

Vegetation of the rock outcrops and screes in the forest-steppe and steppe belts of the Altai and Western Sayan Mts., southern Siberia

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with 10 figures and 2 tables

Abstract. A new concept of classification of petrophytic vegetation, i.e. plant communities on rock outcrops and screes, is proposed for the steppe and forest-steppe belts of the southern Siberian mountains, using the Braun-Blanquet approach and original relevés from the Altai and Western Sayan Mts. In these areas with arid continental climate, the species composition of petrophytic vegetation seems to be less differentiated from the other habitats than is usual in Europe or the Far East. The main habitats of petrophytic vegetation include rock crevices, shallow soils on weathered rock outcrops, disturbed screes with herbaceous vegetation, and shrubberies in less disturbed places. In the proposed classification petrophytic vegetation is divided into three phytosociological classes. The vegetation of moderately dry rock crevices is included in the Eurasian class *Asplenietea trichomanis* (Br.-Bl. in Meier et Br.-Bl. 1934) Oberdorfer 1977 and the alliance *Selaginellion sanguinolentae* Hilbig 2000. Vegetation of disturbed or strongly drought-stressed rock outcrops and screes is included in the class of central Asian steppes, *Cleistogenetea squarrosae* Mirkin et al. ex Korotkov et al. 1991. Within this class, vegetation with predominance of succulent plants is assigned to the alliance *Sedion hybridi* all. nova and xeric rock-crevice vegetation to the alliance *Eritrichio pectinati-Selaginellion sanguinolentae* all. nova. A distinct type of central Asian petrophytic vegetation is assigned to the class *Artemisio santolinifoliae-Berberidetea sibiricae* cl. nova, which includes xeric shrubberies on mobile screes and rock outcrops of different lithology. Seven associations, three subassociations and four communities without syntaxonomic rank are documented in an ordered species-by-relevé table and briefly described with respect to their phytosociological affinities and ecology. The DCA ordination of the relevés was used to demonstrate patterns of floristic differentiation of the higher vegetation units in the Altai and Western Sayan.

Keywords: *Artemisio-Berberidetea*, *Asplenietea trichomanis*, *Cleistogenetea squarrosae*, chasmophytic vegetation, phytosociology, syntaxonomy.

Introduction

The mountain systems of the Altai and Western Sayan are situated in the centre of Eurasia, on the boundary between northern and central Asia (SOCHAVA & TIMOFEEV 1968). The diverse types of steppe, forest and high-

mountain vegetation of these mountains have been studied with different approaches, ranging from the traditional Russian approach based on dominant species (KUMINOVA 1960, RECHAN & KRYLOV 1963, KUMINOVA et al. 1976, 1985, SEDEL'NIKOV 1988, NAMZALOV 1994) to the Braun-Blanquet approach (ZHITLUKHINA & MIRKIN 1987, ZHITLUKHINA 1988, HILBIG 1990, 1995, 2000a, 2000b, HILBIG et al. 1999, ERMAKOV 1995, 1998, ERMAKOV et al. 1991, 1999, 2000a, 2000b, KOROLYUK 2002). However, petrophytic vegetation, i.e. plant communities occurring on rock outcrops, cliffs, screes and talus slopes, is still very poorly known. Besides rather general descriptions of communities applying the dominant approach of traditional Russian geobotany, the only studies of some communities of rock-crevice and scree vegetation that used the Braun-Blanquet approach and data on floristic composition were performed in Mongolia (HILBIG 1995, HILBIG et al. 1999) and southern Tuva (HILBIG 2000a). The diversity of petrophytic vegetation in the Russian part of the Altai and Western Sayan has so far remained nearly unknown (but see KHANMINCHUN 1975).

The purpose of this paper is to identify the main types of petrophytic vegetation in the Russian part of the Altai and Western Sayan, based on field sampling and numerical analysis of relevés. Our aim is also to outline the relationships between vegetation pattern and types of rock habitats with different surface instability, and to compare local patterns with those previously observed in other regions of Europe and northern Asia.

Study area

The study area covers the forest-steppe and steppe belt in the central parts of the Altai and Western Sayan Mts. (Fig. 1) at altitudes between 350 and 1900 m. These mountain systems are intersected by the valleys of the Katun' and Yenisei rivers that run approximately in a south-north direction. The valleys contain numerous rock outcrops, cliffs, and talus slopes. Metamorphic bedrock predominates, most often represented by base-rich chlorite slates, whereas igneous rocks and limestones occupy small areas. The landforms of the ridges that surround the river valleys are very diverse and the slopes tend to be very steep in places. In the Katun' river valley (Altai) a system of high Pleistocene terraces is developed (RUDOY 2002), while the Yenisei valley (Western Sayan) is flooded by a water reservoir some 200 km long and 200 m deep, which was built in 1982.

The climate of the study area is continental in the northern part and ultracontinental in the southern part. The mean annual temperature is between -3 and $+4$ °C, the temperature in the coldest month (January) varies from -31 to -15 °C, in the warmest month (July) from $+16$ to $+19$ °C, and the total annual precipitation is between 220 and 400 mm.

The area is situated in two vegetation belts: forest-steppe and steppe. Forest-steppe occurs in the northern part and is made up of hemiboreal forests, confined to the north-facing or shaded mountain slopes (ERMAKOV et al. 2000a), and meadow-steppes on the drier south-facing slopes. The hemiboreal forests consist of larch (*Larix sibirica*) or a mixture of birch and

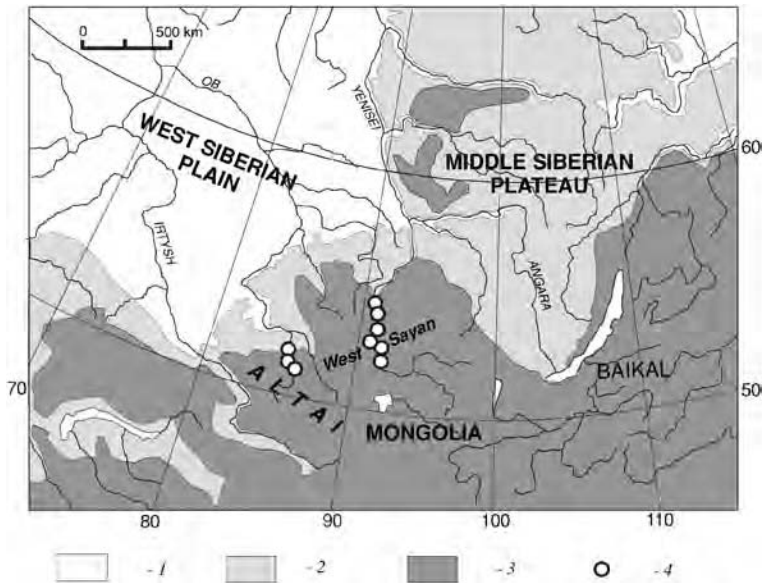


Fig. 1. Locations of the sites of studied rock-outcrop and scree vegetation in the Altai and Western Sayan Mts. 1 – plains and lowlands (altitudes of 0–200 m); 2 – lower plateaus and elevated plains (altitudes of 200–800 m); 3 – plateaus and mountains (altitudes of 800–4000 m); 4 – locations of the study sites.

larch (*Betula pendula*, *Larix sibirica*), in places also with pine (*Pinus sylvestris*). Various types of central Asian steppes predominate in the southern part of the study area. They occupy a broad altitudinal range on the south-facing mountain slopes (400–1800 m, occasionally up to 2000 m) and also predominate at lower altitudes on the north-facing slopes (400–800 m).

Materials and methods

The vegetation of rock outcrops and talus slopes was sampled in the forest-steppe and steppe belts of the central part of the Altai and Western Sayan Mts. in 2000–2003, with the aim of covering a broad range of habitats in different areas. The focus was on vegetation dominated by herbaceous plants or shrubs. Only specific vegetation types of rock outcrops and scree were sampled, whereas the vegetation that was not markedly different from the surrounding sites with more developed soil was not studied. Selected sites were documented with relevés, i.e. plots of 10–100 m² in size where all the vascular plants, and usually also bryophytes and macrolichens were recorded and assigned a cover-abundance value on the Braun-Blanquet scale. A total of 108 relevés were sampled (Fig. 1).

The classification of plant communities was carried out using the Braun-Blanquet approach (WESTHOFF & van der MAAREL 1973). The relevés were

stored in the TURBOVEG database (HENNEKENS & SCHAMINÉE 2001) and classified by TWINSpan (HILL 1979). For every degree of the Braun-Blanquet scale, a new pseudospecies was introduced in TWINSpan, i.e. classification used cover-abundance information. To arrive at floristically and ecologically uniform units, TWINSpan results were manually modified by merging some groups and shifting a few relevés from one cluster to another. In order to check the quality of the resulting classification, another classification of the data set was performed by the cluster analysis, using Ward's method and Euclidean distance, from the STATISTICA software. The values of cover-abundance on the Braun-Blanquet scale were used as input data in this analysis. Detrended correspondence analysis (DCA) ordination using DECORANA (HILL & GAUCH 1980) was carried out in order to show the position of the already distinguished vegetation types along the main gradients.

The classification is presented in a species-by-site table, in which diagnostic species were determined for each vegetation unit using the indicator species analysis (DUFRENE & LEGENDRE 1997). We used a modified version of this analysis (CHYTRÝ et al. 2002), which takes into account only species presences/absences rather than cover-abundances and compares the occurrence of species in the relevés assigned to the considered vegetation unit against all the other relevés in the data set. Compared with other methods used to determine diagnostic species, indicator species analysis tends to underestimate the diagnostic value of rare species. This means that species with a high indicator value must have a high occurrence frequency in the target vegetation unit (CHYTRÝ et al. 2002). Species with an indicator value higher than 40 were considered diagnostic, provided their concentration in the target vegetation unit differed from random expectation at $P < 0.001$ (Fisher's exact test). Indicator values were calculated using the JUICE program (TICHÝ 2002). Species names follow the list of vascular plants of the former USSR (CHEREPANOV 1995; electronic version prepared by D. Geltman). Records of bryophytes and lichens are not shown in the table due to their inconsistent recording in different relevés. Nomenclature of syntaxa follows the rules of the International Code of Phytosociological nomenclature (WEBER et al. 2000).

Results

Classification

Based on the TWINSpan results 12 groups of relevés were distinguished, each with a distinct floristic composition and clear ecological interpretation. The similarity structure among these groups is shown in the cluster analysis dendrogram (Fig. 2), which corresponds well with the accepted classification, thus confirming its robustness. After comparison of these groups with the phytosociological literature, we suggest their syntaxonomic interpretation into three classes, *Artemisio santolinifoliae*-*Berberidetea sibiricae*, *Cleistogenetea squarrosae* and *Asplenietea trichomanis*,

