# Reconstruction of the Late Holocene Environment of Central Yakutia Based on Fossil Invertebrates and Plants from a Buried Lake at the Vilyuy River Valley

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**Abstract:** We present the first record of Holocene fossil insect assemblages from Central Yakutia. A stratigraphic sequence in the locality within the Vilyuy River valley is a buried oxbow. The late Holocene water body inherited an impervious stratum from the late Pleistocene. The organic layer preserved rich fossil assemblages of macrofossils including insects and other invertebrates, plants, and charcoal. The ancient flora and fauna include species that are common in Yakutia as well as those that are rare and absent in the region. The most abundant finds are leech cocoons and bogbean seeds. The macrofossils of some insects were found along with remains of their host plants. Despite the absence of intensive human land use in the area, traces of fires were recorded. The oxbow represents the environment of a floodplain wetland that developed separately from the ecosystem of the adjacent sand dunes.

**Keywords:** insects; freshwater invertebrates; vegetation; gyttja; oxbow; climate

## 1. Introduction

The evolution of a freshwater body has become a classic example of natural succession [1–4]. This succession is especially important for the vast northern regions from Siberia to Northern Europe, as well as Canada and Alaska where wetlands are vast and play an immense role in the life of local ecosystems and indigenous populations [5,6]. Combining observations on modern wetlands with the paleoecological record provides a better understanding of natural processes. Paleolake sediments are an excellent archive that enabled numerous paleoenvironmental studies utilizing different methods of research, from the geochemical and stable isotope composition of lake sediments to micro- and macroremains of plants and animals [7,8].

Insects (particularly beetles) are important members of lake communities, and their remains should be well studied, but the number of papers discussing the paleo-communities of aquatic beetles is very limited. The reason for this is probably rooted in the common paleolimnological research method, which is based on studying sediment cores. Occasionally, even a small volume of sediment from lake cores may contain the remains of beetles and large invertebrates, such as leech cocoons [9]. But in most cases, beetle sampling requires a specific recovery method (see below), operating with a big volume of sediment. Beetles

and caddisflies are recommended for the complex study of the lake sediment as the most visible insects [10,11].

Lacustrine stratigraphic sequences are commonly topped by peat and other organic units. Organic layers are usually a better source of large insect remains than the below-bedded lacustrine sediment. Therefore, the Holocene peat and gyttja are the most popular source of insect macrofossils in paleoecological studies [12–18]. Insects from these deposits are used as proxies for reconstructions of past climates, species distribution, and encasing terrestrial environments.

In contrast to the well-studied entomofauna of famous European sites, the quaternary insects of Central Yakutia (Figure 1) are insufficiently studied. No systematic collection was undertaken until recently, and some insects were occasionally recovered from the bulk samples collected by geologists for routine geological analyses and by curious paleontologists during post-conference field trips in the area. Importantly, such occasional collections [16,17] confirmed the presence of insect remains in the regional Quaternary units.
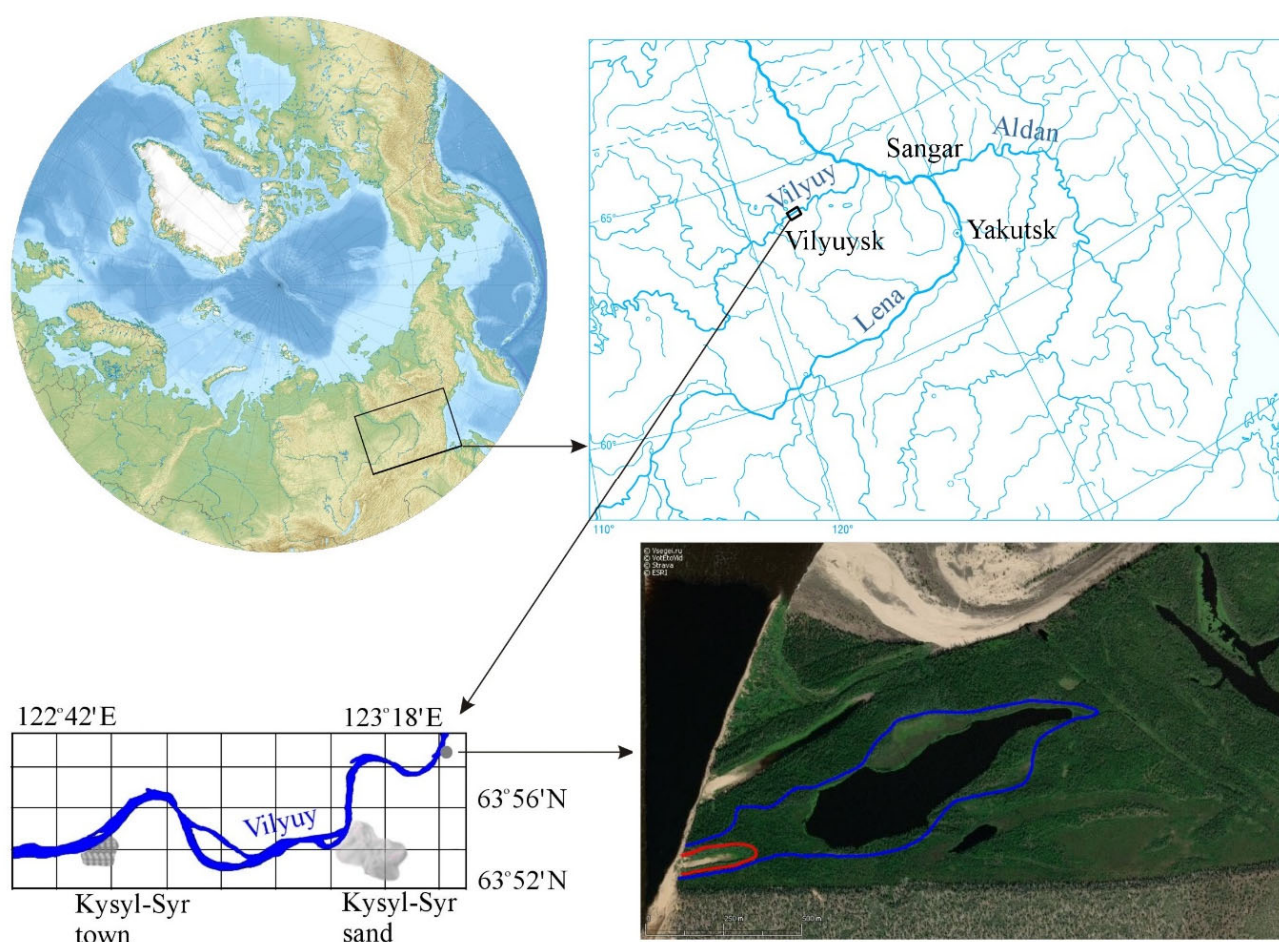


**Figure 1.** Map of the study area. Blue line is outline of large oxbow lake, red line is outline of its dried part.

The possibility of using the fossil record is critical for solving the important question of biogeography about the origin of relict communities. Currently, the extreme climate of Central Yakutia supports cold steppes with a number of relict Pleistocene plants and insects [19,20]. There are two possible explanations of their origin: (1) steppe species which have remained here since the Pleistocene; (2) the region was forested in the Pleistocene and the steppe species migrated into the region in the Holocene from the north, where steppe-tundra occupied most of the land. Steppe insects were absent in fossil insect collections from Central Yakutia [16], which could be due to fragmentary sampling, as the insects

were collected mainly from organic units that mark hydric climatic episodes; thus, this observation needs clarification.

The first unequivocal evidence of the Pleistocene steppe community in the northern part of Central Yakutia was found in the Batagay locality [21]. In contrast to the monotonous insect record from the steppe-tundra localities of northern Yakutia [22], the Batagay sequence formed in contrasting environments, with numerous steppe insects found in one unit. It was still not clear whether the steppe insects were present here from the Pleistocene onwards, surviving locally in some patchy refugia, or if they recolonized the area already in the Holocene, migrating here from their main range outside of the region.

In 2019, we started a large-scale sampling of fossil insects in Central Yakutia. We aimed to fill a gap in the regional paleoentomological record and clarify the origin of the steppe relics. To achieve the second goal, we had to evaluate the taphonomic aspects of the steppe insect record. As most insect macrofossils were previously collected from organic deposits (peat and plant detritus), whereas steppe insects inhabit dry habitats, the steppe taxa had a lesser chance of being preserved in wetland deposits than the hygrophilous taxa.

## 2. Regional Setting

The region is characterized by a cold continental climate. According to meteorological observations [23], the mean temperature of the nearest weather station, Vilyuysk, is $-9.3\,^{\circ}C$; the coldest month is January ($-38.2\,^{\circ}C$); the warmest month is July ($18.0\,^{\circ}C$), and the mean precipitation is 243 mm. The area has continuous permafrost.

The vegetation of Central Yakutia has been formed in a severe climate, but warm summers and the diversity of landscapes provide conditions for great biodiversity [24]. Boreal forests with larch (*Larix gmelinii*), pine (*Pinus sylvestris*), spruce (*Picea obovata*), and occasionally birches (*Betula platyphylla*, *B. pendula*) dominate the landscape, while open grasslands are scattered throughout the region. Importantly, grasslands are more widespread here than in other boreal regions of Siberia. Grasslands include wet meadows with *Alopecurus arundinaceus*, *Elytrigia repens*, and *Hordeum brevisubulatum*, saline meadows with *Goniolimon speciosum* and *Salicornia europaea*, and dry meadows and steppes.

The cold steppe of Yakutia is a unique landscape [25] encased by the boreal forest. The steppe vegetation includes *Stipa capillata*, *Festuca lenensis*, *Kobresia filifolia*, *Carex duriuscula*, *C. pediformis*, *Elytrigia jacutorum*, *Artemisia frigida*, *A. tanacetifolia*, *A. karavajevii*, and *Anemone sylvestris*. Yakutian sand dunes host an even more unique semi-desert community. The vegetation of sand dunes includes such plants as *Thymus sergievskajae*, *Krascheninnikovia lenensis*, *Ephedra monosperma*, *Koeleria skrjabinii*, *K. karavajevii*, *Artemisia karavajevii*, *Phlojodicarpus sibiricus*, and *Rumex graminifolius*; many of the plants are Yakutian endemics.

The Vilyuy River floodplain is typical for Central Yakutia. It is partly covered with ancient and modern dunes, but most of the floodplain is a wetland with sphagnum bogs, wet meadows, and numerous lakes. The forest is dominated by *Larix gmelinii*; *Betula pendula* grows occasionally, and the undergrowth includes the shrubs *Pinus pumila*, *Juniperus sibirica*, *Betula fruticosa*, and *B. exilis.* Low and prostrate shrubs are represented by *Ledum palustre*, *Chamaedaphne calyculata*, *Andromeda polifolia*, and *Vaccinium uliginosum*. Sedges (*Carex globularis*, *C. caespitosa*) are common in the floodplain. *Calamagrostis obtusata*, *Oxycoccus microcarpus*, and *Caltha palustris* occur on sphagnum bogs.

The Kyzyl-Syr locality in Central Yakutia (Figures 1 and 2) was discovered by a group of scientists from the Melnikov Permafrost Institute during a reconnaissance field trip in 2012. The group worked there from 2012 to 2016 and published several papers [26–28].

