

Aapa mire on the southern limit: A case study in Vologda Region (north-western Russia)

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SUMMARY

The aim of the research was to carry out a multidisciplinary study of a mire possessing a ribbed pattern typical for aapa mires and yet situated in the Vologda Region of Russia, which is farther south than the supposed southern limit of aapa mire distribution. The study shows that the mire lies in its own basin while being part of a complex mire system. Its microtopography is represented by three well-defined elements, namely strings, lawns and flarks, which condition the mosaic structure of the vegetative cover. In terms of flora and vegetation composition, this mire is very similar to Fennoscandian rich aapa mires although it lacks a number of typical western species. Dense, well-developed tree stands on strings are prominent features of this mire. The peat deposit is of fen (predominantly swamp) type. The stratigraphy of the peat deposit demonstrates its secondary nature and the young age of the strings. Dendrochronology showed that the phase of active development of the tree stand began about 200 years ago. Thus, the mire fully corresponds to the concept of an aapa mire, on the basis of (1) characteristic topography; (2) heterotrophic vegetation typical of aapa mires; and (3) secondary nature of the strings and their young age. The studied mire provides habitat for several rare species of vascular plants and mosses, and thus requires protection.

KEY WORDS: geography of mires, mire flora, mire vegetation, palaeoecology, peat deposit, Piyavochnoe mire system, *Liparis loeselii*

INTRODUCTION

Aapa mire is a term proposed by Cajander (1913) to denote large patterned or ribbed fens. It was first applied in the area of present Russia in Karelia and Murmansk Region by Zinserling (1934). A continuous belt of aapa mires within the European part of the USSR was recognised by T.K. Yurkovskaya (1974, 1980a) and, following Ruuhijärvi (1960), she made a suggestion about their pan-boreal range (Yurkovskaya 1992) that was later confirmed by analysis of satellite images (Yurkovskaya 2015). A multitude of studies by different authors had been devoted to aapa mires in the European North of Russia, of which the most complete review was made by Yurkovskaya (1992). Traditionally, three types of aapa mire massifs, differing in morphology and the composition of their vegetation, are distinguished within the territory of European Russia (Yurkovskaya 1992, Sirin *et al.* 2017): (1) northern European forest-tundra (Lapland) aapa; (2) Karelian ring (boreal Fennoscandian) aapa; and (3) Onega-Pechora (north-eastern) aapa. The first type was described in the Kola Peninsula forest tundra (Zinserling 1934) and was later found across

the whole European North of Russia (Yurkovskaya 1980a, 1980b, 1992). In aapa mires in the tundra and forest-tundra zones, boreal Cyperaceae are replaced by subarctic species and strings are usually treeless. The second type was confined to boreal Fennoscandia and the third to the Russian Plain east of Fennoscandia; the approximate border between these two regions is the Onega River (Kutenkov 2006, Kuznetsov *et al.* 2013). Typical of Karelian ring aapa mires is the string-flark pattern in the central parts surrounded by pine-dwarf shrub-*Sphagnum* vegetation. Northeastern aapa mires have a similar topographical structure. However, they frequently form large complex mire systems with ridge-hollow raised bogs. Northeastern aapa mires are distinguished by a continuous moss layer of mainly *Sphagnum* species in flarks, the absence of some west-subatlantic species (*Calluna vulgaris*, *Molinia caerulea*, *Carex livida*, *Sphagnum subfulvum*) and poorer floristic composition in general (Yurkovskaya 1992, Sirin *et al.* 2017). Antipin & Boychuk (2004) and Smagin (2012a) described transitional variants of these types. In northern Europe, an optimal territory for aapa mire development is known in the northern part of

Fennoscandia, where aapa is the dominant zonal type of mire massif and occupies tens of thousands of square kilometres (Ruuhijärvi 1960, 1983; Yurkovskaya 1992).

The southern limit of aapa mires in the European part of Russia has not yet been defined. Moen *et al.* (2017) have provided the most up-to-date map of the distribution of string-flark mires in Europe. However, there are indications in the literature that aapa mires also occur in more southerly locations. For example, around their southern distribution limit, aapa mires have been found in the north of Leningrad Region (Botch 1990), in the south-west and south of Arkhangelsk Region (Antipin *et al.* 2000, Smagin 2012a, Smagin *et al.* 2013), in the south-west of the Komi Republic (Goncharova 2007), and sporadically in the south of Karelia (Yurkovskaya 1992).

The question of whether aapa mires can be found in Vologda Region has remained open until recently. Antipin *et al.* (2000) provided a description of flark-string meso-oligotrophic complexes on the Il'inskoe Mire (situated within the Andoma Upland - the northernmost territory of Vologda Region, close to the border with Karelia and Arkhangelsk Region). The Il'inskoe Mire lacks bryales mosses typical for aapa mires as well as eutrophic species of *Sphagnum* and grasses. Nonetheless, the authors considered these complexes typical for Onega-Pechora aapa mires and supposed that the southern limit of this mire type passes through Vologda Region. However, our field studies did not confirm the presence of aapa mire in the part of the Andoma Upland that is included in Vologda Region, although mires resembling aapa were found nearby in Arkhangelsk Region. Smagin (1999) mentioned aapa complex flarks within Vologda Region but did not precisely indicate the location or give any detailed description of the mire. To the best of our knowledge, there are no other reports of aapa mires being present in this region.

We have been conducting studies of mires in the Vologda Region since 2000 and, in 2007, D.A. Philippov began purposefully searching for mires belonging to the aapa type. Primary interpretation of Landsat 5 and Landsat 7 satellite images yielded several objects to be confirmed or refuted by field studies. 'Aapa-like' mires have been studied within the Babaevskiy, Vashkinskiy and Vytegorskiy administrative districts in the north and north-west of the region. However, it was not until 2015 that we managed to find a mire in Vytegorskiy District that exhibits all the main characteristics of aapa. It is situated in the northern part of the large Piyavochnoe mire system near the village of Konetskaya. Satellite imagery revealed a general

string-flark pattern corresponding to that of 'classic' aapa mire and our field studies led us to the conclusion that this mire indeed belongs to the aapa type. Its southerly latitude increases the scientific interest.

The aim of the present work is to demonstrate, through analyses of spatial structure, flora and vegetation, that this mire belongs to the aapa type; to describe its features; and to reconstruct the formation history leading to the present-day appearance of the mire on the basis of peat stratigraphy and dendrochronological data.

METHODS

Study area

The study area is situated in the north of the Russian Plain at an absolute altitude of 110–165 m, and belongs to the zone of the Valdai Glaciation. The area is located within an ancient erosive lowland where a thick layer of pre-Quaternary deposits covers crystalline bedrock. The uppermost layer of deposits (70–90 m thick) belongs to the Moscovian stage (Carboniferous System) and is represented by marine, predominantly carbonate rocks (limestones, dolomites, marls) (Savinov & Romanova 1970, Skupinova 2007). Because the Carboniferous limestones and dolomites are relatively soluble rocks, the development of karst relief forms is characteristic for this territory. Modern karst formation is reflected in the dynamics of surface hydrological processes, particularly in the fluctuation of lake water levels and in the emergence and disappearance of surface watercourses and even lakes (Kulikovskiy 1894, Kozlov 2012).

The main relief-forming factors of the Quaternary period were the abrasion-accumulative actions of late glacial and post-glacial water bodies, a relict of which is Lake Beloe, as well as biogenic accumulation. Quaternary deposits of considerable thickness are represented by moraines, glaciolacustrine, lake, mire, alluvial and aeolian deposits. At present, the area is a flat, terraced, very weakly drained glaciolacustrine plain, slightly inclined towards Lake Beloe and belonging to the Volga-Baltic hydrological system. On a significant part of the territory, groundwater discharges into surface waters allowing widespread paludification (Savinov & Romanova 1970).

The study area is situated on the boundary between two global basins - the Atlantic Ocean basin and the inland Eurasian runoff area. The density of the river system is less than 0.5 km km⁻² and lakes occupy 10–15 % of the area. The average annual runoff is 300–350 mm. The area is characterised by

excessive humidity. Annual precipitation is 550–600 mm, 56–58 % of which falls in liquid form. Total solar irradiance is 101–105 W m⁻² and direct normal irradiance is 47–51 W m⁻². The average annual temperature is + 2.0 to + 2.5 °C. The duration of the frost-free period is 105–110 days. The sum of active temperatures is 1550–1600 °C. Prevailing winds are from the south-east in January and from the north-west in July (Skupinova 2007, Vorobyev 2007).

