

Ecometrics of large herbivorous land mammals in relation to climatic and environmental changes during the Pleistocene

JUHA SAARINEN

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Sciences of the University of Helsinki, for public examination in auditorium XII, University main building, on 16th December 2014, at 12 noon.

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Cover illustration: Juha Saarinen

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ISSN 1798-7911

ISBN 978-952-10-9467-5 (paperback)

ISBN 978-952-10-9468-2 (PDF)

<http://ethesis.helsinki.fi>

Unigrafia

Helsinki 2014

Abstract

The climatic cooling during the Cenozoic (65 Ma – present) culminated in the Pleistocene Ice Ages (ca. 2.6 Ma – 10 000 BP) during which the global climate oscillated between relatively warm climatic phases and very cold and dry glacial phases when extensive continental glaciers formed in the Northern hemisphere. The oscillation between the cold and warm climatic stages caused dramatic cyclic changes in the structure of vegetation varying at its extreme between relatively humid forests and very dry and cold mammoth steppes in Europe. These constantly changing and harsh climatic and environmental conditions caused strong extinction and evolution pressures on mammalian species. In this thesis I will discuss how two major ecometric variables, body size and diet, of large herbivorous land mammals have varied during the Pleistocene and how these patterns are connected with climate, environmental conditions and competing mammal species.

Mammals diversified and started to occupy the niches of large vertebrates after the Late Cretaceous mass extinction which caused the extinction of large non-avian dinosaurs. The frequency of maximum body size in archaic mammal orders shows a significant global peak in the Middle Eocene (ca. 40 Ma) as a result of the diversification and niche filling after the Late Cretaceous mass extinction, but after that maximum size frequency in mammalian orders was low until it peaked significantly again the Pleistocene Ice Ages. This indicates that the Pleistocene climatic and environmental conditions favoured particularly large body sizes in mammals. The overall “harshness” of the Ice Age climate (seasonal, mostly cold and

dry conditions and often rapid climatic changes) could have favoured large body sizes in large terrestrial mammals through mechanisms which are more complicated than the often cited benefit of large size for heat conservation (Bergmann’s rule). Large size increases the ability to survive over seasonal shortages of resources such as food and water and enables long-distance migrations to areas of better resource availability. On the other hand, strong erosional processes caused by glaciers produced fertile soils and harsh climates reduced the chemical defences of plants, which resulted in seasonally high primary production and plant quality, which would have enabled herbivorous mammals to grow into large sizes during seasons of high productivity.

The main factor driving fine-scale body size variations in ungulate populations has been shown by several studies to be resource availability, which is regulated by primary productivity, plant quality, population densities of the ungulate species (intraspecific resource competition) and interspecific resource competition. The comparisons of ungulate body sizes from Middle and Late Pleistocene of Britain and Germany with vegetation openness (percentages of non-arboreal pollen from associated pollen records) show that species with different ecological strategies have different body size patterns in relation to the vegetation structure. The connection between body size patterns and ecological strategies could explain the different responses of body size to vegetation openness. Species which tend to have relatively small group sizes (e.g. deer) show on average larger body sizes in environments where the vegetation structure is open, whereas gregarious, open

adapted species (e.g. horses) tend to have smaller average body sizes in open habitats. I suggest this is because open habitats favour large body size in ecologically flexible species with small group sizes due to high resource availability and quality per an individual (relatively low population densities), less size-restricted manoeuvrability and enhanced capability to escape predators, whereas resource limitations for each individual caused by high population densities can become a limiting factor for individual body size in open-adapted, gregarious species which are efficient open-vegetation feeders and form large groups in open habitats. In closed environments, the body size of the open-adapted, gregarious species is not limited by high population density which enables them to attain larger individual sizes.

Dietary signals of the key ungulate species in Middle and Late Pleistocene Europe based on mesowear analyses are on average significantly positively correlated with vegetation openness (non-arboreal pollen percentages) at locality-level. However, there are significant interspecific differences. While most of the species show positive correlations between their mesowear signal and non-arboreal vegetation, others, especially the red deer (*Cervus elaphus*), do not show any correlation. Instead, the mesowear signal of the red deer is significantly more abrasive dominated when other browse-dominated feeders, especially the roe deer (*Capreolus capreolus*) are present. This indicates that interspecific competition can obscure the effect of available plant material in the diet of ecologically flexible species. This should be taken into account when interpreting the feeding ecology of the key species in palaeocommunities, and especially when attempting to reconstruct palaeoenvironmental conditions from dietary proxies of mammals. Such attempts should ideally be based on as complete dietary analyses of fossil herbivore faunas as possible.

In order to extend the palaeodietary and palaeoecological analyses based on mesowear signals of herbivorous mammals, a new tooth wear-based dietary analysis method was developed for elephants and other lamellar toothed proboscideans, based on measuring occlusal relief of their molar teeth as angles. The benefits of that approach compared with other available methods are that it is easy-to-do, fast and robust, and it gives consistent and comparable results for species with different dental morphologies. The preliminary results from that study indicate that the angle measurement method is a powerful tool for reconstructing proboscidean diets from the fossil record.

