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Estimation of individual age and season of death in woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799), from Sakha-Yakutia, Russia

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ABSTRACT

A unique find of a woolly rhinoceros skull bearing both nasal and frontal horns is described from a thermokarst lake of the Bol'shaya Chukoch'ya River basin in north-eastern Republic of Sakha (Yakutia), Russia. Based on counts of cementum layers of the maxillary first molar and dark and transverse bands of the nasal and frontal horns a correlation of individual age records within these structures is established. Both estimations of individual age are agreed as well as three other age estimation criteria followed from cranial characteristics, general aspects of dentition and tooth wear pattern. Thus, the number of horn bands, which is equal to 30 or 31, does express the individual age at the moment when the woolly rhinoceros died. The tooth cementum and both horns are proved to be recording structures of woolly rhinoceroses which can be used as precise individual age estimation criteria. The season in which death occurred is also discussed.

1. Introduction

The horns of the woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799), are much more rare finds than any other hard parts of this mammal, including both cranial and postcranial complexes. This fact reflects an original composition of horns which are mostly keratinaceous structures and are easily separated from the skull. By their composition horns are comparable with other soft tissues and are best preserved almost exclusively in the permafrost with highest density as found in north-eastern Siberia [chiefly, the northern Republic of Sakha (Yakutia) and the western Chukotka Autonomous Okrug, the Russian Federation]. The only deviation of this pattern was the finds of some woolly rhinoceros horns and even entire mummies in an ozokerite "paleoswamp" of the fore-Carpathian region in western Ukraine. These finds were in relatively unusual taphonomic conditions containing a unique combination of clays, oil, and brine. These conditions provided a burial site favorable for soft tissue preservation (Bayger et al., 1914; Nowak et al., 1930; Kotarba et al., 2008). Horns which have been naturally uncovered during the summer permafrost melting are destroyed by natural weathering. It is also difficult to preserve these rare fossils during lengthy expeditions.

Nonetheless, the woolly rhinoceros horns have been well known for 230 years. These horns were originally described by Pallas (1769) from Siberia. Pallas was the first to introduce the term "filament" to denote an elementary unit of a horn which is today described as "fiber" or "tubule". Many years later, Siberian fossil horns were studied by Eichwald (1835) who was the first scientist to suggest a correlation between the number of transverse bands of a horn with the individual age of a woolly rhinoceros. This suggestion was refuted by Brandt (1849).

It was only in the last quarter of the 20th century that new investigations of woolly rhinoceros horns were pursued. Fortelius (1983) carefully examined a horn specimen of possible Siberian origin from the University of Helsinki Museum of Paleontology (Finland). He reproduced the original figures of Brandt (1849) and supported Eichwald's (1835) interpretation of transverse bands of horns as annual increments. Fortelius (1983) augmented Eichwald's opinion by references to Klevezal and Kleinenberg (1967) who compiled a significant set of data on the distinct appearance of annual increments in bones, tooth cementum and dentin in various large boreal mammals living in severe seasonal conditions. He also noted the presence of similar increments in the teeth of woolly mammoths and woolly rhinoceros, but could not prove his theory which warranted further studies. Later, some researchers considered that the number of paired dark and light zones (transverse bands) in woolly rhinoceros horns were indicative of an individual's age and the result of seasonal fluctuations in horn growth (Garutt, 1995, 1998). Horn development might also be interrupted when senility was reached (Chernova et al., 1998). Unfortunately, no scientist justified his/her position with any firm evidence. Moreover, growth increments might be periodic formations which do

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not indicate a specimen's age with precision. Even structures possessing apparent annual increments, such as tooth dentine and cementum, may get two layers during a year (Klevezal, 1988). Therefore, a much more complicated pattern of periodic increments is observed in some cases.

An examination of the maxillary first molar (M1) in the white rhinoceros, *Ceratotherium simum*, indicates that cementum layer counts corresponded approximately with age despite difficulties in interpreting lines due to their bifurcation in places. One pair of light and dark zone is normally formed each year (Hillman-Smith et al., 1986). However, this might not be the case for woolly rhinoceroses which lived in very different environmental conditions of the Ice Age high latitudes. A unique set of horns and skull of the same woolly rhinoceros allows us to clarify the nature of the horn's periodic banding pattern by comparing the number of dark and light paired zones with the number of annual layers in the cementum from a M1. We will also attempt to distinguish the season in which the animal died.

2. Materials and methods

2.1. Occurrences and preservation state

A complete skull with nasal and frontal horns belonging to the same woolly rhinoceros was recovered in 2008 from a thermokarst lake on the right bank of the Bol'shaya Chukoch'ya River in the Khallerchen Tundra [north-eastern Republic Sakha (Yakutia), Russia]. The sample moved to the lake during the summer permafrost melting. The geological age of the sample is the Late Neopleistocene. These specimens (F-2527, F-2528, and F-2529) are housed in the "Ice Age" Museum, Moscow, Russia.

The almost complete skull of F-2527 is in a very good state of preservation (Figs. 1C and 2A, B). The skull cavities bear relatively large pebbles and cases of recent caddis flies (Limnofilidae). Four teeth are preserved in the left maxilla (P4, M1–M3) (Fig. 1A, B) and two teeth are intact in the right maxilla (M1 and M2). The alveoli of the second premolars (P3) are almost occluded by bone tissue while those of the third premolars are not completely occluded (Fig. 1A). It is difficult to determine if these teeth were functional at the rhinoceros' death or were discarded from extreme wear. The attrition of the masticatory surfaces is significant especially that of P4 and M1 (Fig. 1A, B).

