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Phytosociological classification of mire vegetation of the Udyl' Federal Nature Reserve (Khabarovsk krai, the Russian Far East)

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ABSTRACT

The vegetation of peat mires within the Udyl' Federal Nature Reserve, located on the left bank of the lower Amur River in the Ul'chskii District of Khabarovsk Krai, was investigated. Employing the Braun-Blanquet floristic classification approach, we identified 10 associations, 2 subassociations, 10 variants, and 3 community types, which belong to 6 alliances, 4 orders, and 3 classes. The affiliation of two additional community types with higher syntaxonomic units remains unresolved. Among the syntaxa recorded, 9 associations and 2 subassociations are described as new; one association is revised based on previously published data. A new monotypic class, Carici minutae–Salicetea brachypodae cl. prov., is proposed to encompass the vegetation of shrubby tussock-sedge minerotrophic mires in the southern Russian Far East, which are subject to regular inundation during spring and summer high-water periods. Two new alliances are established: Carici minutae–Salicion brachypodae **all. nov.** and Sphagnion alaskense **all. nov.** Syntaxonomic ordination was performed using Non-metric Multidimensional Scaling (NMDS) based on a Bray-Curtis distance matrix of median species abundances. The degree of similarity among syntaxa was assessed through hierarchical clustering.

Keywords: mire vegetation, Braun-Blanquet classification, phytosociology, syntaxonomy, boreal mires, *Sphagnum*, Udyl' Federal Nature Reserve, Lower Amur lowlands, Russian Far East.

РЕЗЮМЕ

Лапшина Е.Д., Филиппов И.В. Фитосоциологическая классификация растительности болот федерального заказника "Удыль" (Хабаровский край, российский Дальний Восток). Проведено изучение растительности торфяных болот федерального заказника "Удыль", расположенного на левобережье в нижнем течении р. Амур, на территории Ульчского района Хабаровского края. На основе флористической классификации Ж. Браун-Бланке в растительном покрове выделено 10 ассоциаций, 2 субассоциации, 10 вариантов и 3 типа сообществ из 6 союзов, 4 порядков 3 классов. Принадлежность к высшим единицам еще 2 типов сообществ не установлена. Из выделенных синтаксонов 9 ассоциаций и 2 субассоциации описаны как новые, еще одна ассоциация актуализирована по ранее опубликованным материалам. Предложено выделение нового монотипного класса Carici minutae–Salicetea brachypodae cl. prov., включающего растительность кустарниково-кочкарноосоковых минеротрофных болот на юге Дальнего Востока, регулярно заливаемых в период весенних и летних паводков. Описаны 2 новых союза Carici minutae–Salicion brachypodae **all. nov.** и Sphagnion alaskense **all. nov.** Ординация синтаксонов проведена методом неметрического многомерного шкалирования (NMDS) по медианному обилию видов. Степень сходства между синтаксонами оценена методом иерархической кластеризации.

Ключевые слова: растительность болот, классификация Браун-Бланке, фитосоциология, синтаксономия, бореальные болота, *Sphagnum*, федеральный заказник "Удыль", Нижнеамурские низменности, российский Дальний Восток

The Udyl' Federal Nature Reserve is located on the left bank of the lower Amur River, within the Ul'chskii District of Khabarovsk Krai (51°42'–52°24'N 139°30'–140°12'E). Its central feature is Lake Udyl', one of the largest lakes in the Lower Amur region, with a water surface area of 330 km² and a catchment area of 12 400 km². The reserve was established primarily to protect rare and endangered waterbirds associated with the lake's wetland system – including *Anser cygnoides*, *Haliaeetus pelagicus*, and *H. albicilla* – all of which are listed in the IUCN Red List, the Red Data Book of the Russian Federation, and regional Red Data Books, as well as to conserve their habitats.

In accordance with the reserve's primarily zoological focus, its avifauna and ichthyofauna have been relatively well studied. The vegetation cover, however, remains poorly investigated to date. Only the most general information on the vegetation of the broader regions encompassing the Lake Udyl' area is available (Sochava 1962, Karpenko 1964, Man'ko & Rozenberg 1967, Nechaev 1970). The first detailed account of the mire vegetation of the Udyl'–

Kizin Lowland, within which a substantial portion of the Udyl' Nature Reserve is situated, was provided by Yu.S. Prozorov (1974). Based on a combination of three criteria – vegetation, soil, and microtopography – he developed a detailed classification of mire communities. The data on microtopography, peat depth, and peat soil properties presented therein retain their scientific value; however, a phytosociological classification of the mire vegetation of this region has not been carried out to date.

A detailed study of the vegetation cover, including the mires that occupy approximately 60 % of the reserve's land area (excluding the lake surface), is essential for identifying the most valuable plant communities from a conservation perspective – particularly those associated with the habitats of numerous rare vascular plants, bryophytes, and other species – as well as for vegetation mapping.

The aim of the present study was to describe the community diversity of mire vegetation within the Udyl' Nature Reserve and adjacent territories, and to develop a phytosociological classification of mire community types.

MATERIAL AND METHODS

Study area

The territory of the Udyl' Nature Reserve is representative of the Lower Amur region, fully reflecting its key natural characteristics – from the monsoon climate and low-mountain and lowland topography to the characteristic mid-taiga forests and meadow-mire landscapes. The total area of the reserve is 132 700 ha, of which more than one-quarter, in the lowest-lying central part, is occupied by the shallow Lake Udyl'. The lake has average summer depths of 2–3 m (maximum 5 m), stretches 44 km from southwest to northeast, and ranges from 5 to 11 km in width.

The northern and northwestern parts of the reserve consist of a gently sloping foothill plain with low hills reaching 100–120 m in height. The highest terrain in the eastern and northeastern parts is formed by a mountain massif separating the lake basin from the Amur floodplain, with its highest point at Mt. Gidal (476 m a.s.l.). The southern end of the lake lies within the heavily waterlogged lacustrine-alluvial Udyl'–Kizin Lowland, which grades southward into the Amur floodplain. The surface of the low lake-river terrace is covered by peat mires with peat deposits 0.5 to 4 m thick (Prozorov 1974).

Lake Udyl' is connected to the Amur River via the Ukhta channel and plays an important role in regional water regulation. The flood period in the Amur basin averages 110–170 days, with 5 to 15 flood events occurring during the summer–autumn season, resulting in regular and prolonged inundation of the shoreline mires of the reserve. Water levels in the lake rise in response to flooding of the Amur, with the highest rises (up to 2 m) occurring in July–August due to monsoon rainfall, and the lowest levels recorded in late March. Major Amur floods are catastrophic events with a recurrence interval of once every 200–250 years (Danilov-Danilyan et al. 2014). The most recent event (July–September 2013) raised water levels in Lake Udyl' by 4 m, inundating the *Sphagnum* mires of the first and second river terraces.

The regional climate is a northern variant of the monsoon type, with relatively warm and humid summers and cold, low-snow winters. The mean annual air temperature is -0.8 to -1.0°C, with a frost-free period of approximately 190 days. Mean January temperatures range from -22 to -27°C (average -25.2°C), and mean July temperatures from +16 to +18°C (average +17.6°C). Mean annual precipitation is 450–480 mm (up to 656 mm), with 70–80 % falling during the warm season. These climatic conditions favour prolonged seasonal frost persistence. In peatlands, permafrost is locally present at depths of 40–50 cm below the surface.

From a geobotanical perspective, the reserve lies within the southern part of the middle taiga subzone. The greater part of the territory is occupied by the lake with its aquatic vegetation, floodplain meadows, mires, and wet larch open woodlands. The forests consist predominantly of secondary birch, and less commonly aspen, stands with scattered old larches, which developed after fires on the sites of primary larch and dark coniferous forests.

The mires occur across three poorly differentiated elevation levels, each associated with particular mire vegetation types determined by hydrological regime and water-mineral nutrition. Along the low shores of the lake and at river mouths, within the regularly flooded zone, a more or less continuous belt of shrubby tussock-sedge mires has developed. At greater distances from the lake, on the slightly elevated first terrace, dwarf shrub–*Sphagnum* mires that are subject to flooding only during the highest water events occur; these are characterised by the presence of *Myrica tomentosa*. Extensive areas on the gently sloping and flat surfaces of the second terrace are occupied by dwarf shrub-cotton grass-*Sphagnum* larch open woodland mires – mari (open larch mire woodlands) – and large ridge-hollow and lake-ridge-hollow mire systems fed predominantly by atmospheric precipitation.

Sampling and data analysis

Fieldwork was carried out from 13 to 21 August 2025, predominantly in the southern part of the Udyl' Federal Nature Reserve and in adjacent territories, where the largest mire systems are concentrated. A total of 190 complete geobotanical relevés were made, of which 177 were used for syntaxon characterisation (Fig. 1). Relevés were made in 5 × 5 m plots, with all species – vascular plants, bryophytes, and terricolous lichens – recorded and percentage cover estimated. Bryophyte specimens were collected during the fieldwork for subsequent laboratory identification. In total, 730 bryophyte specimens were collected (approximately 2 000 identifications were made). DNA sequences were obtained for eight morphologically ambiguous *Sphagnum* specimens at the Herbarium Laboratory of the Tsitsin Main Botanical Garden of the Russian Academy of Sciences (Moscow).

An Integrated Botanical Information System, IBIS 7.2 (Zverev 2007), was used for preliminary sorting of relevés and development of the vegetation classification. Species cover in the tables follows the Braun-Blanquet scale: r – solitary or very sparse individuals; + – up to 1 %; 1 – 1–5 %; 2 – 6–25 %; 3 – 26–50 %; 4 – 51–75 %; 5 – 76–100 %. Constancy is given as a percentage: r – <10 %; I – 10–20 %;

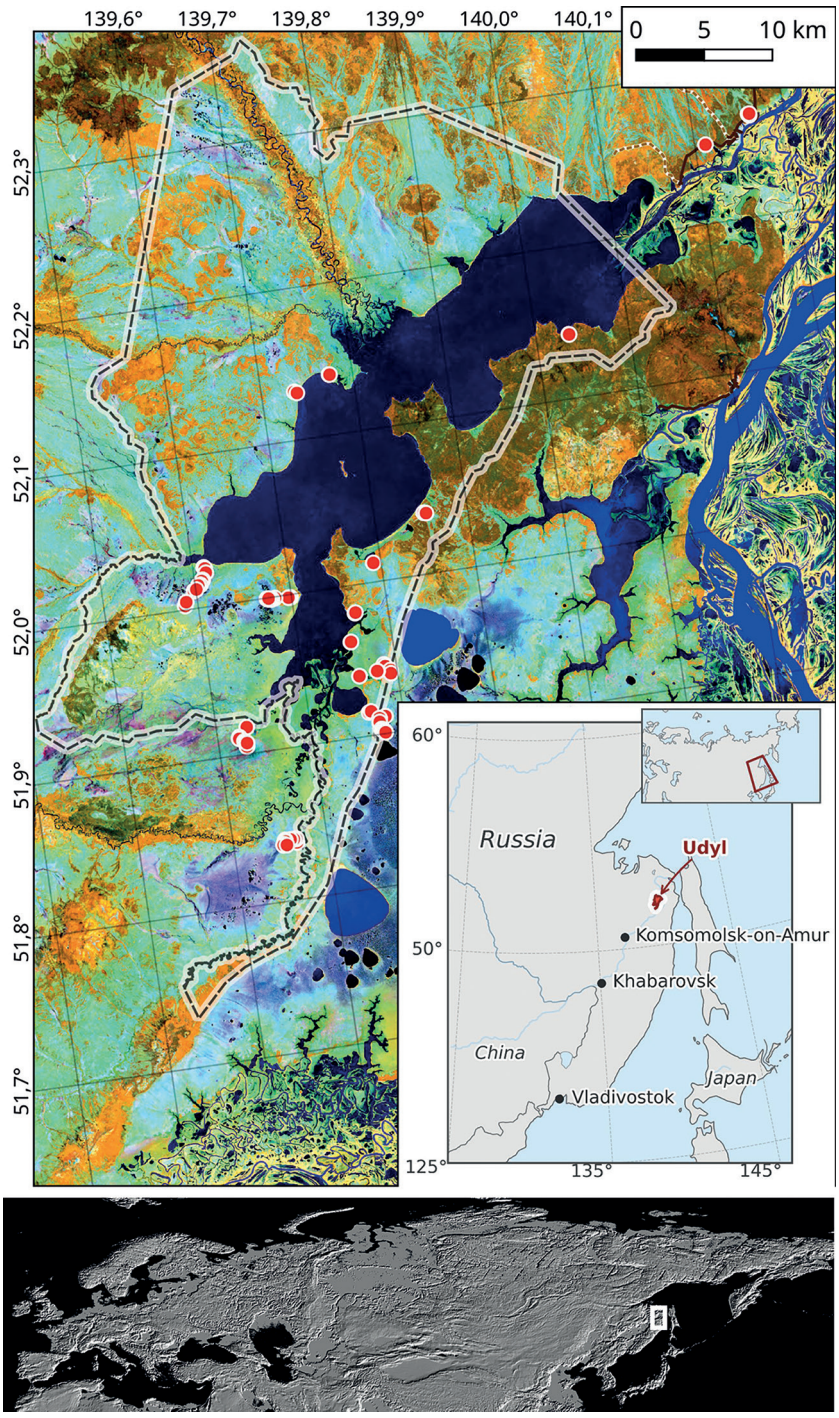

Figure 1 Study area with the location of geobotanical relevés. Dashed line – Udyl' Nature Reserve boundary. Background: Sentinel-2 false colour composite (bands 8-11-4), median composite for July–August 2021–2024; orange – deciduous forests, brown – mixed forests, dark blue – open water, light green – dwarf shrub–*Sphagnum* open larch mire woodlands (mari), pink – ridge-hollow mire complexes

II – 20–40 %; III – 41–60 %; IV – 61–80 %; V – 81–100 %. A synoptic table was compiled based on calculated constancy and median abundance values for each syntaxon.

The concept of diagnostic species was used for syntaxon delimitation, including selective and preferential species (Matveyeva 2006, Lavrinenko & Lavrinenko 2015, Lavrinenko et al. 2016). Diagnostic species represent differential species combinations characteristic of the syntaxon when occurring together, although individually each species may not be differentiating. In syntaxon names, the second element refers to the species from the highest dominant layer (ICPN, Art. 10b). Where vascular plant cover was sparse (25 % or less), the second element refers to the dominant of the moss layer, which determines the structure and physiognomy of the mire communities. The nomenclature of the described syntaxa follows the International Code of Phytosociological Nomenclature (ICPN) (Theurillat et al. 2021). The nomenclature of vascular plants follows Chepinoga et al. (2024), bryophytes – Hodgetts et al. (2020), and lichens – Santesson et al. (2004).

To visualise the floristic similarity among syntaxa, ordination was performed using Non-metric Multidimensional Scaling (NMDS) (Kruskal 1964), based on Bray-Curtis distances (Bray & Curtis 1957). The ordination was carried out on a matrix of median species abundances per syntaxon. The quality of the ordination solution was assessed using the stress value (stress = 0.09, k = 2), which indicates a good representation. The degree of similarity among syntaxa was additionally assessed by hierarchical clustering using Ward's algorithm (Ward D2) with Bray-Curtis distances. All analyses were performed in R using the vegan package (Oksanen et al. 2022).

RESULTS

The mire vegetation of the Udyl' Federal Nature Reserve is characterised by high diversity, which is associated with a relatively broad range of ecological conditions of mire habitats in terms of water-mineral supply type, moisture regime, and degree of waterlogging, as well as the presence of insular permafrost within the mires. Many mire communities of simple or mosaic structure form relatively homogeneous vegetation cover; however, mire vegetation is more commonly represented by extensive mire and mire-lake systems with a regular alternation of different plant community types.

Within the framework of the floristic-ecological classification, the communities of various mire types identified within the Udyl' Nature Reserve and adjacent areas were assigned to six alliances and four orders belonging to three classes: Carici minutae–Salicetea brachypodae cl. prov., Scheuchzerio–Caricetea nigrae Tx. 1937, and Oxycocco–Sphagnetea Br.-Bl. et Tx. ex Westhoff et

al. 1946. For two community types represented by a limited number of relevés, their assignment to higher syntaxonomic units has not yet been determined.

Prodromus

Class
Order
Alliance
Association / Community type
Subassociation
Variant

Carici minutae–Salicetea brachypodae cl. prov.
Salicetalia brachypodae ord. prov.
Carici minutae–Salicion brachypodae **all. nov.**
Sphagno obtusi–Caricetum minutae **ass. nov.**
typicum **subass. nov.**
inops **subass. nov.**

Scheuchzerio–Caricetea nigrae Tx. 1937
Caricetalia nigrae Koch 1926
Sphagno–Caricion canescentis Passarge (1964) 1978
Com. type *Equisetum fluviatile–Sphagnum obtusum*
Stygio–Caricion limosae Nordhagen 1943
Sphagno obtusi–Caricetum meyerianae **ass. nov.**
Com. *Utricularia intermedia–Carex meyeriana*
Scheuchzerietalia palustris Nordhagen ex Tx. 1937
Scheuchzerion palustris Nordhagen ex Tx. 1937
Sphagnetum perfoliati-majoris **ass. nov.**
Carici limosae–Sphagnetum majoris Bogdanowsaya-Guiheneuf 1928
Utricularia intermedia
Irido laevigatae–Sphagnetum papillosi **ass. nov.**
typica
Sphagnum balticum
Sphagnum majus

Oxycocco–Sphagnetea Br.-Bl. et Tx. ex Westhoff et al. 1946
Sphagnetalia medii Kästner et Flössner 1933
Sphagnion alaskense **all. nov.**
Sphagno papillosi–Caricetum middendorfii **ass. nov.**
Carici lasiocarpae–Sphagnetum alaskense **ass. nov.**
Chamaedaphno–Sphagnetum alaskense **ass. nov.**
typica
Myrica tomentosa
Oxycocco–Empetrion hermaphroditi Nordhagen ex Du Rietz 1954
Larici cajanderi–Sphagnetum fusci **ass. nov.**
typica
Sphagnum alaskense
Com. *Larix cajanderi–Sphagnum angustifolium*
Sphagnion lenenses Lapshina et al. 2023
Carici middendorfii–Sphagnetum lenenses **ass. nov.**
typica
Sphagnum fuscum
?
?
Com. *Larix cajanderi – Sphagnum girgensohnii* s.l.
Com. *Larix cajanderi–Polytrichum commune*

The original relevés are presented in diagnostic tables (Tables 1–5) and summarized in a synoptic table (Table 6). The physiognomy of most described communities is illustrated by photographs (Figs 2–3). To visualize the results of the classification, ordination of all syntaxa was performed using NMDS (Fig. 4), which separates and displays clusters on a two-dimensional plane as point aggregations. Hierarchical clustering was performed to assess the degree of similarity among the syntaxa (Fig. 5). Descriptions of the distinguished syntaxa are provided below.

Vegetation of minerotrophic mires regularly flooded by river and lake waters

In the zone of regular flooding along the shores of Lake Udyl', reedgrass-tussock sedge communities with a more or less developed shrub layer (*Salix brachypoda*, *Spiraea salicifolia*, *Betula ovalifolia*) are widespread. We treat these shrub–tussock sedge communities within a distinct new class replacing the European-West Siberian class Frangulatea in the southern Russian Far East. Within the Udyl' Nature Reserve, these communities are represented by one association with two subassociations.

Sphagno obtusi–Caricetum minutae ass. nov.

(Table 1, rel. 1–17; Table 6, syntaxon 1; Fig. 2A, Fig. 4, Fig. 5, clusters 1.1, 1.2)

Holotypus: relevé 4 (author's number – 140E25ud) in Table 1, Khabarovsk krai, Ul'chskii District, Udyl' nature reserve, 13.08.2025, author E.D. Lapshina.