Tiivistelmä (in Finnish)

Kenotsooisella ajalla (65 miljoonaa vuotta sitten–nykyaika) maapallon ilmasto on lämpimän alkuvaiheensa jälkeen muuttunut enimmäkseen kylmemmäksi, keskileveyksillä kuivemmaksi ja kausittaisemmaksi. Tämä ilmaston pitkäaikainen kehitys huipentui pleistoseeniin eli jääkausiaikaan, joka vallitsi noin 2,6 miljoonaa – 10 000 vuotta sitten. Pleistoseenijalla ilmasto vaihteli voimakkaasti ja sen seurauksena pohjoisella pallonpuoliskolla esiintyi vuorotellen melko lämpimiä ilmastovaiheita joiden aikana metsät olivat hallitsevia elinympäristöjä ja kylmiä glasiaalivaiheita, jolloin kylmän ja kuivan ilmaston seurauksena syntynyt aro- ja tundrakasvillisuuden vyöhyke, niin kutsuttu mammuttiaro, levittäytyi laajalle alueelle pohjoisessa Euroasiassa. Eläimistön piti sopeutua näihin voimakkaisiin ilmaston ja elinympäristöjen muutoksiin. Tässä väitöskirjassa selvitän miten kenotsooisen ajan globaalien ilmaston vaihtelut vaikuttivat nisäkkäiden ruumiin koon evoluutioon ja keskityn tarkastelemaan tarkemmin miten suurten kasvinsyöjänisäkkäiden ruumiin koko ja ravinto vaihtelivat ympäristön ja kasvillisuuden muutosten mukaan keski- ja myöhäis-pleistoseenin Euroopassa.

Liitukauden lopun massasukupuutossa (noin 65 miljoonaa vuotta sitten) suurten maaselkärankaisten ekologisia lokeroita hallinneet dinosaurukset hävisivät, mikä mahdollisti nisäkkäiden voimakkaan monimuotoistumisen niiden levittäytyessä vapaaksi jääneisiin suurten maaselkärankaisten ekolokeroihin. Tämä laukaisi eksponentiaalisen ruumiin koon ylärajan kasvun useissa nisäkslahkoissa kenotsooisen ajan alkupuolella, mutta keski-eoseenijän (noin 40 miljoonaa vuotta sitten) jälkeen maksimikoon evoluutio tasoittui ja alkoi seurata ilmaston muutoksia.

Sama ilmiö on nähtävissä maksimikoon esiintymisfrekvenssissä hyvin erilaisissa nisäkslahkoissa ja maailmanlaajuisesti. Erityisen voimakas maksimiruumiinkoon esiintymisen huippuvaihe on pleistoseenin jääkausijalla, mikä viittaa siihen että ilmaston kylmeneminen ja siihen liittyvät ympäristönmuutokset suosivat erityisen suuren ruumiin koon kehittymistä useimmissa nisäkslahkoissa. Tämän ilmiön aiheuttivat todennäköisesti monet ilmaston ja ympäristöjen muutoksiin liittyvät tekijät, jotka ovat monimutkaisempia kuin usein esitetty suuren koon hyöty ruumiinlämmön ylläpitämiseksi kylmässä ilmastossa (niin kutsuttu Bergmannin sääntö). Suuri koko auttaa nisäkkäitä selviämään kausittaisesta ravinnon niukkuudesta ja mahdollistaa tehokkaan vaeltamisen ravintokohteita seuraten. Toisaalta jäätiköiden aiheuttama voimakas eroosio tuotti ravintorikkaita maannoksia mahdollistaen suuren kasvillisuuden tuotannon kasvukausien aikana ja kylmät ja karut olosuhteet paransivat ravinnon laatua heikentäen kasvien kemiallisia puolustusmekanismeja. Tämä mahdollisti suuren ruumiin koon kasvattamisen suotuisina vuodenaikoina.

Pääasiallinen suurten kasvinsyöjänisäkkäiden ruumiin kokoa säätelevä tekijä populaatiotasolla on useiden tutkimusten mukaan ravinnon saatavuus, jota puolestaan säätelevät perustuotanto, kasviraivon laatu, nisäkslajin populaatiotiheys (lajinsisäinen ravintokilpailu) ja lajien välinen kilpailu ravinnosta. Keskeisten kasvinsyöjänisäkslajien ruumiin koon vaihtelun vertailu niiden yhteydestä kerättyihin siitepölyaineistoihin keski- ja myöhäis-pleistoseenin Euroopan keskeisiltä fossiililöytöpaikoilta viittaa siihen että erilaisten lajien ruumiin koon vaste kasvillisuuden avoimuuteen vaihtelee riippuen lajien ekologiasta tavalla, joka tukee käsitystämme ravinnon saatavuuden ja populaatiotiheyksien

vaikutuksesta yksilöiden ruumiin kokoon. Lajit jotka esiintyvät tyypillisesti pieninä ryhminä ja ovat ekologisesti joustavia (kuten useimmat hirvieläimet) ovat keskimäärin suurikokoisempia avoimissa ympäristöissä, joissa ravinto on hyvälaatuista ja sitä on runsaasti tarjolla, liikkuvuus on vähemmän rajoittunutta kuin suljetuissa ympäristöissä ja suuri koko on etu petojen välttämiseksi. Suurina laumoina avoimissa ympäristöissä esiintyvät, avoimiin ympäristöihin erikoistuneet lajit (kuten hevoset) ovat keskimäärin pienikokoisempia tällaisissa ympäristöissä mikä johtuu todennäköisesti siitä että suuri populaatiotiheys rajoittaa yksilökohtaista ravintoresurssien saatavuutta. Suljetuissa ympäristöissä tällaisten lajien populaatiotiheydet jäävät pieniksi koska avomaan kasvillisuutta (kuten heinää), jota nämä lajit ovat erikoistuneet hyödyntämään, on tarjolla vähemmän ja se esiintyy laikuittaisemmin, jolloin populaatiotiheys ei rajoita yksilökohtaista ruumiin kokoa ja keskimääräinen ruumiin koko on suurempi.