The study area belongs to the southern part of the middle taiga zone (Isachenko & Lavrenko 1980), within the West-Russian longitudinal phytogeographical sector (Yurkovskaya, 2012). The territory is highly paludified - the area of mires is 29.6 % (Filonenko & Philippov 2013). According to the mire regionality of Europe (Moen *et al.* 2017), the study area belongs to the typical raised bog region near the boundary between the Northeastern and East-Baltic subregions. The following mire types prevail: open and pine treed *Sphagnum* raised bogs with dwarf shrubs and cottongrass, open and treed by pine and birch herb-*Sphagnum* transitional mires, and rich-herb-sedge and sedge-hypnales eutrophic mires on peat soils (Abramova 1965).

The Piyavochnoe mire system is over 20 km long and covers an area of more than 80 km². The mire complex is composed of several raised bog and fen massifs (in this regard it is similar to a raised bog - aapa-mire system, according to Laitinen *et al.* 2007), and a series of intra-mire primary lakes and mineral islands. Part of the Piyavochnoe mire is included in the list of objects requiring protection (VRCPPD 1978) as a valuable natural source of cranberry. However, the status of the mire as protected within a specially protected natural territory was never adopted as an official regulation.

Field methods and data collection

Field investigations were carried out near the village of Konetskaya in the north-western part of the Piyavochnoe mire system (60° 46' 30" N, 36° 52' 00" E) in September 2015 and September 2016 by the authors of this article. Geobotanical relevés were made according to a standard technique (Philippov *et al.* 2017) with determination of species composition and projective cover (%) of species for individual layers of vegetation. Owing to the heterogeneity of the vegetation associated with the microrelief, relevés were made for the three main forms of microtopography (strings, lawns and flarks) on each sample plot within their natural contours. The area of relevé sites varied from 20 to 400 m². In total, 15 relevés were made for five sample plots, i.e. three relevés (string, lawn and flark) to each sample plot. Four sample plots were selected in different parts of

the main massif, representing the most widespread vegetation of each microtopographical element, and one sample plot was selected at a small site with similar patterning located to the south, across a raised bog within the Piyavochnoe mire system (Figure 1b, 1c). Specimens of higher plants were delivered to the herbaria of the Russian Academy of Sciences (RAS) Institute for Biology of Inland Waters (IBIW) and Karelian Research Centre (PTZ).

Peat thickness was measured on each sample plot. On three of the plots (2, 4, 5) peat samples were taken from strings and flarks for macrofossil analysis. Peat was sampled using a Russian peat borer (“torfyanoj bur Instorfä”). Each 25 cm of a core of the whole organic deposit was taken separately. If a well-defined peat stratification was noticed, samples were taken in accordance with the boundaries of layers. In total, 145 peat samples were taken from six cores. Botanical macrofossil analyses and decomposition degree analyses of the samples were made using a microscope at a precision of 5 % in the Laboratory of Mire Ecosystems, Institute of Biology, Karelian Research Centre RAS (Petrozavodsk, Russia) by N.V. Stoikina and E.L. Talbonen. Stratigraphical diagrams of peat composition were built using “Korpi” software (Kutenkov 2013).

Dendrochronology was studied on two sample plots (1 and 3), located at a distance of 700 m from each other. Cores were taken from the largest pine trees, 50 cm above the mire surface, using a Swedish increment borer. Additionally, cross-sections of standing deadwood were collected. Four cores and one cross-section were taken on Sample Plot 1, and seven cores and two cross-sections on Sample Plot 3. Cores and cross-sections were sanded with a sandpaper disc. Measurements were performed using a binocular microscope MSP-1 (LOMO PLC) followed by analysis of scanned images using Quantum GIS software. Measurements on cross-sections were performed in four radial directions, and the data were averaged. To restore synchronisation and precise timing of each increment, the entire series of chronologies was cross-dated. Absolute values of increments were used in the work, avoiding any standardisation. The total age of the trees was determined as the sum of the age determined from cores and the period of growth from the root collar to the height where it was cut, assuming a growth rate of 5 cm year⁻¹ (Vernodubenko 2011). Tree chronologies were compared with long-term total annual precipitation data from the nearest meteorological stations (Bulygina *et al.* 2014, Novakovskiy & Elsakov 2014).

Plant nomenclature follows the reviews by Tzvelev (2000) and Ignatov *et al.* (2006).

RESULTS

Structure

The main mire massif that we investigated, near the village of Konetskaya, lies within a separate basin in the very north of the Piyavochnoe mire system. The aapa type massif has an area of approximately 2 km²

and abuts a raised bog to the south; the boundary is located along a mineral ridge which outcrops as a chain of forested mineral islands (Figure 1b). The bog and aapa mire are separated by a marginal fen (lagg) which has formed along the chain of islands. To the west and north, the massif is bounded by narrow strips of marginal forested mire; down the

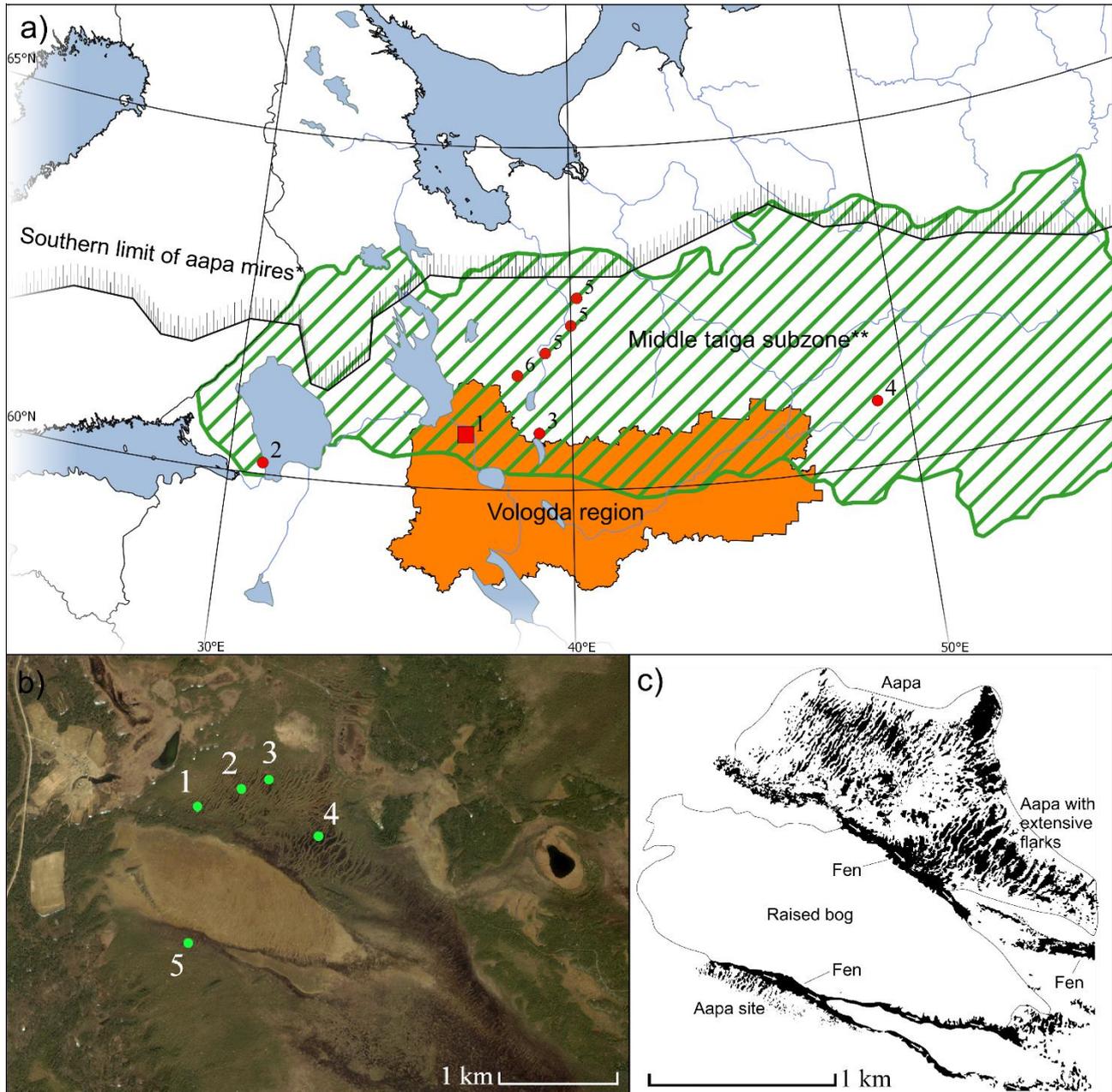


Figure 1. Locations of the study area and previously reported sites. a) Southern aapa mire locations: 1 = present study; 2 = Leningrad Region (Botch 1990); 3 = Arkhangelsk Region, near Vozhe Lake (Smagin 2012a); 4 = Komi Republic (Goncharova 2007); 5 = Arkhangelsk Region (Kuznetsov *et al.* 2013); 6 = Arkhangelsk Region (Smagin *et al.* 2013); *southern distribution limit of string-flark mires after Moen *et al.* (2017); **middle taiga subzone of European Russia after Isachenko & Lavrenko (1980). b) Sample plots (GeoEye satellite image obtained through the Yandex Maps service). c) Schematic representation of the Piyavochnoe mire system.

slope to the south-east, aapa complexes are replaced by fen which discharges into a tributary of the Vatkoma River.