The association comprises shrub-tussock sedge–*Sphagnum* communities of minerotrophic (eutrophic) groundwater-fed mires in the Amur River basin that are regularly inundated by river and lake waters.

Diagnostic species: *Betula ovalifolia*, *Carex mituta* (dom.), *Salix brachypoda*, *Spiraea salicifolia*, *Sphagnum obtusum*, *S. orientale*, *Warnstorfia pseudostraminea*.

Structure and composition. Shrub cover ranges from 20 to 60 %, more rarely reaching 80 % or being absent altogether. The main lower shrub sublayer, 60–80 cm in height, is formed in varying proportions by *Spiraea salicifolia* and *Salix brachypoda*, above which a taller upper sublayer (5–30 %) is often developed, consisting of *Betula ovalifolia* shrubs 1.5–2.5 m tall. *Salix myrtilloides* is also frequently present at low abundance. In the dense herb layer (cover 50–80 %), *Carex minuta* and *Calamagrostis langsdorffii* dominate, sometimes accompanied by *Glyceria spiculosa* and *Sanguisorba parviflora*. *Comarum palustre* occurs between the tussocks, occasionally reaching 20 % cover but usually comprising 3–5 %. *Galium trifidum*, *Lysimachia thyrsiflora*, and *Scutellaria regeliana* occur at low abundance. The moss layer is generally well developed (15–70 %, usually 30–50 %) and is composed mainly of *Sphagnum obtusum* with the participation of *S. orientale* and *S. squarrosum*. *Climacium dendroides*, *Sphagnum fimbriatum*, *Polytrichum swartzii*, and *Warnstorfia pseudostraminea* are constantly present at low abundance. The rare peat moss species *Sphagnum mirum* was recorded exclusively in these communities and only on two occasions.

Distribution and ecology. Shrub-reedgrass-tussock sedge mires are widespread along the low shores surrounding Udyl' Lake and in the lower reaches of rivers flowing into the lake. Floodwaters play the principal role in the hydrological regime of these mire types, regularly inundating them during summer–autumn floods. The duration of flooding varies widely depending on the topographic position of a particular site and the duration of the flood period. As a result, the communities develop a strongly tussock microrelief formed by large, dense *Carex minuta* tussocks reaching 20–40 cm in height and 20–25 cm in diameter.

The peat thickness of the lakeshore reedgrass-tussock sedge and shrub-reedgrass-tussock sedge mires varies from 30 to 150 cm, usually being about 50 cm.

Sphagno obtusi–Caricetum minutae typicum subass. nov.

(Table 1, rel. 1–10; Fig. 2A, Fig. 5, cluster 1.1)

Holotypus: relevé 4 (author's number – 140E25ud) in Table 1, Khabarovsk krai, Ul'chskii District, Udyl' Nature Reserve, 13.08.2025, author E.D. Lapshina.

Table 1. Eutrophic and mesotriphic willow and birch shrubs reed grass-tussock sedge communities. Association Sphagno obtusi–Caricetum minutae (1): 1–10 – subass. typicum (1.1), 11–17 – subass. inops. (1.2). 18–19 – Community type *Equisetum flufiatile–Sphagnum obtusum* (2).

Subassociation	**typicum (1.1)**										**inops (1.2)**							**2**		**Constancy and abundance**		
Cover (%): shrubs	80	20	40	80	30	40	20	35	50	60	0	0	15	1	0	5	0	0	0			
dwarf shrubs	3	0	0	1	0	0	0	0	0	0	0	0	5	0	0	15	0	0	0			
herbs	60	70	70	40	70	50	80	55	80	80	60	50	50	80	50	60	80	60	40			
mosses	50	70	25	50	15	30	50	50	20	35	100	90	30	50	70	50	90	100	100			
Number of species	21	17	12	18	12	15	16	19	11	16	13	11	15	13	8	17	9	15	16			
Relevé nr. by author	139E25ud	114F25ud	141E25ud	140E25ud	149F25ud	113F25ud	176E25ud	112F25ud	142E25ud	175E25ud	193E25ud	164F25ud	165F25ud	150F25ud	163F25ud	194E25ud	192E25ud	170E25ud	144F25ud			
Relevé nr. in the table	**1**	**2**	**3**	**4***	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15***	**16**	**17**	**18**	**19**	**1.1.**	**1.2.**	**1**
Diagnostic species of the ass. Sphagno obtusi–Caricetum minutae																						
Carex minuta ***C-S***	2	1	3	2	3	1	3	1	3	2	3	2	2	3	2	2	3	.	.	V	V	V
Sphagnum obtusum	2	4	2	3	2	2	3	3	2	3	5	5	2	3	1	3	2	5	5	V	V	V
Sphagnum orientale ***C-S***	1	+	1	1	.	+	1	+	2	1	1	2	.	+	4	1	5	.	.	V	V	V
Glyceria spiculosa ***C-S***	+	2	.	1	1	2	1	2	.	+	+	+	1	1	.	+	.	.	.	V	IV	IV
Warnstorfia pseudostraminea ***C-S***	1	r	+	+	.	+	+	+	+	+	.	r	.	.	+	.	+	.	.	V	III	IV
Salix brachypoda ***C-S***	3	+	2	3	2	2	2	2	1	2	.	.	.	.	.	+	.	.	.	V	I	III
Spiraea salicifolia ***C-S***	2	2	2	3	+	2	1	2	3	2	.	.	.	+	.	.	.	.	.	V	I	III
Climacium dendroides	1	+	+	+	1	+	.	+	+	+	.	.	.	.	.	.	.	.	.	V	.	III
Sphagnum squarrosum	1	.	.	2	.	1	.	2	.	+	.	.	.	.	.	.	.	.	.	II	.	II
Diagnostic species of the com. type *Equisetum flufiatile–Sphagnum obtusum*																						
Equisetum flufiatile	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.
Carex lasiocarpa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.
Carex limosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.
Menyanthes trifoliata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.
Oxycoccus palustris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.
Pediculari sadamsi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Lobelia sessilifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.
Diagnostic species of the Carici minutae–Salicion brachypodae																						
Betula ovalifolia	2	+	.	2	2	+	+	1	.	2	.	.	2	+	.	1	.	.	.	IV	III	IV
Galium trifidum	+	+	.	+	.	.	1	+	.	+	.	.	.	+	.	.	.	.	.	III	III	III
Polytrichum swartzii	+	.	.	.	.	.	+	.	.	.	+	+	.	.	+	.	+	.	.	I	III	II
Scutellaria regeliana	.	+	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	II	.	II
Diagnostic species of the Calamagrostietea langsdorffii																						
Calamagrostis langsdorffii	3	3	2	2	2	2	2	2	2	3	3	2	3	3	2	3	3	.	.	V	V	I
Sanguisorba parviflora	.	r	.	.	+	.	+	.	.	.	.	+	+	+	.	+	.	.	.	II	IV	III
Carex pseudocuraica	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	I	I	I
Gentiana triflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	II	I
Other species																						
Comarum palustre	2	1	1	1	+	1	2	1	2	1	+	.	+	2	.	+	.	.	.	V	III	V
Lysimachia thyrsiflora	.	+	+	.	.	+	+	.	1	.	2	2	.	+	1	.	2	+	+	III	IV	III
Salix myrtilloides	.	r	.	+	r	.	1	+	+	.	r	.	1	+	.	+	.	.	.	III	III	III
Sphagnum fimbriatum	1	.	.	+	.	.	.	+	.	.	.	.	+	.	.	+	.	.	.	II	II	II
Chamaedaphne calyculata	1	.	+	1	.	.	.	.	.	.	.	.	+	.	.	1	.	.	.	II	II	II
Myrica tomentosa	.	r	.	.	r	.	.	.	.	r	.	.	+	+	.	.	.	.	.	II	II	II
Anemonidium dichotomum	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	I	.	I
Carex chordorrhiza	.	.	.	r	.	.	.	.	.	.	1	.	.	.	.	+	.	r	+	I	II	I
Eriophorum russeolum	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.	+	.	.	.	III	I
Sphagnum alaskense	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	+	.	.	II	I
Polytrichum jensenii	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	r	.	.	II	I
Straminergon stramineum	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	.	.	.	.	I	I	I
Sphagnum mirum	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	I	.	I
Sphagnum imbricatum	+	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	I	I	+

Note. Species found in 1 relevé: *Andromeda polifolia* (13 r), *Aulacomnium palustre* (16 +), *Betula platyphylla* juv. (1 r), *Calamagrostis neglecta* (19 +), *Calliergon cordifolium* (1 1), *Caltha membranacea* (18 r), *Drepanocladus aduncus* (8 r), *Eriophorum gracile* (19 +), *Galium davuricum* (3 +), *Iris laevigata* (13 +), *Lathyrus pilosus* (1 +), *Parnassia palustris* (19 r), *Sphagnum warnstorfii* (16 r), *Warnstorfia fluitans* (18 r).

GPS coordinates (WGS 84) (N, E) and dates: **1** – 51.93996, 139.75951, 13.08.2025; **2** –51.96298, 139.75590, 13.08.2025; **3** – 51.96296, 139.75552, 13.08.2025; **4** –51.93996, 139.75925, 13.08.2025; **5** – 51.98153, 139.76445, 16.08.2025; **6** – 51.93995, 139.75949, 13.08.2025; **7** – 51.98186, 139.76515, 16.08.2025; **8** – 51.93995, 139.75949, 13.08.2025; **9** – 51.96314, 139.75581, 13.08.2025; **10** – 51.98150, 139.76442, 16.08.2025; **11** – 52.02596, 139.61205, 18.08.2025; **12** – 52.02615, 139.61241, 18.08.2025; **13** – 52.02525, 139.61299, 18.08.2025; **14** – 51.98195, 139.76517, 16.08.2025; **15** – 52.02625, 139.61201, 18.08.2025; **16** – 52.02530, 139.61281, 18.08.2002; **17** – 52.02607, 139.61171, 18.08.2025; **18** – 52.14234, 140.03548, 16.08.2025; **19** – 52.14247, 140.03552, 16.08.

Authors. E.D. Lapshina (**E** – in the author's relevé nr.), I.V. Filippov (**F**).

Diagnostic species (next to the name of the taxon): ***C-S*** – Carici minutae–Salicion brachypodae.

* – nomenclatural types (holotypes).

Diagnostic species, structure and composition, distribution and ecology are the same as in the association.

Sphagno obtusi–Caricetum minutae inops subass. nov.

(Table 1, rel. 11–17; Fig. 5, cluster 1.2)

Holotypus: relevé 15 (author's number – 163F25ud) in Table 1, Khabarovsk krai, Ul'chskii District, Udyl' Nature Reserve, 18.08.2025, author I.V. Filippov.

Diagnostic species: *Carex mituta*, *Sphagnum obtusum*, *S. orientale*, *Warnstorfia pseudostraminea.*

Structure and composition. The communities of the subassociation are characterized by a poorer species composition. The shrub layer is less developed than in the typical communities or may be absent altogether. The more mineral-demanding species *Spiraea salicifolia* and *Salix brachypoda* almost completely disappear from the shrub layer.

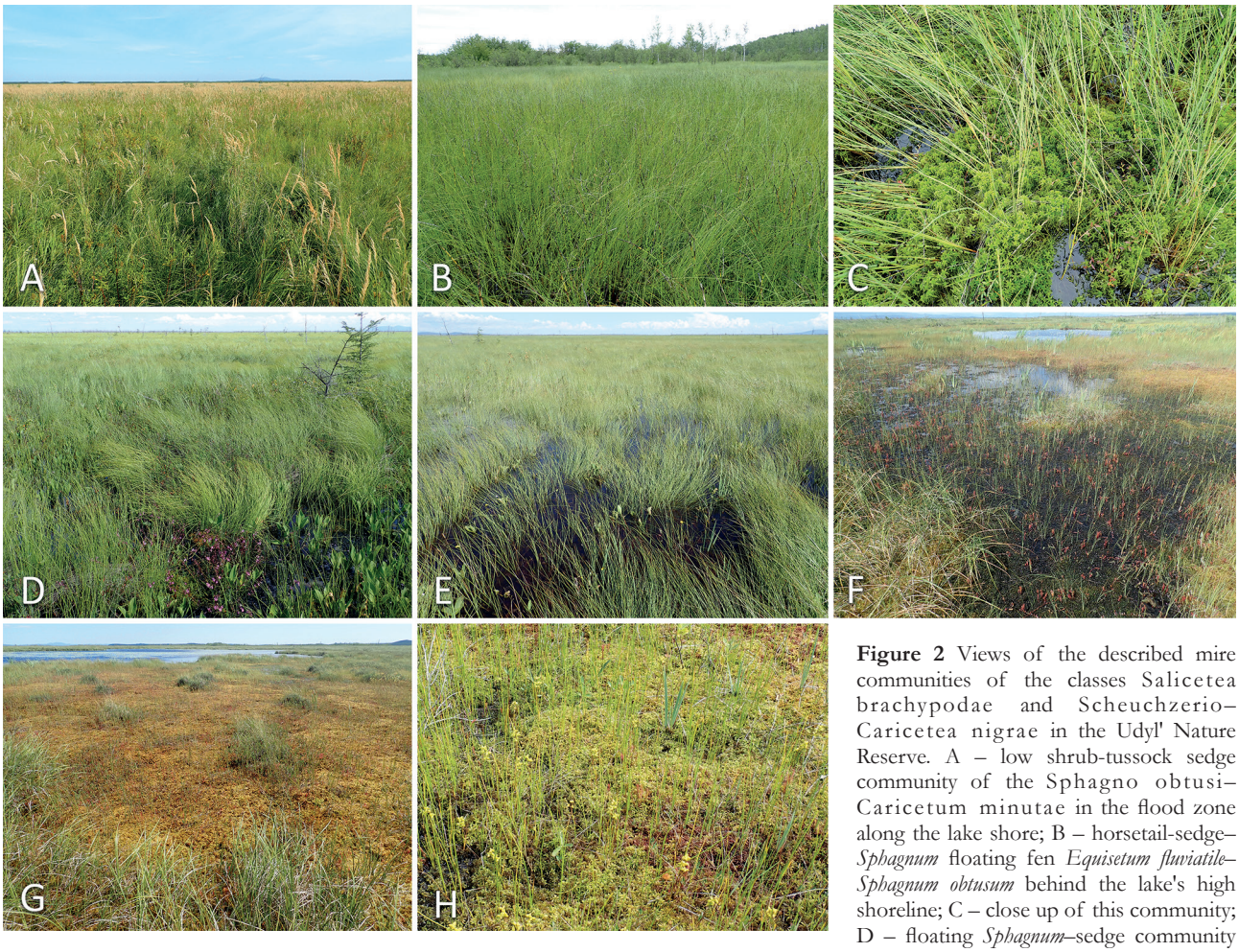

Figure 2 Views of the described mire communities of the classes Salicetea brachypodae and Scheuchzerio–Caricetea nigrae in the Udyl' Nature Reserve. A – low shrub-tussock sedge community of the Sphagno obtusi–Caricetum minutae in the flood zone along the lake shore; B – horsetail-sedge–*Sphagnum* floating fen *Equisetum fluviatile–Sphagnum obtusum* behind the lake's high shoreline; C – close up of this community; D – floating *Sphagnum*–sedge community of the Sphagno obtusi–Caricetum meyerianae in hollow of aapa-like mire complex; E – community type *Utricularia intermedia–Carex meyeriana* in waterlogged hollow of aapa-like mire complex; F – *Sphagnum* carpet of the Sphagnetum perfoliati-majoris in central part of hollow within the lake-ridge-hollow mire complex, periodically flooded by lake water during the monsoon rains; G – slightly raised flat *Sphagnum* lawn of the Irido laevigatae–Sphagnetum papillosi var. typica in the lake-ridge-hollow mire complex; H – close up of this community

In the herb layer, *Calamagrostis langsdorffii* predominates, while the abundance of *Lysimachia thyrsiflora* increases.

Distribution and ecology. The communities of the subassociation are usually confined to isolated depressions between sandy ridges within restricted areas of the floodplain terrace and do not occupy large areas. They represent a later developmental stage of floodplain mires and replace the communities of the typical subassociation as peat accumulates and mineral nutrient conditions become progressively poorer.

The class Scheuchzerio–Caricetea nigrae encompasses the full diversity of sedge-moss vegetation of fens and transitional mires, both rich and poor in mineral nutrients, as well as waterlogged habitats (flarks and hollows) of ombrotrophic bogs.

Within the Udyl' Nature Reserve, 5 associations with variants and 2 community types belonging to 3 alliances were identified: Sphagno–Caricion canescentis, Stygio–Caricion limosae, and Scheuchzerion palustris.

Vegetation of mesotrophic quaking mires with mixed water supply

Floating mat mires (quaking mires) were studied along the eastern shore of Udyl' Lake, where they develop in lagoons separated from the lake by high beach ridges. Due to the presence of water layer within the peat deposit, the surface of these mires is not flooded, only the floating peat surface fluctuates, while the water table throughout the growing season remains stable at a depth of 10–15 cm below the moss surface.

Communities recorded in one of these mires were assigned, within the Braun-Blanquet floristic-ecological classification framework, to the alliance Sphagno–Caricion canescentis Passarge (1964) 1978 of the order Caricetalia nigrae Koch 1926.

Community type *Equisetum fluviatile–Sphagnum obtusum* (Table 1, rel. 18–20; Fig 2B, Fig. 4, 5, cluster 2)

This community type includes horsetail–*Sphagnum* and *Menyanthes*–horsetail–*Sphagnum* phytocoenoses developing in floating mat mires with water layers within the peat deposit.

The herb layer is two-tiered. The upper sublayer (10–20 %), 40–60 cm tall, is formed by *Equisetum fluviatile* with minor admixture of *Carex lasiocarpa*, *C. rostrata*, and *Calamagrostis neglecta*, whereas the lower sublayer is characterized primarily by *Menyanthes trifoliata* (1–10 %) and *Carex limosa* (3–10 %). *Carex chordorrhiza*, *Galium trifidum*, *Eriophorum gracile*, *Lobelia sessilifolia*, *Lysimachia thyrsiflora*, *Parnassia palustris*, and *Pedicularis adunca* occur at low abundance. The moss layer forms a

continuous carpet dominated by *Sphagnum obtusum*. *Oxycoccus palustris* locally grows abundantly across the moss surface, its cover occasionally reaching 30–60 %.

Vegetation of meso-oligotrophic flarks and hollows of aapa mires

Aapa mires (string-flark fens) represent a rare mire type within the Udyl' Nature Reserve. The vegetation of meso-oligotrophic flarks and hollows of aapa mires is represented by one association and one community type.

Sphagno obtusi–Caricetum meyerianae ass. nov. (Table 2, rel. 1–5; Table 6, syntaxon 3; Fig. 2C, Fig. 4, 5, cluster 3)

Holotypus: relevé 2 (author's number – 136F25ud) in Table 2, Khabarovsk krai, Ul'chskii District, Udyl' Nature Reserve, 15.08.2025, author I.V. Filippov.

Diagnostic species: *Carex meyeriana*, *Sphagnum obtusum*.

Structure and composition. The shrub layer is absent, only scattered dwarf shrubs of *Andromeda polifolia*, *Chamaedaphne calyculata*, and *Salix myrtilloides*, 5–20 cm tall, occur sparsely. In the herb layer (30–50 %), *Carex meyeriana* and *Menyanthes trifoliata* predominate. *Utricularia intermedia* spreads across the surface of the water-saturated peat (fluid) peat between the sedge tussocks (5–10 %, locally reaching 40 % in patches). *Carex lasiocarpa*, *C. limosa*, *Juncus stygius*, *Iris laevigata*, *Scheuchzeria palustris*, and *Utricularia minor* occur at low abundance but with high constancy, more rarely encountered are *Equisetum fluviatile*, *Eriophorum gracile*, *E. russeolum*, *Lobelia sessilifolia*, and *Pedicularis adunca*. The loose moss carpet (cover 30–70 %) is formed by *Sphagnum obtusum* and *S. orientale* in varying proportions.

