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# Vegetation Diversity of Screes and Taluses of The Pamir and South-Western Tian Shan in Middle Asia

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**Abstract** This paper presents the results of phytosociological research on scree vegetation of the Pamir and south-western Tian Shan. We collected 222 phytosociological relevés during field studies conducted in 2015–2019, applying the Braun-Blanquet approach. We identified 21 plant communities on mobile and stabilized screes of colluvial cones, aprons and fans, inhabiting mainly the montane and alpine belts in several ranges (e.g. Peter the First, Alichur, Shugnan, Shachdarian, Darvaz, Rushan, Vanch, Fergana, Kyrgyz and Terskey ranges). As a result we provide the first comprehensive hierarchical syntaxonomic synopsis of scree communities at montane and alpine elevations in the eastern Middle Asia. The collected vegetation relevés represent the majority of the variation among the phytocoenoses of gravel, pebble, cobble and rock block slides and screes in the montane and alpine belts. As a result of field studies and Twinspan analyses, nine associations were identified on screes of the Pamir and western Tian Shan. All these communities were assigned to the *Sileno brahuicae-Lactucetalia orientalis* Nowak et al. 2021. Additionally, within the nitrophilous compact gravel screes one subassociation of *Corydalidetum kashgaricae trigonelletosum gontscharovii* was distinguished. In the most arid zone two additional plant associations and one subassociation were identified in gravelly semi-deserts zone. The main factors determining the species composition of the studied associations are scree mobility, rock particle size, elevation above sea level and slope inclination. Our research revealed considerable diversity of scree habitats of montane and alpine belts what might be astonishing regarding harsh environment of this mountainous territory. However, a great number of lineages that evolved here and particularly rich species pool of this habitat in Middle Asia facilitate remarkable diversity among vegetation of taluses and screes. The distinctiveness of species composition is additionally enhanced by high degree of endemism of chasmophytic habitats in the eastern part of Middle Asia. Despite recent developments, the prominent chasmophytic vegetation of Middle Asia still needs thorough studies focused on its relationship to semi-desert, tall-forb and petrophytic communities of high mountains of the Pamir, Hindu-Kush, Kunlun and Central Tian Shan.

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**Keywords** *Artemisio-Berberidetea* · Colluvial cones · Montane and alpine vegetation · Chasmophytes · Syntaxonomy · Tajikistan · Kyrgyzstan

## Introduction

The territory of Tajikistan encompasses a vast area of mountain ranges and highly elevated plateaus in the Pamir-Alai mountain system (also called Hissaro-Alai). Almost half of the country's area is made up of bare, rocky land dominated by rupicolous habitats. Tajikistan has very diverse climate, landscape and habitat conditions (Nobis et al. 2020; Nowak et al. 2020b). Located between the continental Asian deserts in the west and south, and the great mountain ranges of Tian Shan, Kunlun, Hindu-Kush and Karakorum in the north, east and south-east, having all vertical belts from hot to permafrost deserts, it offers an outstanding range of biotopes for plants and vegetation. This extraordinary complexity of climatic influences, phytogeographical divisions and diverse land geomorphology affect the floristic composition and richness of plant species of this country. Despite that the territory of Tajikistan is still far from being sufficiently investigated in terms of floristics and taxonomy, one can approximately assess that the vascular flora of Tajikistan consists of ca 4,300 species assigned to 116 families (Nowak et al. 2020c). Approximately 30% of vascular plant species known from Tajikistan are generally accepted endemics of the country (Nowak et al. 2011). Chasmophytic habitats in Tajikistan, a country with a high degree of isolation and a position within the borderland of different phytogeographical regions, are particularly species-rich (composing more than 35% of the country's flora) and additionally act as a refuge for many narrowly distributed plants. More than half of them inhabit scree and rocky habitats. Scree phytocoenoses also harbour the most numerous representation of exclusive endemics of this territory (Nowak et al. 2011). Because of this considerable floristic richness, the mountains of Middle Asia have been recognized by Conservation International as one of the 35 so-called hotspots of biodiversity (Mittermeier et al. 2005) and as one of the eleven most important focal points of scientific studies and conservation efforts (Giam et al. 2010).

The vegetation of taluses and screes has been studied continuously in recent decades, mainly in Europe and in Southwest and Central Asia. Research conducted in the Carpathians and the Sudetes Mts (e.g. Valachovič et al. 1997; Kosinski 2001; Sanda et al. 2008; Chytrý 2009), the Alps (e.g. Pott 1995), the Mediterranean (Mucina et al. 1990; Mota Poveda et al. 1991; Ortiz and Rodríguez-Oubiña 1993; Dimopoulos et al. 1997; Deil et al. 2008) and Crimea (Ryff 2016) is summarized in the work of Mucina et al. (2016). In Africa, few studies concerning rupicolous vegetations have been published (e.g. Deil and Hammoumi 1997). In Asia and the Taurus (Hein et al. 1998; Parolly 1998; Eren et al. 2004), the Caucasus (Ermolaeva 2007; Golub et al. 2009; Belonovskaya 2012; Belonovskaya et al. 2014), the ranges of northern Iran (Klein 1987, 1988; Noroozi et al. 2014) and the Altai (Ermakov et al. 2006; Polyakova 2010; Polyakova and Valachovič 2019) have been investigated. After initial studies (Dzhuraev 1970, 1972a,b) the first comprehensive research in the area of the western Pamir-Alai on scree vegetation were conducted in recent years (Nowak et al. 2015, 2016). According to vertical zonation and the size of rock debris (fine or coarse gravel, pebble, cobble and rock blocks), several plant communities were distinguished in the alpine belt, among others *Anaphallidetum zeravschanicae*, *Angelicetum ternatae*, *Feruletum foetidissimae*, *Feruletum sumbuli*, *Stellarietum turkestanicae* and *Tetrataenietum olgae* (Nowak et al. 2016). At lower elevations, in the colline and montane belts, additional scree communities were investigated, for example *Caccinietum dubiae*, *Corydalidetum kashgaricae*, *Eremostachyetum tadschikistanicae* and *Zygophylletum atriplicoidis*. As the phytogeographical differences in Middle Asia are considerable, particularly between the western Pamir-Alai and the Eastern Pamir, this contribution has to be supplemented by research of the eastern Pamir-Alai and the western Tian Shan to complete our knowledge on scree vegetation diversity.

Despite their fairly widespread occurrence in Middle Asia, vegetation of gravel slopes from the *Cymbalario-Parietarietea diffusae* class have not been mentioned so far from Tajikistan. This thermophilous chasmophytic vegetation of walls is known from the Mediterranean region and the winter-mild Atlantic to subcontinental regions of temperate Europe, the Middle East and North Africa (Mucina et al. 2016). In Middle Asia it occurs not only on anthropogenic structures like walls or road escarpments, but very frequently on compact gravel deposits on hill slopes and river escarpments. Additionally, semi-desert vegetation has been reported from scree-like habitats in arid areas of northern Pakistan

(Eberhardt 2004; Peer et al. 2007). It is too early to judge the final systematic position of this type of vegetation, but temporarily it can be classified as semi-deserts or stony steppes (*Ajanio-Cleistogenetea songoricae*).

A geobotanical survey aimed at a detailed description of petrophytic vegetation was initiated in western Tajikistan in the year 2008, in both rock and scree habitats. Until now, the vegetation of these habitats of the Pamir-Alai and Tian Shan has been partially studied in various elevational belts mainly in western Tajikistan (e.g. Nowak et al. 2014a,b,c, 2016). However, the area of the eastern Pamir and the relation of Pamir-Alai and Tian Shan vegetation is still insufficiently investigated and has a lot of gaps in terms of classification, phytogeography and vegetation ecology.

The purpose of this paper is to complete the knowledge on scree vegetation of eastern Middle Asia and identify the main types of chasmophytic vegetation inhabiting stable and unstable screes in the mountains of the Pamir and the western Tian Shan Mts. Below we outline communities of screes and taluses of different particle sizes and bedrock types of the Pamir and western Tian Shan that are included in the vegetation of *Artemisio santolinifoliae-Berberidetea sibiricae*, which inhabits mainly the montane and alpine belts. Using data available from our own phytosociological research, we have attempted to address the following questions: (1) What is the diversity of the talus and scree vegetation of montane and alpine belts in the Pamir and western Tian Shan? (2) What is the relation of vegetation pattern to environmental variables in the area under study? (3) What is the relationship of scree vegetation recognized in the study area with that previously observed in other regions of Europe and Asia?

## Material and methods

### Study area

The vegetation survey was conducted in the eastern part of Middle Asia (the Pamir – in eastern Tajikistan and western Tian Shan – in Kyrgyzstan) within an area ca 150,000 km$^2$ (Fig. 1). Because of considerable phytogeographical differences between the Pamir-Alai and the Tian Shan Mts, the research aims at comparing the scree vegetation of both areas including Alai, Transalaian, Alichurian, Shachdarian, Shugnan, Sarikol, Yazgulem and Peter the First ranges in Pamir-Alai and Trans-Ili Alatau, Kyungey Ala-Too, Terskey Ala-Too, Songkol, Fergana, Kyrgyz and Chatkal Mountains in Kyrgyzstan.

Different vegetation types of the study area are shaped by a strongly varied landscape and human activity, particularly the grazing of sheep, goats, yaks, camels and horses. The study area is dominated mainly by steppes and chasmophytic vegetation; however, tall forb communities and hay meadows also contribute importantly to the landscape at intermediate elevations and at the bottoms of river valleys. Alpine grasslands in the subalpine and alpine belts are used generally as summer pastures, and at highest elevations, *Kobresia* mats serve as winter pastures. In addition, the wide terraces of lowland river valleys and also floodplains of the alpine rivers offer a suitable habitat for grasslands and alpine swards. On saline pans and marshes, mainly at higher elevations, halophytic vegetation dominate. Forested areas in Tajikistan cover less than 23% of the total country area, with a clear declining tendency because of human impact. The main type of forest vegetation in Tajikistan are juniper stands forming a subalpine open wood zone. The 'stony' and bare character of the highland landscapes of eastern Middle Asia makes this territory particularly suitable for different types of chasmophytic communities. The vast rupicolous habitats of eastern Middle Asia extend across a long elevational gradient. The sites under study were located between 800 and 4,300 m a.s.l. (mean 2,360) and in different habitats in terms of aspect, inclination, bedrock and particle size.

The geological structure of the study area is very complex. Outcrops of rocks formed from the Precambrian to the present age are very common. Only a few geological surveys have been published for Tajikistan (cf. Nedzvedskiy 1968). The middle and higher parts of the Hissar Mts are largely composed of extrusive rocks, mainly granite, granitoid and syenite. Some igneous outcrops also occur in the Darvaz and Kuraminian Mts and in the western Pamir ranges. In the Turkestan and Zeravshan Mts, Cambrian and Silurian sediments predominate. The rocks here are generally limestone, marble, dolomite, dolomitic shale, clay shale, phyllitic schist and argillaceous slate. Several kinds of metamorphic rocks are also present within the study area, with the most common migmatic gneiss, conglomerates and metamorphic mudstones. Along the Talas-Fergana Fault in Kyrgyzstan there are Cretaceous-Eocene sedimentary rocks up to two kilometres thick in the Fergana Basin.