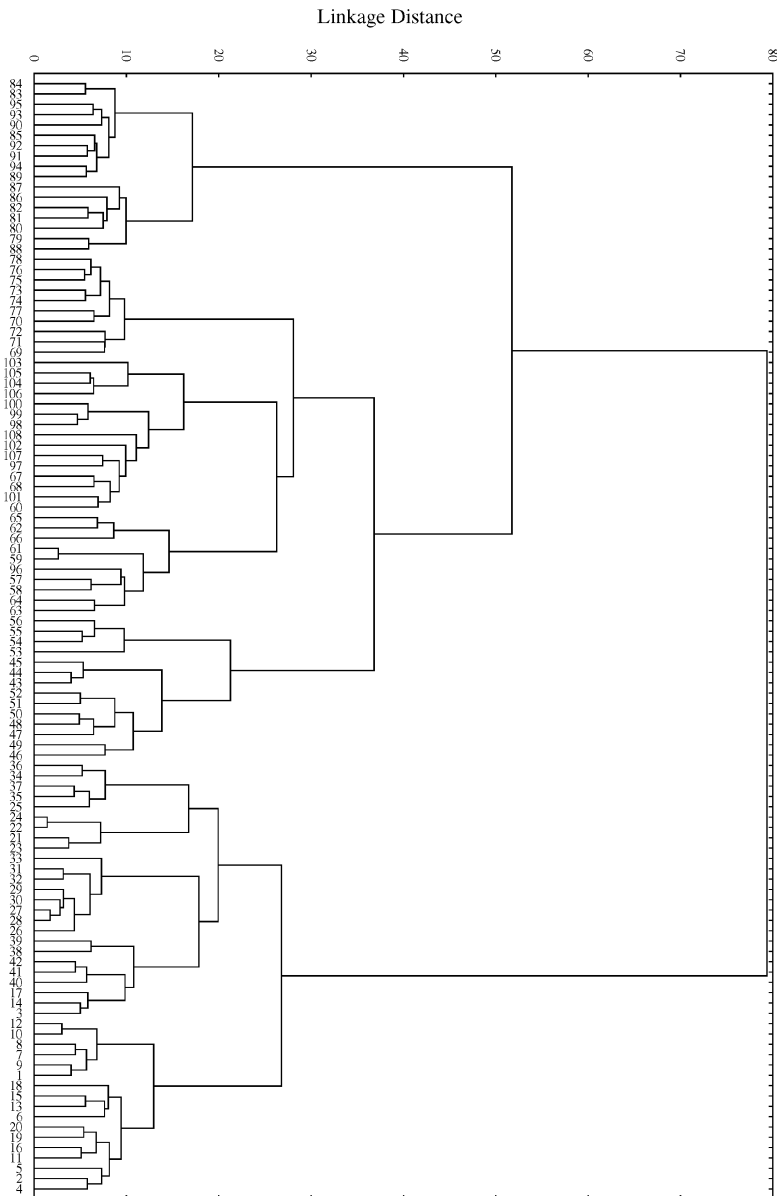


Fig. 2. Dendrogram of 108 relevés of rock-outcrop and scree vegetation (Ward's method, Euclidean distance). 1–20 – *Atraphaxido pun-gentis*-*Artemisietum rutifoliae*, 21–33 – *Vincetoxico sibirici*-*Berberidetum sibiricae*, 34–37 – *Thalictrum foetidum*-*Grossu-laria acicularis* comm., 38–42 – *Elytrigio geniculatae*-*Artemisietum santolinifoliae*, 43–52 – *Grossulario acicularis*-*Spirae-etum trilobatae*, 53–56 – *Sambucus sibirica*-*Grossularia acicularis* comm., 57–66 – *Kitagawio baicalensis*-*Sedetum hybridi*, 67–78 – *Spiraeo trilobatae*-*Sedetum hybridi*, 79–95 – *Galio coriacei*-*Selaginellum sanguinolenta*, 96–100 – *Woodisia ilven-sis*-*Selaginella sanguinolenta* comm., 101–108 – *Hylotelephium populifolium*-*Selaginella sanguinolenta* comm.

and 12 associations or informally named communities roughly corresponding to the associations. The informal names (community) were used if there remained some doubts as to whether the vegetation type has a stable floristic composition that is repeated in similar habitats over larger areas. Some of the associations are subdivided into subassociations, which represent their ecological and geographical differentiation. In some cases the missing data from other areas of Siberia or central Asia do not yet make it possible to propose syntaxa at the level of order or alliance. The proposed taxonomic scheme is as follows:

ARTEMISIO SANTOLINIFOLIAE-BERBERIDETEA SIBIRICAE cl. nova hoc loco

Artemisio santolinifoliae-Berberidetalia sibiricae ordo nova hoc loco

Artemision rutifoliae all. nova hoc loco

Atraphaxido pungentis-Artemisietum rutifoliae ass. nova hoc loco

stipetosum orientalis subass. nova hoc loco

typicum subass. nova hoc loco

spiraetosum mediae subass. nova hoc loco

Grossulario acicularis-Berberidion sibiricae all. nova hoc loco

Vincetoxico sibirici-Berberidetum sibiricae ass. nova hoc loco

Thalictrum foetidum-*Grossularia acicularis* community

Elytrigio geniculatae-Artemisietum santolinifoliae ass. nova hoc loco

Grossulario acicularis-Spiraetum trilobatae ass. nova hoc loco

Sambucus sibirica-*Grossularia acicularis* community

CLEISTOGENETEA SQUARROSAE Mirkin et al. ex Korotkov et al. 1991

Helictotrichetalia schelliani Hilbig 2000

Sedion hybridi all. nova hoc loco

Kitagawio baicalensis-Sedetum hybridi ass. nova hoc loco

Spiraeo trilobatae-Sedetum hybridi ass. nova hoc loco

Eritrichio pectinati-Selaginellion sanguinolentae all. nova hoc loco

Galio coriacei-Selaginellum sanguinolentae ass. nova hoc loco

ASPLENIETEA TRICHOMANIS (Br.-Bl. in Meier et Br.-Bl. 1934) Oberdorfer 1977

Order ?

Selaginellion sanguinolentae Hilbig 2000

Woodsia ilvensis-*Selaginella sanguinolenta* community

Hylotelephium populifolium-*Selaginella sanguinolenta* community

Description of syntaxa

Artemisio santolinifoliae-Berberidetea sibiricae

The class includes central Asian petrophytic vegetation. It is widespread in semi-arid and arid climatic sectors of mountain systems of southern Siberia, northern Mongolia and northern parts of Middle Asia. Communities of the

Artemisio-Berberidetea occupy mobile screes and exposed rocks of different lithology. Scares are formed of stones of metamorphic or granitic rocks up to 60 cm in diameter or small stones and gravels from other bed-rocks such as slates and limestones. Across the entire geographic range, these communities are in contact with zonal types of steppes: Festuco-Brometea at the north-western periphery of the mountain systems and Cleistogenetea squarrosae in their central parts. A typical feature of the class is the predominance of drought-adapted shrubs and semi-shrubs that form a layer with a cover of 10–60%. Herb species are represented by perennial, obligate or facultative petrophytic plants, which are never dominant. Bryophytes and lichens never form a distinct layer. Only *Rhytidium rugosum* and *Abietinella abietina* have higher cover and constancy in some communities. Species richness (without epilithic cryptogams) usually varies between 5–20 species per relevé.

Character species occurring over the whole range of the class are xerophilous shrubs *Artemisia santolinifolia*, *Berberis sibirica* and *Grossularia acicularis*, and xerophilous herbs *Clematis glauca*, *Elytrigia geniculata*, *Erysimum flavum*, *Euphorbia tshuiensis*, *Panzerina canescens*, *Seseli buchtormense*, *Vicia costata* and *Vincetoxicum sibiricum*. Distributions of other character shrub species such as *Artemisia rutifolia*, *Atraphaxis laetevirens* and *A. pungens*, as well as of some herbs (e.g. *Scutellaria grandiflora*, *Stellaria dichotoma*, *Stipa orientalis* and *Youngia tenuicaulis*) are confined to the main part of the class range in the steppe altitudinal belt. In the moderately humid climate of the forest-steppe zone these species occur occasionally. Differential species, including *Allium senescens*, *Artemisia gmelinii*, *Chelidonium majus*, *Ephedra monosperma*, *Euphorbia humifusa* and *Tribulus terrestris*, show high constancy values in the Artemisio-Berberidetea sibiricae but also occur in zonal steppes of the Cleistogenetea squarrosae; some of them are also found in ruderal vegetation. Regional differential species for the western and south-western parts of the class range are *Galium paniculatum*, *Lonicera microphylla* and *Spiraea trilobata*.

Within the Artemisio santolinifoliae-Berberidetea sibiricae we distinguish one order, Artemisio santolinifoliae-Berberidetalia sibiricae (with the same character and differential species as the class), and two alliances, Artemision rutifoliae and Grossulario acicularis-Berberidion sibiricae. The nomenclatural type of the class Artemisio santolinifoliae-Berberidetea sibiricae is the order Artemisio santolinifoliae-Berberidetalia sibiricae (holotypus), and the nomenclatural type of this order is the alliance Artemision rutifoliae (holotypus).

Artemision rutifoliae

The alliance represents the most drought-adapted communities of the Artemisio-Berberidetea. They occur within the altitudinal belt of dry steppes of the Cleistogenetea squarrosae in the southern part of the Western Sayan Mts., Tannu-Ola Mts., and ridges situated in the arid intermountain basins of Tuva and northern Mongolia. The relevés available from

the Western Sayan were included in a single association, *Atraphaxido pungentis*-*Artemisietum rutifoliae*. Diagnostic species of the alliance are therefore identical with those of this association. The *Artemision rutifoliae* is a westerly distributed vicariant of the *Spiraeion aquilegifoliae* Hilbig 2000, which includes scree vegetation in Mongolia and Dauria. The latter contains many eastern Siberian and Manchurian-Daurian species, such as *Amygdalus pedunculata*, *Haplophyllum dauricum*, *Lespedeza dahurica*, *Lilium pumilum*, *Pulsatilla ambigua* and *Spiraea aquilegifolia*. *Spiraeion aquilegifoliae*, as well as another Mongolian-eastern Asian alliance, *Ulmion pumilae* Mirkin et al. ex Hilbig 2000, should be included in the *Artemision santolinifoliae*-*Berberidetea sibiricae*, as well as some vegetation types described from southern Mongolia by WESCHE & RONNENBERG (2004). The nomenclatural type of the alliance *Artemision rutifoliae* is the association *Atraphaxido pungentis*-*Artemisietum rutifoliae* (holotypus).

Atraphaxido pungentis-*Artemisietum rutifoliae*

Diagnostic species: *Achnatherum sibiricum*, *Artemisia rutifolia*, *Atraphaxis pungens*, *Elytrigia geniculata*, *Panzerina canescens*, *Scutellaria grandiflora*, *Vicia costata*.

Nomenclatural type of the association is relevé EN138–2001 (holotypus; no. 10 in Table 1).

This association is typical of steep erosion-prone slopes. It is widespread in areas with an arid ultracontinental climate, namely in the deep valleys of the Yenisei and Khemchik rivers in the Western Sayan, where it occupies the driest mobile scree slopes of large stones on south-facing slopes at altitudes of 560–1500 m. More rarely, it occurs on south-facing cliffs of metamorphic rocks. In sites with well-developed soil the association is replaced by the zonal dry steppes of the *Cleistogenetea squarrosae*.

Subassociation A. p.-A. r. *typicum* unites scree communities that are widespread in the deep valley of the Yenisei river where they occur on south-facing slopes at altitudes of 560–800 m. The diagnostic species of this subassociation are identical with those of the association.

The subassociation A. p.-A. r. *stipetosum orientalis* includes communities of the driest scree slopes in the southern part of the Western Sayan. They occur on steep slopes adjacent to the arid Central Tuva intermountain basin at altitudes of 600–800 m. Diagnostic species are *Artemisia frigida*, *Euphorbia humifusa*, *E. tshuiensis*, *Schizonepeta annua* and *Stipa orientalis*. Nomenclatural type of the subassociation is relevé EN130–2001 (holotypus; no. 1 in Table 1).

Subassociation A. p.-A. r. *spiraeetosum mediae* includes scree communities at higher altitudes. They occur on less dry southern slopes adjacent to small rivers, tributaries of the Yenisei, at altitudes of 700–1100 m. The diagnostic species of this subassociation include *Allium senescens*, *Artemisia dracunculus*, *Euphorbia monosperma*, *Poa transbaicalica* and

Table 1. (cont.)

