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Northernmost Record of the Merck's Rhinoceros *Stephanorhinus kirchbergensis* (Jäger) and Taxonomic Status of *Coelodonta jacuticus* Russanov (Mammalia, Rhinocerotidae)

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Abstract—A lower jaw of *Stephanorhinus kirchbergensis* from the Mus Khaya locality on the Yana River in Yakutia is described. This jaw was previously designated as a paratype of *Coelodonta jacuticus*, but morphological and morphometric analysis has shown that it actually belongs to a typical *S. kirchbergensis.* Morphometric parameters of the holotype (skull) of *C. jacuticus* fall within the range of intraspecific variation of *C. antiquitatis.* The same results of a morphometric study were obtained for the subspecies *Coelodonta antiquitatis pristinus* and *C. a. humilis.* This suggests that *C. jacuticus*, *Coelodonta antiquitatis pristinus,* and *C. a. humilis* are invalid taxa which should be regarded as junior synonyms of *C. antiquitatis.* The find of *S. kirchbergensis* in northern Yakutia is the northernmost occurrence of this species.

Keywords: Stephanorhinus kirchbergensis, *Coelodonta jacuticus*, *C. antiquitatis*, *C. a. pristinus*, *C. a. humilis*, morphology, systematics, Middle–Late Neopleistocene, Yakutia

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INTRODUCTION

The overwhelming majority of rhinoceroses recorded in Russia belong to *Coelodonta antiquitatis* (Blumenbach, 1799). Occurrences of rhinoceros corpses or skeletons are usually of great interest, while individual finds of isolated bones receive little attention of researches. Little attention is also given to the other fossil rhinoceros species, *Stephanorhinus kirchbergensis* (Jäger, 1839). Its remains are rather scarce and usually isolated. They are frequently incorrectly identified in collection of museums and scientific organizations. This is connected with poor diagnostic value of a number of skull parts and elements of the postcranial skeleton of *S. kirchbergensis* and *C. antiquitatis.* To distinguish between these species, the teeth (intact or slightly worn), bones of the facial and occipital skull region, lower jaws, and metapodia are most important. As available material is fragmentary, identification is complicated in connection with the absence of detailed descriptions of many skeleton fragments of *S. kirchbergensis* belonging to the same individual.

The remains of Merck's rhinoceros considered below are only the fourth record in Eastern Siberia. Previously, a skull from the Irkutsk Region (Brandt, 1877; Billia, 2008), teeth from the Vilyui River (Dubrovo, 1957), and a skull from the Chondon River have been described from this vast territory (Kirillova, 2016) (Fig. 1).

In 1964, V.F. Goncharov found a lower jaw of a large rhinoceros in yellowish gray sand at the base of the Mus Khaya outcrop (lower reaches of the Yana River, northern Yakutia; 70°43′ N, 135°25′ E) (Fig. 1). This specimen was referred to the woolly rhinoceros *C. antiquitatis* and stored in the Geological Museum of the Diamond and Precious Metals Geology Institute of the Siberian Branch of the Russian Academy of Sciences in Yakutsk (IGABM, specimen no. 400). Subsequently, Lazarev (2008) designated this jaw as a paratype of *Coelodonta jacuticus* Russanov, 1968. Along with the jaw of rhinoceros, a tooth of *Mammuthus primigenius* (Blumenbach, 1799) of the so-called early type with the plate frequency of 8.5 per 10 cm was found. Similar buried sands of the Yana–Omoloi interfluve were referred by Dementiev et al. (1963) based on geomorphological data and bedding to the second half of the Middle Neopleistocene. However, these authors indicated that this sand had yielded a number of spruce and pine forms that are absent in the upper horizon of icy loams. Based on these data, Goncharov (1968) assumed that these sand

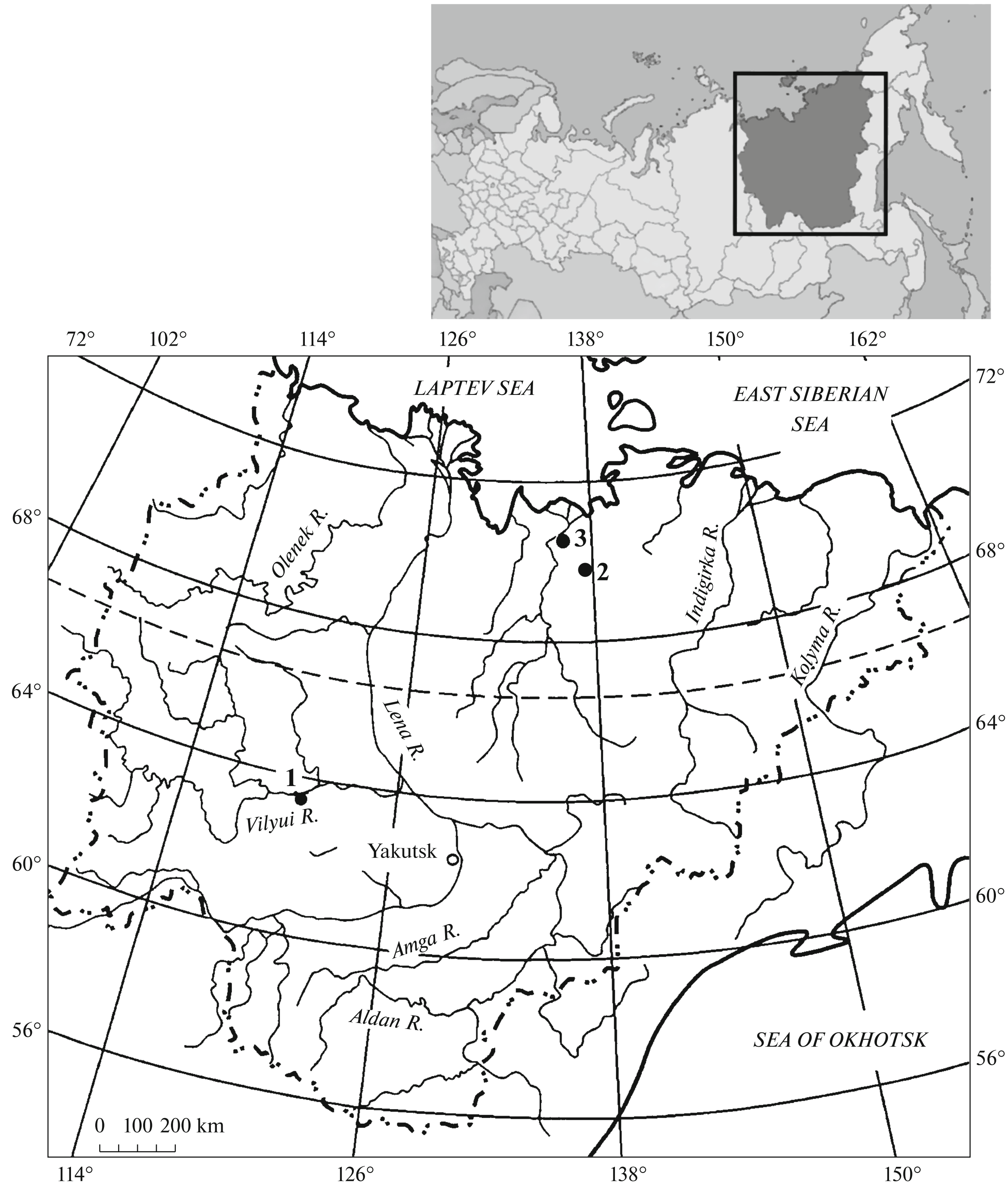

Fig. 1. Localities of Merck's rhinoceros in Yakutia: (1) Vilyui River, mouth of the Tyalychima River (Dubrovo, 1957); (2) Chondon River (Kirillova et al., 2017), (3) Yana River, Mus Khaya locality.

