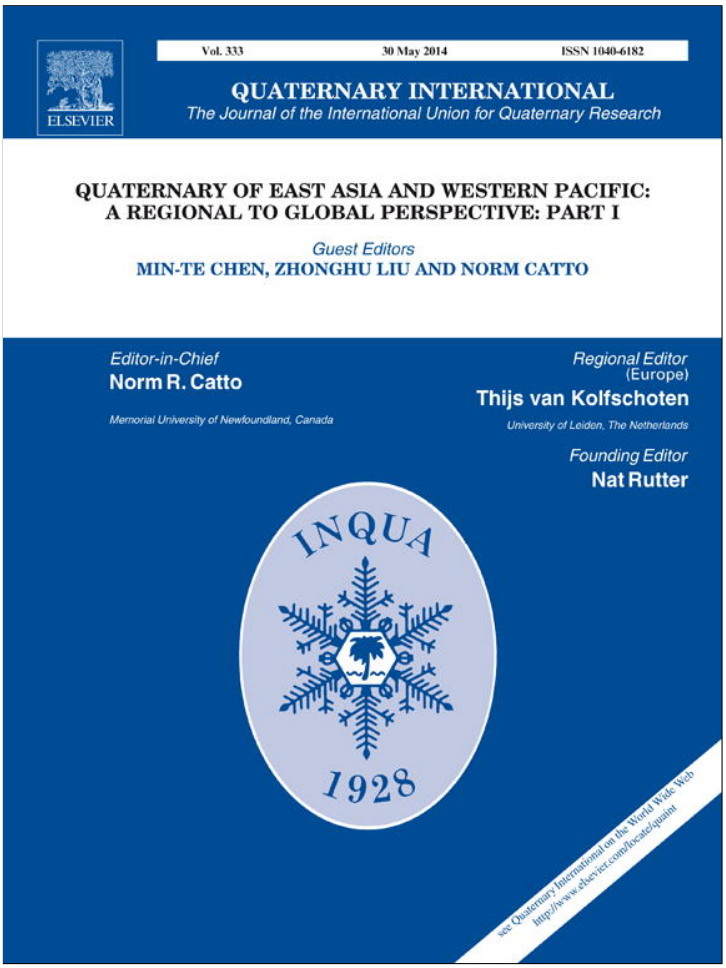

Quaternary International 333 (2014) 86–99

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Juvenile remains of the "woolly rhinoceros" *Coelodonta antiquitatis* (Blumenbach 1799) (Mammalia, Rhinocerotidae) from the Tomsk Priob'e area (southeast Western Siberia)

A.V. Shpansky

Tomsk State University, Geology and Geography, Prospect Lenina 36, 634050 Tomsk, Russia

ARTICLE INFO

Article history:
Available online 23 February 2014

ABSTRACT

Ontogenetic studies based on fossil mammals are rather scarce, including for the "woolly rhinoceros" *Coelodonta antiquitatis* (Blumenbach 1799). In this paper, for the first time, the earliest age stages (from 6 months to 3.5 years) of *C. antiquitatis* have been studied on the basis of several lower jaw fragments and limb bones from two Late Pleistocene sites along the Ob' (at Krasny Yar and near Kargasok) in the Tomsk Priob'e area (Tomsk region, southeast Western Siberia). As opposed to other mammalian species (e.g. mammoths), the absence of great concentrations of *C. antiquitatis* juvenile remains (possibly due to the palaeoecological features of this taxon) has to be emphasized. Finds of skulls, jaws, and isolated milk molars are very rare, particularly in those cases of individuals younger than three years. Therefore, the remains from Krasny Yar, belonging to individuals characterized by different ages, represent a unique case.

A large series of osteological material on the mandibles with functioning milk teeth and forming permanent teeth, belonging to calves from 6 months to 3.5 years of age, is described. For the first time, a large series of *C. antiquitatis* tubular bones of different individual ages (from birth to adulthood) is described, and the order and age of epiphysis adhering is revealed. The proportions of tubular bones (ratio between epiphysis and diaphysis) remain the same in stages 3–5 of individual progress (over 3 years of age). An assumption about *C. antiquitatis* sizes in different ontogenetic stages and the rate of growth is made. The body size for one-month-old calves is approximately 72 cm in shoulder height and about 120 cm in length. Well-known ontogenetic studies concerning modern African rhinoceroses (*Diceros bicornis* L. 1756 and *Ceratotherium simum simum* [Burchell, 1817]) as well as other ontogenetic studies performed on *C. antiquitatis* juvenile dental material have also been taken into consideration in this paper.

1. Introduction

Juvenile skeletal remains of the woolly rhinoceros are rarely found, much less commonly than mammoth juvenile remains. Finds of rhinoceros juvenile skeleton fragments of an age of about 6 years as well as remains of *Coelodonta antiquitatis* (Blumenbach 1799) of about 12 years from Yakutya (Lazarev et al., 2010; Boeskorov, 2012) are well-known, even if the size of a new-born and a sucking-rhinoceros remains unknown, at least at present. As a general rule, works mainly concern jaws with primary teeth (Garutt, 1992; Shpansky and Billia, 2006).

Ontogenetic studies based on fossil mammals are rather scarce, including for the "woolly rhinoceros" *C. antiquitatis*. As opposed to other mammalian species (e.g. mammoths), the absence of great concentrations of *C. antiquitatis* juvenile remains (possibly due to the palaeoecological features of this taxon) has to be emphasized. Finds of skulls, jaws, and isolated milk molars are very rare, particularly in the cases of individuals younger than three years.

In this paper, for the first time, the earliest age stages (from 6 months to 3.5 years) of *C. antiquitatis* have been studied on the basis of several mandibular fragments and limb bones found in two Late Pleistocene sites along the Ob' situated in the Tomsk Priob'e area (southeast Western Siberia). The remains from one of the two sites (Krasny Yar), belonging to some individuals characterized by different ages, represent a unique case.

E-mail address: shpansky@ggf.tsu.ru.

http://dx.doi.org/10.1016/j.quaint.2014.01.047
1040-6182/

In the present study, rather well-known ontogenetic studies concerning the living African rhinoceroses, the "black rhino" *Diceros bicornis* L. 1756 (Schaurte, 1966; Dittrich, 1974) and the "southern white rhino" *Ceratotherium simum simum* (Burchell, 1817) (Hillman-Smith et al., 1986) have also been taken into consideration, as well as other ontogenetic studies performed on a large amount of *C. antiquitatis* juvenile dental remains which were carried out by Garutt (1992, 1994). The results of this research showed that development, eruption phases, and teeth replacements differ slightly and essentially coincide. Garutt (1992, 1994) developed a technique of definition of individual age on the basis of degree of wear on examined teeth. The author defined 10 age stages, noting the lack of material of the earliest age stages, corresponding to the age of sucking young animals (from 1.5 months to 1.5 years).

Sciences indicate an age of about 25,650 ± 420 BP (SB RAS-5201)–18,505 ± 215 BP (SB RAS-5555), which may be correlated with the Karginsky–Sartansky horizon (Western Siberian regional stratigraphy). As for the palaeontological site near Kargasok, a Late Pleistocene age (Karginsky horizon, in the Western Siberian regional stratigraphy; MIS 3) is ascertained. Both the stratigraphical positions and the specific structures of the two sites have previously been described by Shpansky (2003, 2006).

The material is housed in the Palaeontological Museum collections of Tomsk State University in Tomsk, and consists of eight *C. antiquitatis* juvenile upper and lower jaw fragments, and 31 limb bones (radii, ulnae, tibiae, and metapodiali) (Table 1). Documentary data of the IPEE 3751-35 lower jaw from the Shirokostan Peninsula (Laptev Sea) (Garutt, 1992) are used for comparison.

Table 1
Researched material on *Coelodonta antiquitatis* from Krasny Yar in age groups, collected from 1991 to 2012.

Bones	Embryo and new-born	Juvenile 3 years old	Juvenile 3–7 years old	Young adult 7–14 years old	Adult species older than 14 years old	%*
1. Skulls and their fragments		2			1	0.8
2. Mandibles		4	2	1		1.8
3. Teeth		1			69	17.5
4. Vertebra: 64 (total)						16.0
Cervical				4	27	
Thoracic				1	18	
Lumbar				3	8	
Sacral					1	
Caudal					2	
5. Ribs (+sternum)					9	2.3
6. Scapulae					6	1.5
7. Humerus			2	1	4	1.8
8. Ulnae				2	12	3.5
9. Radius	1		2	6	11	5.0
10. Carpals				1	46	11.8
11. Metacarpals		2		1	21	6.0
12. Pelvis	1				1	0.5
13. Femur					1	0.3
14. Patella					6	1.5
15. Tibia + fibula		1	1	1	9	3.0
16. Astragals					40	10.0
17. Calcaneal					28	7.0
18. Tarsus					12	3.0
19. Metatarsus		1			14	3.8
20. Phalanges: 12 (total)						3.0
First					4	
Second					5	
Third					3	
Total (minimal number of species):	2 (1?)	11 (4?)	7 (2)	21 (3)	358 (32)	399 (42)

The following abbreviations are used in the text: IPEE – A.N. Severtsov Institute of Ecological and Evolutionary Problems, Russian Academy of Sciences (Moscow); PM TSU – Palaeontological Museum of the Tomsk State University; TPU – Tomsk Polytechnic University; IDPMG – Institute of Diamond and Precious Metals Geology SB RAS (Yakutsk); ZAPUJ – Zoological Museum, Jagiellonian University (Krakow, Poland); TOKM – Tyumen Regional Museum of Local History (Tyumen).

