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Analysis of ^{13}C and ^{15}N isotopes from Eurasian Quaternary fossils: Insights in diet, climate and ecology

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Summarising conclusions

In this dissertation, a vast amount of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from bulk collagen of Quaternary mammalian bone, tusk, antler and teeth samples are presented and discussed. Most of these data are measured at the Centre for Isotope Research (CIO), Groningen ($n > 400$). The dataset consists of samples from various localities within Eurasia and are taken from human fossils, but mainly from fossils of various animal taxa including extinct species such as woolly mammoth (*Mammuthus primigenius*), straight-tusked elephant (*Palaeoloxodon antiquus*), wild horse (*Equus mosbachensis*), Siberian unicorn (*Elasmotherium sibiricum*), woolly rhinoceros (*Coelodonta antiquitatis*) and giant deer (*Megaloceros giganteus*). Many of these faunal species belong to the typical ‘mammoth steppe fauna’.

The results shed light on dietary and habitat characteristics of these animals through time and space. But also on the habitat characteristics of coeval living hominins, as they were exposed to the same environmental and climatological circumstances. Moreover, dietary information of animals is relevant for hominins sharing the same region, as in turn the animals may have been part of the hominins’ diets, or the animals may have competed for the same food resources. Fossil skeletal remains are abundantly found at archaeological sites.

Archaeologists reconstruct the past, usually based on a limited amount of available data. Stable isotope analyses, however, offer a relatively cheap, fast, objective, controllable and nowadays widely available, valuable and unique contribution to the palaeoenvironmental reconstruction and to the scientific debates. For instance, the numerous $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from Holocene woolly mammoths from Wrangel Island provide a clearer picture of the circumstances in which mammoths lived just before the ultimate extinction of the species (see Chapter 3). The Holocene $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values remain remarkably similar through time and are the same as those of Late Pleistocene woolly mammoths from the Northeastern Siberian mainland (**RQ 2**). Minor differences are observed in samples with an LGM age, but the post-LGM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from North-eastern Siberia are similar to those pre-dating the LGM. This continuity or recovery of stable isotope values sharply contrasts to published data of woolly mammoths and other large herbivores samples from Europe and Alaska, which revealed significant changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values; changes that are related to climatic fluctuations during and/or after the LGM. Moreover, the data reveal that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Holocene woolly mammoths from Wrangel Island are similar to these of the Late Pleistocene mammoths from the North-eastern Siberian mainland, while they diverge from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth samples from Alaska, despite the fact that both regions are geographically rather close (**RQ 1**). The stable isotope data indicate that the stable isotope composition of vegetation on Wrangel Island was similar to that of other parts of West-Beringia and not to that in Alaska, despite the proximity to Central Beringia and Alaska. The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between Wrangel Island and Central Beringia and Alaska can be used

in further research on the way in which Central Beringia might have acted as ecological barrier that prevented (an earlier) migration of specific species to East Beringia (RQ 4).

Although changes in habitat and/or diet cannot be unconditionally ruled out based on diachronic similarity of stable isotope data, climate change would most probably be reflected as changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the fossil bones. Therefore, the stable isotope data provide supporting evidence that climate change was not the direct cause of the ultimate extinction of the woolly mammoth. This way, the stable isotope data add to the debate on the cause of the megafauna extinctions towards the end of the Pleistocene (RQ 3).

Another example of a valuable contribution of stable isotope research to the scientific debate, forms the analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data of fossil material from various mammal taxa and multiple find horizons from the key archaeological site Schöningen (see Chapter 6). Seemingly contradicting results achieved by analysis of different proxies, hampered the possibility to get a clear picture of the environmental circumstances in which the hominins operated at this locality. The isotopic data from faunal remains indicate that during the climatic Reinsdorf Interglacial optimum the landscape was forested, alternating with open areas, whereas during depositional level 4 the landscape was more open. The $\delta^{13}\text{C}$ values seem to be too low to be indicative for a steppe landscape. This is supported by the faunal record of depositional level 4 that does not include species that are indicative for glacial conditions (RQ 8).