Kyzyl-Syr Sands is a modern sand dune field (*tukulan* in Yakut) near the Kyzyl-Syr settlement on the right bank of the Vilyuy River. The main section (point 366) is located at 63°54′ N, 123°16′ E, in the area of active dunes. The dune field continues downstream, where it is covered by mixed forest. The main source of the dune deposits is a late Pleistocene aeolian sand that belongs to the Do'olkuminskaya Suite, a common subsurface deposit in the region.
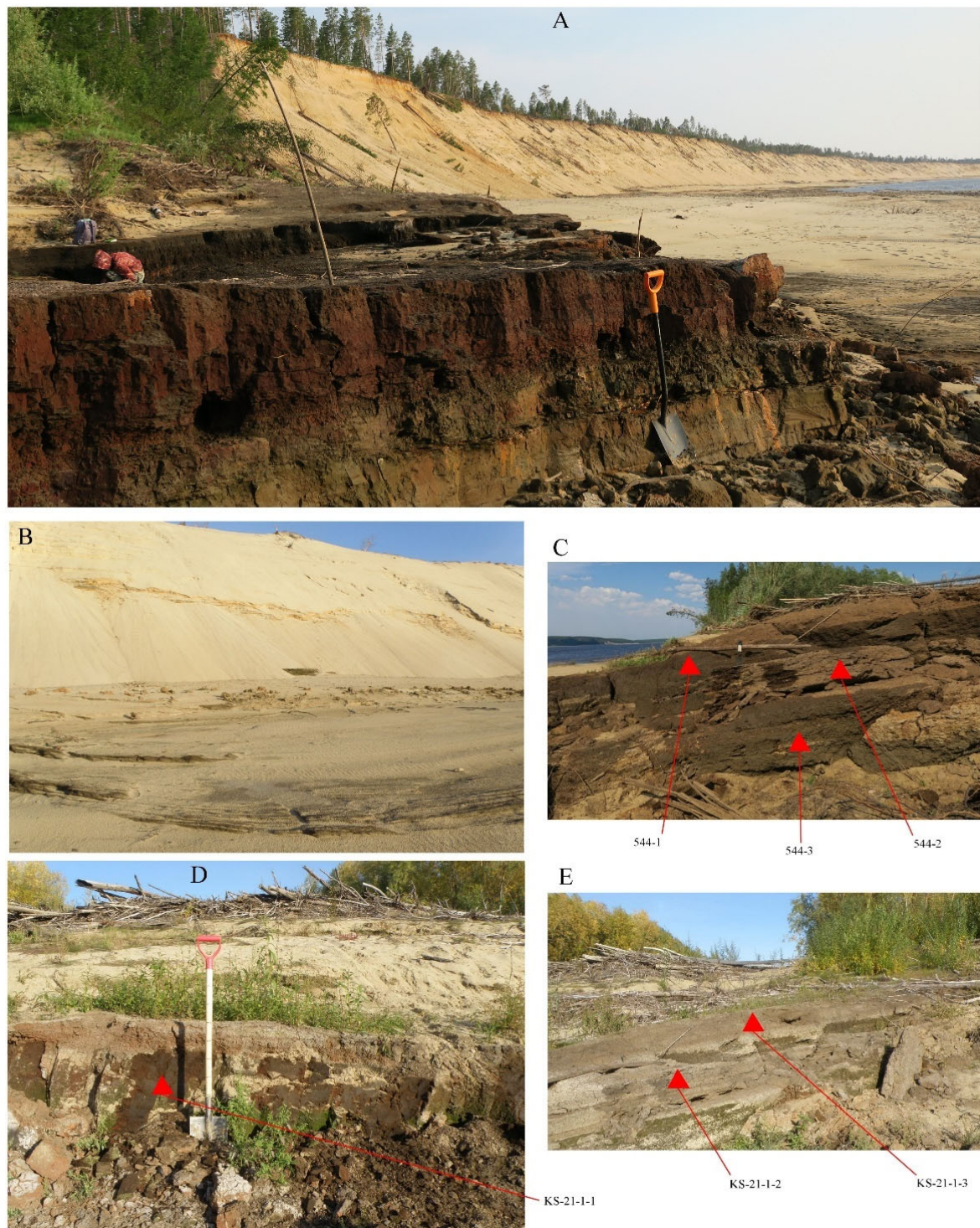
**Figure 2.** Photos of the Kyzyl-Syr section. (**A**)—The section at the Vilyuy River, (**B**)—alluvial layer of plant detritus at the base of the high terrace, (**C**)—organic layer (OL) and location of June 2021 samples, (**D**,**E**)—OL and location of samples collected in September 2021.

The lower unit of the main section exposed two layers of loosely packed organic deposits (allochthonous detritus) (Figures 2B and 3). Radiocarbon dating yielded an MIS (marine isotope stage) 3 age of the unit (39.9 and 44.4 ka for the upper and lower layers correspondingly, Figure 2); the unit was described as an alluvial sequence with sediments grading from channel to floodplain deposit [27].
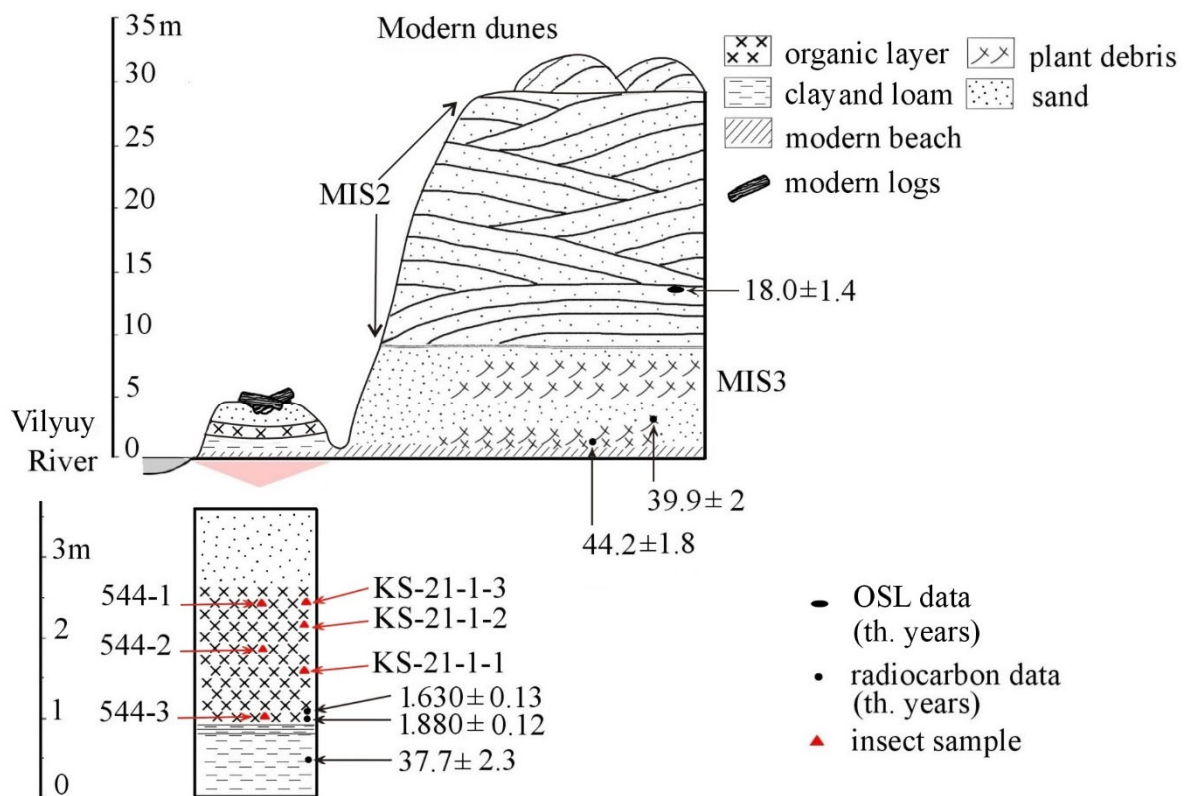
**Figure 3.** General stratigraphy of the Kyzyl-Syr section.

When the section was revisited in 2019, the researchers discovered a small exposure with an organic-rich layer (Figure 2A,C–E) at the base of the floodplain terrace (point 544), about 10 km downstream from the main section (63°58′ N, 123°24′ E). Field observations led to two hypotheses: (1) the organic layer (OL) at the base of the low floodplain terrace is relatively young (of the Holocene age); (2) the OL is a continuation of the MIS3 detritus bedded at the base of the nearby Pleistocene section.

After re-examining the section in September 2021, uncertainty about the age of the OL returned. Riverbank erosion allowed the tracing of the organic bed strike-wise. The OL was exposed for about 20 m along the riverbank and at the edges of the old river channel. In September, the channel was dry and covered by sand and driftwood. In its central, lowermost position, the OL was bedded below the dry river channel, but both sides of the layer followed the saucer shape of the river channel. Since the OL at the base of the original section (Figure 2C) followed the shape of the Holocene channel, it could not be of the MIS3 age. The late Holocene age of the OL was later confirmed by radiocarbon dating.

## 3. Materials and Methods

Two samples from the base of the OL (Figure 3) (depth 275–270 cm) were submitted for radiocarbon dating; the best-preserved fragments of twigs (MPI-162) and wood (MPI-227) were selected from the original sediment samples.

Radiocarbon dating was carried out in the Geocryology Laboratory of the Permafrost Institute SB RAS in Yakutsk (MPI). The laboratory uses the classical method of liquid scintillation with an ultra-low-level liquid scintillation spectrometer–radiometer Quantulus 1220. Benzene is produced by direct synthesis using vacuum pyrolysis without the stage of preliminary charring. This method allows us to increase the carbon output and decrease the minimal sample weight required for the analysis. The dating technique requires 12–20 g of carbon for wood samples and 30–50 g for peat.

Calibration of radiocarbon dates was performed using the OxCal 4.3 program for a 95% significance level using the IntCal20 radiocarbon age calibration curve [29].

Insects and seeds were extracted from the OL by wet sieving. Wet sieving usually produces a mix of different macrofossils including charcoal, chitinous fragments of insects and other invertebrates, calciferous shells of ostracods and molluscs, small mammal bones, and seeds and other parts of plants. Sometimes, peat and gyttja contain numerous insect remains visible to the naked eye, articulate body fossils among them, but in our samples visual examination was not productive; only wet screening allowed the recovery of macrofossils from the sediment.

The volume of each sample was approximately 15 L for K-1 samples and 10 L for 544 samples.

To wet sieve, we used soft nylon screens with meshes of 0.4 and 0.1 mm. The smaller mesh allowed us to collect remains of freshwater invertebrates, eggs, and small seeds. The larger mesh allows for a much faster screening, catching larger macrofossils. Wet-sieved samples were air-dried in the field, and the dry material was further sieved in the laboratory through a nest of soil sieves of 5, 2, 1, 0.5, and 0.25 mm to ease the manual picking of macrofossils. The macrofossils of more than 2 mm were picked from the fraction using a head magnifier, while smaller macrofossils were picked under a stereoscopic microscope.

The organic material from the OL was cemented (gyttja-like) and highly hydrophobic, barely absorbing water. Adding soap and hydrogen peroxide, which usually helps to disintegrate solid clay sediments, did not work here; we had to break the sample up by hand.

All groups of excavated subfossils play their role in paleoenvironmental reconstruction. The macroremains of plants and insects require certain classification. Classifications of plant macroremains are based on their growth form and/or biome [30] and some parameters of plant communities [31,32]. Here, we used a combination of the growth forms and biomes that correspond to certain environments of Central Yakutia. The system of ecological grouping of insect macroremains is more standardized [22,33,34] and was created specifically for the description of the steppe-tundra insect communities of northern Yakutia. Invertebrates are represented by soil animals, such as earthworms and oribatid mites, and water inhabitants.

## 4. Results

A twig fragment was collected for radiocarbon dating from the organic-rich loam immediately below the OL (depth 310 cm from the day surface); this sample was considered a better source of 14C than the OL itself. Radiocarbon dating yielded the date 37,745 ± 2300 BP (Table 1) which attested the MIS3 age of the unit. The OL was considered a part of the lower unit of the main section that yielded two similar radiocarbon dates (Table 1) [27]. Additional radiocarbon dating of the OL material (1860 ± 120 and 1630 ± 130) showed sharp disconformity, indicating the late Holocene age of this unit.