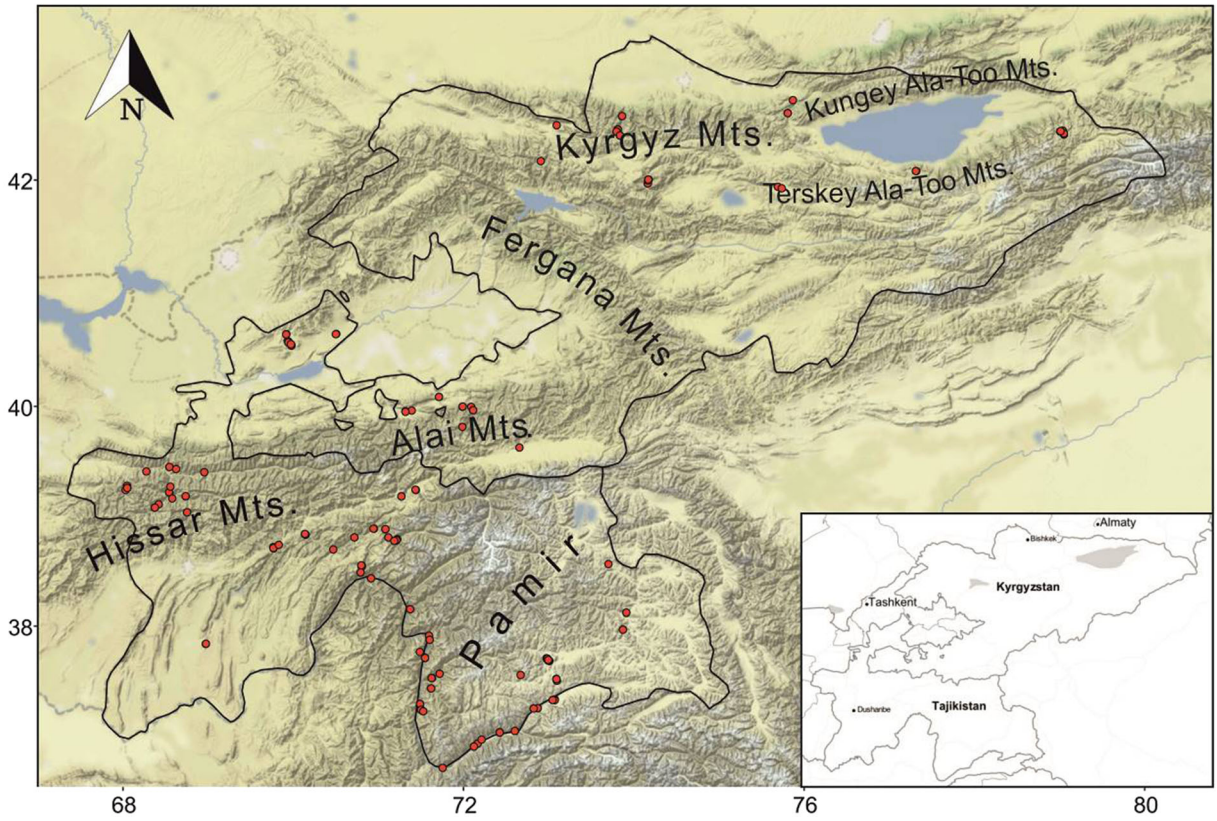


**Fig. 1** Study area and spatial distribution of relevés.

To the east of the Fergana Range there are no Cretaceous or Paleocene sediments. Continental deposits accumulated from the Eocene (e.g. marl, conglomerate) to limestones in the central Tian Shan Mountains in the Oligocene and Miocene are frequent there (Moores and Fairbridge 1997).

It is difficult to characterize the climatic conditions of the region with such a variable orography and intermediate position between the main bioclimatic zones of the Irano-Turanian and Central Asiatic regions with influences of the Indo-Indochinese climate from the south and the Euro-Siberian climate from the north. The study area stretches across a transition zone of the Temperate and Irano-Turanian types of macrobioclimates, with the first one characterized by a summer precipitation peak unlike winter precipitation and additionally higher continentalism (Djamali et al. 2012). There are four main types climatic zones within the research area: (1) the warm, continental, Irano-Turanian climate in the Fergana Basin. The surroundings of Jalalabad and Osh are characterized by winter precipitation that achieves its peak in March, with up to 80 mm and a yearly average of ca 200–250 mm. The temperatures reach 20°C in April and rise to an average of 34°C in June to August. During these months, precipitation is scarce, amounting to 0–10 mm per month. Snow and frost occur from December to February, with averages not falling below −3°C and with extreme values of −27°C in some years; (2) the warm humid, continental climate in the Tian Shan and Pamir-Alai ranges. In this area the average temperature in June is around 22°C in the colline and montane zones and drops to 10°C in the alpine belt. The lower limit of perpetual snow in the western Tian Shan is at 3,000–3,300 m a.s.l. Annual precipitation ranges here from about 500 mm on the northern slopes to ca 1,000 mm on the southern; (3) the cold semi-arid climates of the Issik-Kul basin, central and western parts of the Alai Valley and foothills and plateaus in the colline, montane and subalpine belts. These areas are clearly distinguished by lower precipitation with the average of ca 200–400 mm per year. The distribution of precipitation during the year is similar to the temperate climate, with the maximum in May – July (up to 70 mm). The temperatures exceed the value of

20°C only in summer, with the annual average of ca 10°C; (4) the cold desert climate of the easternmost sections of the Alai Valley and the eastern Pamirian Plateau. Unlike the west Pamir or Tian Shan ranges, this area is distinguished by significant aridity with less than 100 mm mean annual precipitation. Only in May and August does the average monthly precipitation exceed 20 mm. The average yearly temperature slightly exceeds 0°C, with the minimum dropping far below −30°C in January – February (Latipova 1968; Narzikulov and Stanyukovich 1968; Safarov 2003). However, within all these zones a lot of local anomalies occur, caused by orography, wind conditions and elevational differences (Fig. 1).

## Data sampling and data analyses

For five successive vegetation seasons (2015–2019), 222 relevés were collected in screes in the Pamir and the southwestern Tian Shan Mts. The size of each vegetation relevé was generally 10 $m^2$. Because of community physiognomy and the homogeneity of vegetation, we sampled several relevés with a surface of 1 $m^2$ on fine-grain-gravel scree (e.g. with *Corydalis kashgarica* and *C. fimbrillifera*). In each relevé, all vascular plant species were recorded using the seven-degree cover-abundance scale of Braun-Blanquet (Westhoff and van der Maarel 1973). Cryptogams were not recorded because of their negligible abundance and importance in the scree communities in the study area. The aim of the survey was to cover a broad range of habitats in relation to elevational range, size of rock debris, exposition and inclination. For each plot, geographical coordinates were measured with the help of a GPSMAP 60CSx device with an accuracy of ± 5 m, using the WGS84 reference frame. In the tables, latitude and longitude are given in degrees, minutes and seconds. The type of rock was determined through an analysis of lithology, pore geometry, mineralogical components, texture, permeability, hardness and pH, performed by a professional geologist (see the Acknowledgements). The gravel size was determined directly in field by measuring the diameter of five randomly selected particles.

Data were stored in the Vegetation of Middle Asia database (Nowak et al. 2017) and analysed in R (R Core Team 2020) and JUICE software (Tichý 2002). A modified TWINSPAN analysis (Roleček et al. 2009) provided an initial idea of the data structure and resolution. The cover-abundance scale was transformed using the four-step interval scale with cut-off levels at 0%, 5%, 10% and 25%. As the plots were selected fairly objectively, we downweighted rare species using the chord distance as a measure of cluster heterogeneity (Roleček et al. 2009). Taxa identified only at the genus level were omitted during the analysis. Diagnostic species were identified using the phi coefficient as a fidelity measure (Chytrý and Tichý 2003). Group size was standardized, and the Fisher exact test ($P < 0.05$) was applied. Species with a phi coefficient greater than 0.20 were considered diagnostic for a particular cluster. Diagnostic taxa for alliances were defined as those with a phi coefficient ≥ 0.15 in at least two clusters within this alliance (with the exception of the 1 cluster which is very distinct). Species with a frequency greater than 40% were defined as constant and those with a maximum cover value exceeding 20% as the dominant species of an individual cluster (plant community). For translation of the TWINSPAN results into phytosociological associations, we chose the highest division that still yielded floristically well characterized 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 the geographical range, certainty of the taxonomic status of the diagnostic species and the ICPN recommendations (Theurillat et al. 2021). During the division the habitat profile and authors' field experience were used to find the comprehensive and ecologically interpretable results of classification. Besides the new plant communities, already known associations were identified within the dataset: *Angelicetum ternatae* Nowak et al. 2015, *Feruletum koso-polianskyi* Nowak et al. 2015, *Corydalidetum kashgaricae* Nowak et al. 2016 and the subassociation of *Feruletum foetidissimae mediasietosum macrophyllae* Nowak et al. 2015 (Nowak et al. 2015, Nowak et al. 2016).

To check the floristic-sociological classification and to highlight the relationships between relevés, non-metric multidimensional scaling (NMDS) was performed (no downweighting of rare species, response data were log-transformed). Species cover values of the seven-degree Braun-Blanquet scale were transformed to a percentage scale (r, +, 1, 2, 3, 4, 5 to 0.1, 1, 5, 15, 37.5, 62.5 and 87.5, respectively). The differences in environmental factors (elevation, inclination, gravel size, temperature, precipitation) and vegetation variables (cover of herbs, species richness and Shannon diversity index) between groups were assessed using the

Kruskal–Wallis rank sum test (function '*kruskal.test*') with multiple comparison based on Dunn's test using the function *'dunnTest'* in the 'FSA' package (Ogle et al. 2018) in R.

A synoptic table with the constancy degree values of all species is given in Table S2. Only species reaching the first constancy class (20%) in at least one column are presented. For newly-described associations, the International Code of Phytosociological Nomenclature was adhered to (Theurillat et al. 2021). According to the 4th version of the ICPN, we assigned the type relevés with the reference to the supplementary materials (Table S1). All mentioned syntaxa are arranged into a syntaxonomic overview at the beginning of the description in the Results section. As the most significant attributes of the habitat, we considered spatial structure and environmental characteristics, mainly the presence of unstable rock debris or gravel deposits creeping or sliding down on mountain slopes. When analysing the possible class assignment of the particular associations, we considered mainly the *Thlaspietea rotundifolii* Br.-Bl. 1948, as a syntaxon comprising the alpine scree vegetation of Europe; the class *Heldreichietea* Parolly 1998, which is related to talus of the east Mediterranean region; the *Lamio tomentosi-Chaerophylletea humilis* Belonovskaya 2012 reported from screes in the Caucasus (Belonovskaya 2012) and *Artemisio santolinifoliae-Berberidetea sibiricae*, which has been proposed to include vegetation types of scree and rocky slopes of Central Asia (Ermakov et al. 2006). All of these syntaxa represent climax stage and stable, species-poor vegetation types inhabiting extreme, unstable environments.

The species nomenclature followed mainly the Plant List and for some exceptions Cherepanov (1995). Plant material collected during field studies was deposited in the Herbarium of Middle Asia Mountains, hosted at OPUN (University of Opole, Poland) and KRA (Jagiellonian University, Poland). Supplementary tables (Table S1–S2) and figures (Fig. S1–S2) are available in the Figshare Digital Repository (https://doi.org/10.6084/m9.figshare.13102361; Nowak et al. 2021).

## Results

### Synopsis of syntaxa

Based on our phytosociological survey, the hierarchical system of screes and taluses syntaxa in the Pamir and south-western Tian Shan in Middle Asia is as follows (numbers of clusters according to TWINSPAN classification (Fig. 2):

Class: *Artemisio santolinifoliae-Berberidetea sibiricae* Ermakov et al. 2006

Order: *Artemisio santolinifoliae-Berberidetalia sibiricae* Ermakov et al. 2006

Alliance: unknown

1. Community of *Scutellaria oligodonta-Lonicera semenovii* (cluster 1)

Alliance: *Artemision rutifoliae* Ermakov et al. 2006

2. *Allietum galanthii* Nowak et al. 2021 (cluster 4)

3. *Nepetetum floccosae* Nowak et al. 2021 (cluster 5)

4. *Helianthemetum songarici* Nowak et al. 2021 (cluster 6)

5. Community of *Lagochilus kaschgaricus-Crepidifolium akagii* (cluster 7)

Order: *Sileno brahuicae-Lactucetalia orientalis* Nowak et al. 2021

Alliance: *Ferulo foetidissimae-Vicion kokanicae* Nowak et al. 2015

6. *Angelicetum ternatae* Nowak et al. 2015 (cluster 10)

7. Community of *Ferula bucharica* (cluster 11)

8. *Perovskietum scrophulariifoliae* Nowak et al. 2021 (cluster 13)

9. *Eremuretum turkestanicae* Nowak et al. 2021 (cluster 14)

10. *Feruletum koso-polianskyi* Nowak et al. 2015 (cluster 15)

11. *Feruletum foetidissimae mediasietosum macrophyllae* Nowak et al. 2015 (cluster 16)

Alliance: *Ferulion grigoriewii* Nowak et al. 2021

12. Community of *Bunium badachschanicum* (cluster 17)

13. *Crambo schugnanae-Feruletum grigoriewii* Nowak et al. 2021 (cluster 19)

Class: *Cymbalario-Parietarietea diffusae* Oberd. 1969

Order*: Tortulo-Cymbalarietalia* Segal 1969

Alliance*: Parietario judaicae-Hyoscyamion aurei* S. Brullo et Guarino 1999

14. *Corydalidetum kashgaricae* Nowak et al. 2016

14.1. *Corydalidetum kashgaricae trigonelletosum gontscharovii* Nowak et al. 2021 (cluster 8)