Relévé number	1234 56 78901234 567890 1234 567890123 4 567 89012 3456 7890123456 789012345678 9012345678901234 5 67890 12345678	1 11111111 1
<i>Leonurus dimidiatus</i>
<i>Paezera lanata</i>
<i>Lappula</i> sp.
<i>Silene repens</i>
<i>Euplexum sibiricum</i>
<i>Iris ruthenica</i>
<i>Allium</i> sp.
<i>Oxytropis strobilacea</i>
<i>Scabiosa ochroleuca</i>
<i>Stevnia cheiranthoides</i>
<i>Stipa capillata</i>
<i>Allium splendens</i>
<i>Artemisia obtusiloba</i>
<i>Chenopodium hybridum</i>
<i>Thalictrum minus</i>
<i>Claudia aprica</i>
<i>Potentilla longifolia</i>
<i>Scorzonera radiata</i>
<i>Gypsophila paniculata</i>
<i>Dendranthema sinuatum</i>
<i>Veratrum nigrum</i>
<i>Schizonepeta multifida</i>
<i>Campanula glomerata</i>
<i>Hieracium x robustum</i>
<i>Tephrosia integrifolia</i>
<i>Hieracium umbellatum</i>
<i>Rubus matsururanus</i> (E2)
<i>Iris tigrina</i>
<i>Euphorbia alpina</i>
<i>Euphorbia discolor</i>
<i>Linaria</i> sp.
<i>Selaginella borealis</i>
<i>Carex macrorura</i>
<i>Cruciata krylovii</i>

Species with two or one occurrences: *Agropyron cristatum* 38; + 39; 1; *Alyssum lenense* 41; + 42; + *Arabis sagittata* 96; + 97; + *Trifolium terrestris* 3; + 6; + *Aureofystea caerulea* 15; + 38; + *Allium antisopodum* 17; + 81; + *Veronica pinnata* 18; + 82; + *Euphorbia* cf. *esula* 21; 1; 49; + *Chamaenerion angustifolium* 21; + 23; + *Helictotrichon sibiricum* 39; + 87; + *Acronoxon alpinum* 46; + 72; + *Elymus gmelinii* 47; + 77; + *Aconitum anthoroides* 48; + 68; + *Asterophora litifolia* 50; + 51; + *Pentaphragma parvifolia* (E2) 51; 2; 52; 2; *Elymus multiflorus* 54; + 69; + *Lamium album* 55; + 60; + *Artemisia vulgaris* 56; + 66; + *Thestium refractum* 59; + 61; + *Artemisia sibirica* 60; + 101; + *Arabis pendula* 62; + 64; + *Dichodon ceratoides* 62; + 65; + *Dendranthema zawadskii* 67; 1; 71; 1; *Astragalus sibiricus* 71; + 72; + *Potentilla tenuicaulis* 72; + 74; + *Veronica spicata* 73; + 74; + *Anagallidum dichotomum* 79; + 88; + *Euphorbia uvalensis* 80; + 85; + *Poa* sp. 81; + 102; 1; *Seseli* sp. 83; 1; 102; + *Caragana altaica* var. 83; + 84; + *Erysimum albicum* 84; + 102; + *Spiraea hypericifolia* (E2) 85; 1; 86; 1; *Bergenia crassifolia* 101; 1; 102; 1; *Polypodium vulgare* 101; + 102; + *Cystopteris fragilis* 101; + 108; + *Meibomia cucullata* 102; 1; 108; + *Calamagrostis parviflora* 103; 2; 108; + *Caragana frutes* (E2) 103; 2; 104; + *Pinus sibirica* (f.) 104; + 106; + *Artemisia* sp. 2; 1; *Dryopteris fragrans* 5; + *Setaria* sp. 6; + *Cannabis* sp. 14; + *Kochia* sp. 19; + *Asparagus officinalis* 19; + *Chenopodium* sp. 23; + *Spiraea crevata* (E2) 30; + *Symbrium heteromallum* 38; + *Calystegia* sp. 41; + *Androsace maxima* 41; + *Androsace delavignai* 46; + *Cheerophyllum pinnatifidum* 46; + *Pentaphragma fruticosum* (E2) 50; + *Gymnocarpium robertianum* 50; + *Juncus sativa* (E2) 52; + *Melica alissima* 53; 1; *Nezpetta sibirica* 59; + *Lappula heterocaulis* 59; + *Populus tremula* (E2) 60; + *Carex* sp. 60; + *Convolvulus arvensis* 60; + *Galatella macrocarpa* 66; + *Pteridium aquilinum* 66; + *Ziziphora chitropodoides* 68; 2; *Dracocephalum peregrinum* 68; + *Viola macrocarpa* 70; + *Meibomia porphyranica* 71; + *Potentilla chinensis* 71; + *Polygnum alpestre* 72; + *Thalictrum petaloides* 77; + *Lappula redowitzi* 79; + *Astragalus melilotoides* 80; 2; *Potentilla turczanowiana* 83; + *Potentilla* sp. 85; + *Carex amurensis* 86; 1; *Potentilla bykura* 86; + *Calamagrostis epigeios* 87; 2; *Stipa pennata* 87; 1; *Festuca valesiaca* 87; + *Lycichia sibirica* 87; + *Thestium repens* 87; + *Potentilla pensylvanica* 88; 2; *Cerastium arvense* 90; + *Coluria geoides* 96; 2; *Saxifraga sibirica* 97; + *Circaea alpina* 101; + *Gymnocarpium* sp. 101; + *Paeonia* sp. 101; + *Artemisia ochroleuca* 102; + *Viola arvensis* 104; + *Dianthus superbus* 105; + *Androsace* sp. 107; + *Artemisia sibirica* 108; + *Leptopus tenuiflorus* 108; + *Rubus saxatilis* 108; +

Table 2. Header data of the relevés from Table 1. Author abbreviations: NE – N. Ermakov, MC – M. Chytrý, MV – M. Valachovič, MH – M. Hájek, PH – P. Hájková, JR – J. Roleček, PS – P. Šmarda.

Relevé no.	Database no.	Field no.	Author	Date M/D/Y	Plot size (m ²)	Altitude (m)	Aspect	Slope (°)	Cover shrub layer (%)	Cover herb layer (%)	Cover moss layer (%)	Locality
1	19429	EN130-2001	NE	8/29/2001	100	750	S	45	10	40	0	W Sayan, Khem-Terek river mouth
2	19430	EN131-2001	NE	8/29/2001	100	800	S	60	25	15	0	W Sayan, Khem-Terek river mouth
3	19438	EN166-2001	NE	9/1/2001	100	580	S	45	3	55	0	W Sayan, Kolbak-Mys
4	19439	EN167-2001	NE	9/1/2001	100	600	S	70	10	10	0	W Sayan, Kolbak-Mys
5	19458	EN201-2001	NE	9/3/2001	100	560	W	40	30	10	0	W Sayan, M. Shugur river mouth, opposite side of the Yenisei
6	19464	EN207-2001	NE	9/3/2001	100	560	S	60	25	10	0	W Sayan, Urburn river mouth
7	19431	EN132-2001	NE	8/29/2001	100	800	S	40	35	15	0	W Sayan, Khem-Terek river mouth
8	19435	EN136-2001	NE	8/30/2001	100	700	S	45	10	20	0	W Sayan, Khem-Terek river mouth, 800 m upstream
9	19436	EN137-2001	NE	8/30/2001	100	700	S	45	25	15	0	W Sayan, Khem-Terek river mouth, 800 m upstream
10	19437	EN138-2001	NE	8/30/2001	100	750	SSE	55	25	15	0	W Sayan, Khem-Terek river mouth, 800 m upstream
11	19440	EN168-2001	NE	9/1/2001	100	600	S	50	20	10	0	W Sayan, Kolbak-Mys
12	19442	EN170-2001	NE	9/1/2001	100	580	S	60	45	5	0	W Sayan, Kolbak-Mys
13	19443	EN171-2001	NE	9/1/2001	100	700	S	60	18	5	0	W Sayan, Kolbak-Mys
14	19456	EN199-2001	NE	9/2/2001	100	750	S	30	20	65	0	W Sayan, M. Shugur river valley, lower part
15	19444	EN172-2001	NE	9/1/2001	100	650	S	45	40	10	0	W Sayan, Kolbak-Mys
16	19454	EN197-2001	NE	9/2/2001	100	800	S	20	10	50	0	W Sayan, M. Shugur river valley, lower part
17	19455	EN198-2001	NE	9/2/2001	100	800	SSE	30	15	65	0	W Sayan, M. Shugur river valley, lower part
18	19457	EN200-2001	NE	9/2/2001	100	700	S	40	10	30	0	W Sayan, M. Shugur river valley, lower part
19	19461	EN204-2001	NE	9/3/2001	100	550	W	35	25	10	0	W Sayan, M. Shugur river mouth, 1 km up the Yenisei stream
20	19462	EN205-2001	NE	9/3/2001	100	600	SW	30	20	10	0	W Sayan, M. Shugur river mouth
21	77	MV007	MV+NE	8/8/2003	100	580	ESE	40	10	5	0	W Sayan, Bolshaya Kerema, opposite to the Us river mouth
22	79	MV009	MV+NE	8/8/2003	40	601	SE	40	15	3	0	W Sayan, Bolshaya Kerema, opposite to the Us river mouth
23	19388	EN101-2003	NE	8/8/2003	100	580	E	40	10	5	0	W Sayan, Us river mouth, opposite side of the Yenisei
24	19391	EN103-2003	NE	8/8/2003	100	600	SE	40	15	4	0	W Sayan, Kerema river mouth
25	19424	EN125-2001	NE	8/29/2001	100	650	S	15	85	3	2	W Sayan, Khem-Terek river mouth
26	19425	EN126-2001	NE	8/29/2001	100	650	S	40	20	30	0	W Sayan, Khem-Terek river mouth

Table 2. (cont.)

Relevé no.	Database no.	Field no.	Author	Date M/D/Y	Plot size (m ²)	Altitude (m)	Aspect	Slope (°)	Cover shrub layer (%)	Cover herb layer (%)	Cover moss layer (%)	Locality
27	19426	EN127-2001	NE	8/29/2001	100	700	S	40	25	20	0	W Sayan, Khem-Terek river mouth
28	19427	EN128-2001	NE	8/29/2001	100	700	S	40	40	20	0	W Sayan, Khem-Terek river mouth
29	19428	EN129-2001	NE	8/29/2001	100	750	S	30	30	30	0	W Sayan, Khem-Terek river mouth
30	19432	EN133-2001	NE	8/29/2001	100	700	S	45	25	30	0	W Sayan, Khem-Terek river mouth
31	19433	EN134-2001	NE	8/30/2001	100	700	S	50	45	5	0	W Sayan, Khem-Terek river mouth, 1 km upstream
32	19434	EN135-2001	NE	8/30/2001	100	750	S	40	50	10	0	W Sayan, Khem-Terek river mouth, 600 m upstream
33	19441	EN169-2001	NE	9/1/2001	100	650	SW	30	40	20	0	W Sayan, Kolbak-Mys
34	19448	EN187-2001	NE	9/2/2001	100	1000	S	15	50	15	0	W Sayan, M. Shugur river basin, middle part
35	19450	EN189-2001	NE	9/2/2001	100	900	E	12	65	5	5	W Sayan, M. Shugur river basin, middle part
36	19451	EN190-2001	NE	9/2/2001	100	850	S	20	45	25	4	W Sayan, M. Shugur river basin, middle part
37	19453	EN194-2001	NE	9/2/2001	100	850	N	10	70	3	10	W Sayan, M. Shugur river basin, middle part
38	129	MC046	MC+JR+PS	8/9/2003	100	618	SSE	52	2	20	1	W Sayan, Malye Ury valley, left side near the mouth
39	130	MC047	MC+JR+PS	8/9/2003	100	596	S	52	3	30	5	W Sayan, Malye Ury valley, left side near the mouth
40	19394	EN107-2003	NE	8/9/2003	100	1000	S	40	10	80	0	W Sayan, Idzhir ridge, near Bazaga
41	19403	EN116-2003	NE	8/10/2003	100	705	S	40	10	60	0	W Sayan, Kerema river mouth, 3 km down the Yenisei
42	19405	EN118-2003	NE	8/10/2003	100	800	S	40	5	70	0	W Sayan, Kerema river mouth, 3 km down the Yenisei
43	19477	EN14-2002	NE	6/8/2002	80	530	S	40	60	7	0	Altai, Chemat, 15 km S
44	19478	EN15-2002	NE	6/8/2002	100	515	S	40	60	5	0	Altai, Chemat, 14 km S
45	19479	EN16-2002	NE	6/8/2002	100	480	S	35	40	3	0	Altai, Chemat, 19 km S
46	19480	EN17-2002	NE	6/8/2002	100	540	S	30	30	50	0	Altai, Chemat 19 km S
47	19482	EN19-2002	NE	6/8/2002	100	550	SW	15	60	5	6	Altai, Kuyus, 4 km N
48	19483	EN19-2002	NE	6/8/2002	100	530	SW	25	20	5	0	Altai, Kuyus, 4 km N
49	19484	EN21-2002	NE	6/8/2002	100	600	S	30	70	5	0	Altai, Kuyus 2 km N
50	19485	EN22-2002	NE	6/9/2002	100	600	W	40	40	15	0	Altai, Chemat, 38 km S
51	19486	EN23-2002	NE	6/9/2002	100	580	SW	40	50	15	0	Altai, Chemat, 36 km S
52	19487	EN24-2002	NE	6/9/2002	100	610	E	30	50	5	0	Altai, Chemat, 34 km S
53	19488	EN25-2002	NE	6/9/2002	100	550	NW	20	40	10	3	Altai, Chemat, 15 km S
54	19490	EN27-2002	NE	6/9/2002	100	600	S	40	25	8	5	Altai, Kubra river mouth

Table 2. (cont.)

