К ВОПРОСУ О ВРЕМЕНИ И СРЕДЕ ОБИТАНИЯ STEPHANORHINUS KIRCHBERGENSIS JÄGER 1839 (MAMMALIA, RHINOCERATIDAE) НА АЛТАЕ И СЕВЕРО-ВОСТОКЕ РОССИИ [On the time and environment of Stephanorh...

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On Time and Environment of *Stephanorhinus kirchbergensis* Jäger 1839 (Mammalia, Rhinoceratidae) in Altai and Northeastern Russia

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Abstract—The remains of the extinct Merck's rhinoceros (*Stephanorhinus kirchbergensis* (Jäger 1839)), well studied in Western Europe, are rare in Russia. However, thanks to the work of a number of researchers, the geography of the finds and the reconstructed range of the species have been significantly expanded. The time of the optimal existence of Merck's rhinoceros in Yakutia is now recognized as the Middle Pleistocene; the latest finds, dating from the beginning of the late Pleistocene, are known from the southeast of Western Siberia. We provide new radiocarbon dates for the root of a tooth and bone tissue from a previously unstudied lower jaw of the Merck's rhinoceros from Altai (AltR), whose taxonomic identity we confirm using genomic analysis. Both dates provide an age estimate of around 40 thousand years, which corresponds to the Karginsky time (MIS 3), and are the youngest for the species on the territory of Russia. The pollen spectrum from the soil filling the bone canal characterizes plant communities of open landscapes with forest areas on the upland or in the floodplain, and reflects either local features of the environment or communities of the cold stage within the Karginsky interstadial. A second Merck's rhinoceros from the Chondon River (ChR), in extreme northeast Yakutia, was determined by previous researchers to have lived either 45–70 thousand years ago or during the beginning of the Middle Pleistocene. Considering what habitats were available in the region, we propose that the ChR could have lived during the last—Kazantsevo—interglacial (MIS 5e) or later. Both finds, AltR and ChR, extend the temporal range of the species existence.

Keywords: Merck's rhinoceros, age, environment, Altai, northeastern Russia, ancient DNA

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INTRODUCTION

Merck's rhinoceros ("tandem" rhinoceros *Dicerorhinus merckii*, *Stephanorhinus kirchbergensis* (Jäger 1839) in the modern taxonomy), an extinct representative of one of three genera of large Pleistocene rhinos (*Coelodonta*, *Elasmotherium*, *Stephanorhinus*), is scarce in Russia's geological record. In Western Europe, the fact that the remains are confined to interglacial deposits led to their identification as belonging to interglacial or "forest" rhinoceros (Alekseeva, 1977; Burkanova et al., 2020). For a long time, special publications on this species were based mainly

Fig. 1. Locations of the remains of Merck's rhinoceros studied: Altai rhinoceros (AltR), specimen F–887; Chondon rhino (ChR), specimen F–4160.

on West European materials. Despite a fairly large number of remains, a nearly complete skeleton was first discovered only in 2016 in Poland (Kotowski et al., 2017).

The first finding in Russia was from the Irkutsk region (Cherskii, 1874). Later, remains from localities of the Russian Plain as part of the Khazar faunistic complex were described (Gromova, 1932; Belyaeva, 1939). Interest in Merck's rhinoceroshas revived in the early 21st century. A series of articles were published with revision and description of new findings in Russia (Billia, 2007, 2008, 2008a, 2010, 2014; Shpansky and Billia, 2012; Shpansky, 2016).

The reconstructed range of this rhinoceros, which previously covered the greater part of Europe and a significant part of Asia, except for its southern and northern territories (Billia and Zervanovà, 2015), has been significantly expanded to the north due to the findings on the Chondon River in northern Yakutia (Kirillova et al., 2016) and to east in Primorye (Kosintsev et al., 2020) and to the revision of earlier findings (Shpansky and Boeskorov, 2018). The latest time of its existence on the territory of Russia was determined as the Middle Pleistocene for Yakutia (Shpansky, 2017) and the beginning of the Late Pleistocene MIS 5 for the southeastern part of Western Siberia (Shpansky, 2017; Shpansky and Boeskorov, 2018).

On the territory of Russia, in situ findings of Merck's rhinocerosare rare; it is difficult to correlate the lifting specimens of age beyond the capabilities of 14C method with geological layers, like for the Chondon rhinoceros.

In Southern Siberia, the remains of Merck's rhinoceroscome from the Chumysh River in Altai (Vasil'ev et al., 2014, 2015; Shpansky, 2016) from the Late Pleistocene deposits widely represented in this area.

The goal of this study was to refine the spatiotemporal boundaries and conditions for the existence of this exotic rhinoceros based on two findings from distant regions of Russia: the Chumysh River in Altai and the Chondon River in Northeastern Russia (Fig. 1).

MATERIALS AND METHODS

(1) The skull of an adult Merck's rhinoceros from the Chondon River in Northern Yakutia, specimen F–4160, hereinafter referred to as the Chondon rhinoceros (ChR) described earlier (Kirillova et al., 2016, 2017).

(2) The mandible of an adult Merck's rhinoceros (Fig. 2), specimen F–887, hereinafter referred to as the Altai rhinoceros (AltR). Found in 2005 on the towpath of the Chumysh River near the village of Pobeda (Tselinnyi District, Altai krai). The mandible is well preserved; the incisal part and diastema are absent; roundness is noticeable. The inner bone canal contained soil (yellow medium-grained sand with a silty component), from which spores and pollen were isolated.