The nasal and frontal horns (F-2528, and F-2529, respectively) are almost complete and in a good state of preservation (Figs. 1C and 3B).

Transverse band patterns and horn preservation were compared to other woolly rhinoceros horns with well-expressed transverse banding from the collection of the "Ice Age" Museum:

The nasal horn (F-2361) from the Malyy Anuy River (c. 17 km upstream of the village of Anyuysk, Chukchi Peninsula), with only the axial part preserved, belonged to a young animal. This was determined by the small number of transverse bands (Fig. 3A);

F-370 and F-371 of the same specimen from the Terekhtyakh River valley (north-eastern Sakha-Yakutia) is unique in its completeness and excellent preservation although it is only a fragment of a midsagittal section of the nasal horn F-558 from the Drevniy gold mine in the vicinities of the village of Cherskiy (lower Kolyma River, Sakha-Yakutia).

2.2. Methods of individual age estimation

The individual age of the Bol'shaya Chukoch'ya River woolly rhinoceros was evaluated using four different age estimation criteria:

(1) cranial characteristics, especially conditions of sutures between skull bones;
(2) a general dentition pattern and the degree of attrition of tooth masticatory surfaces in comparison with the scale worked out by Hillman-Smith et al. (1986) for extant white rhinoceros;
(3) a general dentition pattern and the degree of attrition of tooth masticatory surfaces in comparison with the scale worked out by Garutt (1992a) for woolly rhinoceros;
(4) counts of the number of layers in the cementum of the maxillary first molar in accordance with the method developed by Klevezal (1988). The upper M1 tooth was impregnated with BF-2 (Bakelite-formaldehyde glue) and coated with polyepoxide. After this hardening M1 was cut in sagittal plane and polished. The resulting surface was examined by reflected light through the Leica StereoZoom 6 Photo microscope and photographed with a Nikon Coolpix 4 500 digital camera. The age of the tooth was estimated by counting the number of layers in the cementum of the dental root and interroot pad. The reliability of the results was evaluated against a 5-grade scale of results arrived at by successive counts of the number of layers in accordance with Klevezal's (1988) method. The M1 was selected for measurements, because this tooth erupted relatively early in the animal's life and grew continuously as established in extant white rhinoceroses (Hillman-Smith et al., 1986).

Regular growth increments of the nasal horn F-2528 were well-expressed for measurements and were selected for study. The number of transverse bands for both the nasal and frontal, horns (F-2528 and F-2529) was counted. Each band consists of two zones; they were counted according to their successive appearance in a different color, density, microrelief and state of preservation. In the nasal horn F-2528 the bands from 8th to 30th are more expressed while the previous apical ones are almost invisible (Fig. 3B). The counting and measuring of the bands were evaluated in the areas where they were more clearly expressed. This included the seven basal bands at the posterior surface of the horn and the following 16 bands of the anterior surface. Other bands were measured on the right horn facet in several series by using an oblique light installed at various angles to the facet surface in each successive series. The boundaries of bands and those of their subdivisions (zones) were marked by pins and measured with a millimeter-scale line. Precise measurements depended on the degree of expression of the band boundaries which decreased from the horn base to its apex.

2.3. Terminology

The term "recording structures" is applied in the following discussion. The term was coined for the structures of animals including bones, tooth dentine and cementum and the horny matter of claws and horns. It is believed that these recording structures are affected by changes in the physiological and morphological conditions during the formation of their newly formed parts. These changes are fixed in the appearance of such recording structures (Klevezal, 1988, 2007).

The tooth cementum increments are noted as "layers" while horn increments are called "bands." Each of the bands consists of two zones. One zone is lighter and more dense and the other is darker and looser.

We prefer the term "filament" following Pallas (1769) and Ryder (1962) to the term "tubule" which commonly suggests a hollow structure while the term "fiber" is commonly restricted to hair. These are the keratinaceous lamellar filaments which compose the bulk of a horn. These filaments are arranged in parallel along the

