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The structure and dynamics of the vegetation of Gladkoe Mire in the upper reaches of the sinking Uzhla River (Vologda Region)

Stanislav A. Kutenkov[1], Dmitriy A. Philippov[2]*

[1] *Karelian Research Centre, Russian Academy of Sciences, ul. Pushkinskaya 11, Petrozavodsk, Republic of Karelia, 185610 Russia*

[2] *I.D. Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok 109, Nekouz District, Yaroslavl Region, 152742 Russia*

**philippov_d@mail.ru*

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The purpose of this paper is to study the interaction of mire and river ecosystems affected by karst processes. The research was carried out in 2016 in the headwaters of the sinking Uzhla River in Gladkoe Mire (in the northwest of the Vologda Region). The composition of flore of the mire, comprising 149 species of higher plants, is described for the first time. We recorded 17 species that are protected and rare for the region, and two species (*Hamatocaulis lapponicus* and *Warnstorfia tundrae*) are recorded in the region for the first time. The vegetation in the central part is predominantly eutrophic herb-hypnum fen communities, along the river and mesoeutrophic forested mire communities at the mire margin. Based on the stratigraphy of peat deposits of five mire areas, it is shown that the formation of the river bed occurs on a pre-existing mire, leading to a reduction of fens and an increase in mire afforestation.

Keywords: mire hydrology, forested mire, fen, flora, peat deposit, Red Data Book, Vologda Region.

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Introduction

Sinking rivers are a unique geographic phenomenon associated with the karst topography. In this case, the river is captured by a karst sinkhole and continues as a subterranean river. Uzhla River, located in the southern part of the Vytegra District (northwest of the Vologda Region) is an example of such a river (Fig. 1A). This small river (length 25 km, basin area 313 km^2) begins in Uzhelskoe Lake, and then in two sections becomes subterraneous, and then comes back to the surface again, before entering the Kovzha River near the village of Uzhla (part of the Volga-Baltic waterway; Caspian Sea basin). The middle and lower reaches of the Uzhla River are relatively well studied. It has been shown that in the middle course (2–2.5 km downstream from the northern part of Gladkoe Mire) the river drops into an underground channel, which is a karst cave 3 m wide and 2 m high, at a depth of 64 m at the mouth and with a likely length of about 6 to 7 km. The velocity of water flow in the subterraneous section is about 0.5 m/s, and water flow calculations indicate the existence of additional underground tributaries (Bagulina, 2000; Garkusha, 2000; Kozlov, 2012).

We focused on the upper Uzhla River basin, where Gladkoe Mire is located (Fig. 1A, B). It is in this part of the basin that the river channel sinks for the first time and reappears in the central part of the mire.

We are not aware of studies of mires associated with sinking rivers, although in general, studies of karst

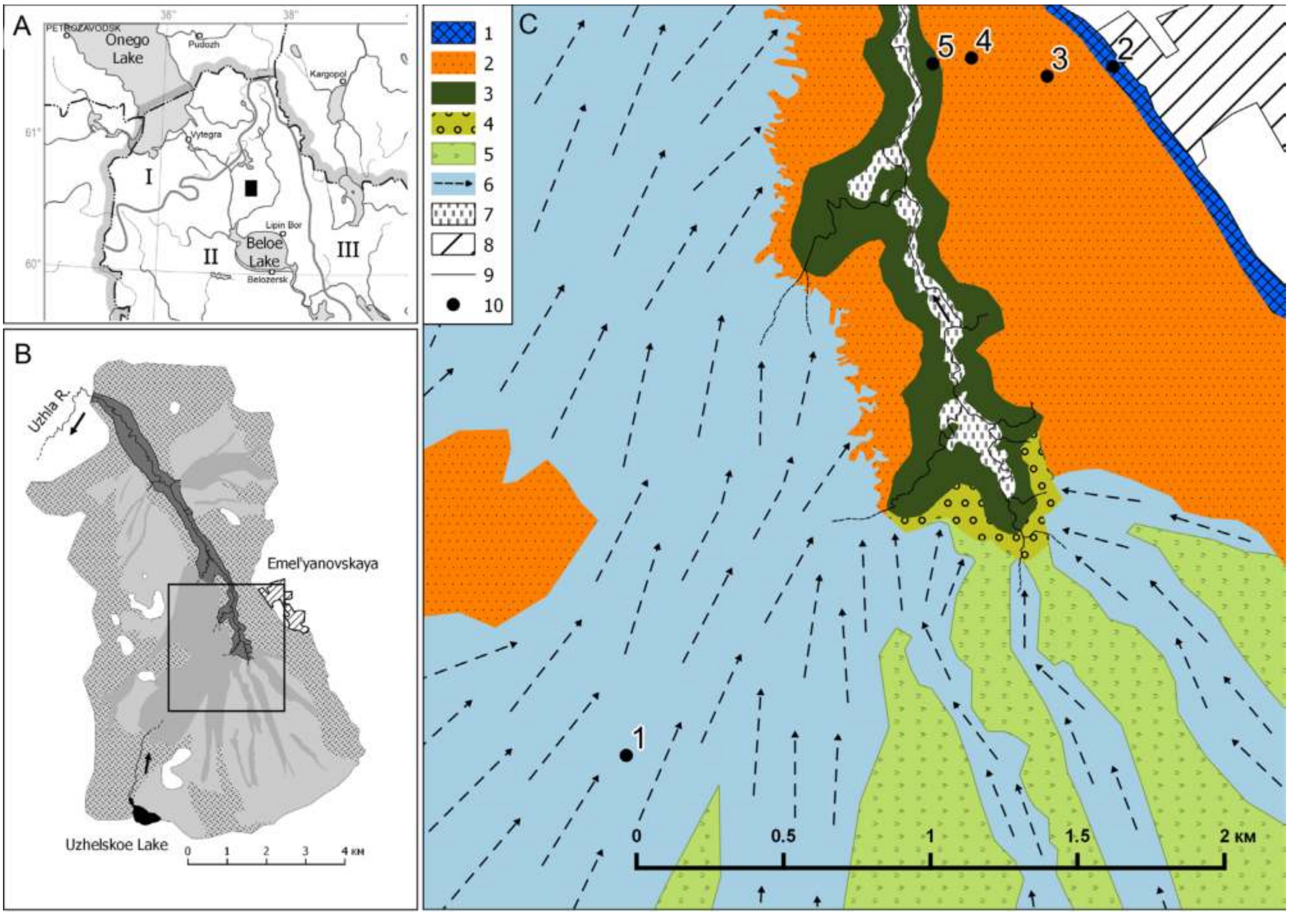

Fig. 1. Gladkoe Mire. **A** – geographical position of the mire within the north-west of the Vologda Region (according to: Skupinova, 2007); **B** – general scheme of the mire; **C** –central part of the mire. I – III – drainage basins (I – basin of the Baltic Sea, II – basin of the Caspian Sea, III – basin of the White Sea); 1–7 – biotopes (1 – birch-spruce margins; 2 – bog-grass pine forests and herb-sphagnum pine forests; 3 – bog-grass pine forest; 4 – young birch forest on peat; 5 – sphagnum lawns; 6 – mire; 7 – floodplain meadows); 8 – former village (Emel'yanovskaya); 9 – watercourses; 10 – places of sampling peat.

mires and mires of karst regions have been carried out relatively regularly in recent years both in Russia (Aschepkova and Semikolennykh, 2014; Galanina and Philippov, 2018; Galanina et al., 2015; Martynenko et al., 2012; Puchnina and Churakova, 2010; Volkova, 2010, 2012; Zatsarinnaya, 2015; Zatsarinnaya et al., 2011) and abroad (Booth et al., 2004; Gaudig et al., 2006; Ireland and Booth, 2012; Mouser et al., 2005; O'Driscoll and Parizek, 2003; Whittington et al., 2007). We are also not aware of any previous research into the flora and vegetation of Gladkoe Mire. Previously, we performed botanical studies of several mires located 20–35 kilometers from Gladkoe Mire. These include Kemskoe Mire (Kucherov and Kutenkov, 2014; Sofronova et al., 2014), Piyavochnoe Mire (Kutenkov and Philippov, 2019), and a series of mire massifs along the shore of Kovzhskoe Lake and near the village of Mirnyi (Philippov, 2010, and unpublished).