Relevé no.	Database no.	Field no.	Author	Date M/D/Y	Plot size (m ²)	Altitude (m)	Aspect	Slope (°)	Cover shrub layer (%)	Cover herb layer (%)	Cover moss layer (%)	Locality
55	19491	EN28-2002	NE	6/9/2002	100	600	S	35	35	15	7	Altai, Kuba river mouth, 1 km up the Chermal river
56	19492	EN29-2002	NE	6/9/2002	100	580	S	35	20	20	6	Altai, Kuba river mouth, 1 km up the Chermal river
57	61	MH059	MV+MH+PH	8/10/2003	100	808	SE	39	35	60	5	W Sayan, Bolshaya Kerema river mouth
58	68	MH066	MV+MH+PH	8/12/2003	100	699	S	50	15	80	3	W Sayan, Talovka valley near the mouth
59	78	MV008	MV+NE	8/8/2003	30	580	E	35	20	70	3	W Sayan, Bol'shaya Kerema, opposite to the Us river mouth
60	83	MV013	MV	8/12/2003	10	566	S	35	10	15	1	W Sayan, Talovka valley near the mouth
61	19389	EN102-2003	NE	8/8/2003	100	580	E	35	20	70	2	W Sayan, Us river mouth, opposite side of the Yenisei
62	19412	EN125-2003	NE	8/12/2003	100	560	SSE	35	15	65	2	W Sayan, M. Kashkanak river mouth
63	19413	EN126-2003	NE	8/12/2003	100	560	S	30	30	20	0	W Sayan, M. Kashkanak river mouth
64	19414	EN127-2003	NE	8/12/2003	100	550	S	30	30	65	3	W Sayan, M. Kashkanak river mouth
65	19418	EN131-2003	NE	8/12/2003	100	550	E	35	15	60	2	W Sayan, M. Kashkanak river mouth
66	19420	EN133-2003	NE	8/12/2003	100	600	S	35	30	70	4	W Sayan, Talovka river mouth, opposite side of the Yenisei
67	19476	EN13-2002	NE	6/8/2002	100	500	S	40	3	40	0	Altai, Chermal, 15 km S
68	19481	EN18-2002	NE	6/8/2002	70	500	SSE	30	0	35	0	Altai, Chermal, 19 km S
69	19489	EN26-2002	NE	6/9/2002	100	570	S	3	0	20	60	Altai, Kuba river mouth
70	19493	EN30-2002	NE	6/9/2002	5	550	S	40	0	60	10	Altai, Uazhan, 5 km down the Chermal river
71	19494	EN31-2002	NE	6/9/2002	10	600	W	30	0	70	25	Altai, Uazhan, 4 km down the Chermal river
72	19497	EN34-2002	NE	6/2/2002	7	550	SW	5	0	50	15	Altai, Uazhan, 3 km down the Chermal river
73	19499	EN36-2002	NE	6/9/2002	25	480	SW	5	0	45	10	Altai, Cherga, 4 km down the Sema river
74	19500	EN37-2002	NE	6/11/2002	5	540	S	10	0	35	10	Altai, Cherga, 7 km S
75	19501	EN38-2002	NE	6/11/2002	15	580	SW	40	0	55	10	Altai, Cherga, 1 km S
76	19502	EN39-2002	NE	6/11/2002	30	600	SE	30	0	50	10	Altai, Cherga
77	19503	EN40-2002	NE	6/11/2002	25	520	SW	25	0	55	10	Altai, Cherga
78	19504	EN41-2002	NE	6/11/2002	15	500	SW	60	0	60	15	Altai, Cherga, 2 km down the Sema river
79	35	MH033	MV+MH+PH	8/3/2003	100	584	SE	40	0	30	1	W Sayan, Sarla valley near the mouth
80	50	MH048	MV+MH+PH	8/8/2003	100	555	SSE	25	0	50	30	W Sayan, Bol'shaya Kerema river mouth
81	52	MH050	MV+MH+PH	8/8/2003	100	694	ESE	28	0	50	40	W Sayan, Bol'shaya Kerema river mouth
82	60	MH058	MV+MH+PH	8/9/2003	100	799	SW	37	2	25	10	W Sayan, Alan-Art valley near the mouth

Table 2. (cont.)

Relevé no.	Database no.	Field no.	Author	Date M/D/Y	Plot size (m ²)	Altitude (m)	Aspect	Slope (°)	Cover shrub layer (%)	Cover herb layer (%)	Cover moss layer (%)	Locality
83	81	MV011	MV+MH+PH	8/10/2003	25	814	SE	75	0	35	15	W Sayan, Bol'shaya Kerema, ridge above the Enisei river
84	80	MV010	MV+MH+PH	8/10/2003	25	687	SW	80	0	20	20	W Sayan, Bol'shaya Kerema, opposite to the Us valley mouth
85	123	MC040	MC+JR+PS	8/8/2003	100	550	SW	26	3	65	15	W Sayan, Us valley, right side near the mouth
86	127	MC044	MC+JR+PS	8/8/2003	100	550	S	19	5	40	25	W Sayan, Us valley, right side near the mouth
87	132	MC049	MC+JR+PS	8/9/2003	100	592	NE	27	0	40	15	W Sayan, Yenisei valley, between the MaIye Ury and Alan-A
88	19346	EN59-2003	NE	8/3/2003	9	620	S	60	2	30	3	W Sayan, Sarly river mouth
89	19347	EN60-2003	NE	8/3/2003	12	600	SSW	50	5	30	2	W Sayan, Sarly river mouth, 3 km upstream
90	19348	EN61-2003	NE	8/3/2003	12	600	S	65	4	30	4	W Sayan, Sarly river mouth, 3 km upstream
91	19379	EN92-2003	NE	8/7/2003	12	600	S	80	5	35	0	W Sayan, Sarly river mouth
92	19380	EN93-2003	NE	8/7/2003	8	650	S	30	2	40	2	W Sayan, Sarly river mouth
93	19392	EN104-2003	NE	8/9/2003	15	1000	SSW	70	4	30	5	W Sayan, Idzhir ridge, near Bazaga
94	19393	EN106-2003	NE	8/9/2003	15	1000	S	60	2	20	2	W Sayan, Idzhir ridge, near Bazaga
95	19396	EN109-2003	NE	8/9/2003	15	1000	S	70	2	30	4	W Sayan, Idzhir ridge, near Bazaga
96	139	MC056	MC+JR+PS	8/11/2003	100	589	SSE	48	5	35	10	W Sayan, Talovka valley, left side near the mouth
97	140	MC057	MC+JR+PS	8/11/2003	4	610	SE	35	0	30	5	W Sayan, Talovka valley, left side near the mouth
98	19415	EN128-2003	NE	8/12/2003	6	550	S	80	4	20	5	W Sayan, M. Kashkanak river mouth
99	19416	EN129-2003	NE	8/12/2003	9	600	SE	75	2	20	4	W Sayan, M. Kashkanak river mouth
100	19417	EN130-2003	NE	8/12/2003	9	550	E	80	4	30	4	W Sayan, M. Kashkanak river mouth
101	76	MV006	MV	8/7/2003	12	909	N	85	0	40	75	W Sayan, Sarla valley
102	82	MV012	MV	8/10/2003	25	1038	NNE	80	0	20	60	W Sayan, Bol'shaya Kerema, ridge above the Yenisei river
103	19314	EN27-2003	NE	7/31/2003	10	560	S	75	6	40	25	W Sayan, Podporozhnaya Sosnovka valley, near the mouth
104	19315	EN28-2003	NE	7/31/2003	12	560	S	65	5	25	4	W Sayan, Podporozhnaya Sosnovka valley, near the mouth
105	19341	EN54-2003	NE	8/2/2003	100	570	S	70	10	10	4	W Sayan, Golaya river mouth, opposite side of the Yenisei
106	19342	EN55-2003	NE	8/2/2003	12	560	S	75	5	10	3	W Sayan, Golaya river mouth, 2 km downstream the Yenisei
107	19349	EN62-2003	NE	8/3/2003	9	560	S	70	3	15	5	W Sayan, Sarly river mouth, 3 km upstream
108	19377	EN90-2003	NE	8/7/2003	16	580	SSW	70	10	35	20	W Sayan, Sarly river valley, lower part

Spiraea media. Nomenclatural type of the subassociation is relevé EN204–2001 (holotypus; no. 19 in Table 1).

A community with predominance of *Artemisia rutifolia* was described from Mongolia by HILBIG (1995). This community is species-poor, consisting of drought-adapted petrophytic plants, and can be included in the *Artemision rutifoliae* as a separate association.

Grossulario acicularis-Berberidion sibiricae

This alliance includes communities of moderately dry and dry mobile screes occurring in the forest-steppe and steppe belts of the Altai and Western Sayan. Compared with the previous alliance, it is related to a more humid and less continental climate. This is indicated by the absence of a large group of drought-adapted plants (e.g. *Allium senescens*, *Artemisia rutifolia*, *Atraphaxis laetevirens*, *A. pungens*, *Scutellaria grandiflora*, *Stellaria dichotoma*, *Stipa orientalis* and *Youngia tenuicaulis*), which are constant in the *Artemision rutifoliae*. *Grossulario acicularis-Berberidion sibiricae* communities mainly occur in the narrow parts of the large river valleys (except the Katun' and Yenisei), where they usually occupy the lower and middle parts of steep south-facing slopes. Occasionally these communities occur in the more arid altitudinal belt of dry steppes as very narrow vegetation strips in the humid, lowest parts of screes, near the river terraces. In such places the *Grossulario-Berberidion* is in contact with the *Artemision rutifoliae*, the latter always occupying the drier and higher parts of the screes. Diagnostic species of the alliance are *Artemisia gmelinii*, *Berberis sibirica*, *Cotoneaster melanocarpus*, *Galium verum*, *Grossularia acicularis* and *Spiraea media*. Nomenclatural type of the alliance *Grossulario acicularis-Berberidion sibiricae* is the association *Grossulario acicularis-Spiraeetum trilobatae* (holotypus).

Vincetoxico sibirici-Berberidetum sibiricae

Diagnostic species: *Artemisia santolinifolia*, *Berberis sibirica*, *Caragana pygmaea*, *Chelidonium majus*, *Vincetoxicum sibiricum*.

Nomenclatural type of the association is relevé EN135–2001 (holotypus; no. 32 in Table 1).

This association occurs in the steppe belt of the Western Sayan where it occupies the lowest parts of steep slopes with chloride slate screes. The stands are species-poor, with less than 10 species per relevé; however, most of these species are obligate petrophytes. The mean vegetation cover varies between 40 and 70%. The shrub layer has a cover of 30–60% and consists of obligate and facultative petrophytes (*Artemisia santolinifolia*, *Berberis sibirica*, *Caragana pygmaea* and *Ephedra monosperma*). The herb layer always plays a subordinate role, with a cover of 5–15%; it consists of petrophytes and xerophytes that are common in the surrounding dry steppes.

Thalictrum foetidum-*Grossularia acicularis* community

Four relevés of this community were made in the Shugur river valley, a right tributary of the Yenisei. The community occupies screes of hard metamorphic rocks on slopes of various aspects, at altitudes of 800–1000 m. It is characterised by the predominance of shrub layer and a poorly developed herb layer. Besides these, some drought-adapted mosses (*Rhytidium rugosum* and *Abietinella abietina*) frequently attain a high cover.

Elytrigio geniculatae-Artemisietum santolinifoliae (Fig. 3)

Diagnostic species: *Achnatherum sibiricum*, *Artemisia frigida*, *A. santolinifolia*, *Caragana pygmaea*, *Chamaerhodos erecta*, *Cleistogenes squarrosa*, *Erysimum flavum*, *Goniolimon speciosum*, *Helictotrichon altaicum*, *Poa transbaikalica*, *Potentilla acaulis*, *Schizonepeta annua*, *Spiraea media*, *Vicia costata*.

Nomenclatural type of the association is relevé EN118–2003 (holotypus; no. 42 in Table 1).

This association occurs on the gravel screes of south-facing steep slopes of the central part of the Western Sayan. The small-sized stones support drought-adapted plants that are otherwise common in the surrounding steppes on well-developed soils. The obligate petrophyte *Artemisia santolinifolia* forms a monodominant shrub layer with a cover of 40–80%. The other above mentioned diagnostic species, which are typical of dry steppes or screes (scree species include *Elytrigia geniculata*, *Erysimum flavum* and *Vicia costata*), show high constancy values but never dominate.

Artemisia santolinifolia dominated communities varying in floristic composition and belonging to different associations are widespread in the central Asian mountain systems. Some of them were described from Mongolia by HILBIG (1990, 1995) and WESCHE & RONNENBERG (2004).

Grossulario acicularis-Spiraeetum trilobatae (Fig. 4)

Diagnostic species: *Caragana arborescens*, *Cotoneaster melanocarpus*, *Galium paniculatum*, *Grossularia acicularis*, *Lonicera microphylla*, *Polygonatum odoratum*, *Spiraea trilobata*, *Thalictrum foetidum*.