15. Community of *Corydalis fimbrillifera* (cluster 9)

Class: *Ajanio-Cleistogenetea songoricae* (Mirkin in Kashapov et al. 1987) Mirkin et al. 1988

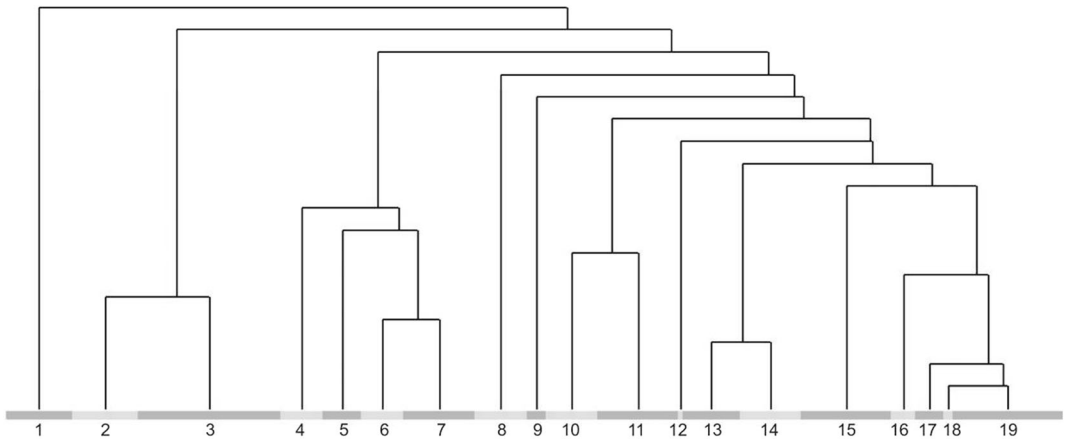


**Fig. 2** Dendrogram illustrating the assignment of relevé groups identified by TWINSPAN to particular syntaxonomical units: 1 – community of *Scutellaria oligodonta-Lonicera semenovii*; 2 – *Artemisio glaucinae-Salsoletum paulseni*; 3 – *Cousinio pannosae-Artemisietum skorniakovii*; 4 – *Allietum galanthii*; 5 – *Nepetetum floccosae*; 6 – *Helianthemetum songarici*; 7 – comm. of *Lagochilus kaschgaricus-Crepidifolium akagii*; 8 – *Corydalidetum kashgaricae trigonelletosum gontscharovii*; 9 – community of *Corydalis fimbrillifera*; 10 – *Angelicetum ternatae*; 11 – community of *Ferula bucharica*; 12 – community of *Lagochilus seravschanicus*; 13 – *Perovskietum scrophulariifoliae*; 14 –; *Eremuretum turkestanicae*; 15 – *Feruletum koso-polianskyi*; 16 – *Feruletum foetidissimae mediasietosum macrophyllae*; 17 – community of *Bunium badachschanicum*; 18 – community of *Patrinia intermedia* and *Salvia bucharica*; and 19 – *Crambo schugnanae-Feruletum grigoriewii.*

Alliance: *Piptathero gracilis-Artemision brevifoliae* Eberhardt 2004

16. *Artemisio glaucinae-Salsoletum paulseni* Nowak et al. 2021 (cluster 2)

17. *Cousinio pannosae-Artemisietum skorniakovii* Nowak et al. 2021 (cluster 3)

17.1. *Cousinio pannosae-Artemisietum skorniakovii leymetosum lanati* Nowak et al. 2021

*Incertae sedis*:

Community of *Lagochilus seravschanicus* (cluster 12)

Community of *Patrinia intermedia* and *Salvia bucharica* (cluster 18)

(We refrain from describing these two communities because of the very scarce sample material with only one or two relevés.)

**Description of plant communities of scree and talus vegetation of the Pamir and south-western Tian Shan in Middle Asia (*Artemisio santolinifoliae-Berberidetea sibiricae*)**

The Central Asian rupicolous communities of *Artemisio santolinifoliae-Berberidetea sibiricae* Ermakov et al. 2006 are widely distributed across southern Siberia, Mongolia and north-eastern limits of Middle Asia (Polyakova 2010). They occupy rock outcrops and screes in the Altai, Tian Shan, Sayan and Tarbagatai and develop in the strongly continental climate.

**1. Community of *Scutellaria oligodonta-Lonicera semenovii* (Fig. 2, cluster 1, 14 relevés)**

**Diagnostic species**: *Callianthemum alatavicum, Cerastium tianschanicum, Dasiphora parviflora* (= *Potentilla parvifolia*), *Dracocephalum imberbe, D. stamineum, Geranium saxatile, Leontopodium fedtschenkoanum, Lonicera semenovii, Neotorularia korolkowii* (= *Neotorularia sulphurea*), *Poa albertii* subsp. *albertii* (= *Poa litvinoviana*), *Ranunculus popovii, Scutellaria oligodonta, Semenovia transiliensis, Spiraea hypericifolia, Valeriana ficariifolia*

**Constant species**: *Lonicera semenovii*

**Dominant species**: *Dasiphora parviflora, Dracocephalum imberbe, Lonicera semenovii, Spiraea hypericifolia*

**Floristic and habitat characteristics:** This vegetation is composed of typical Central Asian species sometimes restricted only to central Tian Shan (Kyrgyzstan and Xinjiang in China, e.g. *Scutellaria oligodonta*; eFloras 2020It occupies the typical screes of alpine belt in Ak-Shyyrak and Terskey Ala-too (Fig. S1). It was noted between 3,300 and 3,650 m a.s.l (mean approx. 3,500 m a.s.l.), mainly on stony debris (mean stone size was approx. 12 cm). The community prefers steep slopes up to 60° (mean ca 37°) with southern expositions. Both the cover of herbs and the species richness are moderate, reaching on average 30% and 9 taxa in a

plot, respectively. The pattern of the studied plots reveals the compositional heterogeneity of this community. It includes patches of different successional stages with some having considerable shrub layer with *Spiraea hypericifolia* as dominant species. Additionally, in some cases the species from rock ledges or crevices contribute considerably to this vegetation (e.g. *Dracocephalum imberbe* or *Dasiphora parviflora*).

**Alliance: *Artemision rutifoliae* Ermakov et al. 2006**

Phytocoenoses of this vegetation occupy the rocky outcrops, shelves, ledges and typical screes in Central and Middle Asian regions in Irano-Turanian climate area with strong continental influence. They occur in the steppe zone; however, the main diagnostic taxa (including *Artemisia rutifolia*) are typical chasmophytes with the ecological optimum in more or less stable rocky debris.

**2. *Allietum galanthii* Nowak et al. hoc loco (Fig. 2, cluster 4, 9 relevés)**

**Type relevé**: Table S1, succesive number 17, holotypus hoc loco

**Diagnostic species**: *Agropyron cristatum* (= *Agropyron pectinatum*), *Allium galanthum, Asperula ferganica, Chesneya ferganensis, Cicer songaricum, Dracocephalum diversifolium, Isatis minima, Linaria bungei* (= *Linaria transiliense*), *Piptatherum latifolium, Scutellaria adenostegia, Silene quadriloba* (= *Melandrium quadrilobum*)

**Constant species**: *Agropyron cristatum, Allium galanthum, Chesneya ferganensis, Scutellaria adenostegia*

**Dominant species**: *Agropyron cristatum, Allium galanthum, Chesneya ferganensis, Dracocephalum diversifolium*

**Floristic and habitat characteristics:** The main diagnostic species of this association is distributed in Central Asia and inhabits loose screes in the montane belt at elevations of 500–2,000 m a.s.l. in Kyrgyzstan, Mongolia, NE China and southern Siberia (Kovalevskaya 1968). The association was found in Kyzyl-Oy Valley in Kyrgyz Range (Fig. S1) on northern, mostly on north-eastern slopes (Fig. S2) at elevations of 1,700–1,900 m a.s.l. (Fig. 3a). Its stands have distinct, sparsy physiognomy with clear domination of *Allium galanthum*. Plots have been found on gravel or cobble screes (1–30 cm in diameter, Fig. 3c) of limestone rocks with inclination of approx. 40° (Fig. 3b). The association prefers northern aspects of sunny, unstable screes. Vegetation plots of the association are poor or moderately rich in species in comparison to other associations, with an average number of species per relevé equal to eleven (Fig. 4c). The total cover of vascular plants in the phytocoenoses has the intermediate values of approx. 35% and varies between 20% and 50% (Fig. 4a, 5a).

**3. *Nepetetum floccosae* Nowak et al. hoc loco (Fig. 2, cluster 5, 8 relevés)**

**Type relevé**: Table S1, successive number 25, holotypus hoc loco

**Diagnostic species**: *Artemisia pamirica, Cousinia buphtalmoides, Elymus schrenkianus* (= *Roegneria schrenkiana*), *Lonicera pamirica, Nepeta floccosa* (= *N. vakhanica*), *Ribes heterotrichum*

**Constant species**: *Nepeta floccosa*

**Dominant species**: *Nepeta floccosa, Ribes heterotrichum*

**Floristic and habitat characteristics:** *Nepetetum floccosae* is supposedly distributed in alpine belt of Eastern Pamir in Tajikistan (Fig. 5c, 6e) as well as in northern Hindukush in Afghanistan and Kun-lun Shan in Xinjiang and Xizang provinces in China (eFloras 2020). Plots of this association have rarely been recorded along the upper section of the Vakhan Valley (Fig. S1). It was noted within the range of elevations from 3,450 to 3,750 m a.s.l. (Fig. 3a), in alpine belt of semi-desert vegetation of the Central Asian phytogeographical zone. This association occurs on fine debris screes (mean gravel size ca 8 cm; Fig. 3c). Plots of *Nepetetum floccosae* were found on relatively gently sloping escarpments with the mean inclination of approx. 27° (Fig. 3b). The association prefers south-eastern and southern expositions (Fig. S2). The phytocoenoses were observed on limestone and dolomite shale debris. The association is characterized by a sparse herb cover with the mean close to 25% (Fig. 4a). The species richness was very low, with the average six species and maximum of ten species per plot (Fig. 4c). Despite the herbaceous character of this vegetation, occasionally shrubs compose the clear layer with *Ribes heterotrichum* as the most abundant.

**4. *Helianthemetum songarici* Nowak et al. hoc loco (Fig. 2, cluster 6, 9 relevés)**

**Type relevé**: Table S1, successive number 34, holotypus hoc loco

**Diagnostic species**: *Allium setifolium, Allium weschniakowii, Alyssum linifolium* (= *Meniocus linifolius*), *Astragalus oxyglottis, Dracocephalum*