This paper aims to analyze the composition of higher plant communities, the structure of vegetation and its dynamics (based on the stratigraphy of peat deposits) of Gladkoe Mire, located in the upper reaches of the sinking Uzhla River.

Preliminary results of this work were reported at the IX meeting in memoriam of Ekaterina Alexeevna Galkina (St Petersburg, February 2018) and published in the Proceedings of that conference (Kutenkov and Philippov, 2018).

Material and methods

Research area

The study area is located in the north of the Russian Plain, at absolute elevations of 110–165 m, and belongs to the Valdai glaciation zone. The territory is located within an ancient erosion depression. The crystalline basement in the study area is covered by a thick layer of pre-Quaternary sediments, the upper 70–90 meters of which belong to the Moscovian Stage (Middle Carboniferous) and is represented by marine, mainly carbonate rocks (Savinov and Romanova, 1970; Skupinova, 2007). The presence of the latter contributes to the development of karst landforms. The ongoing karst formation is reflected in the dynamics of surface hydrological processes, in particular in the fluctuation of the level of water bodies, the emergence and sinking of surface waterways and even lakes (Bergshtresser, 1838; Kulikovsky, 1894; Vorobyev, 2005). In general, the territory is a hilly moraine plain of the geomorphological region of the Belozero-Kirillov ridges, which are the marginal formations of the Valdai glaciation (Buslovich et al., 2001).

The analyzed territory belongs to the Kemsko-Itkol'skiy mire district (Abramova, 1965). The study area is located in the southern part of the middle taiga and is characterized as highly paludified – the area of mires is 26.7% (Filonenko and Philippov, 2013). The mire areas under study are dominated by mesotrophic shrub-sedge and sedge-tussock fens, and the rest are raised hollow-hummock and pine-shrub-sphagnum bogs, as well as eutrophic hygrophilic herb-hypnum mires. Mires are of topogenous and limnogenous origin (Abramova, 1965; Philippov, 2010).

Gladkoe Mire is located in an ancient lake depression (Garkusha, 2000) at absolute elevations of 140–145 m, and has a relatively flat bottom composed of blue clay. According to field exploration research carried out in 1949 by the Leningrad branch of the Rostorfrazvedka institute, the mire has an area of 26.47 km^2 (of which 17.05 km^2 are within the boundaries of an industrial deposit), the average depth of peat deposits is 2.75 m (maximum 4.3 m). The fen type of peat deposits, with low stump content, prevails, the degree of decomposition is 20–35%, the ash content is 1.7–6.8% (Torfyanoi fond.., 1970). Slightly north of this peatland (according to the same cadastral source) is the Bolshoe Mire. Based on the lab-analytical studies carried out in 1952, its area is 33.10 km^2, of which 19.02 km^2 are within the boundaries of a productive peat deposit, the average depth is 2.29 m, and a fen type of peat deposit predominates.

An analysis of the territory based on satellite imagery results (Landsat 7) and our field studies showed that these two objects are actually parts of the one mire and lie in the same depression of the primary bottom. The formal separation is associated with the presence of afforested medium peat (depth of deposits up to 2–3 m) mire sites between objects not accounted by the peat cadastre. Also, the latter did not take into account a number of other afforested areas along the periphery/margins of the mire.

According to our data, the actual area of Gladkoe Mire (the unified mire system), is 62 km^2, of which 27 km^2 are afforested areas, 10 km^2 overwatered fens, 3 km^2 floodplain complex, and the rest (22 km^2) are occupied by various open and lightly covered sphagnum lawns. There are several in-mire islands (the area is 1.5 km^2; was not taken into account in the calculation of the mire area). Not a single part of the mire has been subjected to drainage reclamation and peat extraction. A small marginal part of the mire in the continuation of the meadows near the village of Emel'yanovskaya previously located here was used for hay cropping.

Methods

Field studies were carried out by the authors in September 2016 in the central part and near the eastern edge of Gladkoe Mire in the vicinity of former village of Emel'yanovskaya (N 60°36′20″ – 60°42′38″, E 37°22′15″ – 37°29′38″) in accordance with the tutorial by Philippov et al. (2017). To study the dynamics of the mire vegetation and the influence of the river on its course, a series of four sections was laid along a profile about 0.7 km long from the eastern shore of the mire near the uninhabited village of Emel'yanovskaya to the river floodplain, 1.7 km downstream from the appearance of the incised channel. Peat was sampled separately in the central fen part of the mire, 1.5 km southwest of the river (Fig. 1C). At these five plots, peat samples were taken bed-by-bed to the entire depth of the organic deposits using a Russian peat borer (″Torfianoy bur Instorfa″) with a step of 10–20 cm, and where pronounced changes in peat layers were present, along their borders. A total of 89 peat samples were selected. Botanical analysis of peat and the degree of its decomposition was performed by E.L. Talbonen using the microscopic method in the Laboratory of mire ecosystems of the Institute of Biology, Karelian Research Centre, Russian Academy of Sciences. Stratigraphic diagrams of peat composition were constructed using the Korpi software (Kutenkov, 2013). A short description of the vegetation was carried out at the places of peat extraction (dominant and characteristic species were indicated in all layers of phytocenoses, and the height of the stand). Floristic descriptions were compiled for individual mire sites (forested mire, fen, riverine areas, etc.) and for the entire Gladkoe Mire. The nomenclature of plants follows mainly the reports of N.N. Tsvelev, M.S. Ignatov and N.A. Konstantinova (Ignatov et al., 2006; Konstantinova et al., 2009; Tsvelev, 2000).

Results and discussion

Composition of higher plants

We recorded 149 species of higher plants belonging to 95 genera, 57 families on Gladkoe Mire: Marchantiophyta – 4, Bryophyta – 42, Equisetophyta – 4, Lycopodiophyta – 1, Polypodiophyta – 2, Pinophyta – 3, Magnoliophyta – 93. *Hamatocaulis lapponicus* and *Warnstorfia tundrae* were recorded for the first time for the Vologda Region bryoflora (Sofronova et al., 2018), and *Scorpidium revolvens* was also newly reported for the bryoflora of the mires of the north-west of the Vologda Region (Philippov and Boychuk, 2008). The main diversity is concentrated on afforested mire sites (~110 species), while open sites are relatively poor (~40 species). The following is a list of species, grouped alphabetically within divisions and families.

Marchantiophyta

Aneuraceae H. Klinggr.: *Aneura pinguis* (L.) Dumort.

Marchantiaceae Lindl.: *Marchantia polymorpha* L. ssp. *polymorpha*

Myliaceae Schljakov: *Mylia anomala* (Hook.) Gray

Ptilidiaceae H. Klinggr.: *Ptilidium pulcherrimum* (Weber) Vain.

Bryophyta

Amblystegiaceae Kindb.: *Amblystegium serpens* (Hedw.) Bruch et al., *Campylium protensum* (Brid.) Kindb., *C. stellatum* (Hedw.) C.E.O. Jensen

Aulacomniaceae Schimp.: *Aulacomnium palustre* (Hedw.) Schwägr.

Brachitheciaceae Schimp.: *Sciuro-hypnum curtum* (Lindb.) Ignatov

Bryaceae Schwägr.: *Bryum pseudotriquetrum* (Hedw.) P. Gaertn., B. Mey. et Scherb., *B. weigelii* Spreng.

Calliergonaceae (Kanda) Vanderp., Hedenäs, C.J. Cox & A.J. Shaw: *Calliergon cordifolium* (Hedw.) Kindb., *C. giganteum* (Schimp.) Kindb., *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs, *Warnstorfia exannulata* (Bruch et al.) Loeske, *W. tundrae* (Arnell) Loeske

Dicranaceae Schimp.: *Dicranum majus* Turner, *D. polysetum* Sw.