2. Sites, geological ages, and material

Part of the material was found along the Ob' at Krasny Yar village (about 105 km north of Tomsk, in Krivosheino district, Tomsk Region). The remaining material comes from the same river near Kargasok (about 400 km northwest of Tomsk, in Kargasok district, Tomsk Region) (Fig. 1).

As far as the Krasny Yar palaeontological site is concerned, ^{14}C data provided by the Siberian Branch of the Russian Academy of

3. Description of the odontological and postcranial material

A detailed description of the *C. antiquitatis* juvenile odontological and postcranial material from Krasny Yar and Kargasok is given below.

3.1. Odontological material

PM TSU 5/3312 – a maxillary fragment on which only the second deciduous molar (D^2) and the third deciduous molar (D^3) are preserved (Fig. 2). Apart from the anterior portion of the D^3 ectoloph, both teeth are well-preserved and not very worn. Palatally, before the D^3, a part of the D^1 alveolus is also preserved.

PM TSU 5/3313 – a maxillary fragment with the D^3 only (Fig. 2), very well-preserved and only a small part of a worn tooth. After the D^3, the D^4 vestibular alveoli are present. Under the vestibular-mesial root, the maxillary foramen was observed.

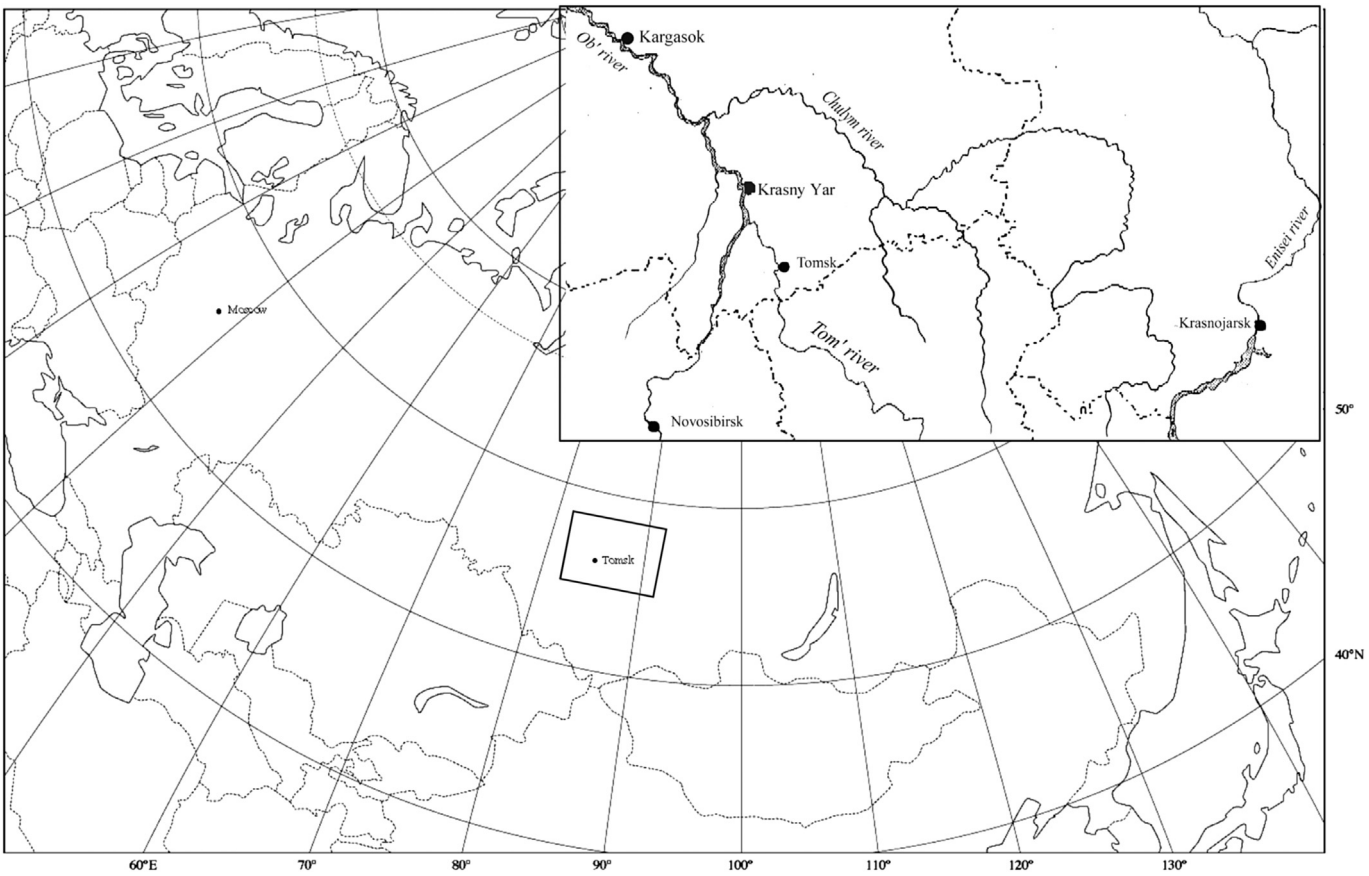

Fig. 1. Sketch showing the geographical localization of Krasny Yar (Krivosheinsky district) and Kargasok (Kargasoksky district) in Tomsk Region (southeast Western Siberia).

PM TSU 5/2588 – a mandibular horizontal branch fragment, very low with thin walls (Fig. 2), preserving the D_1 and the D_2 deciduous molar alveoli. The D_3 and the D_4 were growing. After the D_4, the anterior portion of the first permanent molar (M_1) alveolus is also present. On the D_3 only the exterior part of the parastilid and the back of the hypoconid show signs of initial wear. The D_4 is coming out from its alveolus, and only the metaconid and the protoconid are overhanging the jaw. The root system was not developed. The maximum length of D_3–D_4 is 81.5 mm. The alveolus for M_1 has porous walls with relief, which indicates the initial formation stage of the tooth. The mental foramen is under the back part of the D_3 alveolus. The branch height at the level of the back edge of the D_3 alveolus is 40 mm, and its thickness is 30.5 mm.

PM TSU 11/32 – a horizontal lower jaw branch fragment with the D_2 and the D_3 (max length = 66.3 mm) damaged at the symphysis and after the D_3 alveolus (Fig. 2). The D_3 is more erased than the D_3 on the 5/2588 specimen, but a little bit less than the D_3 on the 5/2351 lower jaw fragment (on which the D_4 was growing up, see below). On this basis, the D_4 development was at an intermediate stage. Possibly the whole occlusal surface of the tooth was developed and the root system was starting its formation process. The two mental foramina are situated under the D_1 alveolus; the distance between them is 13 mm. The medial surface of the symphysis form indicates incomplete fusion of lower jaw branches and remaining synchondrosis between horizontal branches. Ventrally, the horizontal branch appears greater in comparison with the 5/2588 specimen. The branch height at the level of the back edge of the D_3 alveolus is 44 mm, while its thickness is 32.6 mm.

PM TSU 5/2351 – a mandibular horizontal branch fragment preserving the D_3 and the D_4. This last tooth was growing in the lower jaw before D_3 was lost (Fig. 3). The third premolar (P_3) formation is evident under the D_3 even if the P_3 root system was not generated, and its future occlusal surface presents rounded outlines and is not enameled (Fig. 3). The D_3 lies at an eruption initial stage, while the D_4 was still growing up. The maximum length of the D_3–D_4 complex is 83.5 mm. Occipitally, the great cavity for the M_1 formation is preserved. The horizontal branch appears to be larger than those of both the 5/2588 and 11/32 specimens, but smaller than that of the 5/1269 mandibular fragment. The branch height at the level of the back edge of the D_3 alveolus is 56 mm, while its thickness is 39.5 mm.

PM TSU 5/1269 – a horizontal lower jaw branch fragment – the biggest one among the five lower jaw branch fragments – preserving the D_2, the D_3, and the D_4 (Fig. 3). The teeth were in a phase of initial degree of deletion (particularly D_2 and D_4) and are densely adjoining. The maximum length of the D_2–D_4 series is 98 mm. Both the D_1 and the M_1 alveoli were preserved. The M_1 alveolus is represented by a wide and deep cavity provided by smooth walls which indicates that the first molar was in a formation stage. The morphology of the lower portion of the alveolus would indicate that the root system was starting its formation process. The mental foramen is between the D_1 and D_2 alveoli. The horizontal branch appears rather large and dense; the ventral part shows a remarkable thickness. The height of the jaw at the D_3 level is 70 mm, the greatest thickness at the same level is 42 mm. In the frontal part of the symphysis there is a large alveolus (round shape, upward) of a cutting tooth (I_1).