Suurten kasvinsyöjänisäkkäiden ravinto vaihteli keski- ja myöhäis-pleistoseenin Euroopan löytöpaikoilla ja olisi keskimäärin merkittävästi yhteydessä kasvillisuuden rakenteeseen. Useimmat lajit söivät keskimäärin voimakkaammin hampaita kuluttavaa ravintoa (pääasiassa heinää) avoimissa ympäristöissä, mikä voitiin todeta vertailemalla keskimääräisiä hampaiden purupinnan kulumismuotoja fossiilisissa kasvinsyöjänisäkäsyhteisöissä samojen löytöpaikkojen siitepölyaineistoihin. Tästä on kuitenkin poikkeuksia, erityisesti pleistoseenin Euroopan löytöpaikoilla yleinen, runsas ja ekologisesti joustava isokauris eli saksanhirvi (*Cervus elaphus*). Sen ravinto on sen sijaan keskimäärin kuluttavampaa (runsaammin heinää sisältävää) löytöpaikoilla, joilla esiintyy runsaasti muita samankaltaista lehtevää kasviainesta hyödyntäviä lajeja,

erityisesti metsäkaurista (*Capreolus capreolus*). Tämä viittaisi siihen että lajien välinen kilpailu saa ekologisesti joustavan isokauriin muuttamaan ravinnonkäyttöään riippumatta kasvillisuuden rakenteesta. Tämä havainto osoittaa että käytettäessä kasvinsyöjänisäkkäiden ravinnonkäyttöanalyysijä elinympäristöjen paleoekologisessa rekonstruoinnissa tulee olla varovainen ja tulkintojen tulisi mahdollisuuksien mukaan perustua mahdollisimman kattavaan nisäkäsfauunan analysointiin.

Laajentaaksemme mahdollisuuksia nisäkkäiden makroskooppiseen hampaiden kulumismorfologiaan (niin kutsuttuun mesowear-analyysiin) perustuvien ravinnonkäyttöanalyysimenetelmien hyödyntämiseen fossiilisten nisäkäsyhteisöjen analysoinnissa, kehitimme uudenlaisen, kulmamittauksiin perustuvan menetelmän hampaiden purupinnan suhteellisen topografian mittaamiseen norsuilla ja niiden fossiilisilla sukulaisilla (Proboscidea). Tällaisen menetelmän etuna on sen helppokäyttöisyys, nopeus ja vertailukelpoisuus verrattuna muihin ravinnonkäyttöanalyysimenetelmiin. Alustavien tulostemme mukaan menetelmä antaa erinomaisia tuloksia norsueläinten ravinnon kuluttavuudesta, mikä osoittaa erityisesti heinäkasvien määrää kasvinsyöjien ravinnossa.

Acknowledgements

This PhD thesis was funded by the Finnish Graduate School of Geology, Nordenskiöld Samfundet and the dissertation completion grant of the University of Helsinki. Travel grants for the research visits during this work were granted by the Finnish Graduate School of Geology, Nordenskiöld Samfundet and IMMPS Research Coordination Network of the National Academy of Sciences (USA).

I owe my greatest thanks to my supervisors Prof. Mikael Fortelius, Prof. Heikki Seppä and Docent Jussi Eronen, whose highly constructive, insightful and encouraging advice and comments have been essential for this work. All the supervisors have also contributed to the original research articles. I would like to thank Mikael Fortelius and Jussi Eronen also for supporting me in the applying and organising of the several museum visits and other research collaboration abroad, which have been essential for this work and for my development as a scientist. I owe special thanks to my scientific advisor Prof. Adrian Lister from the Natural History Museum of London, whose contribution has been significant. His expertise and constructive suggestions during this work have had a great influence on my scientific thinking. Several others have contributed as co-authors of the research articles included in this study.

This work would not have been possible without great opportunities to visit several prominent museums and research institutes around the world and to study their fossil mammal collections. Those are: the Natural History Museum of London (NHM), University Museum of Zoology in Cambridge (UMZC), Sedgwick Museum in Cambridge (SMC), Torquay Museum (TM), Ipswich Museum (IM), British Geological Survey in Nottingham

(BGS), in Great Britain, Staatliches Museum für Naturkunde in Stuttgart (SMNS), Staatliches Museum für Naturkunde in Karlsruhe (SMNK), Research Station of Quaternary Paleontology of the Senckenberg Institute in Weimar (IQW), in Germany, the American Museum of Natural History in New York (AMNH), Page Museum in Los Angeles, in USA, and Tsavo Research Station (Tsavo East National Park) and the National Museums of Kenya in Nairobi (KNM), in Kenya. I owe special thanks to the curators and museum assistants who provided me the access to the collections and helped me with all the logistics. Those people are: Andrew Currant and Philippa Brewer (NHM), Matthew Lowe (UMZC), Matthew Riley (SMC), Barry Chandler and Clare Jones (TM), Ann Ainsworth (IM), Louise Neep and Paul Shepherd (BGS), Reinhard Ziegler (SMNS), Dieter Schreiber (SMNK), Prof. Ralf-Dietrich Kahlke (IQW), Jin Meng, Judith Galkin, Ross McPhee and Eileen Westwig (AMNH), John Harris and Shelley Cox (Page Museum), Shadrack Ngene (Tsavo Research Station) and Mary Muungu (KNM). During the proboscidean mesowear research I was affiliated with the University of Nairobi and Kenya Wildlife Service from 2011 to 2012. I would especially like to thank Dr. Faith Karanja, Daniel Kiarie, Prof. Lucy Irungu and Dean of the Faculty of Veterinary Medicine Prof. John Njenga Munene for arranging my affiliation with the University of Nairobi. I would like to thank Prof. Samuel Kasiki for accepting my affiliation with the Kenya Wildlife Service.