beds should be assigned to the Kazantsevo Interglacial of the Late Neopleistocene. Subsequently, the sandy beds on the Mus Khaya outcrop, which have yielded the rhinoceros jaw considered here, were referred to the Kemyulken Formation and, to the first half of the Middle Neopleistocene (Fig. 2). The pollen–spore assemblage from this formation is characterized by uniform proportions (within 20%) of tree–bush and grassy–shrub associations, including mostly small birches, alder, and dwarf cedar (up to 4–6%); there are also rare larch, spruce, large birches, willows, and diploid pines. Herbs compose 35–40% of pollen grains

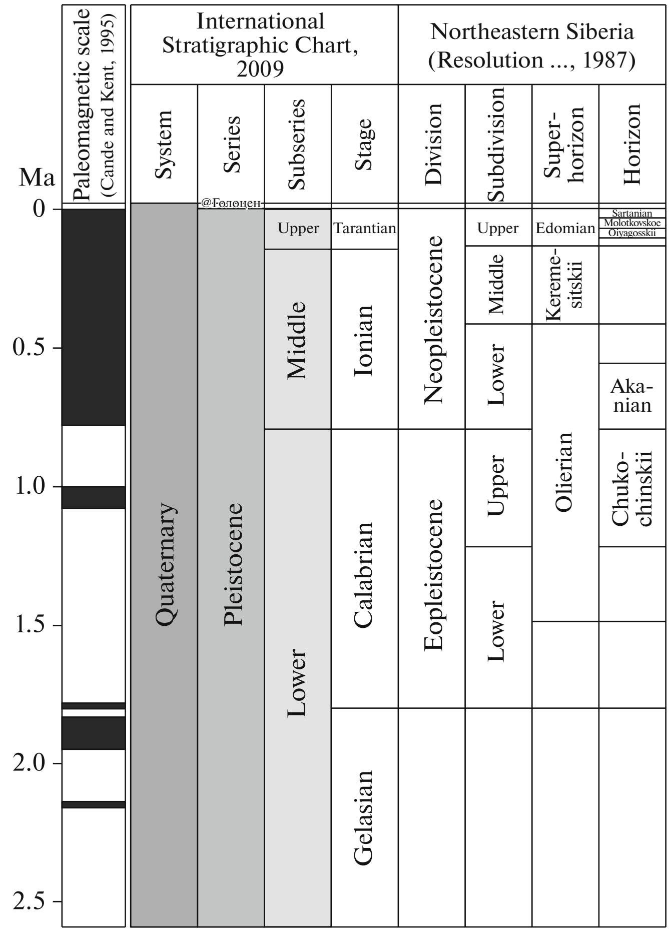

Fig. 2. Correlation of units in the International Stratigraphic Chart (*GTS,* 2009) and Regional Stratigraphic Chart of northeastern Russia (MSK Resolution ..., 1987) stratigraphic circuits.

and are represented by wormwoods, sedges, grasses, Ericales, Caryophyllaceae. About 20% of spores belong to the Siberian club moss; spores of green and sphagnum mosses (4–8%), lady ferns, and horsetails are less frequent. The spore-pollen spectrum corresponds to a warming, forest–tundra and tundra–steppe type of vegetation of northern Yakutia (*Resheniya* ..., 1987). The jaw (specimen IGABM, no. 400) is strongly mineralized; the bone is dark brown, in places, dark fulvous, almost black; in breaks, bone substance is dark brown; the teeth (enamel and roots) are mostly dark brown, in places, black. This color is usually characteristic of bones and teeth of mammals coming from the beds of northern Yakutia older than the Upper Neopleistocene. For example, bone remains of mammals from the Early Neopleistocene Oleier Fauna are usually dark brown, dark gray, almost black (Sher, 1971). Mammal remains coming from overlying icy loesslike and loamy deposits of the Upper Neopleistocene are usually lighter, from light yellow to yellowish light brown or grayish light brown (Vereschagin, 1979; Lazarev, 2008). The extent of mineralization and color of bone remains undoubtedly depend on sedimentary conditions; nevertheless, the color of specimen IGABM, no. 400 may be evidence of a significant geological age, not younger than the Middle Neopleistocene (MIS10–MIS11).

Abbreviations used in the present study are as follows: (GM KGU) Geological Museum of Kazan State University; (IGABM) Diamond and Precious Metals Geology Institute of the Siberian Branch of the Russian Academy of Sciences, Yakutsk; (PM TGU) Paleontological Museum of Tomsk State University; (TOKM) Tomsk Regional Museum; (YaNTs) Yakut Scientific Center, Yakutsk; (YaFSOAN) Yakut Subsidiary of the Siberian Branch of the Academy of Sciences, Yakutsk; (SMNS) Stuttgart Museum of Natural History, Germany.

MATERIAL AND METHODS

The following specimens were analyzed: specimen IGABM, no. 400, left mandibular ramus with teeth; IGABM, nos. 311 and 104/5, skulls; IGABM, no. 603, tooth M2. Analyzing morphological characters of the skull and lower jaw, we also examined specimens PM

Table 1. Morphological distinctions in the lower jaw structure of the woolly and Merck's the rhinoceroses

Stephanorhinus kirchbergensis	*Coelodonta antiquitatis*
Symphysis narrow, longitudinally concave	Symphysis wide and flat
Ventral margin of horizontal ramus slightly curved	Ventral margin of horizontal ramus will curved strongly ventrally
Horizontal ramus oval in transverse plane	Horizontal ramus pear-shaped in transverse plane, with expansion in ventral part
Articular process positioned at angle to sagittal plane of jaw; buccal end raised	Articular process positioned perpendicular to sagittal plane of jaw
Premolar crowns vertical; molar crowns directed anteriorly	Tooth crowns vertical
Metalophid on molars narrower than hypolophid	Metalophid on molars wider than hypolophid
Internal valleys of teeth open, rapidly narrowing toward base	Internal valleys of teeth partially covered by expansion of posterointernal ends of lophids; valleys deep, weakly narrowing toward base

TGU, nos. 1/51 and 62/2, GM KGU, no. 739 and published data on *S. kirchbergensis* and *C. antiquitatis* from localities of Europe and Siberia (Gromova, 1935; Borsuk-Bialynicka, 1973; Kahlke, 1977; David, 1980; Shpansky and Pecherskaya, 2009; Tong and Wu, 2010; Shpansky and Billia, 2012; Shpansky, 2016).

The lower jaw and dental measurements were performed following the method developed by Shpansky (2016). To distinguish between the woolly and Merck's rhinoceroses, which sometimes occur together in this territory, we used the characters introduced previously (Gromova, 1935; Shpansky, 2016) in the description of lower jaws (Table 1).

Skulls of *C. antiquitatis* were measured according to the scheme shown in Fig. 3: (1) skull length measured from the apex of the occipital crest to anterior margin of the nasals; (2) condylobasal length; (3) dental row length; (4) ratio of the molar to premolar rows (M series/P series); (5) rostral width at the anterior end of the nasals; (6) skull width in the anterior part of orbits; (7) width at the temporal constriction (the least sinciput width between the external edges of temporal fossae; (8) greatest width at zygomatic arches; (9) width at the articular fossae measured at the external edges; (10) width at the occipital crest taken from above; (11) occiput width at the mastoid tubercles, at the most strongly projecting points of mastoid processes; (12) width of the occipital condyles; (13) skull width at M3 measured between buccal walls of M3; (14) greatest width of choanae; (15) width of the nasal septum in the area of choanae; (16) skull height from the top of the base of the nasal horn to the palatine (frequently coincides with the anterior edge of P2 alveolus), perpendicular to the skull length; (17) skull height at the posterior edge of M3 to the highest point of the frontals; (18) occipital height from the upper edge of the foramen magnum to the occipital crest; (19) occipital height from the lower edge of condyles to the occipital crest (two measurements of the occipital height are necessary, because the upper edge of the foramen magnum is very changeable in shape and frequently has a significant dorsal concavity); (20) length of the nasal incisure; (21) width of the nasal incisure; (22) length of the nasal callous under the horn; (23) width of the nasal callous under the horn; (24) length of the frontal callous under the horn; (25) width of the frontal callous under the horn; (26) width of the foramen magnum; (27) height of the foramen magnum; (28) palatal width from within between M3; (29) palatal width from within between P2.