PM TSU 5/4811 – a horizontal lower jaw branch fragment. The fragment is a right horizontal branch with remaining D_2–D_4 (Fig. 3). The jaw is broken anteriorly along the symphysis, and a part

Fig. 2. *Coelodonta antiquitatis* (Blumenbach 1799); Late Pleistocene (Karginsky–Sartansky horizon, in regional stratigraphy; MIS 3–2); Ob' at Krasny Yar (Krivosheino district, Tomsk Region, southeast Western Siberia); maxillar fragment (PM TSU 5/3312) with the second and the third deciduous molars, (1) occlusal view and (2) vestibular view; maxillar fragment (PM TSU 5/3313) with the third deciduous molar, (3) occlusal view and (4) vestibular view; mandibular fragment (PM TSU 5/2588) with the third and the fourth deciduous molars, (5) buccal view and (6) occlusal view; Late Pleistocene (Karginsky horizon, in regional stratigraphy; MIS 3); Ob' River, near Kargasok (Kargasok district, Tomsk Region, southeast Western Siberia); mandibular fragment (PM TSU 11/32) with the second and the third deciduous molars, (7) buccal view and (8) occlusal view.

of the diastem and the D_1 alveolus was preserved. The jaw is broken along the back edge of the M_1 alveolus. The D_1 alveolus is represented by two holes of considerable sizes. The D_2–D_4 teeth are in the initial stage of showing wear. The general length of primary teeth D_2–D_4 is 96.8 mm (including alveolus D_1 – 117.5 mm). The M_1 alveolus is a deep cavity with smooth walls and a flat bottom. The form and condition of the M_1 alveolus indicate a forming tooth and the most initial stage of M_1 teething. The main part of the tooth crown was in its alveolus and the root system was not formed. The mental foramen is on the level of the back edge of D_1 alveolus. The horizontal branch is rather large, and the lower part has a non-significant thickening. The jaw height under D_3 is 59 mm, while the greatest thickness is 40 mm. The general condition of individual jaw development is close to the PM TSU №5/1269 specimen.

PM TSU 5/553 – a left mandibular horizontal branch fragment without teeth (Fig. 4). The teeth alveolus is well-preserved. Their form indicates which teeth had functioned and which ones were still in the teething process. In the jaw, alveolus walls of the five constant P_2-M_2 teeth remained. The alveolar socket of back root D_1 also remained. The P_2 alveolus consists of two well-formed sockets, but a barrier between them is considerably lower (~10 mm) than the upper edge of buccal alveolus wall, which means incomplete teething. The main part of the buccal wall of the P_3 alveolus is smooth, set in its tooth crown, but the alveolus is expanded at the top. The alveolus bottom is divided into a well-detached radicular cavity; this indicates that the tooth root system was developing, as well as the initial stage of teething. The primary D_3 was absent in the jaw. The P_4 alveolus is narrowing at the top and has a smooth concave bottom with open gnathic canals. The primary D_4 continued to function in the jaw, and the P_4 was at the stage of crown forming. The M_1 alveolus consists of two parts corresponding to tooth roots, demonstrating its high place and brygmus.

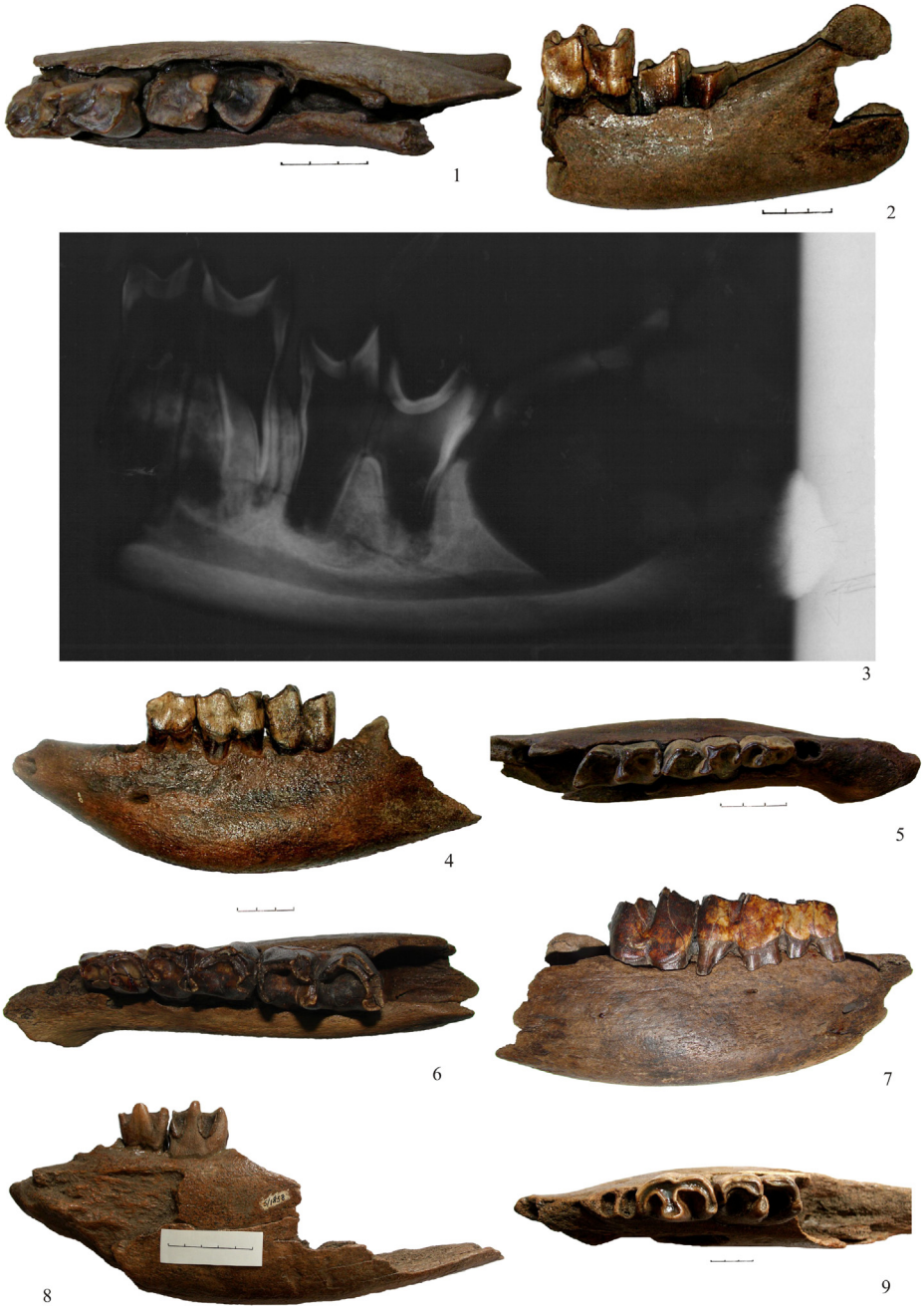

Fig. 3. *Coelodonta antiquitatis* (Blumenbach 1799); Late Pleistocene (Karginsky–Sartansky horizon); Ob' River at Krasny Yar (Krivosheino district, Tomsk Region, southeast Western Siberia); mandibular fragment (PM TSU 5/2351) with the third and the fourth deciduous molars, (1) occlusal view, (2) buccal view and (3) roentgenogram; mandibular fragment (PM TSU 5/1269) with the second, the third and the fourth deciduous molars (4) buccal view and (5) occlusal view; mandibular fragment (PM TSU 5/4811) with the second, the third and the fourth deciduous molars (6) buccal view and (7) occlusal view; mandibular fragment (PM TSU 5/1858) with the third and the fourth premolars, (8) buccal view and (9) occlusal view.

The M_2 alveolus reflects the primary stage of teething. Its root system had not been formed: root sockets were just forming and the jaw canal is open. The alveolus walls are vertical without narrowing at their top, suggesting the start of the rising of the chewing surface over the superior edge of the alveolus. Therefore, the jaw belongs to an animal that died in the period of its active primary-permanent teeth replacement. The dental formula may be presented as follows:

$$p2\frac{d3^{?}}{p3\uparrow}\frac{d4}{p4\uparrow}m1m2\uparrow$$

On the basis of the teeth ratio, the jaw belongs to a young animal about 3–3.5 years old, corresponding to the third age stage proposed by Garutt (1992).