The aapa mire has well-defined microrelief with alternation of *Sphagnum* strings, herb-hypnales flarks and low *Sphagnum* lawns (Figure 2). The strings are 20–35 cm high, 5–20 m wide and stretch across almost the whole mire massif for 400–600 m. The flarks are completely isolated and contain water 10–30 cm deep. Flark width varies from 1–3 m to 25–30 m and 30–55 m in the waterlogged south-eastern part of the massif. The length of the flarks is 150–400 m. Low (5–20 cm) *Sphagnum* lawns 2–5 m wide have developed along the downslope sides of strings. Some depressions between strings are completely covered by lawns. Isolated rounded hummocks up to 10 m in diameter have developed in large flarks. The proportions of different microforms vary between different parts of the mire. Flarks usually prevail,

reaching their maximum development in the south-eastern part of the mire.

An additional small (0.09 km²) site with a similar pattern is located to the south of the raised bog. The string-flark pattern here is less distinct, with lines of hummocks crossing flarks and low lawns occupying the main area. The flarks discharge into a marginal fen to the north.

Flora

In the aapa sites of the Piyavochnoe mire system, we identified a total of 112 species of higher plants (70 vascular plants and 42 mosses) (see Appendix). Our research allowed us to find four moss species never previously recorded in the north-west of Vologda Region (Philippov & Boychuk 2008), namely *Calliergon richardsonii*, *Cinclidium stygium*, *Dicranum bonjeanii* and *Meesia triquetra* (Sofronova *et al.* 2018).

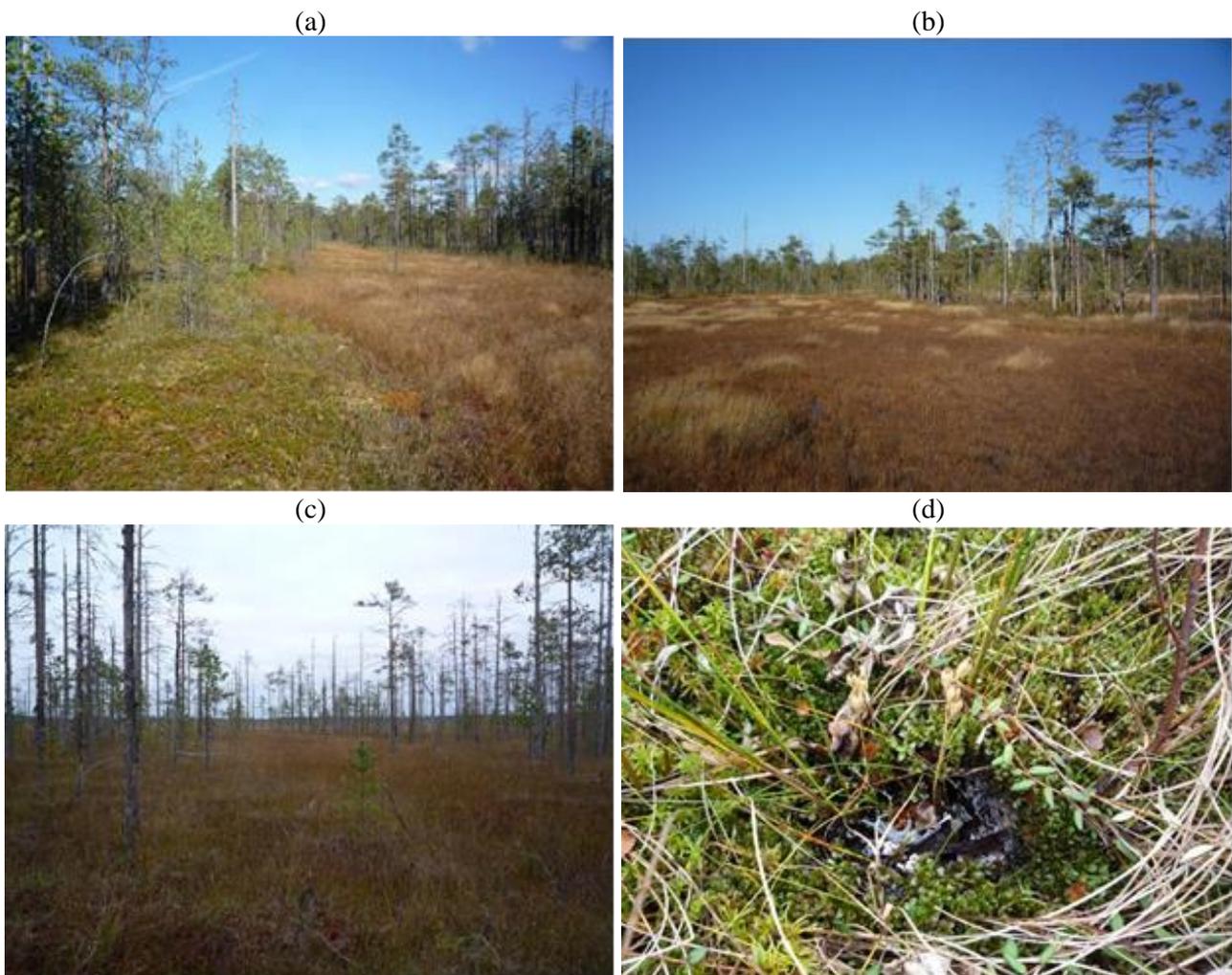


Figure 2. Piyavochnoe mire system: (a) string-flark microtopography (Sample Plot 2); (b) flark-dominated pattern (Sample Plot 4); (c) under-developed string-flark pattern (Sample Plot 5); (d) *Liparis loeselii* in autumn. Photos: D.A. Philippov.

The Piyavochnoe aapa sites were found to be inhabited by 17 species (13 vascular plants and four mosses) that are included in the second edition of the Red Data Book of Vologda Region (Suslova *et al.* 2013, GVR 2015). These species (listed according to their conservation status) were as follows: Critically Endangered (CR): *Juncus stygius*, *Liparis loeselii*; Endangered (EN): *Hammarbya paludosa*; Vulnerable (VU): *Carex omskiana*; Near Threatened (NT): *Drosera anglica*, *Rhynchospora alba*, *Trichophorum alpinum*, *Utricularia minor*; Data Deficient (DD): *Calliargon richardsonii*; biological control required: *Dactylorhiza incarnata*, *Epipactis palustris*, *Empetrum hermaphroditum*, *Moneses uniflora*, *Utricularia intermedia*, *Sphagnum contortum*, *S. jensenii*, *S. subsecundum*. No special studies of algal flora have been conducted on Piyavochnoe mire. However, analysis of several water samples has yielded the discovery of a new species of desmid, named *Euastrum kossinskiae* Anissimova et Philippov (Anissimova & Philippov 2018).

Vegetation

In accordance with the structure of the microrelief, the vegetation has a mosaic structure of string, lawn and flark communities which may be attributed to three different groups of associations (Appendix).

Strings

Strings are covered by pine - herb - shrub - *Sphagnum* communities. All strings possess a well-developed pine tree stand of 6–12 m height with up to 50 % canopy cover. A shrub layer of *Salix* spp., *Alnus incana*, *Frangula alnus*, *Juniperus communis* sometimes develops in the understorey. Also, single specimens of *Picea abies* are present.