Hylocomiaceae (Broth.) M. Fleisch.: *Hylocomium splendens* (Hedw.) Bruch et al., *Pleurozium schreberi* (Brid.) Mitt., *Rhytidiadelphus triquetrus* (Hedw.) Warnst.

Meesiaceae Schimp.: *Meesia triquetra* (Jolucl.) Ångstr.

Mniaceae Schwägr.: *Cinclidium stygium* Sw., *Plagiomnium rostratum* (Schrad.) T.J. Kop., *Rhizomnium pseudopunctatum* (Bruch et Schimp.) T.J. Kop., *R. punctatum* (Hedw.) T.J. Kop.

Plagiotheciaceae (Broth.) M. Fleisch.: *Plagiothecium denticulatum* (Hedw.) Bruch et al.

Polytrichaceae Schwägr.: *Polytrichum strictum* Brid.

Pylaisiaceae Schimp.: *Calliergonella cuspidata* (Hedw.) Loeske, *Ptilium crista-castrensis* (Hedw.) De Not.

Scorpidiaceae Ignatov & Ignatova: *Hamatocaulis lapponicus* (Norrl.) Hedenäs, *H. vernicosus* (Mitt.) Hedenäs, *Scorpidium revolvens* (Sw. ex anon) Rubers, *S. scorpioides* (Hedw.) Limpr.

Sphagnaceae Martynov: *Sphagnum angustifolium* (C.E.O. Jensen. ex Russow) C.E.O. Jensen, *S. centrale* C.E.O. Jensen, *S. contortum* Schultz, *S. fallax* (H. Klinggr.) H. Klinggr., *S. flexuosum* Dozy et Molk., *S. fuscum* (Schimp.) H. Klinggr., *S. magellanicum* Brid. aggr., *S. obtusum* Warnst., *S. squarrosum* Crome, *S. subsecundum* Nees, *S. teres* (Schimp.) Ångstr., *S. warnstorfii* Russow

Thuidiaceae Schimp.: *Helodium blandowii* (F. Weber et D. Mohr) Warnst.

Equisetophyta

Equisetaceae Rich. ex DC.: *Equisetum fluviatile* L., *E. palustre* L., *E. pratense* Ehrh., *E. sylvaticum* L.

Lycopodiophyta

Lycopodiaceae Beauv. ex Mirb.: *Lycopodium annotinum* L.

Polypodiophyta

Dryopteridaceae Ching: *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *D. cristata* (L.) A. Gray

Pinophyta

Cupressaceae Bartl.: *Juniperus communis* L.

Pinaceae Lindl.: *Picea abies* (L.) Karst., *Pinus sylvestris* L.

Magnoliophyta

Apiaceae Lindl.: *Angelica sylvestris* L., *Thyselinum palustre* (L.) Rafin.

Araceae Juss.: *Calla palustris* L.

Asparagaceae Juss.: *Majanthemum bifolium* (L.) F.W. Schmidt

Asteraceae Dumort.: *Cirsium palustre* (L.) Scop., *Crepis paludosa* (L.) Moench, *Ligularia sibirica* (L.) Cass., *Solidago virgaurea* L. s.l.

Betulaceae S.F. Gray: *Alnus incana* (L.) Moench, *Betula humilis* Schrank., *B. nana* L., *B. pubescens* Ehrh.

Caprifoliaceae Juss.: *Linnaea borealis* L., *Lonicera pallasii* Ledeb.

Caryophyllaceae Juss.: *Stellaria graminea* L.

Cyperaceae Juss.: *Baeothryon alpinum* (L.) Egor., *Carex appropinquata* Schum., *C. cespitosa* L., *C. chordorrhiza* Ehrh. ex L. fil., *C. diandra* Schrank, *C. dioica* L., *C. globularis* L., *C. irrigua* (Wahlenb.) Smith ex Hoppe, *C. lasiocarpa* Ehrh., *C. limosa* L., *C. omskiana* (Meinsh.) Jalas, *C. pauciflora* Lightf., *C. rhynchophysa* C.A. Mey., *C. rostrata* Stokes, *C. vesicaria* L., *Eriophorum angustifolium* Honck., *E. gracile* Koch., *E. latifolium* Hoppe, *E. vaginatum* L., *Rhynchospora alba* (L.) Vahl

Droseraceae Salisb.: *Drosera anglica* Huds., *D. rotundifolia* L.

Empetraceae S.F. Gray: *Empetrum nigrum* L.

Ericaceae Juss.: *Andromeda polifolia* L., *Chamaedaphne calyculata* (L.) Moench, *Oxycoccus palustris* Pers., *Vaccinium myrtillus* L., *V. vitis-idaea* L., *V. uliginosum* L.

Grossulariaceae DC.: *Ribes nigrum* L.

Juncaceae Juss.: *Juncus filiformis* L., *J. stygius* L., *Luzula pilosa* (L.) Willd.

Lamiaceae Lindl.: *Scutellaria galericulata* L.

Lentibulariaceae Rich.: *Utricularia intermedia* Hayne, *U. minor* L.

Menyanthaceae Dumort.: *Menyanthes trifoliata* L.

Onagraceae Juss.: *Chamaenerion angustifolium* (L.) Scop.

Orchidaceae Juss.: *Dactylorhiza incarnata* (L.) Soo, *D. maculata* (L.) Soo, *Hammarbya paludosa* (L.)

O. Kuntze, *Malaxis monophyllos* (L.) Sw., *Platanthera bifolia* (L.) Rich.

Oxalidaceae R.Br.: *Oxalis acetosella* L.

Pediculariaceae Juss.: *Melampyrum pratense* L., *Pedicularis palustris* L.

Poaceae Barnhart: *Agrostis stolonifera* L., *Calamagrostis canescens* (Web.) Roth, *C. neglecta* (Ehrh.) Gaertn., Mey. et Scherb., *Poa pratensis* L.

Polygonaceae Juss.: *Acetosa fontano-paludosa* (Kalela) Holub, *Bistorta major* S.F. Gray

Primulaceae Juss.: *Naumburgia thyrsiflora* (L.) Reichb.

Pyrolaceae Dumort.: *Moneses uniflora* (L.) A. Gray, *Orthilia secunda* (L.) House, *Pyrola rotundifolia* L.

Ranunculaceae Juss.: *Caltha palustris* L.

Rhamnaceae Juss.: *Frangula alnus* Mill.

Rosaceae Juss.: *Comarum palustre* L., *Filipendula ulmaria* (L.) Maxim., *Padus avium* Mill., *Rosa majalis* Herrm., *Rubus arcticus* L., *R. idaeus* L., *Sorbus aucuparia* L.

Rubiaceae Juss.: *Galium palustre* L., *G. trifidum* L.

Salicaceae Mirb.: *Salix aurita* L., *S. caprea* L., *S. cinerea* L., *S. lapponum* L., *S. pentandra* L., *S. phylicifolia* L., *S. rosmarinifolia* L.

Saxifragaceae Juss.: *Chrysosplenium alternifolium* L.

Scheuchzeriaceae Rudolphi: *Scheuchzeria palustris* L.

Valerianaceae Batsch: *Valeriana officinalis* L. s.l.

Violaceae Batsch: *Viola epipsila* Ledeb.

Populations of 17 species of higher plants protected and rare in the region were found within the boundaries of this mire (Resolution ..., 2015; Suslova et al., 2013):

1/CR – *Juncus stygius*;

2/EN – *Hammarbya paludosa*;

2/VU – *Carex omskiana*;

3/LC – *Ligularia sibirica*, *Malaxis monophyllos*;

3/NT – *Baeothryon alpinum*, *Drosera anglica*, *Rhynchospora alba*, *Utricularia minor*;

biological control required species – *Betula humilis*, *Dactylorhiza incarnata*, *Moneses uniflora*, *Platanthera bifolia*, *Rubus arcticus*, *Salix lapponum*, *Utricularia intermedia*, *Sphagnum contortum*, *S. subsecundum*.