Moreover, the results show the important addition that stable isotope analysis can make to results achieved by other archaeological methods. The application of stable isotope analysis is not limited to the individual but suitable for detecting and comparing inter- and intraspecific, diachronic and spatial patterns of feeding behaviour and habitat use (see Chapter 3 and 5). Stable isotope data offer another perspective on, and form a valuable addition to, results achieved by analytic methods focussing on for instance morphology, dental wear, and dental calculus analyses. This is illustrated by the stable isotope data from the Siberian unicorn (*Elasmotherium sibiricum*), presented in Chapter 4. The species has extremely high-crowned rootless molars. This morphological feature is regarded as an adaptation to very abrasive food, such as eating tubers. When eating plant roots, a lot of sand comes along, which means that the animal's teeth are likely to wear down fast. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the Siberian unicorn point to a very specialised diet and $\delta^{13}\text{C}$ values support the consumption of underground plant parts. Its very specialised diet, its specialized habitat, the assumed low population size and its slow reproductive rate may have made the Siberian unicorn prone to extinction in the face of environmental change (RQ 6).

Another example of a significant addition to dental morphological information is the $\delta^{15}\text{N}$ values of the horses from Schöningen (see Chapter 6), which are lower than all other investigated herbivore species at the site. Although horses are generally considered to be typical obligate grazers, the $\delta^{15}\text{N}$ values may point to a browsing diet for the horses at Schöningen. Morphologically, the horse molars diverge from these found in

other periods and sites, with unfamiliar pointed cusps and a dental wear pattern indeed indicative for a substantial part of browse in their diet (**RQ 9**).

The Schöningen results from well-preserved bone collagen (**RQ 7**) illustrate, in addition, that the age of fossils does not have to be per se a limiting factor to analyse their stable isotope ratios. Instead, the current research makes clear that it is worth examining the organic fraction from fossils (far) beyond the radiocarbon timescale, in cases that the burial context or the physical appearance of the fossil remains suggest good preservation. Indeed, if the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of bone collagen from old samples were categorically on forehand excluded because of their age, we would mistakenly miss potentially important information.

For instance, stable isotope information of the straight-tusked elephant would never have been recovered if fossils with an age higher than 50 ka were disregarded. The straight-tusked elephant samples from Schöningen (see Chapter 6) and the North Sea area (see Chapter 4) revealed that these elephantids show a distinctive pattern of $\delta^{15}\text{N}$ values higher than those of coeval living herbivorous large mammals. A similar discrepancy of $\delta^{15}\text{N}$ values between woolly mammoths and co-occurring Late Pleistocene herbivores is commonly observed. An all-encompassing explanation for the divergence is not yet established. Likely, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of bulk collagen samples will not be good enough to solve this puzzle. Although more study is necessary to get precise insight into the complex cycling of single amino acids through the metabolic network (McMahon and McCarthy, 2016; O'Connell, 2017), analysis of the $\delta^{15}\text{N}$ composition of single compounds from woolly mammoths and straight-tusked elephants may eventually give the solution. A study of compound-specific isotopes of different Pleistocene large herbivore and carnivore species carried out by Schwartz-Narbonne *et al.* (2015) pointed towards a dietary (as opposed to a physical) explanation for the high mammoth $\delta^{15}\text{N}$ values. However, the data from straight-tusked elephants make an elephantid-specific physiological adaptation a more plausible cause for the observed high $\delta^{15}\text{N}$ values and form a promising basis for further investigation and debate (**RQ 5**).

The research in this thesis emphasises the importance of sufficient amounts of data. As shown in the case of the extensive dataset of Siberia, prior claims based on just a few data showed to be off the point. Outliers occur, but the problem is that others build on such data, whilst the data do not form a good base. We must continue to look extremely critically at claims made on the basis of a small amount of data. To date, discussing small datasets of stable isotopes from bulk collagen can actually be avoided for many species and localities. Given the current sophistication of isotope measurement technology, low costs and fast sample throughput, statements should nowadays be based on relatively large data sets. In addition to create a sound base for outlier analysis and other statistical evaluation, large data sets ensure that diachronic and spatial patterns can be analysed. Often, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is automatically measured with collagen ^{14}C dating. Much of the data presented in this dissertation has been obtained in this way. By publishing such

data, it would be easier to discuss a (few) stand-alone data point(s) in comparison to relevant readily available $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Also, applications such as isotope mixing models and estimating reservoir effects likely benefit from higher amounts of available ^{14}C dated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data. Moreover, techniques such as ZooMS probably increases the future amount of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data, since it enables to identify bone parts which lack morphological diagnostic features relatively simply at species level (Richter *et al.*, 2011; Stewart *et al.*, 2014; Welker *et al.*, 2015). Therefore, likely more frequently bone fragments will be sent in for ^{14}C , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. This way, ZooMS opens the possibility to investigate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data of bone assemblages that may be important but that previously, without morphological species identification, would have been ignored. It will improve our understanding of associated assemblages that itself may be inappropriate or too valuable for destructive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis, and to feed isotope mixing models with valuable data of potential important, but otherwise overlooked, dietary resources.