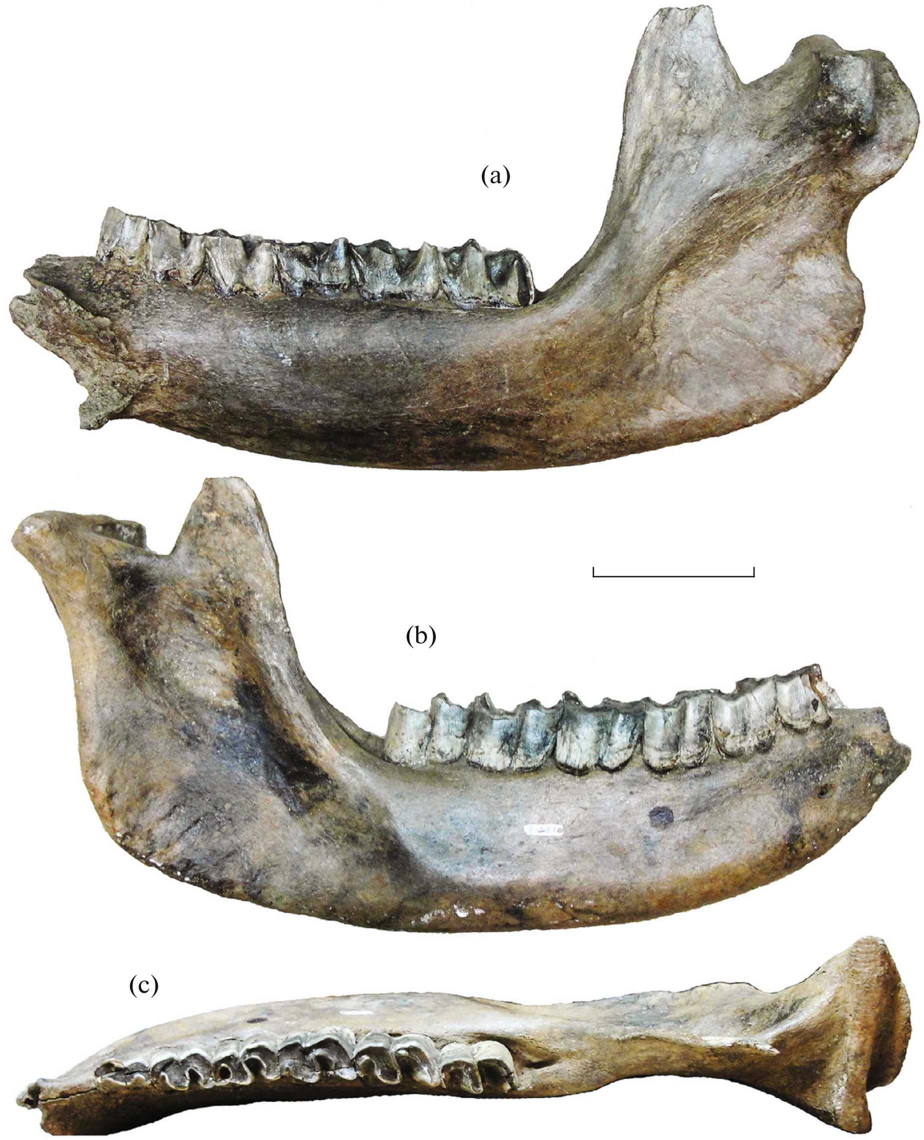

Fig. 2. Mandible of Merck's rhinoceros from the Chumysh River (Altai), specimen F–887. (a) lingual; (b) buccal; and (c) top views. Photo. Scale 1 cm. Shidlovskiy National Alliance "Ice Age."

Both samples are stored at Shidlovskiy National Alliance "Ice Age."

Morphometry. The mandible and teeth were measured by conventional methods (von den Driesch, 1976; van der Made, 2010) using an electronic caliper with an accuracy of up to 1 mm. Notation for cheek teeth (premolars and molars): P and M are upper, and p and m lower.

Enamel microwear was studied using the equipment of the Multiaccess Center (MC) "Instrumental Methods in Ecology" at the Institute of Ecology and Evolution, Russian Academy of Sciences. The teeth of AltR were studied by macro- and microscopic morphological techniques. The images were obtained at various magnifications using a Sony Alpha 5000 digital camera (Sony Corporation, Japan) and a Keyence Digital Microscope VHX-1000 (Keyence Corporation, Japan) and edited with the Adobe Photoshop Elements 11 computer program (Adobe Systems, Inc., United States). Measurements of the enamel width and microrelief images were performed using TESCAN ATLAS software (TESCAN, Czech Republic). The dimensions of some enamel elements were processed by variation statistics.

Pollen analysis. Laboratory processing of soil from the mandibular bone canal was performed at the Laboratory of Continental Ecosystems of the Mesozoic and Cenozoic of Tomsk State University (Tomsk) by separating the organic and inorganic fractions with a heavy liquid based on KI and CdI_2 solutions (Grichuk,

Table 1. GenBank numbers of mitochondrial genomes of the samples used for molecular and phylogenetic analysis

Species name	GenBank no.
Sumatran rhinoceros (*Dicerorhinus sumatrensis*)	NC_012684.1
Woolly rhinoceros (*Coelodonta antiquiatis*)	NC_012681.1
White rhinoceros (*Ceratotherium simum*)	NC_001808.1
Black rhinoceros (*Diceros bicornis*)	NC_012682.1
Indian rhinoceros (*Rhinoceros unicornis*)	NC_001779.1
Javan rhinoceros (*Rhinoceros sondaicus*)	NC_012683.1
Merck's rhinoceros (*Stephanorhinus kirchbergensis*), specimen F–4160	KX646743.1
Malay tapir (*Tapirus indicus*)	NC_023838.1

1940) modified by additional ultrasonic treatment. The remains were analyzed at the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg). Pollen and spores were determined in temporary glycerol preparations using an Olympus BX51 microscope with magnification of ×400 and a reference collection of modern pollen and spores of the Institute of Plant and Animal Ecology and a guide atlas (Beug, 2004). Counting was carried out up to 500 pollen grains of terrestrial plants, with parallel registration of spores of higher spore plants and nonpollen palynomorphs. The amount of pollen of trees, shrubs, and grass was taken to be 100%.

