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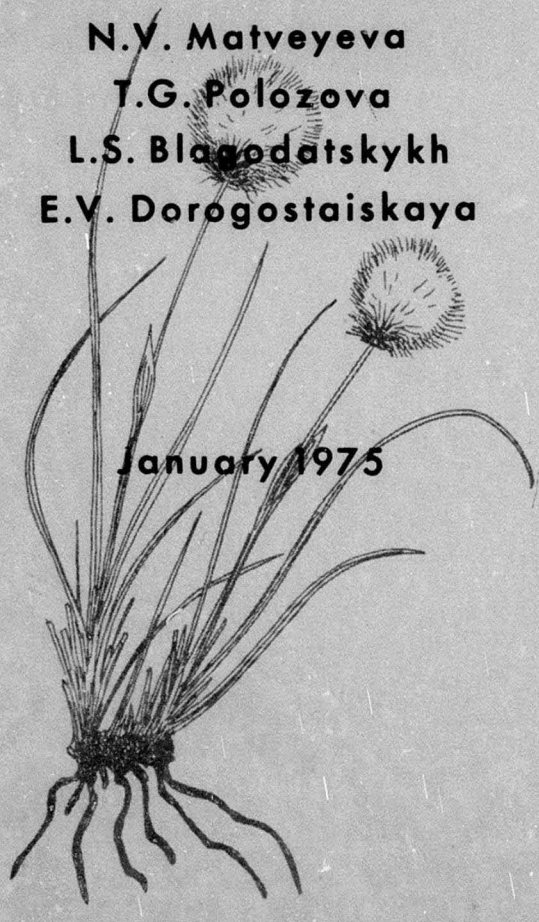

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A BRIEF ESSAY ON THE VEGETATION IN THE VICINITY OF THE TAIMYR BIOGEOCOENOLOGICAL STATION

by

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Geobotanical investigations undertaken along the right hand bank of the Pyasina River near the mouth of its tributary, the Tareya, are quite few. Until 1965, when complex biogeocoenological investigations were started by the V. L. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R. in the settlement of Tareya, there existed some information about the plant cover of this area only in the work by A. N. Vinogradova (1937). During the last several years, a series of papers have appeared, devoted mainly to questions of the vegetation pattern around the station (Matveyeva 1968, 1969 B, Boch, Vasilevich and Ignatenko 1969), and also to the knowledge of biomass in the main types of the tundra (Khodachek 1969).

At present, the border of the subzone of the Arctic Tundra extends to the south of the mouth of the Tareya (Geobotanical map of the U.S.S.R., scale 1:4,000,000) and the area investigated by us, thus, is included in this subzone. Referring to this area as Arctic Tundra came about because of the brevity of the visits by botanists here and a lack of thorough investigations of its vegetation.

F. V. Sambuk (1937) distinguished six subzones in Taimyr: 1) the dissociated arctic aggregations, 2) the mountain tundras of the Byrrang chain, 3) the moss-*Eriophorum* tundras, 4) the moss-shrub tundras, 5) the forest tundra, and 6) the open *Larix* forest. He indicated that the southern borders of the first two subzones reached to the mouth of the Tareya, the southern shore of Taimyr Lake and to the river of Bolshaya Balakhnya. The author furnishes descriptions of the basic associations typical of each subzone. From his description it is not difficult to establish that our research area belongs to the moss-*Eriophorum* and the moss-shrub tundra subzones (in the mentioned paper, the characteristics of the vegetation for these two subzones are treated together).

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[1]The present work was carried out by collaborators of the Taimyr biogeocoenological station. The schemata of the vegetation investigated were made with the active assistance of O. M. Afonina and Yu. Zharkova, the surveying work on the vegetation profile was made by O. Voloshin and I. N. Safronova. The lichens were determined by Kh. Kh. Trass and T. Kh. Piin at the Tartu University, and great help with the determination of mosses was given by I. I. Abramov and A. L. Abramova. In the preparation of the manuscript for printing, an active part was played by L. L. Zanokha. To all mentioned above, the authors express their deep gratitude.

According to the geobotanical division of the U.S.S.R. in 1947, the area of the right hand bank of the Pyasina River is included in the Central Taimyr district of the moss and lichen tundras belt of the Arctic Tundra Region. From our point of view, this more correctly reflects the location of the subzonal border between the Arctic and the Typical Moss-Tundra of Western Taimyr in the area of the central course of the Pyasina.

In the literature on tundra management, there has hitherto been no uniform zonal subdivision of the Tundra area. A summary by V. D. Aleksandrova (1971 B) is devoted to the principles of zonal division of the arctic vegetation. In it, an attempt is made to compare the points of view of different authors and, in addition, to furnish the original divisions and the characteristics of the units distinguished. The area around the mouth of the Tareya does, according to this division, belong to the Northern Belt of the Sub-Region of the Subarctic Tundra, which corresponds to the Subzone of the Typical Tundra (Gorodkov 1916) or to the Subzone of the Moss-lichen and Shrubby Tundra (Sochava and Gorodkov 1956). In favor of this division speaks the considerable participation of hypo-arctic elements in the flora (*Betula nana, Salix pulchra, Vaccinium Vitis-Idaea,* and *Pyrola grandiflora*) in the moist communities, sufficiently wide distribution on the water divides of the *Betula nana* and *Salix reptans* tundras, the great closeness of the vegetation cover in the basic tundra types, and the presence of shortgrass meadows with a rich floristic composition.

Before going into a concrete description of the vegetation, we will pause over some general peculiarities in its composition and structure, and also the characteristics of distribution of the plant communities. One of the most important traits, which we consider necessary to stress, appears to be the unbroken density of the vegetation cover over the larger part of the area around the station, which is guaranteed mainly by the development of a thick moss cover. The latter is due to the fact that the depth of the snow cover on the water divides varies from 40 to 60 cm. In all the places where the snow blows away in spring and fall and in winter reaches a depth of not more than 20 cm, a spotty tundra of various kinds develops (on the elevated flat banks of the Pyasina and the upper parts of the slopes in brook valleys).

The area occupied by the spots amounts to 20-30% in these tundras, but because the majority of the spots usually are found in a state of development, the actual open ground is, as a consequence, not more than 5-10%. Because of this, a fully closed system of the roots of flowering plants is found in the subsoil. On steepest and strongly wind-blown slopes, there is a plicated, spotty tundra of arctic type (Govorukhin 1960), where sod-free surface amounts to 60-70%, but in the area under consideration it is insignificant.

The tundra communities are characterized by a rich floristic composition. Thus, in a single definite community there may be counted from 100 up to 130-140 species, including flowering plants, mosses and lichens. Most numerous are the species of lichens (40-50), then the angiosperms (35-40) and last come leafy mosses and liverworts (30-40). If evaluating them on basis of phytocoenotic significance and comparing them on measured coverage and abundance, then the mosses occupy first place; they dominate in mass and cover the soil up to 80-90%. The lichens, on the other hand, have a minimal coverage, but are characterized by a high frequency; they are usually met with in every area of the communities, but in small quantities. In this respect, the angiosperms occupy an intermediate position; their projected coverage in the above-ground layer does usually not exceed 30-40%, but a large part of roots and rhizomes is located in the moss-cover, forming a dense network, which holds together the mossy turf.

The greatest floristic richness is characteristic for communities, developed on slopes with a southerly exposure, and its maximum is attained on steep banks of Pyasina. Bogs and swampy area are, in contrast, characterized by poor species composition; lichens are almost absent, the number of angiosperms reaches 10-15 species, and mosses dominate both in number of species and as to mass.

As the basic unit, with which we operate for the description of the vegetation, appears the plant community or phytocoenosis. On the whole, for the understanding of this unit, we confine ourselves to the definition given by V. N. Sukachev (Sukachev et al., 1957). But following a series of authors (Yaroshenko 1931, 1950; Ramensky 1938; Mazing 1963), we consider it necessary to introduce into the concept and definition of the phytocoenosis an indication of the defined spatial extent. We agree with A. A. Nitsenko (1968) that because the vegetation cover can be separated into phytocoenoses, the conditions of the environment must also be distributed among "larger or smaller localities". The above-mentioned authors connect the distribution of the phytocoenoses with the forms of meso-relief. Also we believe that the spatial extent of a phytocoenosis can be measured in the same units as an horizontal extent of the meso-relief elements. In spite of the great diversity of the tundra vegetation, in the tundra zone as well as in all other zones, the distinction of phytocoenoses as territorial units is both possible and feasible.

For the overwhelming majority of tundra communities, the countour mosaic is the most peculiar (Matveyeva 1970 A, 1970 B). Micro-aggregations appear as structural elements of the phytocoenoses. They are associated with various elements of the nano-relief, the formation of which is connected with the cryogenic processes carried on in the ground. The latter appears not the only, but the most characteristic, broadly distributed and also as the most stable factor for the formation of micro-aggregations in the tundra zone (in addition, communities may be made up of micro-aggregations of zoogenic, phytogenic and other origin). The presence of micro-relief, usually in connection with thermokarst or frost-cracking of the ground, appears as the cause for the formation of a combination of plant aggregations which approximate to the steppe and semi-desert complexes, or, on a more general level, to the micro-combinations (Isachenko 1969). As such micro-combinations in our research area could be included polygonal bogs, bog-tundra complexes in the upper reaches of brook valleys, complexes of swampy tundras on high water divides and combinations of *Dryas*-sedge-moss tundras with swampy sedge-*Eriophorum* thermokarst sinkholes. As elements of such complexes or micro-combinations appear phytocoenoses or fragments of them, which do not occupy large areas and are more or less regularly repeated in genetically uniform territories.

GENERAL DESCRIPTION OF THE VEGETATION

Within the limits of the station area it is possible to distinguish the following elements of the landscape profile, which are characteristic in general for the Taimyr lowlands: the undulating hills of the water divides with an absolute height of 40-50 m, composed of quaternary marine sediments; the remnants of hills and ridges on the surface of an ancient alluvial terrace, 30-35 m high; the water-collecting depressions in the upper valleys of small rivers and brooks, falling out into Pyasina; the swampy lake-depressions between the hills (the elevation of the hills and ridges in relation to the depressions does not exceed 10-15 m); the slopes of the brook and river valleys; the cliffs of the right-hand bank of Pyasina; and the sandy and silty bars in the floodplain of Pyasina (Figures 1 and 2).

The flat parts of the not very high water-divides and the very gentle, sometimes slightly concave slopes of the hills, weakly drained, with sufficiently thick snow-cover in wintertime, are occupied by *Dryas*-sedge-moss small-hummocky tundras. The characteristic trait of these tundras is the density of the vegetation cover. The dominant angiosperms are *Carex ensifolia* spp. *arctisibirica*[1)] (15-30%) and *Dryas punctata* (10-20%), and the dominant mosses are

[1)] = *Carex Bigelowii* Torr. ssp. *arctosibirica* (Yurtsev) Love & Love (translator's remark).

Tomenthypnum nitens (30-40%), *Hylocomium splendens* var. *alaskanum* (30-40%) and *Aulacomnium turgidum* (10-20%). The density of the vegetation cover is caused basically by the development of a thick moss cover (the general coverage of the mosses is 90%). The lichens do not play an important role in the composition of the vegetation cover, on the whole they occupy less than 1% of the area. The coverage of the angiosperms is 30-40%, even if basically they are characterized mainly by two species; the rest of the species occur sporadically. The abundance and coverage of species varies according to the small-hummocky nano-relief characteristic of tundras of this type. As a result of thermokarst in the tundras of the type described, there is often developed very wet sedge-cottongrass waterholes (*Carex stans*[2] - *Eriophorum angustifolium*), some of which are eventually converted into small lakes.

On the more elevated water divides on the ancient marine terrace (Danilov, Popov and Smirnova 1971), composed of heavy loam, the character of the vegetation changes somewhat in a condition of increased moisture. Although, still, the dominant species remain *Tomenthypnum nitens*, *Aulacomnium turgidum*, *Ptilidium ciliare*, *Dryas punctata* and *Carex ensifolia* ssp. *arctisibirica* an essential admixture begins to form of *Betula nana* (the prostrate form), *Salix reptans* and dwarf shrubs *Cassiope tetragona*, *Vaccinium Vitis-Idaea* and *Pyrola grandiflora*. In such a shrub-dwarf shrub-sedge-moss tundra, the abundance of lichens is reduced.

Between the *Dryas*-sedge-moss and the shrub-dwarf shrub-sedge-moss tundras appear a row of transitional types. As co-dominants the above-mentioned species may be found separately and sometimes in various combinations of 2-3 species. In the moss-cover, in relation to the increase in moisture content of the soil, there appears to be a tendency to mono-dominance: if in better drained habitats, 3-4 species of mosses usually appear as almost equally dominating, then in a moister habitat *Tomenthypnum nitens* will be the most dominant of them all. The presence of the small hummocks nano-relief partly breaks the general tendency: even in a wet tundra dominated by *Tomenthypnum nitens* and *Ptilidium ciliare* and a high abundance of *Betula nana*, xerophilous species develop on the hummocks. However, usually in such tundras the area, occupied by unfavorable elements of the nano-relief, is bigger than the area of hummocks.

Usually the extent of the communities of the described types of tundras is large. They occupy an area of several hectares, and borders between various communities are gradual and often difficult to distinguish, as not only qualitative changes in composition occur, but also quantitative changes in the distribution of the same species. Thus, by definition, a difficulty is presented not only in the delimitation of various taxonomic units, but in the actual separation of plant communities and the determination of their borders in nature.

The most elevated and flat parts of the water sheds are occupied by the complex of swampy sedge-*Eriophorum* water pits (in thermokarst depressions), dwarf birch and willow-mossy tundras, and fragments of *Polytrichum*-tundras, which are connected with flat elevations of the micro-relief of various levels. The sedge-*Eriophorum* water pits are wettest and are found in various stages of swamping (20% of the surface). They have variable form, in part they are strongly oversaturated, on others water is standing, and some are developed into small pools. The surface of the water hollows is 10-20 m^2. Their floristic composition is poor; it consists of about 10 species of angiosperms, and 6-7 mosses. Lichens are absent. The dominants are *Carex stans*, *Eriophorum angustifolium*, *Dupontia Fischeri*, *Meesia triquetra*, *Drepanocladus vernicosus*, *Calliergon sarmentosum*, *Calliergon Richardsonii* and *Polytrichum Jensenii*.

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[2] = *Carex aquatilis* L. ssp. *stans* (Drej.) Hulten (translator's remark).

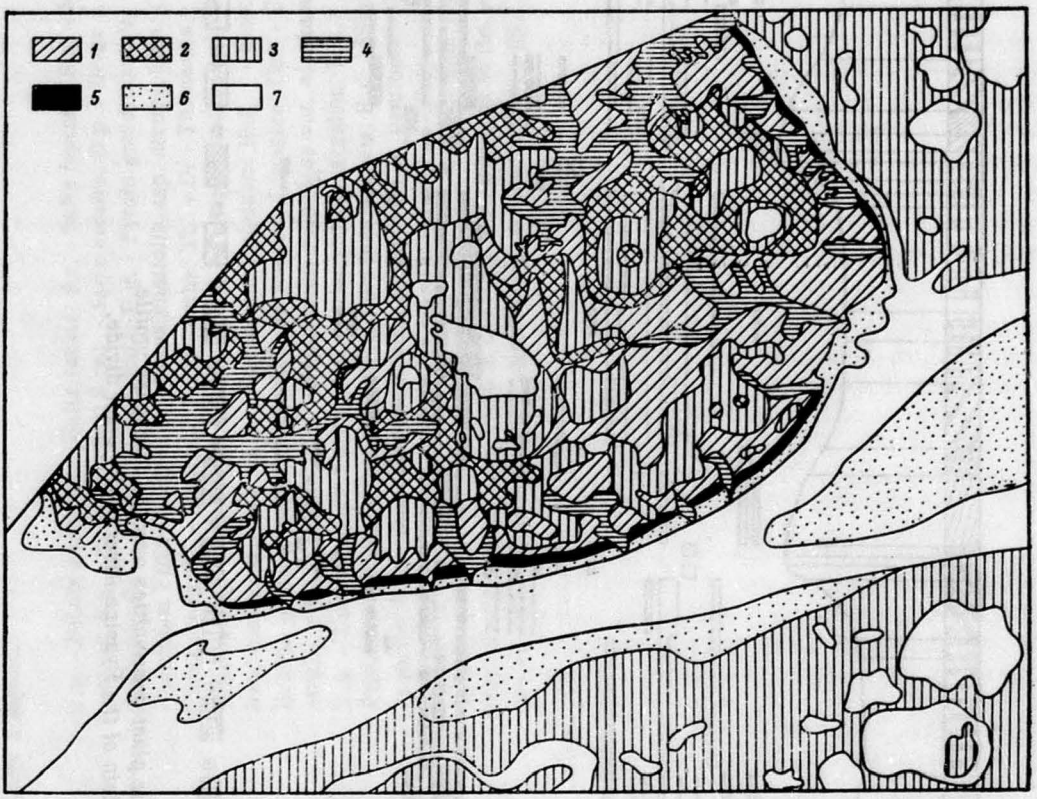

Figure 1. Schematic map of the distribution of basic vegetation types in the vicinity of the station.

Vegetation of the water divides: 1 - Combination of *Dryas* sedge-moss, *Dryas* moss, and herb-*Dryas* tundra with average humidity and good drainage; 2 - Combination of shrub-sedge-moss and dwarf shrub-sedge-moss tundra with high humidity and fragments of boggy tundra and bog communities. Vegetation of lake depressions and areas of accumulated water in the collapsed basins of the upper reaches of the waterways: 3 - Combination of sedge-*Hypnum* and shrub-sedge-*Hypnum* polygonal bogs with shrub-sedge-moss polygonal boggy tundra. Vegetation of brook valleys: 4 - Combination of willow-*Tomenthypnum*, dwarf shrub-*Hylocomium* tundras on slopes with a southern and eastern exposure, *Cassiope*-moss, herb-*Tomenthypnum*, willow-*Drepanocladum* aggregations on north- and west-facing slopes and sedge-, low grass-, and *Eriophorum*-moss communities in the bottoms of the valleys. Vegetation of the ravine slopes of Pyasina and Nera rivers: 5 - Combination of *Dryas*-moss, herb-moss, herb-grass and sparse herb aggregations on the convex parts of the slopes and willow-, and *Equisetum*-moss aggregations in the hollows between them. Vegetation of silty and sandy bars: 6 - *Equisetum* - *Arctophila-Eriophorum*, willow-*Eriophorum-Tomenthypnum*, and willow-sedge-moss aggregations; 7 - Lakes.

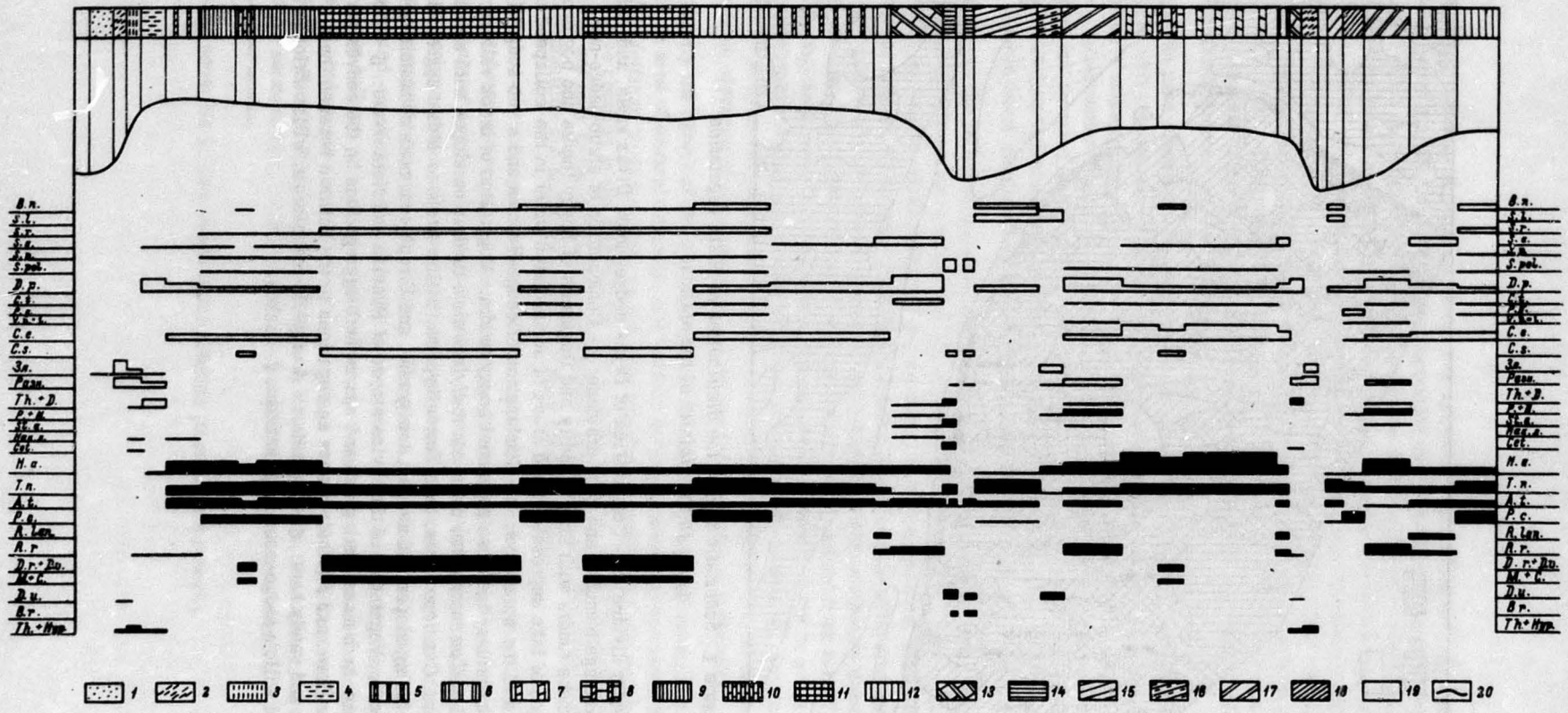

Figure 2. Distribution of basic plant communities over the landscape profile (SSE-NNW) from the floodplain of the Pyasina River to the water divide.