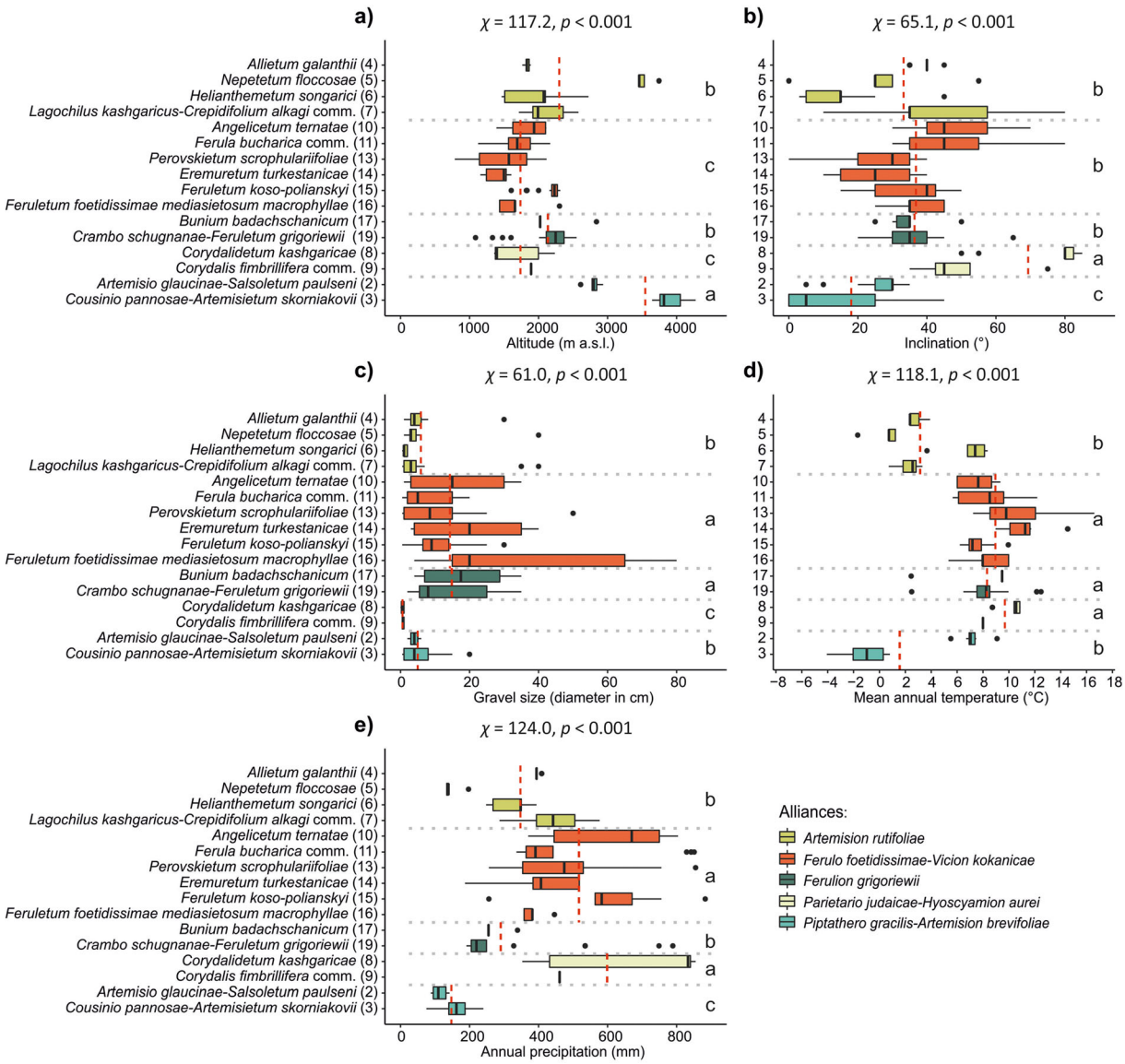


**Fig. 3** Boxplots showing the median (line), quartiles, outliers and the ranges of: a – elevation, b – inclination, c – gravel size, d – mean annual temperature and e – sum of annual precipitation for particular syntaxonomical units. The red line indicates mean values of alliances. Values of $\chi^2$ and $p$ for the Kruskal–Wallis rank sum tests for vegetation groups are presented. Different letters indicate significant differences between the alliances based on the post-hoc Dunn's test. The numbers on the y axis represent the TWINSPAN analysis cluster numbers.

*heterophyllum, Helianthemum songaricum, Koeleria macrantha* (= *Koeleria cristata*), *Salsola drobovii, S. gemmascens, Scorzonera pubescens, Stipa caucasica, S. drobovii, S. lipskyi, Zygophyllum atriplicoides*

**Constant species**: *Helianthemum songaricum, Stipa caucasica*

**Dominant species**: *Dracocephalum heterophyllum, Helianthemum songaricum, Stipa caucasica*

**Floristic and habitat characteristics:** *Helianthemetum songarici* is distributed across the alpine belt of Pamir-Alai and western Tian Shan ranges, with additional occurrence area in north-eastern China and Mongolia (eFloras 2020). In Tajikistan and Kyrgyzstan this association has considerable elevation range from ca 1,500 to 2,800 with the mean of 1,950 m a.s.l. (Fig. 3a). This vegetation is very distinct as it has a

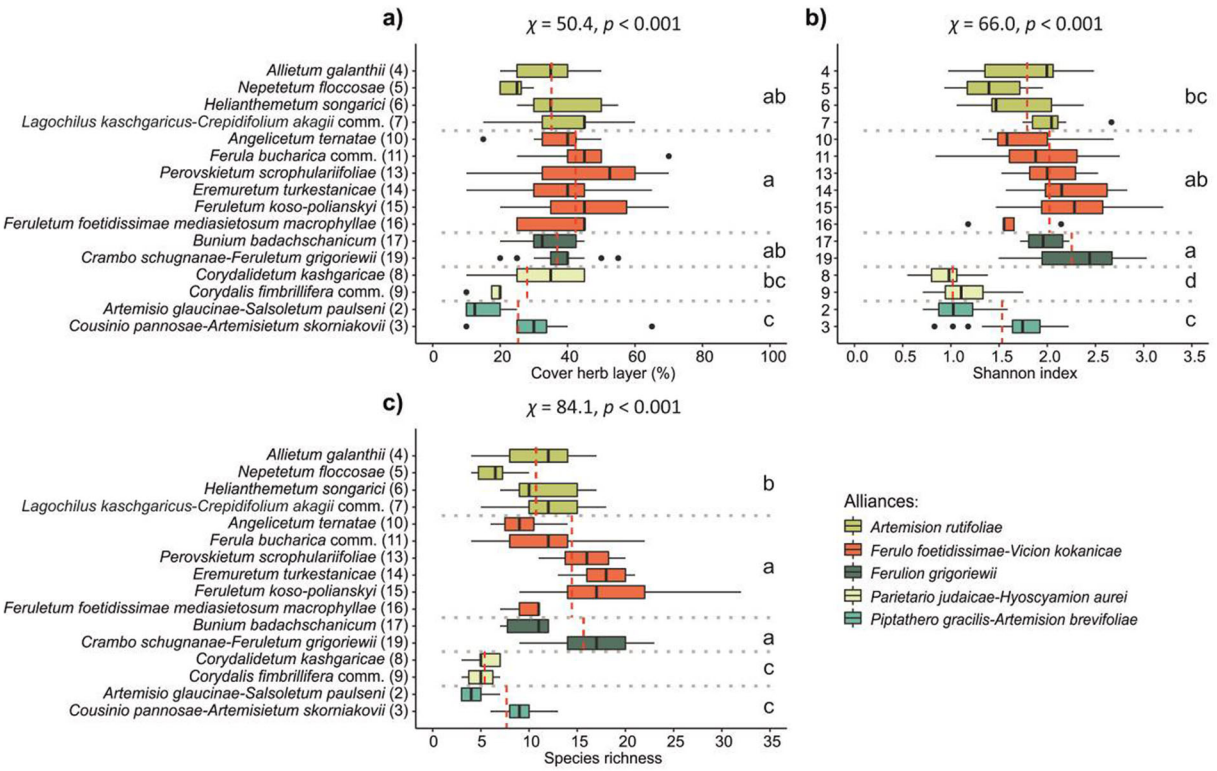


**Fig. 4** Boxplots showing the median (line), quartiles, outliers and the range of the: a – cover of the herb layer, b – Shannon diversity index and c – species richness for particular syntaxonomical units. The red line indicates mean values of alliances. Values of $\chi^2$ and $P$ for the Kruskal–Wallis rank sum tests for vegetation groups are presented. Different letters indicate significant differences between the alliances based on the post-hoc Dunn's test. The numbers on the y axis represent the TWINSPAN analysis cluster numbers.

physiognomy formed by dwarf shrubs or small herbaceous plants on gently sloping hills with sunny expositions (Fig. 5f). Plots of this association were found in Zeravshan, Turkestan, Fergana and Terskey Alaa-too ranges (Fig. S1). It occupies fairly gentle slopes with the mean inclination of approx. 15° (Fig. 3b) on north-western and southern expositions (Fig. S2). The substrate was preferably alkaline rock, mainly limestone or dolomite. The tiny gravel debris (ca 1 cm in diameter, Fig. 3c) is creeping down and mingled with clay and silt deposits with some ingredient of soil. Within the sampled plots, between seven and seventeen species were noted (mean 12, Fig. 4c). The total cover of herb layer was relatively high, up to 55% with the mean value of approx. 40% (Fig. 4a). Due to habitat similarities (gentle slopes, warm, sunny locations) the association harbour a number of typical steppe species like *Alyssum linifolium*, *Bromus laneolatus*, *Stipa drobovii* and *S. lipskyi*.

**5. Community of *Lagochilus kaschgaricus-Crepidifolium akagii* (= *Youngia tenuicaulis*) (Fig. 2, cluster 7, 15 relevés)**

**Diagnostic species**: *Acantholimon alatavicum, Artemisia rutifolia, Carex turkestanica, Crepidifolium akagii* (= *Youngia tenuicaulis*), *Ferula tschimganica, Galagania ferganensis* (= *Korovinia ferganensis*), *Lagochilus kaschgaricus, Potentilla asiae-mediae* (= *Potentilla multifida*), *Stipa caucasica*

**Constant species**: *Artemisia rutifolia, Stipa caucasica*

**Dominant species**: *Acantholimon alatavicum, Artemisia rutifolia, Carex turkestanica, Patrinia intermedia, Pilopleura tordyloides, Stipa caucasica*

**Floristic and habitat characteristics:** This fairly heterogeneous group includes vegetation distributed mainly in the Kyrgyz range with some outposts in neighbouring mountains (Fig. S1). The typical plots of this community occupy steep slopes with gravel or pebble rock screes of south-eastern and eastern


**Fig. 5** Photographs of scree vegetation belonging to the: a – *Allietum galanthii* in the Talas Mts near Ming-Kush, Kyrgyzstan; b – *Angelicetum ternatae* in the Turkestan Range near Matcha, Tajikistan; c – *Nepetetum floccosae* in the Alichur Mts close to Alichur in the Eastern Pamir, Tajikistan; d – *Eremuretum turkestanicae* in the Kuraminian Mts near Adrasmon, Northern Tajikistan; e – *Crambo schugnanae-Feruletum grigoriewii* in Khuf in the Western Pamir, Tajikistan; and f – *Helianthemetum songarici* – Zeravshan Mts near Sorvoda, Tajikistan. All pictures were taken by A. Nowak.

exposition (Fig. S2). It is dominated by typical scree species like *Artemisia rutifolia* or *Patrinia intermedia*; however, this group includes also plants that inhabit frequently rock ledges (*Crepidifolium akagii* and *Rhinactinidia limoniifolia*). That is why we leave it rankless. The internal heterogeneity of the community is also apparent in species composition and richness. The typical scree plots have up to eighteen species, which is much more compared to species-poor plots of rock pebble debris or ledges with only five taxa. In the study area this vegetation can be found in montane and subalpine belts at ca 1,900 to 2,600 m a.s.l. with the mean of ca 2,150 m a.s.l. (Fig. 3a). The average cover of the herb layer was moderate, approx. 40%, ranging from 15 to 60% (Fig. 4a).

**Order: *Sileno brahuicae-Lactucetalia orientalis* Nowak et al. hoc loco**

**Nomenclatural type: *Ferulo foetidissimae-Vicion kokanicae* Nowak et al.** 2015

**Diagnostic species:** *Callipeltis cucullaris*, *Eremopoa persica, Galium spurium, Lactuca orientalis* (= *Scariola orientalis*), *Pachypterygium brevipes, Papaver*