Part of this PhD work was done in collaboration with the IMPPS (Integrating Macroecological Patterns and Processes across Scales) Research Coordination Network funded by the US National Academy of Sciences

and hosted by Felisa Smith, Morgan Ernest and Kathleen Lyons. Working in the IMMPS research group was important for the beginning of my international research collaboration, and the papers I and II in this thesis were produced as a result of that collaboration. The IMPPS project has also resulted in other significant publications, which were not included in this thesis. Also, I would like to thank the various people who have reviewed the research articles and the synopsis included in this thesis for their insightful comments which have helped me to improve this work.

Several other people deserve my gratitude for important and interesting discussions. I would especially like to thank Aleksis Karme for the rich conversations, research ideas and adventures we have shared during these years. Kari Lintulaakso was the greatest companion and collaborator I could have hoped for during our participation in the IMPPS Research Coordination Network meetings in Santa Fe, USA, between 2008 and 2012. Laura Säilä collected the mesowear angle data of Rancho la Brea mammoths during the elephant mesowear research project and was the second person after myself to test and apply the angle measuring method I developed for proboscidean tooth surfaces. I had valuable discussions with Pierre Mauries and Silvia Pineda at the beginning of this PhD project. I have also shared a lot of thoughts and insights with Pirkko Ukkonen and Diana Pushkina, both of them great specialists on Pleistocene mammal faunas and palaeoecology. I would also like to thank Pasquale Raia, Mark Bell, Peter Heintzman and Ursula Göhlich for our productive collaboration on mammal body size evolution research.

I thank the personnel of the Department of Geosciences and Geography, University of Helsinki, for the supportive and friendly working environment. I would like to thank all my friends and relatives for all the great times

we have shared in and out of work during these years. My mother Anneli Saarinen and my grandparents Jaakko and Inkeri Saarinen have always supported me in every possible way. Their support and encouragement has been of greatest importance for my whole life and for this work. My beloved Iita has my dearest gratitude for all her support and love during these years. Finnish nature with its peaceful, mighty forests and hardy wildlife has been and will always be an endless source of inspiration, recreation and admiration for me.

“If you know how big an animal is, where it lives and what it eats you already know most of what there is to know about it.”

- Peter Andrews

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Publications I - IV

List of original publications

This thesis is based on the following publications:

- I Smith, F.A., Boyer, A.G., Brown, J.H., Costa, D.P., Dayan, T., Ernest, S.K.M., Evans, A.R., Fortelius, M., Gittleman, J.L., Hamilton, M.J., Harding, L.E., Lintulaakso, K., Lyons, McCain, C., S.K., Okie, J.G., Saarinen, J., Sibly, R.M., Stephens, P.R., Theodor, J., Uhen, M.D. 2010. The evolution of maximum body size of terrestrial mammals. *Science*, 330, 1216-1219.
- II Saarinen, J., Boyer, A.G., Brown, J.H., Costa, D.P., Ernest, S.K.M., Evans, A.R., Fortelius, M., Gittleman, J.L., Hamilton, M.J., Harding, L.E., Lintulaakso, K., Lyons, S.K., Okie, J.G., Sibly, R.M., Stephens, P.R., Theodor, J., Uhen, M.D., Smith, F.A. 2014. Patterns of maximum size evolution in Cenozoic land mammals: intrinsic biological processes and extrinsic forcing. *Proceedings of the Royal Society B*, 281, 20132049.
- III Saarinen, J., Eronen, J., Fortelius, M., Seppä, H., Lister, A. In review. Patterns of body mass and diet of large ungulates from Middle and Late Pleistocene of Western Europe and their connections with vegetation openness. Submitted to *Paleontologia Electronica*.
- IV Saarinen, J., Karme, A., Cerling, T., Uno, K., Säilä, L., Kasiki, S., Ngene, S., Obari, T., Mbuu, E., Manthi, F.K., Fortelius, M. In press. A new tooth wear -based dietary analysis method for Proboscidea (Mammalia). *Journal of Vertebrate Paleontology* (2015).

The publications are referred to in the text by their roman numerals.

Author's contribution

- I Major role in data collection as a part of the IMPPS Research Coordination Network. Significant contribution to analyses and discussion about the results.
- II Fully responsible for the research idea, data arrangement and figures. Major contribution to original data collection as part of the IMMPS Research Coordination Network. Mostly responsible for analyses and writing the article. Minor role in the likelihood ratio analysis.

- III Fully responsible for data collection, analyses and figures. Mostly responsible for planning the study and writing the article.
- IV Fully responsible for data collection, measuring methodology and analyses. Mostly responsible for planning the study, writing the article and making the figures.

Abbreviations

Ma	Millions of years ago
BP	Before present
MIS	Marine isotope stage
MxSF	Maximum size frequency
BM	Body mass
NAP	Non-arboreal pollen

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Fig 2 *Climatic variations based on deep sea oxygen isotope record since the Pliocene (3.5 Ma) (Walker and Lowe 2007), 16*

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Fig 4 *Molar tooth morphology types of some large herbivorous mammals and their application in mesowear analyses, page 22*

1. Introduction

The Cenozoic (ca. 65 Ma – present) has been a time of drastic changes in global climate, which are reflected in the evolution of organisms and changes in the ecology of plant and animal communities. After the thermal maximum phases at the Palaeocene and Early Eocene (ca. 60–48.6 Ma), the trend has been towards cooler and, at least in mid-latitudes, dryer climate, ultimately leading to the Pleistocene Ice Age (ca. 2.6 Ma – 10 000 BP) (Zachos et al. 2001, Zachos et al. 2008, figure 1).

(e.g. Simpson 1953, Rensch 1959, Vrba 1980, Vrba 1987, Janis and Fortelius 1988, Vrba 1992, Alroy 1998, Janis et al. 1998, Alroy et al. 2000, Barnosky 2001, Muhlbacher et al. 2011, Raia et al. 2012, Raia et al. 2013, Evans and Janis 2014, paper I, paper II). Recently, much of the research has concentrated on the mechanisms which have driven the evolutionary patterns observed in various mammal lineages (e.g. Alroy 1998, Alroy et al. 2000, Raia et al. 2012, Raia et al. 2013, paper I, paper II).

