochkareva 1986; Kinzikaeva 1988; Rasulova 1991) indicate that there are almost 200 species typical of subalpine meadows (occurring in forb steppe between altitudes of 2,300 and 3,100 m a.s.l.). This group includes more than 30 endemic species, including *Allium glaciale*, *A. paulii*, *Astomaea galiocarpa*, *Astragalus irinaea*, *A. macronyx*, *A. pauperiformis*, *Cicerbita zeravschanica*, *Corydalis macrocentra*, *Cousinia macilentia*, *C. tomentella*, *Dianthus pamiralaicus*, *Fragaria bucharica*, *Gagea capusii*, *G. minutissima*, *Galatella hissarica*, *Hedysarum cisdarvasicum*, *Iris parvula*, *I. tadshikorum*, *I. zaprjagajevii*, *Poa bactriana*, *Primula baldshuanica*, *P. lactiflora*, *Silene erubescens*, *Taraxacum comitans*, and *T. nuratavicum*. This vegetation type is not only species rich and unique, but also has a distinctive use, which is relatively intensive grazing. The most important animals that graze on the subalpine and alpine forb steppes are sheep and goats. Cows are occasional grazers, but mainly in relation to patches of vegetation of the *Artemision dracunculi* occupying the lower valley sections along watercourses. The floristic composition of forb steppe potentially originated during a particular evolutionary episode that occurred in Middle Asia in the Eocene-Miocene and was related to aridisation and the Paratethys Sea retreatment. The palaeo-šhiblyak (a single Tertiary vegetation formation) evolved, and consequently juniper stands, today's šhiblyak and subalpine steppes and tall-forbs, all with a very distinct taxonomic composition. The specific geographic distinction and environmental conditions that create the refuge and cradle for a number of species are important when considering the establishment of a new vegetation class (Kamelin 1973; Loidi 2020).

Conclusion

Our study has expanded the knowledge of the open habitat vegetation in the Pamir-Alai Mountains and contributed to the consistent hierarchical classification of meadow, tall-forb, and steppe communities in the eastern Irano-Turanian region (Nowak et al. 2016a, 2018, 2020; Swacha et al. 2023). The syntaxonomic position of some of the distinguished communities is still unclear, hence further research on the floristic composition and habitat requirements for the vegetation of Middle Asia is required, especially in the vegetation of alpine and subalpine grasslands of Hindu-Kush, Kopet-Dagh and Tian Shan.

However, subalpine and alpine forb steppe, which has a dynamic ecological relationship with the upper zone of juniper woodlands, cryophilous steppes and cushion-tragacanthic vegetation, is a very interesting and distinct grassland type in Middle Asia. To some extent it can be compared to the transitional steppe meadows of *Galietaia veri* Mirkin et Naumova 1986 which grow inbetween the *Molinio-Arrhenatheretea* and *Festuco-Brometea* in Euro-Siberia (Mucina et al. 2016). Like the meadow steppes of China or southern Siberia (Yamalov et al. 2003; Tishkov et al. 2020), they should be studied in detail and distinguished at class

or order level. It will be important to assess the relationship of this vegetation type to the *Astragalo microcephali-Brometea tomentelli* known from Anatolia and to other montane steppes from the Middle East. A final decision on whether the forb steppes of Middle Asia should be distinguished at the class or order rank requires further surveys and careful comparative research. It will also be necessary to extend the analyses to the rest of the region, particularly tall-forb vegetation, steppes and alpine grasslands. In the near future, analyses and descriptions of syntaxa from these similar habitats will be completed and it will then be possible to present a comprehensive vegetation classification system for Tajikistan and neighbouring areas. We would like to undertake further investigations in order to describe the classes of forb steppes with *Eremogone griffithii* and *Nepeta podostachys* under the name *Eremogono griffithii-Nepetetea podostachyos*, and alpine grasslands with *Festuca alaica* and *F. kryloviana* under the name *Festucetea alaico-krylovianae*.

Significant areas of grassland vegetation in Middle Asia provide an important source of forage for livestock. A serious threat to grassland biodiversity in this region is posed by both climate change and land use intensification. Further research on grasslands in this part of the world is required to understand the impact of these changes.

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Data availability

Primary data are stored in the Vegetation of Middle Asia database (<http://www.givd.info/ID/AS-00-003>; Nowak et al. 2017) which are available in the Global Vegetation Database sPlot (Bruehlheide et al. 2019).

Author contributions

AN, MN and SŠ planned the research, conducted the field sampling and identified the plant species. AN, SŠ and GS performed statistical analyses. SN prepared the analytical tables, while all the authors participated in the writing of the manuscript and verification of plants in herbarium.

Acknowledgements

The authors would like to thank Firuza Illarionova from the Dushanbe Nature Protection Team for assistance and help in organising the expeditions. The project was partially supported by the National Science Centre, Poland, no. 2019/35/B/NZ8/03358.