Distribution and ecology. *Menyanthes*–sedge (*Carex meyeriana*)–*Sphagnum* communities occupy extensive waterlogged flarks 10–20 m in diameter within meso-oligotrophic aapa-like string-flark complexe. The flark surface is finely hummocky, formed by sedge tussocks semi-submerged in fluid peat. Only the tops of the tussocks rise 3–5 cm above the water surface.

Community type *Utricularia intermedia–Carex meyeriana* (Table 2, rel. 6–9), Table 6, syntaxon 4; Fig. 2D, Fig. 4, 5, cluster 4)

Carex meyeriana communities were recorded in the most waterlogged flarks of the same mire system as the previous association. In these flarks, the water level remains 10–20 cm above the surface throughout the growing season. Only the tops of the sedge tussocks rise above the water surface, while the cover of *Carex meyeriana* reaches 30–40 %. *Utricularia intermedia* and *U. minor* spread across the surface of the fluid peat, whereas only sparse shoots of *Carex limosa*, *Juncus stygius*, *Rhynchospora alba*, and *Scheuchzeria palustris* emerge above the water surface. The moss layer is absent.

All communities with the participation of *Carex meyeriana* in the Udyl' Nature Reserve were recorded and described exclusively within a single extensive mire system in the upper reaches of the Bol'shoy Daikon River. This mire system is situated on the gently sloping surface of the first terrace above the floodplain and developed under the influence of continuous surface runoff and discharge of comparatively mineral-poor groundwater.

Vegetation of waterlogged hollows of meso-oligotrophic and oligotrophic bog complexes

The vegetation of waterlogged oligotrophic *Sphagnum* hollows is represented by communities of the alliance Scheuchzerion palustris, within which three associations were described in the Udyl' Nature Reserve.

Sphagno perfoliati-majoris ass. nov. (Table 2, rel. 10–26; Table 6, syntaxon 5; Fig. 2E, Fig. 4, 5, cluster 5)

The association comprises strongly waterlogged meso-oligotrophic *Sphagnum* communities of the central parts of hollows affected by flooding from intramire pools within ridge-pool-hollow mire complexes under the monsoonal climate of the southern taiga and southern part of middle taiga zone of the Lower Amur region.

Holotypus: relevé 18 (author's number – 186E25ud) in Table 2, Khabarovsk krai, Ul'chskii District, Udyl' Nature Reserve, 17.08.2001, author E.D. Lapshina.

Diagnostic species: *Drosera anglica*, *Sphagnum majus*, *S. perfoliatum*, *S. papillosum*.

Structure and composition. Shrubs and dwarf shrubs are absent or represented only by scattered individuals of *Andromeda polifolia* and *Myrica tomentosa*, 15–20(30) cm tall. In the herb layer (total cover 10–25 %), *Carex limosa* and *Rhynchospora alba* occur at low abundance but with high constancy, while *Drosera anglica* is abundant in the lower sublayer. The continuous moss carpet is formed by *Sphagnum majus* and *S. perfoliatum* in varying proportions, accompanied at low abundance by *S. papillosum* and, more rarely, by *Sphagnum balticum* and *S. lindbergii*. *Utricularia intermedia* and *U. minor* occur occur with high constancy between *Sphagnum capitula*.

Distribution and ecology. The communities occupy the central, most waterlogged parts of extensive hollows and floating mats periodically flooded from adjacent intramire pools during periods of monsoonal rainfall. Throughout the growing season, the water table remains at the level of the *Sphagnum* capitula. Communities of the association occur in various ridge-hollow and ridge-pool-hollow mire systems in the southern and southeastern parts of the reserve.

Carici limosae–Sphagnetum majoris Bogdanowsaya-Guiheneuf 1928

The association comprises sedge–*Sphagnum* communities with a sparse, low-productive graminoid layer and dominance of *Sphagnum majus* in the continuous moss carpet.

The association is widespread in the mires of European Russia and Western Siberia, where it has usually been described under the name Caricetum limosae subass. sphagnetosum majoris Boch et Smagin 1993 [Art. 2b, 5] (Vegetation … 2025), from which the association in its typical form was originally described.

Lectotypus: relevé 4, Bogdanowsaya-Guiheneuf 1928: 310; Kaliningrad Province, Shuvalov peat mire; author: I.D. Bogdanowsaya-Guiheneuf. The community type includes *Carex limosa* (6 %), *Scheuchzeria palustris* (4 %), and *Sphagnum majus* (*S. dusenii*) with 100 % cover (Bogdanowsaya-Guiheneuf 1928).

In the Lower Amur mires, the association is represented by a distinct variant characterized by the minor admixture of regional species such as *Iris laevigata* and *Pedicularis adunca*, as well as by the sporadic occurrence of *Drosera anglica* and *Utricularia intermedia*, which are absent from the typical communities.

Variant Utricularia intermedia (Table 2, rel. 27–33; Table 6, syntaxon 6; Fig. 4, 5, cluster 6)

Diagnostic species: *Carex limosa*, *Sphagnum majus* (dom.).

Structure and composition. The sparse herb layer (5–15 %, rarely up to 30 %), 15–20 cm tall, is formed by *Carex limosa*. *Carex rotundata*, *Eriophorum russeolum*, *Rhynchospora*

Table 2. Communities of the alliances Stygio–Caricion limosae and Scheuchzerion palustris. 1–5 – Association Sphagno obtusi–Caricetum meyerianae (1), 6–9 – community type *Utricularia intermedia–Carex meyeriana* (2). Associations: 10–26 – Sphagno perfoliati-majoris (3), 27–33 – Carici limosae–Sphagnetum majoris (4).

Assotiation / com. type	1					2				Sphagno perfoliati-majoris (3)																	Carici limosae–Sphagnetum majoris (4)							Constancy and abundance			
Cover (%):dwarf shrubs	20	0	5	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0				
herbs	40	30	35	60	40	40	45	50	35	20	5	5	20	25	5	10	10	30	10	15	20	15	15	10	10	10	15	10	45	10	7	5	15			
mosses	70	30	30	65	30	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	90	100	100	100	100	100	100	100	100	100			
Number of species	17	11	16	18	10	15	9	11	11	8	10	14	10	10	9	10	11	11	7	11	8	9	10	13	11	10	7	7	9	7	7	5	5			
Relevé nr. by author	162E25ud	136F25ud	134F25ud	164E25ud	140F25ud	168E25ud	142F25ud	167E25ud	141F25ud	160F25ud	157E25ud	150E25ud	162F25ud	119F25ud	129F25ud	148E25ud	214E25ud	186E25ud	121F25ud	190E25ud	185F25ud	131F25ud	186F25ud	216E25ud	215E25ud	217E25ud	167F25ud	210E25ud	133E25ud	204E25ud	170F25ud	180F25ud	106F25ud			
Relevé nr. in the table	**1**	**2***	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18***	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**1**	**2**	**3**	**4**
Diagnostic species of the ass. Sphagno obtusi–Caricetum meyerianae																																				
Carex meyeriana	3	2	2	3	1	3	2	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	4	.	.
Sphagnum obtusum	3	2	2	3	3	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	V	1	.	+
Sphagnum orientale	3	2	2	2	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	.	+	.
Carex lasiocarpa	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV	.	.	.
Diagnostic species of the ass. Sphagno perfoliati-majoris																																				
Sphagnum majus	.	.	.	.	.	.	.	.	.	**3**	**4**	**5**	**5**	**3**	**3**	**2**	**3**	**5**	**3**	**5**	**5**	**2**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	.	.	V	V
Drosera anglica	.	.	.	.	.	.	.	.	.	1	1	1	1	+	+	+	1	2	+	1	+	1	+	1	1	1	1	1	.	+	+	+	.	.	.	V	IV
Sphagnum perfoliatum	.	.	.	.	.	.	.	.	.	3	2	1	1	1	3	4	5	4	1	3	2	1	4	3	2	1	.	.	.	.	.	.	.	.	.	V	.
Sphagnum papillosum	.	.	.	.	.	.	.	.	.	1	1	2	+	+	+	2	+	2	.	1	.	1	.	1	1	+	.	+	.	.	.	.	.	.	.	V	I
Diagnostic species of the Stygio–Caricion limosae																																				
Utricularia intermedia	2	1	2	2	2	2	3	3	2	+	+	+	2	r	+	.	r	+	1	3	2	1	1	1	+	+	+	+	.	.	+	.	.	V	4	V	III
Utricularia minor	+	+	+	+	.	+	.	+	.	.	.	.	.	r	.	.	+	.	.	.	1	.	+	+	+	.	.	.	.	.	.	.	.	.	IV	2	II	.
Juncus stygius	+	+	r	.	.	+	+	+	r	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	III	4	II	.
Diagnostic species of the Scheuchzerion palustris and Scheuchzerietalia palustris																																				
Carex limosa ***St-C***	+	+	+	1	1	+	+	1	+	.	1	1	.	2	+	2	.	1	1	.	+	+	1	1	+	+	2	1	2	2	1	1	1	V	4	IV	V
Scheuchzeria palustris ***St-C***	+	+	.	+	+	+	+	.	+	.	.	.	+	.	.	+	.	2	.	1	+	.	.	+	.	1	.	.	.	.	.	.	.	IV	3	III	.
Rhynchospora alba ***St-C***	.	.	.	.	.	+	1	.	+	+	1	+	+	.	+	1	1	2	.	1	.	1	+	+	2	+	.	+	.	r	.	+	.	.	3	V	III
Sphagnum balticum	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	+	.	+	.	+	.	.	r	.	2	+	.	1	.	1	.	.	.	III	III
Sphagnum lindbergii	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	.	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	II	.
Eriophorum russeolum	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	1	.	.	.	III
Diagnostic species of the Scheuchzerio–Caricetea nigrae																																				
Menyanthes trifoliata	2	2	1	2	2	2	+	2	1	2	.	+	1	2	+	.	.	1	.	.	1	.	1	1	1	1	.	.	.	.	.	.	.	V	4	IV	.
Andromeda polifolia	2	.	1	2	.	+	.	+	.	.	.	r	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	III	2	II	.
Eriophorum gracile	+	.	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III	2	.	.
Oxycoccus palustris	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	.	.	.	.	+	+	+	.	.	+	+	.	.	.	.	.	II	II
Carex chordorrhiza	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.
Other species																																				
Equisetum fluviatile	+	.	r	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III	3	.	.
Salix myrtilloides	1	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III	1	.	.
Iris laevigata	.	+	+	.	.	+	+	+	+	.	.	r	.	+	.	r	.	.	+	.	.	+	.	r	.	.	.	.	.	+	.	r	.	+	II	4	II	II
Pedicularis adunca	.	.	.	+	+	.	.	.	.	+	.	+	+	.	.	.	.	.	.	+	.	.	.	r	.	+	.	.	.	.	+	.	.	II	.	II	II
Glyceria spiculosa	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	I	2	.	I
Drosera rotundifolia	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	II	.	.	I
Lobelia sessilifolia	.	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
Hamatocaulis vernicosus	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.
Sphagnum compactum	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.
Cladopodiella fluitans	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.
Myrica tomentosa	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.
Chamaedaphne calyculata	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	I	.	.	I
Carex rotundata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	II

Note. Species found in 1 relevé: *Warnstorfia fluitans* (1 +)

GPS coordinates (WGS 84) (N, E) and dates: **1** – 51.91100, 139.62248, 15.08.2025; **2** – 51.91073, 139.62264, 15.08.2025; **3** – 51.91160, 139.62256, 15.08.2025; **4** – 51.90865, 139.62775, 15.08.2025; **5** – 51.90742, 139.62927, 15.08.2025; **6** – 51.90489, 139.62958, 15.08.2025; **7** – 51.90431, 139.63043, 15.08.2025; **8** – 51.90515, 139.62973, 15.08.2025; **9** – 51.90431, 139.63043, 15.08.2025; **10** – 51.90152, 139.77740, 17.08.2025; **11** – 51.83697, 139.65291, 14.08.2025; **12** – 51.84002, 139.66112, 14.08.2025; **13** – 51.90067, 139.77856, 17.08.2001; **14** – 51.83996, 139.66734, 14.08.2025; **15** – 51.83729, 139.65316, 14.08.2025; **16** – 51.83991, 139.66446, 14.08.2025; **17** – 5.99885, 139.67616, 19.08.2025; **18** – 51.90240, 139.77576, 17.08.2001; **19** – 51.83989, 139.66387, 14.08.2025; **20** – 51.90075, 139.78067, 17.08.2025; **21** – 51.99876, 139.67364, 19.08.2025; **22** – 51.83713, 139.65373, 14.08.2025; **23** – 51.99876, 139.67364, 19.08.2025; **24** – 51.99929, 139.67439, 19.08.2025; **25** – 51.99828, 139.67403, 19.08.2025; **26** – 51.99957, 139.67398, 19.08.2025; **27** – 52.01813, 139.60857, 18.08.2025; **28** – 51.99875, 139.67900, 19.08.2025; **29** – 51.94401, 139.78816; 13.08.2025; **30** – 52.01233, 139.60062, 18.08.2025; **31** – 52.01719, 139.60744, 18.08.2025; **32** – 51.99878, 139.67856, 19.08.2025; **33** – 51.94426, 139.78843, 13.08.2025.

Authors. E.D. Lapshina (**E** – in the author's relevé nr.), I.V. Filippov (**F**).

Diagnostic species (next to the name of the taxon): ***St-C*** – all. Stygio–Caricion limosae.

* – nomenclatural types (holotypes).

alba, and *Scheuchzeria palustris* occur at low abundance, while *Drosera anglica*, *Oxycoccus palustris*, and *Utricularia intermedia* are present in the lower sublayer. *Sphagnum majus* dominates the continuous moss carpet, sometimes with minor admixture of *S. balticum* and *S. papillosum*.

Distribution and ecology. Communities of the association develop in strongly waterlogged hollows of patterned ombrotrophic mires in the boreal and hemiboreal zones of Eurasia. The water table is situated at the moss surface or 1–2 cm below it. Within the mires of the Udyl' Nature Reserve, these communities occupy the central, most waterlogged parts of extensive hollows and floating mats that are not influenced by flooding from adjacent intramire pools during periods of snowmelt and monsoonal rainfall.

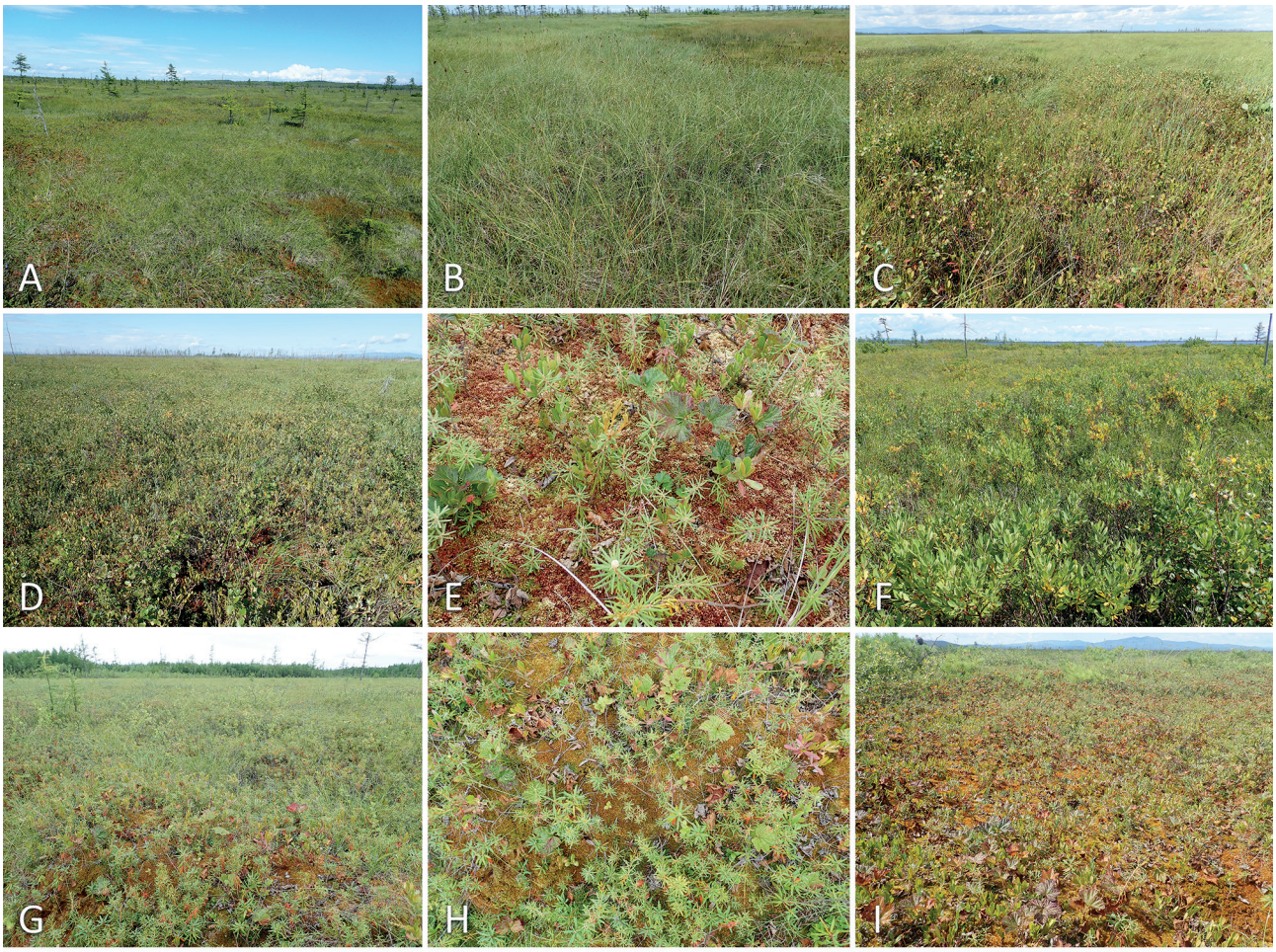

Figure 3 Views of the described mire communities of the class Oxycocco–Sphagnetea in the Udyl' Nature Reserve. A – tall sedge–*Sphagnum* community of the Sphagno papillosi–Caricetum middendorfii occupy an intermediate position between high ridges and waterlogged hollows in the ridge-hollow raised bog complex; B – close up of this community; C – dwarf shrub–sedge–*Sphagnum* community of the Carici lasiocarpae–Sphagnetum alaskense on a soft loose *Sphagnum* ridge 20–30 cm high in the ridge-hollow mire complex; D – dwarf shrub–*Sphagnum* community of the Chamaedaphno–Sphagnetum alaskense var. typica widespread on the low lake's terrace; E – close up of this community; F – *Myrica*–dwarf shrub–*Sphagnum* community of the Chamaedaphno–Sphagnetum alaskense var. Myrica tomentosa regularly flooded by lake water during the monsoon rains; G – general view of the Larici cajanderi–Sphagnetum fusci with a destroyed larch layer due to a fire; H – close up of this community; I – dwarf shrub–cloud berry–*Sphagnum* community of the Carici middendorfii–Sphagnetum lenenses with *Pinus pumila* on the frozen ridges in the ridge-hollow-lake raised bog complex; J – close up of this community

Note. A physiognomically and ecologically similar association was described from Western Siberia under the name Scheuchzerio palustris–Sphagnetum jensenii Lapshina et al. 2024. It is characterized by the dominance of *Sphagnum jensenii* and *S. majus* in the moss layer and is distributed mainly in the northern part of the forest zone in continental regions of northern Eurasia (Lapshina et al. 2024).

