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The MIS 3–2 environments of the middle Kolyma Basin: implications for the Ice Age peopling of northeast Arctic Siberia

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The Kolyma region is historically famous for the unique finds of large Pleistocene fauna, yet, until very recently, absent of the time-corresponding occupation sites. Quaternary geology and palaeontology investigations (2013–2019) in the middle reaches of the Kolyma River (NE Yakutia) have delivered new evidence on the Last Glacial (MIS 4–2) to Early Holocene sub-arctic ecosystems and the past landscape dynamics retrieved from the fossiliferous bodies exposed from thawed grounds. The palaeoecology multi-proxies from the MIS 3 (55–24 ka) cryolithic formations document riparian, larch-dominated northern forests and open parklands with backwater channels, marshlands and lakes. The abundant skeletal remains of Pleistocene ungulates and carnivores, as well as relic flora point to long-term biomass-rich interstadial ecosystems and favourable Palaeolithic occupation habitats. Utilized animal bones, worked mammoth ivory and stone tools show the presence of pre-modern humans in the northeast Russian Arctic >45 000 years ago. Flaked mammoth tusks suggest persistence of settlement during the Last Glacial Maximum in xeric and extremely cold (sub)arctic tundra. The postglacial climate shifts triggered major environmental and hydrological transformations. The final Pleistocene/Early Holocene warming brought restructuring of the Last Ice Age landscape and vanishing of the periglacial tundra-steppe replaced by the present-day larch-dominated Siberian taiga. The mid-Last Glacial human ecology records from the geographical limits of northeast Siberia have fundamental relevance for the reconstructions of the time trajectories and the natural conditions of peopling of Beringia.

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Permafrost regions of north and northeast Siberia (Fig. 1A) are famous for the extraordinary findings of Pleistocene fossil fauna and flora, most of which originate from the Taimyr Peninsula and Yakutia (Sher 1971; Vereshchagin 1974; Ukraintseva 1979; Lazarev & Tomskaia 1987; Andreev *et al.* 2002, 2003; Mol *et al.* 2003; Lazarev 2008; Vartanyan *et al.* 2008; Boeskorov, 2010; Maschenko *et al.* 2013, 2015; Boekorov *et al.* 2014; Cheprasov *et al.* 2015; Plotnikov *et al.* 2016; Kirillova *et al.* 2020).The exceptional preservation of the organic remains including soft-tissues (Solomonov 2009; Boeskorov *et al.*2013; Chernova *et al.*2015; Zimmermann *et al.* 2017) is because of the presence of deeply frozen ground persisting from the Last Ice Age (Balobaev 1991; Duchkov 2006; Grosse *et al.*2013; Fedorov *et al.* 2018) and the thick cryolithic depositional sequences. The first expeditions to these remote regions were carried out in the early 1900s, following the news of frozen mammoth carcasses (Zalenskiy 1903; Pawlow 1906; Sukachev 1914; Flerov 1931; Gromova 1935). The scientific validation of such reports prompted investigations inspired by intriguing questions about the antiquity of human colonization of these extreme northern areas and the environments in which these people had lived.

The initial peopling of the Russian Sub-arctic and Arctic has become a key research issue in terms of timing, natural conditions and forms of cultural adaptations in high-latitude Eurasia. The northern Palaeolithic dispersal has been long a matter of discussion (Mochanov 2010; Derevianko 1990; Kashin 2003; Plumet 2004; Derevianko *et al.* 2005; Mochanov & Fedoseeva 2007; Rolland 2008; Hufthammer *et al.* 2019). Environmental studies in recent decades allowed for more detailed interpretations of the Last Glacial history, the evolution of past ecosystems and climate dynamics (e.g. Gualtieri *et al.* 2003; Leshchinskiy 2006; Maschenko *et al.* 2006; Astakhov & Svendsen 2008; Lozhkin *et al.* 2008; Velichko & Vasil'ev 2008; Chlachula 2011; Wetterich *et al.* 2011; Svendsen *et al.* 2014; Kotlyakov *et al.*2017). Collectively, these efforts and the new scientific findings contribute to the reconstruc-

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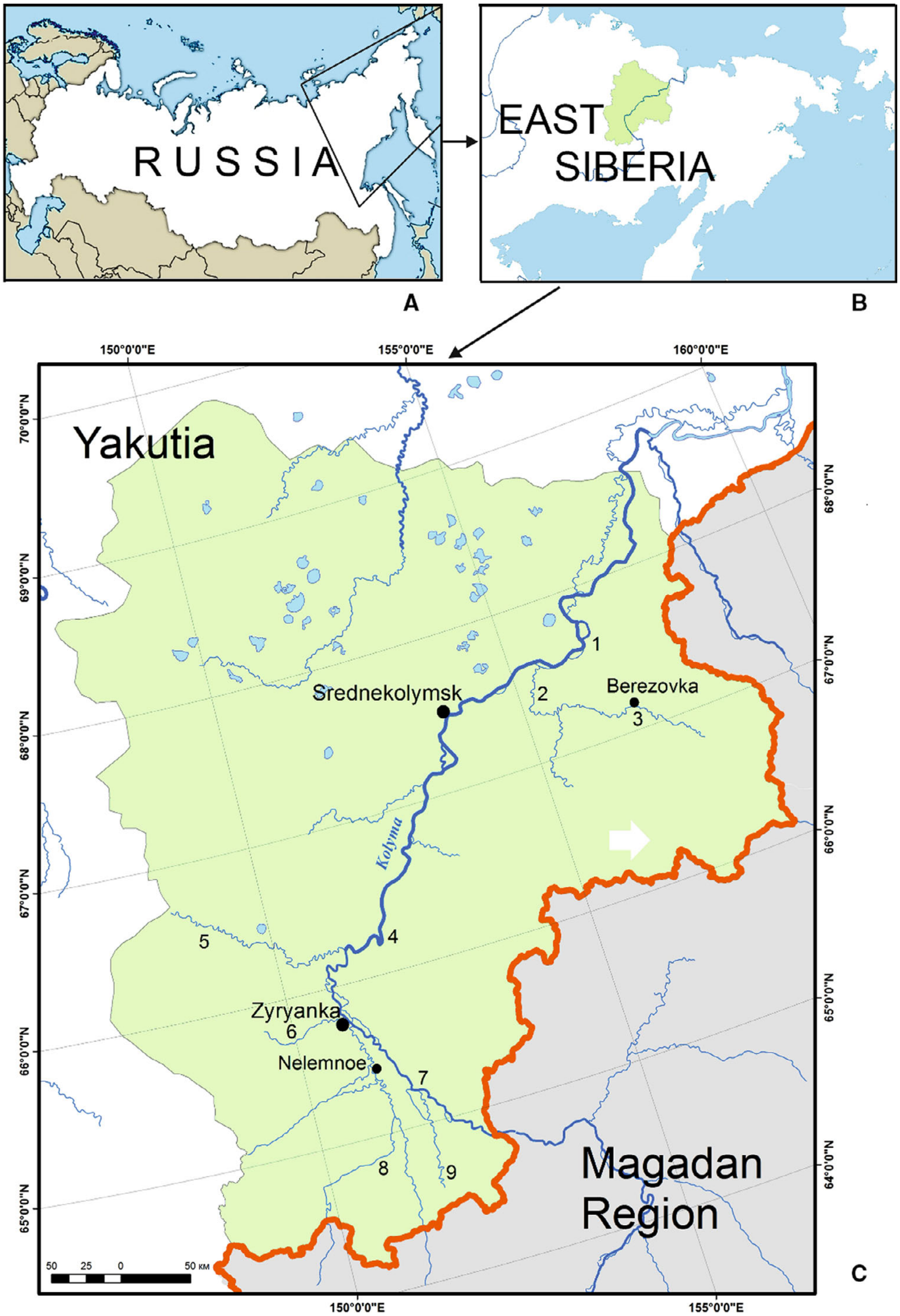