Figure 2 legend.

1 - Silty bars with separate mats of *Poa alpigena* and *Arctophila fulva*; 2 - Herb-grass aggregation; 3 - Herb-moss aggregation; 4 - Lichen-herb-moss tundra; 5 - *Dryas*-sedge-moss spotty tundra; 6 - Dwarf shrub-*Hylocomium* spotty tundra; 7 - Sedge-*Hylocomium* spotty tundra; 8 - The same with combination of *Eriophorum*-moss waterholes; 9 - *Dryas*-sedge-moss small-hummocky tundra; 10 - The same with a combination of sedge-*Eriophorum*-moss waterholes; 11 - Bog-tundra polygonal complex; 12 - Shrub-dwarf shrub-sedge-moss tundra; 13 - Lichen-*Dryas* small-hummocky eroded tundra with small polygons; 14 - Willow-*Drepanocladus* tundra on the upper and sedge-willow-*Drepanocladus* tundra on the lower parts of slopes; 15 - Willow-*Tomenthypnum* tundra; 16 - Grass-willow-*Drepanocladus* tundra; 17 - Herb-dwarf shrub-moss tundra; 18 - Dwarf shrub-moss tundra; 19 - river-beds of Pyasina and brooks; 20 - Line of relief.

B.n. - *Betula nana*; S.l. - *Salix lanata*; S.r. - *Salix reptans*; S.a. - *Salix arctica*; S.p. - *Salix pulchra*; S.pol. - *Salix polaris*; D.p. - *Dryas punctata*; C.t. - *Cassiope tetragona*; P.g. - *Pyrola grandiflora*; V. v-i. - *Vaccinium Vitis-Idaea*; C.e. - *Carex ensifolia* ssp. *arctisibirica*; C.s. - *Carex stans*; *3* - grasses; Pa3H - herbs; Th. + D. - *Thamnolia vermicularis* + *Dactylina arctica*; P + N - *Peltigera aphthosa* + *Nephroma expallidum*; St a. - *Stereocaulon alpinum*; HaK - crustaceous lichens of the *genera Ochrolechia, Pertusaria, Lecanora*; Cet. - *Cetraria nivalis* + *C. cucullata*; H.a. - *Hylocomium splendens var. alaskanum*; T.n. - *Tomenthypnum nitens*; A.t. - *Aulacomnium turgidum*; P.c. - *Ptilidium ciliare*; R. lan. - *Rhacomitrium lanuginosum*; R.r. - *Rhytidium rugosum*; D.r. + D.v. - *Drepanocladus revolvens* + *D. vernicosus*; M. + C. - *Meesia triquetra* + *Calliergon sarmentosum*; D.u. - *Drepanocladus uncinatus*; B.r. - *Bryum cryophilum*; Th. + Hyp. - *Thidium abietinum* + *Hypnum revolutum*. The width of the stripes corresponds to the projected cover of the species; maximum 60%, minimum (line) 1-5%.

The flat surface at lower leaves is occupied by fragments of a dwarf birch-moss tundra (30% of the surface). The dwarf birch thicket is dense, rising high above the surface of the moss turf. It does not form erect shrubs, however. Its cover is a projected 30% of the surface. In the dwarf birch tundra of this type, there is a smaller scale heterogeneity: the lowest level is occupied by mats of *Betula nana*, between them are spots of naked ground surrounded by raised borders covered with *Carex ensifolia* ssp. *arctisibirica*, *Dryas punctata*, *Salix pulchra* and *Vaccinium Vitis-Idaea*. In the moss-cover dominate *Tomenthypnum nitens*, *Hylocomium splendens* var. *alaskanum*, *Aulacomnium turgidum*, *Dicranum angustum*, and *Ptilidium ciliare*. There are few lichens, they grow mainly on raised borders around the spots.

On the flat surface at middle level are found fragments of a *Salix*-moss tundra (30% of the area). Dominants are *Salix reptans* and *Dryas punctata*, in the moss layer *Aulacomnium turgidum*, *Hylocomium splendens* var. *alaskanum*, *Polytrichum strictum* and *Ptilidium ciliare*. The mosses form fairly pure synusia. There are a few lichens.

The fourth element of the complex is fragments of *Polytrichum* tundras (20% of the general area of the complex). It is represented by an accumulation of *Polytrichum strictum* hummocks. The thick moss cover creates unfavorable conditions for the growth of angiosperms: the latter are very few and their projected coverage does not exceed 5-10%; the plants are found in a depauperate condition, many of their parts die off, especially the twigs of *Salix pulchra*. In these habitats there are noted about 10 angiosperm species (basically *Salix reptans*, *S. pulchra*, *Carex stans*, *Festuca cryophila*,[1)] and *Senecio atropurpureus*). Besides *Polytrichum strictum*, among the mosses, *Aulacomnium turgidum* is abundant; the remaining species occur as an admixture. The lichen coverage amounts to 2-3%, generally of species from the genera *Cladonia* and *Cetraria*.

The composition of the vegetational complex on the high water divides can vary somewhat. Sometimes, in addition to the communities mentioned above, there are, within the complex, fragments of *Eriophorum*-moss communities with spots of naked ground, in which are found tussocks of *Eriophorum vaginatum*. On the whole, in spite of some variation, such complexes may be treated as one type - swampy, shrub-moss tundras. Their occurrence is related to thermokarst having developed on the flattest parts of the water divides. Their distinguishing character appears on the whole to be floristic poverty, but more important - in comparison with other tundra communities - is the part of hypo-arctic elements in their flora.

These peculiar and characteristic vegetation complexes are formed also in the upper reaches of brook valleys. The soil surface is broken by frostcracks into large, irregular polygons, 15-35 m in diameter. The watery hollows form here a system of winding waterways in the direction of the valley. These are the wettest habitats; in them grow, together with *Carex stans* and *Eriophorum angustifolium*, also *E. medium*, *E. Scheuchzeri*, *Dupontia Fischeri*, *Comarum palustre*, *Caltha arctica*, and *Cardamine pratensis*.

The surface of the polygons stays for a short time in a waterlogged condition, but then quickly dries out. Thus, the regimen of moisture is here more similar to that of the tundra than to that of the boggy areas. The low-center polygons are occupied by plant aggregations with *Carex stans and Eriophorum angustifolium* and in the moss cover dominate *Drepanocladus revolvens* and *Tomenthypnum nitens*. On the raised border habitats of the polygons develop tundra shrubs such as *Betula nana*, *Salix pulchra* and *S. reptans*; well represented are also dwarf

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[1)] = *Festuca rubra* L. ssp. *Richardsonii* (R.Br.) Hulten (translator's remark).

shrubs like *Dryas punctata, Vaccinium Vitis-Idaea, Cassiope tetragona, Ledum decumbens, Pyrola grandiflora,* and *Ramischia obtusata*[1], and on the raised borders there are also such species, rare for the area investigated, as *Andromeda polifolia, Rubus Chamaemorus* and *Lycopodium Selago*[2]. The high surface polygons are occupied by dwarf birch-moss and willow-moss tundras. This is the second type of habitat (along with the vegetation complexes on the high water divides), where the dwarf birch dominates. The birch reaches 0.5-0.7 m in height. On the raised parts of the polygons, there are often fragments of *Dryas*-sedge-moss tundras, which are so typical for the water divides.

The complexes in the upper reaches of the brooks are distinguished from the above described complexes of swampy tundras on the elevated water divides by the fact that fragments of bog-communities occupy larger areas here and the surface of the ground is broken into polygons of irregular form. The formation of the complexes of a given type is related, rather than to thermo-karst, to frost-cracking of the ground, which makes it similar to polygonal bogs. Although the correlation of the elements of the complexes may change somewhat in relation to increased or decreased paludification, the vegetation of such water-collecting depressions may belong to one bog-tundra polygonal type.

An important space in the area investigated is occupied by lake depressions with arctic polygonal bogs. The drying up of the lakes occurs due to the strongly draining influence of brooks; all the lake depressions are drained. The character of the vegetation of the different bog-masses changes in relation to the duration of their existence as bogs (after the water is lowered). All stages of bog-development may be seen from its very beginning, when the surface of the entire mass has still not been divided into separate polygons, and when frost-cracks can be guessed at just by the change in color of the vegetation cover: along cracks "paths" of open *Carex stans* stands with a light green color are observed against a background vegetation of *Carex chordorrhiza* and *C. rotundata* of a gray-green color. In the next development stage the mass is already broken up by frost-cracks into distinct polygons of 7-10 m diameter, around which start to form raised borders, formed by crumbly cushions of *Aulacomnium turgidum.* The surface of the polygons remains in a waterlogged condition all summer with just the slightly higher borders for a short time uncovered by water. For the somewhat older bog-massives, a regular division into tetragons is characteristic. These are bordered by raised borders and separated by troughs along the frost-cracks. The polygons have a concave surface and in the center of the bog-massive water is standing in them all summer long; the raised borders are dry; on the edges of the bog-complex the bottoms of the polygons dry out, often towards the end of the summer. The vegetation in the center of the polygons is distinguished by a rather high degree of uniformity (the nano-relief so characteristic for tundra communities, has usually not developed here); the dominating angiosperms are: *Carex stans, C. chordorrhiza, Hierochloe pauciflora, Eriophorum medium,* and *Salix reptans,* and of mosses, moisture loving species of the genera *Drepanocladus* and *Mnium.* On the raised borders has developed a vegetation, close to that of tundra: dominants are *Dryas punctata, Salix reptans, Carex stans, Hylocomium splendens* var. *alaskanum,* and *Aulacomnium turgidum.* In the troughs, the vegetation approaches that of the polygon centers, but still poorer in floristic composition: *Carex stans* dominates together with moss species of the genera *Drepanocladus* and *Mnium.*

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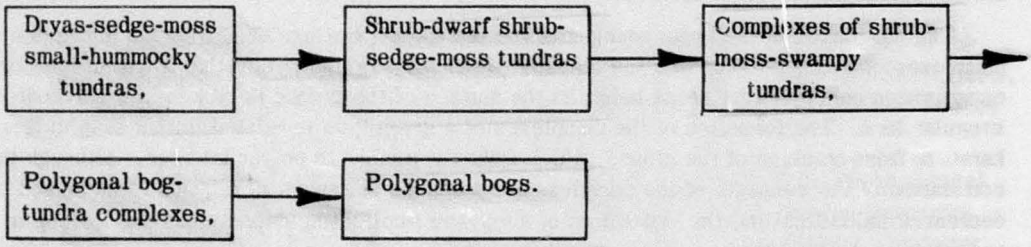
[1] = *Orthilia (Pyrola) secunda* (L.) House ssp. obtusata (Turcz.) Hulten (translator's remark).

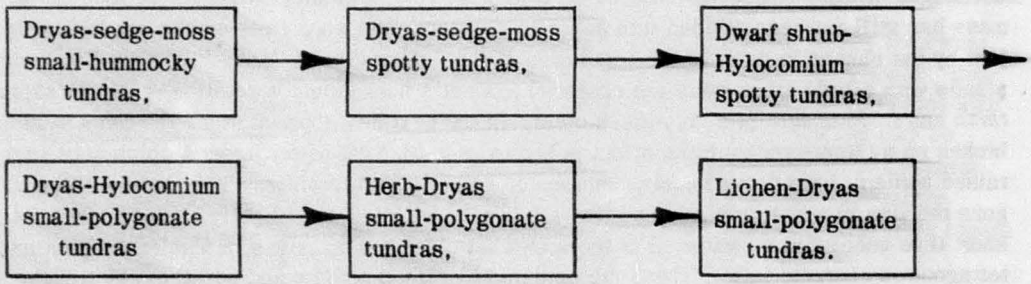
[2] = *Huperzia Selago* (L.) Bernh. (translator's remark).

On the whole, the vegetation of the bogs in our area is similar to that of bogs in other areas of the Arctic, in particular to bogs around the lower Lena (Petrovsky 1959).

The above described types form a row of units of vegetation cover, replacing one another in the direction of increasing factors of moisture and depth of snow cover on a basis of change in soils from loamy (on the water divides) to peaty (in bogs). This series may be represented by the following schema:



Another ecological series of communities on water divides follows along the moisture gradient of increasing drainage and diminished snow-cover on basis of a change from loamy soil to soils of a light mechanical composition:



In conditions, generally close to those in which *Dryas*-sedge-moss small-hummocky tundras develop, but differing by more drained soils and a less deep snow-cover, *Dryas*-sedge-moss spotty tundras are widely represented with a composition of dominants not different from that of the above described small hummocks (*Carex ensifolia* ssp. *arctisibirica*, *Dryas punctata*, *Tomenthypnum nitens*, *Hylocomium splendens* var. *alaskanum*, *Aulacomnium turgidum*). Usually, they occupy flat habitats along the margin of the main banks of Pyasina, which are well drained not only by Pyasina itself but also by its small tributaries; in addition, they occupy elevated and convex parts of the water divides. As clearly distinguishing characters for the spotty tundra appear the presence of spots of bare ground and in connection with them of a not completely continuous vegetation cover. As a result of the formation of a nano-relief, which is represented here by three elements (spots, raised borders and troughs), the vegetation in the spotty tundras is still more diversified than in the small-hummocky ones. In accordance with the three nano-relief elements, three micro-aggregations can be distinguished. The distinction of the vegetation in accordance with different nano-relief elements is in a high degree quantitative rather than qualitative. There is a row of specific species, characteristic for the spots, usually from the

groups of crustaceous lichens: species of the genera *Lecanora, Baeomyces, Rinodina, Pertusaria, Ochrolechia, Toninia* and *Lecidea*. An important role for the revegetation of a spot in the early stages is usually played by *Toninia lobulata* in this type of tundras.

Between the spotty and the small-hummocky *Dryas*-sedge-moss tundras there exist transitional types (and in the case, when they border to each other, a transitional belt can be distinguished; Aleksandrova 1971 A), for which spots of bare ground are characteristic, but not so regularly as in the spotty tundra. The differences in structure of such tundras are caused by the irregular distribution of snow cover in connection with cryogenic processes, taking place in the soil, as a result of which, in localities the least protected by the snow cover, spots of bare ground appear. Thus, on the slopes of brook valleys, spotty and small-hummocky tundras are strictly related to convex (without or with little snow cover) and concave habitats respectively. According to the community of dominants and the genetic closeness, these two types of tundra are distinguished by their spatial structure and the presence of differential species. This was, at the time, the reason why we gave the *Dryas*-sedge-moss small-hummocky tundras and the spotty tundras the rank of ecologically conditioned variants of a single association, but did not separate them into independent units (Matveyeva 1968). Until this time, in the literature, the problem remains open whether the spotty tundras belong to the corresponding associations of communities with a continuous cover from which they appear to have originated, or if they should be distinguished as special units (Sochava 1930; Andreyev 1932; Gorodkov 1935; Govorukhin 1936; Avramchik 1937; Vinogradova 1937; Dushechkin 1937). The solution to this problem is, apparently connected with the fact, that up to now there is no single approach to the concept of the size of an association on the whole. The existence of plant communities with similar floristic composition and sets of dominants, but with different spatial structures and special sets of differentiating species is a phenomenon widely distributed in the tundra zone.

Along with improved drainage (close to brooks), the composition of the vegetation on the spotty tundra begins to change, at the same time as the character of its distribution is retained. The spots of bare ground are almost deprived of vegetation, there is a lack of crustaceous lichens, even of *Toninia lobulata*, the surface of the soil is smooth without traces of frostboils; the spots are in the very first stage of vegetation development. On the borders, the vegetation, surrounding the spots (there is hardly any nano-relief here and raised borders around the spots are absent) is, as before, dominated by *Dryas punctata*, but the abundance of *Carex ensifolia* ssp. *arctisibirica* is diminished, and instead there grows a combination of *Salix arctica, S. polaris* and *Cassiope tetragona*. In the moss cover, *Hylocomium splendens* var. *alaskanum* dominates with an admixture of *Rhytidium rugosum* and *Rhacomitrium lanuginosum*. Depending on its location in the relief, a dwarf shrub-*Hylocomium* spotty tundra may be somehow distinguished by the size of the spots,the degree of its vegetation development and its floristic composition (not of the dominants but of the secondary species).

Close to the brook valleys, the dwarf shrub-*Hylocomium* tundras change into *Dryas*-moss, herb- and lichen-*Dryas*-small polygonate tundras. The diameter of the polygons diminishes to 50 cm, their surfaces stay flat to convex.

As dominant vegetation on the polygons appears *Dryas punctata* (70-80%), which in these conditions is spread over and pressed to the surface of the ground so that the thickness of the plant mat does not exceed 1-2 cm. Sometimes the *Dryas*-carpet completely covers the surface of the polygons, but more often it forms the border vegetation around the polygon, in the center of which the soil remains open with lichens of the genera *Ochroleuca, Pertusaria* and *Lecanora*. The floristic composition of such tundras is usually variable, generally because of an abundance

of legumes and herbs. The polygons are split by narrow frost-cracks. In such a case, when the cracks are about or more than 10 cm wide, they are colonized by mosses (in *Dryas*-moss tundras) such as *Hylocomium splendens* var. *alaskanum* or *Rhytidium rugosum;* where the cracks are less than 5 cm, they are usually deep (up to 10-15 cm) and have steep, not vegetated sides (in herb- and lichen-*Dryas* tundras). Usually, such tundras are related to well drained soils of a light mechanical texture and are situated in the upper part of steep slopes of brook valleys.

On the very steepest parts of the slopes, the polygons, parted by frost-cracks into separate pieces, begin to slip down. The character of the vegetation of the surface of the polygon is in such cases preserved, but the nano-relief is sharply changed: the polygons develop into elevated bumps between which collects soil deprived of vegetation. Such sites are subjected to strong water and snow erosion; here may take place a catastrophic washing away of soil together with its vegetation turf, which will lead to erosion of the ground, its warming, deep thawing of the permafrost, the development of thermokarst and, finally, *in toto*, to the formation of negative forms of relief in the shape of many spurs and brooks of ravine type.

As a zonal vegetation type, developed on flat water divides on loamy soils of medium moisture, may be considered the *Dryas*-sedge-moss small-hummocky tundras.

Now we turn to the description of the vegetation in the river valleys. The right hand bank of the Pyasina is characterized by the presence of a dense network of brooks. The majority of them fall out directly into Pyasina, but a few belong to the system of its tributaries, Nera and Tananka-Tar. The length of the brook channels varies from one to a few kilometers. In addition, the larger brooks have a great many tributaries, and their banks are cut by very many deep channels in which, to the middle of summer, there is still snow and after snowmelt, these channels turn into waterways. The slopes of the brooks, oriented in different directions, have alternating convex and concave parts. Variability due to the external conditions is the cause for the large variety of the vegetation in the valleys: its character changes markedly in regards to exposure and steepness of the slopes and in connection with this to the depth and durability of the snow cover, to the warming of the soil and to the depth of thawed out permafrost.