The main species of the field layer are *Betula nana*, *Empetrum hermaphroditum*, *Carex lasiocarpa*, *Menyanthes trifoliata*; those of the ground layer are *Sphagnum fuscum*, *S. angustifolium* and *S. warnstorffii* (see Appendix). The *Sphagnum* mosses are arranged in the order given above along the centre–margin gradient of each string. Dwarf shrubs are well-developed in the centres of strings, while mesomorphic grasses are mainly confined to the marginal parts of strings. Complete isolation of sites with only oligotrophic species does not occur. An independent dense layer formed by *Phragmites australis* was seen on some strings.

In total, 67 species were encountered in the five relevés made for strings, which is a rather high number. Of these species, 29 were highly constant (registered in 3–5 relevés). Mean richness per plot was 37 species.

Lawns

Lawns encircling strings and low hummocks are formed by the minerotrophic *Sphagnum* moss species *Sphagnum warnstorffii*, *S. teres*, *S. centrale* and *S. sect. Subsecunda*. The main species of the field layer are *Andromeda polifolia*, *Carex lasiocarpa*, *Menyanthes trifoliata*, *Oxycoccus palustris*, *Scheuchzeria palustris* and *Trichophorum alpinum* (see Appendix). Low pines, *Betula nana* and *Phragmites australis* are also present in the lawns.

The total number of species recorded in lawns is 66, and one-third of them are highly constant. The average richness is 32 species per plot.

Flarks

In wet flarks, both the ground layer and (especially) the field layer are sparse. Among the herbs, together with *Carex lasiocarpa* and *Menyanthes trifoliata* (which are widespread across all microforms), *Rhynchospora alba*, *Trichophorum alpinum* and *Scheuchzeria palustris* cover large areas and *Utricularia intermedia* and *U. minor* are abundant underwater. *Scorpidium scorpioides* is a dominant species in the ground layer (see Appendix).

The total number of species recorded in flarks is 52. Twenty-one species are highly constant and the mean richness is 26 species per plot.

Peat deposit and palaeocommunities

The depth of the peat deposit increases from the margins to the central axis of the massif, where it reaches a depth of 190–660 cm below the flark surface. Peats of eutrophic fen type with a 25–35 % degree of decomposition are predominant. The main peat-forming species are sedges (*Carex lasiocarpa*, *C. limosa*, *C. chordorrhiza* and others), *Scheuchzeria palustris*, *Eriophorum* spp. and bryales (*Scorpidium* spp., *Meesia triquetra*, *Calliargon* spp.) with, to a lesser degree, eutrophic *Sphagnum* species, *Menyanthes trifoliata* and other species (Figure 3b).

Basal layers differ between sampling plots, reflecting various initial stages of mire formation. In the deepest part (Sample Plot 4), a layer of liquid clay with a high content of mire plant remnants including seeds of sedges underlies the peat deposit. The lower layer of the peat deposit, where wood macrofossils are almost completely absent, corresponds to the sedge - *Menyanthes* - hypnales community (Figure 4). At Sample Plot 2, mire formation started from a forest stage (Figure 3b). The basal layer of peat contains remnants of pine, birch, horsetail and other typical species for paludified forests. This layer contains charcoal particles and is abruptly replaced by a birch-sedge (*Carex lasiocarpa*) layer 10–15 cm from the mineral bottom. Birch then gradually

disappears from the communities, being replaced by fen peat forming species. On the southern aapa mire site (Sample Plot 5), mire formation apparently began from open sedge - *Scheuchzeria* fens; their peats are characterised by a high degree of decomposition and an abundance of sedge seeds (Figure 3b).

At all plots, the further course of mire development was accompanied by periodic alternations of the main peat-forming species while preserving the general fen character of vegetation. One of the most significant changes was registered at 200–210 cm below the flark surface at Sample Plot 2 and Sample Plot 4, where a rapid shift in the predominant peat-forming species from

Scheuchzeria palustris and *Eriophorum* spp. to sedges, *Menyanthes trifoliata* and *Hypnum* mosses occurred (Figure 3b). Similar changes were seen at Sample Plot 5 at depth 150 cm; although here, while the share of *Scheuchzeria* decreased, it was still among the main peat-forming species. Such changes reflect fluctuating flow and may be conditioned by the processes of karst development generally changing the hydrological situation on adjacent ground. At Sample Plot 2, the water supply was apparently so great that the aquatic plants *Nuphar* and *Sagittaria* began appearing in the communities, and their remnants along with sedges and *Menyanthes* were found at depths of 100–175 cm (Figure 4). At

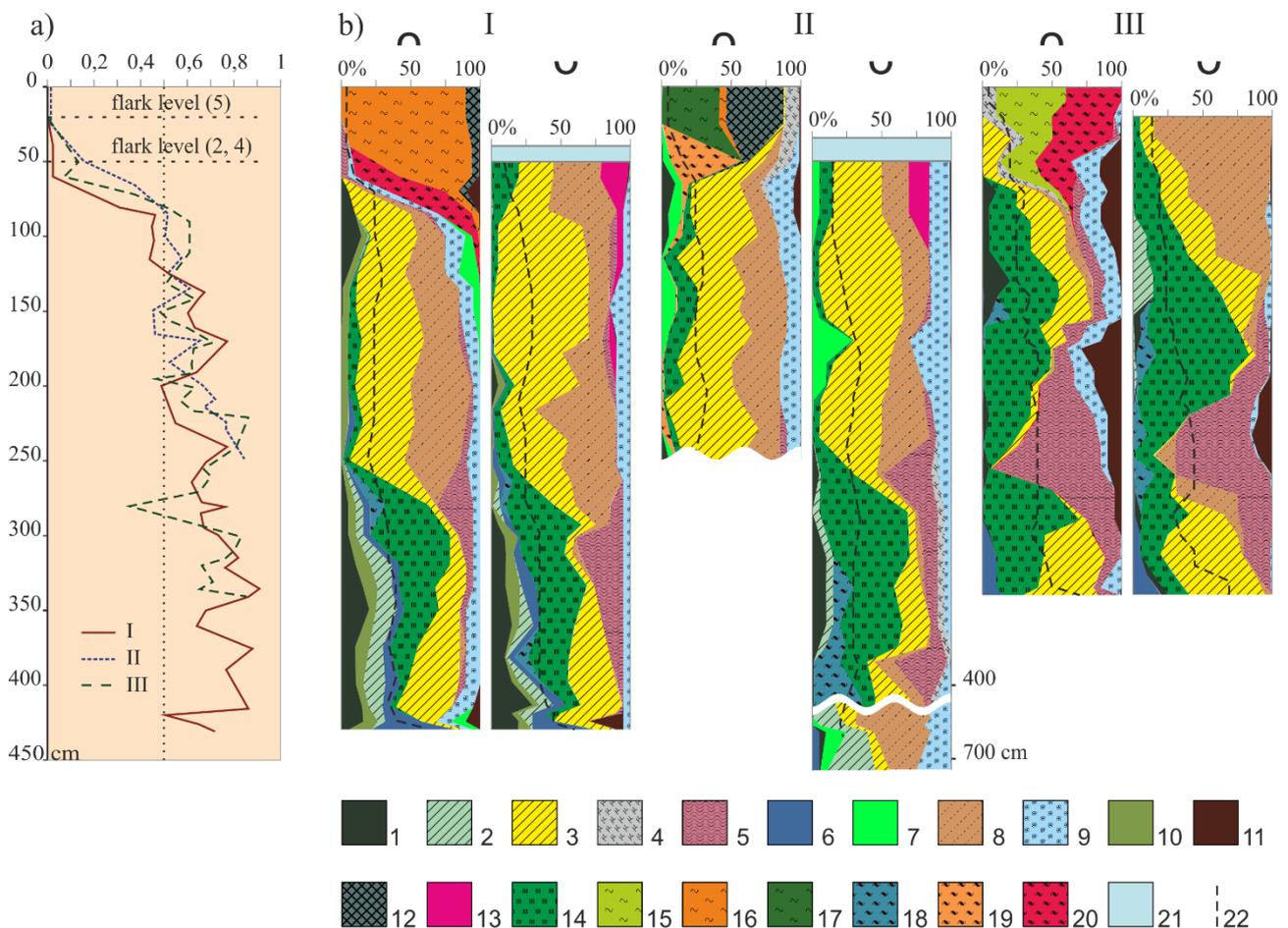


Figure 3. Macrofossil compositions of string and flark peat deposits. a) Similarity (Sørensen-Czekanowski's index) of the macrofossil compositions of string and flark peat deposits from three sample plots (for above-flark levels, data for flark-surface peat are used). b) Macrofossil compositions of string (∩) and flark (∪) peat deposits: I= Sample Plot 2; II= Sample Plot 4 (the uppermost 250 cm of a > 650 cm core of string peat was analysed, more detail is given in Figures 4 and 5); III= Sample Plot 5. Macrofossils (1–20): 1= *Betula*; 2= *Carex rostrata*; 3= *Carex* spp. (*C. lasiocarpa* + *C. limosa*, *C. chordorrhiza*, *C. omskiana*); 4= Dwarf shrubs; 5= *Eriophorum*; 6= *Equisetum*; 7= Herbs; 8= Hypnales (*Scorpidium scorpioides*, *S. cossonii*, *Meesia*, *Calliegon*, *Warnstorfia*, etc.); 9= *Menyanthes*; 10= *Phragmites*; 11= *Pinus*; 12= *Polytrichum* + *Aulacomium*; 13= *Rhynchospora* + *Baeothryon*; 14= *Scheuchzeria*; 15= *Sphagnum angustifolium*; 16= *S. fuscum*; 17= *S. russowii*; 18= *S. centrale* + *S. sect. Subsecunda*; 19= *S. teres*; 20= *S. warnstorffii*.

the present time, these species are absent from the studied part of the mire, although they are common and frequently abundant in different water bodies of the Vologda Region.