PM TSU 5/1858 – a horizontal lower jaw branch fragment with the P_3 and the P_4 (Fig. 3). The P_3 is scarcely worn, while the P_4 is in its initial stage of deletion. The metaconid is separated from the protoconid. The P_3 length is 34 mm, its width is 23 mm. The P_4 length is 40 mm, its width is 24.5 mm. The maximum P_3–P_4 complex length is 72.5 mm. The P_2 alveolus and the anterior portion of the M_1 one are preserved. The mental foramen is under the P_2 alveolus. The horizontal branch is large and dense, the

greatest height under the M_1 is 103 mm, and its thickness at the same level is 55 mm. Some dimensions of the lower jaw are given in Table 2.

Young animals' radiuses are the most numerous from the group of tubular bones (Table 1). Among them there is a very little example of an embryo or a new-born animal, a diagonally

Table 2
Sizes of mandibles of *Coelodonta antiquitatis* calves from Tomsk Priob'e.

Measurement, mm	5/2588	11/32	5/2351	5/1269	5/4811	5/553
Individual age	6–10 months	1–1.5 years	1.5–2 years	2–2.5 years	1.5–2.5 years	3–3.5 years
Length of tooth row D_1–D_4	~130	84 (D_{1-3})		114.5	118	
Length of tooth row P_{2-4}						103
Length of tooth row P_2–M_2						C125
Jaw height in front of D_2/P_2	33.5	39		54	46	48.5
Height between D_3 and D_4/P3 and P_4	40	45	56	70	56.5	C65
Height behind D_4/P_4	52.5		61	63	60	C71
Thickness of a horizontal branch on the level of D_4/P_4	32.5	C35	39.4	42	39.8	~52

A very well-preserved and rather well-developed isolated first upper molar (PM TSU 5/3489) was not yet ready to come into use. It was certainly still preserved inside its maxillary bone. Its walls appear fairly thick, smooth, bright, and acovered by enamel. The bulbus pulparis is also remarkably developed. The tooth length is 41 mm, its width is 40 mm. Some dimensions of the teeth are given in Table 3.

damaged radius (PM TSU 5/1402) without both epiphyses (Fig. 6). Both the cranial and the caudal surfaces of the diaphysis are smooth. The first one is transversally rounded while the second one is flat and curved along its sagittal plane. Two radiuses are without epiphysis; although they have large ends and well-developed surfaces for connecting epiphysis, there was no accreting process. Considering the bone sizes and general

Table 3
Dimensions (in mm) of the *Coelodonta antiquitatis* upper and lower deciduous molars on the upper and lower jaw fragments coming from Krasny Yar and Kargasok, and from the Shirokostan peninsula (Laptev Sea).

Specimens	Individual age	D^1		D^2		D^3		D^4		
		L	W	L	W	L	W	L	W	Locality
PM TSU 5/3312	2.5–3.5 years	–	–	31.5	32.7	38.4	37	–	–	Krasny Yar
PM TSU 5/3313	2–3 years	–	–	–	–	39.5	37.5	–	–	Krasny Yar
		D_1		D_2		D_3		D_4		
Specimens	Individual age	L	W	L	W	L	W	L	W	Locality
PM TSU 5/1269	2.0–2.5 years	–	–	25	15	35	18.4	39	20	Krasny Yar
PM TSU 5/2351	1.5–2.0 years	–	–	–	–	39.5	19.6	43	19.8	Krasny Yar
PM TSU 5/2588	6–10 months	–	–	–	–	39	19	41.2	19.3	Krasny Yar
PM TSU 5/4811	1.5–2.5 years			23.5	15	34.7	19.4	39	21.7	Krasny Yar
PM TSU 11/32	1.0–1.5 years	–	–	27.7	15.3	38	20.7			Kargasok
IPEE 3751-35*	1.0–1.5 years	20	11	28	16	37	20	–	–	Shirokostan

D^1, D^2, D^3, D^4 = first, second, third, and fourth upper deciduous molars.
D_1, D_2, D_3, D_4 = first, second, third, and fourth lower deciduous molars.
L = length; *W* = width.

3.2. Postcranial material

From Krasny Yar, only three upper arm bones relate to young animals (Fig. 5). Two (PM TSU 5/4235 and PM TSU 5/3620) have relatively remarkable sizes (Table 4), even if they are much smaller in comparison with those of old species. The proximal epiphyses are extremely gnawed, considering that the lengths of the diaphyses are not completely represented. The large size PM TSU 5/2989 humerus has a not yet adherent epiphysis, but this is peculiar to the young animal group about 8–12 years in age.

development, one may suppose that they relate to young animals 3–5 years old (Fig. 6; Table 5). Six more bones have relevant sizes and connected proximal epiphysis. The epiphyseal joint between the proximal epiphysis and diaphysis is closely shagged, but clearly evident. The sizes of these bones (taking into account distal epiphysis) are relevant in comparison with the bones of adult animals, in length as well as in width (Figs. 6 and 7). In accordance with the features of these bones, one may suppose that they relate to young animals 10–14 years old in the stage of maturity.

Table 4
Sizes of humerus of young woolly rhinoceroses from Krasny Yar.

Collection number	Individual age	Measurement, mm[a]				
		1	2	3	4	5
PM TSU 5/4235 dex	Juvenile 5–7 years old	C160	C99	C59	52.5	
PM TSU 5/3620 sin	Juvenile to 7 years old	C183	C112	78	54	
PM TSU 5/2989 dex	Young adult 8–12 years old	265	C135	C80	68	C140
PM TSU (*n* = 4)	Adult	C365–452	153–170	120–131	77–88	203–225

[a] 1-diaphysis length; 2-distal end width; 3-medial diameter of distal end; 4-narrowest width of diaphysis; 5-width of proximal end.

Table 5
Sizes of radius bones of young woolly rhinoceroses from Krasny Yar.

Collection number	Individual age	Measurement, mm					
		1	2	3	4	5	6
PM TSU 5/1402 sin	Embryo or a new-born	127.5	35/19	C54	C34	51	30
PM TSU 5/4914 sin	Juvenile of 3–5 years old	223	47/26	C75	61	91.3	63.2
PM TSU 5/3633 dex	Juvenile of 3–5 years old	235	54/35	90	67.5	C94	C68
PM TSU 5/4915 dex	Young adult of 7–9 years old[a]	286	56/34	112	69.5	–	–
PM TSU 5/4030 dex	Young adult of 7–9 years old[a]	289.5	58/31.5	109	71	101	–
PM TSU 5/1639 sin	Young adult of 10–14 years old[a]	313	60/37	120	70	98	60
PM TSU 5/4032 dex	Young adult of 10–14 years old[a]	314	60.7/40	118	78	108.5	72
PM TSU 5/4913 sin	Young adult of 10–14 years old[a]	320	55.5/37	C97	C69	92.5	–
PM TSU 5/1392 sin	Young adult of 10–14 years old[a]	330	63/45	120	76	110	70
PM TSU ($n = 9$)	Adult	344–424	58.4–71.3/37–48	104–122	68–89	107–130	64.5–82

1- diaphysis length (full length for adult); 2- width/diameter of diaphysis; 3- width of proximal end; 4- diameter of proximal end; 5- width of distal end; 6- diameter of distal end.

[a] Proximal epiphysis is connected, which is why measurements take it into consideration.

Fig. 4. Horizontal left branch of the PM TSU 5/553 lower jaw belonging to a young animal 3–3.5 years old.

Fig. 5. Humerus of a young *Coelodonta antiquitatis*, frontal view: 1 – PM TSU 5/4235, belongs to a young animal 5–7 years old; PM TSU 5/3620, belongs to a young animal 7 years old; PM TSU 2989, belongs to a young specimen 10–14 years old.

Metapodial bones of young animals are represented by three metacarpal bones and one metatarsale IV. A second metacarpal [Mc II] (PM TSU 5/2722) with the proximal epiphysis but without the distal one (Fig. 8a) is also available. Its proximal articular surface is very well-preserved, while the medial one presents a damaged caudal protuberance. Another second metacarpal [Mc II] (PM TSU 5/864) is also large and can be compared in size with that of a mature animal (Fig. 8b), but it has no adherent epiphysis. In the place of epiphysis attachment, a distal surface of the diaphysis has four outstanding lumps, shifted to diaphysis edges and divided by grooved hollows. It possibly belongs to an individual 10–12 years old and may relate to the group of young animals. A third metacarpal [Mc III] (PM TSU 5/178) with very well-preserved proximal epiphysis (articular surface included), but without the distal one (Fig. 8c) was also collected. The two medial articular surfaces appear rather damaged. As opposed to the two other specimens, 5/2722 (see above) and 5/2460 (see below), the bone is very dense and its dimensions are close to those of the adult rhinoceroses. A left fourth metatarsal [Mt IV] (PM TSU 5/2460) with a very well-preserved proximal epiphysis but without the distal one (Fig. 8d) was also found. Its proximal articular surface as well as both the medial and the latero-caudal ones are very well-preserved. Some dimensions of the above mentioned metapodials are given in Table 6. All metapodial bones, except for the PM TSU 5/864 s metacarpal, are not of large size and they might relate to young animals 3 years old.

Table 6
Dimensions (in mm) of the *Coelodonta antiquitatis* juvenile postcranial remains coming (=metapodial) from Krasny Yar.