**Table 1.** Results of the radiocarbon and optically stimulated luminescence (OSL) dating.

| Lab. No | Depth (m) | Radiocarbon Ages BP | Calibrated Age BP IntCal20 | Material | Reference |
|---|---|---|---|---|---|
| MPI-156 | 3.1 | 37,745 ± 2300 | 43,190 ± 2810 | shrub remains | Figure 3 in this study |
| MPI-227 | 2.75 | 1860 ± 120 | 1780 ± 150 | wood | Figure 3 in this study |
| MPI-162 | 2.7 | 1630 ± 130 | 1530 ± 130 | shrub remains | Figure 3 in this study |
| MPI-36 | 30 | 39,900 ± 2000 | 44,540 ± 2240 | plant debris | Figure 3 [27] |
| MPI-38 | 33 | 44,200 ± 1800 | 47,730 ± 2280 | plant debris | Figure 3 [27] |
| MPI-43 | 0.1–0.2 | 3320 ± 90 | 3560 ± 110 | moss, sedge | Figure 9 [27] |
| MPI-48 | 1.2–1.3 | 3990 ± 90 | 4470 ± 150 | peat | Figure 9 [27] |
| MPI-52 | 1.3–1.4 | 5840 ± 100 | 6650 ± 120 | peat with wood | Figure 9 [27] |
| MPI-57 | 1.6–1.7 | 8250 ± 100 | 9230 ± 130 | gyttja | Figure 9 [27] |
| OSL | | | | | |
| RLQG 2265-035 | 23 | 18,000 ± 1400 | | quartz sand | Figure 3 [27] |

We collected three samples (Figure 3, samples 544-1, -2, and -3) for the analysis of insect and plant remains in June of 2021 during a permafrost field school (Figure 2C). Finally, the section was revisited in September of 2021 and three more samples (samples KS-1-1, -2, and -3, Figure 2D,E) were collected (Figure 3 samples KS). Both series of samples were collected from the lower, middle, and top parts of the unit corresponding with the stratigraphic layers within the unit.

*4.1. Section Stratigraphy*

The section exposed the following stratigraphic layers, bottom to top (Figure 3):

1. Layer at 0–75 cm: bluish-grey gleied loam with reddish ferruginous spots and plant inclusions, solid, bedding is unclear.
2. Layer at 75–85 cm: laminated loam deposit with alternating light and dark laminae, several mm thick.
3. Layer at 85–90 cm: brown loosely packed organics with admixture of sand and silt.
4. Layer at 90–160 cm: dark brown and reddish-brown consolidated gyttja-like organic material with fragments of grasses, wood, and spruce cones.
5. Layer at 160–360 cm: modern alluvial sand with logs in the central part of the section.

At the edges of the depression, the modern soil covers the OL.

Two samples from the depth of 275–270 cm (at the base of OL) (Figure 3) yielded the following radiocarbon dates: twigs 1630 ± 130 yr. BP (MPI-162) or Cal BP 1530 ± 130 and wood 1880 ± 120 yr. BP (MPI-227) or Cal BP 1780 ± 150).

*4.2. Macrofossils*

The macrofossils included fragments of beetles, resting eggs (ephippia) and shells of small planktonic crustaceans, statoblasts of freshwater bryozoans, cocoons of annelids including earthworms and leeches, and numerous cones, cone scales, needles, fruits, and seeds of trees and herbs.

4.2.1. Insects and Other Invertebrates

The insect remains were relatively well preserved (Figure 4) except for a few fragments with a thinned edge (Figure 4R), which were probably redeposited from the underlying Pleistocene unit. The richest group is Coleoptera—174 fragments of 61 species from 14 families (Table 2). In addition to the beetles, the insect assemblage includes Hymenoptera (ants and cocoons of sawflies), Trichoptera (larval cases), Diptera (a head capsule of Chironomidae larvae and puparia of Brachycera), and Neuroptera (cocoons). The diversity of invertebrates is high (Table 2, Figure 5); we found representatives of six phyla: Arthropoda, Annelida, Platyhelminthes, Bryozoa, Mollusca, and Porifera. The diversity of insects and other invertebrates attests for eutrophic conditions in the water body and adjacent loci.

Most of the recorded insects and invertebrates belong to the aquatic group (aq). There are at least two species of whirligig beetles (Gyrinidae) and two species of predaceous diving beetles (Dytiscidae) who live in open water.

A rare find is a minute moss beetle (Hydraenidae) *Limnebius* sp.; this is its first record in the Quaternary fauna of Yakutia. Modern *Limnebius* is not recorded in the region, but the beetles are very small, and it is hard to find them in remote places during casual/random collection. In Europe, *Limnebius* is abundant in some modern wetlands [35] and found in Quaternary deposits [36]. Our fragment probably belongs to *L. truncatellus* (Thunb.), which occurs in Northern Europe and Siberia. This aquatic species lives among vegetation near margins of still and slow-moving water, e.g., in temporary pools.

The weevil *Bagous limosus* Gyll. can be found on aquatic plants or hiding in wet organic matter near water. The larvae feed on various *Potamageton* species [37].

Open water and aquatic vegetation are habitat requirements of leeches of the Erpobdellidae family. We found 440 cocoons, tentatively identified as *Erpobdella octoculata* (L.). These leeches are common in Siberia [38]; they live in slow-moving and still water and feed

on small invertebrates. The leeches attach their cocoons to the lower part of broad leaves of water plants, such as water lilies.



**Figure 4.** Insect remains from the Holocene organic deposits of Kyzyl-Syr. A—*Agonum duftschmidi*, B—*Agonum sexpunctatum*, C—*A. exaratum*, D—*Bembidion transparens*, E—*B. doris*, F—*Gyrinus natator*, G—*Cymbiodyta marginella*, H—*Limnebius* sp., I—*Eucnecosum tenue*, J—*Olophrum rotundicolle*, K—Aleocharinae gen. indet, L—*Porcinolus murinus*, M—*Aphthona violacea*, N—*Donacia splendens*, O—*Hypera viciae*, P—*Tachyerges stigma*, Q—*Bagous limosus*, R—*Ceutorhynchus* sp., S—*Lixus paraplecticus*. Samples: A, C, E—544-1; B, D, F, H, I, M—544-3; G, J, Na, O, Q, R—KS-21-1-3; K, P—KS-21-1-2; L, Nb—544-2. Part of body: A, B, D, Fa, Ga, I, Ja, Na—pronotum; C, E, Fb, Gb, H, Jb, K, L, M, Nb, O, P, Qb, R, Sa, Sb—elytra; Qa—head.

**Table 2.** List of insects and other invertebrates. Ecological groups: aq—aquatic, ri—riparian and bog habitats, mt—wet tundra and bogs inside taiga; direct and indirect indicators of forest or forest-tundra: fo—forest, pl -plant litter, me—meadow, sh—shrubs; indicators of dry environment: dt—cold-resistant xerophilous insects typical for tundra, xe—intrazonal xerophilous insects, st—steppe, ms—meadow-steppe; oth—insects of uncertain habitats.

| Taxa | Eco | 544/3 | KS-21-1-1 | KS-21-1-2 | 544/2 | KS-21-1-3 | 544/1 |
|---|---|---|---|---|---|---|---|
| | | lower | middle | | top | | |
| **Arthropoda, Insecta, Coleoptera** | | | | | | | |
| **Gyrinidae** | | | | | | | |
| *Gyrinus natator* L. | aq | 2 | 0 | 5 | 0 | 3 | 1 |
| *G. opacus* Sahlb. | aq | 1 | 0 | 0 | 0 | 0 | 0 |
| *Gyrinus* sp. | aq | 0 | 2 | 0 | 1 | 0 | 0 |
| **Carabidae** | | | | | | | |
| *Miscodera arctica* (Payk) | me | 1 | 0 | 0 | 0 | 0 | 0 |
| *Elaphrus splendidus* F.-W. | ri | 0 | 0 | 0 | 0 | 0 | 1 |
| *Bembidion* (*Notaphus*) sp. | ri | 1 | 0 | 0 | 0 | 0 | 0 |
| *B.* (*Peryphus*) sp. | ri | 0 | 0 | 0 | 1 | 1 | 0 |
| *B.* (*Diplocampa*) *transparens* (Gebl.) | ri | 1 | 0 | 0 | 0 | 0 | 0 |
| *B.* (*Trepanedoris*) *doris* Pan. | ri | 0 | 0 | 0 | 0 | 0 | 1 |
| *Bembidion* sp. | ri | 0 | 0 | 0 | 1 | 1 | 0 |
| *Dicheirotrichus mannerheimi* Sahlb. | xe | 1 | 0 | 0 | 1 | 0 | 0 |
| *Cymindis* sp. | xe | 1 | 0 | 0 | 0 | 1 | 0 |
| *Agonum* (*Europhilus*) *consimile* Gyll. | ri | 0 | 0 | 0 | 4 | 0 | 0 |
| *A.* (*Europhilus*) *sexpunctatum* L. | ri | 1 | 0 | 0 | 0 | 0 | 0 |
| *A.* (*Olisares*) *duftschmidi* J.Sch. | ri | 0 | 0 | 0 | 0 | 0 | 3 |
| *A.* (*Agonothorax*) *exaratum* Schalb. | ri | 0 | 0 | 0 | 0 | 0 | 2 |
| *Agonum* sp. | ri | 0 | 1 | 0 | 0 | 4 | 0 |
| *Poecilus* (*Derus*) *nearcticus* Lth. | dt | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pterostichus* (*Cryobius*) *brevicornis* (Kby.) | mt | 0 | 0 | 0 | 0 | 0 | 3 |
| *P.* (*Cryobius*) *ventricosus* Esch. | mt | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pterostichus* (*Cryobius*) spp. | mt | 2 | 0 | 3 | 1 | 0 | 0 |
| *Curtonotus torridus* Pz. | xe | 0 | 0 | 0 | 0 | 1 | 0 |
| Carabidae gen. indet. | oth | 0 | 0 | 0 | 0 | 1 | 0 |
| **Dytiscidae** | | | | | | | |
| *Agabus* sp. | aq | 0 | 0 | 0 | 1 | 1 | 2 |
| *Colymbetes* sp. | aq | 1 | 1 | 1 | 1 | 1 | 2 |
| Dytiscidae gen. indet. | aq | 1 | 0 | 0 | 1 | 3 | 1 |
| **Hydrophilidae** | | | | | | | |
| *Cymbiodyta marginella* (F.) | ri | 0 | 0 | 0 | 0 | 1 | 1 |
| *Cercyon* sp. | pl | 0 | 1 | 0 | 0 | 0 | 0 |
| **Hydraenidae** | | | | | | | |
| *Limnebius* sp. | aq | 1 | 0 | 0 | 0 | 0 | 0 |
| **Staphylinidae** | | | | | | | |
| *Eucnecosum tenue* (LeC.) | pl | 2 | 2 | 0 | 1 | 0 | 0 |
| *Olophrum latum* Maekl. | pl | 0 | 0 | 0 | 0 | 1 | 0 |
| *O. rotundicolle* Sahlb. | pl | 1 | 0 | 0 | 5 | 1 | 7 |
| *Olophrum* sp. | pl | 0 | 0 | 1 | 0 | 0 | 0 |
| *Tachyporus* sp. | pl | 0 | 0 | 0 | 1 | 0 | 0 |
| *Stenus* sp. | ri | 0 | 0 | 0 | 1 | 0 | 1 |
| *Lathrobium brunnipes* (F.) | pl | 0 | 0 | 0 | 0 | 1 | 0 |
| *L. longulum* Grav. | pl | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lathrobium* sp. | pl | 1 | 0 | 0 | 0 | 0 | 0 |
| *Gymmusa* sp. | pl | 1 | 0 | 0 | 0 | 0 | 0 |
| Aleocharinae gen. indet | pl | 0 | 0 | 1 | 2 | 0 | 0 |
| *Philonthus* sp. | pl | 0 | 0 | 0 | 1 | 0 | 0 |
| Staphylinidae gen. indet. | pl | 0 | 0 | 0 | 0 | 0 | 2 |