Isolation and analysis of ancient DNA. A single-stranded DNA library was prepared from a DNA extract following (Troll et al., 2019). Quantitative PCR using a 1× Maxima SYBR Green solution showed that the optimum number of PCR cycles for amplification was 12. The DNA library was amplified in a 1× Amplitaq Gold polymerase solution according to this number of cycles. After amplification, it was cleaned on Sera-Mag Magnetic SpeedBeads in a polyethylene glycol solution (18% PEG 8000).

The DNA library was enriched for mitochondrial DNA fragments using a set of biotinylated RNA probes designed to capture mammalian mitochondrial genomes (for details, see Kirillova et al., 2017, Supplementary Table 1). Following protocol version 4.01 from Arbor Biosciences (Ann Arbor, MI), we hybridized the library with RNA probes for 36 h at 65°C. Then it was amplified with a 2× KAPA HIFI polymerase mix and sequenced at the University of California, Santa Cruz, on Illumina MiSeq (paired reads, 75 nucleotides each). We merged reads and assembled the mitogenome according to the protocol by Vershinina et al. (2019) using *Stephanorhinus* cf. *kirchbergensis* as a reference (GenBank: KX646743.1, Table 1) as a reference for mitogenome assembly.

14C dating of AltR was performed twice on the tooth root (dentin) and mandibular bone tissue at the Multiaccess Center "Laboratory of Radiocarbon Dating and Electron Microscopy" of the Institute of Geography, Russian Academy of Sciences (laboratory index $IGAN_{AMS}$), using accelerator mass spectrometry (AMS). Collagen separation for AMS dating followed the standard protocol (Brown et al., 1988) complemented with ultrafiltration (Bronk Ramsey et al., 2004). The samples were graphitized using an AGE3 system combined with a Vario Isotope Select element analyzer (Elementar, Great Britain) and a Precision IRMS (Isoprime, Great Britain) (Nemec et al., 2010; Wacker et al., 2010). Determination of the isotope composition and graphitization of the collagen under study were performed on one sample. The resulting graphites were pressed into NEC targets using a pneumatic press (PSP, Ionplus). The 14C measurement was performed at the Center for Applied Isotope Studies, University of Georgia, United States (CAIS). The $^{14}C/^{13}C$ ratio in graphite was measured on a 0.5 MeV 1.5SDH-1 Pelletron AMS accelerator-mass spectrometer tandem system. All measurements were performed relative to the OXII standard, and the 14C age was calculated using a Libby half-life of 5568 years. The dates were corrected for natural isotope fractionation. The calibration was performed in the CALIB 7.1 program using the IntCal13 calibration curve (Reimer et al., 2013).

RESULTS

A description of the skull of ChR, specimen F–4160, was published previously (Kirillova et al., 2016, 2017).

The mandible of AltR, specimen F–887 (Fig. 2), which belonged to an adult, was well preserved, unevenly colored to dark brown, in some places black, including cancellous bone tissue. The tooth enamel is brownish gray in some places on the surface. The dentitionis complete; the anterior part of p2 is damaged. All teeth have erupted and have functioned; m3 started to wear out recently. The morphological peculiarities of AltR (weak curvature of the ventral part, oval cross section, and constant thickness of the horizontal branch of the mandibular bone; molar crowns inclined forward; the teeth are large relative to the bone height; the overall dimensions of the bone are large) and smooth tooth enamel on the surface (Gromova, 1932; Billia, 2008; Kosintsev et al., 2020) indi-

Table 2. Measurements (mm) of the mandible of Merck's rhinoceros (the values are rounded to integers)

Measurements	Altai, Chumysh River	Shpansky, 2016	Shpansky, Boeskorov, 2018, Table 3	
	F–887	Kindal, Tomsk region	Mus-Khaya, no. 400	Chernyi Yar (Gromova, 1935)
Length from the front edge of the alveole of p2 to the rear edge of the ascending branch (no. 5[1])	495	510	488	478–510
Length from the rear edge of the alveole of m3 to the rear edge of the ascending branch (no. 3[1])	236	221	211	210–250
Length of dental arch p2-m3 (at alveoles) (no. 7[1])	280	289	266	255–283
Length of dental arch p2-4 (at alveoles) (no. 9[1])	119	116	108	108–118
Length of dental arch m1-3 (at alveoles) (no. 8[1])	159	171	158	151–163
Height between m1 and m2 (no. 6[2])	103	108	111	
Height at the back of m3 max (no. 8[2])	115	115	123	121–129
Thickness of the horizontal branch under m3 (no. 36[2])	72	66	63	62–77
Width of the rear edge of the angular segment	75	(54)	66	68–72
Width and diameter of the joint facet pr. condilaris (nos. 14[2] and 21[2])	122/30	124/32	118/28	112–134
Height of ascending branch up to the upper edge of pr. condylaris (no. 15[2])	247	~270	282	260–290
Tooth measurements				
Length/width of p2	–/21		29/21	
Length/width of p3	38/30	40/30	34/27	
Length/width of p4	42/32	44/35	44/32	41/33
Length/width of m1	50/37	54/38	48/37	45/33
Length/width of m2	57/36	58/36	52/38	52–53/35–40
Length/width of m3	53/35	60/36	55/36	59–62/35–40

[1] Number of the feature according to von den Driesch, 1976; [2] number of feature according to van der Made, 2010.

cate that it belongs to Merck's rhinoceros. The measurements are shown in Table 2.

The mandible of AltR is comparable in length to specimensfrom other regions of Russia, although it is somewhat larger than that from Mus-Khaya (specimen 400 from the Yana River, northern Yakutia, Table 2). The small number of specimen, however, did not allow us to reveal sexual dimorphism and individual and geographic variability.

14C age of the Altai rhinoceros. Our dates for AltR: 43000–44000 cal BP (Table 3) currently show the youngest age for Merck's rhinoceros from Russia.