Specimens	*L*	APPD	TPD	DW	DTh	APDD	TDD
Mc II PM TSU 5/2722	119	33	39.5	31.2	23.1	37.5	33.5
Mc II PM TSU 5/864	158	40	50	31	30	39	44
Mc III PM TSU 5/178	129	52	40	43	28	51	38.5
Mt IV PM TSU 5/2460	102.5	29.5	42	25.9	22.2	32	35

L = max length; APPD = antero-posterior proximal diameter; TPD = transversal proximal diameter; DW = min width of the diaphysis; DTh = thickness of the diaphysis; APDD = antero-posterior distal diameter; TDD = transversal distal diameter.

The wing of the left ilium of pelvis (PM TSU 5/3658) has a damaged edge, especially in the area of epiphysis and tuber coxae (Fig. 9). The ilium's collum is broken in front of the acetabulum. The collum's cross-section is of triangular form. In the medial side there is a little nutrient foramen at the bottom of the collum. The form of the wing of ilium is similar to the form of mature species. In the

Fig. 6. Woolly rhinoceros radius bones of different individual ages, frontal view: 1 – PM TSU 5/1402, belonging to an embryo at the last development stage or to a new-born; 2 – PM TSU 5/4914, belonging to a young animal 3–5 years old; 3 – PM TSU 5/3633, belonging to a young animal 3–5 years old; 4 – PM TSU 5/4030, belonging to a young animal 7–8 years old; 5 – PM TSU 5/4915, belonging to a young animal 7–8 years old; 6 – PM TSU 5/4913, belonging to a young animal 10–14 years old; 7 – PM TSU 5/4032, belonging to a young animal 10–14 years old; 8 – PM TSU 5/4031, belonging to a mature animal older than 14 years; 9 – PM TSU 5/3380, belonging to a mature animal older than 14 years.

medial side of the epiphysis, there is a space for a sacrum joint. The minimal collum's width is 45 mm, the cross-section is 28 mm, and the largest width of wing of ilium is 103 mm. On the basis of the bone's size, this may relate to a young animal 1 month old. The demonstrates the really late adherent process of the proximal epiphysis, which occurs after maturity. A joint line between diaphysis and distal epiphysis appears to be well-marked (Fig. 10c).

Table 7
Sizes of tibia of woolly rhino from Krasny Yar.

Collection number	Individual age	Measurement, mm[a]					
		1	2	3	4	5	6
PM TSU 5/2725 dex	Juvenile about 1 years old	170	86	C60.5	43.5/39.5	72	c51
PM TSU 5/4052 dex	Juvenile about 3–5 years old	235	106	C78	58.5/51	94	73
PM TSU 5/2701 dex	Young adult of 12–14 years old[b]	389	121	103	63/56	122	84
$n = 7$	Adult	335–438	C103–143	109–147	62–72/52–69.4	94–118	c73–90

[a] 1-diaphysis length; 2-proximal end width; 3-it's diameter; 4-minimal width/diameter of diaphysis; 5-width of diastal end; 6-it's diameter.
[b] Without proximal epiphysis.

common length of hip-bone could be 200 mm. A mature animal (from Seversk locality, Tom' river) shows the following dimensions: pelvis length – 640 mm, collum width – 83 mm, and the width of the wing of the ilium – 500 mm.

A well-preserved tibia PM TSU 5/2725 of a small size (Fig. 10a) presents large endings and the thin middle part of the diaphysis. The ill-developed relief of the surface joints with epiphysis means considerable meniscus and indicates a young individual, not more than 1 year old. The PM TSU 5/4052 tibia's surface of the joint with distal epiphysis has rather more relief and the same adumbrations as the articulation surface (Fig. 10b). The joint surface with proximal epiphysis is ill-developed. The general bone proportions refer to the PM TSU 5/2725 specimen, but the sizes are considerably larger, so they relate to a young animal 3–5 years in age. The very large sizes of the PM TSU 5/2701 tibia, corresponding to the sizes of a mature animal, relate to a young animal with non-adherent proximal epiphysis (Table 7). This

4. Discussion

4.1. Juvenile woolly rhinoceros mandibles

On the whole juvenile jaws, the third deciduous teeth (D_3) were retained, on the three other jaws the fourth ones (D_4) were retained (even if at different developmental stages), but on the two other jaws only the second ones (D_2) were preserved. On the basis of the horizontal branch dimensions, of the D_2 and D_3 degree of wear, the formation degree and the D_4 developments, among the five jaws the youngest one is represented by the 5/2588 specimen followed by the 11/32, the 5/2351, the 5/1269, the 5/4811, the 5/553 and the 5/1858. The first five teeth illustrate in detail the development of primary teeth at the juvenile stage of development of *C. antiquitatis*. The 5/553 specimen reflects the stage of the primary-permanent teeth replacement. The 5/1858 specimen belongs to a mature animal, in which the P_4 had just started to function.

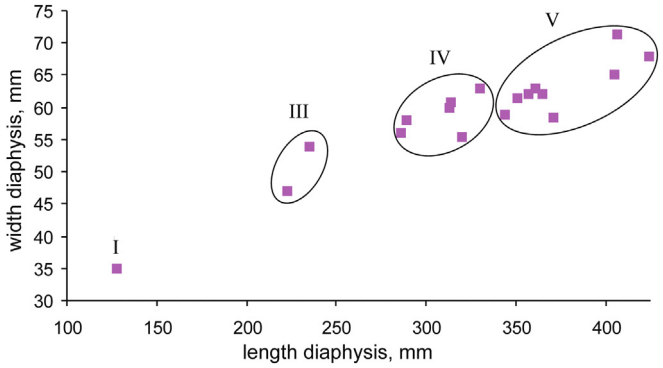

Fig. 7. Width and length correlation of the diaphysis of radius bones of *Coelodonta antiquitatis* from Krasny Yar.

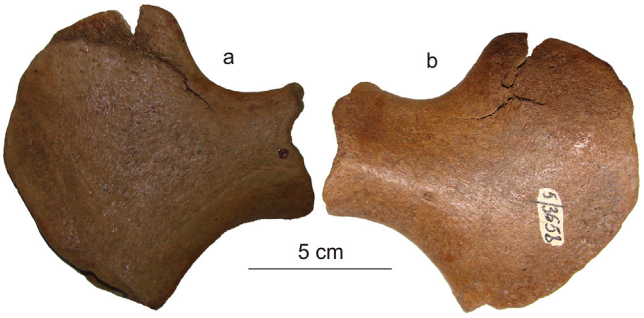

Fig. 9. Pelvis of a new-born *Coelodonta antiquitatis* (PM TSU 5/3658): a – medial view; b – lateral view.

The 5/2588 jaw belongs to the youngest individual because the D_3 was at the earliest stage of deletion and the D_4 just began to come out from its alveolus. Thus the jaw size is the smallest by analogy to the modern African rhinoceroses *D. bicornis* and *C. simum* (Dittrich, 1974; Hillman-Smith et al., 1986). The supposed individual age of the specimen is 6–10 months of postnatal development. The analyses and comparisons of the 11/32 and 5/2351 jaws are given below.

On the 5/1269 and 5/4811 jaws, the D_2 and the D_4 are in an initial stage of deletion while the D_3 is about 25% erased. The greater and well-generated alveolus for M_1 and the rather greater size of the jaw indicate that the age of this individual might be within the limits of 1.5–2.5 years. The 5/4811 jaw has somewhat more worn teeth than those on the 5/1269 jaw, but this difference is insignificant and they can be related to one age group. The presence of a well-preserved alveolus of the cutting tooth I_1 means that the woolly rhinoceros has rather huge forward cutting teeth in the juvenile stage. Mature individuals lose these teeth, and the alveolus gradually closes, representing barely noticeable hollows on the fore edge of simphysis. On the 5/1858 jaw, the P_4 had started to be erased, while P_3 is about 30% erased. The jaw sizes and the condition of the teeth indicate an animal age within the time span of 10–14 years.

On the five jaws, the D_3 is the most erased tooth, in advancing expulsion. The D_2 is a slightly less erased than the D_3. The D_4 expulsions begin later (5/2588 and 5/2351), but becomes level rather quickly with D_2 (5/1269). By this time, the D_3 is 30% erased, but the paraconid is not yet erased and not merged with the parastylid. On the milk molars, the valleys are deep and traces of cement are not present on them, unlike on the P_4 of young-adult individuals (5/1858) where the cement fills the edges of the valleys. On the D_3-D_4, the buccal walls of both metalofid and hypolophid are flattened, because their occlusal surface has sharp angular outlines. On these teeth, the posterior valley is deeper than the anterior one and has triangular outlines.

On both the 11/32 and 5/2588 jaws, the D_1 alveolus has considerably greater size than that on the 5/1269 specimen, the last one belonging to an individual of older age, indicating a D_1 gradual loss and the assumption of the alveoli. This indicates a slightly earlier D_1 expulsion, possibly about 7–9 months (cf. Garutt, 1992)

Fig. 8. Metacarpal and metatarsal bones of a young *Coelodonta antiquitatis*: a – PM TSU 5/2722 II metacarpal; b – PM TSU 5/864 II metacarpal; c – PM TSU 5/178 III metacarpal; d – PM TSU 5/2460 IV metatarsal.