A distinct group is formed by mire communities of slightly rised *Sphagnum* caperts dominated by *Sphagnum papillosum* in oligotrophic and meso-oligotrophic mires. Within the Udyl' Nature Reserve, these communities are represented by two associations.

Iridi laevigatae–Sphagnetum paillosi ass. nov. (Table 3, rel. 8–39; Table 6, syntaxon 7; Fig. 2F, Fig. 4, cluster 7; Fig. 5, cluster 7a, b, c)

Holotypus: relevé 14 (author's number – 179E25ud) in Table 3, Khabarovsk krai, Ul'chskii District, Udyl' nature reserve, 17.08.2025, author E.D. Lapshina.

Diagnostic species: *Sphagnum balticum*, *S. majus*, *S. papillosum* (dom.)

Structure and composition. Among dwarf shrubs, *Andromeda polifolia* (5–10 cm tall) occurs with high constancy. In some communities, small shrubs of *Myrica tomentosa*, 10–15(20) cm tall, form a noticeable admixture. Their total cover does not exceed 5–10 %. In the sparse herb layer (total cover 5–15 %), the most common species are *Carex limosa*, *Drosera anglica*, *Oxycoccus palustris*, *Rhynchospora alba*, and *Scheuchzeria palustris*; more rarely encountered are *Carex middendorffii*, *Iris laevigata*, *Menyanthes trifoliata*, *Pedicularis adunca*, and *Utricularia intermedia*. *Sphagnum papillosum* dominates the moss layer, but toward the centers of the waterlogged hollows it is replaced by *Sphagnum balticum* in combination with *S. majus*.

Distribution and ecology. Communities of the association are relatively widespread in ridge-hollow and ridge-pool-hollow mire complexes with oligotrophic dwarf shrub (*Chamaedaphne calyculata*)–cottongrass–*Sphagnum* (*S. alaskense*) ridges, with or without *Myrica tomentosa*, and extensive meso-oligotrophic hollows of rounded shape reaching 20–25 m in width. *Sphagnum papillosum* forms extensive flat areas with an even moss surface, often dissected by shallow (up to 5 cm deep) wet depressions and water-filled runnels. These communities develop as a broad belt along the periphery of large hollows or occupy the entire area of less waterlogged hollows. More rarely, they form floating mats around intramire pools. The water table is situated at a depth of 5–15 cm.

Based on differences in the species composition of the moss layer, three variants were distinguished: typica, Sphagnum balticum, and Sphagnum majus.

Variant typica (Table 3, rel. 8–17) occupies an intermediate position among all communities with respect to the water table, which is situated approximately 10 cm below the surface, and is characterized by the absence of a noticeable admixture of moss species other than *Sphagnum papillosum*.

Variant Sphagnum balticum (Table 3, rel. 18–27) differs by the constant presence of *Sphagnum balticum*, whose abundance reaches 20–40 %, and by a water table situated at a depth of 15–20 cm.

Variant Sphagnum majus (Table 3, rel. 28–39) is characterized by a noticeable admixture of this species and by the highest water table, approximately 5 cm below the surface.

Communities of the different variants are not sharply delimited from one another in species composition and show gradual transitions, which does not justify their recognition at the rank of subassociation.

Within the first two variants, subvariants may be distinguished that unite groups of communities with the participation of *Myrica tomentosa* and a constant minor admixture of *Iris laevigata* and *Pedicularis adunca*, as well as *Sphagnum perfoliatum* in the moss layer. These species indicate the periodic flooding of their habitats by water from intramire pools.

The **class Oxycocco–Sphagnetea** in the middle taiga of the Lower Amur region includes dwarf shrub–*Sphagnum* communities of predominantly ombrotrophic bogs and dwarf shrub–*Sphagnum* open larch mire woodlands (mari) on peat soils. Within the Udyl' Nature Reserve, the vegetation of this class is represented by four associations with variants and one community type assigned to three alliances: Sphagnion alaskense **all. nov.**, Oxycocco–Empetrion hermaphroditi, and Sphagnion lenense, of which the first is proposed here as new.

Vegetation of (sedge)–dwarf shrub–*Sphagnum* communities with atmospheric and surface-runoff water supply dominated by *Sphagnum alaskense*

Communities dominated by *Sphagnum alaskense*, more rarely by *S. papillosum*, occupy the largest areas within the Udyl' Nature Reserve. We propose recognizing these communities within a distinct new alliance, Sphagnion alaskense **all. nov.** Within the reserve, three associations of this alliance with variants were described.

Sphagno papillosi–Caricetum middendorfii ass. nov.

(Table 3, rel. 1–7; Table 6, syntaxon 8; Fig. 3a, Fig. 4, 5, cluster 8)

Holotypus: relevé 2 (author's number – 211E25ud) in Table 3, Khabarovsk region, Ul'chskii District, Udyl' nature reserve, 19.08.2025, author E.D. Lapshina.

Diagnostic species: *Carex middendorfii* (dom.), *Sphagnum balticum*, *S. papillosum* (dom.)

Structure and composition. Communities of the association are readily distinguished from the low-productive communities of ombrotrophic bogs by the layer of the large sedge *Carex middendorffii* (20–40 %). The lower dwarf shrub layer, 10–15(25) cm tall, is usually formed by *Andromeda polifolia* (10–30 %, more rarely less), with minor participation of *Chamaedaphne calyculata*. The moss layer is composed of *Sphagnum papillosum* and *S. balticum* in varying proportions, accompanied by *Sphagnum alaskense* and *S. lenense* at lower abundance. *Oxycoccus palustris* and *Drosera rotundifolia* grow on the surface of the *Sphagnum* carpet.

Distribution and ecology. Communities of the association occur as small patches ranging from 5 to 100 m², more rarely larger, within ridge-pool-hollow mire complexes with frozen and partially or completely thawed dwarf shrub–*Sphagnum* (*S. lenense*, *S. fuscum*) ridges with *Pinus pumila* and oligotrophic sedge (*Carex limosa*)–*Sphagnum* (*S. majus*) hollows. They occupy relatively low hummocks and carpets along the periphery of the ridges, at their contact with waterlogged hollows.

Note. The dominance of *Sphagnum papillosum* and the participation of *S. balticum* in the moss layer make the communities of the association similar to those of the alliance Scheuchzerion palustris of the class Scheuchzerio–Caricetea nigrae. However, the dominance of *Carex middendorffii* in the herb layer and the constant presence, although at low abundance, of *Andromeda polifolia*, *Chamaedaphne calyculata*, *Drosera rotundifolia*, *Oxycoccus microcarpus*, *O. palustris*, and *Sphagnum alaskense* indicate the affiliation of this association with the class Oxycocco–Sphagnetea.

Carici lasiocarpae–Sphagnetum alaskense ass. nov.

(Table 4, rel. 1–9; Table 6, syntaxon 9; Fig. 2B, Fig. 4, 5, cluster 9)

The association includes shrub birch-dwarf shrub–sedge–*Sphagnum* (*S. alaskense*) communities of hummocks and ridges in waterlogged aapa mires of the Amur River Basin.

Holotypus: relevé 5 (author's number – 161E25ud) in Table 4, Khabarovsk region, Ul'chskii District, Udyl' nature reserve, 15.08.2025, author E.D. Lapshina.

Diagnostic species: *Carex lasiocarpa*, *C. chordorrhiza*, *Glyceria spiculosa*, *Oxycoccus palustris*, *Pogonia japonica*, *Sphagnum alaskense* (dom.), *S. angustifolium*.

Structure and composition. The shrub layer, 30–50 cm tall, is formed by *Betula ovalifolia* (20–30 %). In the dense dwarf shrub layer (30–40 %), 15–20 cm tall, *Andromeda polifolia* predominates, sometimes with admixture of *Chamaedaphne calyculata*. Among the herbaceous species, *Carex chordorrhiza*, *C. lasiocarpa*, *Drosera rotundifolia*, *Glyceria spiculosa*, and *Menyanthes trifoliata* occur at low abundance, together with the rare orchids *Hammarbya paludosa* and *Pogonia japonica*. *Sphagnum alaskense* dominates the moss layer (60–70 %). *Sphagnum angustifolium* occurs with high constancy, while *Aulacomnium palustre* and, more rarely, *S. fuscum*, *S. talbotianum*, and *S. warnstorfii* are present at low abundance. *Oxycoccus palustris* spreads across the surface of the moss carpet.

Distribution and ecology. Communities of the association form soft, loose moss hummocks and ridges alternating with *Menyanthes*–sedge (*Carex meyeriana*) and *Menyanthes*–sedge–*Sphagnum* (*S. obtusum*) waterlogged flarks in meso-oligotrophic aapa-like mires under conditions of continuous surface runoff and discharge of comparatively mine-

Table 3. Sedge–*Sphagnum* communities of low hummocks, ridges and lawns of oligotriphic mire complexes. Associations of the alliances Sphagnion alaskense and Scheuchzerion palustris. 1–7 – Sphagno papillosi–Caricetum middendorfii (1), 8–39 – Iridi laevigatae–Sphagnetum papillosi (2): 8–17 – var. typica (2a), 18–27 – var. Sphagnum balticum (2b), 28–39 – var. Sphagnum majus (2c).

Association	Sphagno papillosi–Caricetum middendorfii (1)							Iridi laevigatae–Sphagnetum papillosi (2)																																	Constancy and abundance				
Subassotiation								typica (2a)										Sphagnum balticum (2b)										Sphagnum majus (2c)																
Cover (%): shrubs / dwarf shrubs	5	20	30	10	10	10	10	1	1	0	5	5	20	0	3	3	3	10	10	1	0	7	3	10	5	3	5	0	0	0	0	0	3	0	0	3	0	1	3					
herbs	30	40	40	20	20	20	25	10	5	10	5	10	15	10	10	15	10	15	10	10	10	10	15	10	15	10	15	20	10	10	7	15	5	10	5	10	10	10	10					
mosses	70	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100					
Number of species	11	6	11	8	6	8	9	8	5	6	6	12	10	14	11	14	13	8	14	9	8	8	12	14	17	12	16	12	10	11	10	11	7	14	9	13	11	14	16					
Relevé nr. by author	145E25ud	211E25ud	212E25ud	181F25ud	183F25ud	184F25ud	187F25ud	127F25ud	179F25ud	213E25ud	209E25ud	154F25ud	207E25ud	179E25ud	161F25ud	183E25ud	159F25ud	218E25ud	196E25ud	197E25ud	151E25ud	169F25ud	185E25ud	122F25ud	187E25ud	184E25ud	189E25ud	149E25ud	156E25ud	147E25ud	128F25ud	154E25ud	178F25ud	158F25ud	117F25ud	124F25ud	156F25ud	118F25ud	120F25ud					
Relevé nr. in the table	**1**	**2***	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14***	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**1**	**2a**	**2b**	**2c**	**2**
Diagnostic species of the ass. Sphagno papillosi–Caricetum middendorfii																																												
Sphagnum papillosum ***I-S***	2	3	3	3	2	4	4	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**4**	**4**	**5**	**5**	**5**	**4**	**4**	**5**	**5**	**5**	**5**	**4**	**4**	**5**	**5**	**5**	**4**	**5**	**5**	**5**	**4**	V	V	V	V	V
Carex middendorfii	2	3	3	2	2	2	2	.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	+	.	+	+	+	.	+	.	.	+	.	.	.	.	.	.	.	V	II	II	I	II
Sphagnum balticum ***I-Sb***	4	3	4	3	5	2	2	.	.	r	+	.	r	.	.	+	.	2	3	3	2	2	2	3	2	2	2	1	1	1	+	+	.	+	.	.	.	.	1	V	II	V	III	IV
Sphagnum majus ***I-Sm***	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	1	.	.	.	.	.	+	.	1	1	1	2	2	2	3	2	2	2	3	2	2	2	3	.	.	II	V	IV
Diagnostic species of the ass. Iridi laevigatae–Sphagnetum papillosi																																												
Myrica tomentosa	1	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1	1	.	r	.	.	.	1	1	1	1	1	.	.	.	.	.	.	.	.	1	.	.	1	I	II	III	I	II
Iris laevigata	.	.	.	.	.	.	.	r	.	.	.	+	.	+	1	+	1	.	.	r	+	.	.	+	+	1	1	r	.	r	.	.	.	+	+	.	+	+	1	.	II	III	III	III
Sphagnum perfoliatum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	+	.	.	+	+	1	.	+	.	1	.	+	.	+	.	.	.	I	III	II
Pedicularis adunca	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	+	.	+	.	.	.	+	.	+	.	+	.	.	.	.	.	.	+	.	r	+	.	.	.	.	II	II	II
Diagnostic species of the Stygio–Caricion limosae																																												
Drosera anglica	.	.	.	+	.	.	.	1	+	1	1	1	+	1	+	+	+	+	1	1	1	1	+	2	+	+	+	1	1	1	+	1	+	+	+	1	+	1	1	I	V	V	V	V
Utricularia intermedia	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	r	.	.	.	+	r	+	.	+	.	.	.	+	.	.	+	.	1	+	r	r	.	I	III	III	III
Juncus stygius	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.	.	.
Diagnostic species of the Scheuchzerion palustris and Scheuchzerietalia palustris																																												
Carex limosa ***St-C***	1	.	.	+	.	.	.	+	1	.	1	.	.	+	+	.	+	+	1	1	1	1	1	+	+	+	1	1	1	.	1	+	+	+	1	1	+	1	+	II	III	V	V	V
Rhynchospora alba ***St-C***	.	.	.	.	.	.	.	1	.	2	.	1	.	1	.	1	+	+	.	+	.	r	1	+	1	1	.	2	1	1	+	2	.	+	+	+	+	+	+	.	III	IV	V	IV
Scheuchzeria palustris ***St-C***	.	.	.	.	.	.	.	.	.	1	.	1	.	1	1	2	1	.	.	+	1	.	1	.	2	1	2	.	.	1	r	1	.	1	.	.	1	+	1	.	III	III	III	III
Carex rotundata	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	+	.	.	1	.	r	.	.	.	.	.	.	.	.	1	.	.	.	.	r	.	.	I	III	I	II
Eriophorum russeolum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	I	I	I
Sphagnum lindbergii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	1	.	.	+	.	.	.	II	I
Cladopodiella fluitans	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	I	.	I	+
Diagnostic species of the Scheuchzerio–Caricetea nigrae																																												
Andromeda polifolia	+	2	3	2	2	2	2	+	+	.	1	1	2	+	.	+	.	2	2	+	+	2	.	2	+	+	+	+	+	+	+	+	1	+	.	+	.	+	+	V	III	V	V	V
Oxycoccus palustris	1	1	2	+	+	+	+	.	+	+	+	+	.	+	+	.	+	.	+	.	+	.	.	+	+	.	+	+	.	+	.	.	+	.	+	+	.	+	+	V	III	III	III	III
Menyanthes trifoliata	.	.	.	.	.	.	.	1	.	.	.	+	.	1	+	+	+	.	.	r	.	.	1	.	+	.	1	+	.	.	+	r	.	1	.	.	1	.	.	.	.	II	III	III
Diagnostic species of the Oxycocco–Sphagnetea																																												
Drosera rotundifolia	r	+	+	.	+	.	+	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	V	I	I	II	I
Chamaedaphne calyculata	+	.	+	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV	.	II	.	+
Sphagnum alaskense	1	.	+	.	.	2	2	.	.	.	.	.	.	.	.	1	.	.	+	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	+	.	III	I	III	II	II
Sphagnum lenense	.	.	1	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	I	.	.	+
Oxycoccus microcarpus	r	.	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	I	.	.	+
Other species																																												
Sphagnum orientale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	I	+	+

Note. Species found in 1 relevé: *Carex canescens* (35 r), *Ledum palustre* (3 +), *Pinguicula villosa* (6 +), *Pogonia japonica* (35 r), *Rubus chamaemorus* (13 +), *Sanguisorba parviflora* (39 r), *Sphagnum compactum* (14 +), *Sphagnum rubellum* (13 r).

GPS coordinates (WGS 84) (N, E) and dates: **1** – 51.84015, 139.66724, 14.08.2025; **2** – 51.99875, 139.67900, 19.08.2025; **3** – 51.99892, 139.67754, 19.08.2025; **4** – 51.99878, 139.67856, 19.08.2025; **5** – 51.99896, 139.67732, 19.08.2025; **6** – 51.99896, 139.67732, 19.08.2025; **7** – 51.99956, 139.67588, 19.08.2025; **8** – 51.83905, 139.65541, 14.08.2025; **9** – 51.99878, 139.67856, 19.08.2025; **10** – 51.99885, 139.67616, 19.08.2025; **11** – 51.99875, 139.67900, 19.08.2025; **12** – 51.90107, 139.77412, 17.08.2025; **13** – 51.99918, 139.68243, 19.08.2025; **14** – 51.91055, 139.77385, 17.08.2025; **15** – 51.90067, 139.77856, 17.08.2025; **16** – 51.90329, 139.77448, 17.08.2025; **17** – 51.90152, 139.77740, 17.08.2025; **18** – 51.99946, 139.67555, 19.08.2025; **19** – 52.01804, 139.60883, 18.08.2025; **20** – 52.01737, 139.60760, 18.08.2025; **21** – 51.84014, 139.65536, 14.08.2025; **22** – 52.01719, 139.60744, 18.08.2025; **23** – 51.90240, 139.77576, 17.08.2025; **24** – 51.83979, 139.66387, 14.08.2025; **25** – 51.90178, 139.77718, 17.08.2025; **26** – 51.90329, 139.77448, 17.08.2025; **27** – 51.90075, 139.77806, 17.08.2025; **28** – 51.84002, 139.66112, 14.08.2025; **29** – 51.83697, 139.65291, 14.08.2025; **30** – 51.83991, 139.66446, 14.08.2025; **31** – 51.83729, 139.65316, 14.08.2025; **32** – 51.83759, 139.65343, 14.08.2025; **33** – 51.99917, 139.68157, 19.08.2025; **34** – 51.90235, 139.77628, 17.08.2025; **35** – 51.83996, 139.66734, 14.08.2025; **36** – 51.84005, 139.66056, 14.08.2025; **37** – 51.90313, 139.77487, 17.08.2025; **38** – 51.83996, 139.66734, 14.08.2025; **39** – 51.84002, 139.66548, 14.08.2025.

Authors. E.D. Lapshina (**E** – in the author's relevé nr.), I.V. Filippov (**F**).

Diagnostic species (next to the name of the taxon): ***St-C*** – Stygio–Caricion limosae, ***I-S*** – Iridi laevigatae–Sphagnetum papillosi: ***I-Sb*** – var. Sphagnum balticum, ***I-Sm*** – var. Sphagnum majus.

* – nomenclatural types (holotypes).

Table 4. Sedge–dwarf shrub–*Sphagnum* and dwarf shrub-*Sphagnum* communities of the alliance Sphagnion alaskense. Associations: Carici lasiocarpae–Sphagnetum alaskense (1), Chamaedaphno calyculatae–Sphagnetum alaskense (2): 10–15 – var. typica (2a), 16–42 – var. Myrica tomentosa (2b).