Tooth microstructure and microwear of the Altai rhinoceros. The dimensions of the investigated fragment of p3 on the chewing surface are 20.26 × 11.4 mm. The surface is polished and contains clearly visible enamel and dentin layers (Fig. 3a). The thickness of the enamel layer ranges from 2.9 to 3.1 mm. The inner layer of enamel with a thickness of 1.4–1.5 mm (~70% of the total enamel thickness) contains regularly spaced enamel prisms with a width of 162.9 ± 22.4 (119.7–185.8) μm and a length of 1195.5 ± 269.6 (782.8–1616.4) μm (n = 10) (Fig. 3b). The distance between the prisms is 193.1 ± 60.5 (140.4–315.6) μm (Table 4). We compared the degree of development of enamel prisms for two Merck's rhinoceros: p3 of AltR and the previously studied M2 of ChR (Kirillova et al., 2017, Fig. 6). It turned out that there were no statistically significant differences between the length and width of enamel prisms in the samples compared ($p > 0.1$), but for M2 of ChR, the width of intervals between prisms was different ($p < 0.1$) and the prisms were located less frequently than for p3 of AltR (Table 4). The insufficient amount of comparative material, however, does not allow us to identify differences in the topography and sizes of enamel prisms determined by the type of tooth, the age of the individual, or the diet and living conditions of the animal. These markers can be very helpful. On the enamel and dentin sur-

Table 3. Results of 14C dating of the F–887 specimen (AltR)

No.	Laboratory no.	Tissue	^{14}C, BP (1σ)	$\delta^{13}C$, ‰	$\delta^{15}N$, ‰	cal BP[i]
1	$IGAN_{AMS}6919$	Dentin	40350 ± 150	20.51	6.00	68.3 (1 sigma) cal BP 43696–44166 1.000 95.4 (2 sigma) cal BP 43478–44372 1.000 Median Probability: 43931
2	$IGAN_{AMS}7224$	Bone	40230 ± 180	20.49	6.53	68.3 (1 sigma) cal BP 43555–44060 1.000 95.4 (2 sigma) cal BP 43345–44298 1.000 Median Probability: 43813

faces, there are a few, but rather large (76 × 74; 100 × 90 μm), oblong or round pits with rough edges (arrows, Fig. 3b).

The size of the fragment with chipped enamel is 32.3 × 10.4 mm; the enamel thickness is 1.9–2.0 mm (Fig. 3c). The dentin surface is punctured by numerous oblong and round pits, the largest ones reaching 556 × 405 and 657 × 408 μm (arrow, Fig. 3d).

Pollen spectrum from the host rock of AltR and general reconstruction of the environment. Pollen and spores from the AltR specimenwere preserved as grains with fine, slightly rounded exine, which is typical for alluvial deposits. No mineralized forms were found, but there were unidentified skeletonized and deformed pollen grains with an indistinct morphological structure. No redeposited pollen grains and spores were found.

The pollen spectrum is dominated by herbaceous plants (68.2%), among which wormwood (*Artemisia* sp. 26.6%), rose family (Rosaceae 11.6%), pigweed (Chenopodiaceae 9.6%), and grasses (Poaceae 7.2%) prevail (Fig. 4, Table 5).

The total content of herb pollen (Herbetum mixtum group) is 11%, including Asteraceae, Polygonaceae, Apiaceae, Fabaceae, and pollen of undetermined taxons (Pollen gen. indet.). Trees and shrubs account for 31.8%, with spruce (*Picea* sp. 14%) and shrub birches (*Betula* sect. Nanae 9%) predominating. There is a small amount of pine (*Pinus* s/g Diploxylon and Haploxylon) and birch (*Betula* sect. Albae) pol-

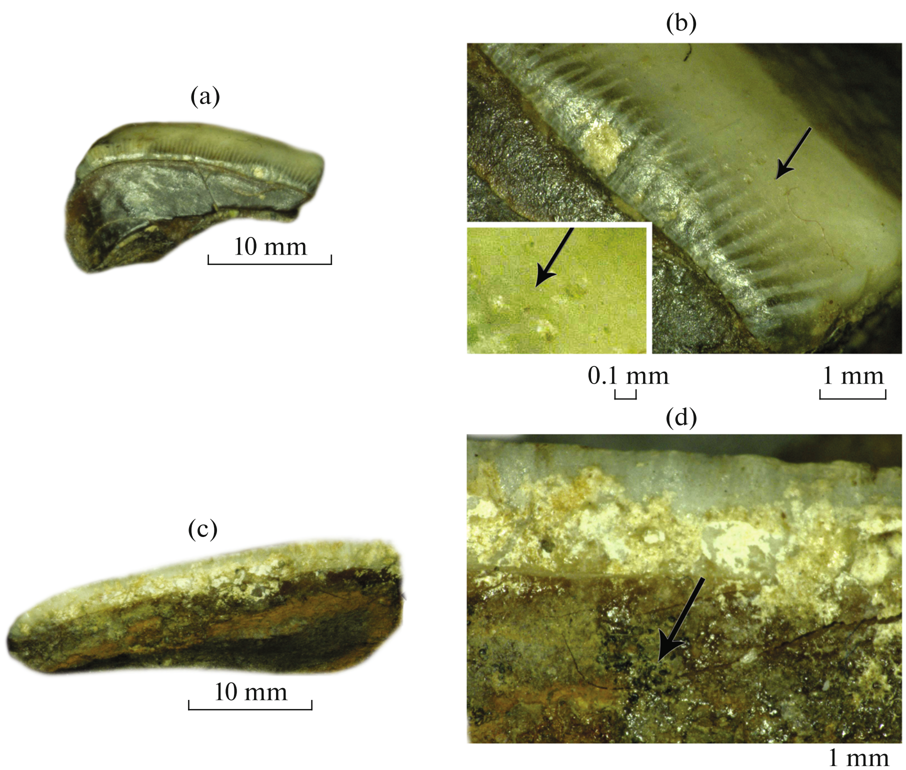

Fig. 3. Enamel microstructure and microwear on two fragments of p3, specimen F–887. (a, b) Chewing surface with a layer of enamel with well-visible enamel prisms and few pits (indicated by arrows). (c, d) Lateral surface with chipped enamel, with a clearly visible layer of dentin with numerous pits (arrow). Micrograph.