Increasingly comprehensive fossil record and methodological improvements have enabled us to answer questions such as what causes the fine-

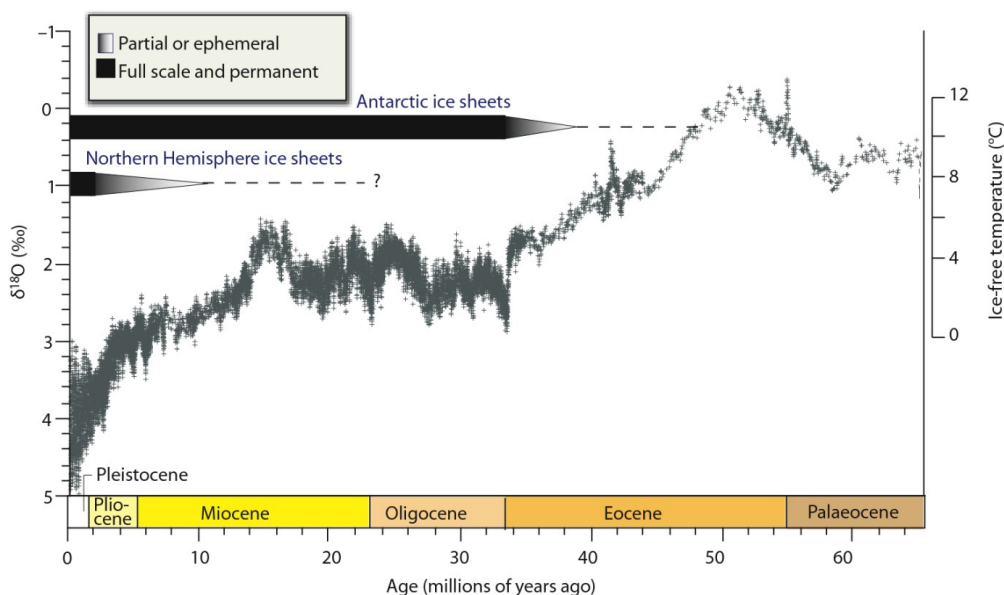


Figure 1. The Cenozoic time scale as millions of years, and fluctuations in $\delta^{18}\text{O}$ (‰) fraction in the deep sea oxygen isotope record, reflecting global temperature oscillations during the Cenozoic. High $\delta^{18}\text{O}$ values indicate cold climate (note that the $\delta^{18}\text{O}$ scale is shown from larger (bottom) to smaller (top) in order to show it as a temperature proxy). Note the drastic cooling and the increased oscillation in global temperatures in the late Cenozoic and especially in the Pleistocene (ca. 2.6 Ma – 10 BP). Ma = mega-annum (millions of years ago), BP = before present. The figure was originally published by Zachos et al. (2008).

The evolution of mammals during the Cenozoic has been a major subject of paleontological research and it has provided some of the most persuasive cases of macroevolutionary patterns recognized in the whole fossil record

scale fluctuations in the evolution of various mammal lineages and how mammals adapted to environmental and climatic changes during the Cenozoic. Taxon-free morphological variables, which can be measured from fossil

bones and teeth of mammals, reflect adaptations to , and phenotypic variation under different climatic and environmental conditions in fossil mammal species and assemblages. These variables are called “ecometrics” (Eronen et al. 2010, Andrews and Hixson 2014, Polly et al. 2014) and they provide a powerful tool for analysing palaeoecology and evolution of mammals in relation to changes in climate and environments through time. Body size and diet are among the most essential ecometric characteristics of mammals which can be analysed from the fossil record and which reflect environmental and climatic conditions.

The Pleistocene Ice Age started when the global cooling trend had reached a point after which periodical glaciation events started in the Northern hemisphere following cyclic changes in the orbit and axis orientation of the Earth (e.g. Hays et al. 1976, Imbrie and Imbrie 1980, Zachos et al. 2001, Lisiecki and Raymo 2005, Lisiecki and Raymo 2007, Walker and Lowe 2007, Zachos et al. 2008, figure 2). Continental glaciation of the Antarctic had started much earlier, already in the Oligocene (Zachos et al 2008). However, at the beginning of the Pleistocene the global cooling intensified the effect of the cyclic changes in the Earth’s orbit and axis on climatic changes, causing summer temperatures to drop periodically low enough for the accumulation of large continental ice sheets (glaciers) in northern Europe and in northern North America (Zachos et al. 2008, Lisiecki and Raymo 2005, Walker and Lowe 2007). Since then the climate oscillated between the extremes of cold glacial maxima and warm interglacial stages in Northern hemisphere, and the changes in climate have often been complex and rapid. In Eurasia the cyclic changes in the Pleistocene climate caused especially dramatic periodical changes in biome distributions and environments. Successions of forest vegetation in

Europe and Northern Eurasia were characteristic for the warm interglacial stages (e.g. Stuart 1976, Svenning 2002, Turner 2002, Bradshaw et al. 2003). During the glacial stages, especially in the Late Pleistocene, continental ice sheets and mountain ranges blocked moisture from reaching the Eurasian inland areas and caused long-term cold and dry high-pressure climates which resulted in the vast mammoth steppe vegetation to spread over the continent (Guthrie 2001). Trampling and grazing by abundant large herbivorous mammals also contributed in maintaining the grass-dominated vegetation of the mammoth steppes (Zimov et al. 1995). Extensive studies on stratigraphic correlation of terrestrial localities with marine isotope stages (warm and cold climatic stages revealed by deep-sea oxygen records), fossil pollen records and fossil faunas have constantly refined our understanding on the complex changes in climate, vegetation and mammal faunas during the Pleistocene (e.g. Stuart 1976, West 1981, Lister 1992, Van Kolfschoten 1995, Schreve 2001a, Schreve 2001b, Schreve and Bridgland 2002, Bradshaw et al. 2003, Bridgland et al. 2004, Roe et al. 2009, Kjellström et al. 2010).