**Table 2.** *Cont.*

| Taxa | Eco | 544/3 | KS-21-1-1 | KS-21-1-2 | 544/2 | KS-21-1-3 | 544/1 |
|---|---|---|---|---|---|---|---|
| | | lower | middle | | top | | |
| **Scirtidae** | | | | | | | |
| *Cyphon variabilis* Thunb | ri | 0 | 0 | 0 | 1 | 1 | 1 |
| **Byrrhidae** | | | | | | | |
| *Cytilus sericeus* Forst. | me | 0 | 0 | 1 | 0 | 1 | 0 |
| *Porcinolus murinus* (F.) | st | 1 | 0 | 0 | 2 | 0 | 0 |
| *Morychus* sp. | xe | 0 | 0 | 0 | 0 | 1 | 0 |
| *Simplocaria semistriata* F. | me | 1 | 0 | 0 | 0 | 0 | 0 |
| **Heteroceridae** | | | | | | | |
| *Heterocerus fenestratus* (Thunb.) | ri | 1 | 0 | 0 | 1 | 0 | 0 |
| **Elateridae** | | | | | | | |
| *Oedostethus femoralis* LeC. | ri | 0 | 0 | 0 | 0 | 2 | 0 |
| Elateridae gen. indet. | ri? | 1 | 0 | 0 | 0 | 0 | 0 |
| **Bostrichidae** | | | | | | | |
| *Stephanopachys substriatus* Payk. | fo | 0 | 0 | 0 | 0 | 1 | 0 |
| **Anthicidae** | | | | | | | |
| *Anthicus ater* Pz. | me | 0 | 0 | 0 | 1 | 0 | 0 |
| **Chrysomelidae** | | | | | | | |
| *Donacia splendens* Jac. | ri | 0 | 0 | 0 | 3 | 4 | 6 |
| *Donacia* sp. | ri | 0 | 1 | 2 | 2 | 0 | 0 |
| *Phaedon concinnus* Steph. | me | 0 | 0 | 0 | 0 | 0 | 1 |
| *Gonioctena affinis* Gyll. | sh | 0 | 1 | 0 | 0 | 0 | 0 |
| *Aphthona violacea* (Koch) | fo | 1 | 0 | 0 | 0 | 0 | 0 |
| *Aphthona* sp. | fo? | 0 | 0 | 1 | 0 | 0 | 0 |
| *Chaetocnema* sp. | me | 0 | 1 | 0 | 0 | 0 | 0 |
| *Galerucella grisescens* Joann. | fo | 0 | 0 | 0 | 0 | 1 | 0 |
| **Curculionidae** | | | | | | | |
| *Tourotaris bimaculata* (F.) | ri | 0 | 0 | 0 | 1 | 0 | 0 |
| *Bagous limosus* Gyll. | aq | 0 | 0 | 0 | 0 | 1 | 1 |
| *Ceutorhynchus* sp. | xe | 0 | 0 | 0 | 0 | 1 | 0 |
| *Phyllobius kolymensis* Kor. et Egorov | ms | 0 | 0 | 1 | 0 | 0 | 0 |
| *P. virideaeris* Laich. | me | 1 | 0 | 0 | 0 | 0 | 0 |
| *Hypera viciae* (Gyll.) | me | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lixus paraplecticus* L. | ri | 1 | 0 | 0 | 0 | 0 | 1 |
| Cleonini gen. indet. | ms | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lepyrus canadensis* Csy. | sh | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lepyrus* sp. | sh | 0 | 2 | 0 | 0 | 1 | 1 |
| *Pissodes* sp. | fo | 0 | 0 | 0 | 0 | 1 | 0 |
| *Dorytomus* sp. | sh | 0 | 0 | 0 | 0 | 1 | 0 |
| *Rhynchaenus* sp. | sh | 0 | 0 | 0 | 0 | 1 | 0 |
| *Tachyerges stigma* Germ. | sh | 0 | 0 | 1 | 0 | 0 | 0 |
| *Isochnus flagellum* Erics. | sh | 1 | 0 | 0 | 0 | 0 | 0 |
| Curculionidae gen. indet. | oth | 0 | 0 | 0 | 2 | 0 | 0 |
| **Arthropoda, Insecta, Hymenoptera** | | | | | | | |
| **Symphyta, Tenthredinidae** | | | | | | | |
| Tenthredinidae gen. indet. (cocoon) | oth | 0 | 0 | 1 | 0 | 0 | 0 |
| **Aculeata, Formicidae** | | | | | | | |
| *Formica* sp. | fo | 0 | 0 | 0 | 1 | 0 | 1 |
| *Formica* sp.? | fo | 1 | 0 | 0 | 0 | 0 | 1 |
| *Camponotus herculeanus* L. | fo | 3 | 1 | 0 | 0 | 2 | 0 |
| **Parasitica, Ichneumonidae** | | | | | | | |
| Ichneumonidae gen. indet. (cocoon) | oth | 0 | 0 | 0 | 0 | 0 | 1 |
| Parasitica gen. indet. | oth | 3 | 0 | 0 | 0 | 0 | 0 |

**Table 2.** *Cont.*

| Taxa | Eco | 544/3 | KS-21-1-1 | KS-21-1-2 | 544/2 | KS-21-1-3 | 544/1 |
|---|---|---|---|---|---|---|---|
| | | lower | middle | | top | | |
| **Arthropoda, Insecta, Neuroptera** | | | | | | | |
| **Chrysopidae** | | | | | | | |
| Chrysopidae gen. indet. (cocoon) | oth | 0 | 0 | 2 | 0 | 2 | 3 |
| **Arthropoda, Insecta, Diptera** | | | | | | | |
| **Chironomidae** | | | | | | | |
| Chironomidae gen. indet. (larvae) | aq | 0 | 1 | 0 | 1 | 0 | 1 |
| Diptera gen. indet. (puparia) | oth | 0 | 0 | 0 | 5 | 3 | 3 |
| **Arthropoda, Insecta, Trichoptera** | | | | | | | |
| **Brachycentridae** | | | | | | | |
| *Brachycentrus subnubilus* Curtis | aq | 3 | 0 | 0 | 4 | 0 | 7 |
| *Micrasema gelidum* McLachlan? | aq | 0 | 0 | 1 | 1 | 0 | 0 |
| **Arachnida, Oribatida** | | | | | | | |
| Oribatida gen. indet. | oth | 0 | 1 | 0 | 0 | 0 | 0 |
| **Arthropoda, Crustacea** | | | | | | | |
| **Branchiopoda, Cladocera, Anomopoda** | | | | | | | |
| **Daphniidae** | | | | | | | |
| *Daphnia* (*Daphnia*) sp. (ephippium) | aq | 74 | 14 | 130 | 10 | 4 | 22 |
| *Simocephalus* sp. (ephippium) | aq | 0 | 0 | 0 | 0 | 0 | 1 |
| *Ceriodaphnia* sp. (ephippium) | aq | 0 | 0 | 2 | 0 | 0 | 0 |
| **Chydoridae** | | | | | | | |
| *Alona affinis* Leydig? | aq | 0 | 0 | 0 | 13 | 0 | 0 |
| **Amphipoda, Gammaridae** | | | | | | | |
| *Gammarus* sp.? | aq | 0 | 1 | 0 | 0 | 0 | 0 |
| **Annelida, Clitellata, Haplotaxida** | | | | | | | |
| **Lumbricidae** | | | | | | | |
| *Eisenia nordenskioldi* (Eisen) | pl | 0 | 0 | 0 | 26 | 1 | 24 |
| Lumbricidae cocoons | pl | 9 | 4 | 9 | 0 | 11 | 0 |
| **Annelida, Clitellata, Hirudinea, Arhynchobdellida** | | | | | | | |
| **Erpobdellidae** | | | | | | | |
| *Erpobdella octoculata* (L)? | aq | 66 | 4 | 57 | 64 | 163 | 86 |
| **Haemopidae** | | | | | | | |
| *Haemopis sanguisuga* (L)? | aq | 12 | 0 | 1 | 5 | 19 | 6 |
| **Platyhelminthes, Rhabditophora, Tricladida** | | | | | | | |
| **Planariidae** | | | | | | | |
| Planarian eggs | aq | 0 | 0 | 0 | 0 | 1 | 0 |
| **Bryozoa, Phylactolaemata** | | | | | | | |
| **Cristatellidae** | | | | | | | |
| *Cristatella mucedo* Cuvier | aq | 6 | 1 | 4 | 3 | 8 | 15 |
| **Mollusca, Bivalvia** | | | | | | | |
| **Sphaeriidae** | | | | | | | |
| *Pisidium casertanum* (Poli) | aq | 0 | 0 | 0 | 0 | 2 | 0 |
| **Porifera, Demospongiae, Spongillida** | | | | | | | |
| **Spongillidae** | | | | | | | |
| Spongillidae gen. indet. | aq | 0 | 0 | 0 | 0 | 37 | 24 |
| sum | | 204 | 39 | 225 | 170 | 296 | 233 |
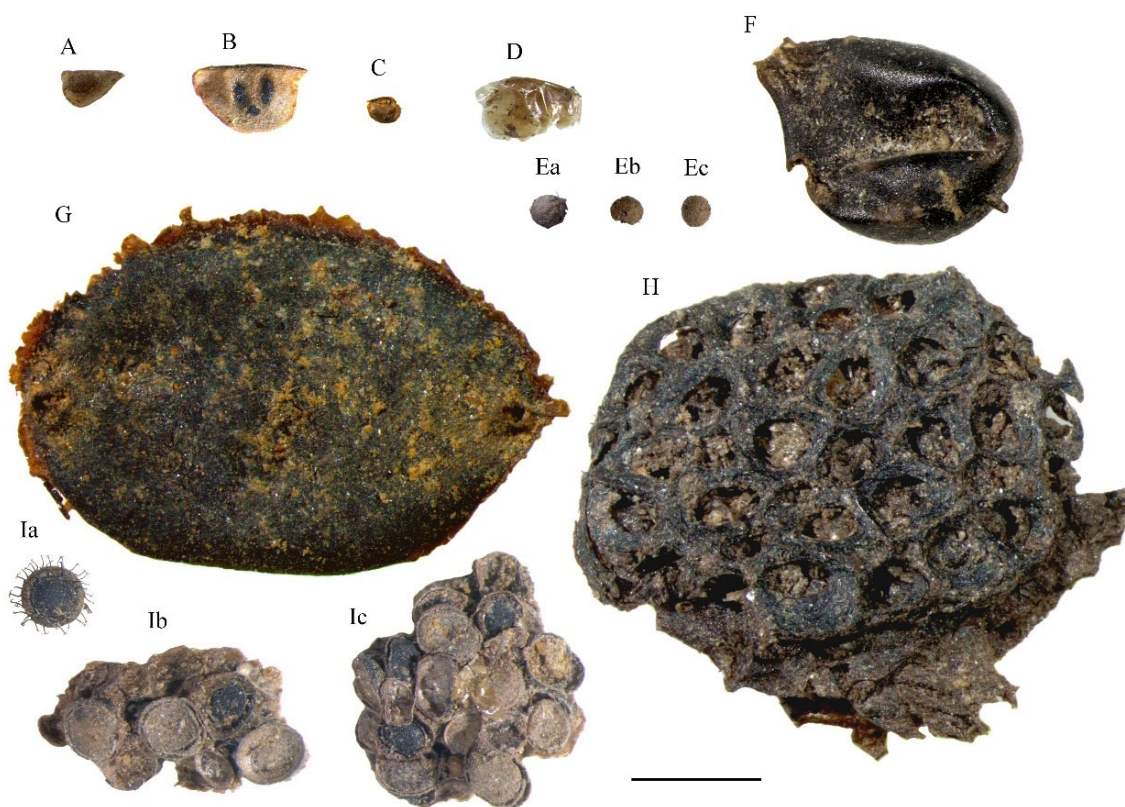
**Figure 5.** Invertebrate remains from the Holocene organic deposits of Kyzyl-Syr. A—*Simocephalus* sp. (ephippium), B—*Daphnia* (*Daphnia*) sp. (ephippium), C—*Ceriodaphnia* sp. (ephippium), D—*Alona affinis*? (shell), E—Spongillidae gemmules (a with spicule, b, c different view), F—*Eisenia nordenskioldi*? (cocoon), G—*Erpobdella octoculata*? (cocoon), H—*Haemopis sanguisuga*? (cocoon), I—*Cristatella mucedo* (a mature statoblast, b, c groups of immature statoblasts). Samples: A—544-1; B—544-3; C, G—ks-21-1-2; D, E, H, I—ks-21-1-3; F—544-2.