It is worth noting that three biological control required species (*Galium triflorum* Michx., *Humulus lupulus* L., *Matteuccia struthiopteris* (L.) Tod.) were discovered along the mineral banks of the river. A rare protected (3/LC) macroalgae, *Batrachospermum turfosum* Bory from the Rhodophyta Division, was also recorded in a mire stream in the central part of Gladkoe Mire. This species is only known in the region from a few records (Chemeris and Philippov, 2010; Noskova et al., 2018; Sadokov and Philippov, 2017). Importantly, *Juncus stygius*, an extremely rare plant for the Vologda Region, was recorded in fen mire sites (Kutenkov and Philippov, 2019; Philippov, 2008a). Two species of mosses, recorded for the first time for the Vologda Region, *Hamatocaulis lapponicus* and *Warnstorfia tundrae*, are predominantly distributed in more northern latitudes (Ignatov et al., 2006).

Vegetation

Most of the mire is treeless and has a relatively even microrelief. Fens approach one another from the southern and western sides to the floodplain of the river (Fig. 2E), located in the center of the mire, and the most extensive of them has an area of more than 6.2 km^2 (Fig. 1C). Some of the fens are fed from external watercourses (streams approaching the mire), part originate directly in the mire. The fens (Fig. 2A) are quite heavily flooded and are occupied by herb-hypnum vegetation. The main background plant is sedge (*Carex chordorrhiza, C. lasiocarpa, C. limosa, C. omskiana, Baeothryon alpinum, Eriophorum angustifolium, Rhynchospora alba*), *Equisetum fluviatile, Scheuchzeria palustris*, swamp grass (*Menyanthes trumolrereustolis Comarum palustre*, *Thyselinum palustre*, *Pedicularis palustris*), as well as shrubs (*Betula nana*, *Andromeda polifolia*, *Oxycoccus palustris*). In the most flooded areas, *Drosera anglica, Hammarbya paludosa, Utricularia intermedia,* and *U. minor* grow. In the mire, in addition to hypnous mosses (*Scorpidium scorpioides, Hamatocaulis vernicosus, Warnstorfia exannulata, Cinclidium stygium, Campylium stellatum,* and several others), sphagnum mosses (*Sphagnum contortum, S. flexuosum, S. obtusum, S. subsecundum*) are also found. In general, the vegetation of fens is close to the **Carex lasiocarpa – Menyanthes trifoliata** mesoeutrophic hollow association widespread in the European north of Russia (Kuznetsov, 2005). Considering the large areas occupied by such fens in Gladkoe Mire, the latter should be classified as sedge and hypnum-sedge mesoeutrophic Eastern European mires (Yurkovskaya, 1992), which are quite widely represented in the Vologda Region (Abramova, 1965; Philippov, 2007, 2008b).

Dwarf shrub-sedge-sphagnum hummocks and ridges with single pines that do not form a regular structure are scattered in the mire. The spaces between fens are covered with mesooligotrophic sphagnum lawns with *Betula nana*, *Chamaedaphne calyculata*, *Oxycoccus palustris*, *Carex lasiocarpa*, *Sphagnum angustifolium*, *S. magellanicum*.

Fens, converging to the center of the mire, are concentrated in streams (Fig. 2B, C), gathering in the Uzhla River. Around the beginning of the pronounced river bed within the mire a birch forest is formed along the peat deposit (Fig. 2D). *Picea abies, Padus avium, Frangula alnus,* and *Rubus idaeus* grow in the undergrowth and underwood. The ground cover is poorly developed (due to abundant leaf litter), and *Vaccinium vitis-idaea*, *Dryopteris carthusiana,* and

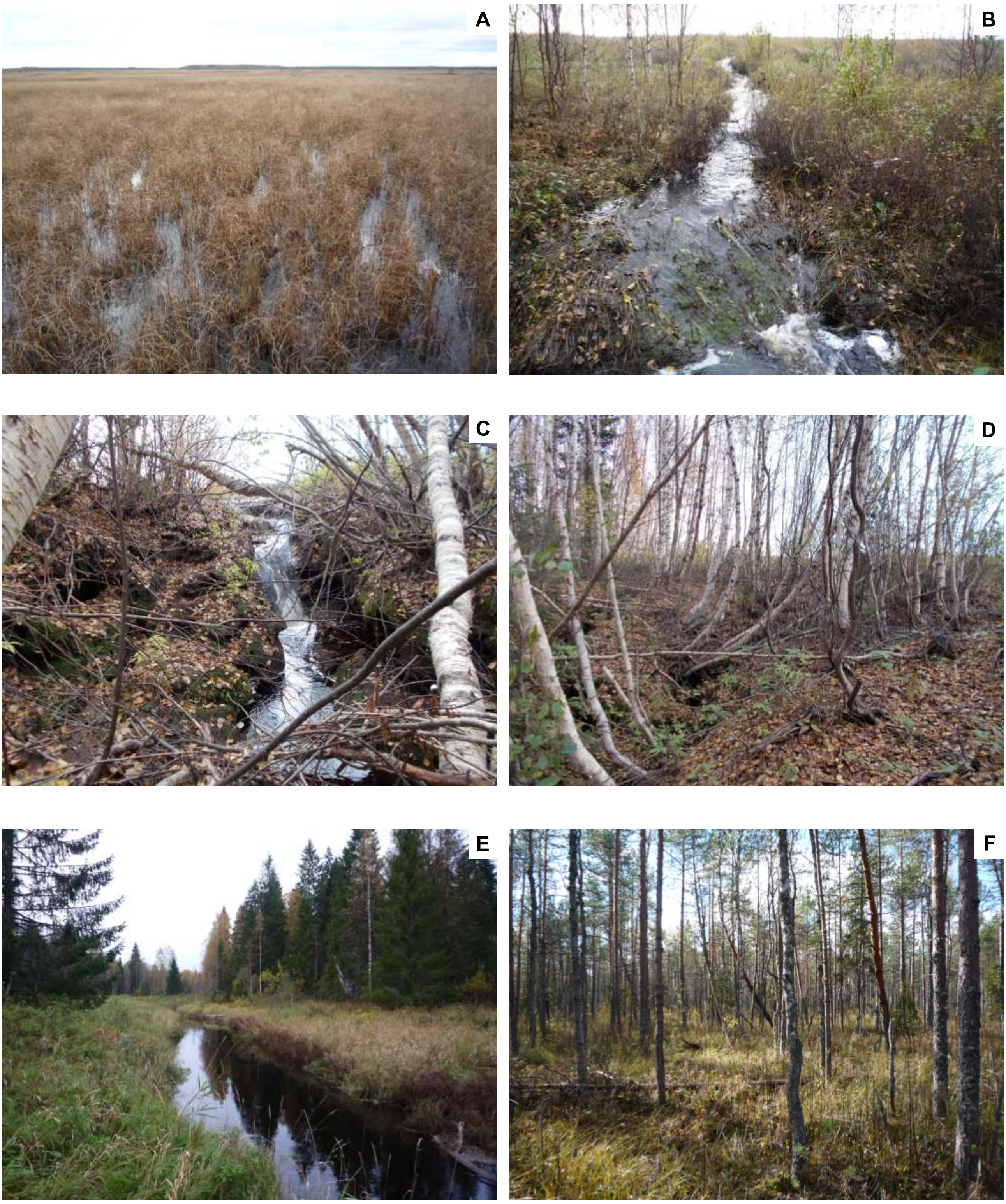

Fig. 2. Gladkoe Mire and Uzhla River. **A** – fen; **B** – mire stream; **C** – destruction of peat deposits by a stream; **D** – subsidence of peat and a change in the shape of birch trunks; **E** – river; **F** –forested mire.

Lycopodium annotinum are found. Streams, going down the slope to the riverbed, cut through the peat deposit, causing its fragmentation and creep. Birch trees growing in such places have bends in their trunks indicating their gradual reclining associated with erosion of peat soils (Fig. 2D).

A grass spruce forest forms along the river banks slightly downstream of the mire. Even further downstream, a small incised floodplain with meanders and elders is present, coastal bars, riverside meadows with characteristic floodplain vegetation surrounded by grassy spruce forest growing on peat (Fig. 2E).