Sexual and age identification of skulls and lower jaws of fossil rhinoceroses was performed by the criteria developed by Borsuk-Bialynicka (1973) and Shpansky (2014).

SYSTEMATIC PALEONTOLOGY

Order Perissodactyla

Family Rhinocerothidae Owen, 1845

Subfamily Dicerorhinae Simpson, 1945

Genus *Coelodonta* Bronn, 1831

Coelodonta antiquitatis (Blumenbach, 1799)

Rhinoceros lenensis: Pallas, 1772, pp. 585, 591–595.

Rhinoceros antiquitatis: Blumenbach, 1799, p. 697.

Rhinoceros tichorhinus: Fischer, 1814, pp. 304–309; Cuvier, 1822, p. 93; Brandt, 1849, pp. 161–416.

Coelodonta Bojei: Bronn, 1831, p. 61.

Rhinoceros (Tichorhinus) antiquitatis: Brandt, 1877, pp. 1–65.

Tichorhinus antiquitatis: Zeuner, 1934, pp. 21–80.

Coelodonta antiquitatis pristinus: Russanov, 1968, pp. 60–66, text-figs. 23–24, 26, and 27.

Coelodonta antiquitatis humilis: Russanov, 1968, pp. 218–220, text-figs. 25, 142, and 143.

Coelodonta antiquitatis jacuticus: Russanov, 1968, pp. 97–102, 214–217, text-figs. 46, 48–50, 138, and 139.

Coelodonta lenensis: Garutt and Boeskorov, 2001, pp. 157–167.

Coelodonta jacuticus (partim): Lazarev, 2008, pp. 51–54, text-figs. 28a, 29a, and 32.

S y n t y p e s. The type series used by I.F. Blumenbach for description of the woolly rhinoceros comes from the southern Urals (Bashkiria) and Germany

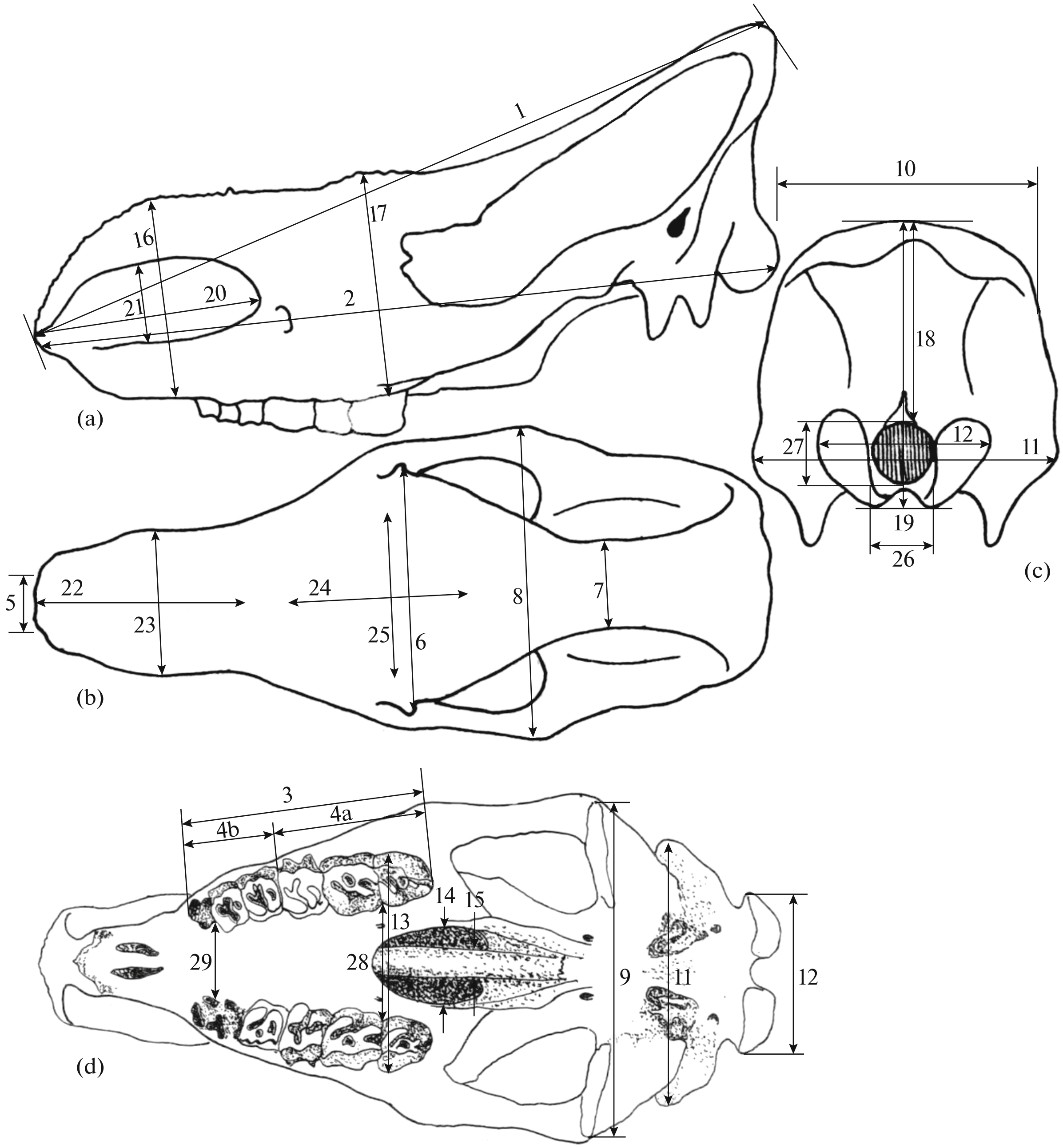

Fig. 3. Scheme of skull measurements in the woolly rhinoceros: (a) lateral view, (b) dorsal view, (c) posterior view, (d) ventral view. For designations, see the text.

(Lower Saxony); the material is listed by Gehler et al. (2007).

D e s c r i p t i o n. See Russanov (1968) and Lazarev (2008).

M e a s u r e m e n t s. See Russanov (1968), Lazarev (2008), and Table 2 of this paper.

C o m p a r i s o n. A comparison of morphometric cranial characters of *Coelodonta antiquitatis, C. nihowanensis,* and *C. thibetana* was provided by Deng et al. (2011) and that of *Coelodonta antiquitatis* and *C. tologoijensis* was performed by Kahlke and Lacombat (2008).