Association	Carici lasiocarpae–Sphagnetum alaskense (1)									Chamaedaphno calyculatae–Sphagnetum alaskense (2)																																	Constancy and abundance			
Variant										typica (2a)						Myrica tomentosa (2b)																														
Cover (%): shrubs / dwarf shrubs	60	60	30	40	70	40	15	30	40	35	60	30	20	80	70	80	90	80	90	80	80	70	30	80	60	70	90	25	40	80	20	90	70	45	70	70	80	60	70	60	80	90				
shrubs	10	30	1	5	50	20	3	20	10	5	1	3	0	2	3	80	50	40	40	30	10	3	20	25	30	1	50	10	15	20	10	40	20	5	30	3	30	15	60	20	60	40				
dwarf shrubs	50	30	30	35	10	20	12	10	30	30	60	25	20	80	70	0	50	40	60	50	70	70	20	60	30	70	60	20	25	60	20	80	50	40	50	70	50	50	10	40	20	80				
herbs	5	10	7	10	15	10	20	50	20	20	15	20	15	20	20	5	5	5	5	20	10	5	15	10	20	5	15	10	15	5	7	20	5	30	30	10	10	15	20	10	20	40				
mosses	100	100	100	100	100	100	100	90	100	100	100	100	100	95	100	95	85	50	80	95	50	85	100	90	100	80	50	100	100	100	100	75	100	100	100	60	90	30	90	80	70	80				
Number of species	23	18	12	18	15	17	13	16	18	15	14	18	10	15	20	19	17	13	22	19	17	17	17	17	16	20	17	17	19	18	16	17	23	15	16	15	23	14	14	19	13	23				
Relevé nr. by author	159E25ud	163E25ud	138F25ud	133F25ud	161E25ud	135F25ud	143F25ud	166E25ud	137F25ud	189F25ud	198E25ud	176F25ud	168F25ud	220E25ud	205E25ud	136E25ud	137E25ud	153F25ud	138E25ud	131E25ud	157F25ud	109F25ud	104F25ud	190F25ud	146E25ud	111F25ud	182E25ud	103F25ud	116F25ud	132E25ud	105F25ud	221E25ud	130E25ud	166F25ud	144E25ud	110F25ud	143E25ud	155F25ud	191E25ud	191F25ud	188E25ud	222E25ud				
Relevé nr. in the table	**1**	**2**	**3**	**4**	**5***	**6**	**7**	**8**	**9**	**10**	**11***	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	1	2a	2b	2
Diagnostic species of the ass. Carici lasiocarpae–Sphagnetum alaskense																																														
Carex lasiocarpa	+	2	+	+	1	1	2	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	.	.	.
Sphagnum angustifolium	1	2	3	1	2	2	2	2	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	V	I	+	+
Oxycoccus palustris	3	1	1	2	2	+	+	+	1	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	.	+	+
Carex chordorrhiza	+	+	+	+	1	+	1	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	.	.	.
Glyceria spiculosa	1	.	.	+	+	+	1	+	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	IV	.	+	+
Pogonia japonica	r	r	.	r	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III	.	.	.
Diagnostic species of the ass. Chamaedaphno calyculatae–Sphagnetum alaskense																																														
Ledum palustre	1	.	.	.	.	.	.	.	.	2	2	2	+	3	3	3	3	2	3	2	3	2	2	2	1	2	3	1	2	3	1	3	2	2	1	2	2	2	1	2	2	1	I	V	V	V
Sphagnum balticum	.	.	.	.	.	.	.	.	.	1	+	+	.	1	2	2	1	.	1	2	+	1	2	.	+	1	1	2	1	2	2	1	2	1	+	+	2	+	2	+	1	1	.	V	V	V
Sphagnum lenense	.	.	.	.	.	.	.	.	.	1	+	+	+	.	+	+	+	.	.	+	.	.	1	.	1	+	1	+	+	1	+	.	+	.	.	.	1	.	.	+	.	.	.	V	III	III
Carex middendorfii	+	+	.	+	.	.	.	.	.	+	1	+	1	+	r	.	.	+	.	1	+	+	1	.	1	+	.	1	+	+	+	.	1	.	1	+	.	.	+	.	+	.	II	V	III	IV
Carex globularis	.	.	.	.	.	.	.	.	.	1	.	+	.	1	+	r	+	.	+	.	.	+	.	+	.	+	.	.	.	.	.	+	.	.	.	.	+	.	.	+	.	+	.	IV	III	III
Sphagnum rubellum	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	1	.	.	+	.	.	.	+	+	.	.	.	.	+	+	+	+	+	.	+	.	+	.	.	+	.	.	.	III	III	III
Diagnostic species of the var. Myrica tomentosa																																														
Myrica tomentosa	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	3	3	3	3	3	1	3	2	2	3	2	3	2	2	2	2	3	2	1	2	2	3	2	3	2	3	3	.	I	V	V
Eriophorum vaginatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	.	+	+	2	+	+	r	+	1	2	+	+	+	1	.	1	1	1	+	1	2	2	1	2	+	.	I	V	IV
Diagnostic species of the alliance Spagnion alaskense and the class Oxycocco–Sphagnetea																																														
Sphagnum alaskense	**5**	**4**	**4**	**5**	**4**	**4**	**5**	**4**	**5**	**5**	**5**	**4**	**5**	**5**	**4**	**5**	**5**	**3**	**5**	**5**	**3**	**5**	**5**	**5**	**5**	**4**	**3**	**5**	**5**	**5**	**5**	**3**	**5**	**5**	**5**	**4**	**4**	**3**	**4**	**4**	**4**	**4**	V	V	V	V
Betula divaricata	2	3	+	1	3	2	1	2	2	1	+	1	.	1	1	1	1	1	1	1	1	1	+	+	.	+	1	+	+	+	1	+	.	+	1	1	+	1	2	1	3	+	V	V	V	V
Chamaedaphne calyculata	2	1	2	2	+	+	.	1	2	2	3	2	1	3	3	3	2	2	3	3	2	2	1	3	2	2	3	2	2	2	2	3	2	2	2	2	3	2	1	2	2	4	V	V	V	V
Andromeda polifolia	2	2	2	2	2	2	2	1	2	+	2	.	2	+	+	+	+	1	+	1	.	1	1	1	2	1	1	1	1	1	1	+	2	1	2	1	+	1	+	1	1	+	V	V	V	V
Drosera rotundifolia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	r	+	+	+	+	+	+	r	+	+	+	+	+	+	.	+	+	+	+	+	r	V	V	V	V
Aulacomnium palustre	+	+	.	+	+	+	.	+	+	.	.	+	.	1	+	+	.	.	+	+	.	.	+	1	.	.	+	+	r	+	+	2	.	.	.	+	1	.	.	2	.	2	IV	III	III	III
Sphagnum fuscum	.	.	1	.	1	2	.	1	.	2	+	2	.	+	2	.	.	1	+	1	+	.	+	.	1	.	2	1	+	+	.	.	1	.	2	.	+	.	1	.	1	.	III	V	III	III
Oxycoccus microcarpus	.	+	.	.	.	+	.	.	+	+	r	1	2	1	+	+	+	r	+	1	.	+	+	1	1	+	.	1	+	1	+	2	1	.	2	+	+	+	+	1	+	2	II	V	V	V
Polytrichum strictum	+	+	.	.	.	.	.	.	+	+	+	1	+	1	1	+	+	+	+	1	+	+	+	2	.	+	+	+	1	1	+	2	1	+	+	+	1	+	.	2	+	1	II	V	V	V
Rubus chamaemorus	.	.	.	.	.	.	.	.	.	2	.	2	.	2	2	1	+	.	1	2	+	+	2	1	1	+	1	1	2	1	+	2	1	2	2	1	+	+	+	+	.	3	.	IV	V	V
Vaccinium uliginosum	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	.	2	+	.	+	1	.	1	.	r	.	.	1	.	.	1	.	1	.	.	1	.	1	.	I	III	III
Smilacina trifolia	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	+	.	+	.	.	1	.	.	.	+	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	r	.	I	II	III
Sphagnum russowii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	2	.	1	.	.	I	I	I
Sphagnum capillifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	+
Diagnostic species of the alliance class Scheuchzerio–Caricetea nigrae																																														
Menyanthes trifoliata	.	+	1	+	+	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV	.	.	.
Other species																																														
Salix myrtilloides	+	.	.	+	+	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III	.	.	.
Sphagnum warnstorfii	+	.	.	+	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	+	+
Sphagnum talbotianum	.	2	.	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	II	.	I	+
Polytrichum jensenii	+	.	.	.	.	.	.	.	.	.	.	1	.	.	1	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	+	I	II	II	II
Sphagnum fimbriatum	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	.	1	.	.	+	.	r	I	.	II	II
Carex minuta	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	II	.	I	II
Iris laevigata	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	I	+
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	+	+
Sanguisorba parviflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	I	+
Calamagrostis langsdorffii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	I	+
Pohlia nutans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	r	.	.	I	+
Scheuchzeria palustris	.	+	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.
Larix cajanderi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	I	+
Pinus pumila	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	I	+
Sphagnum aongstroemii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	I	+
Aulacomnium turgidum	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	I	+	+
Spiranthes sinensis	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	I	.	+	+
Sphagnum imbricatum	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.
Equisetum fluviatile	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.

Note. Species found in 1 relevé: *Betula nana* (20 r), *Calamagrostis neglecta* (1 r), *Calypogeia sphagnicol*a (33 r), *Carex pseudocuraica* (7 r), *C. rotundata* (34 r), *C. tenuiflora* (1 r), *Hammarbya paludosa* (6 r), *Larix cajanderi* (18 +), *Pinguicula villosa* (13 r), *Pleurozium schreberi* (37 r), *Sphagnum compactum* (33 r), *S. obtusum* (1 +), *S. papillosum* (28 +), *Warnstorfia fluitans* (26 r).

GPS coordinates (WGS 84) (N, E) and dates: **1** – 51.9176, 139.63234, 15.08.2025; **2** – 51.91072, 139.62265, 15.08.2025; **3** – 51.90742, 139.62927, 15.08.2025; **4** – 51.91733, 139.63205, 15.08.2025; **5** – 51.91178, 139.62308, 15.08.2025; **6** – 51.91160, 139.62256, 15.08.2025; **7** – 51.90431, 139.63043, 15.08.2025; **8** – 51.90515, 139.62973, 15.08.2025; **9** – 51.91073, 139.62264, 15.08.2025; **10** – 52.13137, 139.73783, 20.08.2025; **11** – 52.01737, 139.60760, 18.08.2025;**12** – 51.99809, 139.69848, 19.08.2025; **13** – 52.01719, 139.60744, 18.08.2025; **14** – 52.13089, 139.73805, 20.08.2025; **15** – 51.99808, 139.69884, 19.08.2025; **16** – 51.94132, 139.78041, 13.08.2025; **17** – 51.94144, 139.77927, 13.08.2025;

Table 4. Continued.

18 – 51.91067, 139.77412, 17.08.2025; **19** – 51.94156, 139.77885, 13.08.2025; **20** – 51.94480, 139.7872313.08.2025; **21** – 51.90313, 139.77487, 17.08.2025; **22** – 51.93838, 139.79261, 13.08.2025; **23** – 51.94526, 139.78567, 13.08.2025; **24** – 52.14001, 139.77527, 20.08.2025; **25** –51.84015, 139.66724, 14.08.2025; **26** – 51.94208, 139.77916, 13.08.2025; **27** – 51.91055, 139.77385, 17.08.2025; **28** – 51.94494, 139.78639, 13.08.2025; **29** – 51.83766, 139.66708, 14.08.2025; **30** – 51.94525, 139.78688, 13.08.2025; **31** – 51.94572, 139.78523, 13.08.2025; **32** – 52.13975, 139.77492, 20.08.2025; **33** – 51.94457, 139.78729, 13.08.2025; **34** – 52.02188, 139.61286, 18.08.2025; **35** – 51.83981, 139.66698, 14.08.2025; **36** – 51.94186, 139.77957, 13.08.2025; **37** – 51.83751, 139.66740, 14.08.2025; **38** – 51.90789, 139.77329, 17.08.2025; **39** – 51.90075, 139.77806, 17.08.2025; **40** – 52.14001, 139.77527, 20.08.2025; **41** – 51.90170, 139.77737, 17.08.2025; **42** – 52.13967, 139.77548, 20.08.2025.

Authors. E.D. Lapshina (**E** – in the author's relevé nr.), I.V. Filippov (**F**).* – nomenclatural types (holotypes).

ral-poor groundwater. The hummocks and ridges are irregular or elongated in shape, 2–7 m across, and weakly oriented perpendicular to the direction of surface runoff. Their height exceeds the water level in the hollows by only 15–20 cm.

Note. Communities of this association occupy an intermediate position between the classes Scheuchzerio–Caricetea nigrae, to which the herbaceous species (*Carex lasiocarpa*, *C. chordorrhiza*, *Menyanthes trifoliata*) belong, and Oxycocco–Sphagnetea, whose diagnostic species include all dwarf shrubs and the dominants of the moss layer. The roots and rhizomes of herbaceous species with higher mineral nutrient requirements are located in the peat below the water table, and dwarf shrubs and oligotrophic *Sphagnum* mosses reflecting the current ecological conditions of the root zone.

Chamaedaphno calyculatae–Sphagnetum alaskense ass. nov.

(Table 4, rel. 10–42; Table 6, syntaxon 10; Fig. 2C, Fig. 4, cluster 10; Fig. 5, cluster 10a, 10b)

The association comprises meso-oligotrophic dwarf shrub–*Sphagnum* communities, with or without *Myrica tomentosa*, dominated by *Sphagnum alaskense* in the moss layer and developing in areas with periodically minor flooding by lake waters poor in mineral nutrients.

Holotypus: relevé 11 (author's number – 198E25ud) in Table 4, Khabarovsk region, Ul'chskii District, Udyl' nature reserve, 18.08.2025, author E.D. Lapshina.

Diagnostic species: *Carex middendorfii*, *Chamaedaphne calyculata*, *Ledum palustre*, *Sphagnum alaskense* (dom.), *S. balticum*, *S. lenense*, *S. rubellum*.

Structure and composition. The shrub layer, when present, has a patchy structure and is formed by *Myrica tomentosa* shrubs 30–50(60) cm tall and scattered small shrubs of *Betula divaricata*. The cover of *Myrica* varies among communities from 5–40 % to complete absence. The dense dwarf shrub layer (40–60 %) is formed by *Chamaedaphne calyculata*, sometimes with greater or lesser participation of *Andromeda polifolia* and *Ledum palustre*, more rarely *Vaccinium uliginosum*. Herbaceous species are few and inconspicuous, their total cover usually not exceeding 5–10 %. *Carex middendorffii*, *Drosera rotundifolia*, *Eriophorum vaginatum*, *Oxycoccus microcarpus*, and *Rubus chamaemorus* occur with high constancy. *Sphagnum alaskense* dominates the moss layer (70–90 %), with minor mix of *Sphagnum balticum*. Other mosses usually present at low abundance include *Sphagnum lenense*, *S. fuscum*, *S. rubellum*, and *Polytrichum strictum*. More rarely encountered are *Sphagnum russowii*, *S. aongstroemii*, *S. fimbriatum*, and *Polytrichum jensenii*.

Distribution and ecology. Meso-oligotrophic dwarf shrub–*Sphagnum* mires dominated by *Sphagnum alaskense* in the moss layer are widespread within the reserve. They occupy an area between shrub-tussock sedge communities in the zone of regular flooding from the lake and oligotrophic dwarf shrub–cottongrass–*Sphagnum* mires and *Sphagnum* larch open woodland mires of ombrotrophic conditions situated at higher elevations. Communities of the association also occur on ridges within oligotrophic ridge-pool-hollow mire complexes in areas periodically flooded by intramire pools.

The surface of the communities is formed by *Sphagnum* hummocks partially coalescing into a continuous cover interrupted by sparse small holes. The relative microrelief amplitude is 20–40 cm. At a depth of 50 cm, patches of seasonally frozen peat may locally persist until mid-August.

Within the association, we distinguish two variants: typica and Myrica tomentosa.

Variant typica (Table 4, rel. 10–15) represents the typical dwarf shrub–*Sphagnum* communities of the association dominated by *Sphagnum alaskense*.

Variant Myrica tomentosa (Table 4, rel. 16–42) is characterized by the constant presence of shrub layer formed by *Myrica tomentosa*, accompanied at low abundance but with high constancy by *Eriophorum vaginatum*. According to our observations, this shrub indicates habitats more or less regularly flooded by the waters of Lake Udyl' and intramire pools during periods of elevated water levels associated with snowmelt and summer–autumn monsoonal rains.

Vegetation of oligotrophic dwarf shrub–*Sphagnum* mires and larch open woodland mires dominated by *Sphagnum fuscum* and *S. alaskense*

Dwarf shrub–*Sphagnum* communities of hummocks and ridges in ombrotrophic bogs dominated by *Sphagnum fuscum* are traditionally assigned to the boreal alliance Oxycocco–Empetrion hermaphroditi. At the southern margin of their distribution in the Lower Amur Basin, they are represented by transitional variants sharing many features with the communities of the alliance Sphagnion alaskense.

Larici cajanderi–Sphagnetum fusci ass. nov.

(Table 5, rel. 19–37; Table 6, syntaxon 11; Fig. 2E, Fig. 4, cluster 11; Fig. 5, cluster 11a, 11b)

The association comprises communities of larch open woodland mires (mari) with scattered larch trees and open dwarf shrub–cottongrass–*Sphagnum* (*S. alaskense*, *S. fuscum*) and dwarf shrub–sedge (*Carex globularis*)–*Sphagnum* communities representing post-fire stages of their recovery. Larch trees in these communities do not play any significant phytocoenotic role due to their extremely low density. Therefore, the dominant species of the moss layer, which determines the ecological conditions of the habitats and the surface structure, is placed in the second position in the association name.

Holotypus: relevé 21 (author's number – 148F25ud) in Table 5, Khabarovsk region, Ul'chskii District, Udyl' Nature Reserve, 16.08.2025, author I.V. Filippov.

Diagnostic species: *Carex globularis*, *Eriophorum vaginatum*, *Sphagnum alaskense*, *S. fuscum*, *Vaccinium vitis-idaea*, *V. uliginosum*.

Structure and composition. At present, natural dwarf shrub–*Sphagnum* larch open woodland mires are represented

Table 5. Dwarf shrub-*Sphagnum* and larch open woodland *Sphagnum* mires of the alliance Sphagnion alaskense. Associations Carici middendorfii–Sphagnetum lenenses (1): 1–5 subass. typicum (1a), 6–18 – subass. sphagnetosum fisci (1b); Larici cajanderi–Sphagnetum fusci (2): 19–25 var. typica (2a), 26–37 – var. Sphagnum alaskense (2b); community types: 38–40 – *Larix cajanderi–Sphagnum angustifolium* (3), 41–43 – *Larix cajanderi–Sphagnum girgensohnii* s.l. (4), 44-46 – *Larix cajanderi–Polytrichum commune* (5).