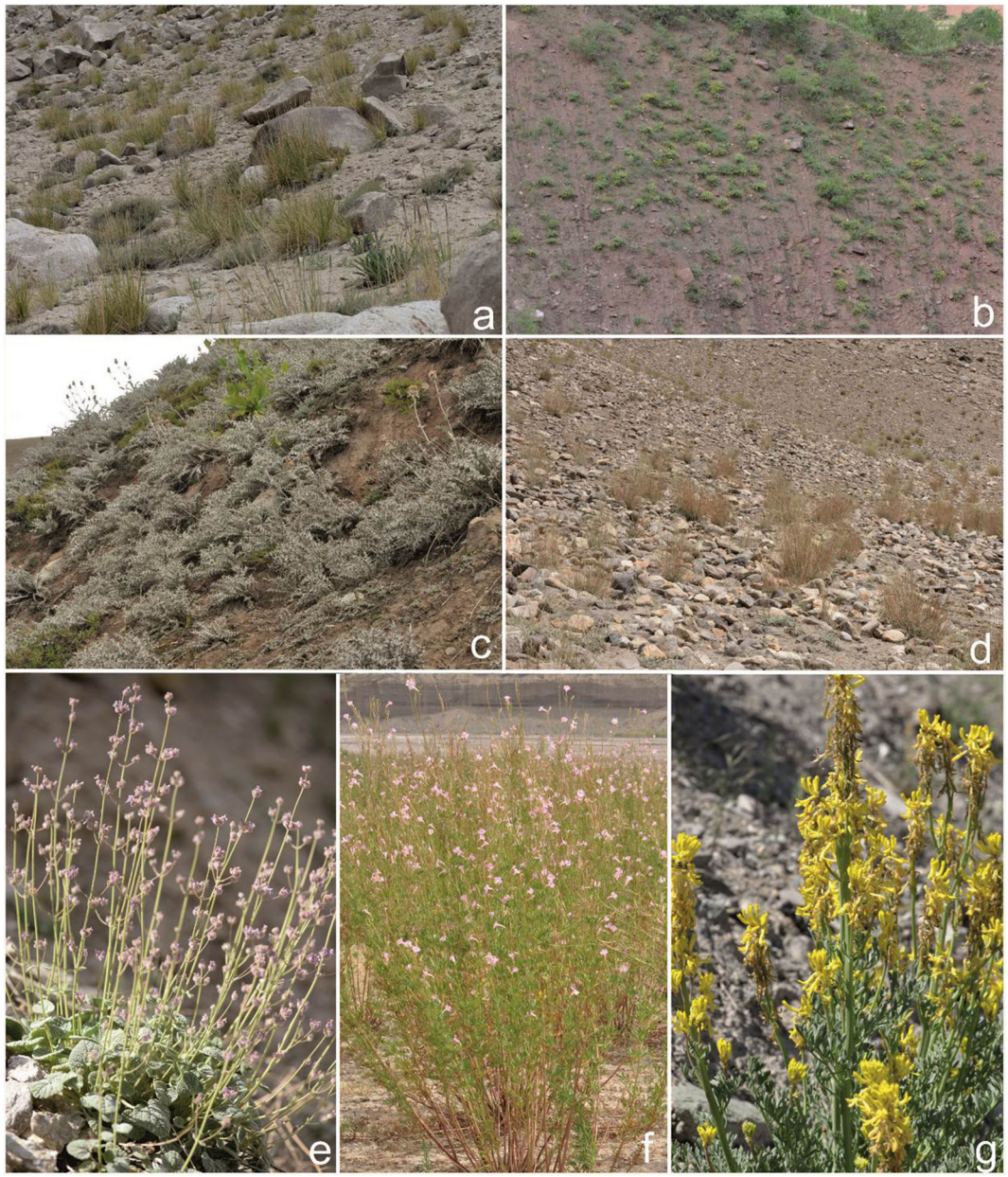


**Fig. 6** Photographs of scree vegetation belonging to: a – the *Cousinio pannosae-Artemisietum skorniakovii leymetosum lanati* near the Chukur-kul Lake in the Eastern Pamir, Tajikistan; b – the *Corydalidetum kashgaricae trigonelletosum gontscharovii* with the domination of *Trigonella gontscharovii* near Childara in the Darvaz Range, Tajikistan; c – the *Cousinio pannosae-Artemisietum skorniakovii* near the Bulyun-kul Lake in the Eastern Pamir, Tajikistan; d – a stand of *Leymus lanatus* in the Alichur Mts. in the Eastern Pamir, Tajikistan; e – a stand of *Nepeta floccosa* in Vakhan Valley near Vrang, Tajikistan; f – a stand of *Incarvillea olgae* on the river Obikhigou terraces near Lyangar,Tajikistan; and g – *Corydalidetum kashgaricae* near Murghab in the Eastern Pamir, Tajikistan. All pictures were taken by A. Nowak.

*pavoninum, Polygonum polycnemoides, Scutellaria intermedia*, *Silene brahuica*, *Trichodesma incanum*

This typical scree vegetation of Middle Asia was provisionally proposed as *Sileno brahuicae-Scutellarietalia intermediae* (Nowak et al. 2016). The order was established for plant communities developed on unstable sediments of taluses and screes dominated by species with an Irano-Turanian distributional range

based on the sampling of western Pamir-Alai ranges. Additional data collected in the eastern Pamir-Alai and western Tian Shan have changed the diagnostic value of the previously assigned species and suggest that *Lactuca orientalis* should be regarded as the main diagnostic taxon of the order instead of *Scutellaria intermedia.* It is typical scree plant of Irano-Turanian region, only occasionally contributing to rock, steppe or forb vegetation (e.g. Nowak et al. 2015, 2016). *Lactuca orientalis* has the core distributional range in Middle and Southwest Asia, but also contribute to scree vegetation on the borderland with Central Asia, having locations mainly in Kyrgyzstan on screes up to 3,800 m a.s.l. (Kovalevskaya 1968; eFloras 2020). The distribution ranges of the most of the diagnostic taxa (*Eremopoa persica, Pachypterygium brevipes, Papaver pavoninum*, *Polygonum polycnemoides, Trichodesma incanum*) are restricted to Irano-Turanian region with few additional typical for its eastern outskirts (e.g. *Nepeta daenensis* or *Eremurus korshinskyi*). This apparent biogeographical border between Central and Middle Asia is in our opinion the crucial argument for establishing the order for scree vegetation with the main compositional element related to western Tajikistan, southern Uzbekistan, Turkmenistan, Iran and other countries of Irano-Turanian region. The distinct differences in climate (see Djamali et al. 2012), particularity the continentality and precipitation influence not only the species composition, but also the weathering patterns and erosion which are important factors for habitat creation for scree vegetation. The gentle slopes of Central Asian subregion with low precipitation, scarce snow cover and high temperature amplitude control the habitat profile and its availability for chasmophytic plants. As has been shown for *Artemisio-Berberidetea* vegetation (Ermakov et al. 2006) the screes of Middle and Southwest Asia occur in the close vicinity of 'stony' tundra steppes (with *Roegneria* spp. *Stipa glareosa* and *S. orientalis*), typical rock vegetation (with e.g. *Asperula oppositifolia*, *Crepidifolium akagi*, *Kudrjaschevia allotricha*, *Poa relaxa*), alpine tall-herbs (with *Elaeosticta allioides*, *E. hirtula*, *Polygonum coriarium*, *Senecio olgae*), high-elevation semi-deserts (e.g. *Kochia scoparia*, *Krascheninnikovia ceratoides*, *Oxytropis chiliophylla*), alpine swards and matts (e.g. *Hedysarum cephalotes*, *Nepeta pamiriensis*, *Oxytropis savellanica*) or fellfield cushion communities (e.g. *Acantholimon* spp., *Gypsophila herniarioides*). The physiognomy of the communities is determined mainly by the harsh habitat of mobile screes with tendency towards drought. The vegetation is moderately abundant, with a mean cover of about 35-40% and a mean species number 10-15. The scree vegetation of Middle Asia has generally herbaceous character, however occasionally the dwarf scrubs or even higher nanophanerophytes contribute significantly to the communities. Such shrubs as, for example, *Atraphaxis*, *Cerasus*, *Colutea*, *Cotoneaster*, *Lonicera*, *Rosa*) occupy more stable screes and form a succeeding successional stage of talus vegetation after its stabilization.

The phytocoenoses assigned to this order inhabit various types of geological substrates, such as limestone, dolomite, marble, granite, syenite, schist or gneiss and reveal weak affinity to particular bedrock type. The main diagnostic species were observed on alkaline, neutral and, rarely, on acidophilous substrates. They grow on various forms of rock debris on colluvial deposits sliding downhill or on solid rocky slopes. The scree substrate material can differ significantly from large rock blocks up to a diameter of 150 cm, cobbles (25–35 cm in diameter), pebbles (10–25 cm), coarse and fine gravel (1–10 cm) and powder-like silt. The community plots were generally found between 800 and 4,300 m a.s.l. (mean 2,400) at various expositions and sloping inclinations.

Due to the substantial differences within scree habitats in Middle Asia, particularly elevation amplitude and biogeographic distinction, the consequent differences in species composition allow to distinguish at least three groups within the proposed order. The first comprises the communities of higher elevations of the western Pamir-Alai, representing the *Ferulo foetidissimae-Vicion kokanicae* alliance. The second was dedicated for montane and colline scree vegetation of the western Pamir-Alai (*Alceion nudiflorae*). The last one, proposed hereby, is coined for the scree vegetation of the montane and alpine communities of Eastern Pamir-Alai (*Ferulion grigoriewii*).

**Alliance: *Ferulo foetidissimae-Vicion kokanicae* Nowak et al.** 2015

This chasmophytic vegetation was recorded on the taluses and screes of the western Pamir-Alai ranges: the Zeravshan, Hissar, Fon, Hazratishoh, Darvaz, Vanch, Turkestan, Peter the First and Karateginian. Considering the distribution of the main diagnostic species, this kind of vegetation can inhabit mountains of alpine relief of the whole Middle Asia. The stands were noted mainly in the subalpine and alpine belts. Only exceptionally some

plots were found below 1,750 m a.s.l. The phytocoenoses of the *Ferulo foetidissimae-Vicion kokanicae* are usually poor in species, having on average thirteen species per plot. Apart from the taxa diagnostic for the alliance and order, the group of species with higher abundance includes *Artemisia persica*, *Atraphaxis pyrifolia*, *Galium spurium* and *Prunus verrucosa* (= *Cerasus verrucosa*).

**7. Community of *Ferula bucharica* (**Fig. 2**, cluster 11, 17 relevés)**

**Diagnostic species**: *Ferula ovina, F. bucharica* (= *Ladygynia bucharica*), *Lactuca glauciifolia, Piptatherum songaricum* (= *Piptatherum kokanicum*)

**Constant species**: *Bromus tectorum*, *Glaucium elegans*

**Dominant species**: *Ferula bucharica, F. foetidissima, F. kokanica, F. ovina, Glaucium elegans, Parietaria judaica, Piptatherum songaricum, Salvia bucharica, Schrenkia golickeana*

**Floristic and habitat characteristics:** Due to considerable differences in species composition, that probably arise from insufficient sampling within this group, we decided to leave it rankless. The community includes plots with various dominant species representing fairly different habitats. *Ferula foetidissima*, *F. ovina* or *Schrenkia golickeana* apparently belong to alpine screes of the Middle Asia; however, *Salvia bucharica* is rather a steppe species while *Parietaria judaica* prefers the nitrophilous wall and steep scree habitats. Particularly interesting is *Ferula bucharica*, an endemic species distributed in south-western Tajikistan, mainly in colline and montane belts of the Ak-tau, Babatag and Darvaz Mts. It occurs in very distinct habitat, a stony, crumbly slopes with deep soil developed within this subhumid climatic zone of the South Tajikistanian and Darvazian phytogeographical subregions. The plots of the association have been found at elevations between 1,100 and 2,200 m a.s.l. (mean approx. 1,650, Fig. 3a). The community inhabits mainly southern and south-western expositions (Fig. S2) with relatively steep inclinations (30–70°, mean approx. 50°, Fig. 3b). The majority of sites are young, unstable landslides with stony debris. Rarely the community inhabits anthropogenic escarpments of roads. It prefers loose debris with rocks of different size, ca 8 cm in diameter on average (Fig. 3c). The association is characterized by moderately abundant herb cover ranging between 25 and 70% (45% on average, Fig. 4a) and is moderately rich in species as well (between 4 and 22 species per plot with 12 taxa on average; Fig. 4c).

**8. *Perovskietum scrophulariifoliae* Nowak et al. hoc loco (**Fig. 2**, cluster 13, 12 relevés)**

**Type relevé**: Table S1, successive number 88, holotypus hoc loco

**Diagnostic species**: *Arenaria serpyllifolia, Artemisia tenuisecta, Ferula koso-poljanskyi, Incarvillea olgae, Linum corymbulosum, Medicago lupulina, Moluccella fedtschenkoana* (= *Otostegia fedtschenkoana*), *Perovskia scrophulariifolia, Plantago lanceolata*

**Constant species**: *Arenaria serpyllifolia*

**Dominant species**: *Ampelopsis vitifolia, Convolvulus spinifer* (= *Convolvulus tragacanthoides*), *Eremurus comosus, Ferula koso-poljanskyi, Incarvillea olgae, Moluccella fedtschenkoana, Zeravschania regeliana*

**Floristic and habitat characteristics:** The phytocoenoses of *Perovskietum scrophulariifoliae* have rarely been spotted on aprons and talus cones of southern Kyrgyzstan in Fergana and Alaian ranges. Occasionally it was also noted on alluvial fans of Zeravshan river in Tajikistan or typical screes on moderately steep slopes (Fig. S1). The diagnostic species is considered an endemic of Middle Asia (Kovalevskaya 1968). The association prefers gentle and planar cones with medium-sized stones and rock debris. The mean diameter of limestone or dolomite boulders was approx. 12 cm (Fig. 3c). Phytocoenoses of *Perovskietum scrophulariifoliae* were found at the moderate elevations from 800 to 2,000 m a.s.l. (Fig. 3a). The phytocoenoses were observed generally on south-western and western expositions (Fig. S2) on slopes of moderate inclinations (mean approx. 25°, Fig. 3b). The communities were fairly rich in species if compared to other scree vegetation. Approximately sixteen species were noted per plot on average (Fig. 4c). The cover of the herb layer ranged between 10 and 70%, with mean value of approx. 45% (Fig. 4a). There is some heterogeneity within the relevés with some plots of distinctly different composition and physiognomy. Hence the group needs still some refinements after collecting additional data. For example, the patches with domination of *Moluccella fedtschenkoana* found on unstable, loose fine debris in Darvaz range, the community with domination of *Zeravschania regeliana* on huge blocks in Kshtut valley or the alluvial vegetation with *Incarvillea olgae* (Fig. 6f) are considerably distinct and needs in-depth analyses.