R e m a r k s. In the skull (IGABM, no. 311) two distinctive characters are recognized: the strongly extended parietal and the small angle (22°) between its surface and the nasofrontal surface (Lazarev, 2008, p. 52) (Fig. 4). Similar characters are recorded by Garutt (1998) in *Coelodonta lenensis* (Pallas, 1772). At the same time, in five skulls figured by Garutt (1998, text-fig. 1), the extension of the occipital crest beyond the occipital plane varies very widely. Among the

Table 2. Skull measurements *of Coeolodonta antiquitatis* from localities of Western and Eastern Siberia

Measurement, mm	Yakutia						Tomsk Region					
	Rusanov, 1968				Lazarev et al., 1998	Boeskorov, unpublished data	Shpansky, unpublished data	Shpansky, 2000	Shpansky and Pecherskaya, 2009			
	"C. a. pristinus" SVGU	*"C. jacuticus"* IGABM no. 311	*"C. a. humilis"* IGABM 104/5 862		Churapcha IGABM 2114	$n = 10$	Kozhevnikovo, Ob River PM TGU no. 62/2	PM TGU 1/51	Chulym River, village of Ezhi[1] 1/153	Chulym River, village of Sergeevo PM TGU 18/128	Shegarka River, village of Babarykino PM TGU 1/53	Kiya River, village of Shinyaevo PM TGU 1/157
Length to apex of occipital crest along straight line	835	806	648	743	706	708–797	830	840	830	–	705	820
Condylobasal length	739	664	611	655	617	–	765	670	720	–	602	695
Dental row length	235	213	190	200	201	198–244	239	208	–	220	223	–
Ratio of M row to P row lengths						–	154/97	132/80	–	145/83	139/88	–
Rostral width	86?	83?	64?		107	–	117	135	118	–	97	115
Width of anterior orbital part	324	253	196	244	236	213–257	C290	358	302	–	247	–
Width at temporal narrowing	95	92	71	67.4	68	55–104	121	136	125	–	111	120
Greatest width at zygomatic arches	361	358	306	360	344	320–360	C347	375	~339	–	327	330
Width at articular fossae						–	C321	364	322	–	320	322
Width at occipital crest (from above)						–	247	246	207	–	173	215

Table 2. (Contd.)

Measurement, mm	Yakutia						Tomsk Region					
	Rusanov, 1968				Lazarev et al., 1998	Boeskorov, unpublished data	Shpansky, unpublished data	Shpansky, 2000	Shpansky and Pecherskaya, 2009			
	"C. a. pristinus" SVGU	*"C. jacuticus"* IGABM no. 311	*"C. a. humilis"* IGABM 104/5 862		Churapcha IGABM 2114	*n* = 10	Kozhevnikovo, Ob River PM TGU no. 62/2	PM TGU 1/51	Chulym River, village of Ezhi[1] 1/153	Chulym River, village of Sergeevo PM TGU 18/128	Shegarka River, village of Babarykino PM TGU 1/53	Kiya River, village of Shinyaevo PM TGU 1/157
Occipital width at mastoid tubercles						–	317.5	306	285	–	263	c262
Width of occipital condyles	176	168	152	152	158	152–178	159	167	167	–	145	164
Width at M3	216*	207*	172*	199*	197*	184–224*	–	212	–	195	184	–
Greatest choanal width						–	71	85	–	~66	68	–
Width of nasal septum near choanae						–	30	–	–	–	–	–
Height from base apex of nasal horn to palatine perpendicular to skull length						–	206	202	~195	–	170	188
Height near posterior edge of M3						–	221	228	–	–	179	199
Occipital depth from upper edge of foramen magnum	191	200	166	173	168	143–207	205	185	163	–	154	175

Table 2. (Contd.)

Measurement, mm	Yakutia						Tomsk Region					
	Rusanov, 1968				Lazarev et al., 1998	Boeskorov, unpublished data	Shpansky, unpublished data	Shpansky, 2000	Shpansky and Pecherskaya, 2009			
	“C. a. pristinus” SVGU	*“C. jacuticus”* IGABM no. 311	*“C. a. humilis”* IGABM 104/5 862		Churapcha IGABM 2114	$n = 10$	Kozhevnikovo, Ob River PM TGU no. 62/2	PM TGU 1/51	Chulym River, village of Ezhi[1] 1/153	Chulym River, village of Sergeevo PM TGU 18/128	Shegarka River, village of Babarykino PM TGU 1/53	Kiya River, village of Shinyaevo PM TGU 1/157
Height from lower edge of near posterior edge of condyles	254	269	234	223	241	217–270	270	260	253	–	226	267
Length of nasal notch							219	208	216	–	195	216
Its width							90	92	87	–	90	95
Length of nasal callosity under horn							280	280	279	–	205	265
Its width	153	145	151	126	162	–	166	188	179	–	130	164
Length of frontal callosity under horn							204	213	238	–	170	240
Its width							181	213	206	–	150	186
Width of foramen magnum							51	56	57	–	50	50
Height of foramen magnum							48	56	67	–	55	69
Palatal width from within between M3							63			85		
Palatal width from within between P2										44		

* Width at the level of M2 (Rusanov, 1968).

[1] The village of Ezhi is situated at the opposite end of the outcrop from the village of Sergeevo.

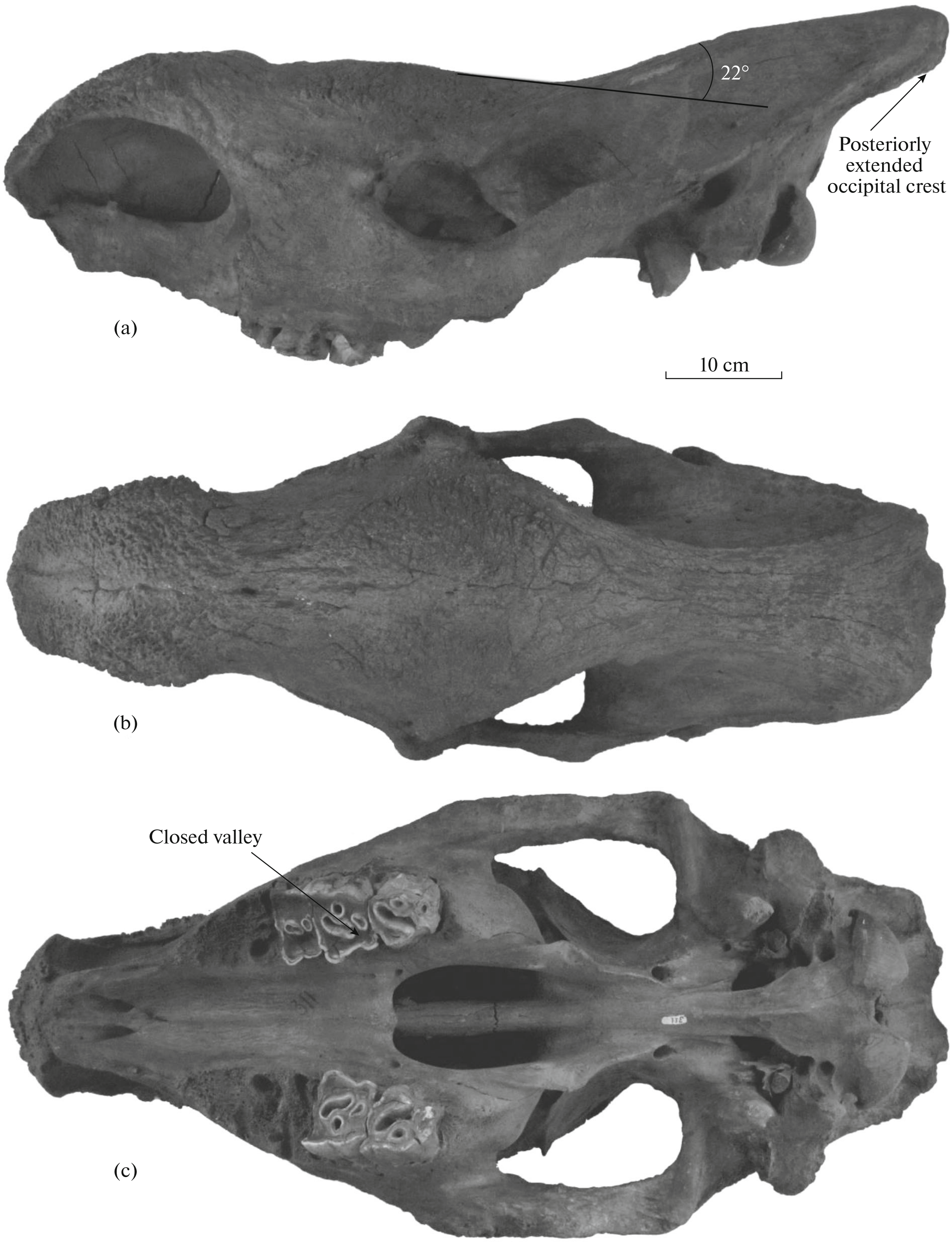

Fig. 4. Skull of *Coelodonta antiquitatis,* specimen IGABM, no. 311; Mamontova Gora locality, Aldan River (Yakutia): (a) lateral view, (b) dorsal view, (c) ventral view. Characters included in the diagnoses by Russanov (1968) and Lazarev (2008) are indicated.