The cocoons of another leech most likely belonged to *Haemopis sanguisuga* (L) (Haemopidae). This leech is widespread in Siberia; it prefers small ponds and can survive out of water for a long time [38]. The leech predates on relatively large prey, including earthworms. The cocoons occur in wet soil.

We also found small plankton crustaceans. Crustaceans are often found in Quaternary deposits and are used with considerable success in paleoenvironmental reconstructions [39–41]. Usually, mainly hard macrofossils survive the wet sieving procedure, such as ephippia or winter eggs of daphnia. Ephippia allow for the identification up to subgenus level. The most abundant ephippia in our samples belong to the *Daphnia* (*Daphnia*) subgenus (Table 2, Figure 5B). These water fleas can live in various water bodies, from large lakes to temporary pools, but large numbers of their ephippia are indicative of a permanent water body rather than a small pool. Solitary ephippia belong to water fleas of the *Simocephalus* and *Ceriodaphnia* genera; they are common members of plankton communities of lakes and ponds.

The extraction of the tiny shells of adult water fleas requires a special technique; these remains rarely survive wet screening, but here we found several shells of Chydoridae water fleas (*Alona affinis* Leydig?). This finding means that the species was abundant in the water body. *A. affinis* is a widespread species with a broad ecological range. The crustaceans feed on detritus and benthic algae that grow on the surfaces of plants and rocks [42].

Statoblasts (survival pods) of the freshwater bryozoan (Phylactolaemata) *Cristatella mucedo* Cuvier are often found in Quaternary deposits of aquatic origin [43]. Statoblasts could be abundant in sediment of freshwater origin, and their species composition can

be used as an indicator of the local and regional climate and environment [44]. We found statoblasts in each sample of the OL. In the top sample (Figure 3), several clusters of connected undeveloped statoblasts were presented. Such clusters could be a part of a caddisfly case (A. Vinogradov, pers. comm.), but more likely the clusters are remains of premature statoblasts without hooks and spines that formed inside colonies of *C. mucedo* at the end of the growing season. Photos of colonies filled with similar statoblasts in clusters of a similar shape are published at http://www.microscopy-uk.org.uk (accessed on 6 March 2020).

Single Bivalvia molluscs *Pisidium casertanum* (Poli) were found in the OL. *P. casertanum* is a widespread species that can live in various water bodies, from lakes and rivers to temporary ponds and swamps [45].

Two top samples of the OL (Table 2, Figure 5) yielded numerous gemmules (internal buds) of freshwater sponges Spongillidae (probably *Spongilla lacustris* (L)). The sponges occupy slow-flowing rivers, lakes, and ponds. Gemmules form mainly in the autumn as a means of survival during the freezing season. In Western Siberia, gemmule-producing sponges are distributed mostly in the steppe-forest zone and southern taiga [46], but *S. lacustris* also occurs in the forest–tundra transition zone and was found in one locality within the southern tundra. *S. lacustris* can grow on a pond bottom or be attached to aquatic macrophytes [47]. The abundance of sponges in the north is low compared to southern regions [46].

Freshwater sponges have been used as a paleoenvironmental indicator [48,49], but this group is rarely mentioned in the literature. In Yakutia, we discovered gemmules for the first time in Quaternary deposits, while modern freshwater sponges are not documented in the region yet.

All six assemblages (Figure 6) are dominated by aquatic species. The share of the aquatic group varies from 62 to 91%. A closely related ecological group, riparian (inhabitants of the water edges), includes 18 species, but their proportion in the samples is low (Table 2).
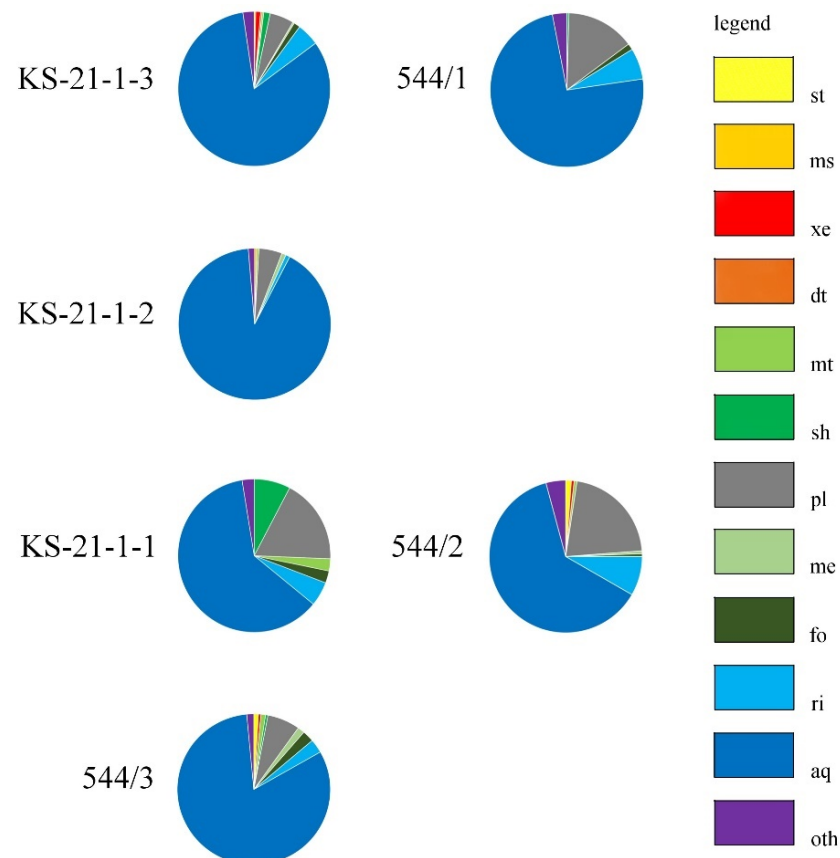


**Figure 6.** Ecological composition of insect–invertebrate assemblages from the Holocene of Kyzyl-Syr.

Some species occur in both the aquatic and terrestrial habitats. The water scavenger beetle *Cymbiodyta marginella* (F.) lives on densely vegetated banks near standing water and in bogs [50]; the beetle can be found in open water [51]. The marsh beetle *Cyphon variabilis* Thunb could be found among wetland vegetation, but its larvae live in water. The leaf beetle *Donacia splendens* Jac. has a similar life cycle. The larvae of the beetle live under water and feed on the roots of *Carex*, *Scirpus*, and *Typha*; the adult beetles occupy the same plants above the water level and probably feed on their flowers [52].

The weevil *Tournotaris bimaculata* (F.) is associated with tall riparian vegetation; the larvae mine the stems of *Typha* [53].

The weevil *Lixus paraplecticus* L. occurs in wetlands and feeds on various Apiaceae, including *Cicuta virosa.* This weevil can occasionally drop from a host plant down into the water and survive, but both the adult and larvae are terrestrial inhabitants [54].

Many other inhabitants of riparian environments were found in the samples. These are ground beetles *Elaphrus splendidus* F.-W., species of the *Bembidion* genus, species of the *Agonum* genus, the rove beetle *Stenus* sp., and the click beetle *Oedostethus femoralis* LeC. These beetles inhabit near-water open grounds.

The next group includes inhabitants of plant litter and soil (pl); this group reaches 21% in the middle of the section (Figure 6). The remains of soft earthworm bodies rarely survive, but their cocoons consist of a solid membrane and can be preserved in deposits. Only one species with a wide range, *Eisenia nordenskioldi* (Eisen), is currently distributed in Yakutia, mainly because of its exceptional resistance to cold [55,56]. The cocoons of *E. nordenskioldi* are large and have a distinctive oval shape (Figure 5). We found many *E. nordenskioldi* cocoons and some small cocoons that may belong to another cold-resistant species *Dendrobaena octaedra* (Savigny) that has not been recorded in the modern entomo-fauna of Yakutia but occurs in the Magadan region. Earthworms prefer wet soil, and in Yakutia *E. nordenskioldi* usually live in floodplains.

Xerophilous terrestrial species are not abundant in any of the layers, but they were recorded in five of the six samples. Most of them occur in the area currently. However, at least one of the species was probably redeposited from the nearby Pleistocene section (Figures 2 and 3) where several steppe species were found. The ground beetle *Poecilus (Derus) nearcticus* Lth. was a common member of the Pleistocene steppe-tundra communities in Yakutia, but extant communities are known only in a few isolated localities in the tundra in North America and Eastern Siberia [18].

### 4.2.2. Plants

The plant remains from the OL belong to 37 taxa (Table 3, Figure 7). All of them (except *Bunias cochlearioides*) are among the modern flora of the region. The plant assemblage includes trees, shrubs, dwarf shrubs, herbs, and water plants. Green mosses (Bryales) are found in each sample, but their proportion is not high. The main precursors for the OL formation were probably sedges and bogbean stems.

The remains of coniferous trees are represented by seeds, cones, and cone scales; we have recorded Dahurian larch (*Larix gmelinii*), Scotch pine (*Pinus sylvestris*), and Siberian spruce (*Picea obovata*). In Central Yakutia, pine occupies dry sandy habitats, such as sand dunes including the Kysyr-Syr *tukulan*. Larch is the most common tree in the Yakutian taiga; it prefers wet habitats. Spruce forests occupy the wet bottoms of river valleys.

The OL samples yielded remains of birches (female catkin scales and fruits). There are trees, such as *Betula platyphylla* that belongs to *Betula (Betula)* sect. *Betula* (former sect. *Albae*) according to the latest taxonomic revision [57], and shrubs, such as *Betula fruticosa* which belongs to *B. (Betula)* sect. *Apterocaryon* (former sect. *Nanae*). Sections became less popular in modern botany as a taxonomic term and are often replaced by the subgenus, but paleobotanists still use them widely, as the sections are recognizable in seeds and pollen and the identification of seeds up to the section level allows us to separate trees from shrubs.

**Table 3.** List of plant remains. Ecological groups: t—trees, the group indicates forests; sh—shrubs, here the group includes dwarf Betula and Alnus, and these shrubs occur on boggy patches inside the forest; psh—prostrate shrubs (mostly Erycaceae); h—hydrophytes (riparian and aquatic plants); h*—hydrophytes inside southern taiga and forest-steppe; hm—hygrophytic and mesohygrophytic (mostly riparian and boggy grasses and herbs); m—mesophitic (meadow and forest grasses and herbs); xe—xero-mesophytic (grasses and herbs of forest-steppe and steppe zones); p—pioneering (grasses and herbs typical for disturbed grounds); oth—other grass and herbs. Plant remains: *n*—needles; *s*—seeds and fruits; *ps*—seeds with perigynia; *ss*—seed scales; *c*—cones; *b*—bracts; *st*—stalk.

