RAPID COMMUNICATIONS IN MASS SPECTROMETRY
Rapid Commun. Mass Spectrom. 2010; **24**: 3146–3150
Published online in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/rcm.4755

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Stable isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) composition of the woolly rhinoceros *Coelodonta antiquitatis* horn suggests seasonal changes in the diet

Alexei V. Tiunov[1]* and Irina V. Kirillova[2]

[1]Institute of Ecology and Evolution RAS, Leninsky Prospect 33, Moscow 119071, Russia
[2]'Ice Age' Museum, All-Russian Exhibition Center, Bld. 71, Moscow 129223, Russia

Received 25 June 2010; Revised 10 August 2010; Accepted 24 August 2010

The extinct woolly rhinoceros *Coelodonta antiquitatis* is a prominent member of the *Mammuthus-Coelodonta* faunal complex, but its biology is poorly known, partly because very few specimens with well-preserved soft tissues have been discovered to date. However, the permafrost-preserved horns of the woolly rhinoceros are recording structures which contain isotopic records of the diet, environmental conditions and physiological status of the animal during most of its life. In this study we report the first data on the pattern of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotopic composition along the nasal horn of woolly rhinoceros. We found systematic variations in $\delta^{13}C$ and $\delta^{15}N$ values associated with morphologically expressed transverse banding of the horn. The comparative analysis of isotopic variation in keratinous tissues of extant and extinct herbivores suggests that the oscillation in isotopic composition of the horn was induced by seasonal changes in the diet. Although the compiled evidence is in part contradictory, we suggest that more positive $\delta^{13}C$ and $\delta^{15}N$ values associated with dark-colored and less dense zones of the horn indicate a summer diet. More dense and light-colored zones of the horn have lower $\delta^{13}C$ and $\delta^{15}N$ values possibly indicating a larger proportion of woody and shrub vegetation in the winter diet. The validity of these conclusions has to be proven in further investigations, but our data underline the potential of isotopic analysis for studies on diet and habitat use by extinct members of Pleistocene fauna.

The extinct woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) is a prominent and famous member of the so-called *Mammuthus-Coelodonta* faunal complex,[1] but its biology is much less known than that of the mammoth, partly because very few specimens with well-preserved soft tissues have been discovered to date. Permafrost-preserved woolly rhinoceros horns have, however, been known in Europe since at least the 18th century.[2,3] As in the extant rhinoceros, *C. antiquitatis* horns are built of keratinous lamellar filaments or fibers which are arranged in parallel along the longitudinal axis and closely packed together within a melanized amorphous polyphase keratin matrix.[4–6]

C. antiquitatis possessed two horns, the much larger nasal one and a shorter frontal one. The characteristic feature of the horns is a more or less regular transverse banding, which is especially obvious in less well-preserved specimens. Each transverse band consists of a pair of layers or zones, one of which is lighter and denser while the other is darker and looser Even in the 19th century the banding had been attributed to annual growth increments of the horn.[7] Although this notion was subsequently questioned by some researchers, recent studies generally agree that the banding reflects seasonal environmental fluctuations. Possibly, the alternating zones are correlated with warmer and colder seasons.[3,8] The width of the transverse bands in *C. antiquitatis* nasal horns is compatible with the annual growth increments in the horns of the extant rhinoceros,[9] and the number of bands corresponds to the woolly rhinoceros age estimations based on the counts of annual dental pad cementum layers and other age estimation criteria.[10] Thus, the horn can be regarded as a recording structure of woolly rhinoceros which contains continuous information on the diet, environmental conditions and physiological status of the animal during most of its life.

The isotopic composition of progressively laid down keratinous tissues such as hair, horns or hooves of vertebrates can provide valuable information on their diet and environment.[11–15] Stable isotope analysis has emerged as a critical tool for resolving spatial and temporal patterns of individual, intraspecific and interspecific resource use.[16] This information is especially important in the case of extinct animals. In particular, the recent isotopic analysis of mammoth (*Mammuthus primigenius*) hairs revealed regular oscillations, attributable to seasonal changes in the diet and/or in physiological status.[17,18]

**Correspondence to*: A. V. Tiunov, Institute of Ecology and Evolution RAS, Leninsky Prospect 33, Moscow 119071, Russia.
E-mail: a_tiunov@mail.ru

This paper reports first data on the isotopic composition of the nasal horn of the extinct woolly rhinoceros. Our main objective was to investigate the changes (if any) in the isotopic composition of carbon and nitrogen of the keratinous tissue along the horn and compare this pattern with morphologically expressed transverse banding. The secondary objective was to analyze published evidence that would help to attribute light- and dark-colored zones of the horn to a particular season.