Table 4. Measurements ($M \pm m$ (limits), $n = 10$, μm) of enamel elements on the teeth of *Stephanorhinus kirchbergensis*: on p3 of the Altai rhinoceros (AltR, sample F–887) and on M2 of the Chondon rhinoceros (ChR, sample F–4160)

Specimen	*L*	*W*	*D**
AltR, F–887, p3	1195.5 ± 269.6 (782.8–1616.4)	162.9 ± 22.4 (119.7–196.1)	193.1 ± 60.5 (140.4–315.6)
ChR, F–4160, M2	1122.5 ± 99.1 (926.9–1244.5)	150.8 ± 27.8 (102.9–191.7)	132.1 ± 15.7 (102.9–158.4)

L is the enamel prism length, *W* is the enamel prism width, *D* is the distance between enamel prisms, and *n* is the number of measurements.
* The differences are statistically valid.

len. Spores of ferns Polypodiophyta and coprophilous fungi Sordariaceae are rare; there is one specimen of green alga of the genus *Pediastrum*.

There are xerophytic (*Artemisia* sp., Chenopodiaceae, Poaceae, etc.), boreal (*Picea* sp., *Pinus* sp., *Betula* sect. Albae), and arcto-boreal (*Betula* sect. Nanae) taxa. This combination is typical for the end of the interstadial or the beginning of stadial intervals.

According to the ratio of the main taxa, the pollen spectrum reflects the vegetation of open landscapes with forest areas on the upland and/or in the river floodplain. The pigwood–wormwood groups alternated with herb–grasses communities; the local forest communities were formed by spruce trees involving birches. Judging by the insignificant percent of pines and birches, there was distant import of their pollen.

Phylogeny. Enrichment of the DNA library for mitochondrial DNA allowed assembly of the complete mitogenome of AltR with an average coverage of 49.86×. Phylogenetic analysis of the complete mitochondrial genomes of extinct and extant rhinoceroses placed the AltR genome together with the previously published mitochondrial genome of ChR; the genetically revealed taxonomy does not contradict the identification of the mandible according to morphological characteristics. Both specimens belong to *Stephanorhinus kirchbergensis* (Fig. 5, Table 1).

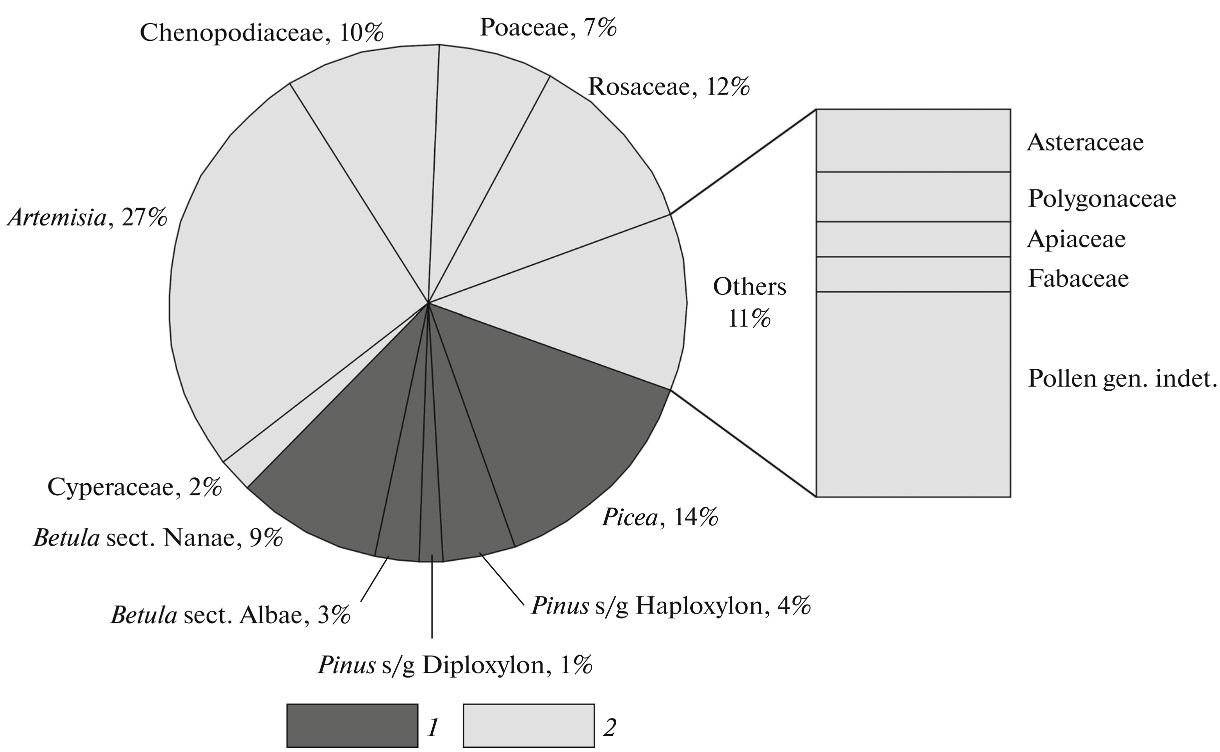

Fig. 4. Pollen spectrum from the soil filling the cavity of the mandible of AltR, specimen F–887: (*1*) herbaceous plants, (*2*) arboreal plants.