**9. *Eremuretum turkestanicae* Nowak et al. hoc loco (**Fig. 2**, cluster 14, 13 relevés)**

**Type relevé**: Table S1, successive number 102, holotypus hoc loco

**Diagnostic species**: *Artemisia namanganica, Bromus scoparius, B. tectorum* (= *Anisantha tectorum*), *Ceratocephalus testiculatus, Eremurus sogdianus, E. turkestanicus, Filago paradoxa, Galium verticillatum, Lactuca undulata, Lappula squarrosa* (= *Lappula consanguinea*), *Linaria popovii, Malva neglecta, Parietaria lusitanica* subsp. *serbica* (= *Parietaria serbica*), *Picnomon acarna*

**Constant species**: *Bromus tectorum, Eremurus turkestanicus*

**Dominant species**: *Bromus tectorum, Crambe cordifolia* subsp. *kotschyana* (= *Crambe kotschyana*), *Eremurus sogdianus, Eremurus turkestanicus, Galium spurium*

**Floristic and habitat characteristics:** The association has been recorded mainly in the northern Tajikistan in Kuraminian range that belongs to south-western Tian Shan (Fig. S1). The main diagnostic species is an endemic plant of the Middle Asia (Kovalevskaya 1968). It forms distinct stands on stony screes of shales and granites in the montane belt (Fig. 5d). The plots of the association have been found at elevations between 1,150 and 1,600 m a.s.l. (Fig. 3a). The community inhabits mainly south-eastern and north-eastern (Fig. S2) slopes with relatively gentle inclinations (mean approx. 25°, Fig. 3b). The majority of sites are old, fairly stabilized taluses and fans. It prefers moderately compacted debris with pebbles and cobbles of the mean size of ca 20 cm in diameter (Fig. 3c). The association is characterized by moderately abundant herb cover ranging between 10 and 65% (40 on average, Fig. 4a). Between thirteen and twenty-one species were recorded in a particular relevé, with an average of eighteen taxa (Fig. 4c).

**Alliance: *Ferulion grigoriewii* Nowak et al. hoc loco**

**Nomenclatural type:** *Crambo schugnanae-Feruletum grigoriewii* Nowak et al. hoc loco

**Diagnostic species:** *Nepeta daenensis*, *Rochelia peduncularis*, *Rosularia glabra*

This scree vegetation includes phytocoenoses inhabiting alpine belt of the Pamir. They occupy immense areas of extend slopes in the western and eastern Pamir, particularly in lower elevations of alpine belt in the river valleys. They grow on typical screes in dry, continental climate of transitional character between Central and Middle Asia. Plots *Ferulion grigoriewii* were recorded in Alichur, Vakhan, Schugnan and Schahdarian Mts. Considering the distribution of the main diagnostic species, the plots of this vegetation could be expected in Hindukush Mts in northern Afghanistan. The patches of *Ferulion grigoriewii* were noted mainly at elevations of (1,100–)2,100–2,300(–2,550) m a.s.l.. They are moderately rich in species, having on average sixteen species per plot. The herbaceous layer is 40% on average. The vegetation period is very short in the Pamir and makes the vegetation almost ephemeral with rapid bloom in early summer and fast disappearance few weeks later with only fruiting Ferulas as a clear resemblance of the association.

**12. Community of *Bunium badachschanicum* (**Fig. 2**, cluster 17, 6 relevés)**

**Diagnostic species**: *Acantholimon lycopodioides, Bunium badachschanicum, Ephedra intermedia, Minuartia litvinovii, Nepeta daenensis, Silene brahuica, Tanacetopsis mucronata*

**Constant species**: *Minuartia litvinovii*

**Dominant species**: *Minuartia litvinovii*

**Floristic and habitat characteristics:** This vegetation is represented by a low number of relevés within the limited area. That is why according to ICPN (Theurillat et al. 2021) we left it rankless. The plots of the community were found in Shugnan and Shakhdarian ranges (Fig. S1) on unstable coarse gravelly screes. The community occupies slopes of moderate inclination (mean 35°, Fig. 3b) on slopes with south-western and western exposition (Fig. S2). The sampling was conducted in the alpine belt at ca 2,000 to 2,800 with the mean of ca 2,150 m a.s.l. (Fig. 3a). The community patches were species-poor with seven to twelve taxa per plot (Fig. 4c) and moderate plant cover reaching up to 45% (mean ca 35%, Fig. 4a).

**13. *Crambo schugnanae-Feruletum grigoriewii* Nowak et al. hoc loco (**Fig. 2**, cluster 19, 23 relevés)**

**Type relevé**: Table S1, successive number 150, holotypus hoc loco

**Diagnostic species**: *Artemisia korshinskyi* (*Seriphidium korshinskyi*), *Cousinia mulgediifolia, C. semilacera, Crambe schugnana, Ferula grigoriewii, Filago arvensis, Polygonum fimbrilliferum, Tytthostemma alsinoides* (*Stellaria alsinoides*)

**Constant species**: *Artemisia korshinskyi, Ferula grigoriewii*

**Dominant species**: *Allium oschanini, Ampelopsis vitifolia, Anaphalis darvasica, Artemisia korshinskyi,*

*Cousinia semilacera, Ferula grigoriewii, Incarvillea olgae*

**Floristic and habitat characteristics:** This is the central, widely distributed association of the Pamirian group of alpine scree vegetation. As the scree vegetation inhabits gentle slopes it neighbours the alpine steppe and forb vegetation (Fig. 5e). This is indicated by the presence of steppic plants (e.g. *Cousinia semilacera*) and tall forb plants (e.g. *Tytthostemma alsinoides*) in the plots. Plots of the *Crambo schugnanae-Feruletum grigoriewii* were found in the alpine belt of the Pamirian ranges (Fig. S1) at elevations of approx. 1,100–2,500 m a.s.l. (mean 2,100, Fig. 3a). The phytocoenosis has been found on alkaline limestone or dolomite coarse gravels or cobbles of ca 15 cm in diameter (Fig. 3c). The association inhabits moderately steep slopes (20°–65° with the average of ca 40°, Fig. 3b) and prevailing north-western, southern and south-western expositions (Fig. S2). The total cover of herb layer ranges between 25 and 55%, with a mean of ca 40% (Fig. 4a).

**Nitrophilous species-poor scree and escarpment vegetation of the Mediterranean region (*Cymbalario-Parietarietea diffusae*)**

Vegetation of thermophilous gravelly slopes or walls occurring in Middle Asia is closely related to *Parietario judaicae-Hyoscyamion aurei* S. Brullo et Guarino 1999. However, unlike European stands, in Tajikistan plots of this vegetation type occur frequently in natural habitats. It prefers fine gravelly slopes with a compacted substrate or the typical screes with fine debris. They are distributed mainly on southern, warm slopes in the colline and montane belts (ca 600–2,200 m a.s.l.). Occasionally they grow also in the arid zone of the Eastern Pamir in the subalpine belt up to ca 3,500 m a.s.l. This vegetation might be a progenitor of Eastern Mediterranean *Cymbalario-Parietarietea diffusae* vegetation.

**14.1. *Corydalidetum kashgaricae trigonelletosum gontscharovii* subass. Nova hoc loco (cluster 8, 11 relevés)**

**Type relevé:** Table S1, successive number 169, holotypus hoc loco

**Diagnostic species:** *Astragalus trachycarpus*, *Corydalis kashgarica*, *Pulicaria salvifolia*, *Trigonella gontscharovii* (= *Melilotoides gontscharovii*, *Melissitus gontscharovii*)

**Constant species:** *Glaucium squamigerum*, *Pulicaria salvifolia*

**Dominant species:** *Astragalus trachycarpus*, *Trigonella gontscharovii*

**Floristic and habitat characteristics:** *Corydalidetum kashgaricae* Nowak et al. 2016 was described from the western Pamir-Alai Mts inhabiting the steep, compact conglomerate screes in the montane belt (Fig. 6g). During the research in similar habitat the community with *Trigonella gontscharovii* was found on steep, crumbly screes mainly in the Darvaz Range (Fig. S1). The only difference is that this community occupies less compacted screes with higher ingredient of clay particles. The main diagnostic species was recorded in the western Pamir-Alai ranges; however, it seems to prefer the subhumid and humid areas of the southern slopes of Hissar and Darvaz Mts. The subassociation occurs on very steep screes and landslides with high rate of surface runoff (ca 80° on average, Fig. 3b). Plots of the vegetation were found mainly in the montane belt, within the elevational range between 1,350 and 2,250 m a.s.l. (mean 1,700, Fig. 3a). The community develops mainly on southern and south-eastern expositions (Fig. S1). The total cover of herb layer reaches moderate values with mean of approx. 30% (from 10 to 45%; Fig. 4a, 6b).

**15. Community of *Corydalis fimbrillifera* (Fig. 2, cluster 9, 4 relevés)**

**Diagnostic species**: *Artemisia porrecta, Corydalis fimbrillifera, Rosularia lutea*

**Constant species**: *Corydalis fimbrillifera*

**Dominant species**: *Corydalis fimbrillifera*

**Floristic and habitat characteristics**: Only few plots of this community were found in the western Pamir Mts (Fig. S1). The species-poor stands of this vegetation are clearly different and separated by the TWINSPAN algorithm. However, because of the scarcity of relevés and supposed anthropogenic disturbances on the sampling sites, we decided to leave it rankless. Plots of the community were found on dry, compact, steep escarpments of roads or natural steep slopes composed of fine gravelly sediments. The community occupies slopes of the inclination up to 70° (Fig. 3b) with northern exposition (Fig. S2). The sampling was conducted in the subalpine belt at ca 1,900 m a.s.l. in the arid zone (Fig. 3a). The found plots were species-poor with a maximum of seven species per relevé (Fig. 4c) and the cover reaching up to 20% (Fig. 4a).

**High-elevation arid steppes and semi-deserts (*Ajanio-Cleistogenetea songoricae*)**

**Alliance: *Piptathero gracilis-Artemision brevifoliae* Eberhardt** 2004

This semi-desert vegetation was originally described from the Hindukush Mts in northern Pakistan

(Eberhardt 2004; Peer et al. 2007). It inhabits arid, high mountain plateaus. The vegetation exhibits sparse plant cover (approx. 5–45%) and low species richness (approx. 3–15) and has often dwarf-shrub or cushion physiognomy. Among species adapted to such harsh environments that contributes to Central Asian screes are: *Acantholimon diapensioides*, *Corispermum hilariae*, *Elymus schugnanicus* (*Roegneria schugnana*), *Krascheninnikovia ceratoides*, *Oxytropis chiliophylla*, *Semenovia pamirica* and *Stipa glareosa.* These plant communities were included in the alliance *Piptathero gracilis-Artemision brevifoliae* Eberhardt 2004 as a mountain dwarf-scrub steppe of high Central Asia.