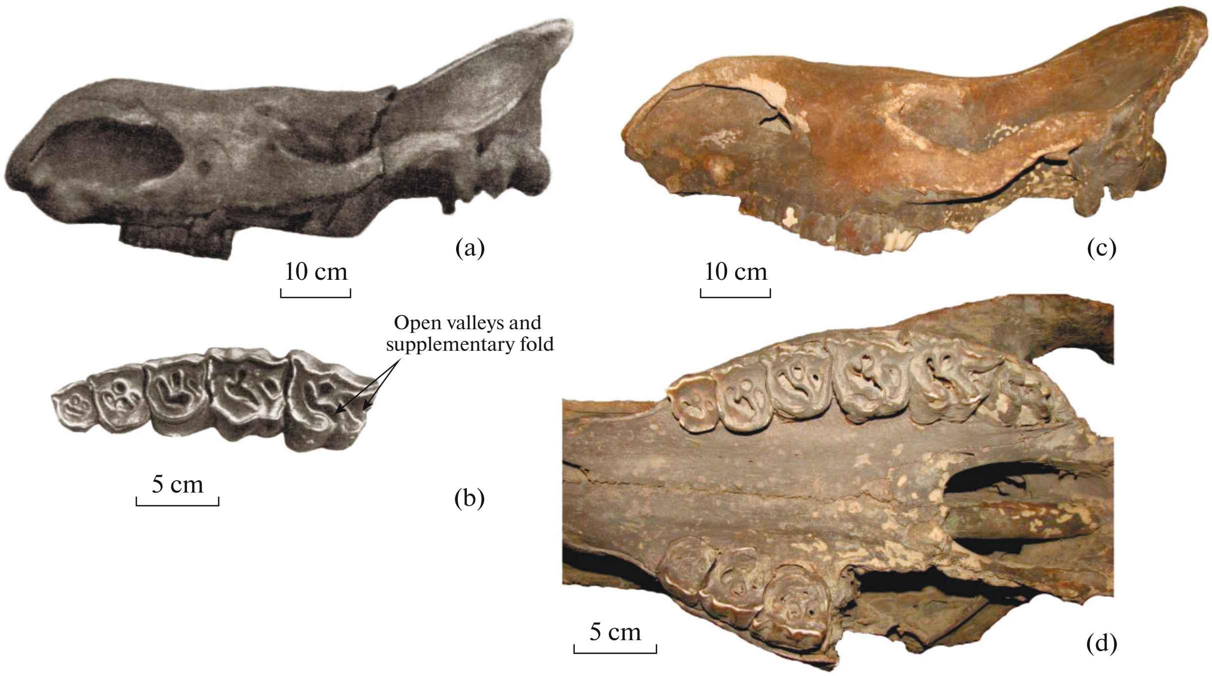

Fig. 5. Skulls of *Coelodonta antiquitatis* from the locality on the Milkere River (Yakutia): (a, b) specimen SVGU, without number (holotype of *Coelodonta antiquitatis pristinus* Russanov, 1968 after Russanov, 1968): (a) lateral view; (b) view of the occlusal surface of the left dental row; Kozhevnikovo (Tomsk Region), Ob River; (c, d) specimen PM TGU, no. 62/2; Late Neopleistocene: (c) lateral view, (d) view of the occlusal surface of the left dental row. The characters included in the diagnosis by Russanov (1968) are indicated.

skulls figured in this study, specimen GM KGU, no. 739 from the Middle Volga River (Garutt, 1998, text-fig. 1d) is most similar to our IGABM, no. 311. The parietal length (828 mm) is greater (806 mm) than in IGABM, no. 311. The study of large samples of skulls of *C. antiquitatis* from Siberia has shown that skull measurements of IGABM, no. 311 are within the range of intraspecific variation of skulls of *C. antiquitatis* Blumenbach (Table 2). The closure of the main and posterior valleys on M2, which was indicated by Russanov (1968) in the diagnosis as a distinctive character of the "Yakut rhinoceros" is connected exclusively with a significant individual age of IGABM, no. 311 and heavy wear of its teeth.[1] The photograph (Fig. 4c) shows that alveoli of P2 and P3 are already closed and M1 is worn almost to its roots. This state of dentition corresponds to the fifth age group of *C. antiquitatis*, i.e., adults and seniors after Shpansky (2014) or old animals after Borsuk-Bialynicka (1973).

The skull (specimen SVGU, without no.) designated by Russanov (1968) as the holotype of *Coelodonta antiquitatis pristinus* Russanov (Figs. 5a, 5b) has measurements and morphological structure typical for the nominative species *C. antiquitatis.* In particular, the skull measurements and M2 structure regarded as diagnostic characters correspond completely to the measurements and morphological characteristics of the skull PM TGU, no. 62/2 from Kozhevnikovo (Tomsk Region), which is similar in the extent of tooth wear (Table 2; Figs. 5c, 5d). A morphometric comparison of the holotype of *C. a. pristinus* with skulls of *C. antiquitatis* from localities of Siberia has shown that it belonged to a large male (Borsuk-Bialynicka, 1973). Its length (835 mm) is slightly greater than in other skulls from Yakutia (708–797 mm), but falls in the range of intraspecific variation of males of *C. antiquitatis* from the Ob River Region near Tomsk (820–840 mm) (Table 2). The large measurements of M2 (the crown is 57 mm long and 64 mm wide) regarded as a diagnostic character of the skull from Milkere is almost the same as the specimen from Kozhevnikovo (the crown is 59.3 mm long and 57.7 mm wide).

The skulls measurements provided by Russanov (1968) for the holotype and paratype of *C. antiquitatis humilis* Russanov fall in the range of intraspecific variation in skulls of females of *C. antiquitatis* (Table 2). Skull IGABM, no. 104/5 is the smallest known individual (the basal length is 648 mm) (Borsuk-Bialynicka, 1973; Lazarev et al., 1998; Shpansky and Pecherskaya, 2009). The basal length of female skulls varies from 650 to 770 mm. One of the smallest skulls from Yakutia belongs to a Churapcha rhinoceros (Lazarev

[1] During storage of the skull (IGABM, no. 311) after the publication of Russanov (1968), the buccal wall of left M3 was damaged (Fig. 4c).

et al., 1998); its basal length is 706 mm. The forearm bones included in the holotype also belong to a very small rhinoceros female. Its radius is 337 mm long, that is, considerably smaller than other specimens from Siberian localities: 374–382 mm for Yakutia (Lazarev et al., 1998), 344-424 mm for the Ob River Region near Tomsk (Shpansky, 2014). A smaller measurement (319 mm) is only known in a young female from the Podbaba locality in Czechia (Borsuk-Bialynicka, 1973).