Nomenclatural type of this association is relevé EN19–2002 (holotypus; no. 48 in Table 1).

The association includes the chasmophytic vegetation of the forest-steppe and steppe altitudinal belts of the northern and central Altai. It occupies mobile screes of metamorphic rocks on steep south-facing slopes of the Katun' river valley, at altitudes of 350–700 m, and also of some side valleys of the Chuya river valley, e.g. Kuyuktanar, where it occurs at altitudes up to 1800 m. Like the Western Sayanian communities of the class, the Grossulario-Spiraeetum trilobatae is characterised by a predominance of petrophytic shrubs that have a cover of 30–60%. They also include shrub species such as *Lonicera microphylla* and *Spiraea trilobata*,



Fig. 3. *Elytrigio geniculatae*-*Artemisietum santolinifoliae* – open stands of *Artemisia santolinifolia* and *Caragana pygmaea* with *Carex pediformis* in the foreground, occurring on a gravelly slope at the foot of cliffs in the Malye Ury valley in the central part of the Western Sayan (photo M. Chytrý).

which appear in the Altai and are characteristic both for the association and higher units. Generally, the Altaian scree communities differ from the Western Sayanian in the presence of mesic shrubs and herbs that are typical of meadow steppes (e.g. *Aconitum barbatum*, *Artemisia gmelinii*, *Caragana*



Fig. 4. *Grossulario acicularis-Spiraeetum trilobatae* – shrub vegetation with *Berberis sibirica* and *Lonicera microphylla* on a scree in the Kuyuktanar valley, a right-side tributary of the Chuya river, Altai (photo M. Chytrý).

arborescens, *Galium paniculatum*, *Polygonatum odoratum*, *Rhododendron dauricum* and *Thalictrum foetidum*). They indicate that the climate of the central Altai is more humid than that of the southern part of the Western Sayan and the adjacent mountain systems of Tuva.

Sambucus sibirica-*Grossularia acicularis* community

This community includes the most humid type of scree vegetation of the *Artemisio santolinifoliae*-*Berberidetea sibiricae*. It occasionally occurs in the forest-steppe belt of the northern Altai and occupies screes with large stones, covering the lowest gentle parts of south-facing slopes and higher parts of the river terraces. The increased humidity is indicated by a group of mesic shrubs and herbs, including *Humulus lupulus*, *Padus avium*, *Rosa acicularis*, *Rubus idaeus*, *Sambucus sibirica*, *Senecio nemorensis*, *Urtica cannabina* and *U. dioica*.

Cleistogenetea squarrosae***Sedum hybridum* rock-crevice and scree communities**

Scree vegetation dominated by succulent plants, *Sedum hybridum* and less frequently *Hylotelephium ewersii*, is related to the forest-steppe altitudinal belt, where it comes into contact with the zonal meadow steppes on the south-facing slopes of mountain ridges. In the more humid northern and north-western peripheral parts of the Altai-Sayan mountain system, they are mainly in contact with the Euro-Siberian steppes of the *Festuco*-*Brometea*, and in the inner parts with the central Asian steppes of the *Cleistogenetea squarrosae*. Unlike the *Artemisio santolinifoliae*-*Berberidetea sibiricae*, the communities with succulent plants avoid mobile screes made up of large blocks. They occur on relatively stable, fine-gravel screes mixed with loamy particles or on south-facing rocks with shallow soil in cracks, hollows and on ledges. These habitats are suitable for plants adapted to moderate drought, which are widespread in zonal meadow steppes, e.g. *Carex pediformis*, *Galium verum*, *Thalictrum foetidum*, *Veronica incana* and *V. spicata*. The communities of succulent plants are characterised by a cover of 50–75%, mean height of 10–25 cm and variable species richness (6–30 species per relevé of 6–100 m²). There are some xerophilous and meso-xerophilous succulent petrophytes (e.g. *Hylotelephium populifolium* and *Orostachys spinosa*) showing high constancy values. Nevertheless, these species are not characteristic of this vegetation type, as they occur in the whole range of rock-outcrop and scree habitats. Based on the current data we have included the Altaian and Western Sayanian rock-crevice and scree communities with *Sedum hybridum* in the new alliance *Sedion hybridi*. Character species of the alliance are *Sedum hybridum* and *Hylotelephium ewersii*, which are also dominants of the stands. Differential species are *Dracocephalum nutans*, *Galium paniculatum*, *Kitagawia baicalensis*, *Phlox sibirica* and *Rhytidium rugosum*. Nomenclatural type of the alliance *Sedion hybridi* is the association *Kitagawio baicalensis*-*Sedetum hybridi* (holotypus).

The position of this alliance in the system of higher syntaxonomic units is unclear. Substrate types supporting the *Sedum hybridum* communities

are favourable for both petrophytic plants and for some widespread drought-adapted species from the surrounding zonal steppes. Steppe species are frequent there, but not dominant. Therefore the *Sedum hybridum* communities contain distinct features of the classes Festuco-Brometea and Cleistogenetea squarrosae. Analysis of the data involved in the current study revealed a stronger floristic relationship between the Sedion hybridi and the Cleistogenetea squarrosae (*Helictotrichetalia schelliani* Hilbig 2000), due to the higher constancy of species typical of southern Siberian and central Asian meadow steppes, e.g. *Allium strictum*, *Artemisia glauca*, *A. gmelinii*, *Caragana pygmaea*, *Carex pediformis*, *Cleistogenes squarrosa*, *Galium verum*, *Kitagawia baicalensis*, *Poa urssulensis*, *Rhytidium rugosum*, *Thalictrum foetidum* and *Veronica incana*.

HILBIG (1990, 1995) described the *Sedum hybridum*-*Sedum* (= *Hylotelephium*) *ewersii* community from Mongolia and subsequently (HILBIG 2000b) included it in the *Thalictrion foetidi* Hilbig 2000 (nomen nudum) and the *Scrophularietea incisae* Hilbig 2000. This community is very poor in species, still it shows floristic relationships with the *Cleistogenetea squarrosae* steppes. The ecological and phytosociological contents of the Mongolian *Scrophularietea incisae* are not clear, because HILBIG (1990, 1995, 2000b) described only one association of this class and some preliminary vegetation units, informally called communities. Currently the assignment of the Sedion hybridi in the class *Cleistogenetea squarrosae* and the order *Helictotrichetalia schelliani* seems appropriate, but it still needs to be tested with larger data sets that will include new relevés from other areas.

Kitagawia baicalensis-Sedetum hybridi (Fig. 5)

Diagnostic species: *Allium strictum*, *Artemisia glauca*, *A. gmelinii*, *Caragana pygmaea*, *Carex pediformis*, *Cotoneaster melanocarpus*, *Dracocephalum nutans*, *Galium verum*, *Kitagawia baicalensis*, *Orostachys spinosa*, *Poa urssulensis*, *Sedum hybridum*, *Spiraea media*, *Valeriana alternifolia*.

Nomenclatural type of this association is relevé MH059 (holotypus; no. 57 in Table 1).

This association was documented in the forest-steppe zone of the central part of the Western Sayan. It occurs in the lower parts of steep, south-facing slopes, on stable gravel screes of chloride slates at altitudes of 300–800 m. It contains an open shrub layer consisting of a combination of mesic and xeric facultative petrophytes (*Artemisia gmelinii*, *Caragana arborescens*, *C. pygmaea*, *Cotoneaster melanocarpus*, *Rosa acicularis*, *Spiraea chamaedrifolia* and *S. media*). The herb layer is dominated by *Sedum hybridum* with a cover ranging mostly between 10% and 20%. A few other plants may have a higher frequency or dominance, e.g. *Carex pediformis*, *Kitagawia baicalensis*, *Poa urssulensis* and *Polygonatum odoratum*). A sparse moss layer, mainly with *Rhytidium rugosum* and *Abietinella abietina*, is typical of most stands.



Fig. 5. *Kitagawio baicalensis*-*Sedetum hybridi* – open stands dominated by *Sedum hybridum* on rock outcrops in the Yenisei valley in the central part of the Western Sayan (photo N. Ermakov).

Spiraeo trilobatae-*Sedetum hybridi*

Diagnostic species: *Galium paniculatum*, *Orostachys spinosa*, *Phlox sibirica*, *Sedum hybridum*, *Spiraea trilobata*, *Thymus serpyllum*.

Nomenclatural type of the association is relevé EN36–2002 (holotypus; no. 73 in Table 1).

This association is widespread in the forest-steppe belt of the northern and central Altai. It occurs in various rock habitats, mainly on south-facing slopes surrounded by zonal meadow steppes, which prevail in places with well-developed soils. The *Sedum hybridum* stands of different size occupy rock outcrops of chloride slate, metamorphic limestone and granite with shallow soil in hollows and larger crevices. They are typical also for the stable loamy-gravelly screes. The association contains some petrophytic shrubs, such as *Spiraea trilobata*. *Sedum hybridum* is the major dominant in herb layer, attaining cover values of 30–80%. Only few petrophytic

species co-dominate in some places, e.g. *Artemisia gmelinii*, *Orostachys spinosa*, *Phlox sibirica* and *Thymus serpyllum*. Other species have low cover and constancy; they are moderately drought-adapted, occurring abundantly in the surrounding zonal meadow steppes. The moss layer is well-developed in most stands and consists of drought-adapted species such as *Abietinella abietina*, *Racomitrium* sp. and *Rhytidium rugosum*.

***Selaginella sanguinolenta* xeric rock-crevice communities**

The drought-adapted rock-crevice vegetation of the southern part of the Western Sayan is represented by *Selaginella sanguinolenta* communities. They are widespread in steppe and forest-steppe altitudinal belts in areas with arid ultracontinental climate in southern Siberia and Mongolia, but are absent in the Altai. *Selaginella sanguinolenta* communities are found on rock outcrops with patchy and shallow soil, usually in crevices, hollows, and on ledges. They predominate in zones of actively weathering metamorphic rocks at altitudes of 550–1200 m. These are found on (1) south-facing slopes of large mountain ridges, (2) slopes of various aspects of eroded mountain ridges situated in the arid intermountain basins and (3) hillsides adjacent to wide and dry river valleys. *Selaginella sanguinolenta* stands occupy rocky sites of any size and form, including isolated stones, rock outcrops and cliffs, and give these places a dark-green colour, which can be recognised from a long distance. On screes, they are replaced by communities of the *Artemisia santolinifoliae*-*Berberidetea sibiricae*. Despite the specific habitat, the drought-adapted *Selaginella sanguinolenta* communities are floristically similar to the surrounding central Asian steppes, which are widespread in the adjacent zonal habitats with well-developed soils. Character species of the central Asian steppe class *Cleistogenetea squarrosae* are common there, including *Artemisia frigida*, *Caragana pygmaea*, *Cleistogenes squarrosa*, *Goniolimon speciosum*, *Heteropappus altaicus*, *Potentilla acaulis* and *P. sericea*. HILBIG (2000b) described the *Selaginellion sanguinolentae* (represented by a single association *Aquilegio-Selaginelletum* with two subassociations) in Mongolia and included it in the *Asplenieta trichomanis*. This solution is optimal for the mesic type of *Selaginella sanguinolenta* communities (*Saxifraga cernua* subassociation of HILBIG 1995), where *Asplenieta* characteristic species such as *Woodsia ilvensis* occur frequently. By contrast, the xeric type of *Selaginella sanguinolenta* communities is characterised by the absence of *Asplenieta* species and predominance of *Cleistogenetea* species. This pattern can be recognised in both Mongolian and Western Sayanian communities. Based on the result of our analysis, we included the *Selaginella sanguinolenta* communities in two classes. The drought-adapted association *Galio coriacei-Selaginelletum sanguinolentae*, described in the current paper, is included in the *Cleistogenetea squarrosae*, *Helictotrichetalia schelliani* and *Eritrichio pectinati-Selaginellion sanguinolentae*, whereas the more mesic communities were assigned in the *Asplenieta trichomanis*.

Galio coriacei-Selaginelletum sanguinolentae (Fig. 6)

Diagnostic species: *Achnatherum sibiricum*, *Alyssum obovatum*, *Artemisia frigida*, *A. gmelinii*, *Aster alpinus*, *Caragana pygmaea*, *Carex pediformis*,



Fig. 6. *Galio coriacei-Selaginelletum sanguinolentae* – rock outcrop in a complex of steppe vegetation dominated by carpet-like stands of *Selaginella sanguinolenta*, with *Orostachys spinosa* on the top. Us valley in the central part of the Western Sayan (photo M. Chytrý).