The cold, dry and dramatically oscillating climates of the Pleistocene had a profound effect on all life on earth, shaping vegetation patterns and animal communities, and creating heavy selection and extinction pressures on organisms (e.g. Kurtén 1968, Geist 1971, Kurtén 1972, Kurtén and Anderson 1980, Lister 1992, Geist 1998, Guthrie 2001). The cold climatic conditions of the Pleistocene increased plant productivity and quality as herbivore food due to the fertile soils generated by intense glacial erosion and the reduced chemical defences and fibrousness of plants, providing abundant resources for large herbivores resulting in the evolution of large species with impressive luxury organs (horns, antlers and tusks) (e.g. Zimov et

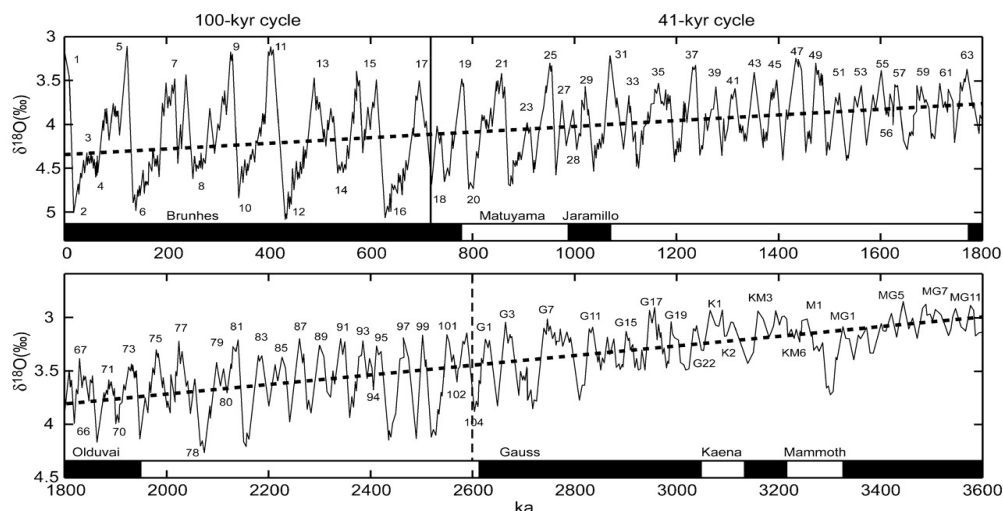


Figure 2. Global deep-sea oxygen isotope ($\delta^{18}\text{O}$) record from 3.5 Ma (Pliocene) until present. High $\delta^{18}\text{O}$ values indicate cold climate and low values warm climate (note that the $\delta^{18}\text{O}$ scale is shown from larger (bottom) to smaller (top) so that the curves indicate temperature changes). There has been a rather constant trend of climatic cooling and intensified oscillations between warmer climatic conditions and colder conditions from the Pliocene to present. The Pleistocene Ice Age started ca. 2.6 Ma when the cooling trend in the climate had reached a point after which the cyclic changes in the axis and orbit of the earth resulted in cyclic fluctuation between cold glacial stages, during which continental ice sheets formed in the Northern Hemisphere, and warm interglacial stages. The figure was originally published by Walker and Lowe (2007) based on the data of Lisiecki and Raymo (2005).

al. 1995, Geist 1998). Early Pleistocene large mammals tended to be relatively generalistic, usually large species adapted to the climatic and environmental changes by flexible ecological strategies (Kahlke et al. 2010, Kahlke and Kaiser 2011), but towards Late Pleistocene, increasingly specialized glacial and interglacial chronofaunas (spatially and temporally shifting mammal assemblages with characteristic species and ecological guild compositions) evolved in Northern Eurasia when the species adapted to different environmental conditions, culminating in the typical Eurasian warm climate or forest adapted “*Palaeoloxodon antiquus* (straight-tusked elephant) assemblage” (Pushkina 2007) and the very specialised cold adapted mammoth steppe megafauna called the “*Mammuthus-Coelodonta* (woolly mammoth-woolly rhinoceros) faunal complex” by Kahlke (1999). The large mammals interacted with their environment and maintained partly open vegetated environments also in the otherwise

forest-dominated environments of Europe during the warm interglacial stages (Svenning 2002).

1.1 Diets, palaeodietary analyses and environments of ungulates

Mammals have adapted to their environments, and thus the species composition of mammal communities reflects environmental conditions. However, there is often considerable plasticity in the ecological strategies of species. During the Miocene (23 – 5 Ma) grassland environments started to spread over continents, especially in the Northern hemisphere, as the result of the gradual cooling and drying of climate. This created a strong selection pressure for herbivores to adapt to feeding on grass. In mammals, this was achieved by changes in the digestive system (e.g. Ilius and Gordon 1992, Gordon 2003, Clauss and Rössner 2014) and by increasing wear-resistance of the molar teeth, which are used for grinding food. Complex enamel patterns and increased crown heights (hypsodonty)

evolved in many large bodied grass-eating mammal lineages (Janis and Fortelius 1988, Fortelius et al. 2002, Janis et al. 2002, Janis et al. 2004, Fortelius et al. 2006, Janis 2008, Damuth and Janis 2011). Since the Miocene, grazing and mixed-feeding mammals have been abundant in open grassland and savanna-like environments, whereas the remaining closed forest environments have still been dominated by browsers and browse-dominated mixed-feeders (Gordon and Prins 2008). Traditionally in ecological and palaeoecological analyses specialized herbivorous ungulates have been classified into three dietary classes, which are browsers (less than 10 % of grass in diet), mixed-feeders (10 – 90 % grass in diet) and grazers (more than 10 % grass in diet) (Janis et al. 2002). In other words, browsers eat woody and non-woody dicotyledonous plants and grazers eat grass (Janis 2008). Mixed-feeders consume variable proportions of both browse and grass in their diet, and they comprise most of the recent ungulate species.