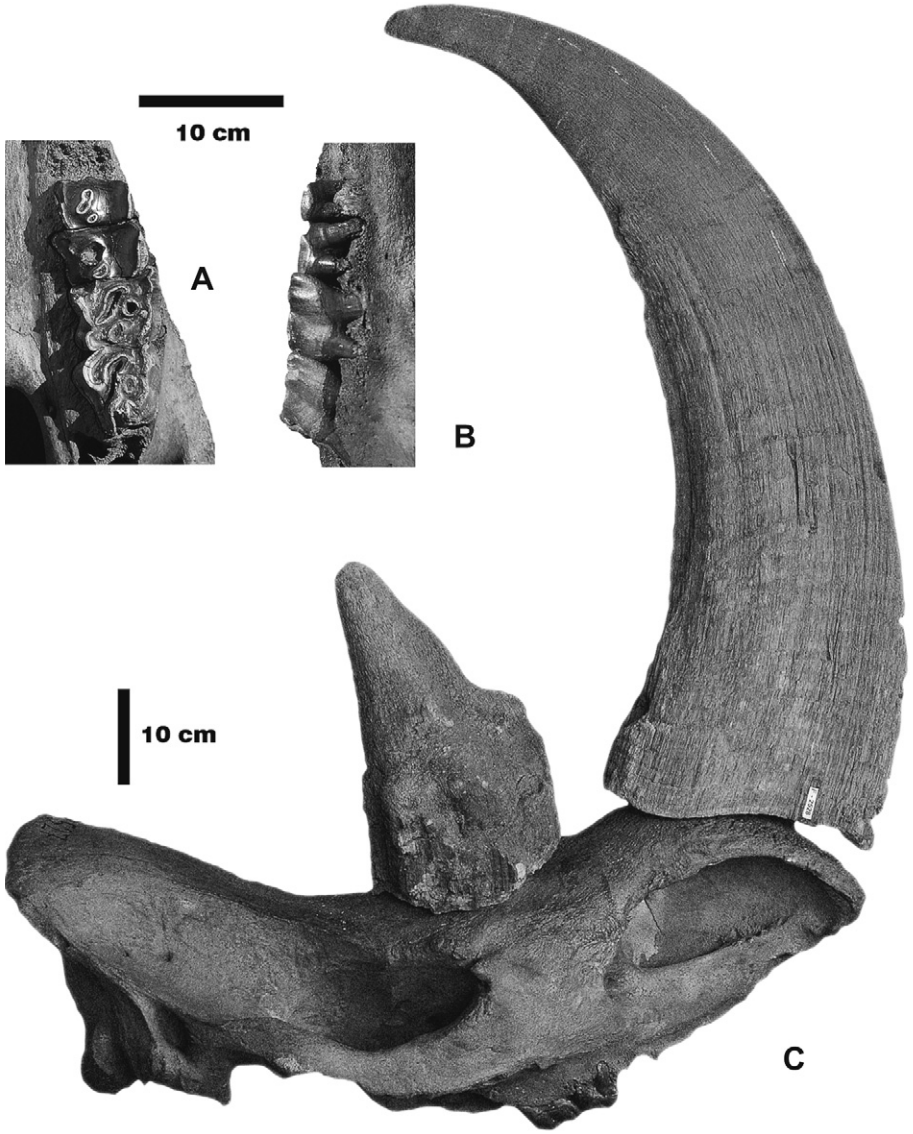

Fig. 1. Skull of woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799), "Ice Age" Museum specimen F-2527, Bol'shaya Chukoch'ya River basin, Sakha-Yakutia, Russia, Late Neopleistocene: A, detail of left maxilla with P4–M3 tooth raw, view from the base; B, same, left lateral view; C, skull with nasal (F-2528) and frontal (F-2529) horns installed at their places, right lateral view.

horn's longitudinal axis and are closely packed together within a melanized amorphous polyphase keratin matrix. This was true in both extant and extinct rhinoceroses (Earland et al., 1962; Ryder, 1962; Chernova et al., 1998; Hieronymus et al., 2006).

3. Results

3.1. The skull

The skull F-2527 is very robust and wide. The box-like shape of its occiput indicates the skull belonged to a male (Garutt, 1992b). Its dimensions are given on Table 1. The major bone sutures of the skull are completely obliterated (Fig. 2A). The process of ageing is expressed by changes in the periosteal resorption of the frontalia; an incipient degradation of bone tissue in the maxillae at the molar level to fully exposed roots in M2; a loss of P2 and P3; an occlusion of the alveoli of the second premolars by bone tissue; and very heavy wear of the molar's masticatory surface down to dentine (Figs. 1A, B and 2B). This set of features is indicative of the onset of the senility stage for the rhinoceros.

The degree of tooth wear of the woolly rhinoceros investigated here corresponds to the tooth wear class XV established for extant white rhinoceroses (Hillman-Smith et al., 1986) which embraces individuals from 30 to 38 years old. Application of the white rhinoceros tooth features to the woolly rhinoceros is suggested because both species were large grazers and shared close similarities in body structure. These similarities include the upper square-lip morphology exemplified in woolly rhinoceros mummies (Nowak et al., 1930); the low head posture indicated by the obtuse angle between the occipital and basal planes of skull (Garutt et al., 1970); and short legs which are evident in completely preserved skeletons and in cave paintings (Fortelius, 1983, Figs. 3 and 6; Fritz and Tosello, 2000, Fig. 1).

In accordance with the age scale developed for woolly rhinoceroses (Garutt, 1992a), the age of the same rhinoceros occurs within limits of the stages C-VIII (adult of 25–30 years old) and C-IX (35–40 years old showing signs of senility).