**16. *Artemisio glaucinae-Salsoletum paulseni* Nowak et al. hoc loco (**Fig. 2**, cluster 2, 14 relevés)**

**Type relevé**: Table S1, successive number 182, holotypus hoc loco

**Diagnostic species**: *Anabasis salsa, Artemisia glaucina* (= *Seriphidium glaucinum*), *Peganum harmala, Salsola paulsenii, S. australis* (= *S. pestifera, Salsola kali subsp. ruthenica*)

**Constant species**: *Anabasis salsa*

**Floristic and habitat characteristics:** The Vakhan corridor in eastern Pamir belongs to the dry, arid climatic zone with precipitation of about 100–150 mm per year. In such conditions the semi-desert vegetation prevails on extensive slopes of Shakhdarian, Hindukush and South-Alichurian ranges. Phytocoenoses of drought adapted species with *Salsola paulsenii*, *S. australis* and *Peganum harmala* were found on southern and south-eastern slopes between Zoogvand and Vrang on mobile, gravelly slopes (Fig. S1). Because the main diagnostic plant *Salsola paulsenii* is distributed additionally in south-western and northern semi-deserts of Tajikistan, this vegetation type can have a larger extent of occurrence in Middle Asia. In the Eastern Pamir the association inhabits the alpine belt at elevations of 2,750–2,950 m (Fig. 3a). The association prefers coarse-grained screes of limestone, schist and dolomite rocks. The plots of the association were found on moderately sloping hills with gentle inclinations (mean approx. 25°, Fig. 3b). The community has a rather open physiognomy due to very scarce abundance of the species (3–7 taxa per plot, Fig. 4c). The total cover of the herb layer ranged between 10 and 25% with a mean value of approximately 15% (Fig. 4a).

**17. *Cousinio pannosae-Artemisietum skorniakovii typicum* Nowak et al. hoc loco (Fig. 2, cluster 3, 30 relevés)**

**Type relevé**: Table S1, successive number 208, holotypus hoc loco

**Diagnostic species**: *Acantholimon velutinum, Ajania tibetica, Artemisia skorniakovii* (= *Seriphidium skorniakovii*), *Astragalus lasiosemius, Cousinia pannosa, Linaria sessilis, Leymus lanatus* (= *Malacurus lanatus*), *Oxytropis trichosphaera, Polygonum mezianum, Stipa orientalis*

**Constant species**: *Artemisia skorniakovii*, *Cousinia pannosa*

**Dominant species**: *Acantholimon velutinum, Ajania tibetica, Astragalus lasiosemius, Leymus lanatus*

**Floristic and habitat characteristics:** The occurrence area of this association is confined to arid zone of high Pamir (Fig. S1). This vegetation is closely related to cold steppes and semi-deserts of the highest plateaus of Central Asia. It supposedly occurs also in Tibet, northern Pakistan and Afghanistan. Plots of *Cousinio pannosae-Artemisietum skorniakovii* inhabits the alpine belt in a distinct Pamirian landscape of gentle hills with sparse vegetation at elevations of ca 3,700–4,300 m a.s.l. (Fig. 3a). The phytocoenoses were scattered on coarse or fine debris cones of fans, aprons, taluses and other land forms. The community develops on gently sloping screes with mean inclination of about 15° (Fig. 3b). *Cousinio pannosae-Artemisietum skorniakovii* inhabit mainly slopes with southern and eastern expositions (Fig. S2). The association is species-poor, having on average nine taxa per plot (Fig. 4c). The mean herb cover value for the association is close to 30% (Fig. 4a, 6c).

Because of habitat differences, mainly the slope steepness it is possible to distinguish within *Cousinio pannosae-Artemisietum skorniakovii* the subassociation dominated by prominent grass of arid plateaus of high Central Asia, *Leymus lanatus*.

**17.1. *Cousinio pannosae-Artemisietum skorniakovii leymetosum lanati* Nowak et al. hoc loco**

**Type relevé:** Table S1, successive number 191, holotypus hoc loco

**Diagnostic species**: *Leymus lanatus* (= *Malacurus lanatus*)

**Constant species**: *Cousinia pannosa, Hedysarum cephalotes, Leymus lanatus, Polygonum mezianum, Stipa orientalis*

**Dominant species**: *Acantholimon velutinum, Leymus lanatus*

**Floristic and habitat characteristics:** *Leymus lanatus* is an endemic plant of highlands of Central Asia with the range restricted to Eastern Pamir. The plots with the domination of this grass were classified together with vegetation of *Artemisia skorniakovii* and *Cousinia pannosa* due to similar floristic composition and similar habitat preferences (Fig. 6a). However, *Leymus lanatus* forms distinct stands on steeper slopes with unstable, coarse, granite debris. Phytocoenoses of *Leymus lanatus* inhabit the highest locations in the Eastern Pamir in the upper alpine belt at elevations of 3,550–4,300 m. The association prefers coarse-grained unstable screes of granite rocks. The plots of the association were found on moderately sloping hills with moderate inclinations (mean approx. 35°) and southern or south-eastern expositions. The average cover of species is moderate with 15–35% (mean ca 30%). As other communities of this arid landscapes, the subassociation is species-poor with low a number of taxa – eight to thirteen taxa per plot.

General floristic features and relations between plant communities

The total number of taxa recorded in the whole dataset (222 relevés) is 570, with only nine exceeding 5% of constancy. The group of species with the highest frequencies includes mainly typical scree plants like *Scariola orientalis* (50 occurrences), *Artemisia rutifolia* (48), *Callipeltis cucullaris* (45), *Galium spurium subsp. spurium* (42), *Eremopoa persica* (40), *Polygonum polycnemoides* (30), *Silene brahuica* (21) and *Artemisia santolinifolia* (21). However, the most frequent species is a steppe-ruderal grass – *Bromus tectorum* (57). There are also species from semi-deserts like *Krascheninnikovia ceratoides* (30) or *Stipa orientalis* (27) with fairly high frequency (Nowak et al. 2020a). All these species are well adapted to surface runoff of rock material and drought conditions. It is worth noticing that the species list of the scree habitat includes an inconsiderable number of taxa that have different ecological profiles, particularly the rock and ruderal plants. Despite the close similarity of rock species this group includes only few taxa in the dataset, for example *Allium oschanini* (7), *Kudryaschewia allotricha* (4) or *Dasiphora parviflora* (3). Also, ruderal plants that often occur in scree or even rock vegetation have insignificant contribution in the screes of the Pamir and western Tian Shan, with only few examples like *Fumaria vailantii*, *Lactuca serriola* or *Malva neglecta* (all 4 occurrences). Representatives of other habitats, as for example xerophytic shrubs (e.g. *Rosa ecae*, *R. huntica*), tall herbs (e.g. *Geranium regelii*, *Lophanthus elegans*) or broad-leaved forests (e.g. *Impatiens parviflora*) were negligible. Hence, as was found for screes of the western Pamir-Alai (Nowak et al. 2015, 2016), the substantial compositional structure of the Pamir and western Tian Shan scree vegetation is almost exclusively typical and unique for this kind of habitat.

As a result of the TWINSPAN classification, five main groups at the alliance level have been distinguished within three classes. The groups are very well distinguished in the NMDS diagram (Fig. 7). The dominant group includes typical screes of Central Asia, namely *Artemisio santolinifoliae-Berberidetea sibiricae*, which is the focal and mostly diverse chasmophytic vegetation in our dataset. It is divided into three main alliances: *Artemision rutifoliae* (typical for the eastern Irano-Turanian region, with strong influences of the continental climate), *Ferulo foetidissimae-Vicion kokanicae* (scree vegetation of the warmer Irano-Turanian subclimate typical for lower Middle Asia) and newly established *Ferulion grigoriewii* that includes scree communities of the Pamir, inhabiting particularly the montane and subalpine belt. Additionally, the first cluster was separated as the most outlying group representing the northernmost plots from the Terskay Alaa-too Mts. That were assigned as the community of *Scutellaria oligodonta-Lonicera semenovii* and left rankless. Within the vegetation of Central Asian screes, the TWINSPAN algorithm positioned the plots representing the class *Cymbalario-Parietarietea diffusae* – nitrophilous vegetation of steep, compacted screes and walls, which is represented by one alliance *Parietario judaicae-Hyoscyamion aurei*. The analysis reveals also vegetation closely related to semi-deserts of Asian highlands that should be assigned to *Ajanio-Cleistogenetea songoricae* and *Artemision brevifoliae* after Eberhardt (2004), who found similar communities in the highlands of Hindukush in northern Pakistan. This group seems to be fairly heterogeneous and needs further studies to clarify and make more consistent the relationships of the communities separated by the algorithm on the left side of the diagram (Fig. 2).

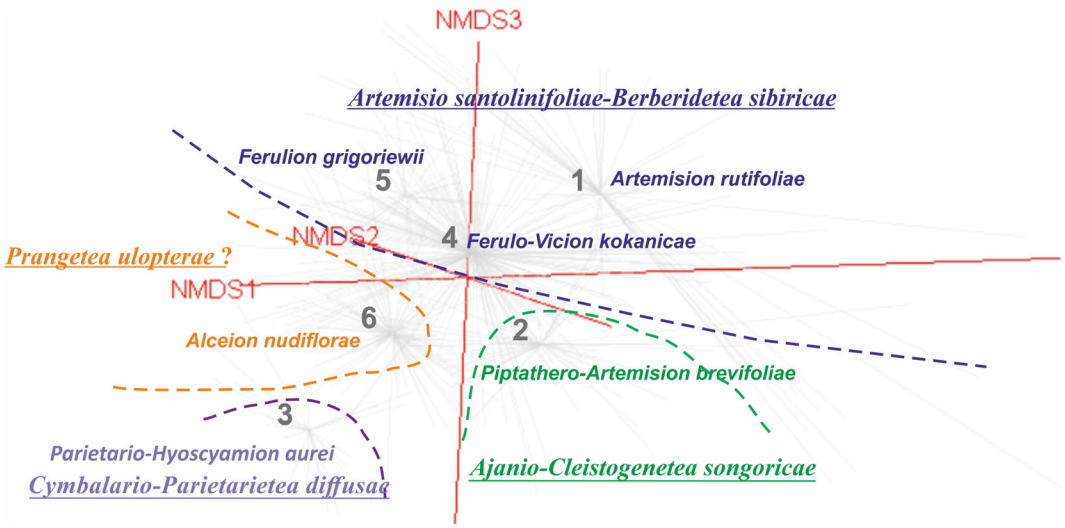


**Fig. 7** NMDS diagram for 222 plots of scree vegetation of Middle Asia with highlighted classes (underlined) and alliances. Note that plots of the *Alceion nudiflorae* alliance (Nowak et al. 2016) were used in the NMDS plot to facilitate the interpretation of the results.

## Discussion

Chasmophytic habitats clearly dominate the landscape of the montane and alpine belts of eastern Middle Asia (Nowak et al. 2020a). Together with zonal steppes, semi-deserts and alpine grasslands the scree vegetation is the most prominent in this region. Like in other ranges with the Mediterranean and Irano-Turanian climate, such as Northern Morocco (Deil 1994; Deil and Hammoumi 1997), Spain (Ortiz and Rodríguez-Oubiña 1993; Galán de Mera et al. 2000), Crete and mainland Greece (Dimopoulos et al. 1997), Bulgaria (Mucina et al. 1990), and Turkey (Hein et al. 1998; Parolly 1998), a diverse relief and alpine orography of the land with rocky canyons, V-shaped valleys, steep slopes, cliffs, solid walls, rocky towers combined with intensive weathering (extreme yearly and diurnal T amplitudes) creates a very diverse habitats (taluses, aprons, fans, cones, rock fields etc.) that promote a diversity of scree vegetation. Additionally, various bedrock types, diversified expositions and inclinations along with different scree mobility and particle size contribute to the very rich mosaic of microhabitats that can harbour a number of vegetation types. Moreover, the mountainous character of a vast area with a lot of ranges and separate massifs reveals the pattern of isolated terrestrial 'islands' serving as evolutionary radiation centres (Snogerup 1971; Deil 1999; Whittaker and Fernandez-Palacios 2007). For example, the montane belt gorges on the great plateaus margins after Oligocen-Miocene uplift of the Pamir and Tian Shan serve as a 'museum' of endemic chasmophytic plants belonging to a number of genera, for example *Andrachne*, *Cephalopodum*, *Cylindrocarpa*, *Fumariola*, *Iskandera*, *Kafirnigania*, *Nathaliella*, *Physochlaina*, *Sergia*, *Spirostegia* or *Uechtritzia*. The changing climate blocked the westerlies and enhanced aridification and the recycling of precipitation patterns (Caves et al. 2016; Bougeois et al. 2018), which triggered the escape of plants to rocks, leading to the development of a number of adaptations to rupicolous habitats, such as new strategies for settlement, reproduction and mitigation of drought stress (Kontopanou and Panitsa 2020). Moreover, chasmophytic habitats have become a cradle of endemism in the high mountains. The highlands of Middle Asia offer particularly suitable conditions for neoendemism. The extensive, deserted territories of Eastern Pamir, a considerably diversified landscape of rocks put a very strong adaptation pressure on plants. A number of species is not able to withstand that kind of harsh environment and disappeared, but a fairly numerous lineages evolved through divergence and reproductive isolation or through hybridization and polyploidy (Kruckeberg and Rabinowitz 1985). Therefore, the species pool of the scree habitat is particularly rich in Middle Asia and thus we can expect remarkable diversity among the plant communities of taluses and screes. This is evidenced by the high degree of endemism both

in the flora of Middle Asia (ca 30%; Nowak et al. 2011) and the share of endemic species in rupicolous communities (see Nowak et al. 2015, 2016).