Chamaerhodos erecta, *Cleistogenes squarrosa*, *Dianthus versicolor*, *Galium coriaceum*, *Goniolimon speciosum*, *Elytrigia geniculata*, *Eritrichium pectinatum*, *Helictotrichon altaicum*, *Kitagawia baicalensis*, *Orostachys spinosa*, *Potentilla acaulis*, *P. elegantissima*, *P. sericea*, *Poa transbaicalica*, *Pulsatilla turczaninowii*, *Selaginella sanguinolenta* (dom.), *Silene graminifolia*, *Veronica incana*.

Nomenclatural type of the association is relevé MH033 (holotypus; no. 79 in Table 1).

The association was described from the southern part of the Western Sayan, where it occurs on dry south-facing slopes of the mountain ridges adjacent to the wide and dry river valleys. It is widespread on rock outcrops where it occupies micro-habitats that contain some layer of shallow soil, e.g. crevices, shallow hollows and ledges.

The most striking feature of the association is the dominance of *Selaginella sanguinolenta*, which attains a cover of 40–80%. The shrub layer is represented only by sparse individuals of *Caragana pygmaea*, *Cotoneaster melanocarpus*, *Spiraea hypericifolia* and *S. media*. Besides *Selaginella sanguinolenta*, other obligate petrophytes also have a high constancy, e.g. *Galium coriaceum*, *Elytrigia geniculata*, *Eritrichium pectinatum*, *Erysimum flavum*, *Hylotelephium populifolium*, *Kitagawia baicalensis*, *Orostachys spinosa*, *Potentilla elegantissima*, *P. sericea* and *Silene graminifolia*. Drought-adapted species of the adjacent zonal steppes (e.g. *Chamaerhodos erecta*, *Cleistogenes squarrosa*, *Goniolimon speciosum*, *Helictotrichon altaicum* and *Potentilla acaulis*) also occur in these habitats. The moss layer is poorly developed, however, it contains some drought-adapted bryophytes such as *Abietinella abietina*, *Polytrichum piliferum*, *Racomitrium canescens* and *Rhytidium rugosum*, and lichens *Cladonia arbuscula*, *C. pyxidata*, *C. rangiferina*, *Parmelia somloensis* and *Peltigera aphthosa*. Exposed bedrocks are covered by numerous species of crustaceous epilithic lichens.

Nomenclatural remark: The class *Cleistogenetea squarrosae*, including the central Asian steppe vegetation, was proposed as a nomen nudum by KONONOV et al. (1985) and MIRKIN et al. (1986). HILBIG (2000b) supposed that this name was validated by KONONOV et al. (1985), but in fact it was not. Although KONONOV et al. (1985) validly described the order *Stipetalia krylovii* Kononov et al. 1985 and assigned it to the class *Cleistogenetea squarrosae*, they did not designate this order as the nomenclatural type of the class, explicitly saying that the nomenclatural type must be selected from a number of (as yet undescribed) Mongolian orders of this class. GOGOLEVA et al. (1987) did not refer to the earlier publication of KONONOV et al. (1985) and again described the order *Stipetalia krylovii* with author citation MIRKIN in GOGOLEVA et al. 1987, and also described the new order *Festucetalia lenensis* Mirkin et al. 1987. She assigned both orders to the *Cleistogenetea squarrosae*. However, both names of the orders are invalid in that publication and so is therefore the name of the class. The reason for this is that in most associations newly described in that paper and assigned to the *Cleistogenetea*, two nomenclatural types were designated (indicated by asterisks in their tables). Both associations within *Stipetalia krylovii* are therefore invalid, and so are the alliances

and the order. Two alliances within *Festucetalia lenensis* are described validly, because they both include a single validly described association (i. e. that with a single nomenclatural type). However, none of these alliances is designated as the nomenclatural type of the *Festucetalia lenensis* order, thus this order name is also invalid. To our knowledge, the oldest validation of the class name *Cleistogenetea squarrosae* was done by KOROTKOV et al. (1991) who assigned to this class the validly described order *Stipetalia krylovii* Kononov et al. 1985, invalidly described order *Festucetalia lenensis* Mirkin in Gogoleva et al. 1987, and ineffectively (in manuscripts) described orders *Stipetalia sibiricae* Arbuzova et Zhitlukhina 1987 and *Thymetalia gobici* Mirkin in Kashapov et al. 1987. As the single validly described order name, *Stipetalia krylovii* Kononov et al. 1985 thus becomes automatically a nomenclatural type of the class, whose correct name is *Cleistogenetea squarrosae* Mirkin et al. ex Korotkov et al. 1991. HILBIG & KOROLJUK (2000) assigned the orders *Stipetalia krylovii* Kononov et al. 1985 (dry steppes) and *Helictotrichetalia schelliani* Hilbig 2000 (meadow steppes) into a newly created class *Agropyretea cristati* Hilbig et Kololjuk 2000. Due to the inclusion of the former order in this class, the class name *Agropyretea cristati* is a nomenclature synonym of the earlier described valid name *Cleistogenetea squarrosae* Mirkin et al. ex Korotkov et al. 1991. In his later paper, KOROLYUK (2002) himself rejected the name *Agropyretea cristati* and used the correct name *Cleistogenetea squarrosae*, along with a superfluous attempt at its validation.

Asplenietea trichomanis

The rock-crevice communities occurring on shaded rocks and cliffs in the forest-steppe belt have been included in the class *Asplenietea trichomanis*. Diagnostic species indicating the affinity of the southern Siberian mesic rock communities to this Eurasian class of rock-crevice vegetation include the mesophilous obligate petrophytes *Asplenium ruta-muraria*, *Cystopteris fragilis*, *Polypodium sibiricum* and *Woodsia ilvensis*. Besides these, there is a large group of mesophilous and moderately xerophilous species that are not present in the more xerophilous association *Galio coriacei-Selaginellatum sanguinolentae*. *Asplenietea* communities are widespread in the forest and forest-steppe belts of the Altai and Western Sayan.

KNAPP (1989) published relevés from the shaded granite rocks in central Mongolia. Besides a rare occurrence of *Asplenium ruta-muraria*, *Cystopteris fragilis*, *Polypodium sibiricum* and *Woodsia ilvensis*, these relevés included *Camptosorus sibiricus*, *Cheilanthes argentea*, *Dryopteris fragrans* and *Selaginella sanguinolenta* as dominant species. The physiognomy of this vegetation is partly similar to the class *Selaginello involventis-Potentillietea dickinsii*, described from Japan and Korea (KOLBEK et al. 1997), which represents a geographic vicariant of the *Asplenietea trichomanis*. At present there are very little data available on *Asplenietea* vegetation in Siberia and central Asia, which makes it difficult to distinguish high-rank syntaxa within this class (HILBIG 2000b). Similar communities are usually classified provisionally into the classes *Cleistogenetea squarrosae* or *Asplenietea trichomanis* (CHYTRÝ et al. 1993, HILBIG 2000b, VALACHOVIČ et al. 2002).

Only two communities within *Asplenieta*, both syntaxonomically unranked, are described in this paper. They can be included in the eastern Mongolian alliance *Selaginellion sanguinolentae*, described by HILBIG (2000b), and the class *Asplenieta trichomanis*.

Woodsia ilvensis-Selaginella sanguinolenta community (Fig. 7)

This community is distributed in the forest-steppe and steppe altitudinal belts of the Western Sayan, where it occupies crevices of various sizes on cliffs formed of chloride slates at altitudes of 550–1300 m. In the steppe belt, the community occurs on the shaded parts of cliffs, in relatively deep crevices with moderately dry, shallow soil. On the south-facing parts of cliffs, the community is replaced by physiognomically similar rocky steppes of the association *Galio coriacei-Selaginelletum sanguinolentae*. By contrast, in the more humid climate of the forest-steppe belt the community is widespread on the south-facing slopes of cliffs. The species indicating moderately dry conditions include *Aleuritopteris argentea*, *Artemisia gmelinii*, *Caragana pygmaea*, *Orostachys spinosa*, *Potentilla sericea* and *Silene graminifolia*.

Hylotelephium populifolium-Selaginella sanguinolenta community

This community occurs in shaded and moist parts of cliffs and stones in the forest-steppe belt and adjacent lower part of the forest belt of the Western Sayan. It occupies crevices, hollows and ledges on cliffs, and occasionally also summits of isolated large boulders. A characteristic feature of the community is the occurrence of mesophilous plants typical of rocky sites: *Asplenium ruta-muraria*, *Bergenia crassifolia*, *Cystopteris fragilis*, *Hylotelephium populifolium*, *Polypodium sibiricum*, *Selaginella borealis* and *Woodsia ilvensis*, and a number of species from the surrounding hemiboreal forests. The community is characterized by a shrub layer of *Caragana arborescens*, *Rhododendron dauricum* and *Spiraea chamaedrifolia*, as well as by the presence of a moss-lichen layer of *Abietinella abietina*, *Lobaria pulmonaria*, *Parmelia* spp., *Peltigera aphthosa*, *P. canina*, *Racomitrium canescens*, *Rhodobryum roseum* and *Rhytidium rugosum*. Some solitary, stunted coniferous trees of *Pinus sibirica* and *P. sylvestris* may also occasionally occur.

Ordination of rock-outcrop and scree vegetation

The pattern of floristic differentiation of higher units of the rock-outcrop and scree vegetation was visualised using DCA ordination. Scatter plots of 82 relevés from the Western Sayan are shown in Figs. 8–9. Axis 1 represents a successive replacement of the major types of chasmophytic vegetation in connection with the lithology of the substratum. Relevés of mobile scree vegetation of the *Artemisio santolinifoliae-Berberidetea sibiricae* (1) occupy the left-hand part of axis 1; next are the communities of the alliance *Sedion hybridi* (2) of the class *Cleistogenetea*, occupying sta-



Fig. 7. *Woodsia ilvensis*-*Selaginella sanguinolenta* community – stands on steep rocky slope with gravel accumulation, dominated by *Woodsia ilvensis* and *Orostachys spinosa*, with carpets of *Selaginella sanguinolenta* in the lowest layer. The Talovka valley in the central part of the Western Sayan (photo M. Chytrý).

ble small-gravel screes mixed with loam, and the right-hand part of axis 1 is associated with rock-outcrop communities of Cleistogenetea (3) and Asplenietea (4). Although the latter two types largely overlap in the space of axes 1 and 2, they are separated into two distinct groups along axis

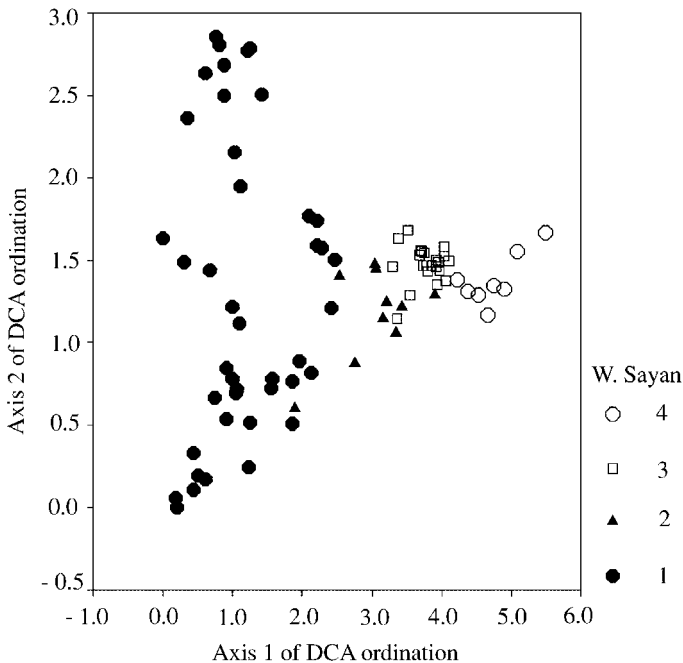


Fig. 8. DCA ordination diagram with axes 1 and 2 of rock-outcrop and scree vegetation in the Western Sayan.

1 – *Artemisio santolinifoliae*-*Berberidetea sibiricae*, 2 – *Cleistogenetea squarrosae* (*Sedion hybridi*), 3 – *Cleistogenetea squarrosae* (*Selaginellion sanguinolentae*), 4 – *Asplenietea trichomanis*.