The slopes facing south, southwest and southeast are usually gentle and relatively even: convex and concave parts are very smooth and transfer gradually from one into the other. The concave parts of the slopes, represented by not very deep channels, are occupied by willow stands of *Salix lanata* and a moss cover where *Tomenthypnum nitens* dominates with an admixture of *Hylocomium splendens* var. *alaskanum, Drepanocladus uncinatus, Campylium polygamum,* and *Ptilidium ciliare.* The willows occupy wide areas in the lower, the gentlest parts of the slopes and also directly along the channels, and ascend from such depressions right up into the water divides and also often onto the top of them. On the convex parts of the slopes, the willowbrush is distributed in a not very wide belt along the water, which soon changes into a herb-dwarf shrub-moss tundra.

In the latter, a well-developed nano-relief is represented by hummocks arranged in "furrows" and by separating them by channels stretching down along the slope. The dominating species of the angiosperms is *Dryas punctata* with the co-dominants *Cassiope tetragona, Vaccinium Vitis-Idaea, Salix polaris* and *S. reptans.* The species composition as noted is very variable (usually around 50 species); and well represented are grasses (*Alopecurus alpinus, Trisetum sibiricum, Arctagrostis latifola*), legumes (*Astragalus umbellatus, A. subpolaris, Hedysarum arcticum*), and herbs (*Polygonum viviparum, Polygonum Bistorta, Senecio resedifolius, Valeriana capitata, Saxifraga punctata,* etc.). In the moss cover along with the widely distributed *Tomenthypnum nitens* (in the channels) and *Hylocomium splendens* var. *alaskanum* (on the hummocks) an

important role is played by *Rhytidium rugosum*. The angiosperms are most abundant on the hummocks and the mosses dominate the troughs together with an important participation (up to 10%) of foliaceous lichens: *Peltigera canina, P. aphthosa*, and *Nephroma expallidum*. The species composition of lichens in such communities is extremely poor (not more than 4 or 5 species) which in general is not characteristic for the tundra communities in the area studied. Usually there can be counted up to 40 species or more. Typically, the fruticose lichens are missing.

Along the steepest part of the slopes, usually on their upper parts, on the most pronounced elements of the nano-relief, there are spots of bare ground in this type of tundra.

A combination of mossy willow brush with herb-dwarf shrub-moss communities is typical for the slopes of the southern faces of the major brooks. In the valleys of the smaller brooks, the latter usually change into herb-*Dryas*-moss tundras (where the nano-relief is not present, *Rhytidium rugosum, Hylocomium splendens* var. *alaskanum* and *Thuidium abietinum* dominate in the moss cover, and the species composition of angiosperms is rich in herbs).

The north-facing slopes are more variable as to the character of their vegetation, which is connected with the greater contrast in the conditions of the environment. Usually rather steep, they are cut by numerous deep channels of ravine type, in which snow remains sometimes as long as to the middle of August. On the convex ridges of the northern slopes, *Cassiope*-moss tundras have developed. Along with the dominant *Cassiope tetragona*, there is an abundant quantity of *Salix polaris* and *Dryas punctata*. In the moss cover which is very thin, *Drepanocladus uncinatus* dominates with an admixture of *Tomenthypnum nitens, Aulacomnium turgidum* and *Ditrichum flexicaule*. In wintertime, such localities are covered by quite deep layers of snow, which in the spring melts fairly quickly so in general they are dry, but cold habitats (because of the exposure). On the contrary, the concave parts of the northern slopes are filled with snow for a quite long time (to the end of July) and are sufficiently wet (running water). Here have developed *Equisetum*-moss-tundras *(Equisetum arvense, Drepanocladus uncinatus, Tomenthypnum nitens)* and willow-moss tundras *(Salix polaris, Drepanocladus uncinatus)* with an abundance of herbs *(Lagotis minor, Oxyria digyna, Ranunculus borealis*[1] *Saxifraga cernua, S. tenuis* and *Pachypleurum alpinum)*.

In more level and dry locations between the ridges, there are not rarely grass-herb-moss tundras, extremely colorful at the height of the vegetation season. Most abundant, and giving a colorful aspect, are *Trisetum sibiricum, Polygonum Bistorta, Ranunculus borealis, Valeriana capitata, Myosotis asiatica, Saxifraga punctata* and *Astragalus umbellatus)*. In the moss cover, *Drepancoladus uncinatus* dominates, but the thickness of the moss cushion is not more than 1 cm.

In the deep valleys of the major brooks, the snow often lasts to the middle of August on the lower parts of the northfacing slopes on negative elements in the relief. The parts surrounding the snowdrifts are occupied by herb-moss communities. In the herbage dominate *Alopecurus alpinus, Ranunculus borealis, R. nivalis, Saxifraga nivalis, S. punctata, Nardosmia frigida*[2], *Eritrichium villosum*, often with a considerable abundance of *Equisetum arvense*. In the moss layer dominate *Tomenthypnum nitens, Drepanocladus uncinatus, D. revolvens, Campylium zemliae* and *Cirriphyllum cirrosum*. In the hollows, gradually melting out under the snow, develop *Ranunculus nivalis, R. sulphureus, R. pygmaeus, Saxifraga tenuis, S. nivalis, S. cernua, S.*

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1) = *Ranunculus acris* L. ssp. *borealis* (Trautv.) Nyman (translator's remark).

2) = *Petasites frigidus* (L.) Franch. (translator's remark).

hyperborea, Phippsia concinna, Carex tripartita[1], and *Taraxacum arcticum.* In the steepest localities in the snow-patch, the ground as a result of erosion often becomes bare, slips or slides gradually down the slope. In such localities, a continuous vegetation cover is absent.

In contrast to the slopes with a southern exposure, the extent of the various communities on the northfacing slopes is limited to about 10, and they often occupy only a few square meters. The communities change gradually along the slope, and the contrast between the vegetation on convex and concave parts of the slope appears very sharp.

Thus, in brook valleys on northfacing slopes there is a characteristic combination of *Cassiope*-moss tundras on convex parts and willow-moss, or herb-grass-moss communities on concave parts and of nival aggregations in places with a long-lasting snow-cover. Immediately along the brook channels, by the water (the width of the open water surface in the upper reaches is 0.5-1 m, at the outlets up to a few meters) stands of *Carex stans, Eriophorum angustifolium* and *E. Scheuchzeri* develops. Sometimes, short grass-moss communities are seen with a not very thick, sparse angiosperm vegetation *(Calamagrostis neglecta, Saxifraga cernua* and *Ranunculus nivalis).* Mosses cover the soil in a compact layer: these are hygrophilous species, *Drepanocladus revolvens, D. uncinatus, Bryum cryophilum, Calliergon sarmentosum* and *Campylium polygamum.* Such lowest habitats are the last of all to emerge from the submersion at the time of spring-flooding and remain strongly waterlogged throughout all the vegetation period. In the upper reaches, where a brook channel has still not formed, on the rather wide bottoms in conditions of running water, a thick growth is formed of *Carex stans, Dupontia Fischeri, Eriophorum angustifolium, E. Scheuchzeri* and *Comarum palustre;* in the moss cover *Bryum cryophilum, Drepanocladus aduncus, Campylium polygonatum* and *Mnium rugicum* usually dominate.

The ancient alluvial terrace of Pyasina (20-25 m above the surface of the river) slopes sharply to the floodplain, the riverchannel coming almost to the foot of the banks, which are strongly undercut by the river at times of flooding. In general, the slope of the bank has a SSW exposure, but being strongly cut by ravines, it also has a combination of other exposures. Characteristic for the bank-slope is a better heating and a deeper seasonal thawing of the soils. The distribution of snow is extremely uneven: on the very edge of the terrace, it is completely blown away, then as one proceeds to the lower parts of the slope and into the depth of the ravines, it may reach a thickness of several meters. The slopes are subjected to constant water and snow erosion, very often to sliding, which hinders the development of vegetation. The nano-relief is formed by flat hummocks of 0.4-0.8 m diameter, which are separated by frost-cracks 0.2-0.5 m wide. Terrace formation is clearly expressed in some places.

The vegetation is denser on the upper and thinner in the lower parts of the slopes. When the heterogeneity reaches a maximum extent almost every hummock sports its own micro-aggregation. The almost complete absence of fruticose lichens is characteristic as well as the unimportance of mosses, especially on the convex parts of the slopes. On the upper part of the slopes have developed herb-*Dryas*-, on the lower portions grass-herb-, and in channels and on northfacing slopes, herbaceous and willow-moss plant aggregations. All the communities of the bank-slope, with the exception of eroded parts, are distinguished by a great variety in species. Here, more than 100 species of angiosperms alone are met. The *Dryas*-aggregations on the upper slopes are characterized by a unique collection of cryophile species, many of which are met with nowhere else *(Koeleria asiatica, Kobresia Bellardi, Carex rupestris, Erysimum Pallasii, Oxytropis Adamsiana,* and *Androsace triflora).*

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[1] = *Carex Lachenalii* Schkur (translator's remark).

Especially variable is the species composition of aggregations, covering the southern slopes. These habitats are well heated, more moist and in winter safely covered with snow. The lower layers are composed of dwarf shrubs as *Salix arctica* and *Dryas punctata;* mosses, *Thuidium abietinum, Drepanocladus uncinatus* and *Hypnum revolutum* are met with in hollows and on the slopes of hummocks; the upper layer is developed by thermophile species of herbs *(Cerastium maximum, Ranunculus borealis, Delphinium Middendorffii, Oxytropis Middendorffii, Polemonium boreale, Myosotis asiatica, Pedicularis verticillata, Erigeron eriocephalus,* and *Arnica Iljinii).*

In the grasslands (30-50 cm high) on the lower part of the slopes, there is an important admixture of grasses (up to 50%, of *Poa glauca, Festuca cryophila, Alopecurus alpinus* and *Trisetum sibiricum).*

The eroded and slipping portions of the slopes, according to the degree of vegetation development, are covered by open herbage composed of *Tripleurospermum phaeocephalum, Myosotis asiatica, Papaver pulvinatum, Arabis septentrionalis, Taraxacum* sp., etc.

In the channels between steep banks where the snow lasts to the middle of July, we have, however, not met with the usual set of nival species. The bottoms of these channels are completely covered with mosses such as *Hylocomium splendens* var. *alaskanum* and *Drepanocladus aduncus,* and of higher plants there reign *Salix polaris* and *S. arctica.*

On the coarse, sandy-pebbly alluvium on the very edges of the Pyasina floodplain, there has developed a thicket of *Salix reptans* and thick stands of *Equisetum arvense* without a moss cover. Besides the species mentioned, here grow *Cerastium jenisejense, Pyrethrum bipinnatum*[1], *Rumex sibiricum,* and *Pedicularis sudetica.* The clay habitats on the floodplain along the river-channel are occupied by *Arctophila*-communities (*Arctophila fulva* covers 30-50%) in which there are usually found *Eriophorum Scheuchzeri, Carex stans, Deschampsia Sukatschewii, Cardamine pratensis,* and *Caltha arctica.* The moss layer is not very thick and consists of *Ceratodon purpureus, Brachythecium Mildeanum* var. *udum, Mnium rugicum, Bryum cryophilum,* and *Aulacomnium turgidum.*

The floodplains of the major right hand tributaries to Pyasina differ by greater occurrence of willow-brush of *Salix reptans* with a small addition of *S. lanata.* Thus, on the floodplain of Nera, close to its mouth along the direction from the river-channel to the base of the bank, there is a succession of the following communities: from an *Equisetum-Arctophila-Eriophorum (Equisetum arvense* 10%, *Arctophila fulva* 15%, *Eriophorum Scheuchzeri* 20%, moss cover practically absent), over a willow-*Eriophorum*-sedge (*Salix reptans* 15%, *Eriophorum Scheuchzeri* 5-10%, *Carex stans* 20%, a moss cover of *Calliergon Richardsonii, Ceratodon purpureus* and *Mnium rugicum* 20%), to a willow-sedge-moss community *(Salix reptans* 25%, *Carex stans* 20%, *Tomenthypnum nitens* 80%, *Orthothecium chryseum* 10%).

The low, inundated sandy islands near the mouths of Nera, Tareya and Tanunka-Tar are covered with willow-brush of *Salix reptans* and a sedge-mat of *Carex stans* with a depauperate species composition.

The above described plant communities and their combinations are principal, most often met with, and they occupy the biggest area of the right-hand bank of Pyasina.

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[1] = *Chrysanthemum bipinnatum* L. (translator's remark).

THE VEGETATION OF THE PERMANENT SITES

Complex biogeocoenological investigations were carried out in the area of Tareya on permanent sites, especially selected for this purpose. The sites were situated along the basic profile of the landscape and went from the floodplain of Pyasina over the mainland slopes onto the water divides (Fig. 2). True enough, not all elements of this profile were covered by the observations made, but the sites were laid out with such calculation that the most widely distributed and typical biogeocoenoses of the area were covered by the investigation. This was done first and foremost for the tundra biogeocoenoses.

In the course of several years, various observations were made on these sites for the purpose of studying the quantitative characteristics of the various components of the biogeocoenoses: micro-climate, soils, observations on the melting of the permafrost, and on the composition and dynamics of microbial and animal colonization of the soils (Compare the preceding symposium!). Further, a determination of the general store of the phytomass has been carried out (Khodachek 1970), and the dynamics of the weight increment of the above-ground plant growth has also been investigated (Polozova and Shamurin 1970).

The report on the vegetation of the permanent sites has not been published. The descriptions and schematic maps below will fill this gap.

The *Dryas*-sedge-moss small-hummocky and the spotty tundras appear to be the zonal types of tundra in the station area. Because of this, their structure and vegetation has been studied especially thoroughly from both qualitative and quantitative points of view (Matveyeva 1968, 1970 A).

Site no. 1

The Dryas-sedge-moss small-hummocky tundra

The site is situated 1.5 km from Pyasina, on the upper part of a very gently N-W sloping hill. The site is poorly drained, throughout all the vegetation period, the soil is found in a very moist condition. A snow-cover is established in the beginning of October; snow-melt begins in the first part of June. The depth of the snow-cover is 40 cm, and the depth of the seasonal thaw of the soil is 50-60 cm. As also in the majority of the tundra communities, the nano-relief of the site is well developed. It has hummocks 10-12 cm in height and 15-30 cm in diameter. They have an irregular shape and, merging together, they form chains, ridges and other nano-elevations. The hummocks are divided by narrow, winding troughs, 15-20 cm broad. The hummocks occupy 60-70% of the area, the troughs 40-30%. In addition, there are also some big spots on the site, 2-3 m in diameter, with increased moisture in which the relation between the area covered by hummocks and troughs, is changed in favor of the troughs. The formation of these depressions is related to the appearance of thermokarst. The soil of the site is tundra gley.

In the community studied, we counted 118 species, of which there are 38 angiosperms, 38 lichens, and 41 mosses (Table 1). As dominants in the vegetation cover appear *Dryas punctata* (10% coverage), *Carex ensifolia* ssp. *arctisibirica* (15%), *Hylocomium splendens* var. *alaskanum* (25%), *Aulacomnium turgidum* (20%) *Tomenthypnum nitens* (20%) and *Ptilidium ciliare* (20%). Of the angiosperms, only *Cassiope tetragona* and *Salix reptans* reach any significant coverage (1%); all the rest of the species occupy unimportant areas. The species listed are characterized by the highest frequency. Beside them, there is a high frequency for *Eriophorum angustifolium*, *Ramischia*

Table 1. Species composition of vegetation aggregations of permanent sites nos. 1 and 2.

Name of species	Spotted tundra			Small-hummocky tundra
	Spots	Raised borders	Troughs	
Angiosperms				
Alopecurus alpinus Smith	+	5	1	+
Arctagrostis latifolia (R. Br.) Griseb.	+	+	+	+
Trisetum sibiricum Rupr.	—	+	—	—
Koeleria asiatica Domin.	+	+	—	—
Poa arctica R. Br.	+	+	+	—
Festuca cryophila V. Krecz. et Bobr.	—	—	+	—
F. brachyphylla Schult.	+	+	—	—
Eriophorum angustifolium Honck.	+	+	—	+
E. vaginatum L.	—	—	—	+
Carex ensifolia (Turcz. ex Gorodk.) V. Krecz. ssp. *arctisibirica* Jurtz.	3	15	6	10
C. vaginata Tausch	—	—	+	+
Juncus biglumis L.	+	+	+	—
Luzula confuza Lindb.	+	+	—	—
L. nivalis Laest.	+	+	+	+
L. tundricola Gorodk.	+	+	+	—
Salix polaris Wahlenb.	+	1	+	+
S. arctica Pall.	+	5	1	+
S. reptans Rupr.	—	+	+	+
S. pulchra Cham.	+	+	+	—
Betula nana L.	—	+	+	+
Polygonum viviparum L.	+	+	+	+
Claytonia joanneana Roem. et Schult.	—	+	+	—
Stellaria ciliatosepala Trautv.	+	+	+	+
Cerastium bialynickii Tolm.	+	—	—	—
Sagina intermedia Fenzl.	+	—	—	—
Minuartia rubella (Wahlenb.) Hiern.	+	+	—	—
M. macrocarpa (Pursh) Ostenf.	+	—	—	—
M. arctica (Stev. ex Sér.) Aschers. et Graebn.	+	+	+	+
Ranunculus sulphureus Soland.	—	—	—	+
R. nivalis L.	+	—	—	+
R. borealis Trautv.	+	—	—	—
Papaver pulvinatum Tolm.	+	+	—	—
Eutrema edwardsii R. Br.	—	+	+	+
Cardamine bellidifolia L.	+	+	+	+
Parrya nudicaulis (L.) Regel	+	+	+	+
Draba micropetala Hook.	+	+	+	—
D. lactea Adams	+	+	+	+
Saxifraga punctata L.	+	+	+	+
S. nivalis L.	+	+	+	+
S. hieracifolia Waldst. et Kit.	+	+	+	+
S. hirculus L.	+	+	+	+
S. cernua L.	+	—	—	+
S. caespitosa L.	—	—	—	+
S. spinulosa Adams	+	+	+	+
S. oppositifolia L.		+	—	—
Dryas punctata Juz.	8	15	2	8
Astragalus umbellatus Bunge	—	+	—	—
A. subpolaris Boriss. et Schischk.	+	+	—	—
Epilobium davuricum Fisch.	+	—	—	—
Pyrola grandiflora Rad.	—	—	—	+
Ramischia obtusata (Turcz.) Freyn	—	+	+	+
Cassiope tetragona (L.) D. Don	+	+	+	1
Vaccinium vitis-idaea L.	—	+	—	+
Androsace bungeana Schischk. et Bobr.	+	+	—	—
Myosotis asiatica Schischk. et Serg.	—	+	+	—
Lagotis minor (Willd.) Standl.	—	+	+	+

Table 1. Continued

Name of species	Spotted tundra			Small-hummocky tundra
	Spots	Raised borders	Troughs	
Pedicularis sudetica Willd.	—	—	—	+
P. dasyantha (Trautv.) Hadač	—	—	—	+
P. hirsuta L.	—	—	—	+
P. oederi Vahl	+	+	+	+
P. capitata Adams	—	+	—	+
Valeriana capitata Pall.	—	+	—	—
Nardosmia gmelinii (Turcz.) DC.	—	+	+	—
Senecio resedifolius Less.	+	+	+	—
Leafy mosses[1)]				
Polytrichum alpinum Hedw.	—	—	—	+
P. juniperinum Hedw.	+	+	+	+
P. strictum Sm.	+	+	+	+
Ditrichum flexicaule (Schleich.) Hampe	10	+	+	+
Ceratodon purpureus (Hedw.) Brid.	—	—	+	—
Distichium capillaceum (Hedw.) B.S.G.	+	—	+	+
D. inclinatum (Hedw.) B. S. G.	+	—	+	—
Oncophorus wahlenbergii Brid.	+	+	+	+
Dicranum elongatum Schleich.	+	2	+	+
D. congestum Brid.	+	+	+	+
D. spadiceum Zett.	+	+	+	2
D. angustum Lindb.	+	+	+	+
D. bongeanii De Not.	+	+	+	+
D. acutifolium (Lindb. et Arn.) C. Jens.	+	+	+	+
Tortella fragilis (Hook. et Wils.) Limpr.	—	—	+	—
Bryoerythrophyllum recurvirostre (Hedw.) Chen	+	—	—	—
Rhacomitrium canescens (Hedw.) Brid.	+	+	+	+
R. lanuginosum (Hedw.) Brid.	3	5	+	3
Tetraplodon mnioides (Hedw.). B. S. G.	—	—	1	+
Splachnum ovatum Hedw.	—	—	—	+
Haplodon wormskjoldii (Hornem.) R. Brown	—	—	+	+
Bryum wrightii Sull. et Lesq.	+	—	—	—
Mnium rugicum Laur.	—	—	—	+
Cinclidium subrotundum Lindb.	—	—	+	—
C. latifolium Lindb.	—	—	—	+
Aulacomnium turgidum (Wahlenb.) Schwaegr.	+	15	5	20
Meesia uliginosa Hedw.	+	—	—	+
M. triquetra (Hook. et Tayl.) Ångstr.	—	—	+	+
Bartramia pomiformis Hedw.	—	+	+	+
Philonotis tomentella Mol.	—	+	—	—
P. fontana (Hedw.) Brid.	—	+	+	+
Myurella julacea (Schwaegr.) B. S. G.	+	—	+	+
Thuidium abietinum (Schwaegr.) B. S. G.	+	+	—	—
Campylium stellatum (Hedw.) Lange et C. Jens.	+	—	+	+
C. polygamum (B. S. G.) Lange et C. Jens.	+	—	+	—
Drepanocladus uncinatus (Hedw.) Warnst.	—	—	+	+
D. intermedius (Lindb.) Warnst.	—	—	+	—
D. revolvens (Turn.) Warnst.	—	—	+	+
D. lapponicus (Norrl.) Z. Smirn. f. *gigas* (Lindb.) Z. Smirn.	—	—	+	—
D. latifolius (Lindb. et Arn.) Broth.	—	—	+	+
D. aduncus Warnst. var. *polycarpus* (Bland.) Mönkem.	—	—	+	—
Scorpidium turgescens (Th. Jens.) Mönkem.	—	—	+	—
Calliergon sarmentosum (Wahlenb.) Kindb.	—	—	+	+
C. giganteum (Schimp.) Kindb.	—	—	—	+
C. richardsonii (Mitt.) Kindb.	—	—	—	+
Tomenthypnum nitens (Hedw.) Loeske	+	1	55	20

[1]A list of the liverworts is found in the paper by A.L. Zhukova in the present collection of papers.