Table 5. Composition and fraction of pollen and spores in the soil from the F–887 specimen (AltR)

Palynotaxa	Number	%
Arboreal pollen sum	159	31.8
Picea	70	14.0
Pinus s/g Haploxylon	23	4.6
Pinus s/g Diploxylon	7	1.4
Betula sect. Albae	14	2.8
Betula sect. Nanae	45	9.0
Sum of pollen of semi-shrubs and grasses	341	68.2
Cyperaceae	11	2.2
Poaceae	36	7.2
Chenopodiaceae	48	9.6
Artemisia	133	26.6
Rosaceae	58	11.6
Asteraceae	9	1.8
Polygonaceae	7	1.4
Apiaceae	5	1.0
Fabceae	5	1.0
Pollen gen. indet.	29	5.8
Total pollen sum	500	100.0
Polypodiophyta	3	0.6
Sordariaceae	18	3.6
Pediastrum	1	0.2

DISCUSSION

In recent years, studies of extinct rhinos in Russia have changed the prevailing understanding of their distribution and time of existence. For example, it turned out that *Elasmotherium sibiricum* J. Fischer 1809 survived until the Late, but not Middle, Pleistocene (Kosintsev et al., 2019). Merck's rhinoceros inhabited the territory up to the coast of the Arctic seas, which shifted the northern border of its reconstructed range by a few hundred kilometers to the north (Kirillova et al., 2016; Shpansky and Boeskorov, 2018). The hornless rhinoceros *Chilotherium* inhabited not only the territories of southern Europe and Central and Eastern Asia, but also the southern part of the Russian Plain (Titov and Tesakov, 2013). Comprehensive research methods provided more information on the distribution and habitat of these rare fossil rhinoceroses.

Environment during the lifetime of the Altai rhinoceros. Both AMC dates for AltR correspond to the Karginsky Interstadial, MIS 3, of the Late Pleistocene in Western Siberia (*Unifitsirovannaya regional'naya stratigracheskaya schema*..., 2000). Paleoecological data for this period indicate the mosaic character of the vegetation and climate in southern Siberia both throughout the entire time of MIS 3 and within other time intervals of the Late Pleistocene (Zykin et al., 2003; Laukhin et al., 2006; etc.), up to the present (Chytrý et al., 2019). This was determined by the local geographic features. According to previously published palynological data, in MIS 3, the greater part of the region was occupied by forests, mainly taiga with predominant spruce, the area of which was shifted to the south of modern forests by 5° (Laukhin et al., 2006, 2015).

In Altai, the pollen spectra from deposits over 44 000–34 000 14C years characterize forests with a significant admixture of broad-leaved species: hornbeam, elm, linden, hazel, etc. (Laukhin et al., 2015). A study of a series of sections of Late Pleistocene deposits in the valley of the upper reaches of the Ob River and its tributaries within the Pre-Altai Plain (Arkhipov and Votakh, 1973; Panychev, 1979) revealed differences in the pollen content of the leading taxa of the arboreal and non-arboreal groups, which reflects changes in the ratio of forest and meadow vegetation both in separate chronological intervals of the Karginsky Interstadial (40 000–24 000 14C years), and for the subsequent Sartan Stadial (24 000–10 300 14C years) (Table 6).

The pollen spectra from deposits 35000–40000 years old corresponding to the time of existence of AltR show that arboreal pollen was predominant (50–80%): *Picea* sp. (dominant), *Pinus sylvestris* L., *P. sibirica* (Loud.) Mayr, *Salix* sp., and *Betula* sp., including herbs (Cyperaceae, Poaceae, Chenopodia-

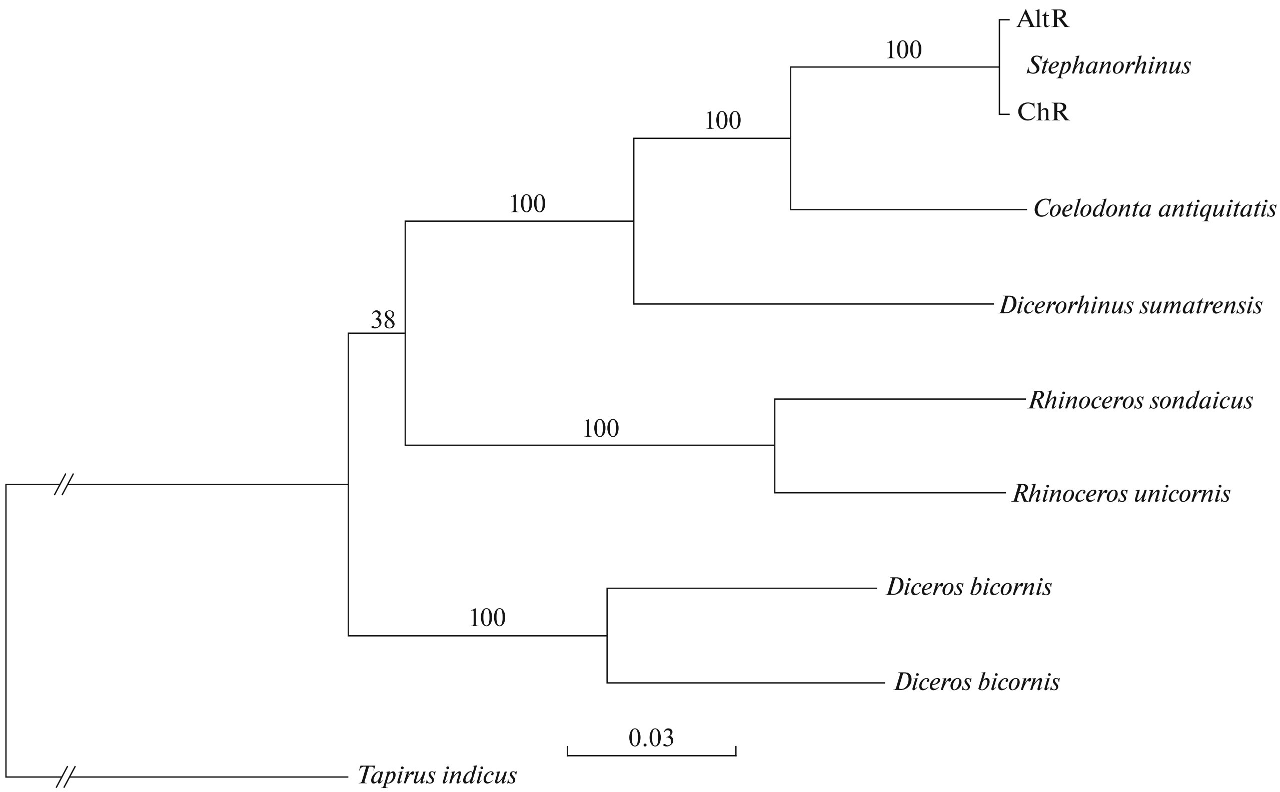

Fig. 5. Phylogeny of extinct and extant members of the family Rhinocerotidae based on molecular analysis of their complete mitochondrial genomes. Figures: support values at the tree nodes obtained by maximum likelihood analysis and 500 bootstrap replicas. The scale indicates the genetic distance between sequences.