Fig. 10. Tibiae of *Coelodonta antiquitatis* of various individual ages: a – PM TSU 5/2725, belonging to a young animal 1 year old; b – PM TSU 5/4052, belonging to a young animal 3–5 years old; c – PM TSU 5/2701, belonging to a young animal 13–14 years old; d – PM TSU 5/4053, belonging to a mature animal.

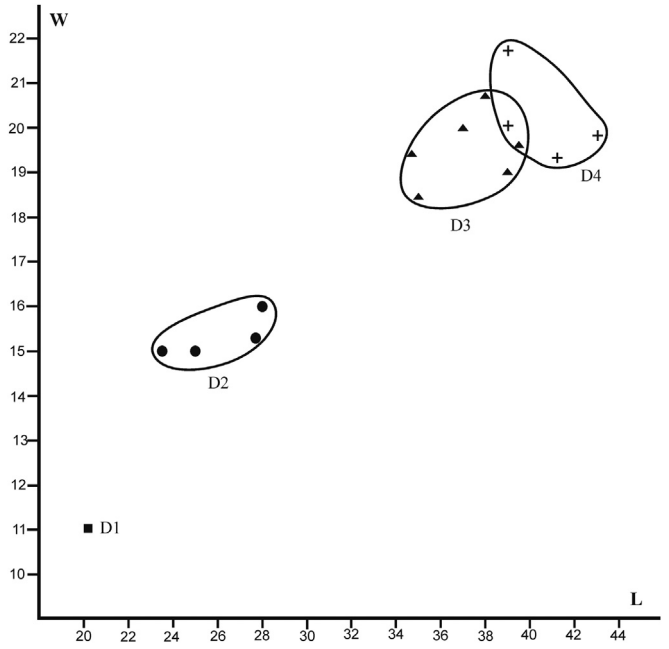

Fig. 12. Lower milk teeth distribution (D1, D2, D3 and D4) in length and width of the crown (in mm): W – crown's width; L – crown's length; measurements correspond to Table 3.

and the beginning of its functioning at least simultaneously with D_4 (probably, at 12–14 months). On the 5/1858 young-adult jaw, the D_1 alveolus is absent, and there is a small hollow from its back root in the jaw of the young animal 5/553 (Fig. 4).

Milk molar width indexes have been calculated, and the resulting graphics are very similar (Fig. 11), with the largest width ratio from the examples of all jaws being similar to D_2. The average relative width for the D_2 is 54.1-(58.9)-64.3%, while for the D_3 it is 49.5-(52.3)-55.5%, and for the D_4 is 47.8-(50.5)-55.1%. By comparison, the permanent teeth width indexes concerning adult animals from the Western Siberian plain are well-marked, with the relative permanent teeth width rather larger than primary ones. It is possible to assume that this distinction is connected with the fact that at the early stages of development young animals live on milk mostly that does not need "firm" crowns (high and wide). One more distinct feature could be the intensive growth of the animal and, as a consequence, rapid teeth change. In adult individuals the greatest relative width concerns P_3, whereas on the basis of this parameter P_2 and P_4 are very close. Among the molars, the greatest relative width concerning the M_1 noticeably exceeds those of the other molars. This feature is possibly correlated with the duration of functioning of these teeth on the mandible. P_3 and M_1 represent the longest functioning teeth. The division of lower primary teeth in length and width of the crown for *C. antiquitatis* (Fig. 12) is similar to *Stephanorhinus kirchbergensis* (Jager, 1839) from Taubach (Kahlke, 1977). A feature of both kinds is a clear separation of D_1 and D_2 and shut-off parameters for D_3 and D_4. Parameters for permanent teeth for both kinds have a considerable shut-off and have no clear distinctions.

Mental foramen on the second stage of ontogenesis shifted from alveolus D_1 to under alveolus D_2. At the stage of primary teeth replacement on permanent and intensive growth in the area of diastema, the back mental foramen shifted forward to the area of trans-incisal narrowing. Intensive growth of the horizontal branch

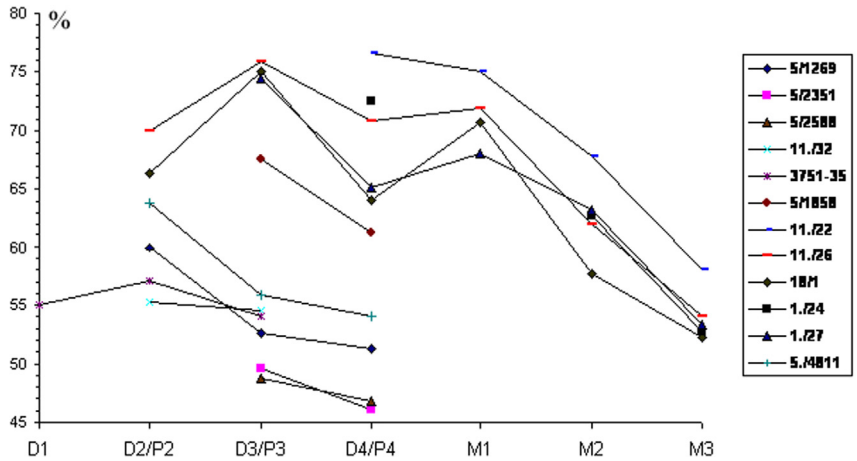

Fig. 11. Width index (width/length of the crown in %) of lower teeth of juvenile and mature species of woolly rhinoceros *Coelodonta antiquitatis* from Tomsk Priob'e. Examples' numbers are in the right column from the PM TSU collection: Krasny Yar – 5/1269, 5/1858, 5/2351, 5/2588, 5/4811; Kargasok – 11/22, 11/26, 11/32; Sergeevo – 18/1; Barlaka river, Lokot' village – 1/24, 1/27; Shirokostan Peninsula – IPEE 3751-35.

in height starts with the permanent before root teeth bud. The lower edge of the horizontal branch of a lower jaw of a juvenile *C. antiquitatis* has clearly marked bowed flection downward. It is one of the most significant features distinguishing *C. antiquitatis* from *S. kirchbergensis*. Moreover, primary teeth of all jaws have a typical structure for *C. antiquitatis*, and a harsh surface of enamel on the outer walls.

(from a new-born to young and adult individuals) from the location of Krasny Yar (Table 1) and some other places of Tomsk Region allowed assessment of some of the main features of structure and individual development of *C. antiquitatis*. The series of material described above (cranial remains, mandibles, and tubular bones of limbs) enabled identification of 5 age groups in the individual development of the woolly rhinoceros (Table 8).

Table 8
Stages of individual development of woolly rhinoceros *Coelodonta antiquitatis*.

Age stages according to Garutt (1992)	Proposed age groups and their morphological characteristics		
	Age group	Individual age (years)	Main morphological features
	1st group	Embryo and new born (up to 1 month)	Eruption and start of upper and lower D2–3; D1 functioning. D4 are still in alveoli
Juvenile S-I and S-II (1–3 years)	2nd group	Young animals (from 2.5 months up to 2.5–3 years old)	Only milk teeth are functioning in upper and lower jaws, forming of permanent teeth is taking place; cranial joints are mobile; diaphyses of tubular bones are growing intensively
Juvenile S-III (3–4 years)	3rd group	Young animals (3–7 years old)	Milk teeth are changed for permanent, M1 starts functioning, then M2, P4 and M3 are teething; cranial joints are not shagged, underplantar calluses are not developed well, flattened; tubular bone sizes are rather large, but epiphyses are not adherent
Sub-mature S-IV and S–V (8–15 years)	4th group	Young adult (7–14 years old)	The start of sexual maturity, by the end of the period P4 and M3 start functioning, upper P2 and P3 abrasion is close to the roots and can fall out, lower p2 and p3 are half-close to the roots, p4 is teething earlier than m3; cranial joints are shagging, but they are seen; underplantar calluses are scalloped, well-seen; epiphysis of tubular bones accreting is not simultaneous (one of the epiphyses, usually a proximal one, is accreting earlier); body growth is slow
Mature S-VI–X (15–45 years old)	5th group	Adult, older than 14	Abrasion of M3, intense abrasion of upper teeth P4 and M1, their falling out and alveolus closing at more than 35 years old; epiphysis joints are completely shagged; body growth is over

The above described lower jaws may be compared with the IPEE 3751-35 juvenile lower jaw preserving the D_1–D_4 (estimated age of about 1–1.5 years) found on the Shirokostan peninsula (east coast of the Laptev Sea) (Garutt, 1992). On the basis of the presence of all the milk molars and of the similar teeth erasing degree, it is possible to place this specimen between the 5/2351 and 5/1269 specimens from the Ob' at Krasny Yar. The D_4 of the IPEE 3751-35 specimen it was not affected by the erasing process, but reached the level of the chewing surface, whereas on the 5/2351 the crest of the D_4 protoconid had not reached the level of D_3. On the 5/1269 and 5/4811 specimens, the crests of both the protoconid and metastilid were affected by the erasing process. The milk molar sizes on the juvenile mandibular fragments from Western and Eastern Siberia are very close (Table 2). Furthermore, these mandibular fragments may be included in the S–1 general age stage, corresponding to 1–1.5 years. They correspond to young animals of the 2nd and 3rd age groups of individual development with a common age interval from 6 months up to 3.5 years (stage S 1–3 according to Garutt, 1992).