Lazarev (2008) substantiated that *Coelodonta jacuticus* Russanov is a separate species, retaining the holotype designated by Russanov (1968), i.e., specimen YaNTs (presently IGABM), no. 311, a skull from a 50-m-high terrace of Mamontova Gora Hill on the Aldan River (Fig. 4). He also retained the age range of distribution of this species, Middle Neopleistocene. The point where the skull (specimen IGABM, no. 311) was found the in geological section Russanov (1968) obviously indicated incorrectly. He wrote that the skull of the rhinoceros no. 311 was found in situ on a 50-meter terrace of Mamontova Gora Hill in the Middle Pleistocene beds. Different researchers investigating this terrace indicated that its lower and middle strata belong to the Middle Neopleistocene (dated by the thermoluminescence method as 300000 ± 5700 and 176000 ± 2000, respectively); the upper strata consisting of covering loesslike loams is dated Upper Neopleistocene (with radiocarbon datings from 26800 to 44000). Just covering loesslike loams have yielded many bone remains of a Late Neopleistocene fauna: *Mammuthus primigenius* (Blumenbach, 1799), *Alces* sp., *Rangifer tarandus* Linnaeus, 1758, *Ovibos pallantis* Ham.-Smith, 1827, *Bison priscus* Bojanus, 1827, *Equus lenensis* Russanov, 1968, and *Coelodonta antiquitatis* (Blumenbach, 1799) (Agadjanian et al., 1973; *Neogenovye ...,* 1979). Agadjanian, investigating in detail Quaternary mammals from the Mamontova Gora locality, assigned all remains of woolly rhinoceroses from this locality to the Late Neopleistocene (Agadjanian et al., 1973). Thus, it is evident that the skull of *"C. jacuticus,"* specimen IGABM, no. 311 comes from the Upper Neopleistocene beds of the 50-meter terrace of Mamontova Gora Hill. The morphological identity of skulls of specimens IGABM, no. 311 and GM KGU, no. 739 from the Middle Volga Region and the Sartanian age (19500 ± 300, GIN-6030) of the Volga specimen also reject the Middle Neopleistocene age of specimen IGABM, no. 311.

Our morphological study of skulls of *C. antiquitatis* from localities of the Tomsk Region and Yakutia have shown that a significant posterior deviation of the occipital crest beyond the occipital plane, so that it overhangs the occipital condyles [diagnostic characters proposed by Russanov (1968) for the establishment of a separate taxon] is observed in old individuals with heavily worn M3 and closed alveoli of molars. The extent of deviation of the occipital crest beyond the occipital plane and the angles between the planes of the parietal and frontal vary within a wide range in the skulls of the same geological age. Therefore, it is plausible that these characters should be referred to as feature individual variation of *C. antiquitatis*. Thus, the characters proposed to be species-specific for *C. jacuticus,* should not be regarded as such.

Lazarev (2008) proposed to take YaNTs (presently IGABM), no. 400, lower jaw from the Mus Khaya outcrop (Yana River), which is redescribed below, for a paratype of *C. jacuticus*. In morphological characters and size, this jaw is typical for *S. kirchbergensis;* therefore, this specimen cannot belong to *C. jacuticus* or other species of the genus *Coelodonta*. Thus, Lazarev established the species *C. jacuticus* based on specimens belonging to different rhinoceros genera; hence, characters that he listed as diagnostic reflect morphological features of *C. antiquitatis* and *S. kirchbergensis* and may not be used in the diagnosis of the species *C. jacuticus*.

The diagnosis of the subspecies *Coelodonta antiquitatis humilis* was based on dimensions of the holotype and paratype: "The skeleton is less massive than in *Coelodonta jacuticus* Russ., the bones[2] are shortened. The skulls of females and males are less than 700 mm and 750 mm long, respectively; at most 200 mm wide at M2; with the dental rows less than 200 mm long. On the last molar (M3), a posterior valley is completely or almost completely absent; the main valley is closed (it is rarely slightly open only in at an early stage of tooth wear)" (Russanov, 1968, p. 218). The features of the M3 structure indicated by Russanov concern strongly worn teeth and are frequently observed in specimens of the fifth age group (Shpansky, 2014). Russanov (1968) did not compare morphological characters with other skulls. Our study has shown that the morphometric parameters of *C. a. humilis* fall in the range of intraspecific variation of *C. antiquitatis*.

In 2008, Lazarev revised the Yakut subspecies of the species *C. antiquitatis* and concluded that *C. a. pristinus* is invalid, since its holotype lacks collection number (only the depository was indicated: Northeastern Geological Department) and "description of the locality, measurements, and diagnostic characters corresponds to that of Middle Neopleistocene rhinoceros" (Lazarev, 2008, p. 51). The skull described by Russanov (1968) belongs to a large male, larger than specimens from Yakutia, but comparable is size to male skulls from Western Siberia (Shpansky, 2000). In fact, Russanov established the new subspecies incorrectly with reference to the International Code of Zoological Nomenclature. To date, the holotype of *C. a. pristinus* has apparently been lost. Russanov included tooth M2 (specimen IGABM, no. 603) from the upper strata of the Mamontova Gora section in the material of the subspecies *C. a. pristinus*. However, the

[2] From the description provided by Russanov (1968), it is evident that the "bones" mentioned by him are in fact fused radial and ulnar bones.

age of these strata has been determined as the Late Neopleistocene (Agadjanian et al., 1973).

Thus, the subspecies *C. a. pristinus* and *C. a. humilis* described by Russanov (1968) from Yakutia and also *C. jacuticus,* which was subsequently ranked by Lazarev (2008) as a separate species, are invalid, because their type specimens correspond in geological age and morphometric parameters to typical Late Neopleistocene *C. antiquitatis*.

M a t e r i a l. Skulls: specimen IGABM, no. 1, vicinity of the town of Vilyuisk, Vilyui River; specimen IGABM, no. 5, Rossypnoe outcrop on the Aldan River; specimen IGABM, no. 311, 50-meter terrace of Mamontova Gora Hill (holotype *Coelodonta jacuticus* Russanov, 1968). Skull: specimen SVGU, without number; Milkere River; specimen IGABM, no. 603, tooth M2, upper strata of the Mamontova Gora section (type of *Coelodonta antiquitatis pristinus* Russanov 1968). Specimen IGABM, no. 104/5, female skull; specimen IGABM, no. 104/3, forearm bones of one individual, covering loess of the Rossypnoe outcrop on the Aldan River; (holotype of *Coelodonta antiquitatis humilis* Russanov 1968). Specimen IGABM, no. 862, male skull, previously designated as a paratype of this taxon; Rossypnoe outcrop on the Aldan River. All specimens come from the Late Neopleistocene of Yakutia.

Stephanorhinus Kretzoi, 1942

Stephanorhinus kirchbergensis (Jäger, 1839)

Coelodonta antiquitatis jacuticus (partim): Lazarev and Tomskaya, 1987, pp. 76–79, pl. VI, fig. 5.

Coelodonta jacuticus (partim): Lazarev, 2008, p. 52, figs. 30a and 31a.

L e c t o t y p e. SMNS, no. 34000.3, left upper M2; Germany, Kirchberg; Middle Neopleistocene.

D e s c r i p t i o n (Fig. 6). Specimen IGABM, no. 400 is a well-preserved jaw of an adult animal. Judging from heavy worn crowns of p4 and m3 (Fig. 6), it is this rhinoceros was more than 35 years of age (Shpansky, 2014). The right ramus of the lower jaw is broken at the posterior edge of the alveolus of p3. In the left ramus of the jaw, the tooth row of p3–m3 is preserved. The jaw is 585 mm long from the rostral margin of the symphysis to the posterior margin of the articular process. The ventral margin of the horizontal ramus is almost even, without a convexity; the lower margin ascends very gently from the level of m1 to the symphysis, with an increase in the angle of inclination in the area of the symphysis. The rostral margin of the symphysis is damaged, but its morphological characters, such as significant narrowing (59 mm wide) and sulcate dorsal surface are distinct (Gromova, 1935; Shpansky, 2016). The horizontal ramus is almost constant in thickness throughout the dental row, with a slightly thinner segment under p3–p4. In the transverse plane, the horizontal ramus is highly oval in shape. The mental foramina (one large in the left jaw and two in the right jaw and also several small foramina) are located approximately under the alveolus of p2. The surface of the horizontal ramus posterior to m3 is wide (57.3 mm), flattened, with a relatively small longitudinal depression; the margins of the area are smoothly rounded rather than sharpened, as Gromova (1935) believed. The ascending ramus is wide; the muscle ridges on the buccal side of the angular region are well developed. The angular part is massive; on the medial side, the marginal part of the corner has a ridgelike surface. The posterior margin of the corner is in line with the posterior margin of the articular head. The medial margin of the postcondylar process is sharp in outline. Its posterior surface forms a wide area slightly concave on the lateral side and positioned almost perpendicular to the longitudinal axis of the jaw. In the woolly rhinoceros, such area is considerably smaller, triangular in outline, and positioned at a significant angle to the longitudinal jaw axis. The articular head is inclined relative to the horizontal plane; its medial margin is lowered and the buccal margin is raised. The premolars are positioned vertical to the alveolar margin of the horizontal ramus and the molars are inclined distinctly anteriorly (Fig. 6a). Tooth measurements are shown in Table 4. The molars row (m1–m3) is large, 158 mm long. Cement is present on tooth crowns near the roots; enamel is 1.5–2.6 mm thick, smooth. The external cingulum is well pronounced on the metalophids of all teeth and on hypolophids of m1 and m2. The internal cingulum is well developed on the metalophid of m1 and m2 and at the base of m3. The tooth crowns are somewhat wider at the root part than at the apex (due to a weak inclination of the buccal walls). In the woolly rhinoceros, tooth crowns are almost constant in width throughout their height. The metalophid of molars is shorter at the crown base than the hypolophid. The dental index (ratio between the m1–m3 and p2–p4 rows) is 152% on the lingual side.