Table 1. Continued

Name of species	Spotted tundra a			Small-hummocky tundra
	Spots	Raised borders	Troughs	
Brachythecium mildeanum (Schimp.) Milde var. *udum* (Hag.) Mönkem.	—	—	—	+
Cirriphyllum cirrosum (Schwaegr.) Grout.	+	+	+	+
Orthothecium strictum Lor.	+	—	—	+
O. chryseum (Schwaegr.) B. S. G.	+	+	+	+
Hypnum bambergeri Schimp.	1	+	+	+
Pseudostereodon procerrimum (Mol.) Fleisch.	+	—	—	—
Rhytidium rugosum (Hedw.) Kindb.	+	10	+	+
Hylocomium splendens (Hedw.) B. S. G. var. *alaskanum* (Lesq. et James) Limpr.	+	35	21	25
Lichens				
Sphaerophorus globosus (Huds.) Vain.	+	+	+	+
Psoroma hypnorum (Vahl.) Grey	+	+	+	+
Lobaria linita (Ach.) Rabenh.	—	—	+	—
Nephroma expallidum (Nyl.) Nyl.	+	1	+	+
Peltigera aphthosa (L.) Willd.	+	5	+	1
P. canina (L.) Willd.	+	+	+	1
P. erumpens (Tayl.) Vain.	+	+	+	+
P. polydactyla (Neck.) Hoffm.	+	+	+	+
P. rufescens (Weis) Humb.	—	—	—	+
P. venosa (L.) Baumg.	+	+	+	+
Solorina saccata (L.) Ach.	+	—	—	+
S. spongiosa (Sm.) Anzi	+	—	—	—
Lecidea tornoënsis Nyl.	+	—	—	+
L. osloënsis Th. Fr.	+	—	—	—
Bilimbia sphaeroides (Dicks.) Koerb.	+	—	—	—
Lopadium pezizoideum (Ach.) Koerb.	+	—	—	+
Toninia lobulata (Smrft.) Lynge	20	+	+	+
Baeomyces carneus (Retz.) Flk.	+	—	—	+
Cladonia amaurocraea (Flk.) Schaer.	+	2	+	+
C. beringiana (Ahti) Trass	+	1	+	+
C. bellidiflora (Ach.) Schaer.	+	+	+	+
C. chlorophaea (Flk.) Zopf.	—	+	+	—
C. degenerans (Flk.) Spreng.	+	+	+	+
C. elongata (Jacq.) Hoffm.	+	1	+	+
C. pleurota (Flk.) Schaer.	+	+	+	+
C. pyxidata (L.) Hoffm.	+	+	+	+
C. rangiferina (L.) Web.	+	0.5	+	+
C. uncialis (L.) Web.	+	+	+	+
Stereocaulon alpinum Laur.	+	+	+	+
Ochrolechia frigida (Sw.) Lynge	+	+		
O. upsaliensis (L.) Mass.	+	+	+	+
Pertusaria bryontha (Ach.) Nyl.	+	+	+	+
P. dactylina (Ach.) Nyl.	+	—	—	+
P. octomela (Norm.) Erichs.	+	—	—	+
Lecanora epibryon Ach.	+	+	—	—
Hypogimnia bitteri (Lynge) Ahti	+	+	—	—
Asahinea chrysantha (Tuck.) Culb. et Culb.	—	+	—	—
Cetraria cucullata (Bell.) Ach.	+	1	+	+
C. ericetorum Opiz.	+	1	+	+
C. islandica (L.) Ach.	—	—	—	+
C. laevigata Rassad.	+	+	+	+
C. nivalis (L.) Ach.	—	—	—	+
Alectoria nigricans (Ach.) Nyl.	+	+	+	—
A. nitidula (Th. Fr.) Vain.	+	+	+	+
A. ochroleuca (Hoffm.) Mass.	+	+	+	+
Cornicularia divergens Ach.	+	+	—	—
Dactylina arctica (Hook.) Nyl.	+	0.5	+	+
Thamnolia vermicularis (Sw.) Ach. ex Schaer.	+	+	+	+
Buellia sp.	+	—	—	—
Rinodina roscida (Smrft.) Arn.	+	—	—	—
R. turfacea (Ach.) Koerb.	+	+	—	—
Physcia constipata (Nyl.) Norrl. et Nyl.	+	—	—	+

Note: Figures = % coverage of species
+ = coverage less than 0.5%.

obtusata, Polygonum viviparum, Arctagrostis latifolia, Salix polaris and *Stellaria ciliatosepala.* Of mosses, beside the dominants mentioned, only *Rhacomitrium lanuginosum* and *Dicranum spadiceum* reach a coverage of more than 1%. All the rest of the species are found in minimal quantities. A high frequency is noted for *Polytrichum juniperinum* and *Distichum flexicaule.* None of the lichens reach any important coverage, the biggest role is played by *Dactylina arctica* and *Peltigera aphthosa.* A great number of species are characterized by very high frequency *(Cladonia elongata, C. amaurocraea, C. pyxidata, Thamnolia vermicularis, Cetraria laevigata, C. ericetorum, C. cucullata* and *Psoroma hypnorum).* In contrast, others are extremely rare *(Cetraria nivalis, Peltigera rufescens, P. venosa, P. erumpens),* and some, especially crustaceous lichens, are so small that it is difficult to detect them in the vegetation cover during usual geobotanical investigations *(Lecidea tornoensis, Baeomyces carneus, Ochrolechia upsaliensis, Lecanora verrucosa, Toninia lobulata, Pertusaria octomela, Lopadium pezizoideum).*

The differentiation of the environment in regards to the various elements of nano-relief and accordingly of various ecological conditions appears the mean cause for the horizontal division of the vegetation in the community studied (Fig. 3). We have called the distinguished aggregations, corresponding to the two elements of the nano-relief, micro-aggregations as far as one can distinguish the break-down of vegetation in all the layers (Yaroshenko 1931, 1950). The distinction between the vegetation on hummocks and that in depressions is, first and foremost, decided by the varying coverage of the angiosperms: on hummocks it reaches 40-50%, in the troughs 10%; secondly, the dominating mosses are distributed in the following way: *Hylocomium splendens* var. *alaskanum* and *Aulacomnium turgidum* are favoring raised nano-features, *Tomenthypnum nitens* and *Ptilidium ciliare* play a significant role in nano-depressions. Beside this type of horizontal division, there is a division within the limits of micro-aggregations inside the individual layers that is related not to outer conditions but to the peculiarities of the form and character of growth, of the different species, and also to the form of association between them (Petrovsky 1960, 1961).

On hummocks, *Hylocomium splendens* var. *alaskanum* forms pure synusia covering the surface of the soil completely; less extensive, but denser, layers are formed by *Aulacomnium turgidum* and *Rhacomitrium lanuginosum. Tomenthypnum nitens* forms fairly extensive synusia in the hollows; *Ptilidium ciliare,* in contrast, is rarely met in a clean aspect; very characteristic is a combination of these two species in equal quantity. The growth form of the species mentioned changes in relation to the local conditions. Thus, *Hylocomium splendens* var. *alaskanum* and *Aulacomnium turgidum* grow on hummocks in a continuous cover, but in hollows they grow as single units; the same can be said for *Tomenthypnum nitens* and *Ptilidium ciliare* on humps.

The lichens are for the most part dispersed in the moss cushion *(Dactylina arctica, Thamniola vermicularis, Cladonia pyxidata, C. pleurota, Cetraria ericetorum);* some form well noticeable physiognomically, single-species *(Cladonia rangiferina, C. beringiana)* or two species *(C. elongata* + *C. amaurocraea)* synusia. The dimensions of these lichen spots are usually small, not more than 5 cm in diameter. Some of the larger patches, 10 cm in diameter, are formed by such foliaceous lichens as *Peltigera aphthosa* and *P. canina.*

Dryas punctata and *Carex ensifolia* ssp. *arctisibirica* form large mats. Usually the area, occupied by one of the species mentioned, exceeds the extent of the nano-relief element: the above- and under-ground parts reach both into hollows and over the hummocks. But more of the shoots (vegetative, and in particular, generative ones) are formed on the hummocks above the moss cover than in the hollows, which also appears to be the reason for the different angiosperm cover on the nano-relief elements investigated. *Cassiope tetragona* and *Salix polaris* also form mat-like growth, but they occupy less surface area than the two above-mentioned species. The

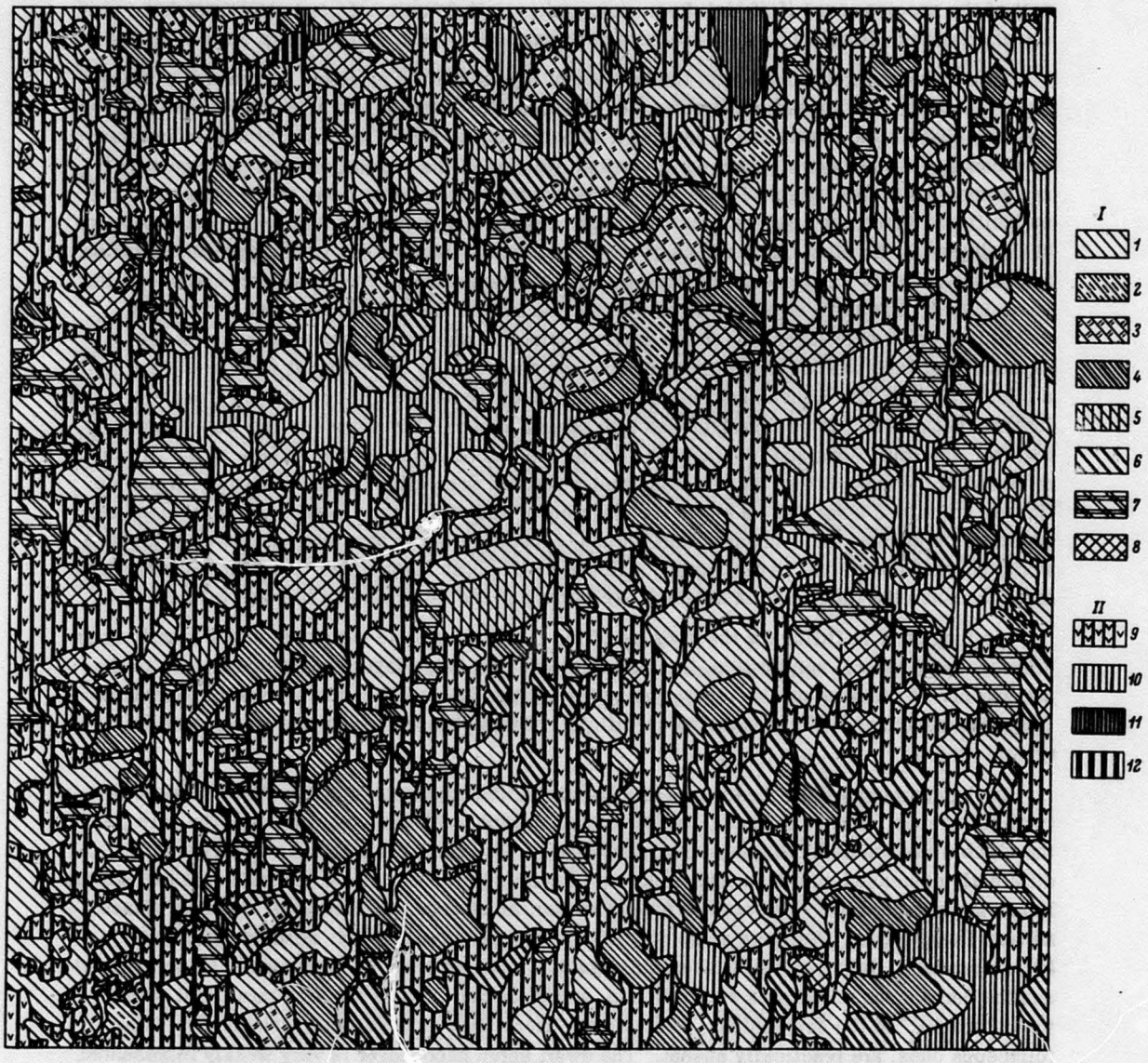

Figure 3. Schematic map of the vegetation of the Dryas-sedge-moss small-hummocky tundra (15x15 m).

The species in the vegetation aggregations mentioned are listed in order of diminishing frequency.

I. Plant agregations on hummocks: 1 - *Aulacomnium turgidum, Carex ensifolia* ssp. *arctisibirica, Dryas punctata,* tufted lichens; 2 - *Aulacomnium turgidum,* fruticose lichens, *Salix reptans;* 3 - *Rhacomitrium lanuginosum, Carex ensifolia* ssp. *arctisibirica,* fruticose lichens; 4 - *Aulacomnium turgidum, Hylocomium splendens* var. *alaskanum, Tomenthypnum nitens, Carex ensifolia* ssp. *arctisibirica, Cassiope tetragona;* 5 - *Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica, Dryas punctata,* fruticose lichens; 6 - *Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica;* 7 - *Tomenthypnum nitens, Carex ensifolia* ssp. *arctisibirica, Dryas punctata, Salix reptans;* 8 - *Ptilidium ciliare, Dryas punctata, Carex ensifolia* ssp. *arctisibirica;* II. Plant aggregations in depressions: 9 - *Tomenthypnum nitens, Ptilidium ciliare, Carex ensifolia* ssp. *arctisibirica;* 10 - *Tomenthypnum nitens, Aulacomnium turgidum, Carex ensifolia* ssp. *arctisibirica;* 11 - *Rhacomitrium lanuginosum, Hylocomium splendens* var. *alaskanum;* 12 - *Carex ensifolia* ssp. *arctisibirica, Ptilidium ciliare, Aulacomnium turgidum.*

rest of the species, even if of high frequency, grow as single units (*Arctagrostis latifolia, Luzula confusa, Eriophorum angustifolium, Polygonum viviparum,* and *Stellaria ciliatosepala).*

Due to its apparent simplicity, the concept of layers and the practical separation of these layers in nature call for some differences of opinion. Not entering into a detailed discussion, we consider that for the separation of layers, it is necessary to follow metrical principles, as the very concept of the layers stands for a vertical division of the vegetation, and consequently it is connected with the height of the plants. The not very large dimensions of the plants and the insignificant differences between them in height create well-known difficulties for the separation of the layers in the plant communities of the tundra zone. Usually, the tundra type of vegetation is characterized by the presence of three layers: the lichen-moss, the herb-dwarf shrub, and the shrub layers. The problem arises as to whether the mosses and the lichens can correctly be united into one single layer, and if the metrical principle should be used as a basis for the separation of layers or the principle of distinction according to life form. It is evident that, as a biological form, the lichens are sharply distinct from the mosses. According to growth-form, the lichens themselves can be distinguished into several groups. When mosses and lichens grow together, the foliaceous and crustaceous lichens are placed either on the surface of the mosses, or buried in the moss cover, which means that a vertical separation exists. However, fruticose lichens are raised some 2-3 cm above the moss cover and to the same height are also raised the vegetative organs of the dominant dwarf shrubs, especially *Dryas punctata.* In the case given it would be more consistent to distinguish a lichen-dwarf shrub layer rather than a herb-dwarf shrub layer, because the difference in height of the herbs and the dwarf shrubs is some 5-10 cm.

As long as it is fitting for the division of the layers to operate with such small quantities as differences of several centimeters, the idea arises to call these layers micro-layers just as the phenomenon of breaking up the vegetation vertically should be called micro-layering (Gorodkov 1935; Aleksandrova 1956); emphasize specificity of this phenomenon for the subzone of the typical tundra.

In the community described we distinguish the following micro-layers[1]: the lichen-moss (with foliaceous forms of lichens), the lichen-dwarf shrub (with fruticose lichens), the herb-, and the shrub (represented by single individuals) layers. The distinction into micro-layers is differently expressed on the various elements of nano-relief. Well developed on hummocks are the lichen-moss micro-layer (*Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Rhacomitrium lanuginosum, Peltigera aphthosa, Thamniolum vermicularis)* the lichen-dwarf shrub (*Dryas punctata, Salix polaris, Cladonia elongata, C. amaurocraea, C. rangiferina, C. beringiana)* and the herbaceous one (*Carex ensifolia* ssp. *arctisibirica).* Shrubs are very rarely met with on the hummocks. In the depressions, a thick moss micro-layer is developed; lichens, including foliaceous ones, are practically absent. The dwarf shrub micro-layer is very weakly represented, only by some *Cassiope tetragona.* The herbaceous micro-layer is less well developed than on the hummocks, due to a lesser coverage of the basic member of the micro-layer studied, *Carex ensifolia* ssp. *arctisibirica. Salix reptans* forms rather dense mats in the depressions.

The community investigated is characterized by a weak differentiation vertically and a fractional separation horizontally. The elements of the horizontal mosaic are few: micro-aggregations, related to the nano-relief elements, not exceeding a diameter of 30 cm, and the dimensions

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[1] A detailed description of the vertical structure of the vegetation along micro-layers is given only for sites 1 and 2, which have been investigated at the greatest detail.

of the synusia within the limits of the various layers are smaller still. Basically, the mosaic of a community is dependent on the formation of the moss synusia, which rather clearly border each other and are well distinguished by color. The differentiation between the vegetational micro-aggregations is rather quantitative than qualitative: the changes lie in the projected coverage of one or the other species.

Site no. 2

Dryas-sedge-moss spotty tundra

It occupies a flat area, slightly inclined towards SE and Pyasina and bordered by the precipitous bank of the river and by two brooks; on the fourth side it changes into a bog-tundra complex. The depth of the snow-cover in wintertime is 20 cm; snow-melt begins the first days of June. The depth of the seasonal thaw in the ground is 60-70 cm. Three elements of nano-relief can be distinguished. The spots of open ground are round or oval and of a medium level. They are surrounded by hummocks (in the form of raised borders), lifting above the surface of the spots by some 5-10 cm. These two elements are separated by not very deep (10-15 cm) troughs in the centers of which frost cracks are usually located. Joining each other, the troughs form a network. The combination of the three elements of nano-relief is regularly and evenly repeated throughout the community. The dimensions of the spots, the raised borders and the troughs were measured as well as the distance between the centers of the spots (Table 2)[1]:

Table 2. Dimensions of nano-relief elements on a site of Dryas-sedge-moss spotty tundra

Measured Data	*Statistical Indices*		
	M±m, cm	*σ, cm*	*V, %*
Diameter of spot	79.20±2.07	20.69	26
Width of raised border	48.25±0.84	8.40	17
Width of trough	30.40±0.88	8.85	29
Distance between centers of spots	192.00±1.32	15.00	8

The number of spots on 100 m^2 averaged 32. Close to the border of the community studied with the boggy polygonal tundra, there appear some small habitats, where the area occupied by troughs increases, which is related to the appearance of thermokarst. The soil of the community studied is tundra gley.