Fig. 1. A, B. Schematic maps of the study area in the middle Kolyma Basin, NE Siberia. C. Location of the investigated localities with the principal palaeontological and archaeological sites, and the fossiliferous sections geo-contextually associated with the Pleistocene cryogenic formations: 1 = Mayachnyy Stream; 2 = Presnyy Stream (a right tributary of Berezovka); 3 = Berezovka; 4 = Irelyakh-Siene; 5 = Ozhogina Stream; 6 = Zyryanka; 7 = Pravokolymskaya Protoka Creek; 8 = Omulevka Stream; 9 = Popovka Stream.

tions of the time frames and the patterns of human behavioural adjustment in the northern territories.

Present-day Yakutia (Fig. 1B) has experienced a most pronounced increase of mean annual air temperature during the last four decades by up to +3 °C on average (Czerniawska & Chlachula 2020), corresponding to the present MAAT of –13/–14 °C along the Arctic coast (the Yana–Indigirka Lowlands) and –15/–17 °C in the interior East (the middle and upper Kolyma) (Danilov & Degteva 2018). The contemporary climate change in the circumpolar regions (Callagham *et al.* 2010; Iijma *et al.* 2010; Turner & Marshall 2011) brings along with transformations of natural habitats, and restructuring of relief and hydrology networks (Costard *et al.* 2007; Konischev 2009), progressing disintegration of the ancient permafrost grounds sealing the Pleistocene-age biotic records. These processes have direct implications for the exploratory fieldwork because of exposures of rich palaeontological localities and new cultural sites released from the ancient cryolithic grounds subjected to seasonal thaw and the ablation-water erosion released from the retreating permafrost.

Quaternary geology, geoarchaeology and palaeontology investigations conducted in the Yana, Indigirka and Kolyma Basins produced new palaeoecology data and early cultural records detailing the temporal framework and environmental contexts of the Late Pleistocene and Early Holocene inhabitation of these geographically remote areas (Bezusko *et al.* 2008; Basilyan *et al.* 2011; Pitulko 2011, 2013; Cheprasov *et al.* 2015, 2018; Pitulko *et al.* 2016, Pitulko *et al.* 2017;) linked to parallel studies in the northern Urals (Svendsen & Pavlov 2003; Astakhov & Svendsen 2008; Svendsen *et al.* 2010). The main issues of the current research remain the recognition of the archaeological occurrences in the cryolithic contexts and the age of the unearthed cultural implements made from organic (bone, tusk, wood) materials, together with the palaeoenvironmental assessment of early human adaptive capabilities to the past (sub)arctic ecosystems.

The Pleistocene occupation of the Kolyma region is still poorly known because of the limited accessibility of this remote area. Studies in the adjoining Magadan Region (Fig. 1C) provided evidence of pre-Holocene (Final Palaeolithic and Mesolithic) settlements exemplified by rudimentarily worked pebble-tool and more elaborate micro-blade stone industries (Orekhov 1988; Slobodin 1999; Slobodin *et al.* 2017) found in shallow and cryogenically disturbed geological settings. On the contrary, systematic field reconnaissance in the middle Kolyma basin delivered several deeply stratified Late Pleistocene sites with cultural inventories sealed in the intact permafrost contexts. The archaeological records and the associated fossil remains provide evidence of the co-existence of people and Pleistocene megafauna (Cheprasov *et al.* 2015, 2018) analogous to that reported from the Yana basin (Pitulko *et al.* 2004; Chlachula *et al.* 2014). The rich palaeontological assemblages include articulated bones and animal-body soft tissues (Boeskorov *et al.* 2013) as well as ivory and other skeletal parts of the large Pleistocene mammals displaying diagnostic traces of anthropogenic use. These fossil materials together with the accompanying palaeoenvironmental proxies improve the present understanding on the Palaeolithic adjustment in this continental territory.

This paper summarizes the results of investigations in the middle and upper Kolyma area conducted during field expeditions in 2013–2019. The main goals of this research were to detail the regional chronology and environmental conditions of the earliest prehistoric peopling of this largely unexplored region during the Last Ice Age complementing the existing records from the northern Kolyma Lowlands.

Study area

The investigated region is located in the easternmost part of Yakutia (the Sakha Republic). The central surveyed sector covers the middle and upper reaches of the Kolyma River valley and its tributaries delimited by the modern settlements Srednekolymsk and Zyryanka (Fig. 1C). The river basin is the southernmost extension of the Indigirka–Kolyma Lowlands with elevations of 50–200 m a.s.l. (Filippov 1964), bordered by the eastern flanks of the Cherskogo Mountains (2500–3000 m a.s.l.) in the west, and by the Yukagir Plateau (1000–1100 m a.s.l.) and the Kolyma Range (1826 m a.s.l.) in the east. The present relief is sculptured by low-elevation hills amid extensive plains of the Kolyma hydrology catchment area (644 000 km^2; Baranova 1957). The regional structural geology is controlled by the Verkhoyansk-Chukotsk tectonic zone (Kolpakov 1998), which comprises granitic and metamorphic rocks overlain by Jurassic and Triassic sandstones and suites of unconsolidated Tertiary sedimentary bodies of a diverse (marine transgressive/continental) origin. Palaeozoic and Mesozoic schist and shale of the Yukagir Plateau (Chubukulakh Mt., 1117 m a.s.l.) represent major denudation remnants of the former (Tertiary) relief (Rusanov *et al.* 1967; Alexeev *et al.* 1986). The youngest (Quaternary) formations, including sandy-gravelly alluvia and silty-clay lacustrine facies, are associated with the primary Pleistocene palaeontological occurrences (Biske 1957; Boeskorov 2005).