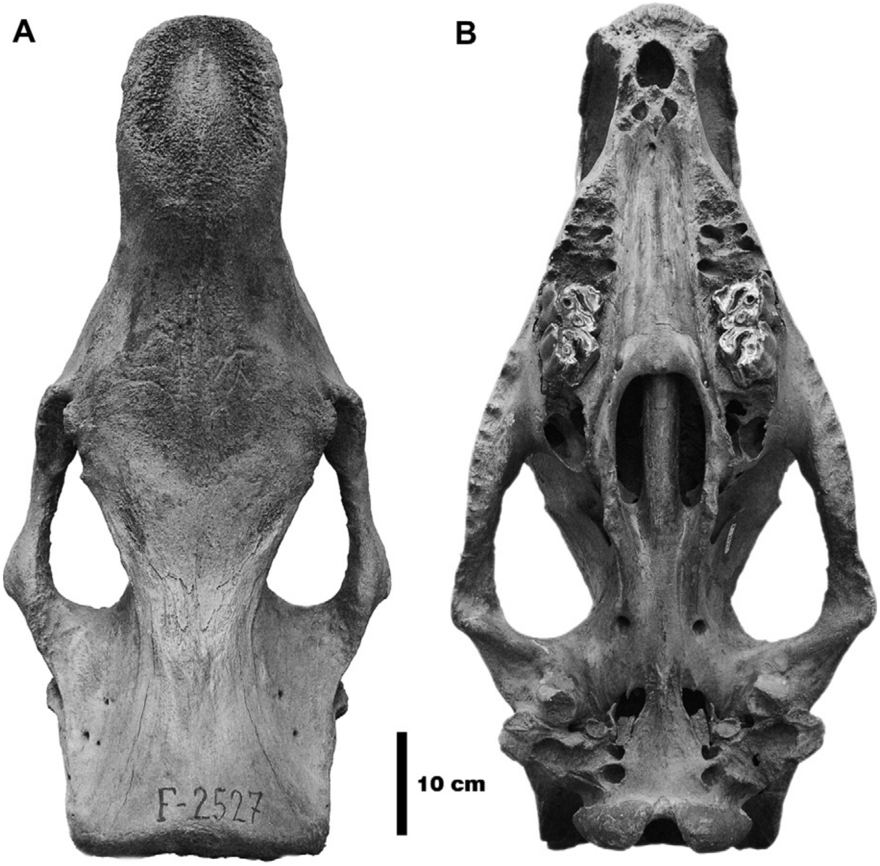

Fig. 2. Skull of woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799), "Ice Age" Museum specimen F-2527, Bol'shaya Chukoch'ya River basin, Sakha-Yakutia, Russia, Late Neopleistocene: A, view from the top; B, view from the base (P4 and M1 are extracted).

3.2. The left M1

The left M1 from the skull F-2527 is 23.8 mm in length along the base of its crown and 55.5 mm wide bucco-lingually (Fig. 1A, B). It has four tooth roots. Three of the roots reveal initial root resorption and the fourth is reduced. The lingual part of the crown is completely worn. The crown height is 10.5 mm on its lingual side. The enamel is preserved on most of the buccal surface of the crown and continues posteriorly. Sufficient increments of the cementum are observed in the interroot pad of the tooth. The masticatory surface is heavily worn. Fig. 4A and B shows that the periodic layers in the cementum of the interroot pad are not equally well-expressed. The interlayer boundary is much more distinct than in other areas. The sharpest boundary between sectors is seen in the seventh and eighth layers. The boundary between the 17th and 18th layers is less distinct, but observable (Fig. 4B).

A cross section of M1 revealed the presence of about 28 well-expressed layers in the cementum of the interroot pad. The reliability grade is 4.5. The resulting number of 28 corresponds to the age of the tooth, but not to the age of the animal. In extant white and black rhinoceroses the eruption of M1 occurs at the age of 1.5–3 years and the tooth cementum does not develop prior to this time (Hillman-Smith et al., 1986; Martin et al., 2008). It is concluded that the individual age of the animal is equal to the number of layers in the cementum plus the age of tooth eruption, that is plus 1–3 years (Hillman-Smith et al., 1986). This data indicates the individual age of the wooly rhinoceros under discussion is about 31 years.

3.3. The nasal horn

The nasal horn F-2528 is flat, wide at the base, and significantly long – 860 mm (linear length from the midpoint of its base to the apex), and gradually curves and tapers to the apex (Figs. 1C and 3B). The lateral blocks of filaments are preserved, but not along the entire length of the horn. Filaments on the right facet run almost up to the apex, but are less well-preserved on the left facet. The medial plane of the horn is partly visible under destroyed lateral blocks of filaments in the posterior and apical parts of the horn. The tip surface of the horn shows some traces of destruction. This could be caused by bioerosion as evidenced when submerged in water over an extended period of time. The foot of the horn base is elongated oval in cross section. The groove in its central part is not expressed very well. The apex is rounded and flattened laterally. The anterior surface of the horn is partly destroyed at the horn base and incipient fractures are observed at the boundaries of the regular increments. The shape of the anterior proximal surface is completely worn and flattened. The apex reveals no wear and the surface shape is rounded. The posterior part of the horn immediately above its base reveals that the boundaries of the regular increments are faulted repeating the convex fault at the foot of the horn base. In the middle part of the horn, measuring from its base, the bands on the working part of the anterior surface tend to be undulated. This undulating structure enabled higher resistance and resilience to the horn against mechanical stress such as a contact with frozen ground during grazing or an opponent's horn during horn-clashing. The principal dimensions of both nasal and frontal horns are provided in Table 2.