| Taxa | Group | KS-21-1-1 + 2 | KS-21-1-3 | 544-1 | 544-2 | 544-3 |
|---|---|---|---|---|---|---|
| **Pinaceae** | | | | | | |
| *Larix gmelinii* (Rupr.) Kuzen | t | 1*n* | 3*c*, 8*s*, 1*ss*, 1*n* | 8*s*, 1*n* | 11*s*, 1*ss*, 1*n* | 1*c*, 1*s* |
| *Picea obovata* Ledeb. | t | 1*c*, 8*s*, 3*ss*, 3*n* | 28*s* | 36*s*, 1*n* | 12*s*, 2*n* | 11*s* |
| *Pinus sylvestris* L. | t | 1*s* | 5*s* | | | 1*s* |
| **Betulaceae** | | | | | | |
| *Betula* (s. str.) sect. *Betula* sp. | t | 5*s* | 1*s* | 1*s* | 1*s* | 6*s* |
| *B. platyphylla* Sukaczev | t | | | 1*ss* | 1*ss* | 1*ss* |
| *B. fruticosa* Pall. | sh | | | 1*ss* | | |
| *B.* cf. *fruticosa* Pall. | sh | | | 1*s* | 1*s* | 1*s* |
| *B.* (s. str.) sect. *Apterocaryon* sp. | sh | | | | 1*s* | 2*s* |
| *Alnus hirsuta* (Spach) Turcz. ex Rupr. | sh | 4*s* | 1*s*, 1*b* | 2*s* | 1*s*, 4*ss* | 1*s* |
| **Rosaceae** | | | | | | |
| *Rubus* cf. *matsumuranus* H. Lev. & Van. | sh | | 1*s* | | 1*s* | |
| *Potentilla* sp. | oth | | | 2*s* | | |
| *Comarum palustre* L. | hm | | 3*s* | 22*s* | 4*s* | |
| **Ericaceae** | | | | | | |
| *Arctostaphylos uva-ursi* (L.) Spreng. | psh | | 2*s* | 1*s* | 5*s* | 2*s* |
| *Vaccinium uliginosum* L. | psh | 1*s* | | | | |
| **Nymphaeaceae** | | | | | | |
| *Nuphar pumila* (Timm) DC | h* | 2*s* | 16*s* | 1*s* | 2*s* | |
| *Nymphaea tetragona* Georgi | h* | 14*s* | 3*s* | 2*s* | 2*s* | 6*s* |
| **Typhaceae** | | | | | | |
| *Sparganium emersum* Rehmann | h | | | 1*s* | | |
| *S. hyperboreum* Laest. | h | | | | | 1*s* |
| **Potamogetonaceae** | | | | | | |
| *Potamogeton perfoliatus* L. | h | 48*s* | 470*s* | 6*s* | 21*s* | 37*s* |
| *P. filiformis* Pers. | h | | | 3*s* | | 3*s* |
| *P. natans* L. | h | | | 1*s* | | |
| **Cyperaceae** | | | | | | |
| *Schoenoplectus lacustris* (L.) Palla | h | 1s | | 1*s* | | |
| *Carex* spp. | hm | 7*s*, 3*ps* | 7*s*, 5*ps* | 19*s*, 8*ps* | 7*s*, 7*ps* | 2*ps* |
| *Eriophorum angustifolium* Honck. | hm | | | | 1*s* | |
| **Ranunculaceae** | | | | | | |
| *Ranunculus repens* L. | m | | | 1*s* | | |
| *R. monophyllus* Ovcz. | m | 2*s* | | | 2*s* | |

**Table 3.** *Cont.*

| Taxa | Group | KS-21-1-1 + 2 | KS-21-1-3 | 544-1 | 544-2 | 544-3 |
|---|---|---|---|---|---|---|
| *Batrachium* sp. | h | | | 1*s* | 1*s* | |
| **Haloragaceae** | | | | | | |
| *Myriophyllum verticillatum* L. | h | | 1*s* | | | 1*s* |
| **Polygonaceae** | | | | | | |
| *Persicaria lapathifolia* (L.) S.F. Gray | hm | 1*s* | | | | |
| **Apiaceae** | | | | | | |
| *Cicuta virosa* L. | hm | | | 2*s* | 5*s* | 3*s* |
| **Menyanthaceae** | | | | | | |
| *Menyanthes trifoliata* L. | hm | 28*s* | 185*s* | 155*s* | 95*s* | 16*s* |
| **Brassicaceae** | | | | | | |
| *Bunias cochlearioides* Murray | xe | | | 1*s* | | |
| Brassicaceae gen. indet | oth | | | 1*s* | | |
| **Lamiaceae** | | | | | | |
| *Dracocephalum ruyschiana* L. | xe | 1*s* | | | | |
| Lamiaceae gen. indet. | oth | | 1*s* | | | |
| **Amaranthaceae** | | | | | | |
| *Corispermum crassifolium* Turcz. | p | 1*s* | | | | |
| Bryales gen. indet. | hm | 4*st* | 3*st* | 5*st* | 8*st* | 1*st* |
| sum | | 158 | 746 | 285 | 192 | 113 |

*B. platyphylla* grows near the section currently, but the northern limit of the species is less than hundred km to the north [58]. The shrub birch *Betula fruticosa* is more typical for tundra regions, but sometimes it can be found on the margins of wetlands within the coniferous forest.

The alder *Alnus hirsuta* can grow either as a small tree or a large shrub; it grows on wet soil and is common along rivers in Siberia.

The Siberian raspberry *Rubus matsumuranus* grows mostly in dry habitats, including forest edges and steep sandy riverbanks; the raspberry can occupy stabilized sand dunes.

The next important plant of the Siberian dry forests and stabilized sand dunes is the dwarf shrub *Arctostaphylos uva-ursi* (bearberry or kinnikinnick). This shrub often creates a continuous cover on sandy soils. In paleosols, buried in Yakutian sand dunes in the last centuries (Ust' Buotama section, the Lena Pillars nature park), the bearberry seeds dominated macrofossil assemblages along with pinecone scales (S. Kuzmina, personal observations). However, only solitary bearberry seeds were found in the Kyzyl-Syr section.

Another low shrub that left seeds in the OL layer is the bog blueberry, *Vaccinium uliginosum* L. This shrub is very common in the north of Yakutia and considerably common in the central part of the region where it prefers wet boggy soil.

While the macrofossils of herbaceous plants originated from various habitats, bog and water taxa were the most abundant. The seeds of two aquatic plants, *Potamogeton perfoliatus* and *Menyanthes trifoliataI*, were abundant in all samples (Table 3). Interestingly, other aquatic taxa such as *Batrachium* sp. and *Myriophyllum verticillatum* are represented here only by solitary seeds, while in other sections of Siberian Quaternary deposits, both taxa are very common and abundant, according to our observations.
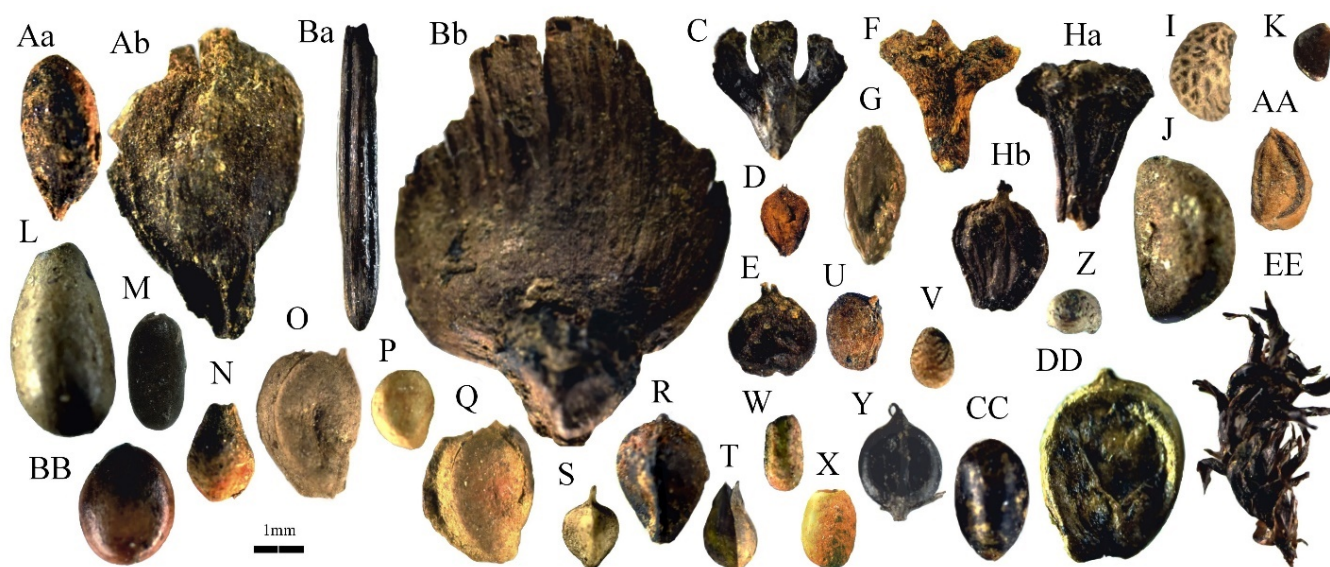
**Figure 7.** Plant remains from the Holocene organic deposits of Kyzyl-Syr. A—*Picea obovata*, B—*Larix gmelinii*, C—*Betula fruticosa*, D—*B.* cf. *fruticosa*, E—*B.* (s. str.) sect. *Apterocaryon* sp., F—*B. platyphylla*, G—*B.* (s. str.) sect. *Betula* sp., H—*Alnus hirsuta*, I—*Rubus matsumuranus*, J—*Arctostaphylos uva-ursi*, K—*Vaccinium uliginosum*, L—*Nuphar pumila*, M—*Nymphaea tetragona*, N—*Sparganium emersum*, O—*Potamogeton perfoliatus*, P—*P. filiformis*, Q—*P. natans*, R—*Schoenoplectus lacustris*, S—*Carex* sp., T—*Eriophorum angustifolium*, U—*Ranunculus monophyllus*, V—*Batrachuym* sp., W—*Myriophyllum verticillatum*, X—*Sparganium hyperboreum*, Y—*Persicaria lapathifolia*, Z—*Comarum palustre*, AA—*Cicuta virosa*, BB—*Menyanthes trifoliata*, CC—*Dracocephalum ruyschiana*, DD—*Corispermum crassifolium*, EE—Bryales gen indet. Samples: A, G, K, O, R, S, Y, BB, CC, DD, EE—KS-21-1-1; B, I, J, W, Z—KS-21-1-3; C, F, N, P, Q, V, AA—544-1; D, E, M, X—544-3; T, U—544-2. Plant remains: Aa, K, L, M, BB, CC—seeds; Ab, Ba—seed scale; Ba—needle; C, Ha—bract scale; D, E, G, Hb, R, S, W, Y—nutlet; F—bract scale; I, J, N, O, P, Q—endocarp; V, X, DD—fruit; Z—achene; AA—semi-fruit; EE—stem and leaves.

Two rare water plants were recorded in the OL. The dwarf water lily *Nuphar pumila* is a widespread species in Northern Eurasia, but its distribution in Yakutia is limited due to the extreme climate. The northern limit of the *N. pumila* range lies exactly on the right bank of the Vilyuy River (except for one isolated locality near Srednekolymsk at the Kolyma River). The second plant is the pygmy waterlily *Nymphaea tetragona*; its main range lies 600 km south of our site (near Aldan River mouth), while single finds are known from northern localities up to the tundra zone [59].

Some plant macrofossils from the OL are of terrestrial origin, but these are not numerous. Some examples are the seeds of *Dracocephalum ruyschiana* and the pods of *Bunias cochlearioides*. The first species prefers forest-steppe ecosystems and spreads along the valleys of large rivers to the north, where it occupies grassy patches among larch and birch forests [60]. *Bunias cochlearioides* has not been recorded in Yakutia previously; this species is common in the meadow-steppes of Europe and South Siberia. The bugseed *Corispermum crassifolium* is a xerophilous species; it often occurs in sand dunes [61].

### 4.2.3. Charred Plant Remains

Charred plant remains were analyzed from six samples (544-1, 544-1, 544-1, KS-21-1-1, KS-21-1-2, and KS-21-1-3) (Tables 4 and 5, Figure 8).

**Table 4.** Fuel fractions in charcoal assemblages.

| Sample Code | Charcoalified Plant Remains, Number of Fragments | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Max Size (mm) | Circularity | Wood | Bark | Roots | Needles | Seeds | Fungal Sclerotia | Total | Vitrified Charcoal |
| 544-1 | | | | | | | | 49 | 49 | |
| KS-21-1-3 | 9 | 0.64 | 50 | 15 | 1 | | 4 | 90 | 160 | 18 |
| 544-2 | 10 | | 27 | 3 | 4 | | | 13 | 53 | 5 * |
| KS-21-1-2 | 7 | 0.43 | 6 | | | | | 43 | 49 | |
| 544-3 | 7 | 0.64 | 3 | 6 | 1 | | | 22 | 32 | 9 |
| KS-21-1-1 | | 0.52 | 9 | 8 | | 1 | | 6 | 24 | 8 |

Note: * The fragments are strongly vitrified; plant anatomical structure is not preserved.