The present climate is very harsh, subcontinental, with an extreme seasonality. The broader study area is the coldest in Eurasia. The average January temperature in the middle Kolyma Basin is –40 °C and the average July temperature is +10 °C. The frost-free period corresponds to 50–70 days per year; the mean annual amount of precipitation is ~200–300 mm (Agroclimate Base 1963; Danilov & Degteva 2018). Except for the north-facing cirque glaciers persisting in the alpine zone of the Cherskogo Mountains (Pobeda Mt., 3003 m a.s.l.) the area did not experience a major ice-coverage during the Last Glacial due to the territorial aridity. During the Last Glacial Maximum (LGM), summer temperature in NE Siberia was ~6–8 °C lower and winter temperature ~12–14 °C lower than the present ones (Frenzel 1992; Velichko 1993). Continuous permafrost underlies the region, reaching 150–300 m in depth (Tochenov 1984; Fedorov *et al.* 2018). Rising spring temperatures trigger

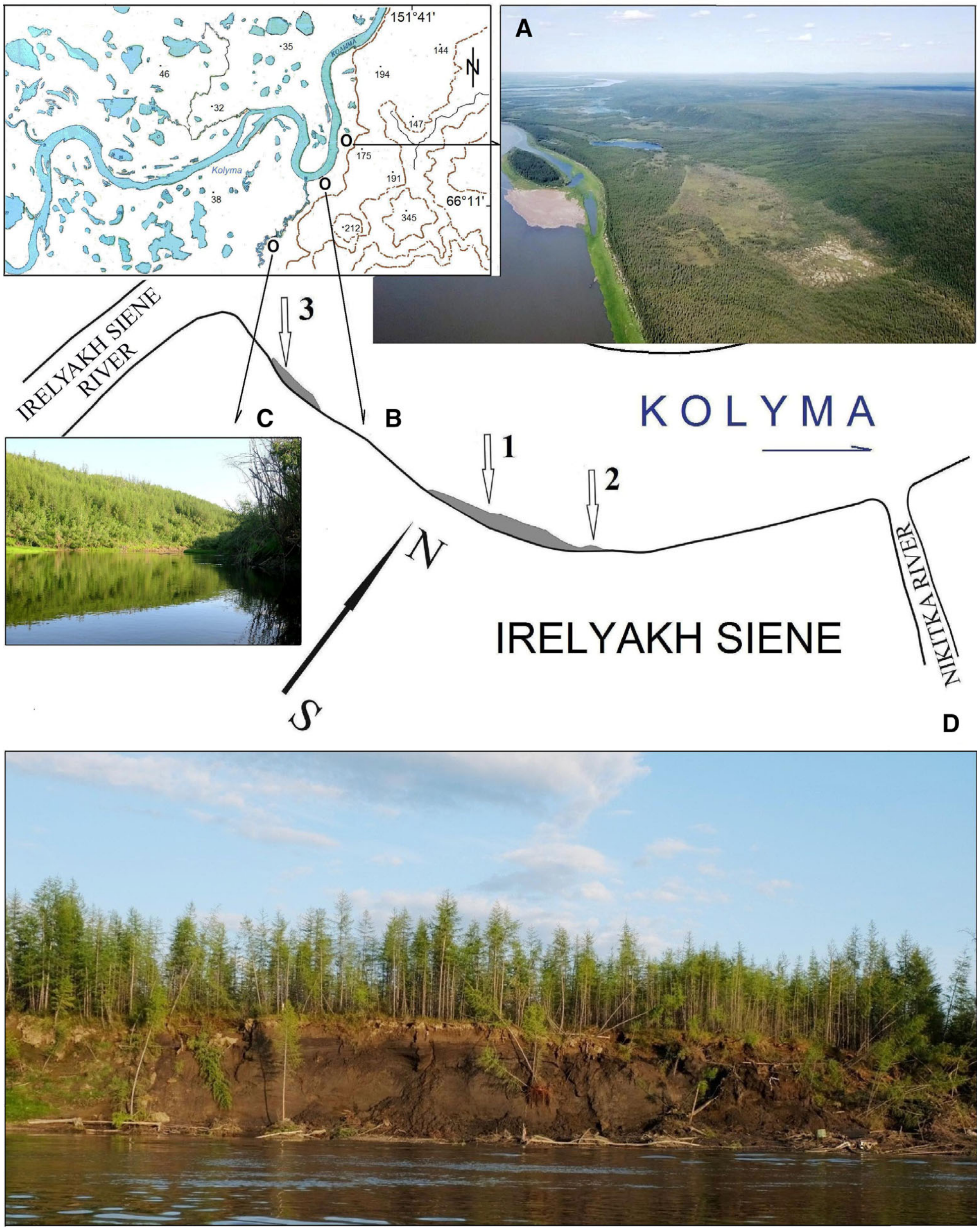

Fig. 2. Geographical position of the Irelyakh-Siene locality in the present geomorphic setting in the middle reaches of the Kolyma River valley (A) with the mapped stratigraphical sections 1–3 (B) and the eponymous Irelyakh-Siene (in Yakutian 'Willow River') River (C). D. A northeastern view of Site 1 with the erosional exposures of the Late Pleistocene cryolithic fossil-bearing deposits along the right bank of the Kolyma River (August 2014).

frozen-ground thaw, and generate mass gravity-flows and thermokarst processes observed across the Kolyma Basin as well as most of Yakutia (Veremeeva & Glushkova 2013; Desyatkin *et al.* 2015; Séjourné *et al.* 2015).

The present landscape is seasonally water-saturated and boggy, with numerous lakes, marshlands and alases (Fig. 2). The Zyryanka and Beryozovka are the main left and right tributaries of the Kolyma, respectively, with marked water-level fluctuations reaching peaks in early summer (June–July). Northern boreal forest and mountain forest-tundra are the principal biotopes in the lowlands and the adjoining foothills, respectively. Larch (*Larix cajanderi*)-dominated taiga characterizes most of the arboreal cover, with willow (*Salix* sp.) and alder (*Alnus* sp.) growths in riparian settings. Sedge-meadows around boggy ponds and mosaic herb-meadows lined by dwarf birch (*Betula nana*) thickets established on elevated, drier locations document the current vegetation diversity characteristic for the intra-continental Siberian regions around the Arctic Circle.