Association	Carici middendorfii–Sphagnetum lenenses (1)																		Larici cajanderi-Sphagnetum fusci (2)																			[3]			[4]			[5]			Constancy and abundance						
Variant	typica (1a)								Sphagnum fuscum (1b)										typica (2a)					Sphagnum alaskense (2b)																																
Cover (%): trees	3	0	0	0	5	0	2	0	0	0	0	0	0	5	0	0	3	1	5	0	0	0	0	0	0	0	1	5	1	0	3	1	0	5	1	7	5	20	25	30	25	0	15	15							
shrubs	1	5	20	0	0	0	20	3	3	20	5	3	0	10	2	4	3	15	5	30	5	3	30	3	2	10	5	2	1	1	5	1	0	10	4	3	1	30	7	15	0	0	0	0	0	0							
dwarf shrubs	50	25	50	15	25	40	60	30	50	40	40	80	30	70	80	90	40	40	40	20	40	80	60	40	80	40	70	70	90	50	55	30	50	80	80	50	80	80	60	80	50	40	40	20	10	30							
herbs	30	30	10	10	25	45	40	15	50	40	25	60	40	10	40	40	30	20	15	20	20	30	15	15	30	35	20	20	10	15	25	15	40	15	30	15	20	5	5	15	10	25	20	10	10	10							
mosses	100	100	80	100	100	95	90	100	100	95	100	100	100	90	100	95	100	100	100	95	90	95	70	100	100	100	90	80	90	100	100	70	100	80	90	100	60	90	100	90	90	100	90	100	100	100							
Tree hight, m 5	0	0	0	4	0	5	0	0	0	0	0	0	6	0	0	4	4	10	0	0	0	0	0	0	0	0	0	0	10	14	3	0	8	10	0	10	12	8	6	10	12	15	10	0	8	6							
Number of species	20	14	14	9	18	18	17	19	18	17	15	17	15	17	19	19	16	20	15	14	17	21	20	18	17	15	16	19	23	15	18	16	16	15	22	22	29	21	19	19	19	17	18	11	11	16							
Relevé nr. by author	126F25ud	173F25ud	130F25ud	175F25ud	125F25ud	181E25ud	150a25ud	177F25ud	201E25ud	152E25ud	172F25ud	206E25ud	203E25ud	182F25ud	200E25ud	219E25ud	188F25ud	208E25ud	107F25ud	153E25ud	148F25ud	172E25ud	155E25ud	108F25ud	135E25ud	171F25ud	158E25ud	177E25ud	178E25ud	152F25ud	132F25ud	146F25ud	174F25ud	134E25ud	174E25ud	147F25ud	173E25ud	224E25ud	226E25ud	225E25ud	194F25ud	196F25ud	195F25ud	223E25ud	193F25ud	192F25ud							
Relevé nr. in the table	**1**	**2**	**3**	**4**	**5***	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21***	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**1a**	**1b**	**1**	**2a**	**2b**	**2**
Larix cajanderi (a)	1	.	+	.	1	.	1	.	.	.	.	.	.	1	.	+	1	1	1	.	+	.	.	.	.	.	.	+	1	+	+	r	1	1	1	1	1	2	1	2	2	3	2	2	2	2	III	II	III	II	V	IV
Larix cajanderi (b)	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2	1	.	1	.	.	r	.	.	.	+	1	1	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	III	I	I	III	III	III
Diagnostic species of the ass. Carici middendorfii–Sphagnetum lenenses																																																			
Sphagnum lenense	**4**	**5**	**4**	**5**	**4**	**4**	**4**	**4**	3	3	3	2	2	2	2	2	1	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	.	+	.	+	r	.	.	.	.	.	.	.	.	.	V	V	V	.	II	II
Carex middendorffii	1	1	+	+	1	.	1	+	.	1	+	+	+	1	+	+	+	1	.	1	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	V	V	V	II	II	II
Pinus pumila	+	1	+	.	1	.	1	+	1	.	1	+	.	1	+	1	1	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	r	.	.	r	.	.	r	.	.	.	.	.	.	.	.	IV	IV	IV	.	II	II
Diagnostic species of the ass. Larici cajanderi–Sphagnetum alaskense																																																			
Sphagnum fuscum	.	.	.	.	+	2	1	2	**4**	**3**	**3**	**4**	**4**	**2**	**2**	**4**	**5**	**3**	**5**	**5**	**5**	**5**	**4**	**4**	**4**	1	1	2	2	3	2	2	3	3	3	3	2	3	4	2	.	.	.	.	.	.	III	V	IV	V	V	V
Sphagnum alaskense	2	1	2	1	2	1	2	2	1	2	3	1	2	4	4	1	1	4	2	2	1	2	2	3	2	**5**	**5**	**4**	**4**	**4**	**4**	**3**	**3**	**3**	**3**	**2**	**2**	+	+	+	.	1	.	.	.	.	V	V	V	V	V	V
Carex globularis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	.	1	+	.	+	.	+	2	+	1	1	1	.	2	2	3	2	2	+	1	+	1	1	1	2	1	1	.	I	+	III	V	IV
Vaccinium vitis-idaea	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	.	+	+	.	1	1	.	1	1	2	2	r	+	+	1	1	1	+	1	1	2	1	2	2	1	+	+	II	.	I	IV	V	IV
Vaccinium uliginosum	2	.	2	.	.	.	.	.	.	+	.	.	.	+	.	.	.	1	1	.	2	1	1	1	.	+	.	2	2	1	.	1	.	.	2	2	2	.	.	.	+	.	.	1	+	1	II	II	II	IV	IV	IV
Diagnostic species of the community types																																																		
Sphagnum angustifolium	.	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	1	.	1	+	3	2	2	4	2	1	.	.	.	I	I	I	I	II	II
Pleurozium schreberi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2	1	1	+	.	+	.	.	.	.	.	.	.	I	+
Ledum hypoleucum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	+	.	.	r	+	+	1	2	2	2	+	.	+	.	.	.	III	I	II
Peltigera aphthosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.
Sphagnum girgensohnii s.l.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	4	5	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	5	5	5	.	.	.	.	.	.
Calamagrostis langsdorffii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	1	1	.	.	.	.	.	.	.	.
Betula platyphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	+	1	.	.	.	.	.	.	.	.	.
Salix myrtilloides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	.	.	.	.	.	.	.	.	.
Diagnostic species of the Oxycocco–Sphagnetea																																																		
Ledum palustre	2	1	3	2	2	2	3	2	2	2	2	3	2	3	3	3	2	2	2	2	2	3	4	2	3	1	3	3	3	3	2	2	3	4	3	2	4	4	4	4	2	2	2	2	2	2	V	V	V	V	V	V
Betula divaricata	1	1	2	.	1	.	2	1	+	2	+	1	.	1	1	+	+	2	1	3	1	1	3	1	1	+	1	1	1	1	1	+	.	2	1	1	1	3	2	2	1	1	2	.	+	+	IV	V	V	V	V	V
Chamaedaphne calyculata	1	2	+	1	2	2	3	2	2	2	2	3	2	2	3	3	2	2	1	1	1	3	2	1	3	3	3	3	3	2	3	2	2	2	2	2	1	2	2	1	.	.	.	.	.	.	V	V	V	V	V	V
Rubus chamaemorus	2	2	1	1	2	3	3	2	3	3	2	3	3	1	3	3	2	2	.	2	2	3	1	1	2	3	1	1	+	.	1	.	2	.	+	+	.	.	.	.	.	.	.	.	.	.	.	V	V	V	V	IV	IV
Polytrichum strictum	1	.	r	.	1	+	+	1	+	1	+	1	.	1	+	+	+	+	+	+	+	1	1	+	+	+	+	2	1	1	1	1	+	2	1	1	2	.	.	.	.	.	.	.	.	.	IV	V	V	V	V	V
Eriophorum vaginatum	1	.	2	.	+	1	1	.	+	1	+	+	+	1	+	.	.	+	.	2	+	1	2	1	2	.	1	2	1	+	2	2	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	IV	IV	IV	V	IV	IV
Drosera rotundifolia	r	+	r	+	r	+	+	+	+	+	+	+	+	r	+	+	+	+	.	+	r	+	+	.	+	+	+	+	+	.	r	.	r	.	+	.	.	.	+	.	.	.	.	.	.	.	V	V	V	IV	III	III
Oxycoccus microcarpus	1	.	.	+	1	1	1	+	+	1	+	2	1	+	+	2	1	+	.	+	1	+	+	.	+	1	+	+	+	+	.	+	.	.	.	.	.	.	+	2	+	.	.	.	.	.	.	IV	V	V	IV	III	III
Andromeda polifolia	1	1	.	+	+	2	+	+	2	1	1	+	2	.	1	+	.	.	.	.	.	+	1	1	+	+	+	1	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V	IV	IV	III	III	III
Sphagnum capillifolium	.	.	.	.	r	+	+	+	1	+	.	.	+	.	.	.	.	+	+	+	+	1	+	+	+	.	.	.	2	+	.	1	+	1	2	2	.	2	1	3	1	1	.	.	.	.	.	.	III	II	III	V	III	IV
Sphagnum balticum	1	+	.	.	+	.	.	1	1	1	.	2	1	+	.	2	1	1	1	.	+	+	.	.	2	1	1	2	2	.	1	2	1	.	2	2	2	.	.	.	.	.	.	.	.	r	III	IV	IV	III	V	IV
Sphagnum rubellum	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	+	.	.	.	.	1	.	.	+	.	1	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	II	II	II	II
Mylia anomala	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	r	+	.	.	+	+	r	r	.	.	.	.	.	.	.	.	.	.	.	.	II	II	II
Other species																																																			
Aulacomnium palustre	.	.	.	.	.	.	.	1	.	.	.	+	.	.	+	1	+	r	+	.	.	+	+	+	.	.	.	.	+	+	.	+	.	1	1	2	2	+	.	+	+	.	+	.	.	+	I	III	II	III	III	III

Table 5. Continued.

Relevé nr. in the table	1	2	3	4	5*	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21*	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	1a	1b	1	2a	2b	2
Cladonia sp.	.	r	.	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	II	I	II	II	I	I
Smilacina trifolia	.	.	.	.	.	r	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	+	1	+	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	I	II	.	II	II
Cladonia rangiferina	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	r	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	II	.	I	I	I	I
Carex rotundata	r	r	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	2	1	.	.	.	II	I	II	I	I
Sphagnum russowii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	r	.	.	.	.	.	r	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	II	II	II	I	I
Pohlia nutans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	+	r	.	.	.	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	II	II	I	I
Polytrichum jensenii	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	+	+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	I	.	+	I	II	I
Betula exilis	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	II	.	.	.
Cladonia sygia	.	1	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	II	II	II	II	.	.
Cladonia arbuscula	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	1	.	.	.	.	.	.	.	I	.	+	I	I	I
Cladonia amaurocraea	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	I	II	II	.	.	.
Aulacomnium turgidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	II	+	.	I	I	I
Dicranum undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	+	.	.	.	.	.	.	I	.	.
Spiraea salicifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	.
Pinguicula villosa	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	+	.	+	+	+
Sphagnum fimbriatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	I	I	I
Warnstorfia trichophylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.
Equisetum sylvaticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	r	.	.	.	.	.	.	.	.
Dicranum polysetum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.
Peltigera sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Sphagnum compactum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	+	+

Note. Species found in 1 relevé: *Cadophogeia muelleriana* (35 r), *Cadophogeia* sp. (37 r), *Cadophogeia sphagnicola* (15 r), *Carex minuta* (18 +), *Cephalozia connivens* (23 r), *Cetraria laevigata* (39 r), *Cladonia crispata* (6 +), *Cladonia stellaris* (41 +), *Dicranum hardmovii* (24 +), *Dicranum montanum* (23 r), *Iris laevigata* (1 r), *Lycopodium dubium* (37 r), *Myrica tomentosa* (8 r), *Peltigera horizontalis* (40 +), *Sphagnum angustrowii* (37 +), *Sphagnum orientale* (46 r), *Sphagnum papillosum* (6 r), *Spiranthes sinensis* (45 r).

GPS coordinates (WGS 84) (N, E) and dates: **1** – 51.83905, 139.65541, 14.08.2025; **2** – 52.01122, 139.59741, 18.08.2025; **3** – 51.83729, 139.65316, 14.08.2026; **4** – 52.00517, 139.58806, 18.08.2025; **5** – 51.84067, 139.65498, 14.08.2025; **6** – 51.91055, 139.77385, 14.08.2025; **7** – 51.84014, 139.65536, 14.08.2025; **8** – 51.99819, 139.69468, 19.08.2025; **9** – 52.01155m 139.59801, 18.08.2025; **10** – 51.83924, 139.65533, 14.08.2025; **11** – 52.01415, 139.60245, 18.08.2025; **12** – 51.99810, 139.69675, 19.08.2025; **13** – 52.00502, 139.58800, 18.08.2025; **14** – 51.99878, 139.67856, 19.08.2025; **15** – 52.01479, 139.60333, 18.08.2025; **16** – 52.13191, 139.73543, 20.08.2025; **17** – 52.13195, 139.73499, 20.08.2025; **18** – 51.99875, 139.67900, 19.08.2025; **19** – 51.94073, 139.79376, 13.08.2025; **20** – 51.83759, 139.65343, 14.08.2025; **21** – 52.01228, 139.79146, 16.08.2025; **22** – 52.04031, 139.85304, 16.08.2025; **23** – 51.83697, 139.65291, 14.08.2025; **24** – 51.93838, 139.79261, 13.08.2025; **25** – 51.93880, 139.79297, 13.08.2025; **26** – 52.01474, 139.60490, 18.08.2025; **27** – 51.83677, 139.65637, 14.08.2025; **28** – 51.91533, 139.76367, 17.08.2025; **29** – 51.91583, 139.77610, 17.08.2025; **30** – 51.91614, 139.76713, 17.08.2025; **31** – 51.83670, 139.65671, 14.08.2025; **32** – 52.04040, 139.85307, 16.08.2025; **33** – 52.00188, 139.58670, 18.08.2025; **34** – 51.94098, 139.79312, 13.08.2025; **35** – 52.01253, 139.79187, 16.08.2025; **36** – 52.04028, 139.85592, 16.08.2025; **37** – 52.03984, 139.85550, 16.08.2025; **38** – 52.26676, 21.08.2025; **39** – 52.26781, 140.26295, 21.08.2025; **40**– 52.26765, 140.26176, 21.08.2025; **41** – 52.26684, 140.26258, 21.08.2025; **42** – 52.26817, 140.26306, 21.08.2025; **43** – 52.26779, 140.26182, 21.08.2025; **44** – 52.25203, 140.21159, 21.08.2025; **45** – 52.25215, 140.21207, 21.08.2025; **46** – 52.25172, 140.21183, 21.08.2025.

Authors. E.D. Lapshina (**E** – in the author's relevé nr.), I.V. Filippov (**F**).

* – nomenclatural types (holotypes).

mainly by secondary communities at different stages of post-fire recovery, as indicated by the highly sparse tree stand, standing dead trunks, and charred stumps. Only occasionally do small groups or solitary living *Larix cajanderi* trees occur, reaching 12–14 m in height and trunk diameters of about 15–20 cm; however, even single trees are often absent. In some such areas, weak regeneration of larch is observed, with saplings 0.5–1.5 m tall.

In terms of species composition and the structure of the lower layers, larch open woodlands and the open dwarf shrub–*Sphagnum* communities formed in their place are similar to one another. Scattered individuals of *Betula divaricata* (1–5 %) form the low shrub layer (30–50 cm tall). The dense dwarf shrub layer (40–80 %), 10–15(20) cm tall, is dominated by *Ledum palustre* and *Chamaedaphne calyculata*, sometimes with a noticeable participation of *Vaccinium uliginosum*. The cover of *Eriophorum vaginatum*, when present, varies from 1 to 15 %. *Vaccinium vitis-idaea*, *Oxycoccus microcarpus*, *Rubus chamaemorus*, and *Drosera rotundifolia* occur at low abundance but with high constancy, while *Carex globularis* and *Smilacina trifolia* are encountered more rarely. In the moss layer, *Sphagnum fuscum* and *S. alaskense* codominate in varying proportions, accompanied by minor admixture of *Sphagnum balticum*, *S. capillifolium*, *Aulacomnium palustre*, and *Polytrichum strictum*.

Distribution and ecology. Communities of the association occur widely on gentle slopes and flat surfaces of river terraces along the periphery of large mire systems. They are supplied mainly by atmospheric precipitation and surface runoff waters. Cottongrass tussocks, *Sphagnum* hummocks, and narrow microdepressions between them form the surface microtopography in most communities. The relative microrelief amplitude is about 20 cm.

Based on the dominance of different *Sphagnum* species, two variants are distinguished within the association: typica and Sphagnum alaskense.

Variant typica (Table 5, rel. 19–25) is characterized by the dominance of *Sphagnum fuscum* in the moss layer. It represents a more advanced stage of mire development associated with peat accumulation and decreasing mineral nutrient availability.

Variant Sphagnum alaskense (Table 5, rel. 26–37) differs by the substantial admixture or even dominance of this species. This variant includes both near-natural and

Table 6. Synoptic table of the syntaxa of mire communities in of the Udyl' Nature Reserve and the adjacent territories