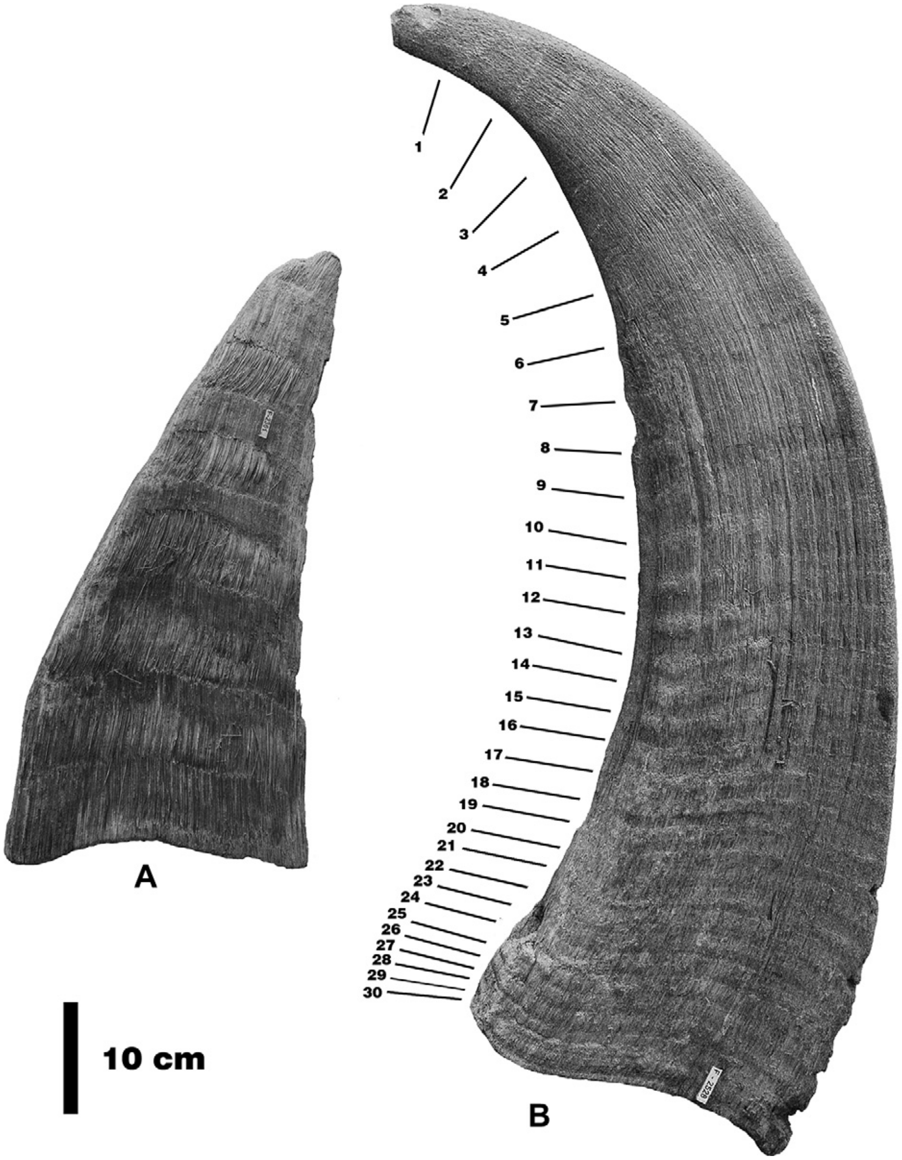

Fig. 3. Nasal horns of woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799), Late Neopleistocene, "Ice Age" Museum: A, specimen F-2361, left lateral view, Anyuysk, Chukchi Peninsula; B, specimen F-2528, right lateral view, Bol'shaya Chukoch'ya River basin, Sakha-Yakutia, Russia, Late Neopleistocene, periodic transverse increments (bands) consisting of a lighter and denser and darker and looser zones each are indicated from the apex (1) to the base (30).

Each transverse band of a regular increment consists of a pair of zones. One is lighter and more dense while the other is darker and more loose. (The discussion of the nature of this difference is beyond the scope of the present paper). The light zones are broader than the dark ones at the apex of the horn. In the middle part of the horn the width of both types of zones is equalized. The light zones again become broader than the dark ones at the base. The expression of the bands is average in microrelief and weak in color. They decrease from the horn base to its apex. This pattern makes it difficult to quantify and measure the number of bands. However, 30 or 31 paired zones (bands) are counted. The foot of the horn base is terminated with a lighter and denser zone. This occurred at the middle stage of the zone formation judging by the comparison of its width with the previous such zone. The measurements of the bands of the nasal horn F-2528 are given in Table 3. Fig. 5 shows the plot indicating the dependence of the band width on the animal's individual age.

3.4. The frontal horn

The frontal horn F-2529 is robust and erect. It is 360 mm long (linear length from the midpoint of its base to the apex) and gradually tapers to the apex. The lateral blocks of filaments are preserved along the entire length of the horn. The foot of the horn base is rounded and extremely concave with an elongated depression running in the anterior–posterior direction. The apex is rounded and both the apex and the anterior surface of the horn are naturally polished. Incipient lateral-vertical fractures are observed at the middle of the horn length which may cause a separation of the lateral blocks of filaments. The bands of increments are not well-expressed along the entire horn length and are stressed by fractures in the horn proximal part and by microrelief irregularities in other parts. The band width slightly increases toward the apex. Light and dense zones of the bands are broader than the dark and loose ones along the entire horn length. The expression of the bands is average in microrelief and weak in color. The number of

Table 1
Cranial dimensions for the Bol'shaya Chukoch'ya River woolly rhinoceros skull (F-2527) in comparison with other woolly rhinoceros skulls from the Middle Urals and Northern Sakha-Yakutia (in mm).

	Skull F-2527	Middle Urals (Kuz'mina and Kuz'mina, 1995)	Sakha-Yakutia (Lazarev and Tomskaya, 1987)
Sample size	1	7	7
Basal length	760	640–700	644–654
Condylobasal length	790	730–800	
Overall length	840	750–900	
Maxillary tooth row length	(225)	223–250	218–226
Palatal length	465	275–305	
Zygomatic breadth	390	320–376	320–360
Mastoid breadth	300	260–320	
Occipital bone breadth at its top	240	195–238	
Nasal bones' breadth (max)	165	157–177	132–198
Postorbital constriction width	140	120–143	

The maxillary tooth row length (P2–M3) is given in brackets because the premolar alveoli are occluded by bone tissue.

bands is 30 or 31. The foot of the horn base is terminated with a lighter and denser zone which occurred at the final stage of the zone formation judging by the comparison of its width with that of the previous such zone.