**Table 5.** Species composition of charcoal assemblages.

| Sample | *Betula* | Ericaceae | *Pinus* | *Picea/Larix* | Sclerotia of | |
|---|---|---|---|---|---|---|
| | | | | | Mycorrhizal Fungi (*Cenococcum* Type) | Saprobic Fungi (*Collybia* Type) |
| 544-1 | | | | | 32 | 17 |
| KS-21-1-3 | 4 | 2 | 4 | 40 | 18 | 72 |
| 544-2 | 1 | | 6 | 20 * | 13 | |
| KS-21-1-2 | 4 | | | 2 | 36 | 7 |
| 544-3 | | | 2 | 2 | 12 | 10 ** |
| KS-21-1-1 | 3 | | | 6 | 5 | 1 ** |

Note: * Five fragments have traumatic resin channels. ** Weathered/cracked.
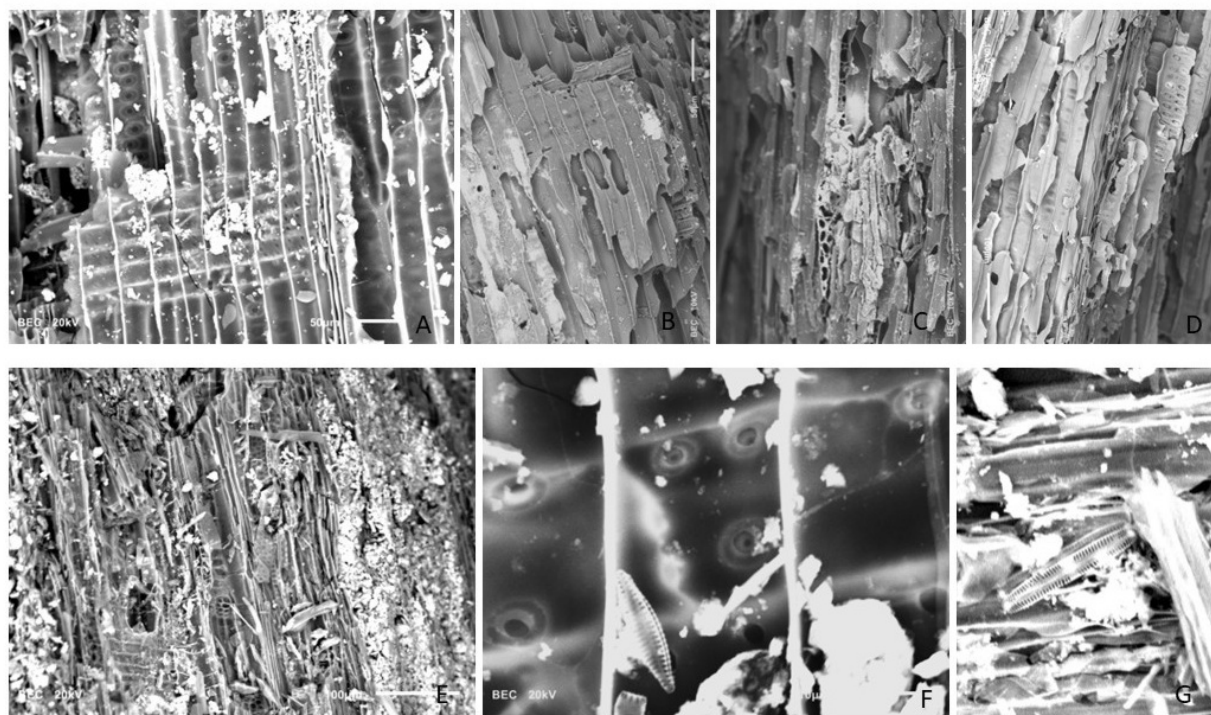


**Figure 8.** Charcoal assemblages from the Holocene organic deposits of Kyzyl-Syr. Charcoal of Picea/Larix from KS-21-1-1 (**A**), KS-21-1-2 (**B–D**), and KS-21-1-3 (**E**) and degraded charcoal of Betula (**F**) from KS-21-1-2, originating from low-temperature burning. Diatoms within crevasses in charcoal from KS-21-1-1 (**F**) and KS-21-1-2 (**G**).

The number of charred fragments varied from 24 to 160 per sample, and the maximum length of the fragments varied from 7 to 10 mm (Table 4). At least in KS-21-1-3, the abundance and large size of the fragments suggest that they originated from in situ burning rather than being transported from afar. Most of the charred material was fungal sclerotia, associated with a root-inhabited organic layer. They were found in all samples; the 544-1 sample contained only sclerotia, while in other samples they comprised from 25 to 88% of the charcoal assemblages. Two types of sclerotia appear to be present in the assemblages. The sclerotia of conifers' mycorrhiza (*Cenococcum* type) were found in all samples; the sclerotia of saprobic fungi (*Collybia* type) were abundant in KS-21-1-1 and, to a lesser extent, in KS-21-1-1 (Table 4). The presence of sclerotia suggests that trees were growing on the site, i.e., the site was forested during some periods. However, the sclerotia are highly buoyant and can be transported by water. The charred fine roots of conifers were found, though not numerous, indicating that indeed there were episodes of reforestation on the site. To be charred, the tree roots had to grow within the organic layer that was later consumed by fire.

The second most numerous fraction was bark; it was as abundant as charcoalified wood or even more numerous in 544-3 and KS-21-1-1 and contributed 30% in 544-1; the number of bark fragments was minimal in 544-2, and in KS-21-1-2, bark was absent. The high charcoal: bark ratio is unusual for forest fires [62] and may indicate that the fire affected dead trees. Interestingly, ~25% of coniferous charcoal fragments from 544-2 have traumatic resin canals similar to "frost calluses" formed during frost damage [63].

The charcoal originated mainly from *Picea/Larix* wood; *Betula* charcoal was found in KS-21-1-1, KS-21-1-2, KS-21-1-3, and 544-2 samples, and in KS-21-1-2, it was more numerous than coniferous charcoal. In all samples, Betula charcoal was dull and fragile, as typical for low-temperature burning; it is possible that green birch wood was scorched by the fire that started in the coniferous forest. Two fragments of Ericaceae biennial shoots were found in KS-21-1-3.

*Pinus* was represented by several charcoal fragments, charred cone scales, and one charred needle, all possibly brought into the site by wind and/or water from the nearby *tukulan*.

The charcoal assemblages from each layer represent the result of more than one fire, as indicated by a high proportion of vitrified charcoal, associated with recurring fires [64]. Moreover, charcoalified wood and, especially, sclerotia had certain indications of erosion, transport, weathering, and post-depositional changes. The charcoal was iron-impregnated in all samples. In KS-21-1-1 and 544-3, the charcoal was iron-impregnated and coated by a thin greyish silt deposit; the sclerotia had an intermittent mud coating. In 544-1, the sclerotia were iron-impregnated and slightly silica-coated. In KS-21-1-2 and 544-2, the sclerotia were mud-coated and Fe-impregnated, with a thin silica film deposited over Fe deposits. Finally, in KS-21-1-3, the sclerotia were weathered, cracked, and Fe-coated; in some sclerotia, a silica coating was visible beneath the iron coating.

The mud coating contained sand particles, indicating that at least a proportion of the sclerotia were eroded from the mineral sediment during erosional events.

## 5. Discussion

Our sampling approach at the Kyzyl-Syr section was based on the assumption that it reflects the classical hydrosere sequence lake–fen–bog [3]. Many studies provided examples of such paleo succession [65–67] in stratigraphic sequences that usually have a basal mineral deposit (gravel, sand, loam, or clay) superposed by gyttja and further peat and finally a paleosol or modern soil at the top of the sequence. Our sequence was seemingly similar, but radiocarbon dating revealed a hidden discontinuity/unconformity, a break in sedimentation that lasted about 36,000 years.

Such misinterpretation of Pleistocene deposits is not uncommon when researchers work with deposits older than the limit of radiocarbon dating. One case is described from the Palisade section at the Yukon River, Alaska [68]. The team was looking for the organic-rich sediment of the Sangamonian age which is usually bedded 2–5 m above the Old Crow tephra (124–10 ka) that is a widespread chronological marker in the region. Assuming

that the age of the deposit was beyond the limit of the radiocarbon dating method, the team did not plan for radiocarbon dating. However, when the macrofossil analysis of the deposit yielded unexpected results, six samples of seeds and insects were submitted for radiocarbon dating that confirmed the Holocene age of the deposit.

Another example shows yet the opposite misunderstanding. The Mamontovy Bysagasa locality at the Laptev Sea coast near Tiksi town in northern Yakutia was initially interpreted as a Holocene section [69]. A relatively low terrace (7 m high above sea level) was composed of sand and plant and woody debris including an in situ larch stump. Such layers with tree remains usually are of the early Holocene age in the region, but the beach under the section was full of bones of Pleistocene large animals, including mammoth bones. A further study has shown that the section consisted of two different units. While the upper 1.5 m of the section represented Holocene sand and organic debris ($^{14}$C about 8.2–9 ka yrs. BP), the lower 5.5 m was melted and compressed Pleistocene silt ($^{14}$C about 28.8 ka yrs. BP). Apparently, the Holocene unit was deposited in a thermokarst lake that formed in the place of the thawing ice-rich Pleistocene sediment.

In the Kyzyl-Syr locality, the Holocene unit is bedded over the impervious loam stratum of the Pleistocene age. The loam is a deposit of the buried river valley system [27] that developed here during the relatively warm and wet climate of MIS3 (Karginsky stratum in Siberian scheme). Alluvial deposits of this stage are exposed nearby at the base of a high sandy bluff (Figures 2B and 3).

The Holocene organic unit (OL) started accumulating in the Vilyuy River valley about 1800 years ago. This last interval in geological history belongs to the Meghalayan Stage Late Holocene, from 4200 cal. yrs. BP onwards [70,71]. According to the Blytt–Sernander scheme that is popular in paleoenvironment studies [72], the water body formed during the Subatlantic humid stage (2.500 cal yrs. BP–present) or in the Roman Warm Period, (RPW; between 2500 and 1600 cal yrs. BP) [73,74].

The term RWP is used here as a stratigraphic unit despite the climate meaning. A warm and humid RPW was recorded in Europe, but in Central Yakutia in the Holocene, the climatic trend was shown to be different. According to the chironomid [75] and diatom [76] record, the water levels in the thermokarst lakes of Central Yakutia were higher during the early and middle Holocene than during the late Holocene. The thermal erosion slowed down in the late Holocene, signaling general cooling in the region.

Pollen data [77,78] suggested that the summer temperatures in the region were up to 1.5 °C warmer than present in the middle Holocene and close to modern or slightly cooler during the Subatlantic interval; some warming has been recorded during the Medieval Warming ca. 1000 cal. yrs. BP. The pollen record reflects a rapid expansion of pine trees in Central Yakutia ca. 5400 cal. yrs. BP, without any abrupt vegetation changes later [79,80].

The gyttja-like consistency of the organic layer indicates that it was accumulated in standing water, and its position within the river valley suggests that it was an oxbow lake. According to our observations, modern floodplain deposits are loosely packed organo-mineral layers that contain detritus along with very coarse organic debris, such as trunks of trees, mixed with alluvial sand. Fine-grained organic layers are not accumulated due to flash flooding and intensive channel erosion.

The fine-textured gyttja-like OL is very unusual for alluvial sequences, while similar units were exposed, for example, during excavations in construction sites in Yakutsk city, where oxbow lakes are common. The natural exposures of oxbow lake deposits are uncommon; the river rarely cuts its own old channels as the erosion affects the opposite bank.

The exposure of the old channel means that the river changed its direction inside the meander belt. The age of the OL helps to estimate the speed of the meander formation. The original riverbank (30–35 m high sand terrace) is visible in the river valley downstream from the section. The depression of the former oxbow lake is approximately 80 m wide and 240 m long; it is aligned with the former riverbank.