The next significant shift occurred in the near-surface layer of peat, reflecting the formation of string-flark complexes. On strings, the thickness of underdeveloped peat with a low degree of decomposition (5–15 %) formed by oligotrophic *Sphagnum* species (*S. fuscum*, *S. russowii*, *S. angustifolium*) is only 25–40 cm. Below, there are slightly more decomposed (10–25 %) eutrophic *Sphagnum* peats formed by *S. warnstorffii* and *S. teres*. In the flarks, the thickness of peat layers corresponding to the current vegetation is around 40 cm.

Parallel boring of strings and flarks showed marked differences in the upper layers along with identical structure of the main stratum of the peat deposit beneath, indicating the youth of the string-flark pattern. Sørensen-Czekanowski's index for flark and string peat layers lying at equal depths greater than 80 cm below the surface varies within a range of 0.5–0.9 (Figure 3a). We assume that these fluctuations

are related to the microdynamics of the vegetation sinusiae on the plots and, possibly, subjective errors of the analyst when visually estimating the proportions of macrofossils. Occasionally, recurrent fluctuations of the index within the range 0.4–0.5 indicate the formation of a mosaic of vegetation coenoses. However, an abrupt decrease of the Sørensen-Czekanowski index beginning at around 80 cm depth evidences the development of pronounced heterogeneity of vegetation cover. The surface layers of string and flark peat display strong differences in macrofossil composition.

Tree stands

Strings and isolated hummocks on Piyavochnoe mire are covered by relatively dense stands of *Pinus sylvestris* f. *uliginosa* Abolin, and a continuous canopy layer has formed in places where strings dominate the microrelief. The trees are 6–12 m tall with trunk diameters up to 20 cm (12 cm on average); canopy coverage on strings is up to 50 %, relative stand density is 0.3–0.5, and stock (determined visually) is up to 100 m³ ha⁻¹. The tree stands are unevenly aged but the main generation is the oldest, aged at 160–200 years.



Figure 4. Peat macrofossil diagram for Sample Plot 4 (flark). Palaeocommunities: 1) *Carex lasiocarpa* + *Rhynchospora alba* - *Scorpidium scorpioides*; 2) *Carex lasiocarpa* - *Scorpidium scorpioides*; 3) *Carex lasiocarpa* + *Menyanthes trifoliata* + *Nuphar*; 4) *Carex* spp. - *Calliergon* + *Meesia*; 5) *Scheuchzeria palustris* + *Eriophorum*, 6) *Carex lasiocarpa* - *Sphagnum centrale*; 7) *Carex* spp. - *Sphagnum* spp. + Bryales, 8) *Carex* spp. - Bryales; 9) *Carex rostrata* + *Menyanthes trifoliata* - *Calliergon*.

Many of the large trees are dead, but fallen pines are relatively rare and all of the same age. The largest trees stand in rows along the central axes of strings, while the margins of strings are covered by smaller trees of a younger generation. Tree stands are depressed to the highest degree in the more waterlogged south-eastern part of the mire (Sample Plot 4). The fraction of dead wood is greater here with almost all large trees being dry. Live trees are less than 6 m tall and belong to *Pinus sylvestris* f. *litwinowii* Sukacz.; many large trees have dry tops.

At the same time, pine macrofossils are almost absent throughout most of the depth of the deposit. At Sample Plot 2, they are recorded in the basal layer, single fragments occur above that level, and it is only from a depth of 60–70 cm upwards in the string peat

that the fraction of pine reaches 10 % (Figure 3a). At Sample Plot 4, pine was registered in the admixture only in the upper one-third of the deposit, reaching 5 % in the string peat at a depth of 50–75 cm; in fact, the layer of wood-containing peat here is only just starting to be deposited (Figure 5). On the southern site (Sample Plot 5), remnants of pine are present in the layer of *Scheuchzeria - Eriophorum* peat at depth 160–275 cm then disappear, reappearing as a 5–15 % pine content in string peat at depth 50–110 cm. Pine remnants are almost completely absent from the upper peat layers in flarks.

The dendrochronological studies indicated three distinct periods of most-active development of tree stands: AD 1825(?)–1842, 1854–1864 and 1884–1904 (Figure 6). The first of these periods is reflected

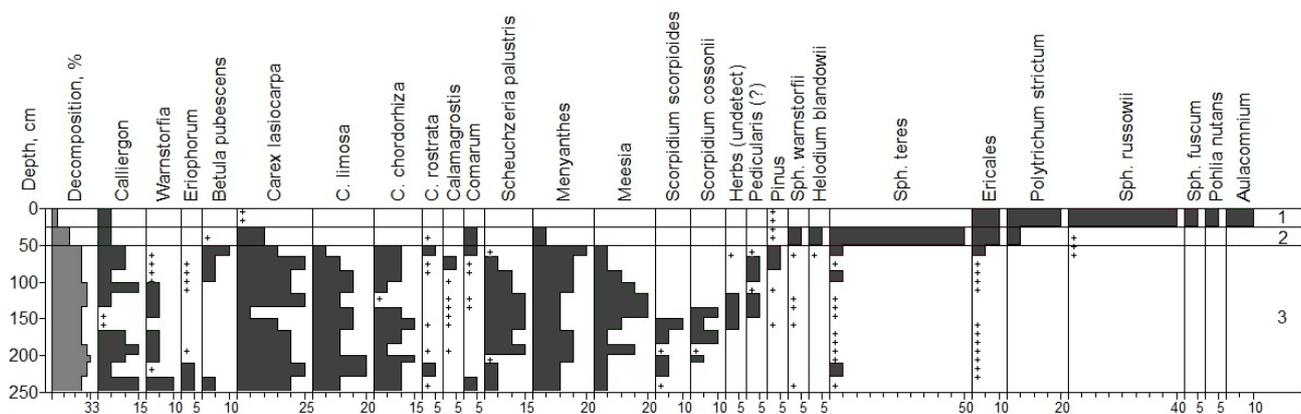


Figure 5. Peat macrofossil diagram for Sample Plot 4 (string; the upper 250 cm).

Paleocommunities: 1) *Ericales - Sphagnum fuscum* + *S. russowii*; 2) *Carex lasiocarpa - Sphagnum teres*; 3) *Carex* spp. + *Menyanthes trifoliata* - Bryales.