Material and methods

The investigations focused on the deeply stratified and radiocarbon-dated sequences of the Pleistocene cryogenic grounds of diverse palaeoenvironmental genesis (lacustrine, alluvial, colluvial), incorporating rich and well-preserved organic remains and early cultural records. The fossils-bearing units occur in patterned geomorphic settings and contextual positions along the Kolyma River banks and its main tributaries.

At the principal sites, biostratigraphical and taphonomic studies enabled the descriptions and interpretations of the intact permafrost-sealed fossiliferous strata along with the remains of the mammoth fauna and fossil flora. Small-size organic residues were retrieved by screen washing. Sediment samples of 10–20 kg each were used. The organic and contextual samples were collected from cleaned and photographically documented profiles for radiocarbon dating, and lithological, mineralogical, sedimentological (sieve and Malvern Mastersizer 2000) and geochemical analyses were conducted, together with complex processing and study of biotic records (fossil wood, pollen, phytolites, molluscs, palaeo-botanical residues and fauna remains). The specific analytical methods followed standard procedures. The excellent conservation and high amounts of palynomorphs in the intact and pollen-saturated organic deposits, fine-grained (silty-clay) sediments and fauna coprolites, allowed high taxonomic precision. The plant species determination followed the works of Reille (1995) and Beug (2004) using combined LM/SEM microscopic studies at 400 and 1000× magnifications (Nikon Alphaphot 2, JEOL JSM–649 OLV) with a minimum of 200 and up to 1000 grain counts per sample. The chronological assessment of the selected pollen samples is based on the ^{14}C ages of fossil fauna obtained from equivalent stratigraphical horizons within the sedimentary succession (Figs 3, 4).

A number of collaborative organizations assisted with the myriad of sample types and analyses. The biotic material was subjected to taxonomic and selective genetic (DNA) assessment of the megafauna species at the Department of Palaeontology, the Mammoth Museum, North-Eastern Federal University in Yakutsk and the Institute of Zoology, Academy of Sciences of Moldova, Kishinev. Analyses of the sites' stratigraphies, sedimentology, lithology and palaeopedology were conducted at the Institutes of Geology, and Geoecology and Geoinformation, Adam Mickiewicz University in Poznan. Palynology and anthracology studies were performed at the IGG AMU and the Institute of Geological Sciences, Masaryk University, Brno; macro-botany at the Faculty of Biology, Lodz University; coprolite parasitology at the South Bohemia University, Ceske Budejovice, and the Northern Science Centre, Tyumen (in progress); palaeo-mycology at the National Museum in Prague. Radiocarbon dating was performed at the Poznan Radiocarbon Laboratory. The ^{14}C calibration was carried out with the OxCal software v4.4.2, r:5 (Bronk Ramsey & Lee 2013) and IntCal13 and IntCal20 atmospheric curves (Reimer *et al.* 2013, 2020) with the probability of 68 and 95% of the true ages of the samples. Satellite images and low-elevation aerial scanning provided additional information on the investigated sites' relief, the Quaternary palaeogeography development of the study area and the present state of permafrost degradation. The synthesized chronostratigraphical and palaeoecological proxy data were integrated into the regional framework of the Late Pleistocene–Early Holocene environmental history of the Kolyma Basin.

Results

Geo-environmental context

The Irelyakh-Siene locality. – The principal palaeontological locality Irelyakh-Siene (latitude 66°11'22.68"N, longitude 151°41'05.05"E, altitude 30–40 m a.s.l.) with evidence of early human presence is located close to the Arctic Circle ~140 km downstream of the Kolyma River from the town (regional centre) Zyryanka, Verkhnekolymskiy District, NE Yakutia (Fig. 1C). The river is bordered on the eastern side by rolling relief elevations (194 m a.s.l.) rising over a ~5-km distance up to 425 m a.s.l. (Fig. 2A). Expanding thermokarst lakes and mass riverbank slumping indicate active permafrost thaw. The nearby area is characterized by meandering streams along the main Kolyma channel, ox-bow lakes and active as well as fossil dried-up thermokarst ponds. The northern coniferous boreal forest constitutes the principal vegetation.

The initial field reconnaissance (2013–2014) mapped seven loci with rich Pleistocene fauna finds. The main site (Irelyakh-Siene 1) exhibits an accumulation of the fossil remains exposed by erosion near the mouth of the Irelyakh-Siene River emptying into Kolyma (Fig. 2B, D). The following (2015) investigations at the Kolyma's right tributary stream Nikita, 350 m north of Irelyakh-Siene 1, documented a Palaeolithic site (Irelyakh-Siene 2) with stone artefacts released from the original cryolithic contexts together with Pleistocene fauna within a ~70-m section. An early occupation place with analogous cultural lithic implements was also mapped at the nearby site on the right bank of the river (Irelyakh-Siene 3; Fig. 2B). The composite locality stratigraphical mapping (2014, 2015, 2019; Fig. 3A, B; Table S1, S2) covered a ~45 000-year time-span and provided the basis for the reconstruction of the past ecosystems, relief transformations and regional climate dynamics in the middle Kolyma area.

The key site—Irelyakh-Siene 1—is contextually enclosed in the Late Pleistocene alluvial and colluvial deposits similar to the other riverside loci mapped in the central and upper Kolyma valley. The site became