EXPERIMENTAL

The nasal horn of the woolly rhinoceros *Coelodonta antiquitatis* was obtained from the deposits in the Panteleikha River valley near Cherskij (Kolyma basin, ca. 68.45′ N, 161.18′ E). The geological age of the deposits is the late Late Pleistocene. The specimen is housed in the 'Ice Age' Museum, Moscow, Russia (collection number F-10). The horn is in a relatively bad state of preservation. The basal and apical ends are missing, and the length of the remaining fragment is about 74 cm. Both lateral surfaces are eroded which made transverse banding very conspicuous: more dense light-colored zones are somewhat convex, whereas dark-colored zones are hollow with individual keratin fibers readily visible on the surface (Fig. 1). There are in total 17 bands left. The width of the bands decreases from the distal (upper) to the proximal (lower) part of the horn (Table 1). This probably reflects the decrease in the horn growth rate with the age of animal.[5,10]

Before taking the samples, the horn surface was cleared from adhering particles with a tough brush, washed with alcohol and dried. Samples were taken along the length of the horn at 10 mm intervals on the right side ca. 30 mm from the frontal edge. The boundaries between dark- and light-colored zones were usually rather sharp; in the distal part of the horn, where the zones were wider (up to 30 mm), several samples were taken within each zone. The samples were taken with a clipper at the depth of 2–3 mm. In addition, eleven sub-surface samples were taken from a greater depth (8–10 mm) using a borer. In total, 82 samples were taken and analyzed. The obtained material was dried overnight at 50°C and stored in a desiccator until analysis.

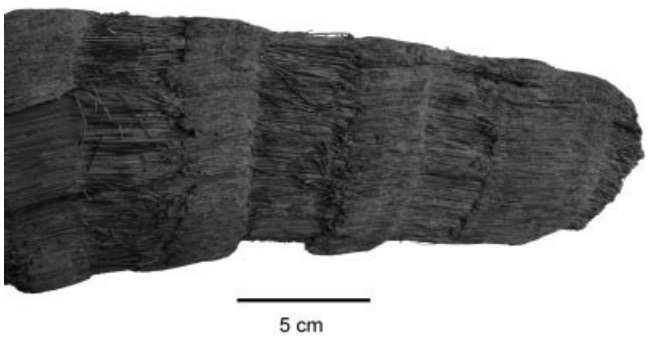

Figure 1. Distal part of the nasal horn of *Coelodonta antiquitatis* with conspicuous transverse banding formed by regular alternation of lighter and denser zones with darker and looser ones. Keratinous fibers are seen in the darker zones. The length of the fragment shown is 23 cm.

Table 1. Size of transverse bands in the horn studied (mm). Each value is the mean from six measurements taken along the circumference of the horn

Band number (from distal end)	Dark-colored zone	Light-colored zone
1	19.3	44.8
2	25.8	27.2
3	30.0	28.5
4	30.0	27.5
5	29.5	31.2
6	18.3	27.8
7	21.5	21.7
8	21.7	16.0
9	18.5	16.7
10	20.5	18.3
11	20.5	17.7
12	18.7	18.0
13	24.7	22.2
14	20.7	13.2
15	16.2	12.8
16	17.0	14.8
17	13.8	12.8

For stable N and C isotope analyses, samples were weighed (500–600 μg) and wrapped in tin capsules. Stable N and C isotope ratios were measured using a continuous-flow mass spectrometer (Delta V Plus, Thermo Electron, Bremen, Germany) coupled with an elemental analyzer (Flash EA 1112, Thermo Electron) through a Conflo IV interface (Thermo Electron). The carbon and nitrogen elemental contents and isotope compositions were measured in the same measurement sequence. After every tenth sample a solid internal laboratory standard (acetanilide) was run as a control. The performance of the mass spectrometer was further monitored by IAEA (Vienna, Austria) reference materials (glutamic acid USGS 40 and USGS 41), analyzed after every thirtieth sample.