Class	I	II						III						?	
Number of releves	17	2	5	4	17	7	32	7	9	33	18	19	3	3	3
Syntaxon number	1	2	3	4	5	6	7	8	9	10	12	11	13	14	15
Diagnostic species of the ass. Sphagno orientale–Caricetum obtusi and the all. Carici minutae–Salicion brachypodae															
Calamagrostis langsdorffii	**V^{3}**	.	.	.	.	.	.	.	.	I^{r}	.	.	.	2^{+}	3^{1}
Carex minuta	**V^{2}**	.	.	.	.	.	.	.	II^{+}	I^{+}	.	I^{+}	.	.	.
Sphagnum orientale	V^{1}	.	V^{2}	.	I^{r}	.	I^{+}	.	.	.	.	.	.	.	.
Comarum palustre	V^{1}	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix brachypoda	IV^{2}	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spiraea salicifolia	IV^{2}	.	.	.	.	.	.	.	.	.	.	.	.	3^{r}	.
Warnstorfia pseudostraminea	IV^{+}	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Betula ovalifolia	IV^{1}	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Glyceria spiculosa	IV^{+}	.	II^{+}	2^{+}	.	I^{r}	.	.	IV^{+}	I^{+}	.	.	.	.	.
Salix myrtilloides	III^{+}	.	IV^{+}	1^{+}	.	.	.	.	III^{+}	.	.	.	.	1^{+}	3^{+}
Climacium dendroides	III^{+}	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sanguisorba parviflora	III^{+}	.	.	.	.	.	r^{r}	.	.	I^{r}	.	.	.	.	.
Lysimachia thyrsiflora	III^{+}	2^{+}	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium trifidum	III^{+}	2^{+}	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum obtusum ***S-C***	V^{3}	**2^{5}**	V^{3}	1^{+}	.	I^{+}	.	.	I^{+}	.	.	.	.	.	.
Diagnostic species of the com. type *Equisetum fluviatile–Sphagnum obtusum*															
Equisetum fluviatile	.	2^{2}	IV^{+}	3^{+}	.	.	.	.	II^{r}	.	.	.	.	.	.
Carex chordorrhiza ***S-C***	I^{+}	2^{+}	III^{+}	.	.	.	.	.	V^{+}	.	.	.	.	.	.
Carex lasiocarpa ***S-C***	.	2^{+}	V^{+}	.	.	.	.	.	V^{1}	.	.	.	.	.	.
Lobelia sessilifolia	.	2^{+}	.	3^{+}	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of the Sphagno obtusi–Caricetum meyerianae and the all. Stygio–Caricion limosae															
Carex meyeriana	.	.	V^{2}	4^{2}	.	.	.	.	.	.	.	.	.	.	.
Utricularia minor	.	.	V^{+}	2^{+}	II^{+}	.	.	.	.	.	.	.	.	.	.
Juncus stygius	.	.	IV^{+}	4^{+}	I^{+}	.	I^{r}	.	.	.	.	.	.	.	.
Eriophorum gracile	.	1^{+}	IV^{+}	2^{+}	.	.	.	.	.	.	.	.	.	.	.
Utricularia intermedia	.	.	V^{2}	4^{2}	V^{+}	III^{+}	III^{+}	.	.	.	.	.	.	.	.
Scheuchzeria palustris	.	.	V^{+}	3^{+}	III^{+}	.	III^{+}	.	II^{+}	.	.	.	.	.	.
Rhynchospora alba ***St-Cc***	.	.	.	3^{+}	V^{+}	III^{+}	IV^{+}	.	.	.	.	.	.	.	.
Iris laevigata	I^{+}	.	III^{+}	4^{+}	II^{+}	III^{+}	III^{+}	.	II^{r}	I^{+}	I^{r}	.	.	.	.
Hamatocaulis vernicosus	.	.	III^{+}	.	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of the all. Scheuchzerion palustris and its syntaxa															
Sphagnum majus	.	.	.	.	**V^{5}**	**V^{5}**	IV^{2}	.	.	.	.	.	.	.	.
Drosera anglica ***St-Cc***	.	.	.	.	V^{+}	IV^{+}	V^{+}	I^{+}	.	.	.	.	.	.	.
Sphagnum perfoliatum	.	.	.	.	V^{3}	.	II^{+}	.	.	.	.	.	.	.	.
Sphagnum papillosum	.	.	.	.	V^{+}	I^{+}	**V^{5}**	**V^{4}**	.	r^{+}	I^{r}	.	.	.	.
Carex rotundata	.	.	.	.	.	III^{+}	II^{+}	.	.	r^{r}	II^{r}	I^{+}	.	.	.
Eriophorum russeolum	I^{+}	.	III^{+}	.	.	III^{1}	I^{r}	.	.	.	.	.	.	.	.
Diagnostic species of the class Scheuchzerio–Caricetea nigrae															
Carex limosa ***Sch***	.	2^{1}	V^{+}	4^{+}	IV^{+}	V^{1}	V^{+}	II^{+}	.	.	.	.	.	.	.
Menyanthes trifoliata	.	2^{1}	V^{2}	4^{1}	IV^{+}	.	III^{+}	.	IV^{+}	.	.	.	.	.	.
Oxycoccus palustris	.	2^{2}	.	.	II^{+}	II^{+}	III^{+}	V^{+}	V^{1}	I^{+}	.	.	.	.	.
Pedicularis adunca	.	2^{+}	III^{+}	.	II^{+}	I^{+}	II^{+}	.	.	.	.	.	.	.	.
Diagnostic species of the syntaxa of the class Oxycocco–Sphagnetea															
Aulacomnium palustre	I^{+}	.	.	.	.	.	.	.	IV^{+}	III^{+}	II^{+}	III^{+}	2^{+}	2^{+}	1^{+}
Sphagnum angustifolium	.	.	.	.	.	.	.	.	V^{2}	I^{+}	I^{+}	II^{+}	3^{2}	3^{2}	.
Pogonia japonica	.	.	.	.	.	.	r^{r}	.	III^{r}	.	.	.	.	.	.
Myrica tomentosa	II^{r}	.	.	.	I^{+}	.	II^{+}	I^{1}	I^{+}	V^{3}	I^{r}	.	.	.	.
Pinus pumila	.	.	.	.	.	.	.	.	.	I^{+}	IV^{+}	I^{r}	1^{r}	3^{+}	.
Sphagnum capillifolium	.	.	.	.	.	.	.	.	.	I^{+}	III^{+}	IV^{+}	3^{2}	2^{1}	.
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	I^{+}	I^{+}	V^{+}	3^{1}	3^{2}	3^{+}
Mylia anomala	.	.	.	.	.	.	.	.	.	.	.	II^{+}	2^{r}	.	.
Diagnostic species of the class Oxycocco–Sphagnetea															
Andromeda polifolia ***S-C***	I^{r}	.	IV^{2}	2^{+}	I^{+}	.	V^{+}	V^{2}	V^{2}	V^{+}	IV^{+}	III^{+}	.	.	.
Sphagnum balticum ***S-C***	.	.	.	.	III^{+}	III^{1}	IV^{1}	V^{4}	.	V^{1}	IV^{1}	IV^{1}	.	.	1^{r}
Carex middendorfii	.	.	.	.	.	.	II^{+}	V^{3}	II^{+}	IV^{+}	V^{+}	II^{+}	.	.	.
Polytrichum strictum	.	.	.	.	.	.	.	.	II^{+}	V^{+}	V^{+}	V^{+}	.	.	.
Eriophorum vaginatum	.	.	.	.	.	.	.	.	.	IV^{+}	IV^{+}	IV^{1}	.	.	.
Rubus chamaemorus ***Ox-Em***	.	.	.	.	.	.	r^{+}	.	.	V^{1}	V^{3}	IV^{1}	.	.	.
Sphagnum lenense ***Sl***	.	.	.	.	.	.	r^{+}	II^{+}	.	III^{+}	V^{3}	II^{+}	.	.	.
Drosera rotundifolia	.	.	III^{+}	.	.	I^{+}	I^{+}	IV^{+}	V^{+}	V^{+}	V^{+}	IV^{+}	1^{+}	.	.
Oxycoccus microcarpus	.	.	.	.	.	.	r^{+}	II^{+}	II^{+}	V^{+}	V^{+}	III^{+}	3^{+}	.	.
Sphagnum fuscum ***Ox-Em***	.	.	.	.	.	.	.	.	III^{+}	IV^{+}	IV^{3}	V^{3}	3^{3}	.	.
Chamaedaphne calyculata	II^{+}	.	II^{r}	.	.	I^{r}	I^{r}	IV^{+}	V^{1}	V^{2}	V^{2}	V^{2}	3^{2}	.	.
Sphagnum alaskense	I^{+}	1^{+}	.	.	.	.	II^{+}	III^{2}	**V^{5}**	**V^{5}**	V^{2}	V^{3}	3^{+}	1^{1}	.
Betula divaricata	.	.	.	.	.	.	.	.	V^{2}	V^{+}	V^{1}	V^{+}	3^{2}	3^{1}	2^{+}
Ledum palustre	.	.	.	.	.	.	.	I^{+}	I^{1}	V^{2}	V^{2}	V^{3}	3^{4}	3^{2}	3^{2}
Vaccinium uliginosum	.	.	.	.	.	.	.	.	.	III^{+}	II^{+}	IV^{1}	.	1^{+}	3^{1}
Carex globularis	.	.	.	.	.	.	.	.	.	III^{+}	I^{+}	IV^{1}	.	.	.
Sphagnum rubellum	.	.	.	.	.	.	r^{r}	.	.	III^{+}	II^{+}	II^{+}	.	.	.
Other species															
Larix cajanderi	.	.	.	.	.	.	.	.	.	I^{r}	II^{+}	IV^{+}	3^{2}	3^{2}	3^{2}
Ledum hypoleucum	.	.	.	.	.	.	.	.	.	.	.	II^{+}	3^{+}	3^{2}	2^{+}
Cladonia sp.	.	.	.	.	.	.	.	.	.	.	I^{r}	I^{+}	3^{+}	.	.
Pleurozium schreberi	.	.	.	.	.	.	.	.	.	r^{r}	.	I^{+}	3^{1}	2^{+}	.
Peltigera aphthosa	.	.	.	.	.	.	.	.	.	.	.	.	2^{r}	2^{r}	.
Sphagnum girgensohnii s.l.	.	.	.	.	.	.	.	.	.	.	.	.	1^{1}	**3^{4}**	.

fire-damaged communities, in which the abundance of *Carex globularis* increases markedly (up to 5–30 %), while the frequency of *Drosera rotundifolia* and *Oxycoccus microcarpus* decreases.

Community type *Larix cajanderi–Sphagnum angustifolium* (Table 5, rel. 38–40; Table 6, syntaxon 13; Fig. 4, 5, cluster 13)

This community type represents oligotrophic dwarf shrub–*Sphagnum* larch open woodland mires (mari) on deep peat deposits (about 1.5–2 m thick) that have remained unburned for a long time.

The tree layer (5–10 %) is uneven-aged and 4–8 m tall. The dense dwarf shrub layer (60–70 %) is formed by *Ledum palustre*, 15–20 cm tall, with admixture of *Chamaedaphne calyculata*. Upper shrub layer (up to 1.2 m tall) is represented by *Betula divaricata* (5–30 %). Among herbaceous species, only *Carex globularis* is usually present, while *Vaccinium vitis-idaea* and *Oxycoccus microcarpus* occur with high constancy. *Sphagnum fuscum* dominates the moss layer, codominating with *S. angustifolium*. *Sphagnum alaskense*, *S. capillifolium*, as well as *Mylia anomala* and *Pleurozium schreberi*, occur at low abundance.

The communities were described from an isolated mire massif in the vicinity of Solontsy village, near the northeastern boundary of the reserve.

Dwarf shrub–*Sphagnum communities* on frozen peat mounds with *Sphagnum lenense*

Communities of frozen peat mounds dominated by *Sphagnum lenense* in such a southern region as the Lower Amur Basin are of relict character and are represented by a single association.

Carici middendorfii–Sphagnetum lenenses Lapshina ass. nov.

(Table 5, rel. 1–18; Table 6, syntaxon 12; Fig. 2F, Fig. 4, cluster 12; Fig. 5, clusters 12a, 12b)

The association comprises dwarf shrub–*Sphagnum* (*S. lenense*, *S. fuscum*) communities with *Pinus pumila* on frozen and partially or completely thawed peat ridges and mounds that have persisted to the present day within large mire systems of the Lower Amur Basin.

Holotypus: relevé 5 (author's number – 125F25ud) in Table 4, Khabarovsk region, Ul'chskii District, Udyl' Nature Reserve, 14.08.2025, author I.V. Filippov.

Diagnostic species: *Carex middendorfii*, *Pinus pumila*, *Sphagnum lenense*, *S. fuscum*.

Structure and composition. Large frozen peat mounds stand out within the mire by groups of sparsely distributed old stunted larch trees (up to 5–7 m tall) and *Pinus pumila* shrubs 0.5–1.5 m high.

Table 6. Continued.

Syntaxon number	1	2	3	4	5	6	7	8	9	10	12	11	13	14	15
Sphagnum girgensohnii s.l.	.	.	.	.	.	.	.	.	.	.	.	.	1^1	**3^4**	.
Equisetum sylvaticum	.	.	.	.	.	.	.	.	.	.	.	.	.	2^+	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	.	.	2^+	**3^5**
Betula platyphylla	I^r	.	.	.	.	.	.	.	.	.	.	.	.	1^+	3^1
Warnstorfia trichophylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2^r

Note. Species with constancy only II and I are not included in the table.

Associations / community types: 1 – Sphagno obtusi–Caricetum minutae, 2 – *Equisetum fluviatile–Sphagnum obtusum*, 3 – Sphagno obtusi–Caricetum meyerianae, 4 – *Utricularia intermedia–Carex meyeriana*, 5 – Sphagnetum perfoliati-majoris, 6 – Carici limosae–Sphagnetum majoris, 7 – Irido laevigatae–Sphagnetum papillosi, 8 – Sphagno papillosi–Caricetum middendorfii, 9 – Carici lasiocarpae–Sphagnetum alaskense, 10 – Chamaedaphno–Sphagnetum alaskense, 11 – Larici cajanderi-Sphagnetum fusci, 12 – Carici middendorfii–Sphagnetum lenenses, 13 – *Larix cajanderi–Sphagnum angustifolium*, 14 – *Larix cajanderi – Sphagnum gigensohnii* s.l., 15 – *Larix cajanderi–Polytrichum commune.*

Characteristic species (next to the name of the taxon): ***S-C*** – Scheuchzerio–Caricetea, ***St-Cc*** – Stygio–Caricetea limosae, ***Sch*** – Scheuchzerion palustris, ***Sl*** – Sphagnion lenense, ***Ox-Em*** – Oxycocco–Empetrion.

The dense (40–60 %) low dwarf shrub layer is formed by *Ledum palustre* and *Chamaedaphne calyculata*, sometimes with participation of *Vaccinium uliginosum* and *Andromeda polifolia*. An upper sublayer, 30–50 cm tall, is formed by shrub birches, mainly *Betula divaricata* and more rarely with a mix of *B. nana*. Among herbaceous species, *Rubus chamaemorus* predominates, while *Carex middendorffii*, *Eriophorum vaginatum*, and *Drosera rotundifolia* occur at low abundance. *Oxycoccus microcarpus* spreads across the surface of the moss carpet. A distinctive feature of communities with near-surface permafrost is the dominance of *Sphagnum lenense*, which is gradually replaced by *S. fuscum* in sites with prolonged persistence of seasonal frost. *Sphagnum alaskense* accompanies these species at lower abundance but with high constancy, whereas *S. balticum*, *S. capillifolium*, and *Polytrichum strictum* occur more rarely.

Distribution and ecology. The frozen peat ridges and mounds that have persisted to the present day are at different stages of degradation. As high ridges thaw and subside, dwarf shrub–*Sphagnum* communities dominated by *Sphagnum alaskense* with admixture of *Sphagnum fuscum* and *S. lenense* develop along their periphery on lower ridges. Scattered *Pinus pumila* shrubs are often retained in these communities. In typical communities, permafrost occurs at a depth of 40–50 cm.

Within the association, two variants are distinguished based on the dominant *Sphagnum* species: typica and Sphagnum fuscum. As additional relevés become available, their rank may be raised to subassociations or even separate associations.

Variant typica (Table 5, rel. 1–8) comprises dwarf shrub–cloudberry–*Sphagnum* communities dominated by *Sphagnum lenense*, whose cover varies between 60 and 95 %.

Variant Sphagnum fuscum (Table 5, rel. 9–18) differs by the predominance of this species in the moss layer and by the higher abundance of *S. alaskense*, varying from 5 to 70 %.

Vegetation of paludified larch forests and dwarf shrub–*Sphagnum* larch open woodland bogs

A distinct group is formed by relevés of paludified dwarf shrub–*Sphagnum* larch forests and open larch woodland bogs represented by two community types. All of them were recorded on small isolated mire massifs in the vicinity of the villages of Kol'chyem and Solontsy, near the northeastern boundary of the reserve, although the same community types also occur within the reserve itself.

Community type *Larix cajanderi–Sphagnum girgensohnii* s.l. (Table 5, rel. 41–43; Table 6, syntaxon 14; Fig. 4, 5, cluster 14)

This community type comprises paludified dwarf shrub–*Sphagnum* larch forests and open woodland mires (mari) on shallow peat deposits (up to 1 m, usually 20–50 cm thick) that have remained unaffected by fire for a long time. They differ by a taller tree stand, 10–16 m high, and by the absence of almost all species of the class Oxycocco–Sphagnetea, except for *Ledum palustre*, which forms a well-developed dwarf shrub layer (20–70 %) up to 40 cm tall, with a noticeable mix of *L. hypoleucum*. *Betula divaricata* shrubs 1.2–2.0 m tall form a sparser upper shrub sublayer. In the herb–dwarf shrub layer *Carex globularis* and *Vaccinium vitis-idaea* are usually present. In the moss layer, alongside *Sphagnum angustifolium*, a distinct species from the *S. girgensohnii* s. l. complex predominates, accompanied by *S. capillifolium*, *S. russowii*, and *Pleurozium schreberi*, whereas *Sphagnum fuscum* is scarce or absent.

Community type *Larix cajanderi–Polytrichum commune* (Table 5, rel. 44–46; Table 6, syntaxon 15; Fig. 4, 5, cluster 15)

This community type represents an early post-fire recovery stage of paludified dwarf shrub–*Sphagnum* larch forest. The tree layer (5–15 %) is formed by young *Larix cajanderi* and *Betula platyphylla* trees 3–7 m tall. Scattered taller (up to 15 m) dead larch trunks are scattered bearing traces of fire. The dwarf shrub layer (10–20 %) is formed by *Ledum palustre* with minor admixture of *L. hypoleucum* and *Salix myrtilloides*. Among herbaceous species, *Calamagrostis langsdorffii* is the most conspicuous (1–5 %). *Vaccinium vitis-idaea* and *Carex globularis* are common in the lower layer. *Polytrichum commune* dominates the continuous moss cover.

NMDS ordination and hierarchical clustering

NMDS ordination and hierarchical clustering revealed a clear separation of the entire set of mire vegetation relevés from the Udyl' Nature Reserve into distinct clusters (Fig. 4, 5). The largest of these correspond to the classes Scheuchzerio–Caricetea nigrae and Oxycocco–Sphagnetea. Shrub-tussock sedge communities occurring in the regularly flooded by lake and river zone occupy a somewhat isolated position. Their species composition cannot be assigned to any of the known classes, thus justifying the description of a new class.

Class Carici minutae–Salicetea brachypodae (Fig. 4, I)

The Far Eastern shrubby tussock-sedge communities of regularly flooded shoreline mires are most similar in ecology and physiognomy to the alliance Salicion cinereae Müller et Görs ex Passarge 1961 of the order Salicetalia auritae Doing 1962, which is currently treated as a distinct class – Franguletea Doing ex Westhoff in Westhoff et Den Held 1969 – both in Europe (Mucina et al. 2016) and in Russia (Morozova 2026).

In its current circumscription, the class Franguletea comprises shrubby (willow and alder-willow) herbaceous

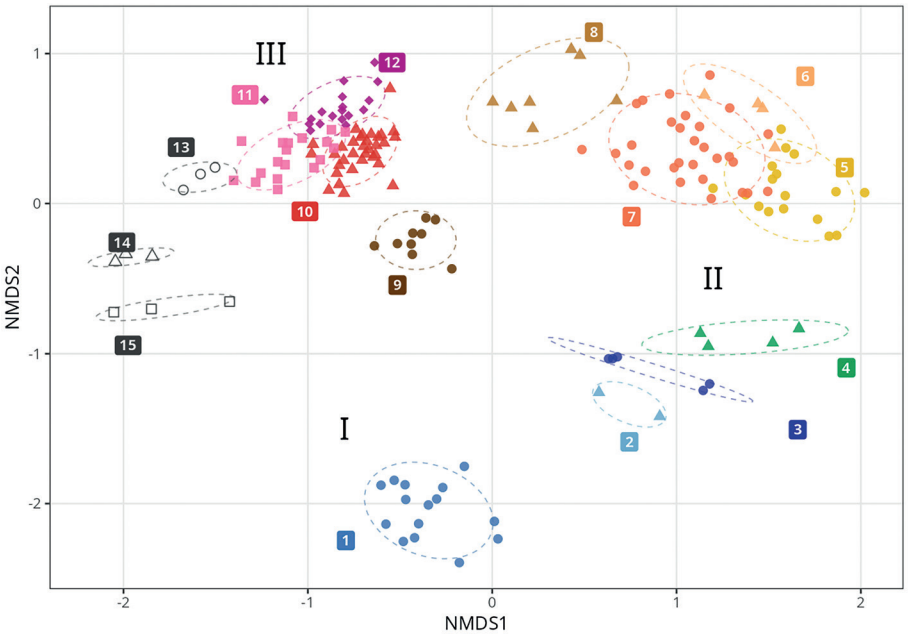

Figure 4 NMDS-ordination of the described syntax (stress = 0.093). Dashed ellipses show 75 % confidence intervals of relevé distribution. I – Carici minutae–Salicetea brachypodae: 1 – Sphagno obtusi–Caricetum minutae); II – Scheuchzerio–Caricetea nigrae: 2 – *Equisetum fluviatile–Sphagnum obtusum* com. type; 3 – Sphagno obtusi–Caricetum meyerianae; 4 – *Utricularia intermedia–Carex meyeriana* com. type; 5 – Sphagnetum perfoliati-majoris; 6 – Carici limosae–Sphagnetum majoris var. Utricularia intermedia; 7 – Irido laevigatae–Sphagnetum papillosi; III – Oxycocco–Sphagnetea: 8 – Sphagno papillosi–Caricetum middendorfii; 9 – Carici lasiocarpae–Sphagnetum alaskense; 10 – Chamaedaphno–Sphagnetum alaskense; 11 – Larici cajanderi–Sphagnetum fusci; 12 – Carici middendorfii–Sphagnetum lenenses; 13 – *Larix cajanderi–Sphagnum angustifolium* com. type. Community types with an uncertain class affiliation; 14 – *Larix cajanderi–Sphagnum girgensohnii* s.l.; 15 – *Larix cajanderi–Polytrichum commune*

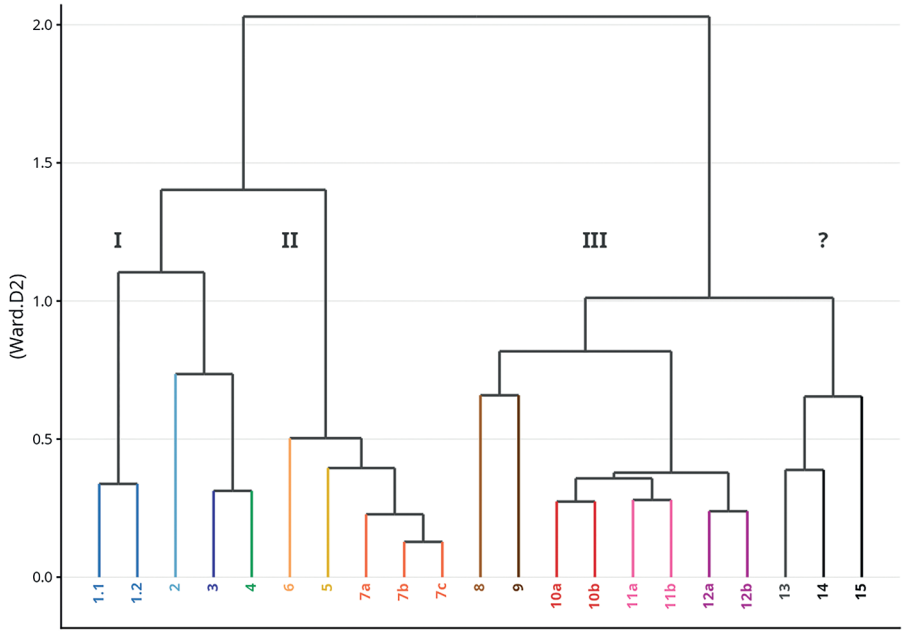

Figure 5 Dendrogram of floristic similarity among the described syntaxa in the Udyl' Nature Reserve. The numbers of syntaxa correspond to the numbers in Fig. 4 with subordinate units (subassociations and variants according to the Prodromus)

communities of waterlogged habitats in Europe and Western Siberia (Morozova 2026). The tussock-sedge communities described here, with a more or less developed shrub layer of willows, *Spiraea salicifolia* and shrubby birches, do not fully conform to the diagnosis of this class. Still less do they correspond, in terms of diagnostic species, to the large-sedge communities of the class Phragmito–Magnocaricetea Klika in Klika et Novák 1941, or to the geographically closer meadow communities of the Far Eastern class Calamagrostietea langsdorffii Mirkin in Akhtyamov et al. 1985. The latter encompassing wet, mesic and steppified meadow communities of the Far Eastern part of Eurasia (Akhtyamov 1995).