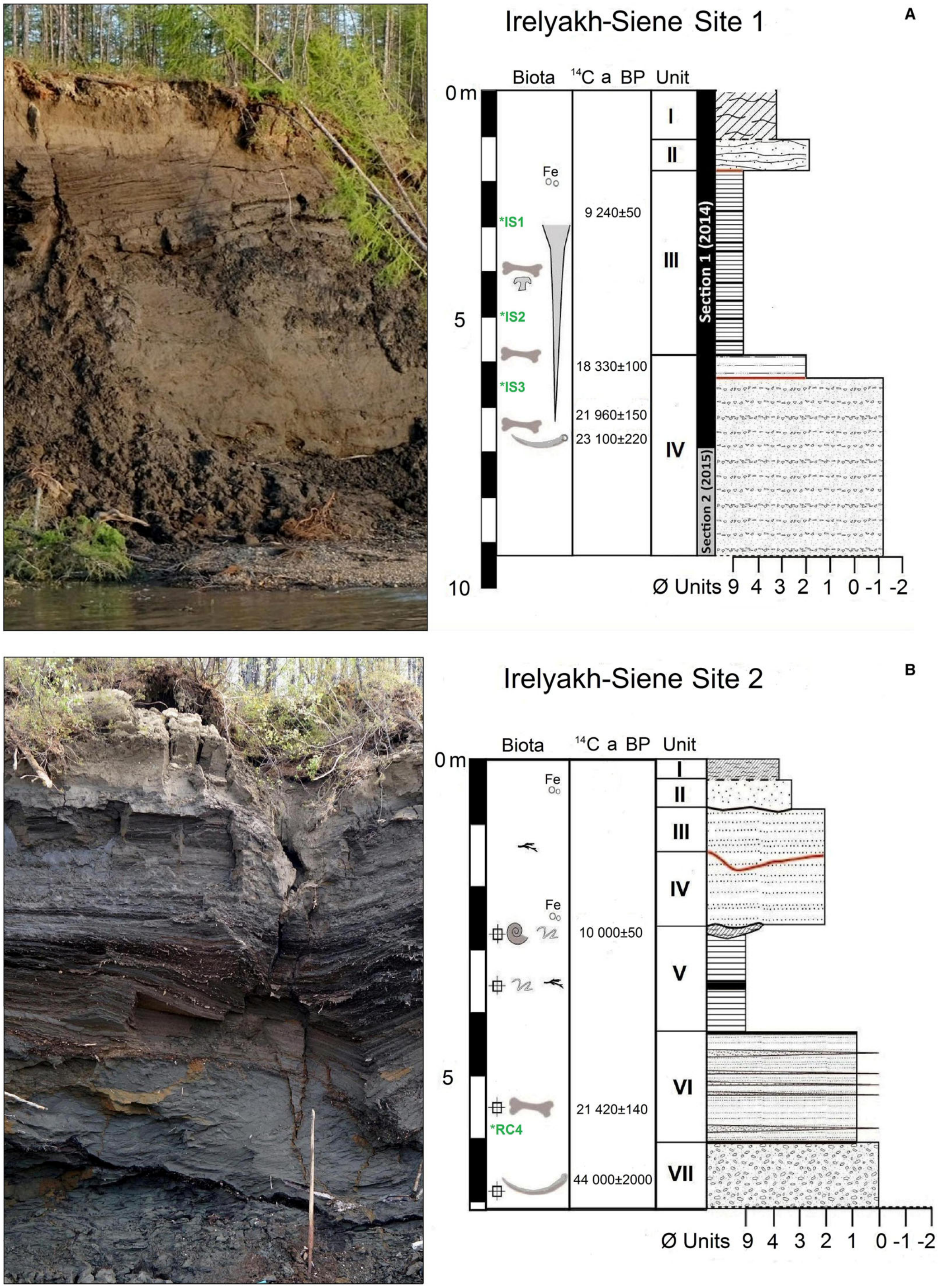

Fig. 3. A. Irelyakh-Siene, Site 1 (2014). Composite stratigraphical log and radiocarbon ages of the sedimentary facies of permafrost-sealed units incorporating fossil biota remains (flora and fauna): Unit I – present tundra-forest soil, partly colluvial; Unit II – interstratified colluvial sands and fine gravels; Unit III – laminated shallow-water dark grey clayey alluvial (overbank) and/or pond deposits; Unit IV – medium to large-size sandy gravel alluvium of a laterally migrating palaeo-channel (detailed description in text). B. Irelyakh-Siene, Site 2 (2015). Stratigraphical log of the main sedimentary and fossiliferous units: Unit I – present forest-tundra soil, partly colluvial; Unit II – sandy sub-surface pedogenic horizon, colluviated and cryogenically distorted; Unit III – laminated sandy alluvium; Unit IV – interstratified clayey back-water/lacustrine deposits; Unit V – massive humic lacustrine clays; Unit VI – overbank/meandering river channel deposit of interstratified laminated clays and fine sands; Unit VII – medium-gravel alluvium of the Kolyma River MIS 3 palaeo-channel. The palaeoenvironmental organic records occur throughout the section in the mid-Last Glacial to Early Holocene Units (VII–III).