The natural abundances of ^{15}N and ^{13}C were expressed in per mil (‰) deviation from international standards:

$$\delta^{15}N \text{ or } \delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000,$$

where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Atmospheric nitrogen and Vienna Pee Dee Belemnite (VPDB) were used as the international standards for nitrogen and carbon, respectively. The standard deviation for replicate measurements ($n = 8$) of glutamic acid or acetanilide was less than 0.1‰ for $\delta^{13}C$ and <0.15‰ for $\delta^{15}N$.

RESULTS

The total C and N contents were lower in surface samples (44.0 ± 0.2[SE] and 14.7 ± 0.1%, respectively) than in subsurface samples (48.4 ± 0.3 and 16.0 ± 0.1%, respectively). However, the C/N ratio of the horn material was remarkably similar in all samples and averaged 3.01 ± 0.01. There was no difference in the total C and N contents or in the C/N ratios between dark- and light-colored zones. In contrast, the $\delta^{13}C$ and $\delta^{15}N$ values changed considerably along the horn, showing a roughly sinusoidal pattern. This pattern was not pronounced in the basal (proximal) part of the horn (about 20 cm), which was formed later in the animal's life. Along

DOI: 10.1002/rcm

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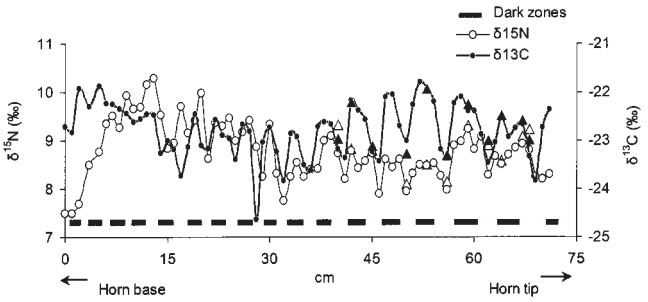

Figure 2. Nitrogen ($\delta^{15}N$, open symbols) and carbon ($\delta^{13}C$, closed symbols) isotope composition of *Coelodonta antiquitatis* horn. Circles: surface samples; triangles: subsurface samples. Surface samples were taken at regular 10 mm intervals. Alternating dark- and light-colored zones of the horn are shown as the broken line below.

the distal part of the horn (formed earlier and having wider bands, Table 1), higher $\delta^{13}C$ and $\delta^{15}N$ values were associated with dark-colored zones, whereas light-colored zones were depleted in both ^{13}C and ^{15}N (Fig. 2). In the distal half of the horn, the positive peaks of $\delta^{13}C$ and $\delta^{15}N$ values tended to be wider than the negative peaks, although the widths of the dark- and light-colored zones were roughly equal.

The total range of $\delta^{13}C$ and $\delta^{15}N$ values was from -24.6 to -21.8‰ and from 7.5 to 10.3‰, respectively. Subsurface samples did not differ from the respective surface samples in $\delta^{13}C$ values, but were slightly more enriched in ^{15}N (on average by 0.2‰, paired *t*-test: $p = 0.005$, $n = 11$).

DISCUSSION

The C/N ratio in structural proteins can be used as a rough indicator of sample preservation.[19] The C/N ratio in the horn samples studied was very similar to the C/N ratio in modern keratinous tissues.[11] This suggests that although the horn surface was physically eroded, the chemical transformation or contamination of keratin was relatively small. Perhaps more important, there was no difference in the elemental contents of C and N or in the C/N ratios between the dark- and light-colored zones, and a very small difference in $\delta^{13}C$ and $\delta^{15}N$ between the outer and inner layers of the horn. Thus, the observed oscillation of isotopic composition was not likely to be an artifact induced by different diagenetic alteration of the horn tissue in dark- and light-colored zones. This is confirmed by preliminary analyses of the individual keratin filaments separated from the horn that showed the same pattern of oscillation in isotopic composition as the bulk horn tissue (data not shown). Moreover, in the distal part of the horn the boundaries between the dark- and light-colored zones were very sharp (Fig. 1), but the changes in C and N isotopic composition were gradual, and minimum $\delta^{13}C$ and $\delta^{15}N$ values were recorded in the middle of the light-colored zones.