ceae, Brassicaceae, etc.). These communities probably formed under conditions of a rather humid, moderately cool climate with predominant forest vegetation (Panychev, 1979). Our data most likely characterize the plant communities of the cold stage within the Karginsky Interstadial, when only local forest communities were preserved among shrub thickets and xerophytic vegetation.

Diet of Altai and Chondon rhinos. We found the following features of microwear to enamel on the chewing surface of the tooth of AltR:

(1) The absence of thick grooves and fine, randomly spaced scratches usually found on the teeth of ungulates.

(2) Few pits on the enamel and their abundance on the dentin surface.

(3) Oblong configuration and large sizes of pits.

In the last few weeks before its death, AltR most likely fed on browse.

The isotopic (nitrogen, carbon) data (Table 3) are close to the data obtained for woolly rhinos of Yakutia (Bocherens, 2015). This does not contradict our data, taking into account the forced diversity of the diet even in "specialized" fossil rhinos (Asperen and Kahlke, 2015).

On the geological age of the Chondon rhinoceros. The lifetime of ChR was initially determined with allowance for two markers: over-extreme 14C dating, on the one hand, and the geological age of deposits, "usually rich in mammalian remains in the region" (Lomachenkov, 1956), on the other (Kirillova et al., 2017). This "calculated" range is probably erroneous, as noted later by Shpansky, one of the authors of the publication on Merck's rhinoceros (Shpansky and Boeskorov, 2018). However, we cannot agree with the geological age proposed in this publication for the following reasons.

(1) The time of existence of Merck's rhinoceros in Yakutia was stated to be the Middle Neopleistocene, but this was not confirmed by other methods: "In our opinion, all findings in Yakutia ... can be attributed to the first half of the Middle Neopleistocene (MIS 11–9), the most ecologically favorable time for the existence of this specialized animal" (Shpansky and Boeskorov, 2018, p. 108).

The environmentally friendly conditions do not always lead to species prosperity, while their absence does not always imply unsuitable conditions. It is important to take into account compliance and adaptability to various types of nutrition, even in such "specialized"species as Merck's "forest" rhinoceros more

Table 6. Ratio of the main pollen in the pollen spectra of Upper Pleistocene deposits of the Ob River and its tributaries within the pre-Altai Plain

Taxa	Arkhipov and Votakh, 1973; Panychev, 1979						Our data
	Ob River					Chumysh River	
	1	2	3	4	5	6	7
Arboreal pollen (AP)	15	88	15	80	60	<5	32
Non-arboreal pollen (NAP)	75	10.5	80	15	40	90	68
Picea	18	2.8	15	100	30	50	44
Pinus sylvesrtis	<5	6.1	40	–	60	20	4.4
Pinus sibirica	<5	42	20	–	<5	20	14.5
Betula sect. Albae	75	5.4	10	–	<5	10	8.8
Betula sect. Nanae	<5	–	<5	–	–	–	28.3
Ephedra	<5	–	–	–	–	<5	–
Artemisia	25	–	10	<5	–	60	39
Chenopodiaceae	25	<5	20	<5	–	20	14.1
Poaceae	30	<5	30	<5	<5	<5	10.6
Cyperaceae	–	<5	<5	<5	30	<5	3.2
Herbetum mixtum	15	<5	25	<5	10	17	31.1

Pollen spectrum from (1) clay loams of the section of deposits I of the terrace above the flood-plain of the Suzun River, age 10950 ± 150 14C years (SOAN-54); (2) clays of the terrace section of the Biya River near the village of Turochak, 13750 ± 70 14C years (SOAN-576); (3) the section of Krasnyi Yar deposits, Ob River, 30870 ± 300 14C years (SOAN-1457); (4) clay loams of a section of the Ob River near the village of Kargopolovo, 32275 ± 420 14C years (SOAN-1254), 32400 ± 2000 14C years (SOAN-23), and 33450 ± 550 14C years (SOAN-744); (5) section deposits of the Bol'shaya Rechka River, 35980 ± 720 14C years (SOAN-436) and 37340 ± 660 14C years (SOAN-1258); (6) blue clays of a section near the village of Kytmanovo, age 24240 ± 2700 14C years (SOAN-31); (7) F–887 specimen.

adapted to branch feed and as the "steppe" *Coelodonta antiquitatis* feeding on grass. The study of microwear on the enamel of the chewing surface of teeth showed that the food of Merck's rhinoceros could have been both leaves and herbs evidently depending on the season, landscape, and other factors (Asperen and Kahlke, 2015); i.e., these rhinos consumed what was available. The ChR pastures included meadows with grass and mixed herbs, moss communities, and possibly sparse larch forests (Kirillova et al., 2017). The vegetation cover of the tundra is heterogeneous, which is associated with the microrelief, the presence of permafrost rocks, and the associated cryogenic processes in the active layer of soil. However, even under extreme conditions with sparse vegetation, more productive herbaceous and subshrub intrazonal associations are found along the lake shores and riversides. It is logical to assume that Merck's rhinoceros, like modern species, fed in the richest food places in river valleys and near water reservoirs.