The mire margins are mostly covered with mesoeutrophic herb-sphagnum pine forests (Fig. 2F). Adjacent uplands, as well as creek and riverside areas, are occupied by spruce and birch forests. The largest afforested massif is located on the eastern edge of the mire, in particular, it completely occupies the space from the original bank to the Unzhla River, 3.7 km along the river.

The edge of this massif near the uplands (up to 70 m wide) is occupied by a spruce-birch swamp-grassy forest. In the ground layer, *Carex appropinquata*, horsetails, forbs, *Calliergonella cuspidata* and *Sphagnum warnstorfii* predominate. Peat depth reaches 2.0 m. Similar hummock-sedge birch forests are periodically found in the margins of eutrophic mires (Kutenkov and Kuznetsov, 2013).

In the main, central part of the forested massif, a mesoeutrophic pine forest develops with a stand height of 12–16 m. The herb-shrub layer contains *Carex lasiocarpa*, *C. appropinquata*, *Menyanthes trifoliata*, *Comarum palustre*, *Bistorta major*, *Equisetum pratense*, *Chamaedaphne calyculata*, and *Oxycoccus palustris*. The moss cover is patchy, *Sphagnum warnstorfii, Calliergonella cuspidata*, and species of the family Mniaceae predominate. The peat depth is 2.5–3 m. The composition of the vegetation corresponds to the **Sphagno warnstorfii – (Carici cespitosae –) Pinetum** association**,** a widespread in carbonate conditions, the **bistortaetosum** subassociation, uniting the Eastern European rich (key) herb-sphagnum pine forests of temperate continental climate (Kucherov and Kutenkov, 2011).

Closer to the Unzha River, the topography becomes prominently sloping, and the pine forest is replaced by meadowsweet spruce forest. The stand height reaches 24–28 m. The dense shrub layer contains *Salix* spp., *Frangula alnus, Sorbus aucuparia,* and *Rubus idaeus. Filipendula ulmaria, Equisetum fluviatile, Calla palustris*, and various ferns grow in the grass-shrub tier. *Rhytidiadelphus triquetrus, Calliergon cordifolium*, and species of the family Mniaceae are found among mosses. The peat depth is about 2 m and decreases towards the riverbed. Similar meadowsweet spruce forests (**Filipendulo – Piceetum**) are characteristic of eutrophic conditions with flowing humidification (Kucherov et al., 2010; Kutenkov and Kuznetsov, 2013).

Deposit stratigraphy

The central part of the mire, herb-hypnum fen

Peat was sampled in the central part of the main fen, in the sedge-bogbean-hypnum community (Fig. 1C, Borehole 1). The depth of the deposit at the sampling site is 2.65 m; a layer of water 15 cm thick was on top of it during sampling (Fig. 3). The degree of decomposition gradually decreases from the bottom to the surface. The benthic layer of the fen deposit consists mainly of horsetail residues, as well as birch, marsh calla, bogbean and reeds. 30–40 cm from the bottom, this is replaced by a bog sedge-bogbean-hypnum layer, which is almost uniform to the surface and corresponds to the current vegetation on the site. As in modern communities, *Carex lasiocarpa* prevails among the remains; in addition to it, the remains of *Carex limosa, C. chordorrhiza, Menyanthes trifoliata, Scheuchzeria palustris*, and *Eriophorum angustifolium* are recorded in the peat. The content of the first two species increases closer to the surface. Of the mosses, *Warnstorfia exannulata* prevails, having its maximum in the lower part of the deposit, *Meesia triquetra* is recorded in the upper part.

The margin of the mire massif

The sample was collected within 50 m of the upland coast in a spruce-birch bog-grass community (Fig. 1C, Borehole 2). The deposit is quite homogeneous, consisting of forest peat with a high degree of decomposition and a predominance of the remains of birch, to a lesser extent spruce and pine (Fig. 4). Herbal residues are associated with woody residues; in the bottom layer, horsetails prevail, in the middle part, i.e., bogbean and closer to the surface *Carex appropinquata*. In addition to them, the remains of reeds, *Carex lasiocarpa, Sphagnum warnstorfii, Calliergon cordifolium,* and *Calliergonella cuspidata* were found. The composition of the deposit, despite some changes in the balance of remains, indicates fairly stable conditions of mire formation and the constant presence of forest communities on the site.

Pine-grass mire in the center of the afforested massif

In 70 m from the coast, the spruce-birch margin is replaced by mesoeutrophic pine growing on peat 2.5–3 m deep. Within it, at different distances from the coast, samples were collected from two boreholes**.**

The structure of the peat deposit 250 m from the shore (Fig. 1C, Borehole 3) is significantly different from the deposit at the edge of the massif. The bottom peat layer, with a high degree of decomposition, almost entirely consists of the remains of birch and horsetail, in a small amount of bogbean and sedge, including *Carex omskiana* (Fig. 5). At 30–90 cm from the bottom, it is gradually replaced by fen peats (sedge-*Scheuchzeria*-hypnum, sedge-*Scheuchzeria*-bogbean-hypnum, sedge-*Scheuchzeria*-sphagnum, or horsetail-bogbean-hypnum-*Scheuchzeria*). Of sedges in fen peat, *Carex lasiocarpa, C. rostrata,*

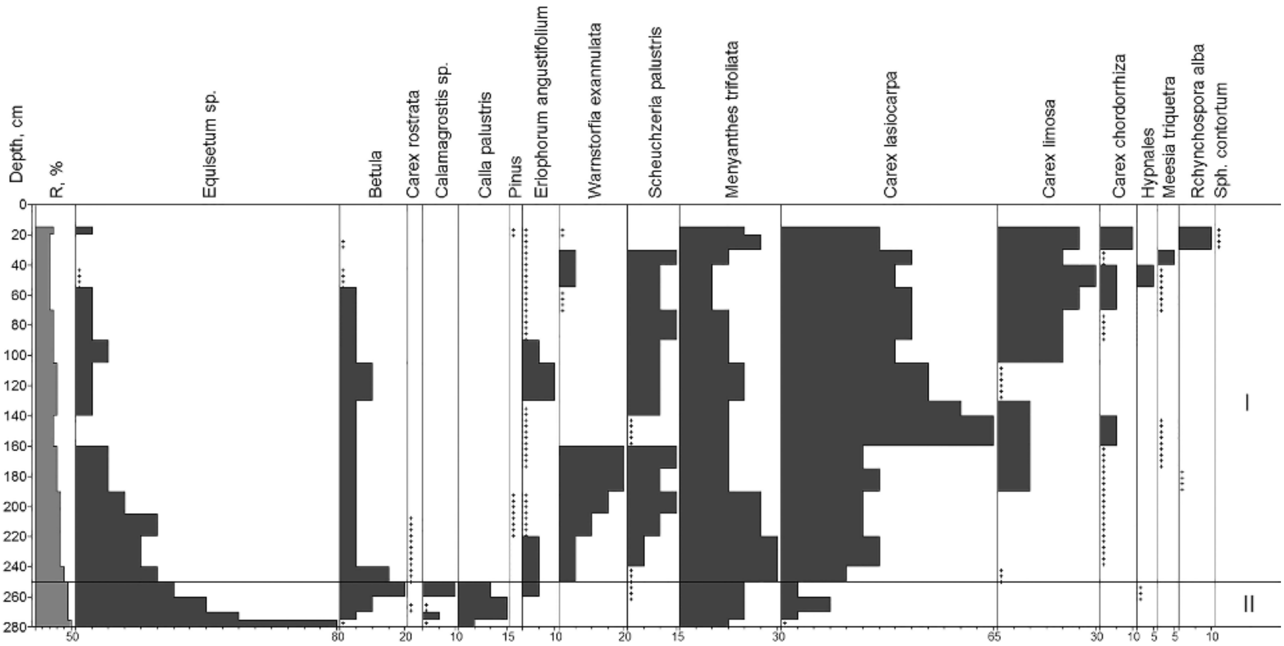

Fig. 3. Stratigraphy of the peat deposit of the central fen (Borehole 1). Paleocommunities: I – fen herb-hypnum (sedge-bogbean-hypnum, sedge, sedge-bogbean); II – birch-horsetail. The top 15 cm are occupied by water.