3.5. *Horns of other woolly rhinoceroses*

Additional samples include the horns F-2361, F-558, F-370, and F-371. The nasal horn F-2361 is of average preservation state (Fig. 3A). The lateral blocks of filaments are absent and only the axial plate is preserved. However, the bands of regular increments are extremely well-expressed as well as their light/dense and dark/loose subdivisions. They reveal a large width which is typical of young animals due to their high rates of filament growth. This is true for both extinct and extant rhinoceros species (Pienaar et al., 1991; Chernova et al., 1998). Darker zones are broader than the lighter ones. The band width decreases toward the base. The well-preserved nasal horn F-558 was bisected in the midsagittal plane for gross anatomical observations. The transverse banding on the cut surface is not distinct enough along the horn length which makes it difficult for the precise counting of bands. The outer surface is weathered and the bands are more expressed. The pair of horns F-370 (nasal) and F-371 (frontal) belongs to the same mature individual. They are extremely well-preserved. The frontal horn is complete, but the transverse bands are not expressed well enough to count with precision.

In general, the horns of the Bol'shaya Chukoch'ya River woolly rhinoceros possess less distinct bands than those of the F-2361 horn, but are more apparent than those of the F-370 and F-371 horns. The least expression of banding is observed on the sagittal section of the F-558 horn despite its state of preservation within the total sample set. The periodic banding is much better expressed on extremely weathered horns. The brighter colored zones are less preserved, but more distinct in their density. The F-2361 horn is less preserved, but the best for measuring and counting the bands within the total sample set. These peculiarities of horn preservation indicate that the horns of the Bol'shaya Chukoch'ya River woolly rhinoceros, which only reveal weak banding, did not experience multiple defrostings–frostings after the animal's death and burial or for a long time on the surface after the melting of the permafrost caps yielding these fossils.

4. Discussion

4.1. *Layered structures of teeth and horns as indicators of the individual age of the woolly rhinoceros*

In extant African mammals, up to two layers can be formed in tooth recording structures during a single year and the secondary layer can be indistinct (Klevezal, 1988, 1996). However, a perfect correlation of estimations of the individual age of the woolly rhinoceros from the Bol'shaya Chukoch'ya River based on several direct counts and indirect approximations indicates that the transversely bands of horns are indeed the annual. As a recording structure, the woolly rhinoceros horn is similar to the cementum in molars. In the case of the rhinoceros individual under discussion its age at death is within the limits of 30–33 years.

The woolly rhinoceros horns resemble the epidermal derivatives of mammals. These include cornified sheaths of bovid artiodactyl horns; baleen plates, and carnivore and pinniped claws (Earland et al., 1962; Ryder, 1962; Chernova et al., 1998; Tombolato et al., 2010). The growth of these derivatives is discontinuous and slows with ageing which allows researchers to use them as

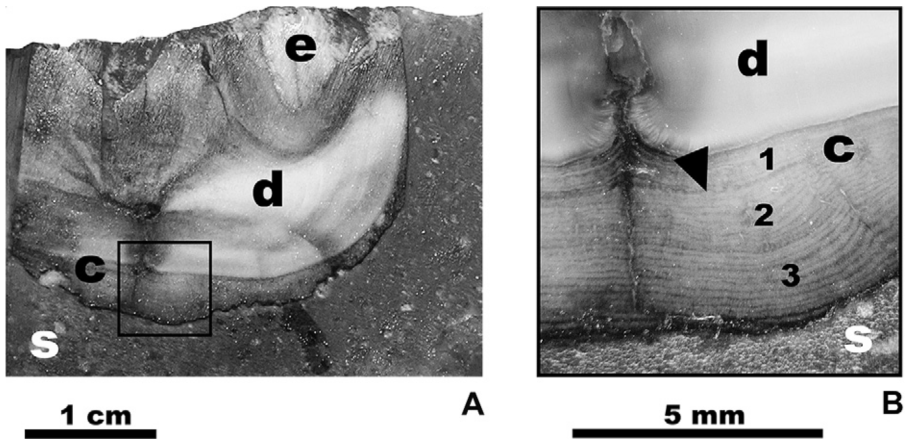

Fig. 4. Upper M1 tooth of woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799), "Ice Age" Museum specimen F-2527, Bol'shaya Chukoch'ya River basin, Sakha-Yakutia, Russia, Late Neopleistocene: A, transverse section; B, enlargement of (A), showing layers in the cementum, the most distinct boundary between them (arrowed), and three main growth sectors (1 to 3). c – cementum, d – dentin, e – enamel, s – synthetic glue.

Table 2
Dimensions of horns of the Bol'shaya Chukoch'ya River woolly rhinoceros.