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[1] Large and small diameters of the spots were measured; from these data was obtained a mean diameter (n=100); in the same manner, the widths of the raised borders and the troughs were measured and from these four numbers a mean value was obtained for each element. The distance between the centers of the spots was achieved thus: the distance was measured from the center of one spot to the centers of the neighboring ones, about 100 measurements in all. The number of spots on a surface of 10 x 10 m was counted and the count replicated 10 times.

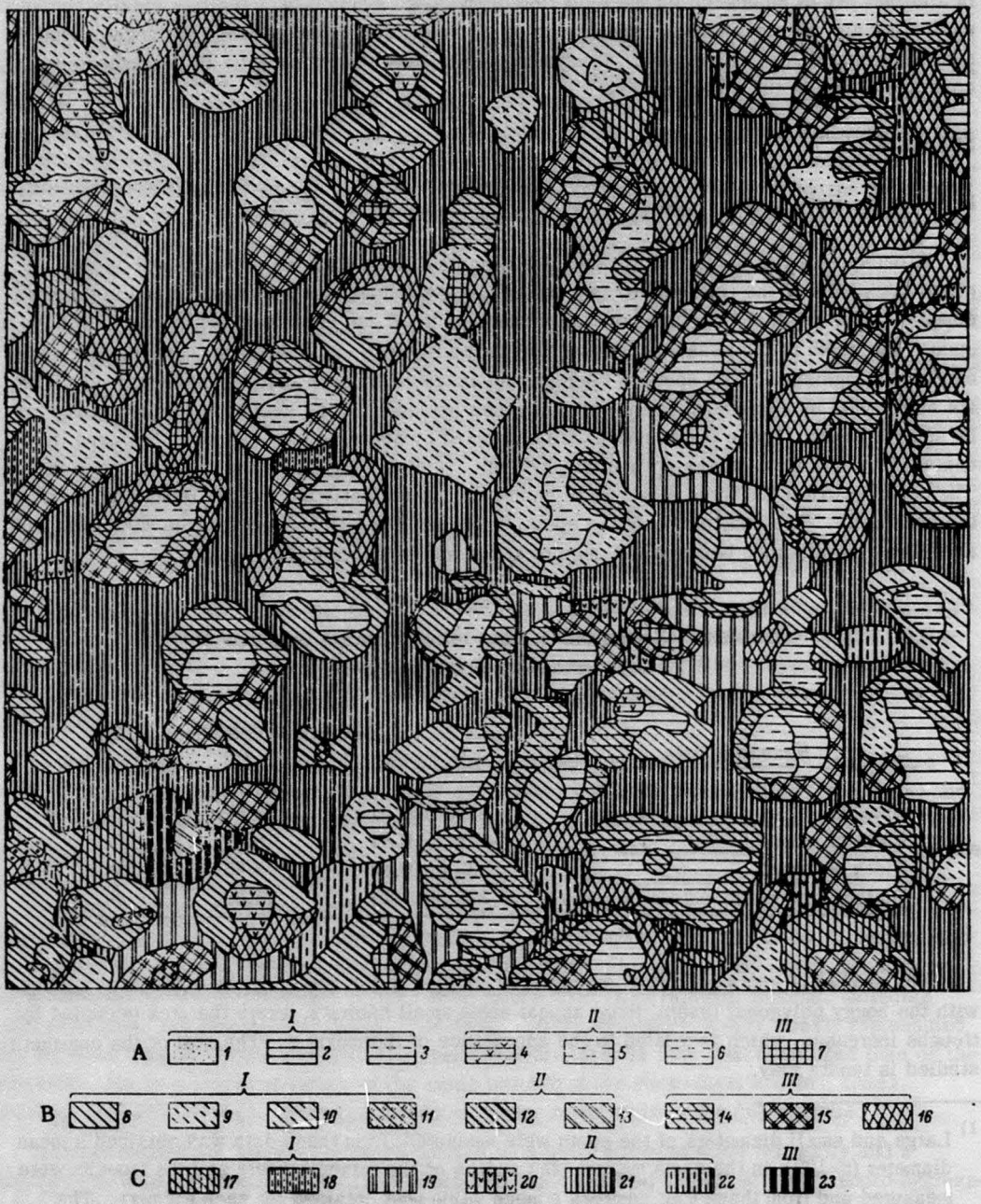

Figure 4. Schematic map of the vegetation of Dryas-sedge-moss spotty tundra (15 x 15 m).

Figure 4 legend.

A. Vegetation aggregations on spots.

I. Growth on dry sites: 1 - single specimens; 2 - *Dryas punctata;* 3 - *Dryas punctata, Carex ensifolia* ssp. *arctisibirica,* crustaceous lichens;

II. Growth on moist sites: 4 - *Hypnum Bambergeri, Dryas punctata;* 5 - *Dryas punctata, Hypnum Bambergeri;* crustaceous lichens; 6 - *Dryas punctata, Eriophorum angustifolium, Hypnum Bambergeri,* crustaceous lichens;

III. Growth completely covering spot: 7 - *Dryas punctata, Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica,* lichens.

B. Vegetation aggregations on raised borders.

I. On the highest sites: 8 - *Dryas punctata, Hylocomium splendens* var. *alaskanum,* fruticose lichens, *Carex ensifolia* ssp. *arctisibirica;* 9 - *Cassiope tetragona, Hylocomium splendens* var. *alaskanum,* fruticose lichens, *Carex ensifolia* ssp. *arctisibirica;* 10 - fruticose lichens, *Carex ensifolia* ssp. *arctisibirica, Hylocomium splendens* var. *alaskanum;* 11 - *Polytrichum strictum,* fruticose lichens, *Carex ensifolia* ssp. *arctisibirica;*

II. On the medium high sites: 12 - *Salix pulchra, Betula nana, Carex ensifolia* ssp. *arctisibirica, Hylocomium splendens* var. *alaskanum;* 13 - *Salix reptans, Carex ensifolia* ssp. *arctisibirica, Hylocomium splendens* var. *alaskanum;*

III. On the low-lying sites: 14 - *Dryas punctata, Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica, Aulacomnium turgidum;* 15 - *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Salix pulchra, Carex ensifolia* ssp. *arctisibirica;* 16 - *Carex ensifolia* ssp. *arctisibirica, Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum.*

C. Vegetation aggregations in troughs.

I. Not very deep ones: 17 - *Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica;* 18 - *Hylocomium splendens* var. *alaskanum, Carex ensifolia* ssp. *arctisibirica, Salix pulchra;* 19 - *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Carex ensifolia* ssp. *arctisibirica;*

II. Deep ones: 20 - *Tomenthypnum nitens, Carex ensifolia* ssp. *arctisibirica;* 21 - *Tomenthypnum nitens, Aulacomnium turgidum, Ptilidium ciliare, Carex ensifolia* ssp. *arctisibirica;* 22 - *Carex ensifolia* ssp. *arctisibirica, Salix reptans, Drepanocladus vernicosus;* 23 - *Carex stans, Drepanocladus revolvens.*

The great variability in ecological conditions appears, obviously, to be the cause why the community investigated is distinguished by its rich floristic composition. We counted 153 species: 57 angiosperms, 46 mosses, 50 lichens (Table 1). As dominants in the vegetation cover appear of the angiosperms: *Dryas punctata* and *Carex ensifolia* ssp. *arctisibirica*, and of the mosses: *Hylocomium splendens* var. *alaskanum*, *Aulacomnium turgidum*, and *Tomenthypnum nitens*. Of the angiosperms, only *Salix arctica* and *S. polaris* reach a significant coverage (1%), but a fairly high incidence is characteristic for the following species: *Cassiope tetragona*, *Arctagrostis latifolia*, *Luzula nivalis*, *Polygonum viviparum* and *Parrya nudicaulis*. All species of lichens occur in insignificant amounts but many of them have a high incidence.

In correlation with the three elements of nano-relief in the community studied, three vegetation micro-aggregations, well separated physiognomically, are distinguished: The vegetation of spots, of raised borders and of troughs (Fig. 4).

Characteristic for the raised border and the trough vegetation are continuously covered soils, in general in form of a thick (5-10 cm) layer of mosses. As dominating species of mosses on the raised borders occur *Hylocomium splendens* var. *alaskanum* (35% coverage) and *Aulacomnium turgidum* (15%). An important role is played also by *Rhytidium rugosum* (10%) and *Rhacomitrium lanuginosum* (5%). The last three mosses usually form clearly bordering synusia, measuring up to several centimeters in diameter; most often of all, *Hylocomium splendens* var. *alaskanum* grows with an insignificant admixture of the other species. Of the angiosperms in the raised borders, *Dryas punctata* (15%) and *Carex ensifolia* ssp. *arctisibirica* (15%) dominate. Important roles are played by the species *Salix arctica* and *S. polaris*. All the rest of the species are met with as single units. A part of these, not occupying any significant area, are characterized by a high frequency (*Arctagrostis latifolia*, *Luzula nivalis*, *Polygonum viviparum*, *Stellaria ciliatosepala*, *Minuartia arctica* and *Parrya nudicaulis*). A series of species, with a frequency less than 5%, may be considered occasional for the community studied. *Tomenthypnum nitens* (55% coverage) dominates in the troughs and *Hylocomium splendens* var. *alaskanum* (20%) and *Ptilidium ciliare* (15%) appear as co-dominants. The rest of the moss species are met in insignificant measures. Of the total number of angiosperms on the site studied, only two play a relatively significant role in the composition of the vegetation cover of the trough micro-aggregation: *Dryas* (2%) and *Carex* (6%); their frequency is 100%. All the rest of the species occur as single units and have a very insignificant coverage. In the troughs, the same species of lichens occur as on the raised borders (with exception of the foliaceous forms) but with still smaller coverage and frequency (close to 5%).

In contrast to the two above described micro-aggregations, the spots do not have a continuous plant cover. As the general coverage of vegetation on them reaches from 5-30%, it is almost impossible to tell which species dominate. Almost all the species of mosses, characteristic for the plant aggregations of the raised borders and the troughs also occur on the spots, but with a negligible coverage; the most important roles are played by *Ditrichum flexicaule*, *Orthothecium strictum* and *Bryum Wrightii*; they sometimes cover up to 10-15% of the surface of the spots. Of the flowering plants *Dryas* and *Carex* are of the greatest importance. Then we must distinguish the group of crustaceous lichens, the majority of which appear as specifically and exclusively related to spots of bare ground. This is, first and foremost, *Toninia lobulata*, the dead layer of which covers some spots up to 20% (its frequency is 92%), but also *Baeomyces carneus*, *Lecanora epilbryon*, *L. verrucosa*, *Rinodina roscida* and *Pertusaria octomella*. Besides the crustaceous lichens, there is a row of species met with only on spots. Among them are: the angiosperms *Epilobium davuricum*, *Cerastium Bialynickii*, *Juncus biglumis*, *Sagina intermedia*,

Saxifraga cernua; the mosses *Orthothecium strictum, Hypnum Bambergii;* the liverworts *Peltolepis grandis;* and the lichens *Solorina saccata* and *S. spongiosa.* A part of the species mentioned were noted by V. N. Adreyev (1938), B. N. Gorodkov (1956) and B. A. Tikhomirov (1957) but some, especially in the group of crustaceous lichens, we are the first to mention.

While the vegetation of the troughs and the raised borders appears relatively uniform, and is found in a relatively stable state of dynamic balance with the surrounding environment, the vegetation on the spots is represented by successional series. In the community studied, all transitions are met with from spots without any vegetation and bare soil to those completely covered by vegetation, to the extent that their vegetation does not differ from the vegetation on the raised border surrounding such a "former spot". In the first stage of becoming covered with vegetation, the soil of the spot is uneven and wrinkled as a result of frost- and thaw-processes; a very unimportant number of species in minimal quantity colonize it, generally along its borders. In the next stage, the surface of the soil is still uneven, but its parts are fastened by live or dead layers of crustaceous lichens of the genera *Tononia, Pertusaria* and *Ochrolechia.* The general coverage of this vegetation is 10-20%. But in comparison with the preceding stage, there is a richer species composition. In the succeeding stages of vegetation the plants do not colonize as single specimens, but as groups, and the vegetation coverage increases up to 40%. In some spots *Dryas punctata* dominates while in others *Carex ensifolia* ssp. *arctisibirica:* generally they appear as growing out from the surrounding borders. The cover of the following mosses increases: *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Hypnum Bambergeri* and *Orthothecium chryseum.* In contrast to that on the raised border, the thickness of the moss cover on the spots at this stage of the vegetation development is insignificant: the mosses grow as plastered to the ground. Already not only specific, crustaceous lichens have colonized the spot, but also those which are common for the surrounding vegetation on the raised borders, both fruticose and tubular forms. In later stages of vegetation development, when the surface of the ground is covered up to 80-90%, the thickness of the vegetation cover is still thin, because of which the surface of the vegetated spots appears concave. Characteristic for such spots is a vegetation cover of up to 20% angiosperms (basically *Dryas* and sedge), and up to 60-70% mosses (variants with *Tomenthypnum nitens* and *Hypnum Bambergeri,* drier ones with *Hylocomium splendens* var. *alaskanum,* and the driest with *Rhacomitrium lanuginosum).* There are also fully vegetated spots with a sufficiently thick moss cushion, so that the surface no longer appears concave, but rather flat or even slightly convex. In the species composition, such fully vegetated spots do not differ from the surrounding raised borders, but quantitatively the correlation of the species is somewhat different: there is a lesser coverage by angiosperms and a greater abundance of lichens.

The most numerous are spots in intermediate stages of vegetation development in the central part of the community. Closer to the steep slope of the river and the brooks, there are little vegetated spots and completely bare spots. The further from the bank in the direction towards the boggy polygonal tundra, the worse is the drainage, and in this condition spots are found, overgrown with mosses, generally *Tomenthypnum nitens* and *Hypnum Bambergeri.* Complete overgrowth is rare there.

Specific species are characteristic for the spots basically in the early stages of vegetation development; later, they cannot compete and are replaced by species from the surrounding vegetation. The biggest role in the vegetation development is played by the cryptogams: Mosses and crustaceous lichens. Colonizing a bare substrate, they appear to help stabilize the ground and form the turf. The phytocoenotic role of angiosperm species specific for spots (such as

Juncus biglumis, Sagina intermedia, Saxifraga cernua and *Epilobium davuricum)* is insignificant. They have practically no part in the process of vegetation development in the spots: individuals of these species have small dimensions, sprout a weak root system and grow as single specimens occupying insignificant areas, thus they have little importance for the stabilization of the ground. Other species, which are not specific for spots, take place in the vegetation cover development.

In the given community, we distinguished several micro-layers, as was done in the small-hummocky tundra. On the spots a lichen-moss micro-layer is developed in fragments. The mosses are distributed in small spots, and the thickness of the moss cover is 1-3 cm. The crustaceous lichens also form small patches 1-2 cm in diameter, and only layers of *Toninia lobulata* occupy sometimes a significant portion of the spots. The lichen-dwarf shrub micro-layer is represented, basically, by *Dryas*, which forms patches of various dimensions and configuration. The rest of the dwarf shrubs, and also the fruticose lichens, occur as single specimens. The herbaceous micro-layer consists of more or less abundant *Carex ensifolia* ssp. *arctisibirica.*

If on the whole the division of layers in the plant communities of the subzone of typical tundras appears to a certain degree conditional (the total active layer of vegetation does not exceed 20-25 cm), this holds to an even higher degree for the spots in the spotty tundras, where also the maximum sparseness of the vegetation cover is observed.

On the raised borders, there are well developed lichen-moss and lichen-dwarf shrub micro-layers. The fruticose lichens are here best developed (in comparison within the micro-aggregations on spots and in troughs), and their coverage reaches 15%. The micro-layer of prostrate shrubs is one of willows *(Salix arctica* and *S. pulchra).* The herbaceous micro-layer is well distinguished, where *Carex ensifolia* ssp. *arctisibirica* forms a thick sward.

In the troughs, the thickest micro-layer is a mossy one, in which *Tomenthypnum nitens* appears as the dominating species. It is possible to speak about a moss micro-layer here, as lichens (foliose forms) and also *Thamniola vermicularis* occur as single specimens. The lichen-dwarf shrub micro-layer is in general not distinct; it consists of just a single mat of *Dryas punctata,* and the fruticose lichens are also very few in number. The shrub-dwarf shrub micro-layer of *Cassiope tetragona* and *Salix arctica* is fragmentarily formed. *Carex ensifolia* ssp. *arctisibirica* forms an open, herbaceous micro-layer.

There is not much to be said of the shrubby micro-layer as the coverage of the only erect shrub *Salix reptans* reaches at the most 1%.

Site no. 3

The bog tundra polygonal complex

It is situated in a depression of an ancient alluvial terrace, 150 m above a ravine from which runs a brook which empties into the Pyasina. The micro-relief of the area is represented by a combination of difficult to distinguish polygons, 15-30 m in diameter, and elongated water pits, separating the polygons, 0.5-6 m in width and 20-40 cm deep. These waterfilled hollows occupy about 20% of the surface of the complex studied. The edges of the polygons do not form clearly distinct, uninterrupted raised borders, although the corners of the polygons can be noticeably raised in relation to the rest of the surface. Depressed centers of the polygons are also absent. The surfaces of the polygons bear traces of secondary cracking and are covered with a network of elongated troughs in various stages of deepening. Actually, we have here a strongly drained and repeatedly modified ancient polygon system.

The vegetation complex characteristically is a combination of two elements differing according to their nature: a tundra element on the raised and a bog element on the depressed micro-relief (Fig. 5). The tundra element is distinguished by a high frequency and high vitality of shrubs. The latter is due to the significant accumulation of snow and the well drained substrate. An investigation of the soil revealed an important accumulation of peat - up to 18 cm on the positive and up to 35 cm in the negative elements of the micro-relief. In connection with this the surface of the permafrost during summer lies rather close to the ground surface (32-35 cm).

The dominating plant aggregation on the positive elements of the micro-relief (about 30% of the area of a polygon) appears to be a willow-*Eriophorum*-moss on the level parts of the polygons. This aggregation has a 3-layer structure: shrubs (25-30 cm tall, 25% coverage), usually *Salix reptans* with an admixture of *S. pulchra* and *Betula nana;* a herbaceous layer (15-20 cm high, 20% coverage), formed of the vegetative shoots of *Eriophorum angustifolium* and *Carex stans; Aulacomnium turgidum, Hylocomium splendens* var. *alaskanum, Tomenthypnum nitens* and *Dicranum angustum* (Table 3) dominate in the moss cover. This aggregation is very rich in species even if the participating species *(Parrya nudicaulis, Saxifraga punctata, Saxifraga hirculus, S. cernua, S. foliolosa, S. hieracifolia, Pedicularis hirsuta, P. capitata, Valeriana capitata, Pyrola grandiflora,* etc.) occur in low frequency.

On the positive elements of the micro-relief, willow-sedge-moss and willow-sedge-dwarf shrub moss aggregations are also widely distributed, with *Salix pulchra* in the upper layer, and *Carex ensifolia* ssp. *arctisibirica, Dryas punctata, Cassiope tetragona,* and *Vaccinium Vitis-Idaea* in the herbaceous-dwarf shrub layer. In the moss-layer, *Hylocomium splendens* var. *alaskanum* dominates.

On the slightly raised border parts of the polygons, aggregations dominated by dwarf birch are characteristic. These are either a pure mat of *Betula nana* 2.5-3 m in diameter and 50-60 cm high with an average coverage of 70-80%, or a more or less discontinuous thicket covering 30-40%. In the first case, there are hardly any flowering plants under the birch mat, but in the less dense thicket, some herbaceous plants have taken root *(Rumex arcticus, Valeriana capitata, Saxifraga punctata)* or some dwarf shrubs *(Dryas punctata, Vaccinium Vitis-Idaea)* occur. *Drepanocladus uncinatus, Hylocomium splendens* var. *alaskanum,* and *Ptilidium ciliare* dominate in the moss cover.

The waterholes are occupied mainly by a sedge-moss aggregation with *Carex stans.* Together with the sedge, there is in places a significant quantity of *Eriophorum angustifolium,* and in small quantity, *E. Scheuchzeri* and *E. medium.* In general, this aggregation is distinguished by a very poor composition of angiosperms, some single specimens of *Saxifraga cernua, Pedicularis sudetica, Comarum palustre* and *Caltha arctica* occur. *Calliergon Richardsonii, Meesia triquetra, Drepanocladus revolvens* and *Cinclidium latifolium* dominate in the moss cover.