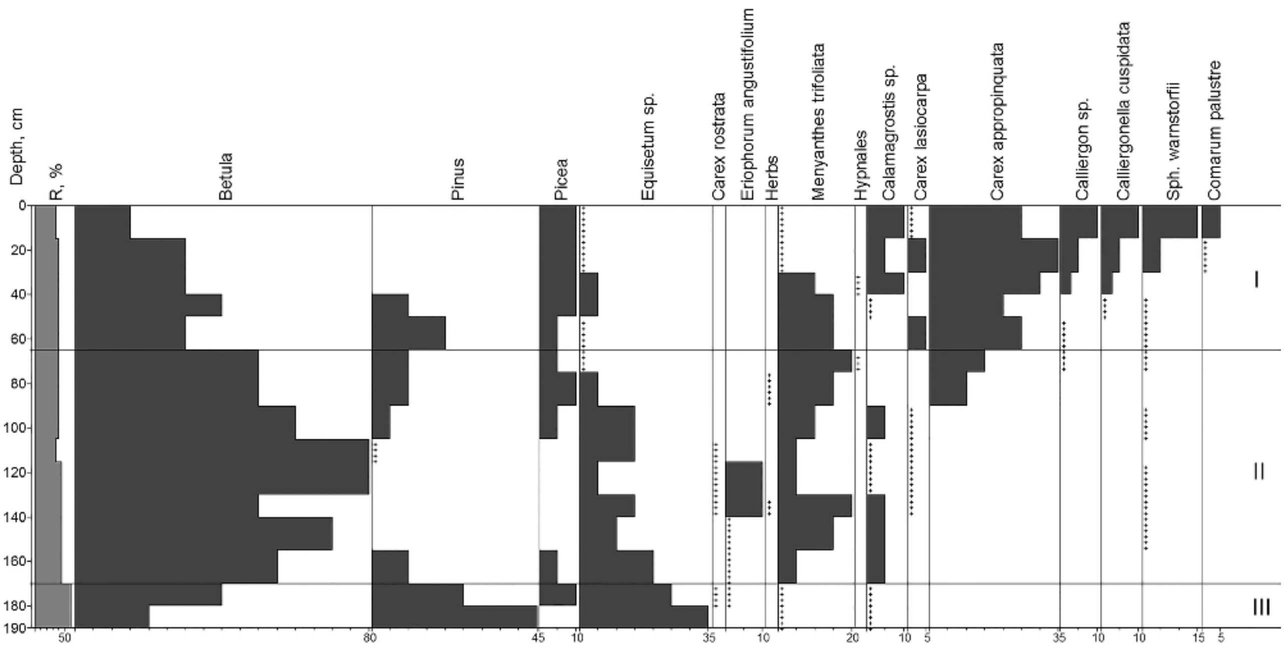

Fig. 4. Stratigraphy of the peat deposit near a meadow (Borehole 2). Paleocommunities: I – birch forest with bog-grass spruce forest; II – birch horsetail-bogbean; III – pine with birch horsetail.

C. limosa, C. chordorrhiza are represented, also there are *Scheuchzeria palustris, Menyanthes trifoliata,* and *Equisetum* sp. Birch (?*Betula nana*) is always present at low content. Of the mosses, *Calliergon* spp., *Warnstorfia exannulata, Meesia triquetra* are found. In the near-surface layer, *Sphagnum contortum*, a characteristic species for eutrophic fens, begins to play a larger role. The ratio of peat formers varies across the deposit; nevertheless, its eutrophic fen character remains unchanged almost throughout its entire thickness.

At a depth of 35 cm from the surface, there is a sharp change in the main peat formers, and *Scheuchzeria, Carex limosa* and fen mosses disappear, while bogbean and *Carex lasiocarpa* remain, and pine, reeds appears, and the content of *Sphagnum warnstorfii* increases. This peat composition corresponds to the modern community of the forested mire.

A borehole selected in the same pine forest 500 m from the upland (Fig. 1C, Borehole 4) 2.5 m deep showed similar dynamics of paleocommunities. The thin bottom layer is composed of the remains of horsetail and *Carex omskiana* and is replaced above the main stratum of peat (sedge-*Scheuchzeria*-hypnum, sedge-*Scheuchzeria*-bogbean-hypnum, horsetail-bogbean-hypnum, sedge-horsetail-bogbean) (Fig. 6.). At a depth of 20 cm, there is also a sharp change in the main peat formers, *Scheuchzeria*, fen sedges and hypnum disappear, the proportion of wood remains increases. In addition to increasing birch content, spruce and pine appear. Remains of *Carex appropinquata, Sphagnum warnstorfii* suddenly appear in large numbers, they are accompanied by reeds, marsh cinquefoil, forbs, and mosses of the family Mniaceae. The composition of the peat is beginning to match the modern community.

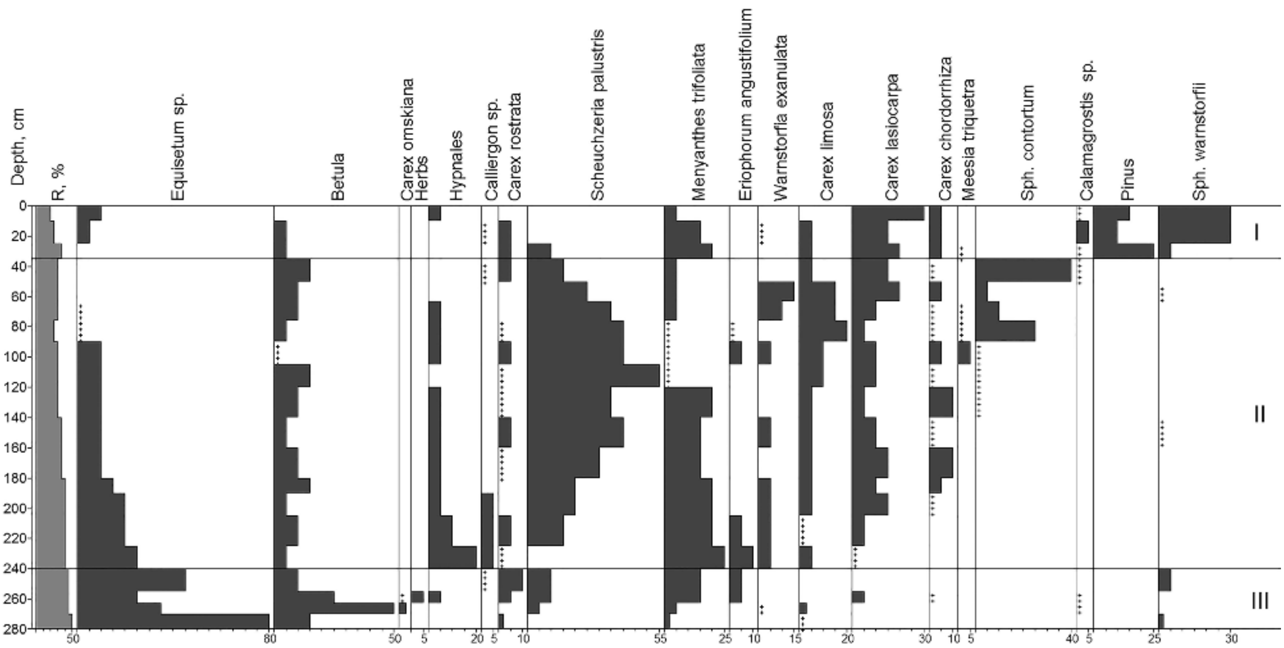

Fig. 5. Stratigraphy of the pine mire deposits on the meadow side (Borehole 3). Paleocommunities: I – sedge-bogbean pine; II – fen herb-hypnum; III – birch-horsetail.