M e a s u r e m e n t s. See Table 3.

R e m a r k s. The lower jaw from Mus Khaya is medium-sized. Morphological characters are similar to those in specimens from Western Siberia and Europe. The teeth are medium-sized for Merck's rhinoceros from localities of Europe: from Moldova, Volga Region, and Taubakh locality (Table 4), but considerably smaller than the teeth from Krasnyi Yar and Kindal (Tomsk Region). The m1–m3 molar row is longer than that of many European specimens (Table 3). In this measurement, the specimen from Taubakh is most similar (157.8–169.9 mm long: Kahlke, 1977). But the molar row is considerably shorter than in the jaw from Kindal (171 mm long) (Shpansky, 2016).

Initially, Lazarev (Lazarev and Tomskaya, 1987) referred this jaw to the woolly rhinoceros subspecies *Coelodonta antiquitatis jacuticus* Russanov. Subsequently, it was designated as a paratype of *Coelodonta*

Fig. 6. Lower jaw of *Stephanorhinus kirchbergensis,* specimen IGABM, no. 400: (a) buccal view and (b) occlusal side view.

jacuticus Russanov (Lazarev, 2008). The lower jaw of specimen IGABM, no. 400 is much larger than that of the woolly rhinoceros and shows a number of significant morphological differences in the shape and outline of the horizontal ramus and symphysis and in the measurements and structure of teeth. In the sulcate dorsal surface of the symphysis it distinctly differs from a wide and flat symphysis of *C. antiquitatis.* The middle part of the horizontal ramus lacks a convexity of the ventral margin, which is observed in the lower jaw of *C. antiquitatis.* In the transverse plane, the horizontal ramus is high oval, whereas in adult *C. antiquitatis,* the horizontal ramus is pear-shaped, with a thickening in the ventral part. The morphological characters indicated by us and the measurements of this jaw and teeth are typical for *S. kirchbergensis* and, consequently, this specimen cannot belong to *C. jacuticus* or the genus *Coelodonta.*

Material. Specimen IGABM, no. 400, lower jaw; Mus Khaya locality, lower reaches of the Yana River, Yakutia; lower Middle Neopleistocene.

DISCUSSION

Paleoecological and Paleozoogeogeographical aspects of the life of *Stephanorhinus kirchbergensis* in Yakutia. Structural features of teeth and lower jaw symphysis give evidence of feeding of the Merck's rhinoceros on leaves and vegetative shoots of bushes and young trees (Gromova, 1935). An indicative feature is structural specialization of the symphysis and angular part of the jaw. The symphysis is narrow, spoon-shaped, with a significant longitudinal concavity of the dorsal surface. This shape of the symphysis combined with a narrow rostral part of the skull allowed the animal to grasp tightly vegetative shoots of plants and to tear off leaves. The diagonal position of the

Table 3. Lower jaw measurements in two-horned rhinoceroses

Measurement, mm	*Stephanorhinus kirchbergensis* Jager							*S. etruscus* Falc.	*Coelodonta antiquitatis* Blum.			
									Western Siberia, Tomsk Region (Shpansky and Pecherskaya, 2009)			Yakutia
	Mus Khaya IGABM no. 400	Kindal (Shpansky, 2016)	Moldova *n* = 3 (David, 1980)	Chernyi Yar *n* = 2 (Gromova, 1935)	Dmitrov GIN without no. (Alekseeva, 1977)	Mosbach (Schroeder, 1903)	Shennongjia (Tong and Wu, 2010) QIII	Mosbach (Schroeder, 1903)	Kargasok PM TGU *n* = 3	SergeevoPM TGU 18/1	Tomsk Region TOKM, *n* = 6	*n* = 5 (Boeskorov, unpublished data)
Length from anterior edge of alveolus of p2 to posterior margin of ascending ramus	488	510	480–486	478–510	–	465	–	425	c450–458*	445	c426–482*	393–433
Length from posterior edge of alveolus of m3 to posterior margin of ascending ramus	211	221	221–254	210–250	–	180–251	–	183–190	–	222	–	–
Length and thickness of symphysis	C121.4/ 60.4	–	–	153–165/–	–	–	106.4–127.2/–	95–125/–	126/(20–26)	137/49	119/18–36.5	122–138/–
Length of dental row p2–m3 (at alveoli) sin/dex	266/–	289	272–290	255–283	–	275–282	–	222–245	219–225	229	218–238.3	196–216
Length of dental row p2–p4 (at alveoli) sin/dex	108/–	116	110–122	108–118	–	123	–	99–104	81	88.5	83–87.5	–
Length of dental row m1–m3 (at alveoli) sin/dex	158/–	171	157–168	151–163	–	157	151.5	138–140	131–132	143	136–144	–
Mandibular depth at p2 sin/dex	90/–	92?	–	90–109	–	–	–	–	50–79	72	49.7–90	60–85

Table 3. (Contd.)

Measurement, mm	*Stephanorhinus kirchbergensis* Jager							*S. etruscus* Falc.	*Coelodonta antiquitatis* Blum.			
									Western Siberia, Tomsk Region (Shpansky and Pecherskaya, 2009)			Yakutia
	Mus Khaya IGABM no. 400	Kindal (Shpansky, 2016)	Moldova $n = 3$ (David, 1980)	Chernyi Yar $n = 2$ (Gromova, 1935)	Dmitrov GIN without no. (Alekseeva, 1977)	Mosbach (Schroeder, 1903)	Shennongjia (Tong and Wu, 2010) QIII	Mosbach (Schroeder, 1903)	Kargasok PM TGU $n = 3$	SergeevoPM TGU 18/1	Tomsk Region TOKM, $n = 6$	$n = 5$ (Boeskorov, unpublished data)
Depth between m1 and m2 sin/dex	111.2/–	108	–	–	113	–	81.6–101.8	–	85–94	108	83–97	–
Depth posterior to m3 sin/dex	122.8/–	115	107–123	121–129	111	108–127	89.3–107.7	80–115	90–108	115	95.5–113	103–110
Thickness of horizontal ramus under m3 sin/dex	62.6/–	66	61–69	62–77	74	–	–	57	52–73	71 (max 73)	56–63.8	–
Width of posterior margin of angular region	66	c54	70–74.5	68–72		–	–	–	–	46.5	–	–
Width and diameter of articular surface of pr. condylaris	117.8/28	123.5/32.5	116–123/–	112–134/–		124/–	–	95–103/–	82/17	109/28	93/20	89–103/-
Height of ascending ramus to upper edge of pr. condylaris	282	~270	273–286	260–290		–	–	–	c245	241	–	–

* Length from incisive edge to posterior angle of jaw.