(2) The upper marker of the time of existence of ChR (beyond the capabilities of the 14C method) cuts off the time period younger than 45000 years. The over-extreme date implies any age older than that. However, there are also the general geological and palaeobotanical data. Here we revise the milestone of 70000 years following the accepted paradigm that Merck's rhinoceros lived in the (relatively warmer) interstadial periods and preferred forest landscapes (which is consistent with the remains of larch branches in the tooth cavities of ChR). These conditions, however, were inherent not only in the Middle Pleistocene. A detailed palynological characterization of the deposits of the Late Pleistocene (Eemian) Interglacial of the Oyogos Yar in Dmitrii Laptev Strait (Andreev et al., 2011) made it possible to reconstruct the temperature rise over the present-day temperatures in July by 9–10°C (Kienast et al., 2011). In the neighboring region, on the coast of the East Siberian Sea, the reconstructed temperature based on palaeobotanical and isotope data at that time was higher than the present-day temperature by at least 8°C (Kirillova et al., 2020).

Thus, acceptable temperature conditions for ChR were not only in the Middle Pleistocene; relatively heat-loving vegetation existed in the extreme north of Yakutia during the Eemian Interglacial, MIS 5e. Accordingly, the Late Pleistocene cannot be excluded as the time of existence of Merck's rhinoceros in the area of the Chondon River.

(3) "During the MIS 3 Molotkov Interstandial, tundra landscapes were widespread on this territory, which were unsuitable for the life of *S. kirchbergensis*" (Shpansky and Boeskorov, 2018, p. 108). The MIS 3

stage of the Upper Pleistocene, the regional name of which is the Karginsky (Molotkov) horizon, stratigraphically has a five-membered structure in the most complete sections in Siberia. According to palynological data, at this time three warmings alternated with two cold stages, of which the last warming was the weakest, and the second cold stage was the most intense. Traces of a climate close to modern or milder have been noted by many researchers, even in the northern sections of the Karginsky Horizon, especially for the Early Karginsky time (Giterman, 1985; Volkova, 2001; Schirrmeister et al., 2002; Lozhkin and Anderson, 2011; Andreev et al., 2011). Repeated climate changes during MIS 3, both coolings and warmings, are also confirmed by paleopedological research (Gubin and Zanina, 2013, 2014). In addition, Pleistocene landscapes were mosaic, which is still preserved in some modern landscapes, both high-latitude and mountainous (Chytrý et al., 2019). The tundra, forest–tundra, and forest vegetation could be combined within one geographic zone, occupying different parts of watersheds and valleys. In the Karginsky (and not only) time, natural events had their own local features (Laukhin et al., 2012, 2015). Thus, the Karginsky Interstadial, the temperature conditions of which were close to modern ones, formally cannot be rejected as a theoretically possible time for Merck's rhinoceros to live in the region, and a finding of its remains from this time would not be surprising.

(4) The conditions of existence of ChR were reconstructed from plant remains, but the conclusion that such "vegetation was characteristic for this latitude at the beginning of the Middle Neopleistocene (MIS 9–11)" (Shpansky and Boeskorov, 2018, p. 108) seems declarative as the authors did not provide any convincing palaeobotanical and other evidence. The vegetation cover of the beginning of the Middle Pleistocene was represented by larch-and-birch forest–tundra (sparse forests). Large areas were occupied by lakes and swamps, as evidenced by the findings of numerous remains of aquatic plants. During the second phase, under conditions of severe, extremely continental climate, the tundra groups with predominant grasses and wormwoods spread. The beginning of the MIS 3 phase is considered by many researchers to be warm, with larch-and-birch forests of the northern sparse taiga type with shrub birch, alder groves, dwarf pine, widespread bog sphagnum, and green mosses (Giterman, 1985). In general, during the warm periods of the Middle and Late Pleistocene, the vegetation was quite similar.

(5) Finally, the fact that Merck's forest rhinoceros "specialized in feeding on branch fodder" is not an indicator of exclusively forest landscapes, it was a "mixed" eater, see above (Asperen and Kahlke, 2015). Also note that larch, the branch remains of which were found in the cavities of the teeth of ChR, now reaches Lake Orotko, located to the north of the middle reaches of the Chondon River (Lomachenkov, 1956) and up to the mouths of the Indigirka, Yana, and Kolyma rivers (Pozdnyakov, 1975).

It would certainly be most reliable to determine the lifetime of ChR (and any other specimenwith over-extreme 14C dating) from in site findings from reliably dated deposits. However, this is not always possible.

Phylogenetic position. The reconstructed phylogenies indicate that the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach 1799) is a sister group to Merck's rhinoceros, and the closest living relative of this group is the Sumatran rhinoceros (*Dicerorhinus sumatrensis* Fischer 1814). The data obtained for AltR are consistent with the previously reconstructed phylogeny of this group (Kirillova et al., 2017).

CONCLUSIONS

Our study made it possible to complement the information about the time and habitat of Merck's rhinoceros in Russia. The finding of AltR ~40000 years old from the Chumysh River "extends" the time of existence of the species, currently attributed to the MIS 5 Eemian Interglacial (Shpansky, 2017), to the end of the Late Pleistocene (MIS 3); this is the latest finding in Russia to date. According to the previously published palynological data, 40000 years ago, forest vegetation was widespread here: spruce trees with birch and shrubs; meadow plant communities were formed by xerophytic and mesophytic herbs (Arkhipov and Votakh, 1973; Panychev, 1979). Our data on the pollen spectra characterize limited forest communities among shrub thickets and xerophytic vegetation and reflect either the local landscape features or the communities of the cold stage within the Karginsky interstadial. Judging by microwear to the tooth enamel, the main food for AltR was the branches of trees and bushes.

For ChR, who lived in open larch forests and grassy pastures and "pushed" the northern border of the range of Merck's rhinoceros far beyond the Arctic Circle, the time of its existence in northeastern Russia may also be extended to the Late Pleistocene (at least to MIS 5e). Further research will clarify the problems of the existence and extinction of the mysterious Merck's rhinoceros.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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