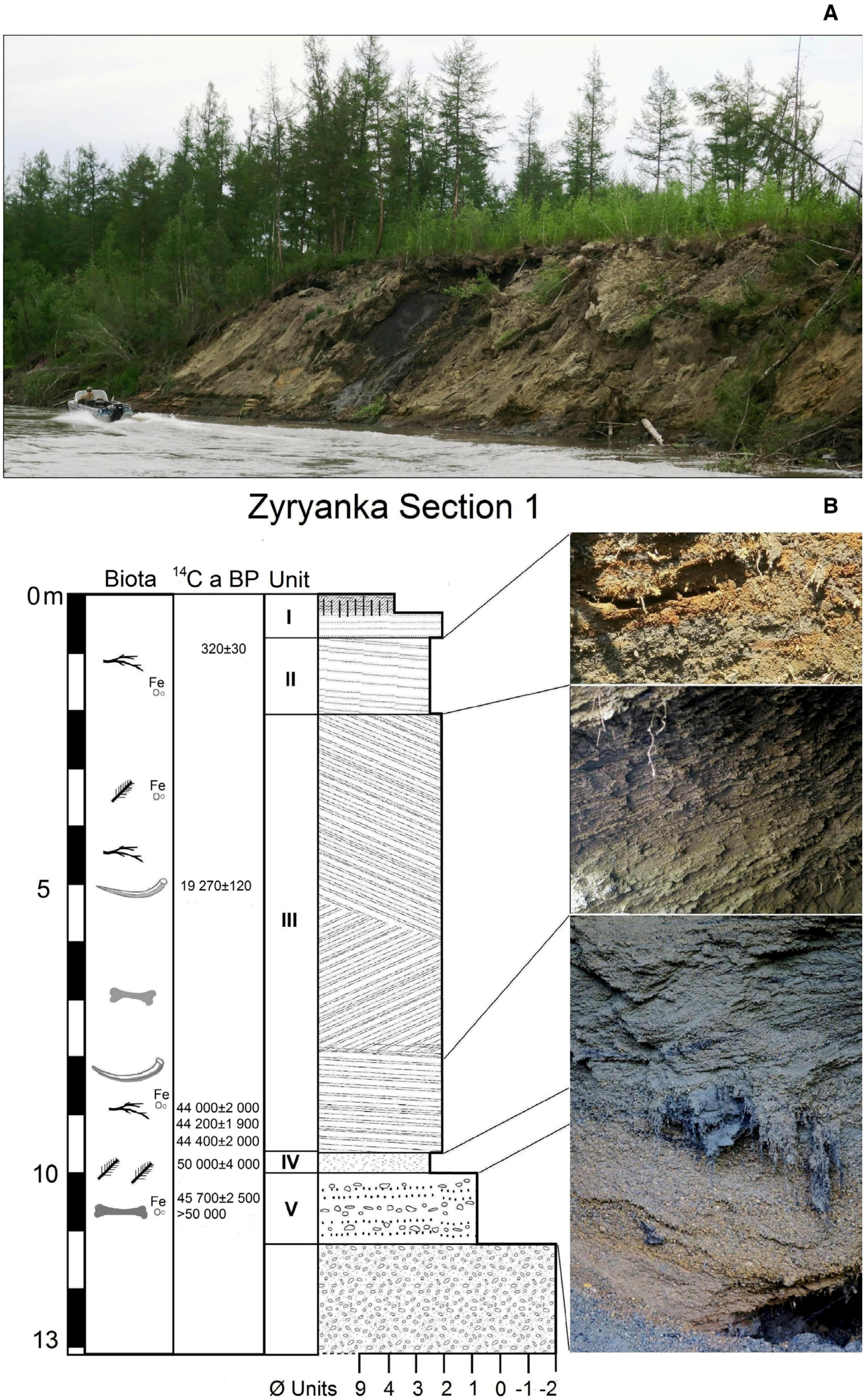

Fig. 4. A. Sections with the Late Pleistocene fossiliferous deposits along the Zyryanka River. B. Zyryanka, Site 1 (2019). A composite chronostratigraphical log with the main cryogenic sedimentary units incorporating fossil organic macro-botanical and faunal remains: Unit I – present tundra-forest soil; Unit II – interstratified colluviated fine-grained sands and silts; Unit III – laminated colluvial MIS 3 interstadial silts with buried organic-rich detritus, fossil wood, twigs, macro-botany remains and fossil fauna; Unit IV – humic, organic-rich overbank or backwater alluvium with fossil leaves and twigs; Unit V – coarse-grained sands and granulae with inclusions of small pebble pockets and lenses of organic material (fossil wood) interbedded by silty-clays; the Zyryanka–Orosu Siene River palaeo-channel alluvium.

exposed by lateral seasonal erosion of the Kolyma River and water pumping for ivory exploration, both disintegrating permafrost grounds. The documented ~11 m (section 2014) stratigraphy (Fig. 3A, Table S1) includes basal fluvial-channel sandy-gravels, ~1.5 m thick (Unit IV) below a suite of interstratified and organic-rich silty-clay beds, ~5 m thick (Unit III), representing the main formation. This is topped by fine-grained colluvial sands, ~0.5–1 m thick (Unit II) and the present forest-tundra soil (Unit I). A massive ice lens underlies the stratigraphical sequence. The Site 1 geology in the bottom part represents an ancient fossil-bearing Kolyma River alluvium (Fig. 6E). The gravels are exposed for about 45–50 m with cryogenically deformed facies and vertically bedded coarse clastic pockets. The overlying dark-grey fine-grained sediments with organic layers represent an overbank palaeo-channel/marginal thermokarst lake deposit incorporating green algae, fossil leaf residues, roots, wood, bark and branches of larch (*Larix* sp.) and birch (*Betula* sp.), all well preserved.

The ~7 m Irelyakh-Siene 2 (sections 2015, 2019) stratigraphy (Fig. 3B, Table S2) is formed by matrix-supported coarse fluvial gravels (Unit VII) corresponding to the basal gravels at Site 1. These are overlain by horizontally laminated sandy silts interspersed by fine sandy-gravels, 1.5–1.7 m thick (Unit VI) grading into humic silty clays, ~1.5 m thick (Units Vc, a) separated by a 0.2-m pedogenic horizon (Unit Vb) below ~2-m-thick fine alluvial sands (Units IV and III) with a colluviated upper part topped by aeolian sands (Unit II) and the present soil (Unit I).

The Site 2 geology illustrates sequenced shifts in the local hydrological palaeo-environment in response to past climate change encompassing the mid-Last Glacial to Early Holocene time-span with a basal riverine channel grading into a shallow low-energy alluvial overbank setting and, eventually, a thermokarst lake. The organic layer (Unit Va) with the freshwater shells indicates an ancient aquatic milieu. The underlying pedogenic horizon (sub-arctic/northern boreal forest-tundra brunisol to gleysol) (Canadian Soil Classification 1987) formed prior to the activation of the river channel on top of the sub-aerially exposed lacustrine pond deposit after the drained thermokarst lake dried up. Subsequently, the local fluvial system migrated over the top of the MIS 3 soil and conformably laid down the stratified alluvial sands. Sometime between the pedogenesis under moderately cool and humid conditions, and the accumulation of the alluvial sands, a cold climate interval triggered the palaeosol cryoturbation. This climatic change may have somehow forced the later alluvial deposition. The onset of the colder climate may have also changed the regional precipitation pattern (became drier) and caused the former permafrost lake to dry up. Colluviation of the uppermost alluvial sands attests to the sediment's sub-aerial exposure and the climate amelioration generating permafrost degradation and top ground instability prior to the present (Holocene) soil formation.

The Zyryanka locality. – The second principal locality with rich Late Pleistocene palaeontological occurrences and palaeoenvironmental proxy-records from the stratified geological context together with evidence of early human occupation was mapped in the Zyryanka River valley – the left tributary of Kolyma, ~40 km downstream of the town Zyryanka (Fig. 1C).

This key chronostratigraphical, archaeological and palaeontological site is positioned at a local brook emptying into the Orosu-Siene River (the left tributary of the Zyryanka River; 65°49'33.53"N, 150°26'25.24"E, 39 m a.s.l.; Fig. 4A). The geomorphic site setting creates a winding depression shaped by erosion of the meandering fluvial channel with a present water capacity (July) of ~2 m^3 s^{-1}. The nearby area is characterized by a flat lowland plain of the Kolyma catchment basin dissected by numerous streams and small tributary rivers seasonally fed by the activated ground ice ablation and drained waters of thermokarst lakes. In the western direction, the landscape of a dense northern taiga raises towards the eastern foothills of the Cherskogo Range at elevations of 300–400 m a.s.l. ~300 km from Kolyma.