The oscillation of C and N isotopic composition was much less regular and consistent in the basal (proximal) part of the horn, and the peaks of $\delta^{13}C$ and $\delta^{15}N$ values occasionally did not coincide. This can be ascribed either to the poor preservation, or more likely to the disruption of the regular growth increments in senescent animals. It is generally agreed that woolly rhinoceroses used their horns not only for display and combat, but also to brush away snow from the ground while feeding in the winter.[3,20] Thus, the basal part of the horn was subjected to regular mechanical impacts and possibly deformations of filament structure. However, along most of the horn length, the oscillations were nearly regular.

In the distal part of the horn (30–70 cm, eight transverse bands) the difference in the isotopic composition among light- and dark-colored zones within single band was on average 1.1 ± 0.1‰ in $\delta^{13}C$ and 0.8 ± 0.1 in $\delta^{15}N$. A similar range of variation in $\delta^{13}C$ values and somewhat larger (up to 2‰) variation in $\delta^{15}N$ values was found in the mammoth hairs,[17] although in this case the higher $\delta^{13}C$ values corresponded to lower $\delta^{15}N$ values, and vice versa. Subsequent studies revealed that the oscillations in the $\delta^{13}C$ values along the mammoth hairs are not consistent among different locations and are generally less pronounced than those in $\delta^{15}N$ values.[18] Iacumin *et al.*[17,18] attributed these oscillations primarily to the seasonal $\delta^{13}C$ and $\delta^{15}N$ changes in the mammoth diet (changes in the isotope composition of plant or in the type of plant) or, only in the case of nitrogen, as a physiological effect related to arid conditions. They suggested that more positive values of $\delta^{15}N$ (and more negative $\delta^{13}C$ values) should record the winter period.

The isotopic composition of carbon and nitrogen in the woolly rhinoceros horn was well within the range reported for mammoth hairs.[17,18] In the horn, however, the patterns of $\delta^{13}C$ and $\delta^{15}N$ values largely correlated (for the distal part of the horn, from 30 to 70 cm: $r = 0.447$, $p = 0.003$) and the attribution of dark- and light-colored zones of the horn to particular seasons remains a challenging task. In their analysis, Iacumin *et al.*[17,18] assumed that the switch to an isotopically distinct diet is reflected in hair keratin with substantial time lag of at least 74 days. This assumption is based on a range of previous publications, but probably implies a full equilibration of the hair with a new dietary isotopic composition.[21] Recent experiments[22–24] have demonstrated that the new isotopic signal appears in the growing hair nearly immediately after the switch from a C3- to a C4-based diet, or vice versa. For example, the proportion of the fast-reacting C isotope pools in the horse hair was estimated as ca. 41% (the fastest pool with half-life of ~0.5 days) and 15% (intermediate pool with half-life of ~4 days).[22] Thus, some changes in the isotopic composition of the hair can be detected within a few days after the diet change, although the time to full equilibration is of the order of months. Similar observations were made on bovine hooves.[13,24] We therefore suggest that the positive $\delta^{13}C$ and $\delta^{15}N$ peaks in the mammoth hairs or rhinoceros horn should correspond to a relatively recent increase in dietary ^{13}C and ^{15}N content.

Unfortunately, the horns or hairs of extinct Pleistocene animals do not provide clear and unambiguous clues that would allow a precise attribution of the isotopic signal to a particular season, diet composition or physiological status of an animal. The information on the seasonality of tissue formation can be derived from H and O stable isotopes ratios,[25–27] although seasonal fluctuations in the isotopic composition of the drinking water and vegetation might be affected by many locally specific processes, including

DOI: 10.1002/rcm

evaporative and reservoir effects,[28] as well as the late melting of the winter snow and its contribution to the water supply in summer.[29] However, some insights can be obtained from the data on the isotopic composition of C and N in keratinous and other tissues of extant animals inhabiting tundra and boreal forests. In particular, Kielland[14] found synchronous oscillations of $\delta^{13}C$ and $\delta^{15}N$ values in the hooves of moose (*Alces alces*) in Alaska. Both C and N were enriched in heavier isotopes (by 0.7–2.7‰) in the summer-formed layers. The oscillations of $\delta^{15}N$ values were ascribed to the dietary changes from deciduous shrubs and woody plants to forbs and possibly aquatic plants. Similar seasonal pattern in $\delta^{15}N$ values was observed in the antlers of caribou (*Rangifer tarandus*) which switch from a shrub-based diet early in the summer to a graminoid-based diet later in the season.[30] This pattern, however, was not found in the blood cells of moose and caribou where the $\delta^{15}N$ values did not differ between seasons, whereas $\delta^{13}C$ values were slightly (0.5–0.6‰) increased in the winter samples.[15]

On the other hand, in a range of geographical locations and ecosystem types (tundra at different altitude and boreal forests) there was a consistent difference in the $\delta^{13}C$ and $\delta^{15}N$ values of the hair and blood samples of co-occurring moose and caribou.[12,15] Relative to moose tissues, caribou tissues were usually enriched in $\delta^{13}C$ and $\delta^{15}N$ values by 2–3‰. This is consistent with the difference in the isotopic composition of plants preferred by moose (shrub and tree leaves) compared with caribou forage, which includes a larger proportion of graminoids, lichen and fungi.