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- 1.1.3. *Smelowskio calycinae-Draconocephalium scrobiculati* ass. nov.**
Holotypus: 9 July 2021; 68.24014 °E; 39.26333 °N; 3617 m a.s.l.; aspect NE; slope 25°; plot area 10 m²; cover herb layer 40%.
Herb layer: *Cousinia franchetii* 2, *Draconocephalum scrobiculatum* 2, *Festuca alaica* 1, *Oxytropis savellanica* 1, *Poa litvinoviana* 1, *Richteria pyrethroides* 1, *Taraxacum minuslobum* 1, *Draba alticola* +, *Eremogone griffithii* +, *Erigeron cabulicus* +, *Geranium regelii* +, *Poa hissarica* +, *Rhodiola heterodonta* +, *Smelowskia calycina* +. [relevé number in Suppl. material 1: 20]
- 1.1.4.a. *Phlomoidetum sarawschanicae* ass. nov.**
Holotypus: 9 July 2021; 68.24319 °E; 39.26071 °N; 3396 m a.s.l.; aspect SE; slope 25°; plot area 10 m²; cover herb layer 60%.
Herb layer: *Ligularia thomsonii* 3, *Artemisia dracunculus* 2, *Nepeta podostachys* 2, *Cousinia franchetii* 1, *Phlomoides sarawschanica* 1, *Poa litvinoviana* 1, *Ziziphora pamiroalaica* 1, *Aconogonon coriarium* +, *Carduus nutans* +, *Cousinia pan-nosa* +, *Eremogone griffithii* +, *Euphorbia sarawschanica* +, *Festuca valesiaca* +, *Geranium regelii* +, *Leucopoa karatavica* +, *Poa bucharica* +. [relevé number in Suppl. material 1: 31]
- 1.1.4.b. *Phlomoidetum sarawschanicae scorzoneretosum acanthocladae* subass. nov.**
Holotypus: 9 July 2021; 68.25277 °E; 39.25765 °N; 3166 m a.s.l.; aspect SE; slope 15°; plot area 10 m²; cover herb layer 40%.
Herb layer: *Artemisia lehmanniana* 3, *Leucopoa karatavica* 2, *Astragalus bactrianus* 1, *Nepeta podostachys* 1, *Phlomoides sarawschanica* 1, *Ziziphora pamiroalaica* 1, *Artemisia dracunculus* +, *Bromus paulsenii* +, *Cousinia franchetii* +, *Festuca valesiaca* +, *Holosteum glutinosum* +, *Ligularia thomsonii* +, *Polygonum fibrilliferum* +, *Scorzonera acanthoclada* +, *Veronica rubrifolia* +. [relevé number in Suppl. material 1: 40]
- 1.1.5. *Alopecuro himalaici-Veronicetum gorbunovii* ass. nov.**
Holotypus: 7 July 2021; 68.3338 °E; 39.09474 °N; 3336 m a.s.l.; aspect NE; slope 20°; plot area 10 m²; cover herb layer 70%.
Herb layer: *Helictotrichon hookeri* 3, *Myosotis alpina* 2, *Potentilla tephroleuca* 2, *Aulacospermum roseum* 1, *Cousinia franchetii* 1, *Delphinium oreophilum* 1, *Festuca alaica* 1, *Geranium regelii* 1, *Koeleria pyramidata* 1, *Oxytropis michelsonii* 1, *Pedicularis krylovii* 1, *Poa bucharica* 1, *Veronica gorbunovii* 1, *Alopecurus himalaicus* +, *Eremogone griffithii* +, *Leymus alaicus* +, *Ligularia thomsonii* +, *Nepeta podostachys* +, *Paraquilegia caespitosa* +, *Potentilla algida* +, *Ranunculus rufosepalus* +, *Tragopogon turkestanicus* +. [relevé number in Suppl. material 1: 71]
- 1.1.6. *Onobrychidetum echidnae* ass. nov.**
Holotypus: 13 July 2021; 68.86781 °E; 39.08468 °N; 3423 m a.s.l.; aspect W; slope 15°; plot area 10 m²; cover herb layer 45%.

Appendix 1. Nomenclature type relevés for the new associations described in this study

Type relevés:

1.1.1. *Morinetum coulterianae* ass. nov.

Holotypus: 28 June 2014; 69.875 °E; 39.41083 °N; 2560 m a.s.l.; aspect W; slope 30°; plot area 10 m²; cover herb layer 65%.

Herb layer: *Morina coulteriana* 3, *Bromus lanceolatus* 1, *Eremopoa persica* 1, *Hyssopus seravschanicus* 1, *Lappula squarrosa* 1, *Poa relaxa* 1, *Scorzonera inconspicua* 1, *Veronica capillipes* 1, *Astragalus pteroccephalus* +, *Cicer macracanthum* +, *Cirsium incanum* +, *Galium spurium* +, *Lipskya insignis* +, *Papaver pavoninum* +, *Trigonella gontscharovii* +. [relevé number in Suppl. material 1: 3]

Herb layer: *Onobrychis echidna* 3, *Potentilla algida* 2, *Geranium regelii* 1, *Poa fragilis* 1, *Crepis pulchra* +, *Euphorbia sarawschanica* +, *Festuca olgae* +, *Ligularia thomsonii* +, *Morina coulteriana* +, *Pedicularis krylovii* +, *Phlomisoides sarawschanica* +, *Scrophularia griffithii* +, *Taraxacum raikoviae* +. [relevé number in Suppl. material 1: 49]

1.2.3. *Erigeronto seravschanici-Eremuretum hissarici* ass. nov.