While the beginning of the OL accumulation coincided with the end of the climatic phase RPW, the lifespan of the oxbow lake is unknown; the 1.5 m of detritus could be accumulated considerably fast, within several centuries.

The macrofossil assemblages of the wetland changed little during its life. All plant, insect, and invertebrate assemblages suggest the existence of a densely vegetated water body with open water. The lake banks were not uniform in vegetation. Shallow boggy edges were occupied by numerous *Menyanthes trifoliata*, various Cyperaceae and Typhaceae formed a fringe of tall herbaceous/grassy vegetation, and there were patches of open ground nearby, hosting numerous ground beetles and rove beetles.

Scrub birch and alder occupied a part of the surrounding wetland. Stabilized sand dunes near the pond provided dry conditions for grasslands with xerophilous plants and insects and pine forest with *Rubus matsumuranus* and *Arctostaphylos uva-ursi*. The reconstructed landscapes are similar to the modern ones in the study area. The climate was similar to the modern climate or slightly warmer.

According to the paleontological evidence, the life in the small water body was rich. The fossil record illustrates many correlations: water lilies and leaches whose cocoons are attached to broad leaves, the weevil *Bagous limosus* and *Potamogeton*, the weevil *Lixus paraplecticus* and *Cicuta virosa*, the weevil *Lepyrus* spp. and willows, and the leaf beetle *Donacia splendens* and sedges.

Sometimes plant and insect records add details to the reconstruction of paleo-communities. We found the weevil *Tournotaris bimaculata* (F.), whose larvae mine the stems of *Typha*. This plant is not recorded here, but other plants of the Typhaceae family, *Sparganium emersum* and *S. hyperboreum*, were found. Tiny seeds of *Typha* could be missed in the sediment; moreover, modern observations on *Tournotaris bimaculata* behavior are not sufficient for excluding its feeding on additional host plants.

The proportions of aquatic and terrestrial taxa changed through time, presumably due to fluctuations in the water level. A similar tendency was observed in charcoal assemblages, as some samples contained a high number of charcoal fragments and various fuel fractions (bark, wood, and even roots and mycorrhizal fungi), suggesting that trees were burned in the wetland during periods of low water level. Charcoal was found in all samples, indicating that fires were common during the entire period of accumulation of the OL. Moreover, the fires were frequently recurring, as indicated by a high proportion of reburned charcoal. The unusual abundance of birch, observed in macrofossils and charcoal, may be a result of the frequent fires.

The stages of reforestation alternated with the stages of site flooding. Charcoal becomes impregnated by iron oxides in water that is enriched in reduced iron compounds when the water warms up to temperatures above 5 °C. The iron deposition was more pronounced in the upper and lower samples than in the samples from the central part of the section, and this may indicate cooler and drier conditions during the formation of the latter. The cocoons of earthworms were found in the same middle part of the unit, attesting to its functioning as the soil.

Finally, numerous diatoms accumulated in crevasses within charcoal fragments (Figure 8), indicating a prolonged submergence of charcoal after the fire and its inclusion into aquatic deposits.

The OL is covered by modern alluvial sands, and some material is brought in from nearby sand dunes by wind. We know that sand dunes (the Pleistocene sand deposit of the D'olkuminskaya Suite) were close to the site during the peat accumulation stage, but sand is nearly absent in the OL. It is probable that the sand dunes were stabilized during the OL accumulation, and the end of the pond life was caused by (or coincided with) the dune activation.

A study of tukulans Kyzyl-Syr and Makhatta (upstream of Kyzyl-Syr, on the left bank of the Vilyuy River) [81] showed that the sand dunes re-activated about 2500 years ago after a period of relatively stable conditions.

The local lenses of the Holocene OL were recorded also in the main body of Kyzyl sands [27,81]. The most prominent OL is bedded in a depression that cuts MIS2 sand down to the surface of MIS3 (Figure 9A). The larger pond existed (probably with interruptions) for about 5 thousand years from the early to the late Holocene [27]. The small lenses of OL, a mixture of green mosses and sedges, are situated within the MIS2 sand (Figure 9B–D). The extent of buried organic lenses is not clear; we estimate their diameter at about 10–30 m, and the layer thickness varies from 0.1 m to 2 m.
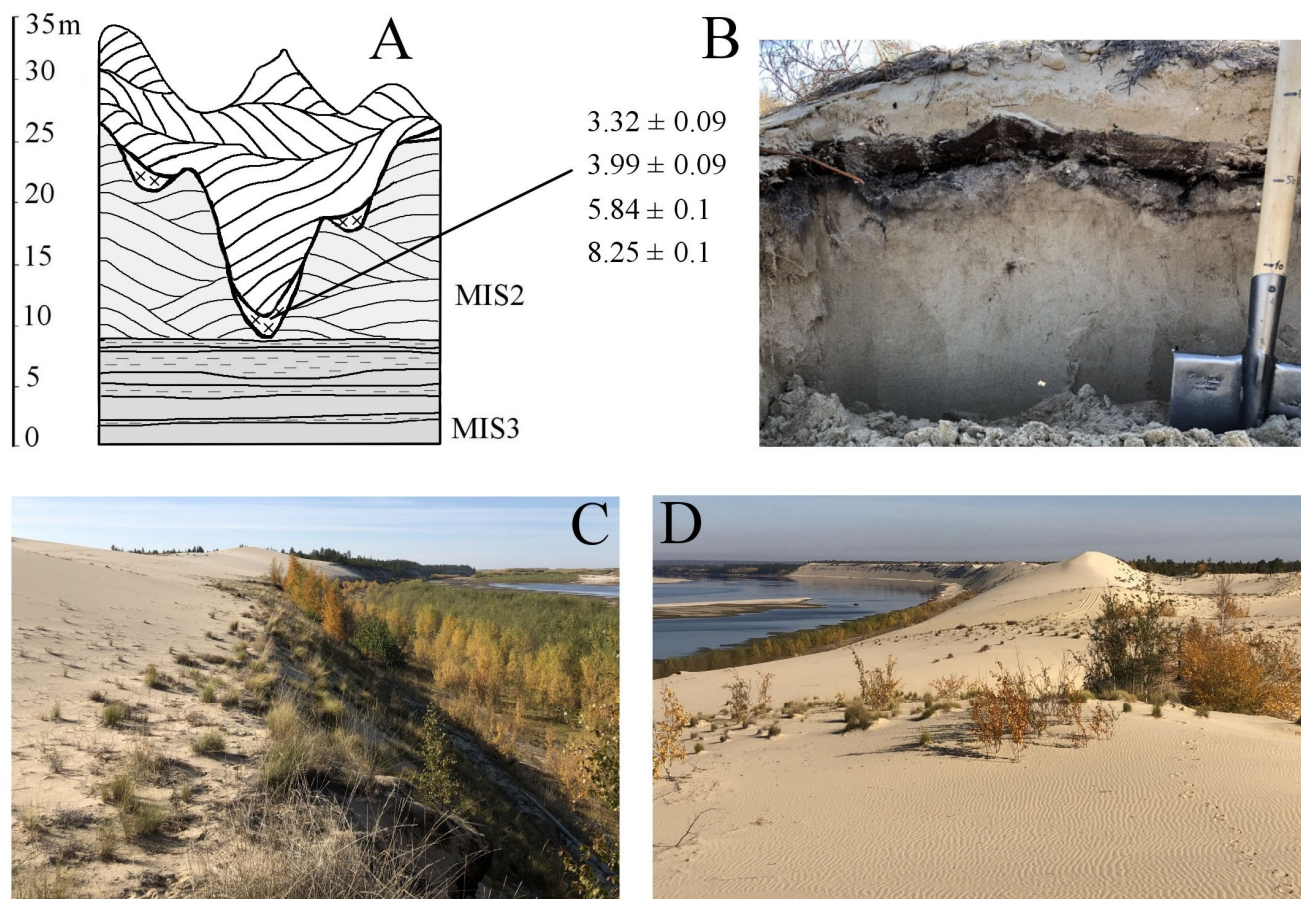


**Figure 9.** An example of a buried late Holocene organic unit in the Kysyl-Syr *tukulan*. (**A**)—A drawing of the section with major stratigraphic layers (after [27]). (**B**)—A buried organic layer, ~10 cm thick, is bedded on and superposed by the sand. (**C**)—Exposure of the organic layer at the top of a high sandy terrace. (**D**)—Depressions on the surface of Kysyl-Syr sand dunes, currently treed, can be filled by water in spring.

Our analysis showed that the invertebrate communities of the small water bodies in dunes differ considerably from that of the buried oxbow lake. The organic layer in one of such ponds, explored for comparison in this study, consisted of felt-like matter derived from green mosses and sedges (Figure 9B). The layer yielded a few insects and numerous eggs, probably from crustaceans of the Triopsidae family (*Triops* sp.?). These tadpole shrimps live in temporary pools. The ponds on sands were less rich due to a restricted nutrient supply; they tended to dry out, but the good location provides the conditions for the renewal of temporary and short-living water bodies to the geological visible system. It is interesting that the assemblages recovered from sediments of this dune pond were dominated by aquatic insects and invertebrates, while the site potentially can be a perfect trap for terrestrial xerophilous insects, similar to such traps in tundra [12,22]. This phenomenon was explained [12] by the effect of a so-called "coastal barrier": dense riparian vegetation hindering the arrival of terrestrial insects to the lakes and their burial in

aquatic sediments. The explanation was applied to wetlands in forested areas and warmer climates, but our study showed that a fringe of vegetation around small interdunal lakes creates a similar "coastal barrier".

The complex history of the area includes at least three stages. (1) During the Karginsky interstadial (MIS3) of the late Pleistocene, a loam layer accumulated within a small area of the wide floodplain valley. The loam created an impervious horizon enabling the formation of the future oxbow lake. (2) With Sartanian (MIS2) cooling, the rivers became shallow [26], and cold deserts became widespread in Central Yakutia. Wind moved sand from dried riverbeds to the land, and stagnant water bodies were rare and short-lived. The sediments of this period were not represented in the studied section. (3) With the Holocene warming and subsequent permafrost melting, running water returned to the area. In some areas of sand dunes, wind erosion exposed impervious Karginsky beds. With the increase in atmospheric precipitation in the Holocene, small pond/lakes were formed in such deflation depressions. In the Holocene, the Vilyui River meandered, rebuilding the valley, cutting sand dunes, and eroding the surface up to the Karginsky beds. (4) Oxbow lakes of various ages formed on the impervious lenses of the Pleistocene alluvial sediment, and one of them was our study site.

## 6. Conclusions

The late Holocene pond at a floodplain terrace inherited its impervious basal layer from an older MIS3 wetland. The life of the pond was typical for a mesotrophic [4] water ecosystem, though the fossil record was diversified by some remains of xerophilous species of insects and plants from nearby dunes.

The late Holocene interdunal water bodies on the high sandy terrace were oligotrophic. The fossil invertebrate assemblages from the dune lake are dominated by aquatic species; terrestrial insects are poorly represented. This observation helps to explain the lack of xerophilous insects in occasional paleoentomological collections from organic units in the region.

The environment of the late Holocene was similar to the modern one, but a number of exotic species of insects and freshwater invertebrates were found in the fossil record. There are three possible reasons for this: (1) a negative impact of modern human activity (e.g., construction of the Vilyui hydroelectric power station upstream that affected the water supply of the river valley), (2) local extinction of relict species due to natural reasons, and (3) the modern fauna of the remote regions of Yakutia is not well studied. The fossil record could provide an objective to search for modern beetles, sponges, and leeches that left tracks in the recent geological record but are not yet recorded in the modern fauna.

The locality is situated close to a long-existing spot of the relict steppe vegetation on sand dunes, but only solitary remains of xerophilous plants and insects were found in the sediment. We think that the dense vegetation around the pond prevented the transportation of seeds and insects from the encasing landscape. Unlike water bodies in treeless landscapes, the sediments of a pond located within the forest accumulated macrofossils that reflect mostly the local environment.

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