A comparison of species lists shows that of the 19 diagnostic species of the class Franguletea and the alliance Salicion cinereae (Morozova 2026), only two species – *Equisetum fluviatile* and *Salix myrtilloides* – occur sporadically and at low abundance in the communities described here. The floristic affinity of the flooded shrubby tussock-sedge communities with the syntaxa of the Far Eastern meadow class Calamagrostietea langsdorffii is limited to a single regionally widespread species, *Calamagrostis langsdorffii*.

For this reason, we propose the new alliance Carici minutae–Salicion brachypodae **all. nov.**, to which we assign the communities described here within the new provisionally proposed order Salicetalia brachypodae ord. prov. and the class Carici minutae–Salicetea brachypodae cl. prov. The names of the new alliance, order, and class are based on *Salix brachypoda* (Trautv. & C.A. Mey.) Kom. – a willow widespread in wet peatland habitats – and *Carex minuta* Franch. (Chepinoga et al. 2024), the dominant of the herb layer, which is also treated as the Far Eastern variety *C. cespitosa* var. *minuta* (Franch.) Kük. (Egorova 1999) or even regarded as a synonym of *Carex cespitosa* L. (POWO).

Diagnostic species of the alliance, order and class: *Betula ovalifolia*, *Carex minuta*, *Galium trifidum*, *Glyceria spiculosa*,

Polytrichum swartzii, *Salix brachypoda*, *Scutellaria regeliana*, *Sphagnum orientale*, *Spiraea salicifolia*, *Warnstorfia pseudostraminea*.

The nomenclatural type of the alliance (holotypus) is the ass. Carici minutae–Salicetum brachypodae **ass. nov.** (Table 1, rel. 1–17, present publication).

The new alliance replaces the European-West Siberian alliance Salicion cinereae in the south of boreal and mixed coniferous-broadleaved zone of the Russian Far East.

The communities of the alliance are well differentiated in multivariate space based on NMDS ordination (Fig. 4, syntaxon 1). They did not form an independent cluster with a high separation threshold on the dendrogram solely due to the relatively small number of relevés available (Fig. 5).

Class Scheuchzerio–Caricetea (Fig. 4, II)

The class Scheuchzerio–Caricetea nigrae comprises the largest number of associations distinguished in this study, which are subdivided into three alliances represented by different numbers of relevés.

The alliance Sphagno–Caricion canescentis is represented by only two relevés of horsetail–*Sphagnum* communities dominated by *Sphagnum obtusum*, described from a quaking mire as a community type (Fig. 4, Fig. 5, cluster 2).

A distinct group is formed by the waterlogged communities of meso-oligotrophic flarks and hollows of aapa mires dominated by the tussock-forming sedge *Carex meyeriana* (Fig. 4, Fig. 5, clusters 3, 4). In terms of habitat conditions and species composition, these communities most closely correspond to the alliance Stygio–Caricion limosae Nordhagen 1943 of the order Caricetalia nigrae Koch 1926. In its current concept, this alliance comprises a diverse range of low-productivity sedge and sedge-moss communities of flarks and hollows in transitional and aapa mires of northern Eurasia, developing under nutrient-poor, weakly acidic conditions (Lapshina & Lavrinenko 2025).

Given the more southerly geographical distribution of the principal dominant, *Carex meyeriana* – occurring in the southern regions of Central and Eastern Siberia, Primorye and the Priamurye, northeastern China, Korea, and the northern islands of Japan – as well as the diversity of communities formed by this sedge (Egorova 1999, Savich 1967), it may be expected that, with the accumulation of additional geobotanical relevés, communities with *Carex meyeriana* will eventually be segregated into a distinct alliance Rhynchosporo albae–Caricion meyerianae **all. prov.**

Another large cluster of the class Scheuchzerio–Caricetea nigrae is formed by communities traditionally assigned in the alliance Scheuchzerion palustris (Figs 4, 5, clusters 5, 6 and 7). In its current circumscription, this alliance comprises low-productivity *Sphagnum* communities of lawns and hollows of patterned oligotrophic raised bogs (Lapshina & Lavrinenko 2025). Despite relatively weak floristic differentiation due to species-poor composition, these communities are subdivided into two major groups: communities of waterlogged hollow with water level at the surface or 1–5 cm below it, and carpet communities dominated by *Sphagnum papillosum*, whose surface lies 10–15 cm above the water table. Statistical analysis of the relevés demonstrates their differentiation at a comparatively high level (Fig. 5, clusters 5, 6 and 7); however, the absence of their own diagnostic species does not allow the *Sphagnum papillosum*-dominated carpet communities to be distinguished as a separate alliance.

Within the Udyl' Nature Reserve, we assign three associations to the alliance Scheuchzerion palustris: Carici limosae–Sphagnetum majoris, Sphagnetum perfoliati-majoris **ass. nov.** and Irido laevigatae–Sphagnetum papillosi **ass. nov.** For the first association, which is widely distributed across the mires of the Eurasian boreal zone, we adopted the original name (Bogdanowsaya-Guiheneuf 1928) and brought it into accordance with the rules of the ICPN. In the mires of the Udyl' reserve it is represented by a distinct var. Utricularia intermedia with a small number of relevés.

The communities of the second association, Sphagnetum perfoliati-majoris **ass. nov.** (Fig. 5, cluster 5), occupy an intermediate position between the alliances Scheuchzerion palustris and Stygio–Caricion limosae, containing numerous species characteristic of the latter – *Carex limosa*, *Drosera anglica*, *Utricularia intermedia*, *U. minor*, *Rhynchospora alba*, *Juncus stygius*. Some of these species are common to both alliances. The association is distinguished by the presence of *Sphagnum perfoliatum*, the rare species southern in the southern Russian Far East. Similar communities with the participation and dominance of *S. perfoliatum* were previously described by us from northern Western Siberia within the association Sphagno perfoliati–Caricetum rotundatae (Lapshina et al. 2022), which we placed in the alliance *Stygio–Caricion limosae*. We currently assign the new association to Scheuchzerion palustris based on the dominance of *Sphagnum majus* in the moss layer; however, its syntaxonomic position may change as additional relevés become available.

The distinguishing feature of the third association, Irido laevigatae–Sphagnetum papillosi **ass. nov.**, is the formation of slightly raised lawns and low flat carpets composed of a continuous layer of the large moss *Sphagnum papillosum*, often with an admixture of other species. These communities develop at the contact zone between elevated hummocks or ridges and waterlogged hollows in raised and transitional mires in regions with moderately continental and monsoon climates, where they frequently cover extensive areas.

Class Oxycocco–Sphagnetea (Fig. 4, III)

The third major cluster correspondsthe class Oxycocco–Sphagnetea, within which five associations with six variants and one community type were distinguished in the Udyl' Nature Reserve (Fig. 4, Fig. 5, clusters 8–13).

Among the entire diversity of communities of the class Oxycocco–Sphagnetea in the Amur River basin, the most widespread are communities dominated by *Sphagnum alaskense*. This species is morphologically most similar to *S. divinum*, recently separated from the *Sphagnum magellanicum* Brid. complex (Hassel et al. 2018). Under the name *S. magellanicum*, however, this species (*S. alaskense*) was previously misidentified in all publications dealing with mire vegetation of the Amur River basin (Katz 1971, Prozorov 1961, 1974, Chakov & Zavgorud'ko 2008, Kutenkov et al. 2022).

Sphagnum alaskense was first described from Alaska (Andrus & Janssens 2003) and occurs in western North America (Alaska, British Columbia, Washington). At present, it has been identified from herbarium specimens throughout the Russian Far East from Chukotka to the southern Kuril Islands (Maksimov & Ignatova 2008). However, this species reaches its maximum development and phytocoenotic optimumin the southern taiga subzone and the mixed coniferous-broadleaved forest zone.

We propose to treat the Far Eastern communities dominated by *Sphagnum alaskense* as a distinct alliance, Sphagnion alaskense **all. nov.**, within the order Sphagnetalia medii.

The new alliance encompasses dwarf shrub–*Sphagnum* (*S. alaskense*) vegetation of raised bogs in the monsoon climate of the Russian Far East, replacing the Euro-West Siberian alliance Sphagnion medii in this region.

The recognition of the new alliance is justified primarily by geographical remoteness and by the regional peculiarities of habitat conditions and species composition. The ecological amplitude of the Sphagnion alaskense is broader than that of Sphagnion medii. The new alliance encompasses not only oligotrophic ombrotrophic habitats but also biotopes more or less regularly flooded during periods of monsoonal rainfall by lake water and nutrient-poor surface runoff. Floristically, communities of the alliance Sphagnion alaskense differ by the presence of *Larix cajanderi* in the tree layer, where present, vs. *Pinus sylvestris* in Sphagnion medii; among shrubs, by the occurrence of the Far Eastern birches *Betula ovalifolia* and *B. divaricata* vs. *B. nana*, sometimes also *Myrica tomentosa*; in the herb layer by presence of *Carex middendorfii* and *Smilacina trifolia*; and in the moss layer, by the dominance of *Sphagnum alaskense* vs. *S. medium/divinum*. Differentiating species relative to Sphagnion medii also include species demanding of mineral-rich conditions, such as *Carex lasiocarpa*, *C. minuta* and *Equisetum fluviatile*.

The nomenclatural type of the alliance (holotypus) is the ass. Chamaedaphno–Sphagnetum alaskense **ass. nov.** (Table 4, rel. 1–42, present publication).

Two further associations assigned to this alliance occupy distinct positions in both the ordination diagram and the hierarchical clustering dendrogram.

The association Sphagno papillosi–Caricetum middendorfii **ass. nov.** (Figs 4, 5, cluster 8) shows affinity to the alliance Scheuchzerion palustris through the dominance of *Sphagnum papillosum* and the participation of *S. balticum* in the moss layer. However, the dominance of *Carex middendorfii* in the herb layer and the constant presence, albeit in low abundance, of *Andromeda polifolia*, *Chamaedaphne calyculata*, *Drosera rotundifolia*, *Oxycoccus microcarpus*, *O. palustris* and *Sphagnum alaskense* indicates that this association belongs to the class Oxycocco–Sphagnetea. *Carex middendorfii–Sphagnum papillosum* communities are likewise assigned to this class in Japan (Hotes et al. 2004, Wang et al. 2025).

The association Carici lasiocarpae–Sphagnetum alaskense (Figs 4, 5, cluster 9) is characterised by the continuous *Sphagnum alaskense* moss carpet typical of the alliance, but differs markedly by the constant presence of a number of species of the class Scheuchzerio–Caricetea nigrae, most notably *Carex lasiocarpa*.

Certain difficulties arose in determining the placement of the dwarf shrub–*Sphagnum* communities of hummocks and ridges in raised bogs dominated by *Sphagnum fuscum* within higher syntaxonomic units (alliances and orders). Traditionally, these communities are assigned to the boreal alliance Oxycocco–Empetrion hermaphroditi (Mucina et al. 2016, Lapshina 2025). At the southern limit of their distribution in the Lower Amur basin, the dwarf shrub–*Sphagnum* communities with *Sphagnum fuscum* acquire certain features of the hemiboreal Far Eastern alliance Sphagnion alaskense **all. nov.** The sparse tree layer, where present, is formed by *Larix cajanderi* vs. *Pinus sylvestris*; *Empetrum hermaphroditum* (*E. nigrum* s. l.) is entirely absent; and *Sphagnum alaskense* forms a notable mix in the moss layer alongside *S. fuscum*, its abundance increasing and being maintained at high levels as a result of recurrent fires.

At the present stage of investigation, we distinguish these communities as the new association Larici cajanderi–Sphagnetum fusci **ass. nov.** on the basis of the dominance or conspicuous participation of *Sphagnum fuscum*, and treat it within the traditional alliance Oxycocco–Empetrion hermaphroditi.

We also assign the community type *Larix cajanderi–Sphagnum angustifolium*, with dominance of *Sphagnum fuscum* in the moss layer, to the same alliance (Figs 4, 5, cluster 13). Its isolated position in the dendrogram is merely a consequence of the small number of relevés.

In the northern boreal and southern tundra zones of northern Asia, the alliance Oxycocco–Empetrion hermaphroditi is replaced by communities of the alliance Sphagnion lenenses Lapshina et al. 2023 of the order Rubo chamaemori–Cladonietalia arbusculae Lapshina et al. 2023, which develop on permafrost peat mounds and raised bogs in the continental regions of eastern Siberia.

The diagnostic species of this alliance and the order Rubo chamaemori–Cladonietalia arbusculae are: *Aulacomnium turgidum*, *Betula nana*, *Cladonia arbuscula*, *C. amaurocraea*, *C. stygia*, *Dicranum laevidens*, *Empetrum hermaphroditum / E. subholarcticum*, *Flavocetraria cucullata*, *Eriophorum vaginatum*, *Orthocaulis binsteadii*, *Rubus chamaemorus*, *Sphagnum balticum*, *S. lenense*, *Vaccinium vitis-idaea* subsp. *minus* (Lapshina et al. 2023, Lapshina 2025).

In the mires of the Lower Amur region, permafrost peat mound communities dominated by *Sphagnum lenense* are of relict character. They are represented by a single ass. Carici middendorfii–Sphagnetum lenenses **ass. nov.**, which from the phytosociological perspective occupies an intermediate position between the alliances Oxycocco–Empetrion hermaphroditi and Sphagnion lenenses. Nevertheless, despite the southerly location of the communities described in the Udyl' Nature Reserve, the constant presence of *Sphagnum alaskense* and the absence or sporadic occurrence in low abundance of other diagnostic species of the alliance Sphagnion lenenses and the order Rubo chamaemori–Cladonietalia arbusculae, we provisionally placed the ass. Carici middendorfii–Sphagnetum lenenses **ass. nov**. into

the hypoarctic alliance Sphagnion lenenses on the basis of the dominance of *Sphagnum lenense* in the moss layer.

All three alliances – Sphagnion alaskense, Oxycocco–Empetrion hermaphroditi and Sphagnion lenenses – show limited differentiation in the hierarchical clustering dendrogram (Fig. 5, clusters 10–12). This is attributable to the narrowly regional character of the relevé dataset: the communities are united by a large block of class Oxycocco–Sphagnetea species, and the syntaxa described represent only the marginal portions of their respective alliances within the broader phytosociological system. With the inclusion of a larger number of relevés from a wider geographical area, the degree of differentiation among alliances will be substantially greater.

In describing the mire vegetation of the Udyl' Nature Reserve, we also provide a brief characterisation of *Betula divaricata*–dwarf shrub–*Sphagnum* larch open woodlands and paludified larch forests with a well-developed tree layer.

The community type *Larix cajanderi–Sphagnum girgensohnii* s.l. encompasses paludified dwarf shrub–*Sphagnum* larch forests and open woodlands (mari) dominated in the moss layer by *Sphagnum* cf. *girgensohnii*. Similar dwarf shrub–*Sphagnum* larch open woodland communities dominated by this *Sphagnum* species have been recorded by us in the northern forest zone of Western Siberia and in the montane forest belt of the Subpolar Urals (unpublished data). The small number of relevés currently available does not allow determination of their position within the higher syntaxa of the regional phytosociological system but these communities may be described at the rank of association with further accumulation of data. The post-fire successional vegetation – *Larix cajanderi–Polytrichum commune* is best retained at the rank of community type.

CONCLUSIONS

The Udyl' Nature Reserve is situated in the shouthern part of the middle taiga subzone and represents a typical area of the Lower Amur region, fully reflecting the main natural features of this territory. Until now, no phytosociological classification of mire vegetation based on the Braun-Blanquet approach has been carried out in the southern Russian Far East, with the exception of a few provisionally described syntaxa of minerotrophic herbaceous mire vegetation in the Jewish Autonomous Oblast and Amur Oblast (Akhtyamov 1987, Dymina 1980, 1985).

Analysis of 177 geobotanical relevés collected in the Udyl' Nature Reserve (Khabarovsk Krai, Ul'chskii District) yielded 10 associations, 2 subassociations, 10 variants and 3 community types belonging to 6 alliances, 4 orders and 3 classes – Carici minutae–Salicetea brachypodae, Scheuchzerio–Caricetea nigrae and Oxycocco–Sphagnetea. The affiliation of 2 community types to higher syntaxonomic units remains undetermined. Almost all associations (9 out of 10) are described as new, one has been nomenclaturally revised. Two new alliances are proposed.

The alliance Carici minutae–Salicion brachypodae **all. nov.** encompasses shrub tussock-sedge communities of minerotrophic mires regularly flooded by river and lake waters in the southern boreal and mixed coniferous-broadleaved zones of the Russian Far East. The new alliance, together with the new monotypic order and class proposed for it, replaces the Euro-West Siberian alliance Salicion cinereae and its corresponding higher syntaxa in the southern Russian Far East.

The alliance Sphagnion alaskense **all. nov.** encompasses dwarf shrub–*Sphagnum* vegetation of raised mires dominated by *Sphagnum alaskense* under the monsoon climate of the Russian Far East, replacing the Euro-West Siberian alliance Sphagnion medii in this region. The new alliance covers not only oligotrophic ombrotrophic habitats but also biotopes more or less regularly flooded by nutrient-poor lake and surface runoff waters during monsoon rains.

As new data accumulate and relevés from a wider area are included in the analysis – particularly from adjacent regions of the Russian Far East, northeastern China and Japan – the degree of differentiation among alliances and classes will be substantially greater.

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