The geology of the Zyryanka Site is broadly analogous to the other investigated sections in the surveyed reaches of the middle and upper Kolyma in the zone of continuous permafrost. The seasonally expanding cryolithic layer, thawing down to 0.5–1.0 m, causes saturation of the top surface with a higher permeability in places covered by up to 1.5-m-thick aeolian sands. The total thickness of the exposed grounds containing Late Pleistocene stratigraphical units is ~12–15 m (Fig. 4B; Table S3). Ice lenses, ice veins and ice wedges dissect in places the surficial geological formations largely consisting of colluviated fine-grained sediments overlying the coarse sandy-gravelly Pleistocene alluvia.

The pilot reconnaissance of the locality in 2014 led to systematic field studies (2015–2019) and the findings of well-preserved fossil fauna including soft tissues and floral remains together with archaeological materials, suggesting an early (pre-LGM) human occupation. Stratigraphy of the site is mapped in three adjacent sections (Zyryanka 1–3), providing a detailed and chronologically consistent picture of the Pleistocene and Holocene geology overlying the Tertiary bedrock. The sequenced occurrences of the Pleistocene-age biota and the cultural finds are associated with the MIS 3 formation delivering affluent multi-proxy environmental archives of the ancient site surroundings.

The Zyryanka stratigraphy (section 1, 2019) includes a basal (~1 m thick) alluvium of coarse, sheetflow sands and small pebbles (Unit V) sealed by an organics-rich deposit (Unit IV). This is overlain by massive (3–6 m) dipping laminated and fossiliferous clayey silts with erosional facies and truncated surfaces (Unit III), covered by interstratified (~1 m thick) and gelifluction-distorted aeolian sands (Unit II) topped by the present forest soil (Unit I).

The composite stratigraphical sequence documents a dynamic past environment. The suite of genetically diverse deposits points to the changing palaeo-landscape in the site vicinity with a past climate-driven ecosystem restructuring. The coarse-laminated sheetflow basal alluvial sands with inclusions of imbricated pebbles (Unit V) indicate a higher-velocity shallow stream with the palaeo-channel position slightly above the present brook level. A shift to a lower-energy back-water or riverine overbank setting is evidenced by the humic silty-matrix stratum (Unit IV) incorporating fossil macro-organic remains (leaves, pieces of moss and wood detritus), and suggesting a perennial flood. A certain temporal hiatus between the two strata is assumed from the distinct erosional boundary and the differential sedimentary composition delimiting the basal stratigraphical units (Fig. 4B). A marked change in the local palaeo-relief is indicated from the subsequent massive accumulation of the dark grey clayey silts forming the sharply dipping laminated beds (Unit III) representing the principal Pleistocene-age cryolithic fossiliferous formation. The great cumulative thickness (up to 6 m) of these gravity-flow deposits and prominent changes in the directional orientation of the single beds in the lower and upper parts of the unit attest to a rather dynamic geomorphic setting characterized by periodic mudflows, generated by cyclic climate variations and burying the formerly exposed organics. The stratigraphical and textural nature of the colluvium points to sequenced depositional processes over several thousands of years under a cool climate with increased atmospheric humidity and marked temperature deviations contributing to the long-term top palaeo-ground instability. A postdepositional distortion in the upper part of the stratigraphical sequence is manifested by fossil frost-wedge casts indicting a shift to very cold and arid periglacial conditions.

The overlying interstratified colluvial silts and sands (Unit II) show periodically changing climates and active geo-settings with surface solifluction and seasonal groundwater fluctuation due to permafrost thaw. Increased aridity and windiness are recorded close to the top surface by up to the 0.5-m-thick laminated aeolian sands deposited from the dried-up Kolyma River banks. Relatively stable conditions account for the formation of the present brunisolic soil (Unit I) under bushy boreal forest vegetation covering the recent ground. Modern permafrost thaw affected the uppermost part of the sections as exhibited by the cryoturbation of Units II and I.

Palaeo-botanical records

The abundant and well-preserved palaeo-botanical records from the stratigraphical contexts of the investigated sites included fossil wood, plants, mushrooms, bryophytes, pollen (Fig. 5) and phytoliths, altogether documenting the successive palaeoecology in the middle Kolyma area over the Karga/mid-Last Glacial interstadial to Early Holocene time-span.

The ancient wood debris and macro-fossil plant remains embedded in the MIS 3 units (Figs 6A, C, 7A–D) are principally represented by Siberian larch (*Larix sibirica*), dwarf birch (*Betula nana*), birch (*Betula* sp.), willow (*Salix* sp.), juniper (*Juniperus* sp.), alder (*Alnus* sp.) as well as peat moss (*Sphagnum*). Of interest is the postglacial *Fomes fomentarius* (L.) J. Kickx f. – a hoof-shaped tree-mushroom with hard outer walls and normal size of 5–50 cm in width, and up to 10 cm vertically layered bark (Fig. 6B). This species grows in broad-leaf warmer boreal and mid-latitude forests (mainly of birch, poplar and beech) hosted by on both living and dead trees (trunks and branches) (Holec 2015). The documented specimen retrieved from the interbedded grey silty and sandy deposit (Unit III/2014) was ^{14}C-dated to ~9.2 ka BP (Table 1), and is an environmental indicator of a milder, sub-humid postglacial climate established in NE Siberia, with a broader geographical distribution in present mid-latitude Eurasia.

The pollen record from the main ^{14}C-dated (Late/final Pleistocene and Early Holocene) stratigraphical units at Irelyakh-Siene 1 (Fig. 5) delivers a picture of markedly changing environments and the vegetation cover at the locality. The intact silty-clay and organic beds contained within the site stratigraphies are not prone to palynomorph reworking post-sedimentary palynomorph reworking and are palaeo-environmentally diagnostic.

The palynomorphs from silty lenses of the upper part of the basal alluvium (stratum IV at approx. –6.5 m; IS 1; Fig. 3A) characterize an open late Last Glacial tundra-steppe dominated by *Artemisia*, Poaceae, Brassicaceae, Ranunculaceae, Rosaceae, Silenaceae, with some cold sub-humid plant species (*Thalictrum*/*Illecebrum*) and just a minor presence of sub-arctic bushes (*Betula nana*, *Juniperus*, *Alnus*, *Salix*). Recorded *Selaginella rupestris* is typical of a boggy setting.