Holotypus: 13 July 2021; 68.87695 °E; 39.06791 °N; 3078 m a.s.l.; aspect SW; slope 20°; plot area 10 m²; cover herb layer 70%.

Herb layer: *Artemisia dracunculus* 3, *Ligularia thomsonii* 3, *Astragalus corydalinus* 2, *Eremurus hissaricus* 1, *Nepeta podostachys* 1, *Prangos pabularia* 1, *Aconogonon coriarium* +, *Adonis turkestanica* +, *Erigeron seravschanicus* +, *Euphorbia sarawschanica* +, *Geum kokanicum* +, *Hypericum scabrum* +, *Iris hoogiana* +, *Jurinea baldschuanica* +, *Poa bucharica* +, *Polygonum aviculare* +. [relevé number in Suppl. material 1: 85]

2.1.1. *Poo alpinae-Swertietum graciliflorae* ass. nov.

Holotypus: 13 July 2021; 68.82547 °E; 39.08888 °N; 3108 m a.s.l.; aspect SW; slope 25°; plot area 10 m²; cover herb layer 80%; cover moss layer 5%.

Herb layer: *Anemonastrum protractum* 2, *Helictotrichon hookeri* 2, *Ligularia thomsonii* 2, *Aconogonon coriarium* 1, *Androsace darvasica* 1, *Calamagrostis anthoxanthoides* 1, *Geranium regelii* 1, *Myosotis alpina* 1, *Poa alpina* 1, *Potentilla grisea* 1, *Potentilla vvedenskyi* 1, *Swertia graciliflora* 1, *Astragalus kokandensis* +, *Cousinia franchetii* +, *Eremogone griffithii* +, *Erigeron vicarius* +, *Gastrolychnis longicarpophora* +, *Klasea algida* +, *Leymus alaicus* +, *Minuartia litwinowii* +, *Oxytropis immersa* +, *Poa bucharica* +, *Polygonum vvedenskyi* +, *Potentilla algida* +, *Rhodiola heterodonta* +. [relevé number in Suppl. material 1: 95]

2.1.2. *Astragalo alpini-Linetum olgae* ass. nov.

Holotypus: 16 July 2021; 71.43625 °E; 39.21032 °N; 2979 m a.s.l.; aspect NE; slope 20°; plot area 10 m²; cover herb layer 90%.

Herb layer: *Linum olgae* 3, *Hedysarum tenuifolium* 2, *Helictotrichon hookeri* 2, *Aconogonon coriarium* 1, *Allium hymenorhizum* 1, *Cousinia stephanophora* 1, *Dictamnus albus* 1, *Erigeron cabulicus* 1, *Gentiana olivieri* 1, *Geranium regelii* 1, *Koeleria pyramidata* 1, *Leymus secalinus* 1, *Ligularia thomsonii* 1, *Myosotis stricta* 1, *Poa pratensis* 1, *Saussurea sordida* 1, *Stachyopsis oblongata* 1, *Thymus minutus* 1, *Astragalus alpinus* +, *Astragalus macropterus* +, *Asyneuma argutum* +, *Bupleurum exaltatum* +, *Carex turkestanica* +, *Crepis pulchra* +, *Eremurus kaufmannii* +, *Erigeron pseudoseravschanicus* +, *Euphorbia sarawschanica* +, *Festuca amblyodes* +, *Oxytropis lehmannii* +, *Petrophragma alpina* +, *Phleum phleoides* +, *Potentilla pedata* +, *Silene tachtensis* +, *Stipa kirghisorum* +. [relevé number in Suppl. material 1: 109]

2.1.3. *Ligulario alpigenae-Solenanthesetum karategini* ass. nov.

Holotypus: 15 July 2021; 71.43342 °E; 39.19788 °N; 3170 m a.s.l.; aspect NE; slope 10°; plot area 10 m²; cover herb layer 80%.

Herb layer: *Geranium regelii* 2, *Ligularia alpigena* 2, *Myosotis alpina* 2, *Pulsatilla campanella* 2, *Aconogonon coriarium* 1, *Carex stenophylla* subsp. *stenophylloides* 1, *Cousinia stephanophora* 1, *Poa litvinoviana* 1, *Saussurea sordida* 1, *Stachyopsis oblongata* 1, *Bistorta elliptica* +, *Carex turkestanica* +, *Erigeron cabulicus* +, *Erigeron pseudoseravschanicus* +, *Gastrolychnis longicarpophora* +, *Leymus alaicus* +, *Nepeta podostachys* +, *Oxytropis lehmannii* +, *Rhodiola heterodonta* +, *Seseli karateginum* +, *Solenanthes karateginus* +, *Veronica gorbunovii* +. [relevé number in Suppl. material 1: 134]

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Supplementary material

Supplementary material 1

The analytic table of Irano-Turanian subalpine forb steppe and alpine grasslands in the Pamir-Alai Mountains.

Link: <https://doi.org/10.3897/VCS.102634.suppl1>