	Nasal horn F-2528	Frontal horn F-2529
Linear length from midpoint of base to apex, mm	860	360
Anterior circumference, mm	1140	360
Posterior circumference, mm	890	330
Anteroposterior foot diameter, mm	290	200
Transverse foot diameter (max), mm	140	185
Anteroposterior diameter at midpoint, mm	220	170
Transverse diameter at midpoint, mm	94	170
Number of transverse bands	30–31	>30
Linear distance from foot to facet base, mm	139	
Weight, kg	11.38	4.50

recording structures. Particularly, claws of Greenland seals show a laminar structure due to discontinuous growth and this structure is expressed in transverse bands. The number of transverse bands is indicative of the seal's individual age (Chapskiy, 1952). However, in terrestrial mammals which use their claws for digging and other activities, the individual age cannot be estimated by claw sheaths due to excessive wear. According to Chapskiy (1952), the growth of claws is restricted to the time of animal molting when the hair and whiskers are replenishing and furfures are being discarded and rejuvenated.

It is noteworthy that the intrinsic nasal horn growth of Bol'shaya Chukoch'ya River wooly rhinoceros, based on direct measurements of its bands (Table 3, Fig. 5), was from 95 to 13 mm per year and progressively reduced with age. A similar horn growth pattern is observed in modern black and white rhinoceroses (Pienaar et al., 1991), although the actual value of mean yearly horn growth may differ. The first apical complete band is only 95 mm in the woolly rhinoceros while the intrinsic growth rate of the nasal horn of both modern African species is about 150 mm in the first year of life (Pienaar et al., 1991). The basis of these differences remains to be investigated.

Table 3
Measurements of transverse bands in the nasal horn (F-2528) of the Bol'shaya Chukoch'ya River woolly rhinoceros (in mm).

Band number from the horn apex	Band width	Lighter & denser zone width	Darker & looser zone width
1		40	
2	95	45	50
3	71	34	37
4	53	28	25
5	57	25	32
6	59	27	32
7	55	28	27
8	49	22	27
9	44	19	25
10	47	22	25
11	38	19	19
12	38	20	18
13	31	15	16
14	32	15	17
15	30	15	15
16	21	11	10
17	22	10	12
18	22	11	11
19	26	13	13
20	23	14	9
21	20	9	11
22	19	9	10
23	20	8	12
24	18	11	7
25	14	8	6
26	14	9	5
27	14	10	4
28	13	10	3
29	16	10	6
30	9	5	4

Live polished surfaces of the nasal (F-370) and frontal (F-371) horn apices indicate the use of both horns for defending an opponent's stabs based on the suggestion that the use of horns for horn-clashing similar to that of extant rhinoceroses is correct. An analysis of the Paleolithic cave painting from the Chauvet Cave in southern France depicting woolly rhinoceroses in confrontation (Fritz and Tosello, 2000, Fig. 1), reveals the use of the frontal horn for defending an opponent's nasal horn thrust. In any case, such a horn wear would not be too high for an individual of about 30 years old.

4.2. *The problem of the estimation of the woolly rhinoceros maturity*

By comparison with other woolly rhinoceros horns described in detail by Fortelius (1983), Chernova et al. (1998), the present pair of horns (F-2528 and F-2529) is the largest except for the length. It is also much better preserved and much more complete. However, the skull size of this individual is not uniquely large. The condylobasal length of skulls of some male woolly rhinoceroses from the "Ice Age" Museum reaches 810 mm (F-46, F-97). The condylobasal length of 800 mm is the largest of the sample set of seven males from the Middle Urals, Russia (Kuz'mina and Kuz'mina, 1995; Table 1). It is assumed that larger horns of woolly rhinoceroses may occur in nature. However, among the skulls from northern Sakha (Yakutia), the present one is the longest (Lazarev and Tomskaya, 1987; Table 1).

The annual layers in the cementum of the M1 of the Bol'shaya Chukoch'ya River wooly rhinoceros are expressed in an irregular pattern and subdivided into three growth sectors by two thicker boundaries (Fig. 4B). The most distinct boundary was between the 8th and 9th annual increments and indicates that at age 10–12 years the animal experienced severe changes in its organism. As a rule, the most significant changes at the postnatal stage of mammal development, which are registered in annual increments, are those related to the onset of sexual maturity (Klevezal, 1988, 1996). The extant white rhinoceros, *C. simum*, and the black rhinoceros, *Diceros bicornis*, become sexually potent between 4 and 5 years old or 7 and 10 years old with females being sexually active earlier (Hillman-Smith et al., 1986). Subsidiary males are able to attain socio-sexual maturity and attain alpha male status for breeding at 10–12 years old (Owen-Smith, 1975; Hillman-Smith et al., 1986). The distinct boundary between about the 8th and 9th annual increments in the M1 pad cementum is, probably, related to the achievement of physiological maturity by the Bol'shaya Chukoch'ya River woolly rhinoceros.

An apparent decrease in the width of annular transverse bands occurs at the same level in horns of woolly rhinoceroses where it is possible to measure the width with precision. (Below the band 11–13 in the horn F-24, below the band 12 in the horn F-27, below the band 11 in the horn F-370, and below the band 10–12 in the horn F-1989). The same pattern is visible on figures of six nasal horns of woolly rhinoceros published by Brandt (1849, Pls IX and X) and reproduced by Fortelius (1983, Figs. 2 and 3): approximately, 12, 12, and 9 (the horn is damaged) on the Fig. 2 in Fortelius (1983) and 11, 12, and 12 on the Fig. 3 in Fortelius (1983). Finally, the same pattern (12/13 band from the apex) is clearly visible in the nasal horn from the Bol'shoy Khomus-Yuryakh River despite the absence of its distal part (Chernova et al., 1998, Fig. 1). It is noteworthy that the stage of growth rate change in woolly rhinoceros horns corresponds approximately to the most distinct boundary in the cementum increments of the molar of the same species (with