An increase in cold-adapted deciduous taxa (*Alnus fruticosa* t., *Betula alba* t., *Salix*, *S. alba* t.) at the expense of *Artemisia* compared to the former pollen record, with some shallow-water-site plants such as *Pediastrum boryanum*, is evident in the overlying layer (Irelyakh-Siene 1, stratum III at –5 m; IS 2), altogether documenting warming up and more humid (final Pleistocene) climates. The proportions of grasses and herbs remain about the same. White birch, willow, alder and the plants growing on water-saturated substrates (Ericaceae, *Epilobium*) and along the lake margins (Polypodiaceae, *Myriophyllum sibirica*) together with aquatic green algae (*Pediastrum boryanum*) indicate a lacustrine setting with boggy ground in corroboration with the sealing or enclosing thick and organic-rich sedimentary facies. Common bilberry (*Vaccinium*), windflowers (*Anemone*),

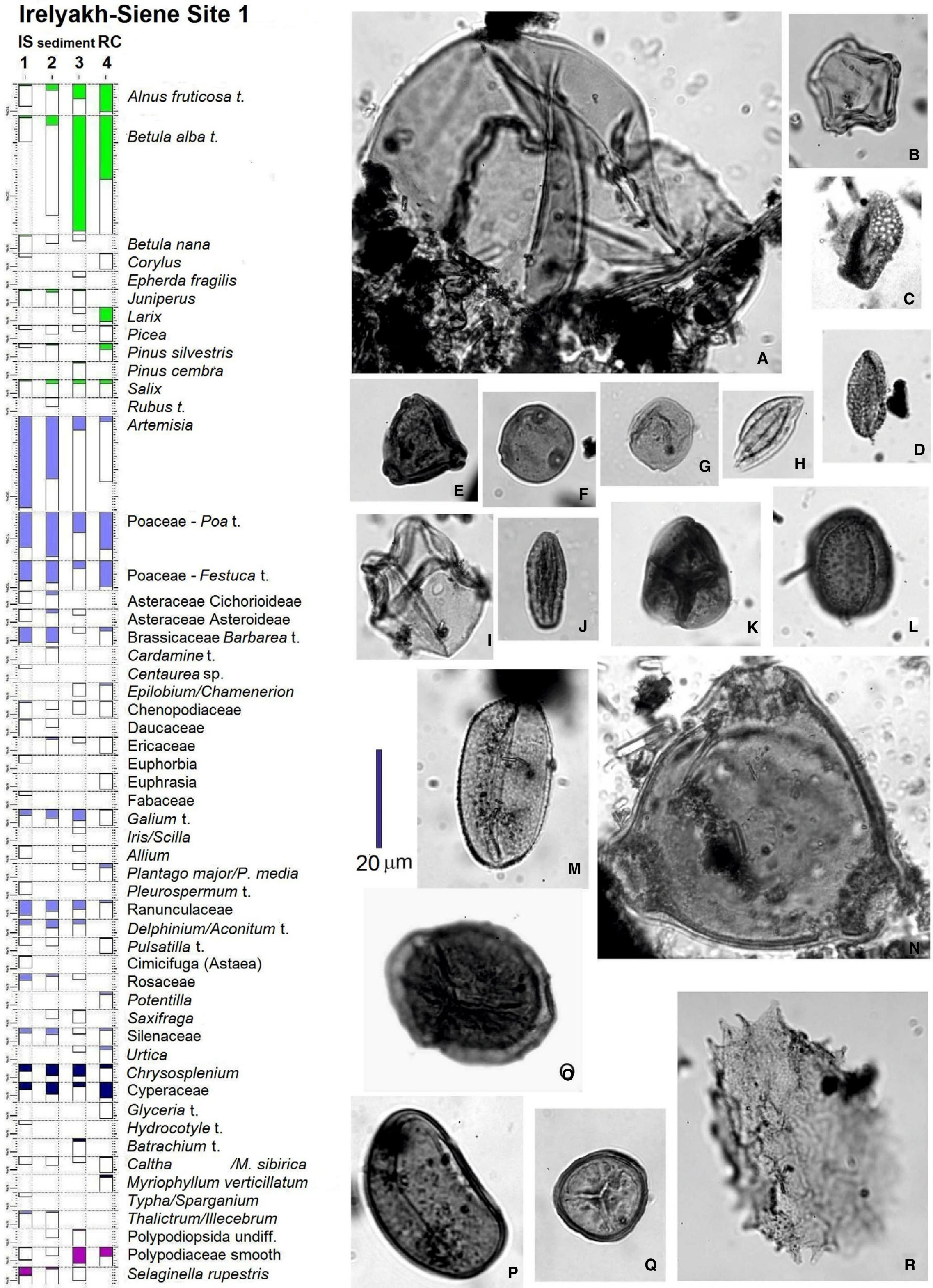

Fig. 5. Irelyakh-Siene. Pollen record: Site 1, samples (IS 1–3): (1) silty clay lenses basal alluvium (–6.5 m); (2) organic clayey lacustrine sediments (–5 m), (3) clayey silt alluvium (–3 m), (4) rhinoceros coprolite/RC (Site 2; –6 m). A. *Larix sibirica* (4). B. *Alnus* (4). C. *Salix alba* type (4). D. *Salix* sp. (3). E. *Betula alba* type (4). F, G. *Betula nana* (3). H. *Juniperus* (2). I. Poaceae/*Elymus* type (4). J. Poaceae/*Delphinium* type (2). K. Poaceae/*Vaccinium* type (3). L. *Anemone* (1). M. *Allium* (3). N. *Chamerion* (4). O. *Selaginella rupestris* (1). P. Polypodiaceae (3). Q. *Sphagnum* (3). R. *Pediastrum boryanum* (2). Magnification 1000× (A–Q); 500× (R). Pollen analysis and photographs N. Doláková (2018).

Fig. 6. Irelyakh-Siene. A. Fossil molluscs (*Novi succinea* – top, *Radix auricularia* – bottom) incorporated in bedded clayey silt back-water/lake deposits, ^{14}C age ~10 ka (Site 2, Unit Va). B. Fossil tree-mushroom (*Fomes fomentarius* L.) incorporated in shallow-water (overbank) and/or pond clay deposits, ^{14}C age ~9.2 ka (Site 1, Unit III). C. Fossil plants, wood and Pleistocene fauna remains eroding from the thawed basal alluvium (Site 2, Unit VII). D. Skull of an adult woolly rhinoceros (*Coelodonta antiquitatis*) (Site 2, Unit VII). E. Molars of the woolly mammoth (*Mammuthus primigenius*) from the upper part of the basal fossiliferous alluvium (Site 2, Unit VII). F. Mammoth (*M. primigenius*) tusk exposed from the fossiliferous sandy gravels (Site 2, Unit VII).