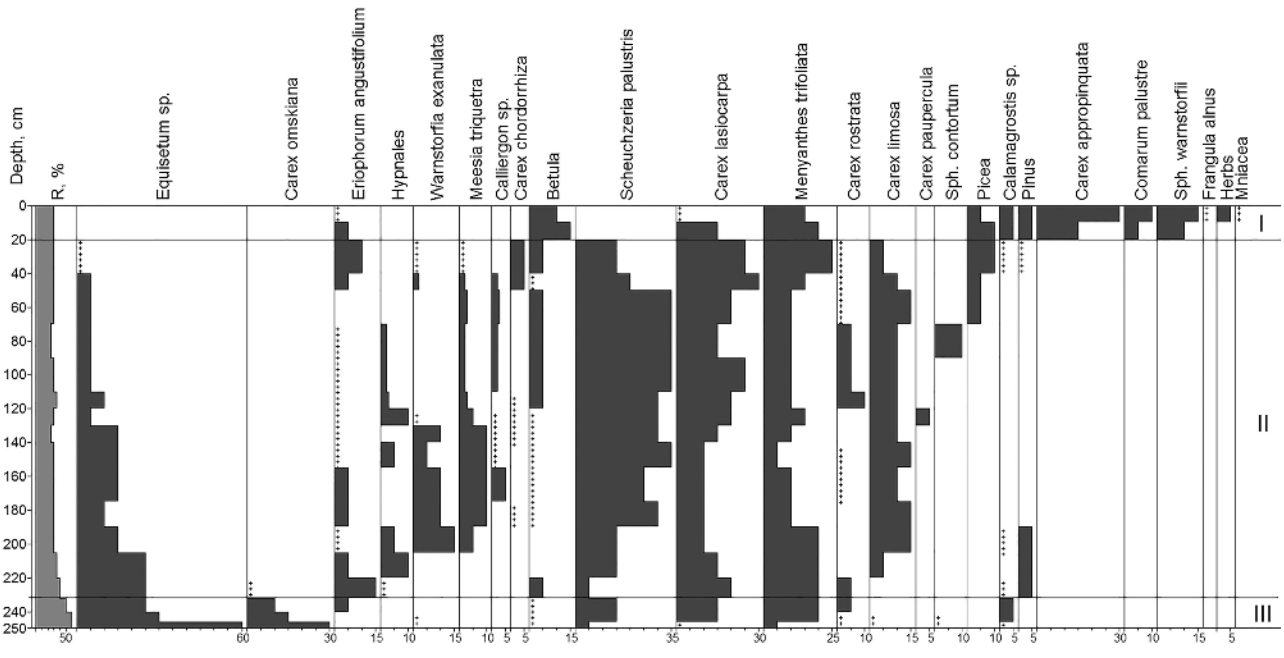

Fig. 6. Stratigraphy of the pine mire deposits on the river side (Borehole 4). Paleocommunities: I – sedge-bogbean pine; II – fen herb-hypnum; III – sedge-horsetail.

Meadowsweet spruce forest near the Uzhla River

Peat depth is about 2 m and continues to decrease towards the riverbed (Fig. 1C, Borehole 5). The deposit here is very similar to the previous site. The bottom layer of the deposit is composed of the remains of horsetail and *Carex omskiana,* and is highly decomposed (Fig. 7). At 20 cm from the bottom, it is replaced by a 30 cm layer of birch-bogbean peat with the participation of *Eriophorum angustifolium* and *Carex lasiocarpa*. The main thickness of the deposit (depth 20–150 cm) consists of medium-decomposed fen (sedge-*Scheuchzeria*-hypnum, sedge-*Scheuchzeria*-bogbean-hypnum) peat. The bulk of its remains is composed of hypnum mosses: *Warnstorfia exannulata, Meesia triquetra, Calliergon* sp., etc. At 20 cm from the surface, the fen peat is covered with well-decomposed forest (spruce with birch) peat with the participation of herbs, and with no remains of mire species. Here the boundary of the upper layer of the peat is most clearly expressed among the studied sites.

Reconstruction of the history of mire development

A generalization of the data from the botanical analysis of peat from four boreholes (taken along a line from the mire margin at the former village of Emel'yanovskaya to the channel of the Uzhla River) allows a detailed reconstruction of the development of this part of the mire system and, to a lesser extent, the entire Gladkoe Mire. The stratigraphic profile obtained shows the presence of significant changes in the conditions of mire formation in the massif to the east of the Uzhla River (Fig. 8).

The most homogeneous deposit is observed in a narrow margin near the upland, where a grassy forested mire was preserved during the entire period of mire formation. On the rest of the forested mire massif, two significant changes are observed in the stratigraphy of the deposit. The main stratum of the deposit is represented here by weakly decomposed (20–35%) fen (*Scheuchzeria*, sedge-*Scheuchzeria*, sedge-bogbean, herb-hypnum and other) peat. They are underlain by a thin bottom layer of a high degree of decomposition, composed of the remains of horsetail and, to a lesser extent, birch and *Carex omskiana*, that is, mire formation began with eutrophic birch-sedge-horsetail communities. The proportion of wood remains in the bottom layer increases somewhat when moving from the center of the mire to its edge, which may be due to the edge effect (center–edge gradient). The widespread occurrence of *Carex omskiana* peat in this layer, which is currently considered very rare in the region (Postanovlenie, 2015), is noteworthy; in modern mire vegetation, this type of sedge is poorly represented.

As the mire grew, with the accumulation of 15–40 cm of deposits, the fairly rapid appearance of the bogbean is recorded as well as *Scheuchzeria*, sedges (*Carex lasiocarpa, C. rostrata, C. limosa, C. chordorrhiza*) and hypnum mosses (*Warnstorfia exannulata, Meesia triquetra, Calliergon* spp.), characteristic of modern fens in the center of the mire on the other side of the Uzhla River. Thus, the entire eastern part of the massif, with the exception of a narrow forest edge, was occupied by mire, including a site with a modern meadowsweet spruce forest near the Uzhla River.

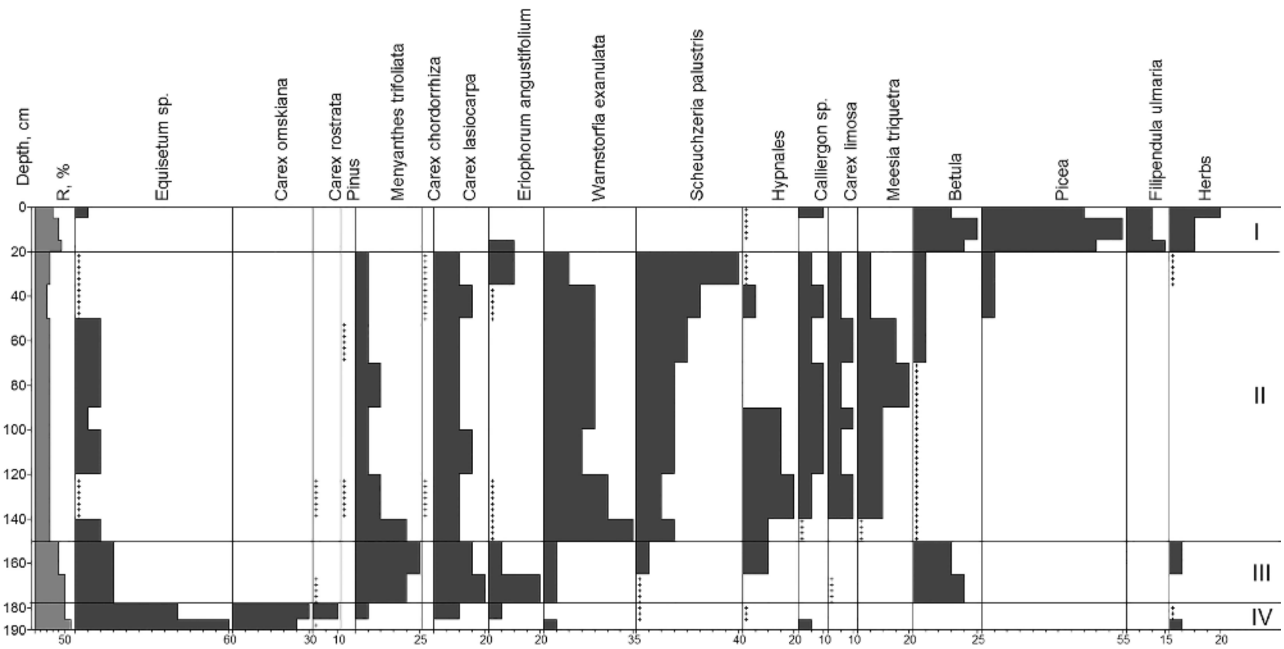

Fig. 7. Stratigraphy of the spruce meadowsweet deposits near the river Uzhla (Borehole 5). Paleocommunities: I – bog-grassy spruce forest; II – fen herb-hypnum; III – birch-sedge-bogbean; IV – sedge-horsetail.