The establishment of a comprehensive hierarchical system of scree and rock habitats of Middle Asia is still not completed. Despite a number of attempts (e.g. Nowak et al. 2014a, c, 2015) for rock habitats and additionally for screes (Nowak et al. 2015, 2016), altogether they were based on approximately 600 relevés. Our current investigation (2017–2019) yielded about 1,000 new relevés, 222 of which were recorded in screes. This significantly supports the improvement of the classification of scree habitats.

The screes of Middle and Central Asia significantly differ from European ones. There is almost no species shared by both areas (Europe and Middle Asia) that is diagnostic for *Thlaspietea rotundifolii* vegetation (Valachovič et al. 1997; Mucina et al. 2016). On the generic level, only a few representatives of the genera *Arabis*, *Oxyria*, *Poa* and, rarely, *Cerastium* that inhabit colluvial deposits both in the Pamir-Alai Mts and European ranges appear in our dataset. Despite some structural similarities, also the class *Lamio tomentosi-Chaerophylletea humilis*, established for chasmophytic vegetation in the Caucasus, is distinct in terms of species composition. However, closer relations to this area are manifested by the presence of species of the genera *Cerastium*, *Corydalis*, *Jurinea* and *Scrophularia* (Belonovskaya 2012; Belonovskaya et al. 2014). Looking at the physiognomical features of Middle Asian scree communities, particularly in south-western Tajikitsan, Fergana Valley and Uzbekistan, the apparent close relation to Iranian vegetation of *Prangetea ulopterae* Klein 1988 is clear (Klein 1987; Noroozi et al. 2014). The dominant taxa which determine the physiognomy of the plant communities are large herbs of the Apiaceae family (e.g. *Tetrataenium olgae*, *Mediasia macrophylla* and species of genera *Angelica*, *Aulacospermum*, *Ferula*, *Semenovia*, *Seseli*). This type of vegetation is called 'umbeliferniki in Russian literature (see Ovchinnikov 1940; Pavlov 1980), meaning vegetation dominated by Apiaceae species. Despite the physiognomical similarity of this type of vegetation, it is still significantly different in species composition. In addition, large Umbelifers occur in Tajikistan in different habitats, for example meadows and pastures (e.g. *Ferula gigantea*, *F. foetida*, *F. tadshikorum*, *F. karatavica*), tall forb communities (e.g. *Prangos* spp., *Ferula kirialovii*, *F. clematidiifolia*, *Heracleum lehmannianum*) or rock habitats (e.g. *Kafirnighania hissarica*, *Ferula botschanzevii*, *F. lithophila*, *F. tschimganica*, *F. ugamica*, *Zeravshania regeliana*). Within the presented scree communities, those included in *Ferulo foetidissimae-Vicion kokanicae* are the most similar to *Prangetea ulopterae*, although they are still very distinct compositionally. Further studies and a survey of a large database are needed to finally resolve the relations between *Prangetea ulopterae* and *Artemisio-Berberidetea*. In the Pamir-Alai it might be possible that both vegetation types occur, as the area straddles two phytogeographical subregions – the Western Asiatic Subregion (Turkestanian Province) and the Central Asiatic Subregion (Central Tian Shan and Tibetan Provinces; see Nowak et al. 2020a). Therefore, the order *Sileno brahuicae-Lactucetalia orientalis* can finally be included in this typically Irano-Turanian vegetation. Plots representing the *Prangetea ulopterae* class might be the westernmost scree vegetation of the Pamir-Alai, namely communities included in the *Alceion nudiflorae* alliance (Fig. 7; Nowak et al. 2016). This vegetation type should therefore be reserved for scree plant communities of the montane and alpine belts of mountain ranges of the western Pamir-Alai, Kopet-Dag, Alborz, Zagroz, western Hindukush and Karakorum Mts, and possibly also the lower belts of the western Himalayas. Species of the Irano-Turanian distributional type are the structural and the main compositional elements of this vegetation. They include *Artemisia persica*, *Callipeltis cucullaris*, *Eremopoa persica, Hypericum scabrum*, *Lactuca orientalis* (*Scariola orientalis*), *Pachypterygium brevipes, Papaver pavoninum*, *Piptatherum purpurascens*, *Polygonum polycnemoides*, *Scutellaria intermedia*, *Silene brahuica* and *Trichodesma incanum*. Phytocoenoses included in this order (*Sileno brahuicae-Lactucetalia orientalis*) occupy scree at different elevations from ca 300–500 up to 4,000–4,500 m a.s.l. Although there is still a considerable overlap between those main vegetation scree types in Middle Asia, the pattern and relation between the Mediterranean *Cymbalario-Parietea diffusae*, western Irano-Turanian *Prangetea ulopterae* and eastern Irano-Turanian *Artemisio santolinifoliae-Berberidetea sibiricae* is fairly clear in our dataset (Fig. 7).

Towards the north and east, and towards higher elevations, the share of typical Irano-Turanian scree species decreases, and dwarf shrubs (e.g. *Artemisia*) and scrubs (e.g. *Atraphaxis*, *Berberis*, *Cerasus*, *Ephedra*,

*Rosa*) take the advantage. This makes this vegetation more similar to *Artemisio-Berberidetea* coined for Central Asia. In addition, prominent components of Middle Asian chasmophytic communities, including taxa of the genera *Acantholimon*, *Corydalis*, *Cousinia*, *Euphorbia*, *Ferula*, *Rheum*, *Scrophularia* and *Scutellaria*, to some extent also occur in Central Asiatic region (Ermakov et al. 2006). For the Western Sayan Mts and Altai, climate continentality with considerable fluctuations in temperature and the aridity of the steppe and forest-steppe belts were indicated as the main determinants of vegetation. These two environmental factors are responsible for weathering dynamics and scree mobility. Extreme diurnal temperature oscillations cause rapid erosion of rock walls and create severe conditions for plants, which, along with their communities, have to adapt to these unfavourable habitats and respond to an unstable and dry substrate. Very similar processes are known from high elevations of the Pamir and from the alpine belts of the eastern Pamir-Alai and western Tian Shan. The harsh environment and strong differences in temperature during the year seem to be essentially the same. The mountains of eastern Middle Asia are generally included in the temperate continental climatic zone (Vladimirova 1968). Although some authors have stressed that Tajikistan is influenced by a Mediterranean-type bioclimate, they have also pointed out that this is rather an oro-mediterranean subtype overridden by extreme and harsh alpine conditions (Rivas-Martínez et al. 2011).

The floristic composition of Central Asian talus vegetation shares some apparent similarities with the researched vegetation plots. The most important seems to be the presence of several common genera of scrubs such as *Atraphaxis*, *Berberis*, *Cotoneaster*, *Lonicera, Rhamnus* and *Spiraea*, and subshrubs such as *Artemisia*. Some species, such as *Artemisia dracunculus, A. santolinifolia*, *A. ruthenica*, *Crepidifolium akagi* and *Stipa orientalis*, occur in both areas. Of course, the particular features of habitats of colluvial cones and of screes with various expositions and particle size are also comparable. For these reasons, regarding physiognomical, structural and environmental similarities, we propose to include the scree vegetation of the montane and alpine belts of the Pamir and western Tian Shan Mts into the class *Artemisio santolinifoliae-Berberidetea sibiricae* Ermakov et al. 2006.

## Environmental features determining the floristic composition of communities

Despite considerable compositional differences between communities due to the high beta diversity of scree vegetation in Middle and Central Asia, there are also other factors controlling the diversity of these plant communities. They are composed of species adapted to frequent disturbances caused by rolling stones and landslides, as well as to a harsh environment with a lack of nutrients and considerable drought. In the study area there are strong environmental and climatic gradients, with a clear increase in humidity towards the north and distinct division between a Mediterranean-like climate in the west and a temperate one in the north-east. As in other studies conducted in Europe and Southwest Asia, plant communities of screes in Middle and Central Asia are influenced mainly by the dynamics of debris runoff, phytogeography, bedrock type and elevation (Valachovič et al. 1997; Parolly 1998; Ermakov et al. 2006). Additionally, the particle size of scree material has an effect on the development of particular vegetation types, but not as strong as has been found for western Pamir-Alai screes (Nowak et al. 2016). *Angelicetum ternatae* and *Eremuretum turkestanicae* are examples of associations with an apparent preference for stable, coarse rock cobble cones. This type of phytocoenoses occupy lower parts of the talus front zone with the largest debris. Additionally, in the Pamir, communities with *Bunium badachschanicum* and *Cousinio pannosae-Artemisietum skorniakovii leymetosum lanati* prefer coarse cobble material; however, they occupy mobile screes with vegetation of a pioneer character. On the opposite extreme of the vegetation variability related to particle size are communities of both species of the genus *Corydalis* (*C. kaschgarica* and *C. fimbrillifera*) and the association of *Helianthemetum songoricae.* The first two communities typically inhabit compact fine gravel debris on steep escarpments whereas the last one prefers sunny, gently sloping hills with stable, fine-grained material. Scree mobility plays important role in the diversification of scree vegetation of Middle and Central Asia. The disturbance rate caused by land runoff is a crucial factor for plant competitiveness and growing abilities. There are scree communities very well adapted to frequent disturbance by a surface rock runoff such as *Allietum galanthii*, *Cousinio pannosae-Artemisietum skorniakovii*, *Feruletum kosopolianskyi* and community of *Bunium*

*badachschanicum*. One example of a plant community that requires stabilized substrates is *Helianthemetum songarici*. Distributed in high mountain landscape, the scree communities of Middle and Central Asia are well adjusted to different elevations and occur along a considerable elevational amplitude, between 800 and 4,300 m a.s.l. The highest-elevated sites (for some plots almost subnival) were occupied by communities of *Scutellaria oligodonta-Lonicera semenovii* and *Cousinio pannosae-Artemisietum skorniakovii.* Among the plots of the second association, plots of the subassociation dominated by *Leymus lanatus* are the highest elevated in the Eastern Pamir. In the lowest, warmest sites the *Perovskietum scrophulariifoliae* and *Eremuretum turkestanicae* communities were found, besides that of *Corydalidetum kashgaricae trigonelletosum gontscharovii.* The size of rock debris combined with the climatic factors also differentiate scree vegetation because they are responsible for soil development and nutrient availability. There is a group of plant communities within the scree vegetation of Middle and Central Asia that prefers deep soils beneath the rocky surface. Communities of *Ferula bucharica* and *Trigonella gontcharovii* in the Pamir-Alai and of *Scutellaria oligodonta-Lonicera semenovii* in the Tian Shan inhabit such humid and soil-rich screes.

## Conclusions and further prospects

This paper reports on the first stage of research into the classification of scree vegetation in Tajikistan. Surely, without sufficient sampling in neighbouring areas, particularly in northern Afghanistan and eastern China, it is hardly possible to reach a definitive conclusion regarding the classification of this rich vegetation. Tajikistan is a 'country of stones' with an immense number of scree or scree-like habitats, sometimes occurring in sophisticated mosaics with bare semi-deserts, 'stony' tall forb communities and petrophytic vegetation. Still, finding the relation between all these communities remains challenging. However, our survey, resulting in 25 associations, four alliances, four subassociations and eighteen communities within one order of scree vegetation (Nowak et al. 2015, 2016), is the first comprehensive treatment that can be used as a base for further refinements and improvements. To obtain a better picture of the classification of the vegetation in the stony landscape of Tajikistan, the rock vegetation of the Eastern Pamir and gravel-bars of alpine rivers have to be surveyed. These habitats harbour a number of different microhabitats for a numerous chasmophytic plants and their relation to typical screes has to be resolved in detail. Additionally, describing the pattern of scree and tall-forb vegetation across the Irano-Turanian region, with a focus on the southern Bukhara and Kopet-Dag ranges in Uzbekistan and Turkmenistan, would be very beneficial in completing the knowledge of scree vegetation of Middle Asia and to find a definitive answer to the question: 'What is the geographical and ecological relation between already established classes *Artemisio-Berberidetea* and *Prangetea ulopterae*?'

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