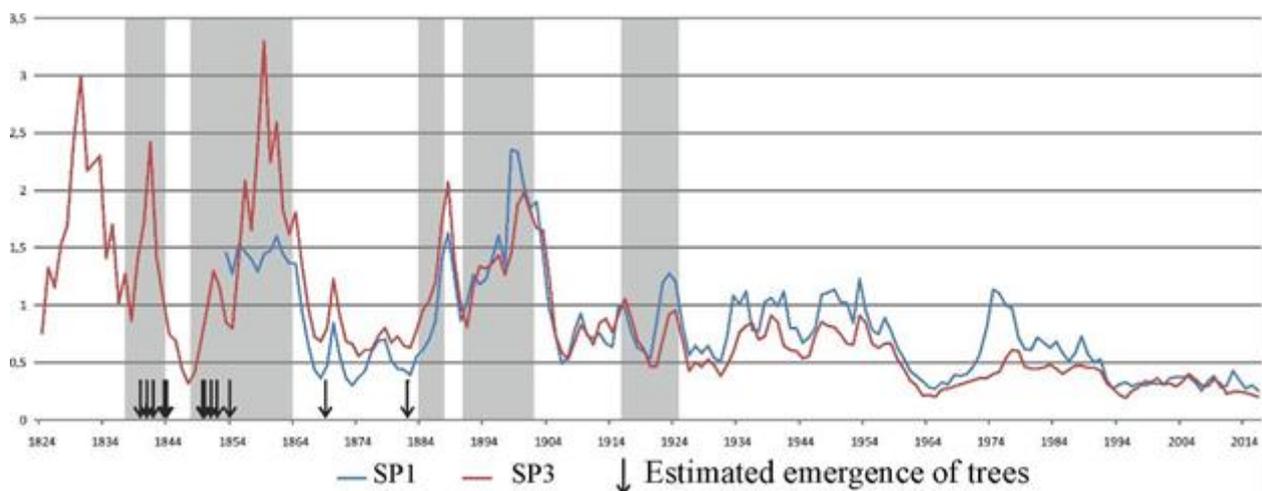


Figure 6. Generalised pine chronologies for Sample Plot 1 and Sample Plot 3. Grey bars mark periods with low (< 500 mm per year) precipitation; no precipitation data were available before the year 1836.

in the chronologies of only two trees but, according to the calculations, most of the other trees analysed established at the end of this period. The second period is recorded in most of the chronologies studied, with the three oldest trees showing a sharp increase in increments to 3–4 mm per year. The average increment for the third period was 1.5 mm per year and the maximum was 2–3 mm per year. By the end of this period the trees (except for the youngest ones) had, on average, reached half of their radius at the time of sampling. Thereafter, tree growth rates generally show a gradual downward trend.

DISCUSSION

Flora

Different types of mires in Vologda Region are inhabited by 308 species of vascular plants and 140 species of mosses (Philippov 2007, Philippov & Boychuk 2008, D.A. Philippov unpublished data). Thus, the Piyavochnoe aapa sites host 25 % of the combined flora of Vologda Region's wetland biotopes. Critically threatened (CR) species found in the study area were *Liparis loeselii* and *Juncus stygius*. *Liparis loeselii* was last recorded in 2013 on a small spring fen in Belozerskiy District (approximately 100 km to the north of our record) (Efimov *et al.* 2014). We found only eleven specimens of this orchid on Piyavochnoe, growing at one spot on the edge of a hypnales flark. Another noteworthy finding was *Juncus stygius*. Over the last ten years, this species has been recorded only on four large mires in the western part of Vologda Region, and it was recently considered to have disappeared from the region (Philippov 2008). The population of *J. stygius* on Piyavochnoe is numerous and its discovery, therefore, creates an opportunity to facilitate the survival of this species in Vologda Region through conservation of the mire in its natural form and condition. All of the other rare species that we have mentioned occur sporadically across the whole or almost the whole territory of Vologda Region, although exclusively on minerotrophic fens and, as a rule, with small or low abundance in the coenopopulations. Almost all of them are abundant in their typical communities within the Piyavochnoe mire system. The exceptions are *Carex omskiana*, *Dactylorhiza incarnata*, *Epipactis palustris*, *Calliergon richardsonii* and *Sphagnum jensenii*, which are found only locally. This may result from lack of data, and further research may reveal additional new locations on the mire.

Vegetation

Strings

The species composition of the string plant communities is close to the hummocky oligotrophic association *Betula nana* - *Carex lasiocarpa* - *Sphagnum fuscum* that is typical for the high strings of Karelian aapa mires as described by Kuznetsov (2005), as well as for the *Menyantho trifoliata* - *Sphagnetum fusci* Blagoveschenskiyi 36 em. Boč 90 association mentioned by Botch & Smagin (1993) and Smagin (2012d) for aapa mires of the European North of Russia in general. Communities of this association represent a succession from grass - *Sphagnum* meso-eutrophic to oligotrophic communities (Kuznetsov 2005). However, the stands of tall *P. sylvestris* f. *uliginosa* Abolin trees seen on Piyavochnoe provide a contrast with Fennoscandian communities, where short *Pinus sylvestris* f. *willkommii* Sukacz is typical. Piyavochnoe also lacks species that are generally less common in the plant communities of the region such as *Calluna vulgaris*, *Oxycoccus microcarpus*, *Trichophorum cespitosum* and *Molinia caerulea*, as well as *Sphagnum papillosum* which is cenotically substituted here by *S. centrale*. At the same time, the roles of several typical species for lawns and flarks (*Carex rostrata*, *Comarum palustre*, *Scheuchzeria palustris*, *Sphagnum warnstorffii*) are increased, evidencing a rather strong mineral nutrition effect. Another typical species for strings is *Dicranum bonjeanii*. Thus, the vegetation of the Piyavochnoe strings differs significantly from that of string types described for Fennoscandian mires (Ruuhijärvi 1960, 1983, Laitinen *et al.* 2005).

One group of string species (*Vaccinium vitis-idaea*, *Melampyrum pratense*, *Moneses uniflora*, *Sphagnum girgensohnii*, *S. russowii*) is more characteristic of forest communities. The presence of this group, along with *Bistorta major* and a large suite of other forest species, brings these communities closer to the *Sphagnum warnstorffii* - (Carici cespitosae-) Pinetum subass. *bistortaetosum* forest of Kucherov & Kutenkov (2011), which is an Eastern European subassociation of rich (spring) herb-rich - *Sphagnum* forested mires with temperate continental climate. Such rich forested mire communities were also recorded in the marginal parts of the Piyavochnoe mire system.

Lawns

The lawn communities are similar to the *Carex lasiocarpa* - *Sphagnum warnstorffii* hummock association (including the sub-association with *Sphagnum teres*) of Kuznetsov (2006), which is

typical for aapa mires from Central Europe to the Urals. The importance of the hummock species *Drosera rotundifolia* and *Sphagnum fuscum* in the species composition of lawns on Piyavochnoe is lower than in Fennoscandian communities of this association Kuznetsov (2006), while *Trichophorum cespitosum* and *Sphagnum subfulvum* (a rare species in Vologda Region) are absent. In contrast, other species such as *Salix rosmarinifolia*, *Carex dioica*, *Melampyrum pratense*, *Pedicularis palustris*, *Straminergon stramineum*, *Helodium blandowii*, *Sphagnum centrale* and *Warnstorfia exannulata* have increased presence, evidencing richer nutrient conditions. The average species richness of 32 species per plot is much greater than seen in this association in Karelia. A special characteristic of the Piyavochnoe site is the absence of *Sphagnum papillosum* (which is typical for aapa mire lawns) and the consequent absence of all plant associations governed by this species, which prefers poorer conditions (Maksimov 1980, Yurkovskaya 1992, Eurola & Huttunen 2006) and is replaced here by *Sphagnum centrale*.

Flarks

The flark communities are similar to the *Carex lasiocarpa* - *Scorpidium scorpioides* association (Kuznetsov 2006), which is confined to the fens and flarks of eutrophic aapa mires. According to the ecological-floristic classification, these communities are close to the *Menyantho* - *Rhynchosporium albae* Smagin 1999 association defined by Smagin (1999, 2012b), which is more characteristic for western aapa mires. However, according to the composition of the moss layer, it is closer to *Comaro palustris* - *Caricetum lasiocarpae* Smagin 2012, which is widely distributed on rich fens and aapa mires throughout the taiga zone of European Russia (Smagin 2012c). The poor-fen species *Eriophorum angustifolium* and *Carex rostrata* are less common and less abundant in flarks on Piyavochnoe mire. Instead, species indicating moving surface water (Eurola & Huttunen 2006: *Eriophorum gracile*, *Pedicularis palustris*), wet conditions in general (*Utricularia intermedia*, *U. minor*), slightly higher nutrient status of flarks (*Juncus stygius*, *Trichophorum alpinum*, *Warnstorfia exannulata*) and conditions at the margins of flarks (*Hammarbya paludosa*), along with rich-fen specialists (*Aneura pinguis*, *Campylium stellatum* s.l., *Sphagnum contortum*), are common on Piyavochnoe. *Cinclidium stygium*, *Calliergon giganteum*, *Hamatacaulus vernicosus* and *Meesia triquetra* are common at Sample Plot 5, where flarks have not reached the stage of complete partition, and in the fens between raised bog and aapa sites. The great

abundance of *Rhynchospora alba* observed on Piyavochnoe is a characteristic feature of western aapa mires, although this species has been found on strings and flarks in both poor and rich aapa mires in locations farther to the east (Yurkovskaya 1992, Antipin & Boychuk 2004, Kutenkov 2006, Goncharova 2007, Smagin 2012a). The abundance of *Scorpidium scorpioides* in the Piyavochnoe flarks is unusual. This typical species for eutrophic flarks on aapa mires has been found in abundance on mires in the south of Arkhangelsk Region (Smagin 2012a, Kuznetsov *et al.* 2013). However, it was not recorded on aapa mires situated at the southern limit of their distribution (Botch 1990, Goncharova 2007, Smagin *et al.* 2013). The total number of species registered in flarks (52) is lower than observed in this association in Karelia (Kuznetsov 2005), but rather high considering the small number of sample plots. The mean richness (26 species per plot) is much higher than in Karelia (15 species).