The less deep parts of the waterholes adjoining the polygons and also the shallow troughs of secondary cracks are occupied mainly by willow-sedge-moss aggregations. The layer of shrubs is not distinct, branches of *Salix reptans, S. pulchra* and *Betula nana* barely rise above the sedge-mat. The shrub coverage is 5-25%, that of *Carex stans* 10-30%. In the moss cover dominate *Calliergon sarmentosum, Drepanocladus latifolius, Meesia triquetra, Tomenthypnum nitens, Aulacomnium turgidum, Polytrichum Jensenii* and *Drepanocladus vernicosus.*

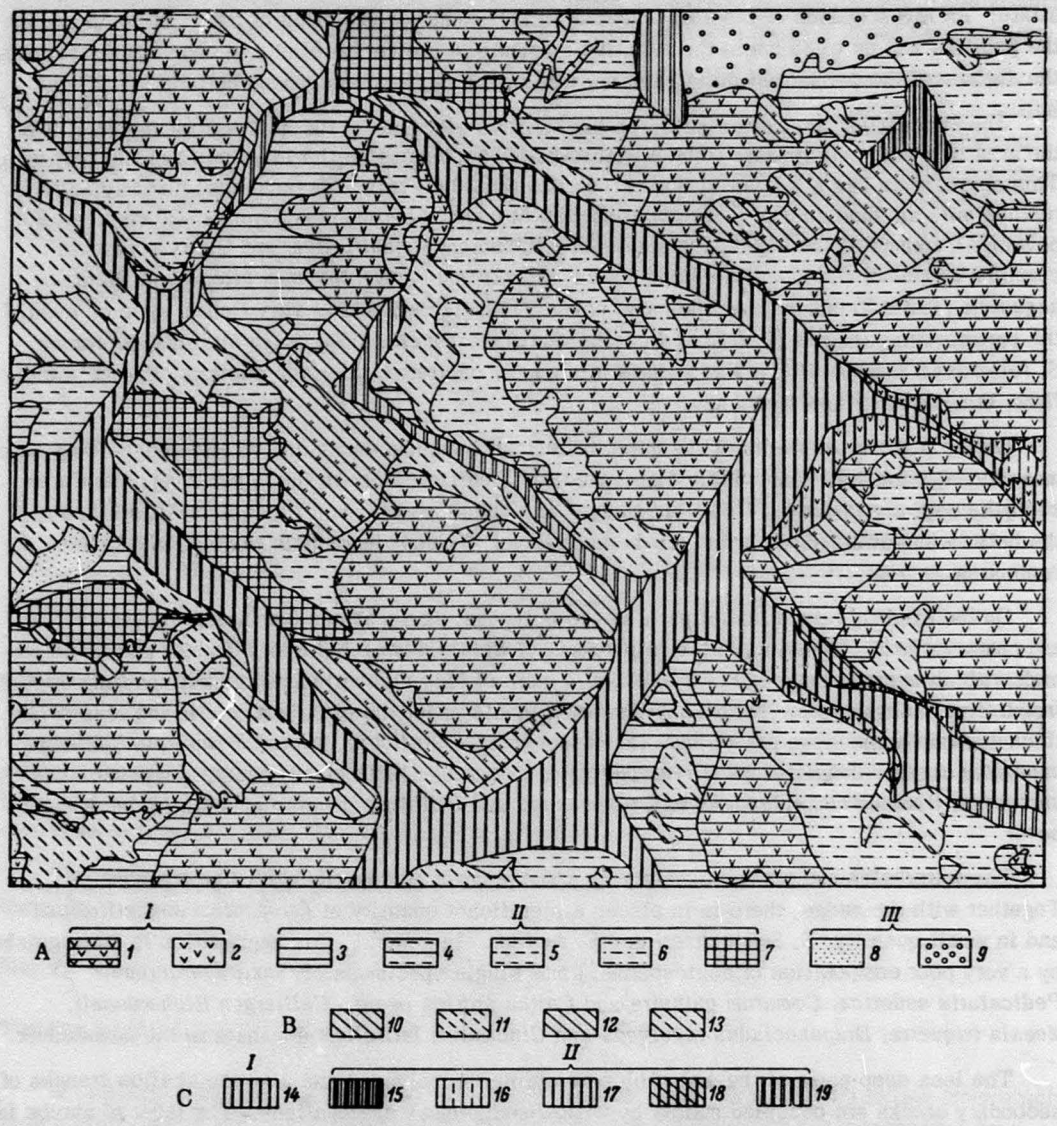

Figure 5. Schematic map of the vegetation of the permanent site (50 x 60 m) on a tundra-bog complex.

Figure 5 legend.

A. Micro-aggregations on polygon surfaces.

I. On depressed sites: 1 - *Salix reptans, Aulacomnium turgidum, Carex stans, Tomenthypnum nitens;* 2 - *Tomenthypnum nitens, Aulacomnium turgidum, Salix reptans;*

II. On raised sites and rather low, not well-defined raised borders: 3 - *Aulacomnium turgidum, Hylocomium splendens* var. *alaskanum, Salix pulchra;* 4 - *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Salix pulchra, Betula nana;* 5 - *Ptilidium ciliare, Aulacomnium turgidum, Salix pulchra, Betula nana;* 6 - *Hylocomium splendens* var. *alaskanum, Dicranum angustum, Salix pulchra, Carex ensifolia* ssp. *arctisibirica;* 7 - *Hylocomium splendens* var. *alaskanum, Salix pulchra, Aulacomnium turgidum, Eriophorum angustifolium;*

III. On hummocks: 8 - *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Dryas punctata, Eriophorum angustifolium;* 9 - *Hylocomium splendens* var. *alaskanum, Dicranum angustum, Dryas punctata, Vaccinium Vitis-Idaea, Carex ensifolia* ssp. *arctisibirica.*

B. Micro-aggregations on raised borders.

10 - *Betula nana, Drepanocladus uncinatus, Ptilidium ciliare;* 11 - *Betula nana, Hylocomium splendens* var. *alaskanum, Salix pulchra, Carex ensifolia* ssp. *arctisibirica;* 12 - *Hylocomium splendens* var. *alaskanum, Betula nana, Aulacomnium turgidum, Cetraria cucullata, Cladonia amaurocraea;* 13 - *Hylocomium splendens* var. *alaskanum, Betula nana, Polytrichum strictum, Vaccinium Vitis-Idaea.*

C. Micro-aggregations in waterholes between the polygons.

I. In very wet and deep ones: 14 - *Calliergon Richardsonii, Cinclidium latifolium, Carex stans, Eriophorum angustifolium, Meesia triquetra;*

II. In shallow ones and on the borders of the deep ones: 15 - *Calliergon sarmentosum, Carex stans, Eriophorum Scheuchzeri, Meesia triquetra;* 16 - *Drepanocladus latifolius, Salix pulchra, Eriophorum angustifolium;* 17 - *Calliergon sarmentosum, Salix reptans, Carex stans;* 18 - *Calliergon sarmentosum, Betula nana, Carex stans;* 19 - *Calliergon sarmentosum, Salix reptans, Betula nana, Carex stans.*

Table 3. Species composition of plant aggregations of the permanent sites nos. 3 and 4

Name of species	Tundra-bog complex		Polygonal bog		
	Polygons	Water-holes	Centers of polygons	Raised borders	Water-holes
Angiosperms					
Lycopodium selago L.	+	—	—	—	—
Hierochloë pauciflora R. Br.	—	—	6—7	—	—
Arctagrostis latifolia (R. Br.) Griseb.	+	—	—	—	—
Calamagrostis holmii Lange	+	—	—	—	—
Poa arctica R. Br.	+	—	—	+	—
Dupontia fisheri R. Br.	—	+	—	—	—
Festuca brachyphylla Shult.	+	—	—	—	—
Eriophorum angustifolium Honck.	3—5	10—30	5—7	—	+
E. medium Anderss.	—	+	2—5	—	+
E. scheuchzeri Hoppe	—	+	—	—	—
Carex chordorrhiza Ehrh.	—	—	10—15	—	—
C. stans Drej.	+	10—30	35—50	+	60—70
C. ensifolia (Turcz. ex Gorodk.) V. Krecz. ssp. *arctisibirica* Jurtz.	2—5	—	—	+	—
Luzula confusa Lindb.	+	—	—	—	—
L. nivalis Laest.	+	—	—	—	—
Salix reptans Rupr.	15—25	15—20	2—5	+	+
S. pulchra Cham.	10—20	5—20	+	3—5	—
Betula nana L.	10—40	10—25	+	5—10	+
Rumex arcticus Trautv.	+	—	—	—	—
Polygonum viviparum L.	+	+	—	+	—
Stellaria ciliatosepala Trautv.	+	—	—	+	—
Caltha arctica R. Br.	—	+	—	—	+
Parrya nudicaulis (L.) Regel	+	—	—	—	—
Draba micropetala Hook.	—	—	—	+	—
Saxifraga punctata L.	+	—	—	+	—
S. hieracifolia Waldst. et Kit.	+	—	—	+	—
S. foliolosa R. Br.	+	—	+	—	—
S. hirculus L.	+	—	—	+	—
S. cernua L.	+	—	—	—	—
Chrysosplenium alternifolium L.	—	+	—	+	—
Comarum palustre L.	—	+	—	—	+
Dryas punctata Juz.	5—15	—	—	3—5	—
Pyrola grandiflora Rad.	+	—	—	—	—
Cassiope tetragona (L.) D. Don	2—10	—	—	—	—
Vaccinium vitis-idaea L. var. *minus* Lodd.	5—10	—	—	—	—
Pedicularis sudetica Willd.	—	—	—	—	+
P. hirsuta L.	+	—	+	+	—
P. oederi Vahl	—	—	—	+	—
P. capitata Adams	+	—	—	—	—
Valeriana capitata Pall.	+	—	—	—	
Senecio atripurpureus (Ledeb.) B. Fedtsch.	+	—	—	—	—
Mosses					
Sphagnum squarrosum Pers.	—	—	—	3—5	—
S. teres (Schimp.) Ångstr.	+	3—5	—	+	—
S. aongstremii Hartm.	—	—	—	+	—
S. subsecundum Nees	—	—	+	+	—
S. orientale Lyd. Sav.	—	+	—	—	—
S. contortum Schultz	—	+	+	—	—
S. platyphyllum Lindb.	—	—	—	+	—
S. riparium Ångstr.	—	+	—	—	+
S. warnstorfianum Du Rietz	+	—	+	3—5	—

Table 3. Continued

Name of species	Tundra-bog complex		Polygonal bog		
	Polygons	Water-holes	Centers of polygons	Raised borders	Water holes
S. fimbriatum Wils.	—	—	—	+	+
S. rubellum Wils.	—	—	—	+	—
Polytrichum jensenii Hag.	—	5	5—7	+	3—5
P. strictum Sm.	5	—	+	5—10	—
Ditrichum flexicaule (Schleich.) Hampe	+	+	+	+	—
Oncophorus wahlenbergii Brid.	+	+	+	+	+
Dicranum elongatum Schleich.	2—3	—	—	2—3	—
D. spadiceum Zett.	—	—	+	+	—
D. angustum Lindb.	3—5	+	+	3—5	+
D. acutifolium (Lindb. et Arn.) C. Jens.	+	—	—	—	—
Rhacomitrium lanuginosum (Hedw.) Brid.	—	—	—	+	—
Tortella fragilis (Hook. et Wils.) Limpr.	—	+	—	—	—
Tetraplodon mnioides (Hedw.) B. S. G.	+		—	+	—
Splachnum vasculosum Hedw.	—	+	—	—	—
Haplodon wormskjoldii (Hornem.) R. Br.	—	—	—	+	—
Pohlia nutans (Hedw.) Lindb.	—	—	—	—	+
Bryum cryophilum O. Må t.	—	—	—	—	+
Mnium curvatulum (Lindb.) Limpr.	—	+	—	—	+
M. rugicum Laur.	—	+	+	—	+
Cinclidium latifolium Lindb.	—	2—3	5—10	—	5—10
Aulacomnium palustre (Hedw.) Schwaegr.	+	—	—	+	—
A. palustre (Hedw.) Schwaegr. var. *imbricatum* Bruch et Schimp.	+	—	—	+	—
A. turgidum (Wahlenb.) Schwaegr.	20—30	+	+	30	5—10
Paludella squarrosa (Hedw.) Brid.	—	+	—	—	+
Meesia uliginosa Hedw.	—	+	—	+	—
M. triquetra (Hook. et Tayl.) Ångstr.	—	3—5	10—20	—	5—10
Bartramia pomiformis Hedw.	—	+	—	—	—
Philonotis fontana (Hedw.) Brid.	+	+	+	—	+
Myurella julacea (Schwaegr.) B. S. G.	—	+	—	—	—
Campylium stellatum (Hedw.) Lange et C. Jens.	+	—	+	+	—
C. polygamum (B. S. G.) Lange et Jens.	—	+	+	—	+
C. zemliae C. Jens.	—	—	+	—	—
Drepanocladus exannulatus (B. S. G.) Warnst.	—	+	—	—	—
D. uncinatus (Hedw.) Warnst.	3—5	—	—	—	—
D. revolvens (Turn.) Warnst.	—	25—30	30—40	—	30—40
D. vernicosus (Lindb.) Warnst.	—	5	5—10	—	3—5
D. lapponicus (Norrl.) Z. Smirn. f. *gigas* (Lindb.) Z. Smirn.	—	—	—	—	+
D. latifolius (Lindb. et Arn.) Broth.	+	3—5	5—10	—	3—10
D. sendtneri (Schimp.) Warnst.	—	+	—	—	—
Scorpidium scorpioides (Hedw.) Limpr.	—	—	—	—	+
Calliergon sarmentosum (Wahlenb.) Kindb	—	10—15	3—5	—	10—15
C. richardsonii (Mitt.) Kindb.	—	5—7	+	—	5—7
Tomenthypnum nitens (Hedw.) Loeske	5—10	10	+	20	+
Brachythecium mildeanum (Schimp.) Milde	—	—	—	+	—
B. mildeanum (Schimp.) Milde var. *udum* (Hag.) Mönkem.	+	+	—	+	+
Cirriphyllum cirrosum (Schwaegr.) Grout.	+	+	+	+	—
Orthothecium chryseum (Schwaegr.) B. S. G.	—	+	—	—	—

Table 3. Continued

Name of species	Tundra-bog complex		Polygonal bog		
	Polygons	Water-holes	Centers of polygons	Raised borders	Water-holes
Hylocomium splendens (Hedw.) B. S. G. var. *alaskanum* (Lesq. et James) Limpr.	15—30	+	—	30—40	—
Lichens					
Nephroma expallidum (Nyl.) Nyl.	—	—	—	+	—
Peltigera aphthosa (L.) Willd.	+	—	—	2—3	—
P. polydactyla (Neck.) Hoffm.	+	—	—	+	—
Cladonia amaurocraea (Flk.) Schaer.	+	—	—	+	—
C. beringiana (Ahti) Trass	—	—	—	+	—
C. elongata (Jacq.) Hoffm.	+	—	—	—	—
C. rangiferina (L.) Web.	—	—	—	+	—
C. uncialis (L.) Web.	+	—	—	+	—
Stereocaulon paschale (L.) Hoffm.	—	—	—	+	—
Parmelia omphalodes (L.) Ach.	—	—	—	+	—
Cetraria cucullata (Bell.) Ach.	+	—	—	+	—
C. ericetorum Opiz	—	—	—	+	—
C. islandica (L.) Ach.	+	—	—	+	—
C. laevigata Rassad.	—	—	—	+	—
Dactylina arctica (Hook.) Nyl.	+	—	—	+	—
Thamnolia vermicularis (Sw.) Ach. ex Schaer.	+	—	—	+	—

Note: Figures = % coverage of species
+ = coverage less than 2%.

Site no. 4

Polygonal bog

It is situated in a lake depression on the surface of the ancient alluvial terrace of the Pyasina river. The bottom of the lake depression is even, very slightly inclined toward the east and a brook; the water flows in this direction at the present time. The shallow lake occupies a very insignificant portion of the depression, the contour of which is clearly marked by a 2-3 m high ledge in the relief.

Over all the area of the depression, there is a clearly distinguishable polygon-rim relief. The polygons have a many-sided form, are 15-20 m in diameter and have rims 1-1.5 m wide, rising 15-30 cm above the central part of the polygon. The polygons are separated from each other by troughs, 1.5-2 m wide, formed as a result of thawing out of the ice wedges. The pits have a depth of 25-40 cm relative to the surface of the raised borders and 10-15 cm relative to the center of the polygons, so that the surface of the polygons during certain periods is drained by the surrounding pits. However, in wet years, water is standing almost all the summer both in the pits and in the depressions on the polygon surfaces. During the period of maximal thawing of the soil, the permafrost is reached at a depth of 40 cm in the pits, at 37 cm under the raised borders and at 45 cm under the bottoms of the polygons.

There is a great similarity between the plant aggregations of the pits and the central depressed parts of the polygons. The vegetation on the raised borders has many general traits in common with the tundra vegetation (Fig. 6). The plant aggregations in the ditches are 2-layered: in the upper layer, *Carex stans* (20 cm in height) dominates, to which sometimes is added some *Eriophorum medium* or some shrubs, the twigs of which do not rise above the sedge mat; the angiosperm composition on the borders is very poor (4-5 species). In the moss-layer predominate *Meesia triquetra, Drepanocladus revolvens,* and *Cinclidium latifolium;* in shallow pits dominate, together with the mosses mentioned, *Calliergon sarmentosum* and *Aulacomnium turgidum* (Table 3).

The central parts of the polygons are distinguished by a very variable composition of species. Dominants are *Carex stans, C. chordorrhiza, Eriophorum angustifolium, E. medium* and *Hierochloe pauciflora,* sometimes in small frequency also willows, *Salix reptans* and *S. pulchra* and birch, *Betula nana,* are met with. The moss-cover is dense (90-95% coverage) and consists of *Drepanocladus revolvens, Meesia triquetra,* and *Cinclidium latifolium.* When the central part is more or less filled with peat, the moss cover usually consists of *Drepanocladus latifolius, D. Vernicosus, Meesia triquetra, Polytrichum jensenii, Calliergon sarmentosum.*

The plant aggregations on the raised borders are more diversified. The most raised corner parts are occupied by *Polytrichum strictum, Dicranum elongatum,* and *Aulacomnium turgidum,* and the lichens *Cetraria islandica, C. cucullata, Cladonia elongata, C. amaurocraea* and *Peltigera aphthosa.* The medium raised borders are occupied by shrub-sedge-moss aggregations with 3 layers. The upper, open shrub layer consists of mats of *Betula nana, Salix pulchra* and *S. reptans* (25-30 cm high), the middle layer of sedge with *Carex stans* (10-15 cm high with 15% coverage) and an addition of *Poa arctica, Saxifraga hirculus, S. punctata, Polygonum viviparum* and *Pedicularis hirsuta;* in the moss layer dominate *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Tomenthypnum nitens, Polytrichum strictum* and *Dicranum angustum;* the lichens present are *Dactylina arctica, Thamnolium vermicularis, Cladonia amaurocraea, Cetraria cucullata,* and *Peltigera aphthosa.* Characteristic for the lowest parts of the raised borders are willow-*Sphagnum* and sedge-*Tomenthypnum* aggregations; in the first, the sedge layer is almost indistinguishable, and in the moss layer *Sphagnum Warnstorfianum* and *S. squarrosum* dominate; in the second group, shrubs are absent, and in the moss cover *Tomenthypnum nitens, Aulacomnium turgidum* and liverworts *Ptilidium ciliare* and *Blepharostoma trichophyllum* predominate.

Site no. 5

Tundra and nival meadow communities on the S-facing main riverbank

The site is situated on steeply (ca. 40°) sloping land on the right hand bank of Pyasina river. The slope has a generally southern exposure, and is deeply cut by deep grooves, which, possibly, were first formed in places where melted ice wedges of an ancient polygonal system. They are some tens of meters long and are in winter filled by snow lasting until the middle of July. The areas between the grooves appear on the floodplain in the form of ridges; their higher more gentle parts are covered by sandy alluvial sediments, their lower, steeper parts by dark-colored, marine silts. Often, the ridges have the form of pyramids, two sides of which are represented by the slopes of two adjacent ravines (with SSW and NNE exposure) while the one (S exposure) towards the river is formed as a result of undercutting by floodwater. Very often parts slip, especially in wet years. The moisture-oversaturated upper layers of the soil together with its vegetation mat slides downslope to the flood-plain, baring the frozen ground in areas of several tens of square meters. The subsequent washing-out of the unstable ground deepens the erosion.