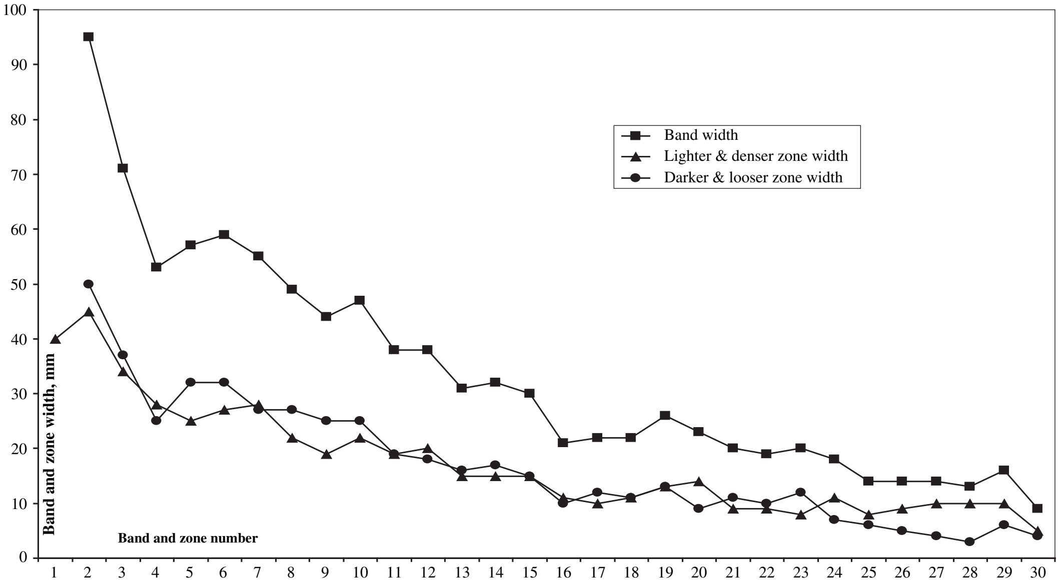

Fig. 5. Plot of the band and zone widths in the nasal horn (F-2528) of woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799), "Ice Age" Museum, Bol'shaya Chukoch'ya River basin, Sakha-Yakutia, Russia, Late Neopleistocene.

addition of three more years gone before the molar eruption, see the paragraph 3.2. above).

4.3. The season of the death of the woolly rhinoceros

The transverse banding of horns expressed in alternation of lighter and denser zones with darker and fragmented ones reflects seasonal environmental fluctuations (Garutt, 1995, 1998). It is possible that this pattern is correlated with the regular alternation of warmer and colder seasons. The alternation of denser and looser zones establishes the difference in the physiological processes occurring during different seasons. This difference is reflected in horns of extant white rhinoceros having been examined by X-ray computed tomography, gross observation of sectioned horns, and light microscopy of histological sections of the horn tissue (Hieronymus et al., 2006). This examination revealed that the difference in color and wear (density) patterns is due to the distribution of a photoabsorbent component (melanin) and a radiodense component (calcium phosphate salts). The concentration of both components was proved to be higher in darker zones due to higher rates of component deposition during the formation of these zones. Because melanin may act to reduce the degree of keratin degradation by absorbing the UV-light entering the tissue (Jimbow et al., 1986; Hieronymus et al., 2006) it would be possible to ascribe the formation of darker zones in woolly rhinoceros horns to polar summer seasons and the lighter ones to polar winter seasons, correspondingly. However, in order to justify this suggestion, studies of the influence of insulation intensity alternations on the growth of horns in extant rhinoceros and of the difference in stable isotope and chemical compositions of horn zones in extinct rhinoceroses are needed.

At present, the season of the specimen's death is established by the examination of teeth only. The annual layers in the cementum of M1 are distinct enough to observe some peculiarities in their formation. The latest light zone is complete, because its width is the same as that of the previous layer as well as that of the last dark zone. A new dark zone has not begun to form. The same pattern is observed on the entire surface of the tooth section. As a rule, a complete growth layer was well-expressed in those mammals which died during the autumn–spring interval (Klevezal, 1988, 1996).

It is quite probable that the Bol'shaya Chukoch'ya River woolly rhinoceros died during a colder season and at the final stages of that interval. In such a case the latest zone to be formed in its nasal horn was the lighter and denser zone. This observation is in agreement with the suggestion that such zones are formed during the polar winter seasons.

5. Conclusions

The horns of woolly rhinoceros are attributed to the recoding structures such as tooth dentin and cementum, claw sheaths, and some others which are indicative of the individual age of an animal. This suggestion is proved by a fairly good correlation of the estimations of the animal's individual age based on the count of layers in the cementum of the M1 tooth (1); conditions of sutures between skull bones (2); general conditions of the tooth system and the degree of tooth wear in comparison to those in extant white rhinoceroses (3); and general conditions of tooth system and the degree of tooth wear in comparison with the scale developed by N. Garutt (1992a) for the wooly rhinoceros (4). In the case of the woolly rhinoceros from the Bol'shaya Chukoch'ya River, the age of its death is within the limits of 30–31 years. The intensity of the dark color itself in horns of woolly rhinoceroses is probably due to differences in the rate of melanin deposition during the horn growth which is shown for extant rhinoceroses (Hieronymus et al., 2006). The season of the animal's death, established by the examination of the annual layers in the outer cementum of M1, is shown to be a colder interval.

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