In diverse ungulate communities, such as the ones in African savannas today, there is typically a succession of species ranging from browsers to grazers (e.g. Jarman 1974, McNaughton and Georgiadis 1986, Janis 2008). This is also evident for Pleistocene palaeocommunities in Europe (see e.g. paper III). Browse and grass are quite different as food resources. Compared to browse, grass is more fibrous, contains phytoliths and may, depending on environmental conditions, gather more exogenous mineral particles, making it abrasive for teeth (e.g. Janis and Fortelius 1988, Fortelius and Solounias 2000, Fortelius et al. 2002, Damuth and Janis 2011). Browse is often more patchily distributed than grass, which is reflected in the grazers and graze-dominated mixed-feeders typically being numerous and gregarious “bulk feeders”, whereas the browsers are typically more scarcely dispersed, more

solitary and more selective feeders (Jarman 1974, Geist 1998, Gordon 2003, Janis 2008). Broadly the trend in the evolution of ungulate faunas since the Miocene has been towards increasing numbers of grazing-adapted species and subsequently a decline in the number of specialized browsing species, but the details are of course much more complex depending on local habitats and resources (Janis et al. 2002, Janis 2008). Dietary adaptations in extant (and Pleistocene Eurasian) ungulate families are variable. Deer (Cervidae) have in general retained relatively unspecialized, browse-based diets required for sufficient nutrient intake for the seasonal growing of antlers (Geist 1998). This is reflected in their relatively unspecialized, mostly low-crowned (brachyodont) and simple dentitions. Also rhinoceroses (Rhinocerotidae) have mostly retained browse-dominated diets and relatively brachyodont dentitions, but unlike the deer, some rhinoceros species such as the Pleistocene woolly rhinoceros (*Coelodonta antiquitatis*) and the extant African white rhinoceros (*Ceratotherium simum*) evolved into specialized grazers with relatively hypsodont dentitions (e.g. Janis 2008). Bovids (Bovidae) and advanced equine horses (Equidae), have thrived in Pleistocene and recent environments by mostly evolving towards increasingly specialized grazing diets (e.g. by increasing hypsodonty and dental complexity) (e.g. Janis 2008). Especially the equine horses are superior in their grazing adaptations (Janis et al. 1994).

Diets of herbivorous mammals are regulated not only by dietary adaptations of the species, but also, perhaps more importantly, by the availability of plants in their environment as well as by ecological relationships with other species. Thus, dietary analyses of fossil herbivorous mammals can provide essential information about the environments and ecological role of species and populations in fossil mammal assemblages.

Analysing palaeodiets of large herbivores from fossil assemblages is potentially a powerful tool not only for understanding the feeding ecology of species and populations of mammals but also for palaeoecological reconstructions based on the connections of the dietary ecology of mammals and their environments. The diet of an herbivorous mammal is not only determined by the dietary adaptations of the species, but also the environment the individual lives in. First, the production of different food stuffs in the environment limits the dietary choices. Second, competition from other herbivores for these food stuffs may prevent an individual from eating the optimal diet. The study of comparative ecomorphology is able to answer questions about the adaptations in species, whereas dietary analyses indicate the actual diets of individuals and populations.

Several methods for dietary analyses based on isotopic composition or tooth wear of fossil and extant mammals have been developed during the last decades, and they form the basis of research on dietary variations between and within species. Stable isotope fractions in tooth enamel offer proxy methods for dietary analyses of several mammal groups. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes differ in C3-photosynthesising plants and C4-photosynthesising plants, so they leave different isotope fractions on the teeth of herbivorous mammals eating them (Lee-Thorp & van der Merwe 1987, Cerling et al. 1997). Thus the diets of herbivorous mammals eating primarily C3-plants can be separated from those utilizing C4-plants, most of which are grasses, by analysing isotope fractions in tooth enamel. This methodology can of course only be used for comparing the fractions of C3 and C4 plants in the diets, but it is useful because strong C4 signal reflects diets based on grasses where C4 grasses dominate (Cerling et al. 1997). The method is, however, rather laborious, requires minor

damaging of the studied specimens for extracting enamel material for the analysis and may contain a risk of contamination. Furthermore, it only reflects the relative amount of C4 grasses in the tropical zone where most grasses are C4 photosynthesising.

The method called microwear analysis is the first proxy method for reconstructing diets of fossil mammals based on tooth wear (Walker et al. 1978), and it is based on counting the abundance of different kinds of microscopic scratches and pits on tooth enamel caused by different kinds of food objects. The hypothesis behind that method is that during the tooth wear abrasive plant material such as grass phytoliths cause long scratches on the worn enamel facets of the teeth, whereas browse does not in which case the microscopic wear pattern is more pitted. The benefit of this method is that it is applicable to virtually all kinds of mammals and it should give consistent results for mammals with very different tooth morphologies. However, the disadvantages are that this is a rather laborious method and it only reveals the last few meals of the animal instead of long-term average dietary signal. Furthermore, it has been suggested that other factors than diet, such as external soil material from the environment, may obscure the dietary signal provided by microwear analysis (Rivals et al. 2010). Ungar et al. (2003) developed a new practical method for analysing microwear surface textures by combining confocal microscopy with scale-sensitive fractal analysis (the dental microwear texture analysis, Scott et al. 2005). This methodological improvement has made dietary analyses based on microscopic tooth wear patterns objective compared to the original method based on visual counting of scratches and pits.