4.2. Some issues regarding the individual development of Coeledonta antiquitatis Blumenbach

The large number of woolly rhinoceros' remains (about 400 bones from a minimum of 42 individuals) of various individual ages

Examination of postcranial skeleton bones of *C. antiquitatis* from Krasny Yar represented by serial fragments of various individual ages allows assumptions about the size and rate of growth of the rhinoceros at different developmental stages. In fossil condition, diaphysis (sometimes damaged) is all that has remained from the tubular bones of a young rhinoceros. That is why in order to discover general size characteristics of a young rhinoceros, it is necessary to accomplish two consecutive tasks.

The first task is exploring the proportion of limbs' long bones (the ratio between diaphysis length, epiphysis length and total length of a bone): humerus, radius, femur and tibia. To accomplish this task, a series of material on tubular bones of young adult and mature animals (the 4th and the 5th age groups) with remaining epiphysis of different stages of epiphysis joints from Krasny Yar (Tomsk Region) was used (Table 9). The examination also includes bones with one joined epiphysis, because it enables evaluation of the ratio between diaphysis and one of the preserved epiphysis lengths. It appeared that the percentage ratio between diaphysis and epiphysis lengths of tubular bones of young adults and mature animals was the same. Absolute bone sizes were different, indicating that this ratio between diaphysis and epiphysis is constant for the individual development of the postcranial skeleton (Table 9).

Table 9
Radial bone proportions of adult woolly rhinoceroses from Krasny Yar.

№	Total bone length, mm	Diaphysis length, %	Proximal epiphysis length, mm	%	Distal epiphysis length, mm	%
5/4031	365	75.9	38	10.4	50	13.7
5/3380	344	77.0	33	9.6	46	13.4
5/117	424	76.4	37	8.7	63	14.9
5/1051	357	77.3	34	9.5	47	13.2
5/2012	371	78.4	30	8.1	50	13.5
5/2080	406.4	75.7	40	9.8	59	14.5
5/2454	350.6	75.4	37	10.6	49	14.0
Average		76.6		9.5		13.9

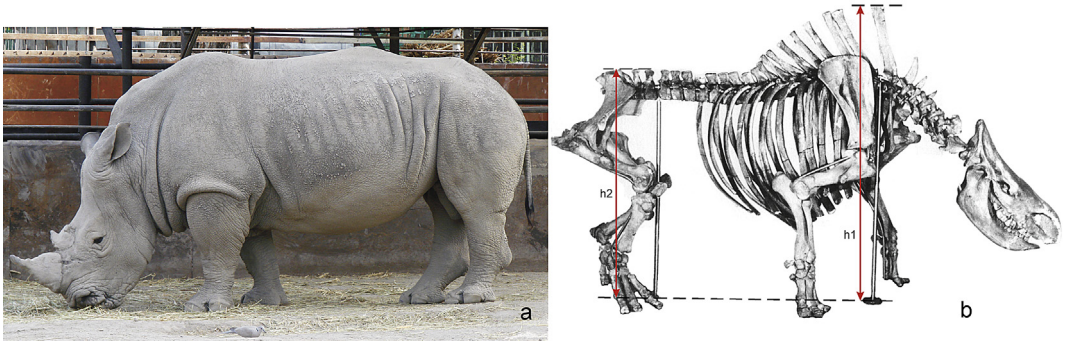

Fig. 13. Static pose of rhinoceros living in the field: a – "white rhino" *Ceratotherium simum* (Burchel), Alma-Ata Zoo (author's photo); b – skeleton of "woolly rhino" *Coelodonta antiquitatis* (Blumenbach), from Podbaba locality (Czech Republic), ZAPUJ 683 (from Borsuk-Bialynicka, 1973). h1 – skeleton height at the shoulder; h2 – skeleton's height at the sacrum. On the skeleton are several construction errors, which lead to the slightly lowered height at the sacrum.

The second task was a calculation of the ratio between limb parts' lengths and the height of woolly rhinoceros' skeletons at the shoulder and at the sacrum. A hypothesis that the correlation of limb parts of a woolly rhinoceros remains without significant changes throughout their lives was suggested. The examination of limb parts was based on published size characteristics and the length of several *C. antiquitatis* skeletons' long bones with various individual ages from Podbaba, Churapcha, Novokuznetsk, and Salairka (Table 10). The comparative limb parts' length of a young adult skeleton from Podbaba (ZAPUJ 683) was smaller than the length of a mature animal, which could create some difficulties during the assembling of the skeleton. These mistakes are noticeable in the back "fracture" between the 8th and 10th thoracic vertebras and angles between bones in knee, hip, elbow and scapular joints. As a result, the caudal part of the skeleton was pulled down and the back was too bent. For some skeletal bones from

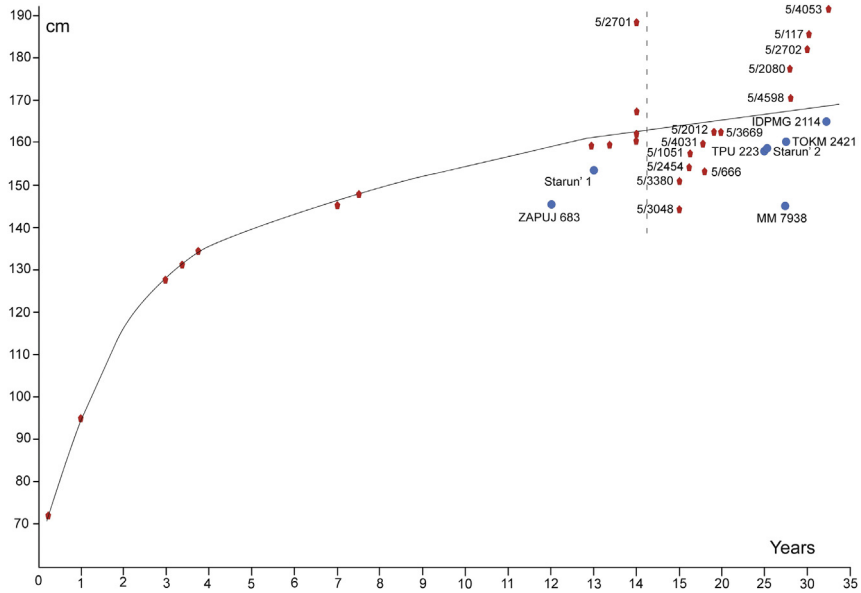

Fig. 14. The woolly rhinoceros' body height change is shown by the curve line according to the individual age, and also in accordance with materials from Krasny Yar (Tomsk Region). Skeletons and corpses from Europe and Siberia are marked with circles.

Novokuznetsk and Salairka, only absolute bone lengths are given. That is why their comparative lengths are overestimated and their average length calculations are not used. The skeleton height was estimated at the shoulder and at the sacrum in static pose (h1 and h2) (Fig. 13). To figure out the probable length of *C. antiquitatis* using the separate skeleton limb pairs available, the ratio between the physiological length (for scapula, humerus and femur), medical length (for radius and tibia) and the height of skeletons at the shoulder and at the sacrum was calculated. All calculations of sizes of young woolly rhinoceroses were made using a correlation of bone parts (diaphysis – epiphysis; Task 1), and a percentage ratio of skeleton limbs.

There were some difficulties in measuring limb proportions, as there are no measures of common length changes of a hand or a foot for skeletons in the literature. These measures were taken from a built skeleton of a Churapchian rhinoceros (IDPMG SB RAS (Yakutsk), sample №2114) with mummified preserved feet, kindly furnished by S.E. Grigoriev (a fellow of the Mammoth Museum, Yakutsk). Measurements from the bearing area to the distal edge of the radial bone and tibia were made respectively. Boeskorov (2012) gives some data of common sizes of woolly rhinoceros' corpses from Starun' and Yakutia. The measurements used here were much smaller than those of Boeskorov (2012). He measured full anatomy length from the wrist (of the foreleg) or ankle (of the hind leg) joints to the distal edge of the hoof's middle digit. There is an angle between the hand and foot bones and bearing area, which is why their total length will exceed the height to which they lift the animal's body.

The radial bone and shin bone are the most numerous in all age groups (Tables 5 and 7), which is why they were taken as the basic material. Based on the selection of woolly rhinoceros' bones from Tomsk Region, a stable ratio between diaphysis and epiphysis lengths for radial and shin bones of 4th and 5th age groups animals was obtained.