3. Along axis 2, the large group of relevés of scree vegetation of the *Artemisio santolinifoliae*-*Berberidetea sibiricae* (1) is subdivided into two main groups: drought-adapted communities of the *Artemisio rutifoliae* in the upper part (SDU values 1.0–3.0) and moderately drought-adapted communities of the *Grossulario acicularis*-*Berberidion sibiricae* in the lower part (0–1.0). Besides, in the central part of the plot, there are a few relevés of scree vegetation in an intermediate position between the two aforementioned alliances on axis 2 as well as between communities of mobile scree (*Artemisio*-*Berberidetea*) and communities of stable screes (*Sedion hybridi*) on axis 1.

A scatter plot of 26 relevés from the Altai is shown in Fig. 10. The main three subdivisions of rock outcrop and scree vegetation along axes 1 and 2 are similar to the pattern revealed for the Western Sayan. Axis 1 represents two major subdivisions of communities, dependent on the substratum type. A group of relevés of mobile large-block scree vegetation of the *Grossulario acicularis*-*Berberidion sibiricae* (1, 2) (*Artemisio santolinifoliae*-*Berberidetea sibiricae*) is in the right-hand part of axis 1.

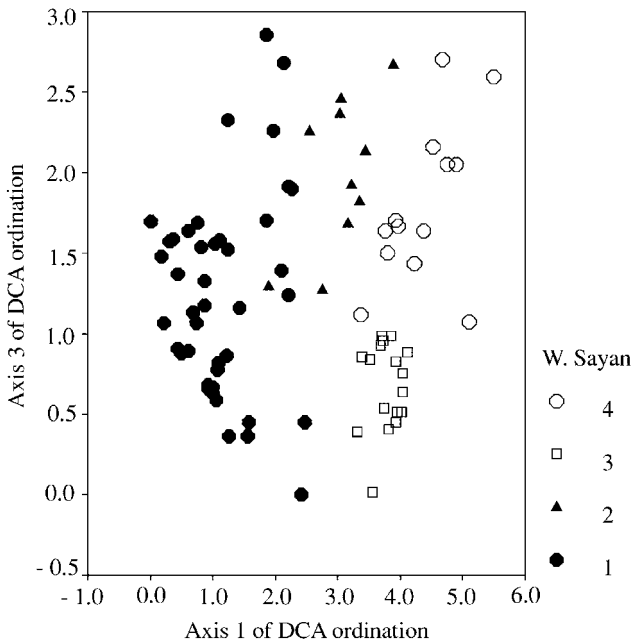


Fig. 9. DCA ordination diagram with axes 1 and 3 of rock-outcrop and scree vegetation in the Western Sayan. Symbols are the same as in Fig. 8.

The left-hand position on axis 1 is occupied by communities of the *Sedion hybridi* (3) (*Cleistogenetia squarrosae*), occurring on relatively stable small-gravel screes mixed with loam, south-facing rocks with shallow soil in cracks, hollows and on ledges. Along axis 2, scree vegetation of the *Grossulario acicularis-Berberidion sibiricae* is subdivided into two main groups: xeric (*Grossulario acicularis-Spiraeetum trilobatae*; 1) in the lower part and mesic (*Sambucus sibirica-Grossularia acicularis*; 2) in the upper part.

Discussion

The Western Sayan and Altai mountains have a rugged topography with steep slopes, strong weathering and active erosion processes, which are supported by an extremely continental climate with remarkable temperature fluctuations and drought. Limestones are very rare and the landscape is formed of a mosaic of more or less weathered metamorphic slates. The stones are partly fixed and partly form instable talus and debris streams, screes and stone-block fields. In places, small cliffs appear among the predominating weathered rocks, which form terraces and hills, but large cliffs or huge rock towers are uncommon.

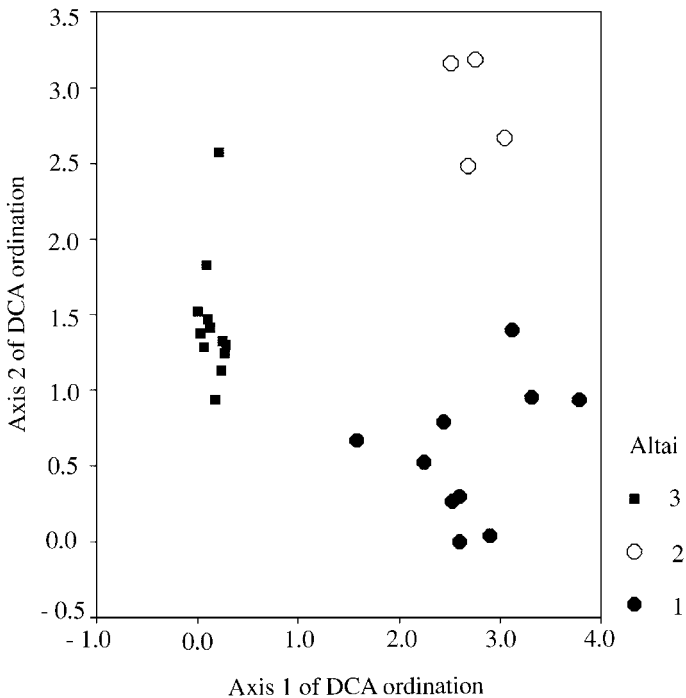


Fig. 10. DCA ordination diagram with axes 1 and 2 of rock-outcrop and scree vegetation in the Altai. 1 – *Grossulario acicularis*-*Spiraeetum trilobatae* (*Grossulario*-*Berberidion*, *Artemisio*-*Berberidetea*), 2 – *Sambucus sibirica*-*Grossularia acicularis* community (*Grossulario*-*Berberidion*, *Artemisio*-*Berberidetea*), 3 – *Spiraeo trilobatae*-*Sedetum hybridi* (*Sedion hybridi*, *Cleistogenetea squarrosae*).

In order to propose a classification scheme of the rock-outcrop and scree vegetation of continental central Asia, a comparison with the established classifications for similar habitats in Europe and the Far East is of crucial importance. The main vegetation classes of rock and scree habitats in temperate Europe are delimited according to the gradient of surface stability, including *Asplenietea trichomanis* (vegetation of solid rocks and wall crevices), *Koelerio-Corynephoretea* (open vegetation of shallow soils on sand or rock outcrops), classes of more closed grasslands on rock outcrops (e.g. *Festuco-Brometea* and *Seslerietea albicantis*), *Thlaspietea rotundifolii* (scree vegetation), and shrub vegetation as a stage of their succession (MUCINA 1997, RODWELL et al. 2002). This kind of habitat pattern, with screes being adjacent to solid rocks and slopes having deep or shallow soil, depending on the inclination, is best reflected in the vegetation pattern of regions with oceanic and suboceanic climates. Similar vegetation patterns to those in Europe were found in Japan and Korea (KOLBEK et al.

1997, 1998). In central Asia, however, vegetation on rock outcrops and screes seems to be less differentiated between habitats, probably due to the overriding effect of the dry continental climate. This fact makes the classification of central Asian plant communities more difficult than in the diversified habitats in Europe or the Far East.

In spite of these difficulties, we tried to implement a traditional scheme of vegetation classification, related to surface instability and soil development, also for the petrophytic vegetation of the Altai and Western Sayan Mts. To some extent we followed HILBIG's (1995, 2000b) proposals for the classification of Mongolian petrophytic vegetation, which used similar principles and is also partly relevant to our study area. The major habitats of petrophytic plants distinguished in the southern Siberian mountains include:

1. Rock crevices. Typical growth forms are bryophytes, small ferns and perennial herbs. In Europe, herbs include, for example, the representatives of the genera *Campanula* and *Saxifraga*, low-growing Caryophyllaceae (e.g. *Cerastium*, *Gypsophila*, *Minuartia*, *Moebria* and *Silene*), and Rubiaceae (e.g. *Asperula* and *Galium*) (MUCINA 1997). Similar types of shaded rocks with extensive moss carpets and occurrence of suboceanic ferns (*Asplenium incisum*, *Camptosorus sibiricus*, *Davallia* spp., *Dryopteris saxifraga*, *Woodsia manchuriensis* and *W. polystichoides*) and selaginellas (*Selaginella involvens* and *S. rossii*) were described in the Far East (KOLBEK et al. 1998). In southern Siberia species with continental distribution ranges are common, such as *Dryopteris fragrans* and *Selaginella sanguinolenta*. Shaded rocks are dominated by ferns (e.g. *Polypodium sibiricum*) and herbs with fleshy leaves, such as *Hylotelephium populifolium*, *Saxifraga spinulosa* and *Sedum hybridum*. The Altaian and Western Sayanian rock vegetation is physiognomically similar in some ways to the eastern Asian *Selaginella involvens* (KOLBEK et al. 1997) and partly to the European vegetation types. However, due to the widespread occurrence of several ferns typical of rock fissures, e.g. *Asplenium ruta-muraria*, *A. septentrionale*, *Cystopteris fragilis* and *Woodsia ilvensis* across large areas of Europe and northern Asia, it seems reasonable to classify the communities of European and Siberian rock and wall crevices into a single class, *Asplenieta trichomanis*. The same conclusion, with some degree of uncertainty, was considered by HILBIG (2000b). The fern vegetation on moist and shady rocks is floristically and physiognomically more similar across Eurasia than the xeric rock vegetation, in which species from the adjacent steppes or other grassland communities frequently occur.

2. Shallow soils on weathered rock outcrops. Vegetation of this habitat type is dominated by plant species adapted to drought stress and considerable temperature fluctuations. In Europe the class *Koelerio-Corynephoretea* (incl. *Sedo-Scleranthetea*) includes vegetation of shallow soils with short-lived vernal therophytes (e.g. *Arabidopsis*, *Cerastium*, *Erophila* and *Veronica*), succulents (e.g. *Sedum* and *Sempervivum*), drought-adapted perennial low-growing dicots (e.g. *Potentilla*), tussock grasses (e.g. *Festuca* and *Koeleria*), bryophytes and lichens. In southern Siberia and Mongolia,

short-lived vernal therophytes are almost non-existent in these habitats, while hemicryptophytes, many of them with succulent features, are dominant, e.g. *Alyssum lenense*, *A. obovatum*, *Goniolimon speciosum*, *Orostachys spinosa* and *Selaginella sanguinolenta*. Numerous drought-adapted plants typical of the surrounding steppes of the Cleistogenetea squarrosae occur there due to the mass effect. There is a series of transitional vegetation types between the zonal steppes and the vegetation types on rock outcrops (KHANMINCHUN 1975). Central Asian steppes are predominantly related to mountain areas and most of their species are adapted to rocky sites. Thus the drought-adapted communities on weathered rock outcrops show distinct floristic similarities to those of zonal steppes and have therefore been included in the Cleistogenetea squarrosae as the *Eritrichio pectinati-Selaginellion sanguinolentae* alliance in the present paper.

3. Disturbed screes with herbaceous vegetation. This habitat is dominated by plant species with an extensive root system and growth forms adapted to the down-slope movement of stone particles. In Europe screes harbour numerous representatives of Brassicaceae (e.g. *Alyssum*, *Arabis*, *Draba* and *Thlaspi*), Scrophulariaceae (*Euphrasia*, *Linaria*, *Scrophularia* and *Veronica*) and succulents of the genera *Saxifraga* and *Sedum* (VALACHOVIČ et al. 1997). Common species widespread on screes both in Europe and Asia are rare, although there are some common genera (e.g. *Alyssum*, *Scrophularia*, *Sedum* and *Vincetoxicum*). On the opposite end of the Eurasian continent, in Korea and Russian Far East there is little information on herbaceous scree vegetation. Many screes in central Asia are overgrown by succulents and combined with shrubs, or form transitional vegetation types to Asplenieta. Two *Sedum hybridum* communities on screes in the study area, occurring in the steppe and forest-steppe belts, are remarkably different from the Scrophularieta as described by HILBIG (1990, 1995, 2000b) from the Mongolian mountains.

4. Shrubberies in less disturbed habitats. In Europe sub-continental steppe shrubberies primarily occur in rocky habitats, but are also able to spread as secondary vegetation in abandoned places. Several shrub genera occur in steppe habitats across large areas from Europe to southern Siberia, including *Berberis*, *Cotoneaster*, *Prunus*, *Rhamnus* and *Spiraea*, often with vicarious species in different areas. Further to the east, in Manchuria and Dauria, these shrubs are replaced by e.g. *Atraphaxis mandshurica*, *Caragana microphylla*, *Securinega suffruticosa*, *Ulmus macrocarpa*, *U. pumila*, and a herb layer with steppe plants such as *Agropyron cristatum*, *Artemisia frigida*, *Cleistogenes squarrosa*, *Koeleria cristata*, *Poa ochotensis* and *Stipa baicalensis* (KRESTOV 2003, QUIAN et al. 2003). Both southern Siberian and Central European shrubberies form a dense layer preventing the development of a ground layer of light-demanding grasses. In the southern Siberian mountains shrub stands of *Artemisia rutilifolia*, *Atraphaxis laetevirens*, *A. pungens*, *Berberis sibirica*, *Caragana pygmaea*, *Cotoneaster melanocarpus*, *Grossularia acicularis*, *Lonicera microphylla*, *Spiraea media*, *S. trilobata* and *Ulmus pumila* develop in the course of succession on infrequently disturbed screes

or rock outcrops, especially if there is some accumulation of soil, e.g. on the margins of talus slopes.