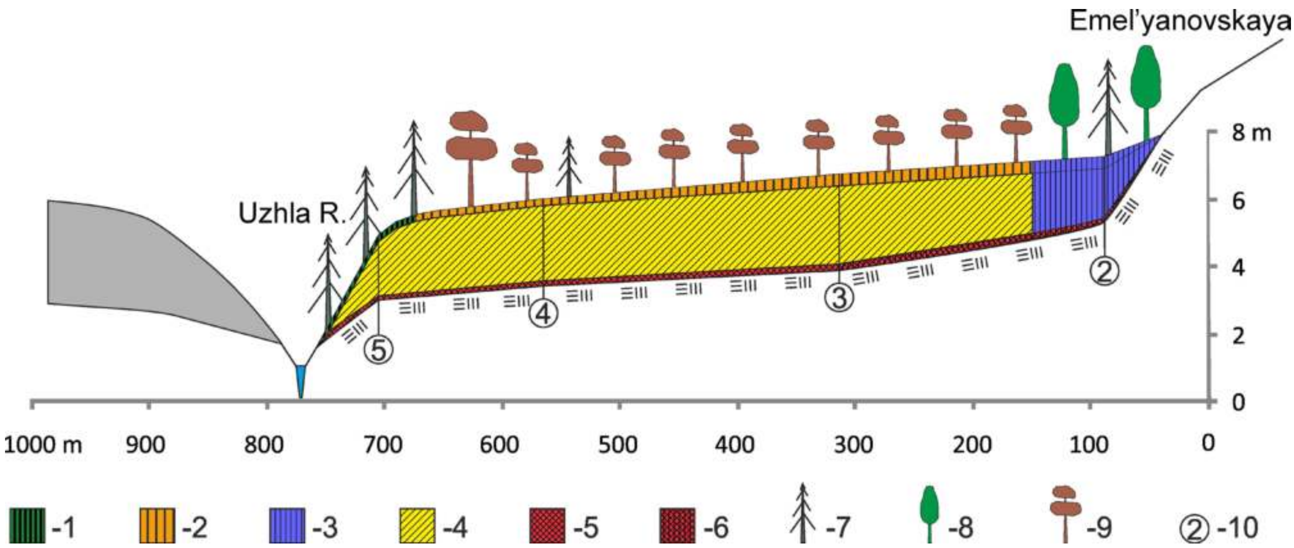

Fig. 8. Schematic section through the peat deposits of the mire massif east of the Uzhla River. 1–6 – peat (1 – forest (spruce), 2 – forest-sedge-bogbean-sphagnum (with pine), 3 – forest (birch), 4 – fen herb-hypnum, 5 – horsetail, 6 – forest-horsetail); 7–9 – tree species (7 – spruce, 8 – birch, 9 – pine); 10 – borehole numbers.

Relatively recently, a second sharp change in peat formation occurred in the deposit. In the surface 20–35 cm layer, *Scheuchzeria* disappeared, and the proportion of fen sedges, bogbeans, and hypnum mosses sharply decreased. The main role was played by wood remains: the content of birch remains increased, while conifers (*Pinus sylvestris* and *Picea* spp.) appeared. They are accompanied by forbs, *Sphagnum warnstorfii*, and in some places *Carex appropinquata*. In general, the top layer of peat reflects the formation of a modern forest community along the fen deposits. Especially noteworthy is the development of spruce peat with a high degree of decomposition directly on top of the *Scheuchzeria* peat in the floodplain part of the mire. A similar change in the composition of peat, simultaneous over the entire width of the mire area, indicates an exogenously induced abrupt change in vegetation.

It is possible that the herb-hypnum fen (presently existing in the southwestern part of the mire) originally occupied a far larger area reaching the eastern margin of the mire. The pronounced channel of the Unzha River cutting through the rock bottom, was formed above a pre-existing fen. The concentration of the surface runoff into the watercourse, its deepening and cutting through the peat deposit, and the formation of a river floodplain led to isolation from the main fen and drying of the eastern part of the mire massif for several kilometers along the formed floodplain and the development of herb-sphagnum pine forest here. Besides, near the river, an additional drainage of the massif occurs, leading to the destruction and drying out of peat. Its thickness gradually decreases towards the river bed. The peat slope is overgrown by a mire-grassy (meadowsweet) spruce forest. Directly along the river bank, peat is completely washed away, and the primary banks (the former bottom of the mire massif), occupied by floodplain meadows, are exposed.

Since the main inflow of water to the mire comes from the south-west, on this side of the river most of the mire have retained a fen character, and changes caused by increasing drainage occurred only within 300 m of the strip along the western bank of the river.

Along the edge of the fen adjacent to the floodplain complex from this side, sphagnum hummocks form, which merge closer to the floodplain into ridges and lawns, supporting more intensive tree growth. It is under conditions of increasing flow and pronounced microrelief that the true mire species, *Hammarbya paludosa* and *Juncus stygius,* also extremely rare for the region, have been recorded. Then begins a pronounced sloping toward the river, first occupied by a herb-sphagnum pine forest, closer to the river by a mire-grassy spruce forest.

Apparently, similar processes at the time also took place downstream on the river (within the northern areas of Gladkoe Mire, which belong to the Bolshoe Mire (Torfyanoy fond..., 1970), where the forming river channel intercepted a watercourse from the mire and caused afforestation of large areas. In places of the modern beginning of the floodplain formation, birch with strongly- and moderately-curved trunks are preserved in the vegetation cover. Together with signs of destruction of peat deposits by water flows, this indicates that the river's advance into the mire presently continues.

Conclusion

This work broadens our understanding of the phytodiversity, typology and stratigraphy of mires in the Vologda Region (Abramova, 1965; Kutenkov and Philippov, 2019; Noskova et al., 2018; Philippov, 2007, 2008b; Philippov and Boychuk, 2008). Gladkoe Mire that we studied in combination with the origin of the twice-sinking Uzhla River is a very unusual natural object, and is also very valuable in terms of biological diversity and environmental transformation. Thus, 149 species of higher plants were found in the mire, of which 18 are protected in the region (1/CR, 2/EN and 2/VU – 1 species each, 3/LC – 2, 3/NT – 4, species biological control required – 9), as well as two species recorded for the flora of the region for the first time.

Within the mire, the formation of a deepened watercourse in fen's place has led to a change in hydrology over a substantial area of the mire. As a result of this, the vegetation developing here underwent a marked transformation; hundreds of hectares of open fens were replaced by forest communities. Also, taking into account channel processes, peat was completely removed/washed off, and the watercourse that is forming (up to the present time) already flows in the mineral banks. It can be assumed that the process of river development (its attack on the mire) will continue further until the river reaches its source Uzhelskoe Lake, or one of the other streams approaching the mire from the south side, completely dividing the mire into two parts. The question remains open whether there is an underground watercourse between Uzhelskoe Lake and the place of appearance of the Uzhla River in the central part of Gladkoe Mire, or the entire water mass follows here along the surface or through the peat mass. The factors that caused the rapid development of the river within the mire is not entirely clear: is this connected with an increase in precipitation, or is it nevertheless associated with the development of karst processes. The purpose of further research can also be an estimate of the speed of the ongoing transformation processes both in the past and in the present (the former can be studied by dating the boundary layers of peat along an existing river bed, and the latter by dendrochronological studies). The natural complex of Uzhla River and Gladkoe Mire is a unique system that has not yet been fully studied, but is of undoubted interest as an object for observation of modern processes of rapid natural ecosystem transformations.

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