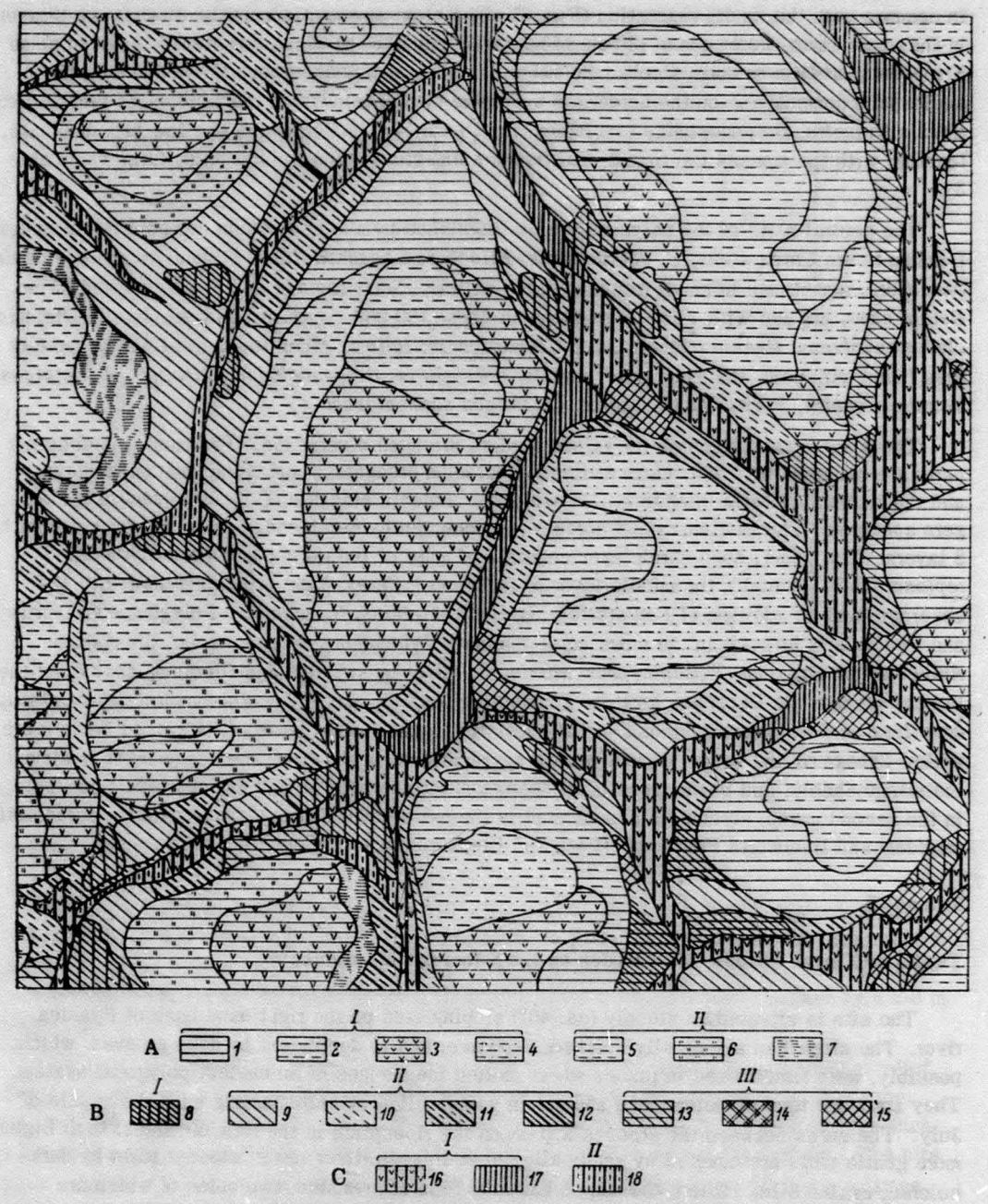

Figure 6. Schematic map of the permanent site (60 x 60 m) on a polygonal bog.

Figure 6 legend.

A. Micro-aggregations in the center of the polygon.

I. On depressed sites: 1 - *Hierochloe pauciflora, Carex chordorrhiza, Drepanocladus revolvens, Cinclidium latifolium;* 2 - *Eriophorum medium, Carex stans, Carex chordorrhiza, Drepanocladus revolvens, Cinclidium latifolium;* 3 - *Carex stans, Drepanocladus revolvens, Meesia triquetra;* 4 - *Eriophorum medium, Carex chordorrhiza, Drepanocladus revolvens, Cinclidium latifolium;*

II. On raised sites: 5 - *Salix reptans, Carex stans, Drepanocladus latifolius, Meesia triquetra;* 6 - *Salix reptans, Eriophorum medium, Carex stans, Meesia triquetra, Calliergon sarmentosum;* 7 - *Salix reptans, Carex stans, Drepanocladus revolvens;*

B. Micro-aggregations on raised borders.

I. On elevated border parts: 8 - *Cladonia* spp., *Polytrichum strictum, Aulacomnium turgidum;*

II. On medium high parts: 9 - *Dryas punctata, Salix reptans, Carex stans, Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Tomenthypnum nitens;* 10 - *Salix reptans, Carex stans, Aulacomnium turgidum;* 11 - *Salix reptans, Carex stans, Aulacomnium turgidum, Hylocomium splendens* var. *alaskanum;* 12 - *Betula nana, Aulacomnium turgidum, Hylocomium splendens* var. *alaskanum;*

III. On low-lying parts: 13 - *Carex stans, Tomenthypnum nitens;* 14 - *Salix reptans, Sphagnum Warnstorfianum, Sph. squarrosum;* 15 - *Salix reptans, Sphagnum Warnstorfianum, Polytrichum strictum, Aulacomnium turgidum;*

C. Micro-aggregations in the waterholes.

I. On depressed surfaces: 16 - *Carex stans, Meesia triquetra, Cinclidium latifolium;* 17 - *Carex stans, Eriophorum medium, Meesia triquetra, Calliergon sarmentosum;*

II. On raised surfaces: 18 - *Salix reptans, Carex stans, Drepanocladus revolvens, Aulacomnium turgidum.*

The upper part of the slope has a crack- and hummock surface. The flat hummocks are from 25-30 cm to 1 m in diameter and are further split by cracks of varying width, their depth from 10-15 up to 50 cm. The cracks are often deepened by trails of the lemmings, and filled with lemming droppings and material thrown out from their burrows under the hummocks. The slow slipping of the hummocks down the slope widens and deepens the cracks further and the hummocks take on the shape of terraces.

Even if the main slope of the river bank on the whole represents the most favorable conditions for the growth of vegetation (with better heated soils, deep - up to 1 m or more - thawing of the permafrost, protection from winds of N and NE direction, good drainage, and a neutral or very slightly acid reaction of the substrate), the river bank slope is not uniform according to the environmental conditions; it is an assemblage of various, often even contrasting habitats. Bareblown, poor in snow-cover, dry spots of the upper parts of the ridges are found next to wind-protected, snow-rich and very wet troughs; the sandy soils are alternating with heavy silts, southfacing slopes alternate with northfacing, lightly sodded, eroded substrates with densely and almost overgrown soils.

Characteristic for the vegetation of the riverbank slope is the very great variation and diversity of the plant aggregations even on similar elements of relief, the presence of open aggregations, the different composition (in comparison with the tundra communities) of life-forms (the frequency of perennial taproot plants, the presence of root-sucker plants and cushion forms), the large proportion of grasses and the rarity of mosses, at least on the positive elements of the slope (Figure 7).

The density of the vegetation diminishes from the top to the bottom along the slope as a result of widely distributed open plant aggregations on eroded parts of the lower slope. In contrast, the height of the herbage improves in this direction from 10-15 to 30-35 cm, apparently because of the increased thickness of the snow-cover and better warming conditions in comparison with the upper parts of the slope (Romanova 1971).

The higher parts of the slope are occupied by dwarf shrub-sedge-moss aggregations, passing from wet tundra to herb-grass aggregations of slopes (Figure 7). The dwarf shrub-sedge-moss aggregations are characterized by a 2-layered composition: a sedge-layer, 8-10 cm high, and a dwarf shrub-lichen-moss layer, 3-5 cm high. In the upper layer, *Carex ensifolia* ssp. *arctisibirica* dominates, in the lower *Hylocomium splendens* var. *alaskanum* and of dwarf shrubs *Dryas punctata*, *Salix polaris* and *S. arctica*. Lichens cover, in places, up to 40% of the surface (Table 4).

On windblown, strongly expressed, steeply sloping parts of the ridges and on S-facing slopes *Dryas* and herb-*Dryas* aggregations dominate; these also have 2-layers: the upper (10-15 cm high) is composed of predominantly grasses, legumes and herbs, the lower (2-3 cm) of a moss-*Dryas* layer, the most important frequency is reached by *Koeleria asiatica* (8%) and *Festuca brachyphylla*, and in the lower by *Dryas punctata* (60-70%) *Cassiope tetragona*, *Salix arctica* and *S. polaris*. Mosses make up 15-20% and consist mostly of *Hylocomium splendens* var. *alaskanum*, *Rhytidium rugosum*, *Distichum capillaceum*, and *Thuidium abietinum*. In driest and open places such xerophilous species as *Kobresia Bellardii*, *Carex rupestris* and *Lychnis sibirica* ssp. *villosula* occur in this aggregation.

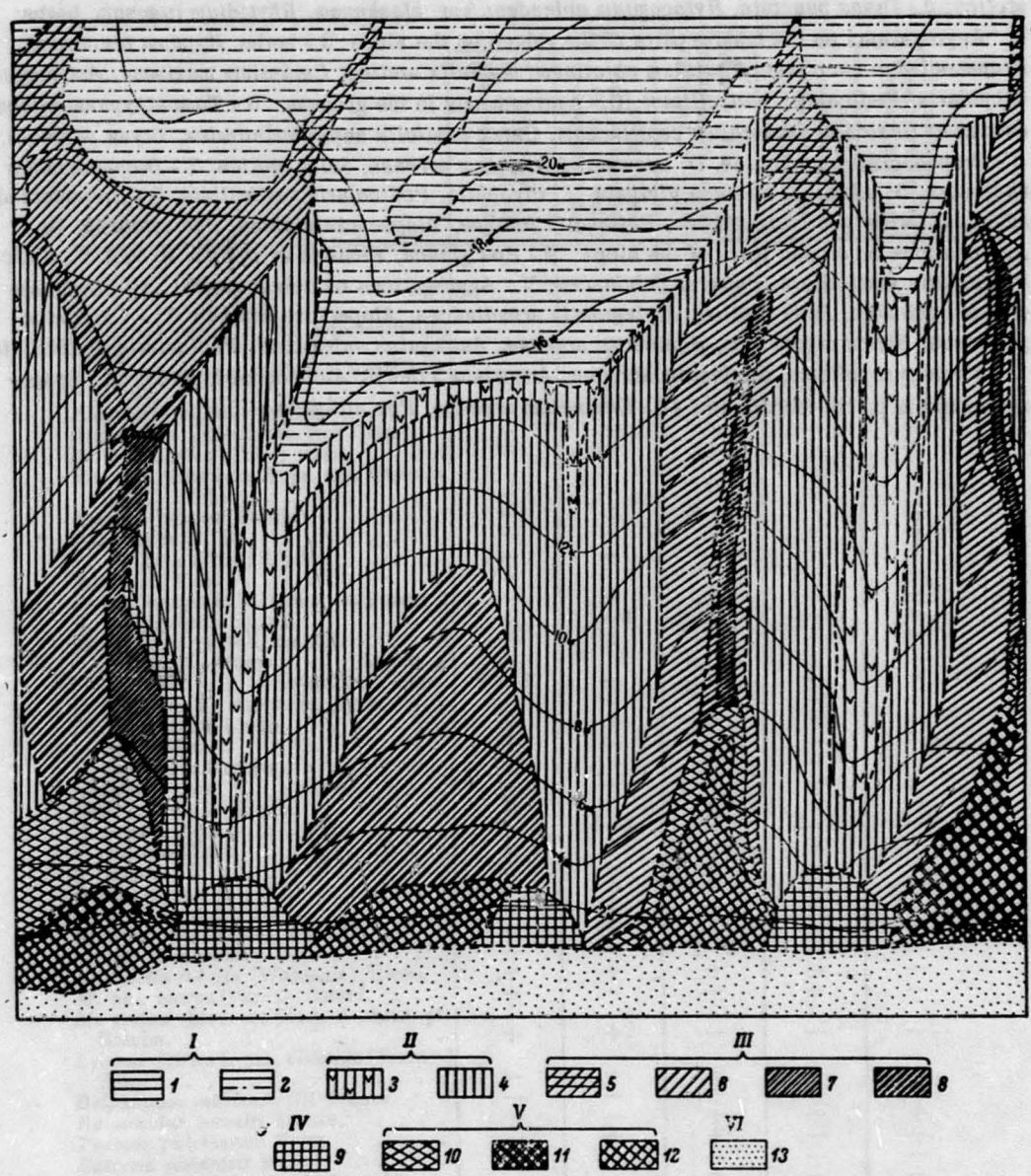

Figure 7. Schematic map of the permanent site (70 x 70 m) on the SSE slope of the main bank of Pyasina river.

Figure 7 legend.

I. Aggregations on the margins of the main bank and on the upper parts of the slope: 1 - *Hylocomium splendens* var. *alaskanum*, *Carex ensifolia* ssp. *arctisibirica*, *Dryas punctata*, *Salix arctica*; 2 - *Dryas punctata*, *Hylocomium splendens* var. *alaskanum*, *Rhytidium rugosum*, herbs; II. Aggregations on the middle parts of the ridges on the slope: 3 - herbs, *Hypnum revolutum*, *Drepanocladus uncinatus*, *Thuidium abietinum*; 4 - *Salix arctica*, *Cerastium maximum*, *Astragalus subpolaris*, *Pedicularis verticillata*; III. Aggregations in the grooves: 5 - *Tomenthypnum nitens*, *Ditrichum flexicaul*, *Distichium capillaceum*, *Carex ensifolia* ssp. *arctisibirica*, *Dryas punctata*; 6 - *Drepanocladus uncinatus*, *D. aduncus*, *Equisetum arvense*, *Salix arctica*; 7 - *Drepanocladus uncinatus*, *D. aduncus*, *Festuca vivipara*, *F. cryophila*, *Pedicularis verticillata*; 8 - *Drepanocladus aduncus*, *Calliergon sarmentosum*, *Philonotis fontana*, *Alopecurus alpinus*, *Poa alpigena*; IV. Aggregations on eroded parts of the slope: 9 - *Poa glauca*, *Festuca cryophila*, *Myosotis asiatica*, *Pedicularis verticillata*, *Papaver pulvinatum*; V. Aggregations on debris cones: 10 - *Drepanocladus uncinatus*, *Salix arctica*, *Arctagrostis arundinacea*, *Alopecurus alpinus*; 11 - *Ceratodon purpureus*, *Bryum cryophilum*, *Equisetum arvense*, *Astragalus subpolaris*, *Pedicularis verticillata*; 12 - *Hypnum revolutum*, *Equisetum arvense*, *Artemisia Tilesii*, *Alopecurus alpinus*; VI. Sparse aggregations on the floodplain: 13 - *Equisetum arvense*, *Poa alpigena*.

Table 4. Species composition of the plant aggregations on permanent site No. 5

Name of species	Vegetation aggregations				
	Dwarf shrub-sedge-moss border of the main bank	Dryas and herb-Dryas on the upper parts of the ridge slopes	Herb-moss and herb on the middle parts of the ridge slopes	Grass-herb-moss and grass-moss on the bottoms of grooves	Herb- and grass-Equisetum-moss on debris cones
Angiosperms					
Equisetum arvense L. ssp. *boreale* (Bong.) Rupr.	+	+	—	+	15—20
Hierochlcë alpina (Liljebl.) Roem. et Schult.	—	+	—	—	—
Alopecurus alpinus Smith	—	—	—	1—20	+
Arctagrostis latifolia (R. Br.) Griseb.	+	+	—	—	—
A. arundinacea (Trin.) Beal.	—	—	—	+	+
Trisetum sibiricum Rupr. ssp. *litoralis* (Rupr.) Roshev.	—	+	7	10	—
Koeleria asiatica Domin	—	3	2—5	—	—
Poa arctica R. Br.	+	+	—	+	—
P. alpigena (Fries) Lindm.	—	—	—	+	+
P. glauca Vahl	—	—	+	1—7	—
Festuca cryophila V. Krecz. et Bobr.	—	—	+	1—3	—
F. brachyphylla Schult.	+	1—3	+	3—30	+
Carex rupestris Bell. ex All.	—	2	—	—	—
C. ensifolia (Turcz. ex Gorodk.) V. Krecz. ssp. *arctisibirica* Jurtz.	15—30	—	—	—	—
C. fuscidula V. Krecz. ex Egor.	—	+	—	—	—
Luzula confusa Lindb.	+	+	+	+	—
L. nivalis Laest.	+	—	—	—	—
L. tundricola Gorodk.	+	—	—	—	—
Lloydia serotina (L.) Reichenb.	+	+	—	+	—
Salix polaris Wahlenb.	2	3	+	+	—
S. arctica Pall.	5—15	1—3	45	2—10	5—8
S. pulchra Cham.	+	+	—	—	—
S. lanata L.	—	—	—	—	+
Oxyria digyna (L.) Hill	—	+	—	+	—
Polygonum viviparum L.	+	+	+	+	—
Stellaria ciliatosepala Trautv.	+	+	—	—	—
Cerastium maximum L.	—	—	1—3	—	—
Minuartia rubella (Wahlenb.) Hiern.	+	+	+	—	—
M. macrocarpa (Pursh) Ostenf.	+	—	—	—	—
M. arctica (Stev. ex Sér.) Aschers. et Graebn.	+	+	—	—	—
Lychnis sibirica L. ssp. *villosula* (Trautv.) Tolm.	—	+	+	—	—
Delphinium middendorffii Trautv.	—	—	+	—	+
Ranunculus borealis Trautv.	—	—	+	—	+
Papaver pulvinatum Tolm.	—	+	+	—	—
Eutrema edwardsii R. Br.	+	—	—	—	—
Erysimum pallasii (Pursh) Fernald	—	—	+	—	—
Arabis septentrionalis N. Busch	—	—	+	—	—
Parrya nudicaulis (L.) Regel	+	+	+	—	+
Draba micropetala Hook.	+	—	—	—	—
D. parvisiliquosa Tolm.	—	+	—	—	—
D. glacialis Adams	—	—	—	+	—
D. hirta L.	—	—	+	—	—
Thlaspi cochleariforme DC.	—	+	+	—	—
Saxifraga punctata L.	+	+	—	—	+
S. nivalis L.	—	+	—	+	—

Table 4. Continued

Name of species	Vegetation aggregations				
	Dwarf shrub-sedge-moss border of the main bank	Dryas and herb-Dryas on the upper parts of the ridge slopes	Herb-moss and herb on the middle parts of the ridge slopes	Grass-herb-moss and grass-moss on the bottoms of grooves	Herb- and grass-Equisetum-moss on debris cones
S. hieracifolia Waldst. et Kit.	—	+	+	+	+
S. hirculus L.	—	—	—	+	+
S. cernua L.	—	+	+	+	+
Potentilla stipularis L.	—	+	+	—	—
Dryas punctata Juz.	3—10	60—70	2—3	+	—
Astragalus subpolaris Boriss. et Schischk.	+	+	2—3	5—7	+
Oxytropis adamsiana (Trautv.) Jurtz.	—	+	3—5	—	—
O. middendorffii Trautv.	—	+	+	—	—
Pachypleurum alpinum Ledeb.	—	+	1—7	+	+
Cassiope tetragona (L.) D. Don	—	5	—	—	—
Androsace bungeana Schischk. et Bobr.	—	+	+	+	—
A. triflora Adams	—	+	+	—	—
A. septentrionalis L.	—	—	+	—	—
Armeria arctica (Cham.) Wallr.	—	+	—	—	—
Polemonium boreale Adams	—	+	3	+	—
Myosotis asiatica Schischk. et Serg.	—	+	2—3	+	+
Eritrichium villosum (Ledeb.) Bunge	—	+	+	+	+
Pedicularis verticillata L.	—	+	7—10	+	—
P. dasyantha (Trautv.) Hadač	—	+	—	—	—
P. oederi Vahl	+	+	—	—	—
P. capitata Adams	+	+	—	—	—
Campanula langsdorffiana Fisch.	—	+	+	—	—
Erigeron eriocephalus J. Vahl	—	—	+	—	—
Antennaria villifera Boriss.	—	+	—	—	—
Tripleurospermum phaeocephalum (Rupr.) Pobed.	—	—	+	—	—
Artemisia tilesii Ledeb.	—	—	+	+	+
Nardosmia gmelini DC.	—	—	—	—	+
Arnica iljinii (Maguire) Iljin	—	—	+	—	—
Saussurea tilesii Ledeb.	—	+	+	—	—
Mosses					
Polytrichum alpinum Hedw.	—	+	+	—	—
P. strictum Sm.	+	+	—	—	—
Ditrichum flexicaule (Schleich.) Hampe	+	+	—	+	+
Ceratodon purpureus (Hedw.) Brid.	—	+	—	+	10
Distichium capillaceum (Hedw.) B. S. G.	+	+	+	—	5—10
D. inclinatum (Hedw.) B. S. G.	—	—	—	+	—
Dicranella subulata (Hedw.) Schimp.	—	—	+	—	—
Oncophorus wahlenbergii Brid.	—	—	—	+	+
Dicranum elongatum Schleich.	—	+	—	—	—
D. congestum Brid.	5	+	—	+	—
D. spadiceum Zett.	+	+	—	+	—
Encalypta alpina Sm.	—	+	+	+	—
E. rhabdocarpa Schwaegr.	—	+	+	+	—
E. rhabdocarpa Schwaegr. var. *leptodon* (Bruch) Lindb.	—	—	+	+	+
Tortula ruralis (Hedw.) Crome	—	+	+	+	—
T. mucronifolia Schwaegr.	—	—	+	+	—
Tortella fragilis (Hook. et Wills.) Limpr.	+	+	—	—	—
Barbula icmadophila Schimp.	—	—	+	—	—
B. unguiculata Hedw.	—	—	—	+	+