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References

- Cherepanov, S. K. (1995): Sosudistye rasteniya Rossii i soprodel'nykh gosudarstv (Vascular plants of Russia and adjacent countries). – *Mir i sem'ya-95*, Sankt-Peterburg. 990 pp. (In Russian).
- Chytrý, M., Pešout, P. & Anenkhonov, O. A. (1993): Syntaxonomy of vegetation of Svjatoj Nos Peninsula, Lake Baikal. 1. Non forest communities. – *Folia Geobot. Phytotax.* **28**: 337–383.
- Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, Z. (2002): Determination of diagnostic species with statistical fidelity measures. – *J. Veg. Sci.* **13**: 79–90.
- Dufrêne, M. & Legendre, P. (1997): Species assemblages and indicator species: the need for a flexible asymmetrical approach. – *Ecol. Monogr.* **67**: 345–366.
- Ermakov, N. (1995): Grass forests classification of southern Siberia and Mongolia. – *Colloq. Phytosoc.* **23**: 259–276.
- (1998): The Altaian relict subnemoral forest belt and the vegetation of pre-Pleistocene mountainous landscapes. – *Phytocoenologia* **28**: 31–44.
- Ermakov, N. B., Korolyuk, A. Yu., Lashchinskii, N. N. (1991): Floristicheskaya klassifikatsiya mezofil'nykh travyanykh lesov yuzhnoi Sibiri (The floristic classification of the mesophilous herb-rich forests of southern Siberia). – SO AN SSSR, Novosibirsk. 96 pp. (In Russian).
- Ermakov, N., Maltseva, T. & Makunina, N. (1999): Classification of meadows of the South Siberian uplands and mountains. – *Folia Geobot.* **34**: 221–242.
- Ermakov, N., Dring, J. & Rodwell, J. (2000a): Classification of continental hemiboreal forests of North Asia. – *Braun-Blanquetia* **28**: 1–131.
- Ermakov, N., Shauro, D. & Maltseva, T. (2000b): The class Mulgedio-Aconitetea in Siberia. – *Phytocoenologia* **30**: 145–192.
- Gogoleva, P. A., Kononov, K. E., Mirkin, B. M. & Mironova, S. I. (1987): Syntaksonomiya i simfitosotsiologiya rastitel'nosti alasov Tsentral'noi Yakutii (Syntaxonomy and symphytosociology of vegetation of the alases of Central Yakutia). – *Izdatel'stvo Irkutskogo universiteta*, Irkutsk. 176 pp. (In Russian).
- Hilbig, W. (1990): Neu beschriebene Pflanzengesellschaften aus der Mongolischen Volksrepublik. – *Feddes Repert.* **101**: 189–206.
- (1995): The vegetation of Mongolia. – SPB Academic Publishing, Amsterdam. 258 pp.
- (2000a): Beitrag zur Kenntnis der Vegetation im tuwinischen Teil des Uvs-nuur-Beckens (Russland). – *Feddes Repert.* **111**: 39–74.
- (2000b): Kommentierte Übersicht über die Pflanzengesellschaften und ihre höheren Syntaxa in der Mongolei. – *Feddes Repert.* **111**: 75–12.
- Hilbig, W. & Knapp, H. (1983): Vegetationsmosaik und Florenelemente an der Wald-Steppen-Grenze im Chentej-Gebirge (Mongolei). – *Flora* **174**: 1–89.
- Hilbig, W. & Koroljuk, Ju. (2000): Sanddünenvegetation im Uvs-nuur-Becken (Mongolei und Tuwa/Russland). – *Feddes Repert.* **111**: 29–37.

- Hilbig, W., Bastian, O., Jäger, E. J. & Bujan-Oršich, C. (1999): Die Vegetation des Uvs-nuur-Beckens (Uvs Aimak, Nordwestmongolei). – Feddes Repert. **110**: 569–625.
- Khanminchun, V. M. (1975): Soobshchestva Selaginella sanguinolenta (L.) Spring v yuzhnoi Tuve (Communities of Selaginella sanguinolenta (L.) Spring in southern Tuva). – Bot. Zh. **60**: 1325–1327. (In Russian).
- Knapp, H. D. (1989): *Camptosorus sibiricus* (L.) Rupp. (Aspleniaceae) – Relikt einer nordmongolischen Laubwaldzone? – Flora **183**: 379–396.
- Kolbek, J., Jarolímek, I. & Valachovič, M. (1997): Plant communities of rock habitats in North Korea: 1. Communities of semi-dry rocks. – Biologia **52**: 503–522.
- Kolbek, J., Valachovič, M. & Jarolímek, I. (1998): Plant communities of rock habitats in North Korea: 2. Communities of moist rocks. – Biologia **53**: 37–51.
- Kononov, K. E., Gogoleva, P. A. & Mironova, S. I. (1985): O dvukh pastbishchnykh asotsiatsiyakh stepei v tsentral'noi Yakutii (On two associations of grazed steppes in central Yakutia). – In: Mirkin, B. M. (ed.): Fitotsenologiya antropogennoi rastitel'nosti, pp. 137–144. – Izdatel'stvo Bashkirskogo universiteta, Ufa. (In Russian).
- Korolyuk, A. Yu. (2002): Rastitel'nost' (Vegetation). – In: Khmelev, V. A. (ed.): Stepi Tsentral'noi Azii, pp. 45–94. – Izdatel'stvo SO RAN, Novosibirsk. (In Russian).
- Korotkov, K. O., Morozova, O. V. & Belonovskaja, E. A. (1991): The USSR vegetation syntaxa prodromus. – Gregory E. Vilchek, Moscow. 346 pp.
- Krestov, P. (2003): Forest vegetation of the easternmost Russia (Russian Far East). – In: Kolbek, J., Šrůtek, M. & Box, E. O. (eds.): Forest vegetation of Northeast Asia, pp. 93–180. – Kluwer Academic Publishers, Dordrecht.
- Kuminova, A. V. (1960): Rastitel'nyi pokrov Altaya (Plant cover of the Altai). – SO AN SSSR, Novosibirsk. 450 pp. (In Russian).
- Kuminova, A. V., Zvereva, Yu. M., Maskaev, Yu. M., Pavlova, G. G., Sedel'nikov, V. P., Koroleva, A. S., Neifeld, E. Ya., Tanzybayae, M. G., Chizhikova, N. M. & Lamanova, T. G. (1976): Rastitel'nyi pokrov Khakasii (Plant cover of Khakasia). – Nauka, Novosibirsk. 423 pp. (In Russian).
- Kuminova, A. V., Sedel'nikov, V. P., Maskaev, Yu. M., Shoba, V. A., Ershova, E. A., Namzalov, B. B., Pavlova, G. G., Maltseva, T. V. & Parshutina, L. P. (1985): Rastitel'nyi pokrov i estestvennye kormovye ugod'ya Tuvinskoj ASSR (Vegetation and natural forage resources of the Tuva ASSR). – Nauka, Novosibirsk. 256 pp. (In Russian).
- Mirkin, B. M., Alimbekova, L. M., Manizabar, N. & Onishchenko, L. I. (1986): Vtoroe priblizhenie floristicheskoi klassifikatsii rastitel'nosti rechnykh poim Mongol'skoi Narodnoi Respubliki (Second approach to the floristic classification of river floodplains of the Mongolian National Republic). – Biol. Nauki **1986/9**: 83–91. (In Russian).
- Mucina, L. (1997): Conspectus of classes of European vegetation. – Folia Geobot. Phytotax. **32**: 117–172.
- Namzalov, B. B. (1994): Stepi yuzhnoi Sibiri (Steppes of southern Siberia). – SO RAN, Novosibirsk & Ulan-Ude. 309 pp. (In Russian).
- Polikarpov, N. P., Chebakova, N. M. & Nazimova, D. I. (1986): Klimat i gornye lesa Yuzhnoi Sibiri (Climate and mountain forests of southern Siberia). – Nauka, Novosibirsk. 225 pp. (In Russian).
- Qian, H., Yuan, X.-Y. & Chou, Y.-L. (2003): Forest vegetation of Northeast China. – In: Kolbek, J., Šrůtek, M. & Box, E. O. (eds.): Forest vegetation of Northeast Asia, pp. 181–230. – Kluwer Academic Publishers, Dordrecht.
- Rechan, S. P. & Krylov, A. G. (1963): Kratkaya kharakteristika lesov pravoberezhya Srednei Katuni (Short description of forests of the right bank of the middle Katun' val-

- ley). – In: Smagin, V. N. (ed.): *Tipy lesov Sibiri (Forest types of Siberia)*, pp. 171–181. – Izdatel'stvo AN SSSR, Moskva. (In Russian).
- Rodwell, J. S., Schaminée, J. H. J., Mucina, L., Pignatti, S., Dring, J. & Moss, D. (2002): The diversity of European vegetation. An overview of the phytosociological alliances and their relationships to EUNIS habitats. – EC-LNV, Wageningen. 168 pp.
- Rudoy, A. N. (2002): Glacier-dammed lakes and geological work of glacial superfloods in the Late Pleistocene, Southern Siberia, Altai Mountains. – *Quatern. Int.* **87**: 119–140.
- Sedel'nikov, V. P. (1988): *Vysokogornaya rastitel'nost' Altae-Sayanskoj gornoj oblasti (High-mountain vegetation of the Altai-Sayan mountain region).* – Nauka, Novosibirsk. 222 pp. (In Russian).
- Sochava, V. B. & Timofeev, D. A. (1968): *Fiziko-geograficheskie oblasti Severnoi Azii (Physical-geographical regions of Northern Asia).* – *Dokl. Inst. Geograf. Sibiri Dal'n. Vostoka* **19**: 3–19. (In Russian).
- Tichý, L. (2002): JUICE, software for vegetation classification. – *J. Veg. Sci.* **13**: 451–453.
- Valachovič, M., Dierssen, K., Dimopoulos, P., Hadač, E., Loidi, J., Mucina, L., Rossi, G., Valle Tendero, F. & Tomaselli, M. (1997): The vegetation on screes – synopsis of higher syntaxa in Europe. – *Folia Geobot. Phytotax.* **32**: 173–192.
- Valachovič, M., Anenkhonov, O. A. & Hodálová, I. (2002): Vegetation along an altitudinal gradient in the Gremyachaya Valley, Barguzinskii Range, Eastern Siberia. – *Biologia* **57**: 83–100.
- Weber H. E., Moravec J. & Theurillat J.-P. (2000): *International Code of Phytosociological Nomenclature.* 3rd edition. – *J. Veg. Sci.* **11**: 739–768.
- Wesche, K. & Ronnenberg, K. (2004): Phytosociological affinities and habitat preferences of *Juniperus sabina* L. and *Artemisia santolinifolia* Turcz. ex Bess. in mountain sites of the south-eastern Gobi Altay, Mongolia. – *Feddes Repert.* **115**: 585–600.
- Westhoff, V. & van der Maarel, E. (1973): The Braun-Blanquet approach. – In: Whittaker, R. H. (ed.): *Classification and ordination of plant communities*, pp. 617–726. – W. Junk, The Hague.
- Zhitlukhina, T. I. (1988): *Sintaksonomiya lesov i subalpijskikh lugov kyginskogo ekologicheskogo profilya (yuzhnaya chast' Teletskogo ozera) (Syntaxonomy of forests and subalpinemeadows of the Kyginskii ecological transect (the southern part of Teletskoe Lake)).* – Ms., VINITI N2146–V88, Moskva. 45 pp. (In Russian).
- Zhitlukhina, T. I. & Mirkin, B. M. (1987): *Sintaksonomiya rastitel'nosti Sayano-Shushenskogo zapovednika. I. Fiziko-geograficheskie usloviya i klass Irido-Laricetea cl. nova (Syntaxonomy of vegetation in the Sayano-Shushenskii Nature Reserve. I. Physical-geographical conditions and cl. Irido-Laricetea cl. nova).* – Ms., VINITI 3357–V87, Moskva. 42 pp. (In Russian).

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