The length of proximal epiphysis of radial bone was measured from the caudal side, in the area where the epiphyseal cartilage has the highest position. The length of distal epiphysis was measured from the medial side, in the area where the epiphyseal cartilage has the lowest position. The mean relative length of diaphysis of the radial bone is 76.6%, proximal epiphysis - 9.5%, and distal epiphysis - 13.9% (Table 9). For sample PM TSU 5/2012, an overestimated length of diaphysis and underestimated length of proximal epiphysis were obtained because of morphological differences in the condition of the dorsal surface of the proximal epiphysis.

The relative length of the shin bone's diaphysis is 76.7%, proximal epiphysis - 14.2%, and distal epiphysis - 9.1%. On the basis of a number of tubular bones of the 4th age group, it was determined that proximal epiphysis joining takes place much earlier on the radial bone (at 7–10 years) than the distal one (about 12–14 years). Large shin bones have earlier distal epiphysis joining. There is not enough material to perform a similar examination of bones of the upper arm and thighbone.

Measurement of long bones' full sizes using preserved diaphyses and then young woolly rhinoceros body sizes from new born to adults produced the following relative sizes. For an animal aged from 1 month, the length of radial bone diaphysis (sample PM TSU 5/1402) is 127.5 mm, the bone's full length could be 166 mm, and the approximate height at the shoulder was72 cm (Fig. 14). A one-year-old rhinoceros's height at the shoulder (according to the size of shin bone sample PM TSU 5/2725) was 95 cm. The dynamics of growth of the length of tubular bones of rhinoceroses showed that the most intensive growth took place before the age of 3–4 years, reaching a shoulder height of 130 cm, after which there is a reduction in growth speed. By the age of 7–

Table 10
Extremity proportions of the woolly rhinoceros skeletons *Coelodonta antiquitatis*.

Location, sex assignment, collection number	Publication	Age group (age)	Skeleton height at the shoulder (H1), mm	Foreleg								Skeleton height at the sacrum (H2), mm	Hind leg							
				Scapula (physiological length)		Humerus (physiological length)		Radius (medial length)		Brush			Femur			Tibia (medial length)			Foot	
				mm	% for H1	mm	% for H1	mm	% for H1	mm	% for H1		mm	% for H1	% for H2	mm	% for H1	% for H2	mm	% for H1	% for H2
Churapcha (Sakha Republic, Russia) female, DPMGI SB RAS, №2114	Lazarev, 1998	5 (adult) 30–35 year	1630	512	31.4	418	25.6	377	23.1	280	17.2	1480	521	32.0	35.2	350	21.5	23.6	230	14.1	15.5
Podbaba (Czech Republic), sex?, ZAPUJ №683	Borsuk-Bialynicka, 1973	4 (young adult)10–12 year	1440	457	31.7	350	24.3	319	22.2	250	17.4	1255	452	31.4	36.0	296	20.6	23.6	200	13.9	15.9
Novokuznetsk (Kemerovo Region, Russia), male?, TPU №223–271	Alekseeva and Rjabchikova, 1974	5 (adult) 20–30 year	About 1570			398	25.4	396 (max)	25.2							371 (max)	23.6				
Salairka (Tyumen' Region, Russia), male, TOKM №2421	Bobkovskaya and Kosintsev, 2005	5 (adult) 25–30 year	1600	?		405	25.3	375	23.4				475	29.7		370 (max)	23.1				
Average					31.6		25.2		22.9		17.3			31.0			21.1			14.0	

10, young animals have body sizes similar to mature species, the height is about 140–150 cm at the shoulder, and further growth is connected with individual peculiarities of animals.

Certain young adults could have very large sizes, indicated by a very large shin bone (sample PM TSU 5/2701), whose length without proximal epiphysis is 389 mm. The length of this incomplete bone exceeds the sizes of mature animal's bones with both joined epiphyses. The calculated height of such an animal at the shoulder could be about 188 cm. The maximal size of adult woolly rhinoceroses of Western Siberia is 190 cm height at the shoulder (Fig. 14). These assumptions are corroborated by the remains of a very large individual found in the Chulym River (Shpansky and Pecherskaya, 2009).

Acknowledgments

The description of cranial remains and lower jaws was discussed with E. Billia (Rome, Italy), the majority of the material was developed with the participation of K.O. Pecherskaya, and the author expresses sincere gratitude to them for their help. The author is grateful to T.V. Chashchina for conducting X-ray work on one of the described mandibles. The author is grateful to S.E. Grigoriev, a fellow of the Mammoth Museum in Yakutsk, for measuring and providing the measurements of common lengths of feet and hands of the Churapchinsky rhinoceros.

References

Alekseeva, E.V., Rjabchikova, E.D., 1974. K voprosu o vozraste lyossovyh porod okrestnotey goroda Novokuznetska (On the question of the age of loess in the surroundings of Novokuznetsk city). In: Voprosy Geography Sibiry [Siberian geography issues, vol. 8. Tomsk State University, Tomsk, pp. 149–154.

Bobkovskaya, N.E., Kosintsev, P.A., 2005. Mammoth (*Mammuthus primigenius* Blum.) and Woolly Rhinoceros (*Coelodonta antiquitatis* Blum.) Skeletons from South of Tumen Region (West Siberia)//Ural and Siberia Faunas at Pleistocene and Holocene Times, pp. 56–80. Chelyabinsk: Rifei.

Boeskorov, G.G., 2012. Some morphological and ecological features of the fossil woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach 1799). Zoologichesky Zhurnal 91 (2), 219–235.

Borsuk-Bialynicka, M., 1973. Studies on the Pleistocene rhinoceros *Coelodonta antiquitatis* (Blumenbach). Palaeontologia Polonica 29, 94.

Dittrich, L., 1974. Beobachtungen zum Milchzahndurchbruch beim Spitzmaul – (*Diceros bicornis*) und Breitmaulnashorn (*Ceratotherium simum*). Säugetierkunde Mitteilungen 22 (4), 289–295.

Garutt, N.V., 1992. Ontogenez zubnoy sistemy sherstistogo nosoroga *Coelodonta antiquitatis* (Blumenbach, 1799) (Ontogenesis of dentition of "woolly rhinoceros" *Coelodonta antiquitatis* (Blumenbach, 1799)). In: Kuzmina, I.E., Baryshnikov, G.D. (Eds.), Istorya Krupnykh Mlekopitayushchikh i Ptiz Severnoy Evrazii, vol. 246. Rossiyskaya Akademiya Nauk (Zoologichesky Institut), St-Petersburg, pp. 81–102 ([Russian, English abstract]).

Garutt, N.V., 1994. Dental ontogeny of the "woolly rhinoceros" *Coelodonta antiquitatis* (Blumenbach, 1799). Cranium 11, 37–48.

Hillman-Smith, K.K., Owen-Smith, N., Anderson, J.L., Hall-Martin, A.J., Selaladi, J.P., 1986. Age estimation of the white rhinoceros (*Ceratotherium simum*). Journal of Zoology 210, 355–379.

Kahlke, H.-D., 1977. Die Rhinocerotidenreste aus den Travertinen von Taubach. Quartarpalaontologie 2, 305–359.

Lazarev, P.A., 1998. Skeleton of the Woolly Rhinoceros from the Churapcha//Mammals of the Anthropogene of Yakutia, pp. 55–97. Yakutsk.

Lazarev, P.A., Grigoriev, S.E., Plotnikov, V.V., 2010. Woolly rhinoceroses from Yakutia//evolution of life on the Earth. In: Proceedings of the IV International Symposium. TML-Press, Tomsk, pp. 555–558.

Schaurte, W.T., 1966. Beiträge zur Kenntnis des Gebisser und Zahnbaues der afrikanischen Nashörner. Säugetierkunde Mitteilungen 14 (4), 327–341.

Shpansky, A.V., 2003. Chetvertichnye Mlekopitayushchie Tomskoy Oblasti i ikh Znachenie dlya Ozenki Sredy Obitaniya (Quaternary mammalian remains from the Tomsk region and their value for an estimation of an inhabitancy). Izd-vo Tomskogo Gosuniversiteta [Tomsk State University Press], Tomsk, p. 162 ([Russian, English abstract]).

Shpansky, A.V., 2006. Quaternary mammal remains from the Krasny Yar locality (Tomsk region, Russia). Quaternary International 142–143, 203–207.

Shpansky, A.V., Billia, E., 2006. Remains of Juvenile "Woolly Rhinos" *Coelodonta antiquitatis* (Blumenbach, 1799) (Mammalia, Rhinocerotidae) from the Tomsk Ob' Region (Western Siberia)//Modern Paleontology: Classical and New Methods. PIN Russian Academy of Sciences, Moscow, pp. 103–108.

Shpansky, A.V., Pecherskaya, K.O., 2009. Pleistocene Large Mammals from the Sergeevo Locality, Chulym River (Tomsk Region)//Modern Paleontology: Classical and New Methods. PIN Russian Academy of Sciences, Moscow, pp. 103–115.