Table 4. Continued

Name of species	Vegetation aggretations				
	Dwarf shrub-sedge-moss border of the main bank	Dryas and herb-Dryas on the upper parts of the ridge slopes	Herb-moss and herb on the middle parts of the ridge slopes	Grass-herb-moss and grass-moss on the bottoms of grooves	Herb- and grass-Equisetum-moss on debris cones
Bryoerythrophyllum recurvirostre (Hedw.) Chen	—	+	+	+	+
Tetraplodon mnioides (Hedw.) B. S. G.	—	+	—	+	—
Pohlia cruda (Hedw.) Lindb.	+	+	+	+	—
Mniobryum wahlenbergii (Web. et Mohr) Jennings	—	—	—	+	—
Bryum cryophilum O. Mårt.	—	—	—	+	+
Bryum sp.	—	—	+	+	—
Mnium orthorrhynchum Brid.	—	+	—	—	—
M. rugicum Laur.	—	+	—	—	—
Aulacomnium palustre (Hedw.) Schwaegr.	+	—	—	—	—
A. turgidum (Wahlenb.) Schwaegr.	2—5	+	—	+	+
Philonotis tomentella Mol.	—	—	—	+	—
P. fontana (Hedw.) Brid.	—	—	—	5	+
Timmia norvegica Zett.	—	—	+	—	—
T. comata Lindb. et Arn.	—	—	+	—	—
T. austriaca Hedw.	+	+	+	+	—
T. austriaca var. *arctica* (Kindb.) Arn.	—	+	+	—	—
Myurella julacea (Schwaegr.) B. S. G.	—	+	+	+	—
Thuidium abietinum (Schwaegr.) B. S. G.	+	+	+	—	—
Campyllium stellatum (Hedw.) Lange et C. Jens.	—	+	—	+	+
C. polygamum (B. S. G.) Lange	+	—	—	+	—
Drepanocladus uncinatus (Hedw.) Warnst.	+	10	30	+	20
D. aduncus (Hedw.) Mönkem.	—	—	—	20—25	—
D. sendtneri (Schimp.) Warnst.	—	—	—	+	—
Scorpidium turgescens (Th. Jens.) Mönkem.	—	—	—	+	—
Calliergon sarmentosum (Wahlenb.) Kindb.	—	—	—	+	—
Tomenthypnum nitens (Hedw.) Loeske	5	+	+	+	+
Brachythecium turgidum (Hartm.) Kindb.	—	—	+	+	—
B. mildeanum (Schimp.) Milde var. *udum* (Hag.) Mönkem.	+	+	+	+	+
Ctrriphyllum cirrosum (Schwaegr.) Grout	—	+	+	+	+
Eurhynchium pulchellum (Hedw.) Jennings	+	+	+	+	—
Hypnum bambergeri Schimp.	+	+	—	—	—
H. vaucheri Lesq.	—	+	+	—	—
H. revolutum (Mitt.) Lindb.	—	5	15	+	+
Rhytidium rugosum (Hedw.) Kindb.	+	+	—	—	—
Hylocomium splendens (Hedw.) B. S. G. var. *alaskanum* (Lesq. et James) Limpr.	25—30	2	+	+	—
Lichens					
Collema tenax (Sw.) Ach. em. Degel.	—	+	—	—	—
Psoroma hypnorum (Vahl) Gray	+	+	—	—	—
Nephroma expallidum (Nyl.) Nyl.	+	+	—	+	—
Peltigera aphthosa (L.) Willd.	—	+	4—5	—	—

Table 4. Continued

Name of species	Vegetation aggregations				
	Dwarf shrub-sedge-moss border of the main bank	Dryas and herb-Dryas on the upper parts of the ridge slopes	Herb-moss and herb on the middle parts of the ridge slopes	Grass-herb-moss and grass-moss on the bottoms of grooves	Herb- and grass-Equisetum-moss on debris cones
Peltigera canina (L.) Willd.	+	+	1—5	+	—
P. erumpens (Tayl.) Lang.	—	+	3	—	—
Solorina saccata (L.) Ach.	—	+	—	—	—
Cladonia amaurocraea (Flk.) Schaer.	+	—	—	—	—
C. elongata (Jacq.) Hoffm.	+	—	—	—	—
C. pyxidata (L.) Hoffm.	+	—	+	—	—
Stereocaulon alpinum Laur.	2	2	—	—	—
Ochrolechia upsaliensis (L.) Mass.	—	+	+	—	—
Pertusaria coriacea (Th. Fr.) Th. Fr.	—	+	—	—	—
Lecanora verrucosa Ach.	+	+	+	—	—
Hypogymnia subobscura (Vain.) Poelt.	—	+	—	—	—
Parmelia omphalodes (L.) Ach.	—	—	+	+	—
Cetraria cucullata (Bell.) Ach.	+	2—3	+	—	—
C. ericetorum Opiz	+	—	+	—	—
C. nivalis (L.) Ach.	+	+	+	—	—
Alectoria nigricans (Ach.) Nyl.	—	+	—	—	—
A. ochroleuca (Hoffm.) Mass.	+	+	—	—	—
Cornicularia divergens Ach.	+	—	—	—	—
Dactylina arctica (Hook.) Nyl.	+	+	+	—	—
Thamnolia vermicularis (Sw.) Ach. ex Schaer.	+	+	+	—	—
Rinodina roscida (Smrft.) Arn.	—	+	—	—	—
Physconia muscigena (Ach.) Poelt.	+	+	—	—	—

Note: Figures = % coverage of the species
+ = coverage less than 1%.

The herb aggregations occupy the slopes of the middle and partly lower sections of the ridge slopes facing the valley. On the S-facing slopes, they are most diversified and rich in composition with a high frequency of legumes (*Oxytropis Adamsiana, O. Middendorffii*, and *Astragalus subpolaris*), louseworts (*Pedicularis verticillat, P. Oederi*), Saxifrages (*Saxifraga punctata, S. cernua, S. spinulosa*) and chickweeds (*Cerastium maximum, Minuartia arctica, M. macrocarpa*). On the edges of the hummocks and in the cracks, there are *Armeria arctica, Draba parvisiliquosa, Minuartia rubella, Thlaspi cochleariforme, Arabis septentrionalis*, etc. A moss layer of *Thuidium abietinum, Hypnum revolutum* and *Drepanocladus uncinatus* is very weakly developed. On the lower parts of the slopes, facing the river, the nival meadow element is strengthened: there is an aspect of *Ranunculus borealis, Myosotis asiatica, Pachypleurum alpinum*, and *Polemonium boreale*, and in places also *Arnica lljinii* and some dandelions. The role of mosses in this vegetation cover is insignificant.

On the north-facing slopes, the herbage is poorer with less legumes and chickweeds; here willows play an increasing role (*Salix polaris* and *S. arctica*) and mosses cover about 50% of the surface, with *Hypnum revolutum* and *Drepanocladus uncinatus* as dominants.

On the eroded parts of the slopes, open plant aggregations often occur with a different degree of the surface sodding by angiosperms (from 2-3 to up to 50%). The bare substrate is colonized by *Tripleurospermum phaeocephalum, Myosotis asiatica, Arabis septentrionalis,* and by *Papaver pulvinatum* earlier then by other plants. They form one-species or mixed herbage. At a later stage, they are joined by grasses such as *Festuca cryophila* and *Poa glauca.* Mosses *Drepanocladus uncinatus, Cirriphyllum cirrosum,* and *Hypnum revolutum* begin growth on already stabilized substrate; in the beginning of the succession, their role is insignificant.

The bottom of the channels are occupied by herb-grass-moss, grass-moss, and *Equisetum*-moss aggregations. In the first two, *Drepanocladus uncinatus, D. aduncus, Ceratodon purpureus* and *Philonotis fontana* dominate in the moss cover; along the waterways, *Calliergon sarmentosum* occurs. The sparse grass herbage consists of *Alopecurus alpinus, Festuca brachyphylla* and *F. cryophila,* and *Trisetum sibiricum.* Besides grasses, in the herbage *Artemisia Tilesii, Oxyria digyna, Pedicularis verticillata, Astragalus subpolaris* and *Polygonum viviparum* are found. The *Equisetum*-moss aggregations are poorer in composition, often with a large amount of *Salix polaris.*

On the firm parts of the channels on debris cones in *Equisetum*-moss aggregations, willow shrubs are colonizing *(Salix lanata);* on the loose substrate, mats of large grasses occur *(Arctagrostis arundinacea* and *Poa alpigena).*

Site no. 6

The anthropogenic vegetation of Tareya settlement

The settlement is situated on the right hand bank of Pyasina river, on a spot with a SSW direction, bordered on one side by the river and on the other by a brook draining into the river. The ancient terrace of Pyasina descends to the river and to the brook in the form of a long slope with a complex relief.

Tareya is a temporary settlement, utilized by fishermen during the fishing season. A description of its vegetation and the composition of the schematic map (Figure 8) was undertaken in 1968. At that time, the settlement consisted of five huts, premises for storing fishing gear and a cold storage for fish. Earlier, there was a base for a geological expedition, which had erected a row of temporary huts of wood, tarpaper and tarpaulin. In 1968, the location, where these had stood, was still clearly visible by their remains, but also by the trampling of the ground and the growth of ruderal plants. Beside them, on the site, there were noted some half-rotten boats, heaps of coal, slag and debris.

In the town area of Tareya, there are no anthropogenous aggregations in the true sense of this word, that is aggregations composed of plants introduced by man onto soils cleared of original vegetation; no experiments with agriculture have been made here. In Tareya and its surroundings, no anthropochore has been found (i.e. plants from other floristic areas, established by man). The vegetation of the settlement, which we call anthropogenous only conditionally, is composed mainly of apophytes (species from the local flora which increase in frequency and sometimes in vigour, winning in the competition against those species for which the influence of man is less favorable or bad).

Figure 8. Schematic map of the area of the village of Tareya.

1.- parts with strongly or completely trampled vegetation; 2 - apophytic aggregations on loose, polluted soil; 3 - semi-ruderal aggregation on polluted alluvial; 4 - *Poa alpigena* aggregations; 5 - *Alopecurus alpinus* aggregations; 6 - *Deschampsia Sukatshewii* aggregations; 7 - Aggregations of *Carex ensifolia* ssp. *arctisibirica* and mosses; 8 - grass-herb aggregations; 9 - *Dryas* aggregations; 10 - fragments of a *Cassiope* tundra; 11 - willow thicket of *Salix lanata;* 12 - aggregations of *Carex stans* and *Arctophila fulva;* 13 - sand and pebble bar; 14 - heaps of coal and slag; 15 - inhabited buildings; 16 - remnants of former buildings or their sites; 17 - old decaying boats; 18 - path-ways.

Basically, under the conditions of the Far North, the influence of man on the ground leads to drainage, better aeration, lowering the surface of the permafrost, or, to temporary loosening or compacting of the soil. Such changes give rise to a gradual disappearance of hydro- and hygrophytes: mosses, sedge, *Juncus*, hydrophilous herbs, also of tundra dwarf, shrubs and prostrate willows; they are replaced mostly by grasses. On loose, anthropogenous substrates, some dicotyledons will also take root.

What the vegetation in Tareya looked like before man's arrival can be judged from the vegetation on an analogous slope some 1.5 km lower along Pyasina. This latter slope is somewhat lower, but has the same exposure. Along the slope to the brook stretches a willow-*Poa* aggregation *(Salix lanata, Poa alpigena).* The main part of the surface is covered with a *Dryas*-sedge-moss tundra. The soils are peaty-gleyic, thixotropic and moist. The moss cover is compact, composed mainly of *Tomenthypnum nitens* (80%), *Aulacomnium turgidum* and *Hylocomium splendens* var. *alaskanum.* The dwarf shrub-grass layer is thin and in depressions almost absent; dominants are *Carex ensifolia* ssp. *arctisibirica* and *Dryas punctata.* All the rest of the species are not numerous *(Salix arctica, S. pulchra, Betula nana, Pyrola grandiflora, Saxifraga cernua,* S. *punctata, Polygonum viviparum, Luzula confusa, Pedicularis Oederi, P. capitata, Minuartia arctica, Lagotis minor, Eriophorum vaginatum, Festuca brachyphylla, Polygonum bistorta, Astragalus umbellatus, Eritrichium villosum* and *Valeriana capitata).*

The vegetation in the town area of Tareya includes the following aggregations: Depressed and sparse *Alopecurus-Poa* aggregations. The vegetation is either trampled completely, or the plants are in a depressed state and of very low vigour. Apparently, the original aggregation - a sedge-*Dryas*-moss tundra - is long since destroyed, and a complete change in the herbaceous and moss layers has taken place. Gleification, which develops in the sedge-moss tundras in the surface horizons, here is found at a depth of 50 cm, and the peaty horizon disappears and humified one appears. The thickness of the active layer is 75-100 cm. The grass-layer is very thin, consisting of generative, but very small shoots of *Poa alpigena* and *Alopecurus alpinus* and, in addition, a very insignificant amount of depressed herbs. The open moss cover, up to 1 cm in thickness, consists of *Ceratodon purpureus, Bryum cirrhatum, B. nitidulum* and *Funaria hygrometrica.*

The aggregation of apophytes on loose, polluted soils. Close to dwellings, there are heaps of soil, refuse and slag. Characteristic for such places is a rather constant set of apophytic-ruderal plants with the dominance of one or another species, which can be explained by the variable relief and the physical and chemical properties of the substrate, and also by an accidental introduction of plants. Understandably, a moss cover is lacking. The dominants are *Descurainia Sophioides, Tripleurospermum phaeocephalum, Artemisia Tilesii, Cerastium maximum, Stellaria peduncularis, Festuca cryophila, F. brachyphylla* and *Arctagrostis arundinacea.* To these species are always added the most common apophytes of Tareya, *Poa alpigena, Alopecurus alpinus,* and *Deschampsia Sukatschewii* and various occasional species.

The dominants, characteristic for the aggregations studied were apparently before man's appearance absent from the sites occupied by them; but all are rather common in the environment of Tareya. Often, they are frequent on the slipping banks of the Pyasina ravines and on loose, moist substrates. They are met with everywhere in the tundra on refuse from burrows and other zoogenic and anthropogenic habitats in loosened soil. To all appearances, not only the friability of the soil, but also the pollution is important since not all, but only certain plants of the open tundra aggregations have settled on anthropogenic substrates. Almost all of these species are noted as characteristic apophytes in other areas of the Far North (Dorogostaiskaya 1972).

The semi-ruderal aggregation on polluted alluvium. This one occurs in conditions of flooding on clay-sandy alluvial deposits of the Pyasina river and its tributary. The soil is condensed sand with lenses of mud, sometimes with included waste matter. A moss cover is lacking. The sites are few, often long-stretched, usually with dominating *Equisetum arvense* (rarely with predominant *Pyrethrum bipinnatum)* and an admixture of *Poa alpigena* and sometimes of *Cerastium Regelii* or a *Taraxacum* sp.

Both *Equisetum arvense* and *Pyrethrum bipinnatum* appear as common plants on alluvials of Pyasina, but in the town area, they are distinguished by much more vigour. Considering them as apophytes, we only underline the fact that here as in other parts of the Arctic, they do not suffer but rather benefit from the influence of man.

Aggregations with dominant Poa alpigena. They occupy a large area in Tareya, but the sites marked 4 on the schematic map, are not always identical. There are two very similar and difficult to delimit variants:

a) the *Poa*-aggregations, situated in the western parts of the settlement on a gentle slope towards the brook and alternating with mats and scrub of *Salix lanata* and *S. reptans.* These sites remain inundated for a long time by the floodwater during the spring. The soil is sandy with a large quantity of clay, indistinctly layered. Mosses cover 20-90% and are 0.5-2 m thick. The soil is not, or only very slightly, sodded. The vegetation is represented by a thin grassland of *Poa alpigena* (not very vigorous) with an addition of herbaceous plants *(Polygonum viviparum, Equisetum arvense, Lagotis minor, Ranunculus borealis, Cardamine pratensis, Carex stans, Nardosmia frigida* and *Astragalus subpolaris);*

b) the *Poa*-aggregations on heights and the quite steep, well drained slopes of hills in the central parts of the settlement. The soil is uniformly sandy with a significant degree of turf and humification of the upper horizon. A moss cover is lacking. The *Poa* forms a thick and dense sod, in places with co-dominant *Trisetum sibiricum* and *Festuca cryophila,* and also with an important addition of *Alopecurus alpinus* and *Arctagrostis arundinacea,* in places also of *Carex ensifolia* ssp. *arctisibirica.* Of the herbaceous plants, there are frequently *Hedysarum arcticum, Pedicularis verticillata, Cerastium maximum, Astragalus umbellatus* and *Saxifraga cernua.*

Apparently, the association with the willow-mat experiences an insignificant anthropogenic influence (trampling and flow of polluted water) and is close to the natural *Poa* meadow, which is often found in the Pyasina river floodplain. The second aggregation is clearly anthropogenic and appears after trampling and pollution, and destruction of plants competing with *Poa.*

The aggregation with dominant Alopecurus alpinus. *Alopecurus alpinus* is a typical, arctic apophyte, widely distributed in all the town area of Tareya and met with as an admixture in the herbaceous layer of almost all the aggregations. The aggregations with *Alopecurus* as the dominant species are correlated with depressions with raised humidity. It has the same soils as the preceding aggregation. Sometimes a moss layer is found. In the herbage there is a noticeable admixture of *Carex ensifolia* ssp. *arctisibirica.* Apparently, this aggregation substitutes for the *Poa* at the appearance of stagnated moisture to which *Poa* is more sensitive. With respects to herb composition, they are similar.

The aggregation with Deschampsia Sukatchewii. It is associated mainly with the lower parts of slopes where there is a brief flooding, also with the flow of polluted water, trampling and pollution with waste matter. There is no moss cover. The surface of the ground is covered with a thick felt of dead and slightly decomposed leaves of *Deschampsia Sukatchewii.* The herbage is very dense and covers about 95% of the soil. The sod of *Deschampsia* is very strong and the

grass frequently sets seeds. Rather often *Poa alpigena, Descurainia Sophioides* and *Tripleurospermum phaeocephalum* also occur. On the whole, it can be said, that under the influence of man the vigour and frequency of *Deschampsia Sukatchewii* is significantly raised and it may be noted as an arctic apophyte.

In addition to the above-mentioned dominating species in the herbage of all the grass aggregations in Tareya, there is a small quantity of *Poa arctica, Dryas punctata, Salix reptans, S. Arctica, Astragalus umbellatus, Myosotis asiatica, Artemisia Tilesii, Polemonium boreale, Senecio resedifolius, Antennaria villifera, Pyrethrum bipinnatum, Polygonum Bistorta, Claytonia Joanneana, Saussurea Tilesii, Pedicularis capitata, Saxifraga hirculus, Armeria arctica, Pyrola grandiflora* and *Stellaria ciliatosepala*.

On the steep slopes with little human traffic, among the anthropogenic vegetation, fragments of the almost undisturbed native vegetation are preserved: aggregations of *Dryas punctata, Cassiope tetragona*, and elements of a grass-herb tundra. Along the shores of the brooks, on sites which dry only towards the end of the summer, there have developed grass-sedge aggregations with predominant *Carex stans*, thickets of *Salix lanata* and *Arctophila fulva*, also hardly subjected to the influence of man.

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