Table 4. Lower teeth measurements in *Stephanorhinus kirchbergensis*

Measurement, mm	Mus Khaya IGABM no. 400	Kindal KF MINS KP-397 (Shpansky, 2016)	Krasnyi Yar PM TGU (Shpansky and Billia, 2012)	Koshkurgan (Khisarova, 1963)	Shennongjia (Tong and Wu, 2010)	Moldova $n = 3$ (David, 1980)	Chernyi Yar $n = 2$ (Gromova, 1935)	Dmitrov (IV sluice) (Alekseeva, 1977)	Poland, ZIN 10743 (Gromova, 1935)	Taubach (Kahlke, 1977)
Length/ width of p2	28.6*/21.4*			32–33.1/15.5	30.5–33.5/ 18.7–20.5	33–34/22.2–26				34.4/23.3
Length/ width of p3	34.5/26.9	40/30		32/–	34.5–36.8/ 25.9–28.6	38–40.5/30–31				39.6–43.7/ 30.4–30.6
Length/ width of p4	44.4/31.9	43.5/35.3			42–43.4/30–32.7	45–46/32–34.5	41/33	45/34	43.5/34.2	41.4–45.2/ 32.8–35.8
Length/ width of m1	48.3/37.1	53.5/37.5	>54/38.7 5-3/1087 dex	54/35	41.8–47.9/ 33.1–37	49–51.3/ 38.2–38.5	45/33	53.5/37.5	48.2/36	46.2–51.8/ 36.3–38.1
Length/ width of m2	52.3/37.6	58.5/35.5	60.6/42.4 5-3/1067 sin	60–62/36–47	51.8–56.5/ 34.6–36.3	52–58/37–39	52–53/ 35–39.5		50/38.5	52.6–60.5/ 36.8–40.2
Length/ width of m3	55.0/35.6	59.5/35.5	63.2/37.3 5-3/3328 sin	47–63/32–42(?)	52.1–60.4/ 32.6–35.7	55–58.1/36–37	59–61.5/ 35–40.3		C60/35.5	55.3–61.8/ 35.8–37.4

* Alveolar.

articular process in relation to the sagittal plane of the horizontal ramus allowed complex movements of the jaw for chewing vegetative food. The significant longitudinal concavity of the occlusal surfaces of upper molars M1–M3 are evidence of a significant role of anteroposterior (longitudinal) movements of the lower jaw (Shpansky and Billia, 2012; Shpansky, 2016). It is plausible that the relatively wide and generally large lower teeth are connected with the treatment of food in the mouth and intended for slowing down the tooth wear. In the woolly rhinoceros, lateral grinding movements of the jaw prevailed, as evidenced by the perpendicular position of the articular process and the flat occlusal surface of the upper buccal teeth. The expanded posterior margin of the angular jaw part allows the development of massive musculature (m. masseter and m. pterygoideus internus) to clench its teeth. This structure of the jaw and teeth in Merck's rhinoceros suggests that it had not only grinding, but also crushing feeding type. Palynological data on the Kemyulken Formation, which enclosed the jaw of *S. kirchbergensis,* suggest that there was temperate climate and forest–tundra and tundra–steppe vegetation in northern Yakutia at the beginning of the Middle Neopleistocene. Therefore, penetration of this species along river valleys into the Far North of Eastern Siberia during the Tobolsk Interglacial appears quite natural.

In the Middle Neopleistocene, Merck's rhinoceros had a huge geographical range from Western Europe to southern Siberia and northeastern China (Billia, 2011; Shpansky, 2017). The find of the Merck's rhinoceros described by us is the fourth East Siberian occurrence. Localities on the Chondon and Yana rivers in Yakutia (70°12′ N, 137° E and 70°43′ N, 135°25′ E, respectively) are the northernmost known points (Fig. 1). In Western Siberia, the northernmost record is the lower jaw from the northern Tomsk Region (59°08′ N, 80°35′ E; Shpansky, 2016, 2017). The assignment of the jaw described from the Yana River to Merck's rhinoceros expands considerably the knowledge of the geographical distribution of *S. kirchbergensis* in Eastern Siberia and shifts the northern boundary of its range north of the Polar Circle.

Stratigraphic distribution of *Stephanorhinus kirchbergensis* in Siberia. To fate, the following three localities of remains of *Stephanorhinus kirchbergensis* have been found in Yakutia: on the Vilyui River (Dubrovo, 1957), on the Chondon River (Kirillova et al., 2017), and on the Yana River, i.e., the jaw described above. Two upper teeth described by Dubrovo (1957) from alluvial deposits on the Vilyui River are typical in size and structure for *S. kirchbergensis.* In her opinion, should be dated as the terminal Lower Pleistocene–basal Middle Pleistocene. Near the teeth of Merck's rhinoceros, there were fragmentary teeth of *Parelephas wüsti* (M. Pawl.) (=*Mammuthus trogontherii* Pohlig). The tooth measurements of the elephant provided by Dubrovo (1957), that is 5.5 plates per 10 cm of the crown length and 2–2.5-mm-thick enamel, correspond to the Khasarian elephant *Mammuthus trogontherii chosaricus* Dubrovo; in our opinion, this suggests that it was not older than the beginning of the Middle Neopleistocene. From tooth cavities of the skull from the Chondon River, plant remains were obtained, including Polaceae, grasses (Dicotyledones), mosses (*Aulacomnium* sp., *Polytrichum* sp.), Ericaceae, branches of willows (*Salix* sp.), birches (*Betula* sp.), and larches (*Larix* sp.) (Kirillova et al., 2016). This composition of remains suggests mixed feeding of *S. kirchbergensis,* which included grassy–leaf and tree–shrub vegetation. This vegetation was characteristic of these latitudes at the beginning of the Middle Neopleistocene (MIS9–MIS11). Shpansky (2017) concluded that a younger geological age (within 48–70 ka) proposed by Kirillova et al. (2017) for northern Yakutia is incorrect. During the Molotkovo Time (MIS3), this territory was covered by tundra landscapes, which were unsuitable for *S. kirchbergensis.* In our opinion, all paleontological records in the territory of Yakutia should be dated the first half of the Middle Neopleistocene (MIS11–MIS9), which was most favorable ecologically for the existence of this specialized animal. At that time it was a member of the East Siberian Faunal Assemblage (Fig. 2). Within Western Siberia, Merck's rhinoceros dwelt for a longer time. The most ancient specimen of *S. kirchbergensis* found in Siberia is a lower jaw from a locality near the village of Dal'nee (Akmolinsk Region, northern Kazakhstan). It comes from the Zhunshilik Formation, which is dated the second half of the Early Neopleistocene (MIS15–MIS16) (Shpansky, 2017). The geologically youngest specimen comes from Bed 6 of the Krasnyi Yar locality (Novosibirsk Region) on the Ob River (Shpansky, 2017). Vasiliev (2005) proposed that the age of the deposits enclosing the lower jaw of *S. kirchbergensis* and skulls of *Mammuthus trogontherii chosaricus* Dubrovo corresponds to the Kazantsevo time of the Late Neopleistocene (MIS5).

CONCLUSIONS

The lower jaw of specimen IGABM, no. 400 is reidentified as *S. kirchbergensis* and, hence, the taxonomic position of some rhinoceros taxa from Yakutia is questioned; this concerns *C. jacuticus,* which Lazarev (2008) regarded as a separate species, and subspecies of the woolly rhinoceros: *Coelodonta antiquitatis pristinus* Russanov, 1968 and *C. a. humilis* Russanov, 1968. As a result of our revision, the above listed taxa are synonymized under the nominative species *Coelodonta antiquitatis* Blum. Thus, in the Middle Neopleistocene, Yakutia was inhabited by two species of two-horned rhinoceroses, *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis,* and, in the Late Neopleistocene, there was only *Coelodonta antiquitatis.*

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