String-flark pattern formation and development of tree stands

Dense stands of *Pinus sylvestris* f. *uliginosa* Abolin are prominent features of strings on this mire, even in comparison with other aapa mires in the extreme south of their range (Botch 1990, Smagin *et al.* 2013). The development of these stands is clearly related to the formation of string-flark relief. Single pine trees are common on the strings of aapa mires; in the case of Piyavochnoe mire, however, the tree stands are extremely dense. The strict arrangement of the largest and oldest trees along the central axes of the strings and the appearance of pine macrofossils in small amounts only in the upper parts of the string deposits indicate that the development of dense pine stands is associated with the development of better-drained conditions on the strings during their formation.

Three distinct periods of most-active development of tree stands were revealed by dendrochronological studies (Figure 6). The first period (1825(?)–1842) is identified on the basis of scant evidence because only two of the trees analysed were present at the time. The increase in annual growth increment during the second period (1854–1864) corresponds to an equal increase in pine of the same age in mesic stands within Vologda Region (Lovelius *et al.* 2013b). A similar period of large increments in hydromorphous pine stands has been reported by other authors (Vernodubenko 2011, Lovelius *et al.* 2013a, Katjutin *et al.* 2017). It is known that the width of the annual rings of coniferous trees in mire habitats is inversely related to the amount of precipitation in the year of formation and the two previous years (Vernodubenko 2011). The period under consideration corresponds to

years with relatively low precipitation (based on data from the weather station in St. Petersburg; Bulygina *et al.* 2014, Novakovskiy & Elsakov 2014) and ends with the very wet year 1864. During the following 19 years, the average growth increment was about 0.7 mm per year. By the time of the third peak of increased growth (1884–1904), most of the trees had already reached the age of 40 years, having passed the period of ‘big growth’. The average increment for this period (1.5 mm per year with maximum 2–3 mm per year) is again equal to the increment of pine in mesic stands (Lovelius *et al.* 2013b). This peak also coincides with a decrease in precipitation (data retrieved from the Vytegor'skaya and Arkhangelsk weather stations). The gradual downward trend in the dynamics of growth thereafter generally corresponds to the age curve. Peaks and dips are less pronounced, although they still correlate with climatic data and are synchronous with the fluctuations of growth in hydromorphic forest types reported in the literature (e.g. Vernodubenko 2011, Lovelius *et al.* 2013a).

Our results indicate that a notable development of tree stands began during the period 1815–1840s. After this, two further periods of favourable conditions contributed to the formation of relatively well-developed stands. After the last of these periods, around 1904, deterioration and stabilisation of hydrological conditions took place in the mire. We assume that a microtopographical pattern suitable for development of the dense tree stand was formed a little earlier than 200 years ago. The trees that appeared at the beginning of this period have now come to the end of their life cycle (Vernodubenko 2011) and many of them are dying. No special studies have been conducted on trees belonging to younger age groups; however, a significant recruitment gap following establishment of the 200-year-old generation can be visually determined.

The secondary nature of strings is a characteristic feature of aapa mire (Bogdanovskaia-Guihéneuf 1936). The small thickness of peat formed from string *Sphagnum* is typical for aapa mire strings (Kuznetsov 1982, Antipin *et al.* 2000, Kuznetsov *et al.* 2013, Smagin *et al.* 2013) and may indicate their recent formation. It is known that intensive growth of a *Sphagnum fuscum* mat allows the formation of a weakly decomposed peat layer 40–65 cm thick over 60–80 years (Muldijarov & Lapshina 1983, Lapshina & Blyakharchuk 1986). Even though the speed of peat formation decreases significantly as the deposit grows, the age of an 80 cm thick layer of string *Sphagnum* peat may be only hundreds of years. This opinion was expressed by Antipin and colleagues (2000). Kuznetsov (1982) showed by radiocarbon dating that the age of strings on Karelian aapa mires

is less than 1000 years. Younger aapa mires with evidently younger strings are also known (Botch 1990, Rehell 2006). In our case, the thickness of the peat layer relating to the string-flark pattern was only 40 cm, indicating the young stage of the pattern. The presence of species typical for previous stages i.e. lawns and flarks (*Carex rostrata*, *Comarum palustre*, *Scheuchzeria palustris*, *Sphagnum warnstorffii*) in the modern vegetation of strings also indicates the successional youth of string-flark patterning on the Piyavochnoe mire. The results on dendrochronology enable us to deduce that the microtopographical pattern was formed a little earlier than 200 years ago. About 100 years ago, the hydrological conditions of the mire finally became identical to the current conditions.

CONCLUSIONS

From the evidence presented here, we can conclude that the Piyavochnoe site fully corresponds to the concept of aapa mire (Cajander 1913, Ruuhijärvi 1960, 1983; Kuznetsov 1982, Yurkovskaya 1992, Laitinen *et al.* 2005, 2008), on the basis of: (1) characteristic topography (occurrence in its own basin, presence of forested margins and relatively more open central part with a string-flark pattern); (2) heterotrophic vegetation typical of aapa mire; and (3) secondary nature of the strings and their young age. Moreover, the vegetation of all topographical elements found here corresponds to that of aapa mire. Special traits of the Piyavochnoe aapa vegetation are the great species richness of the communities and the important role of eutrophic species, which indicates nutrient-rich conditions. The vegetation composition also reflects the successional youth of the complexes. In particular, at Sample Plot 5 the strings still look like rows of *Sphagnum* hummocks with free water flow in between. Strings cover only 5 % of the area of the plot, and small patches of *Sphagnum fuscum* are seen amongst the *S. angustifolium*. The high proportion of constant species (33–43 %) in communities of the same microforms indicates great similarity of communities and monotony of vegetation on the massifs studied.

This is the southernmost aapa mire in the investigated area and, to date, the only one that has been fully described on the territory of Vologda Region. Its latitude is close to that of the most southerly aapa mires described from adjacent regions (Botch 1990, Goncharova 2007, Smagin 2012a, Smagin *et al.* 2013). Therefore, the southern boundary of the sporadic distribution of aapa mires in the north of European Russia can be drawn between

60° N and 61° N, near the southern boundary of the middle taiga subzone.

In general, the aapa sites on Piyavochnoe are floristically more similar to Fennoscandian rich aapa mires than to the poorer sites of north-eastern Onega-Pechora (Yurkovskaya 1980b, 1992; Goncharova 2007, Braslavskaya *et al.* 2017). At the same time, Piyavochnoe lacks a number of the west-subatlantic species that are typical for Fennoscandian mires (*Carex livida*, *Calluna vulgaris*, *Molinia caerulea*, *Trichophorum cespitosum*, *Sphagnum subfulvum*) but rare or absent in this region. Also, in contrast to Fennoscandian (Karelian “ring”) aapa mires, oligotrophic margins are absent here. Instead, aapa mire occurs in a complex with raised bog and eutrophic (rich unpatterned) mire, as previously reported for the similar mires in the south of Arkhangelsk Region (Kuznetsov *et al.* 2013). Thus, in agreement with other researchers (Antipin *et al.* 2001, Antipin & Boychuk 2004, Smagin 2012a, Kuznetsov *et al.* 2013, Kuznetsov 2018), we consider it necessary to define north-eastern rich aapa mire as an independent type within north-western Russia.

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Appendix

Geobotanical descriptions of aapa complexes. Dates: 12 Sep 2015 (Sample Plots 2 and 4), 28 Sep 2016 (Sample Plot 5) and 29 Sep 2016 (Sample Plots 1 and 3). Plot numbers correspond to those given in Figure 1b. The same sample plots were used to evaluate the cover (%) of the ground and field layers and of trees and shrubs. “+” indicates that a single individual was found in the studied sample plot; “++” means species occurrence was less than 1 %.