In both tundra and boreal forest ecosystems the $\delta^{15}N$ values of trees and shrubs are usually lower than those of graminoids, probably due to the association of the woody plants with ecto- or ericoid mycorrhiza.[31–33] C3 plants typically have more negative $\delta^{13}C$ values in closed, forested habitats, and more positive values in open and drier habitats, and this allowed resource partitioning of extinct and extant herbivorous taxa in C3-dominated habitats to be shown.[12,34–37] Work by Heaton[38] also suggests that the $\delta^{13}C$ value in C3 plants generally increases with an increase in temperature and a decrease in water availability. For example, the $\delta^{13}C$ value in prairie graminoids increased on average by 0.5–0.9‰ from spring to middle summer.[39]

This short analysis suggests that the dark-colored zones of the horn were formed during or shortly after the period (summer?) when *C. antiquitatis* was feeding on a more 'caribou-like' diet, which included a large proportion of graminoids. Light-colored zones were probably formed during the cold season when the animals were feeding in a more 'moose-like' style, and consumed larger proportions of shrub and woody vegetation. The very limited data available on the diet composition of *C. antiquitatis* do not contradict this hypothesis. The mummified Starunia rhinoceros was accompanied by tundra-like flora with a substantial contribution of dwarf birches and willows;[40] the significance of shrubs in the diet of woolly rhinoceros was suggested by Flerow.[41] Plant remnants extracted from the mouth cavities of several frost-preserved *C. antiquitatis* heads contained remnants of grasses, as well as of twigs of coniferous (*Picea*, *Larix*) and deciduous trees (*Salix*). Pollen analysis revealed mostly pollen of graminoids and *Artemisia*, but also of *Betula*, *Alnus*, ferns and club-mosses.[20] *C. antiquitatis* possessed rather wide lips and other morphological features typical of a grazer.[3,20,42] Like woolly mammoth, they possibly used grasses and sedges as a dietary staple most of the year. The overall similarity in the diet of two species is suggested by the similar isotopic composition of both soft tissue and bone collagen.[43]

Nevertheless, woody species (*Salix*, *Alnus*, *Betula*, *Larix*, *Picea*) are regularly found in mammoth dung and intestines, though usually in relatively low amounts.[44] Moreover, *Salix* leaves and twigs formed up to 20% of the lower intestine content of a Yukagir mammoth that died in early spring.[45] The woolly rhinoceros could change to a diet that comprised a larger proportion of woody and shrub plant species during relatively short periods of time, and this would explain why the negative peaks of $\delta^{13}C$ and $\delta^{15}N$ are narrower than the positive peaks.

CONCLUSIONS

We found systematic variations in $\delta^{13}C$ and $\delta^{15}N$ values in the horn of extinct woolly rhinoceros, associated with morphologically expressed transverse banding. The comparative analysis of isotopic variation in the tissues of extant and extinct herbivores suggests that the oscillation in isotopic composition of the horn was induced by seasonal changes in the diet. Although the compiled evidence is in part contradictory, we suggest that more positive $\delta^{13}C$ and $\delta^{15}N$ values, associated with dark-colored and less dense zones of the horn, indicate a summer diet that consisted mainly of grasses. The more dense and light-colored zones of the horn have lower $\delta^{13}C$ and $\delta^{15}N$ values possibly indicating a larger proportion of woody and shrub vegetation in the diet. The validity of these conclusions has to be proven in further investigations, but our data underline the potential of isotopic analysis for studies on diet and habitat use by extinct members of Pleistocene faunal complex.

Acknowledgements

We thank F. K. Shidlovskiy (Ice Age Museum, Moscow) for providing material and funding for this study and I.I. Semenyuk (IEE RAS) for the help in the preparation of samples.

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