Microform	strings					lawns					flarks				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Microform percentage	15	30	40	20	5	20	20	10	20	20	65	50	50	60	75
Water level, cm	20–35	20–30	20–30	20–30	15–25	5–15	10–20	5–15	5–20	5–10					
Tree height, m	5–10	2–8	6–12	2–6	5–10	–	–	–	–	–	–	–	–	–	–
Total number of species	50	28	46	31	31	37	22	33	21	42	26	22	25	18	38
TREES and SHRUBS															
<i>Alnus incana</i>	.	.	.	+
<i>Betula nana</i>	7	1	3	15	10	+	1	+	+	10				.	+
<i>Betula pubescens</i>	+
<i>Frangula alnus</i>	+	+
<i>Juniperus communis</i>	++
<i>Picea abies</i>	.	.	+
<i>Pinus sylvestris</i>	50	50	50	25	30	5	+	10	.	30
<i>Salix aurita</i>	++	++
<i>Salix cinerea</i>	++	.	+	.	.	++
<i>Salix phylicifolia</i>	+	+
<i>Salix rosmarinifolia</i>	+	.	+	.	.	+	.	+	.	+	+
<i>Sorbus aucuparia</i>	+
DWARF SHRUBS															
<i>Andromeda polifolia</i>	1	1	+	5	1	5	.	7	5	+	+	+	+	.	++
<i>Chamaedaphne calyculata</i>	.	+	1	15	1	1
<i>Empetrum hermaphroditum</i>	7	25	15	1	2	++	.	+
<i>Ledum palustre</i>	.	.	+	.	++	++
<i>Oxycoccus palustris</i>	5	1	+	3	1	5	30	+	.	1	+	+	+	+	.
<i>Rubus chamaemorus</i>	+	+	+
<i>Rubus saxatilis</i>	+	.	+
<i>Vaccinium uliginosum</i>	1	.	+	1	++	+
<i>Vaccinium vitis-idaea</i>	1	.	+	+	+
SEDGE PLANTS															
<i>Carex canescens</i>	+	5
<i>Carex chordorrhiza</i>	.	.	+	++	.	4	.	+	+	+	7	3	+	.	3
<i>Carex diandra</i>	+	++
<i>Carex dioica</i>	1	.	++	.	+	+	.	+	.	+
<i>Carex echinata</i>	+	+
<i>Carex lasiocarpa</i>	+	+	+	++	10	2	15	1	3	10	5	7	5	+	20
<i>Carex limosa</i>	+	.	.	1	.	3	+
<i>Carex omskiana</i>	+
<i>Carex pauciflora</i>	+	++	+

Microform	strings					lawns					flarks				
Sample Plot №	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
<i>Carex paupercula</i>	+	.	+	.	.	.	+
<i>Carex rostrata</i>	.	.	+	1	+	.	.	.	+	+	3
<i>Carex vaginata</i>	.	.	+
<i>Eriophorum angustifolium</i>	+	.	.	.	+	+
<i>Eriophorum gracile</i>	+	+	+	+	++
<i>Eriophorum latifolium</i>	.	.	+	+	.	+
<i>Eriophorum vaginatum</i>	1	2	5	.	.	+
<i>Juncus stygius</i>	+	.	+	.	1	+	+	+	+
<i>Rhynchospora alba</i>	5	.	5	.	1	20	15	25	.
<i>Scheuchzeria palustris</i>	+	+	+	+	.	2	1	5	2	5	5	3	5	2	.
<i>Trichophorum alpinum</i>	+	+	+	+	35	1	15	1	5	.	+
GRAMINEOUS PLANTS															
<i>Calamagrostis neglecta</i>	+	.	.	+
<i>Phragmites australis</i>	30	.	40	.	.	7	5	15	.	.	+	+	1	.	.
HERBS															
<i>Bistorta major</i>	+	++	+	.	+	+	.	.	.	+
<i>Caltha radicans</i>	+
<i>Cardamine pratensis</i>	+
<i>Comarum palustre</i>	+	+	1	+	5	+	.	.	.	5	+	.	.	.	+
<i>Dactylorhiza incarnata</i>	+	.	.	.	+	.
<i>Dactylorhiza maculata</i>	+	+	+	+	.	+
<i>Drosera anglica</i>	+	+	+	++	.
<i>Drosera rotundifolia</i>	.	+	+	+	+	.	+	.	.	+
<i>Epilobium palustre</i>	+
<i>Epipactis palustris</i>	1
<i>Equisetum fluviatile</i>	+	+	+	.	.	+	+	+	.	+	+	1	+	.	+
<i>Equisetum palustre</i>	+	.	.	.
<i>Galium trifidum</i>	+
<i>Hammarbya paludosa</i>	+	++	+	.	+	.
<i>Liparis loeselii</i>	+
<i>Melampyrum pratense</i>	+	++	+	+	+	+	.	+	+	+
<i>Melampyrum sylvaticum</i>	.	.	+
<i>Menyanthes trifoliata</i>	7	5	20	20	5	5	20	15	15	10	5	5	5	15	20
<i>Moneses uniflora</i>	+	+	.	+	+	+
<i>Naumburgia thyrsoflora</i>	+	.	+
<i>Orthilia secunda</i>	+
<i>Pedicularis palustris</i>	+	+	+	.	+	+	.	+	.	++
<i>Thyselimum palustre</i>	+
<i>Pyrola rotundifolia</i>	+	.	.	.	++	+
<i>Rumex fontano-paludosus</i>	+	+
<i>Utricularia intermedia</i>	10	+	20	2	5
<i>Utricularia minor</i>	3	.	1	+	++
HEPATICAE															
<i>Aneura pinguis</i>	+	3	.	1	.

Microform	strings					lawns					flarks				
Sample Plot №	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
SPHAGNIDAE															
<i>Sphagnum angustifolium</i>	30	20	20	50	60	+	.	.	.	10
<i>Sphagnum centrale</i>	10	+	.	5	10	5	5	5	5	5
<i>Sphagnum contortum</i>	3	.	.	25	.	5	.	+	+	.
<i>Sphagnum fallax</i>	5
<i>Sphagnum fuscum</i>	30	75	30	10	1
<i>Sphagnum girgensohnii</i>	5	.	+	.	+
<i>Sphagnum jensenii</i>	+
<i>Sphagnum magellanicum</i>	+	1	3	1
<i>Sphagnum obtusum</i>	+	.	.	1
<i>Sphagnum riparium</i>	+	+
<i>Sphagnum russowii</i>	1	.	3	+	+
<i>Sphagnum squarrosum</i>	++	.	1	+	.	.
<i>Sphagnum subsecundum</i>	2	5	.	.	.	5
<i>Sphagnum teres</i>	.	.	.	20	.	5	5	3	20	3
<i>Sphagnum warnstorffii</i>	10	.	25	5	25	80	80	75	45	75	+
BRYIDAE															
<i>Aulacomium palustre</i>	+	1	+	+	+	+	+	+	+	+
<i>Brachythecium rivulare</i>	+
<i>Bryum pseudotriquetrum</i>	1
<i>Calliergon cordifolium</i>	3	+	.	.
<i>Calliergon giganteum</i>	5
<i>Calliergon richardsonii</i>	+	.	.	.	+
<i>Calliergonella cuspidata</i>	+	.	+
<i>Campylium protensum</i>	1	.	5	.	.	+	+	+	.	+
<i>Campylium stellatum</i>	+	.	+	+
<i>Cinclidium stygium</i>	15
<i>Dicranum bonjeanii</i>	.	+	+	.	+	.	.	+
<i>Dicranum polysetum</i>	+
<i>Dicranum scoparium</i>	+
<i>Hamatacaulus vernicosus</i>	+	.	5	.	.	+	.	10
<i>Helodium blandowii</i>	.	.	.	+	.	+	.	+	.	++
<i>Hylocomium splendens</i>	+	+
<i>Meesia triquetra</i>	++
<i>Pleurozium schreberi</i>	3	.	++	+	2
<i>Pohlia nutans</i>	.	+	+	.	.	.	+
<i>Polytrichum strictum</i>	+	+	++	.	+
<i>Rhizomnium pseudopunctatum</i>	.	.	.	+	+
<i>Scorpidium scorpioides</i>	30	25	15	15	50
<i>Straminergon stramineum</i>	+	.	+	.	.	+	+	+	+	+
<i>Tetraphis pellucida</i>	.	.	+
<i>Tomenthypnum nitens</i>	+	.	1
<i>Warnstorffia exannulata</i>	++	.	5	+	.	+	+	1	+	+