Mesowear analysis (Fortelius and Solounias 2000) is based on the empirical observation that increasing abrasiveness of plant material

(especially grasses) will wear the tooth cusps blunter and lower than non-abrasive plants which allow tooth-to-tooth wear (attrition) to maintain high occlusal relief and sharp cusps. Why grasses are especially abrasive on tooth enamel is still not totally understood, but whether it is because of high phytolith contents, external grit accumulating on grass leaves or even simply the coarse fibres of plant leaves (e.g. Lucas and Omar 2012, Damuth and Janis 2014, Lucas et al. 2014), the empirical basis of this observation is extensive (e.g. Fortelius and Solounias 2000).

The mesowear analysis is done by visually scoring the cusp shape as sharp, rounded or blunt and the relief (the relative height of the cusps) as high or low (figure 3).

When large samples of ungulate molar teeth are analysed, the mesowear scores reflect the relative amount of abrasive material (mostly grass) in the diet of the ungulate species and local populations/assemblages. The method is easy to use, it can be readily applied to fossil ungulate molars and it gives a robust signal of the abrasiveness of the diet of an herbivorous mammal over a relatively long period of its life.

Selenodonts and plagiolophodont equids

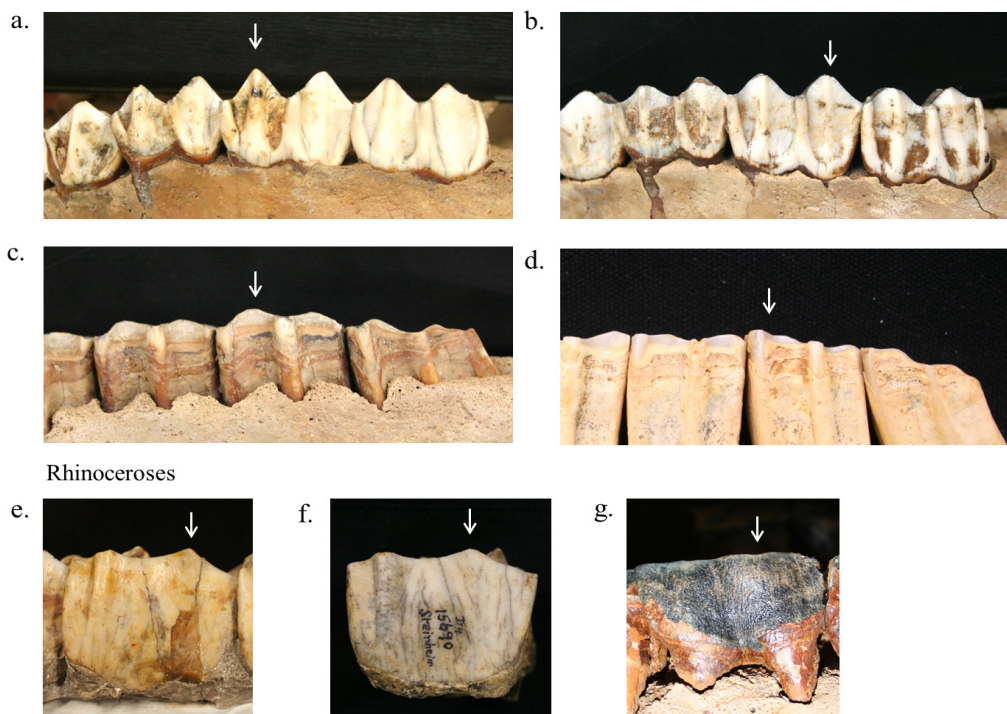


Figure 3. Examples of mesowear scoring of ungulate molars following the original methodology of Fortelius and Solounias (2000). The photos show the buccal (outer or cheek-side) view of upper molar rows (a – d) or second upper molars (e – g), and the arrows point at the sharper buccal cusp of the second upper molar, from which the cusp shape is observed. **Selenodonts and plagiolophodont equids** (high relief: cusp height/tooth crown length ≥ 0.1 ; low relief: cusp height/tooth crown length < 0.1): **a.)** high relief and sharp cusps, **b.)** high relief and rounded cusps, **c.)** low relief and rounded cusps, **d.)** low relief and blunt cusps. **Rhinocerotidae** (high relief: cusp height/tooth crown length ≥ 0.03 ; low relief: cusp height/tooth crown length < 0.03): **e.)** high relief and sharp cusps, **f.)** high relief and rounded cusps, **g.)** low relief and blunt cusps. The example specimens are: **a.)** *Megaloceros giganteus* (SMNS 6517.5.2.67.1), **b.)** *Megaloceros giganteus* (SMNS 6616.10.10.66.4), **c.)** *Equus ferus* (SMNS 6617.7.8.64.4), **d.)** *Equus ferus* (SMNS 31604, SE 19.2.57/10), **e.)** *Stephanorhinus kirchbergensis* (NHM 22020), **f.)** *Stephanorhinus cf. hemitoechus* (SMNS 15690), **g.)** *Coelodonta antiquitatis* (SMNS 6316.2.9.77.3). The photos are not in the same scale.

The mesowear method has been criticised for its subjectivity because each observer has to decide based on visual observation whether the cusp shape is sharp, rounded or blunt and whether the relief is high or low (although this can also be measured objectively), but blind tests have shown that this is not a big problem in practise because observers will mostly score mesowear similarly after a brief introduction to the method (Kaiser et al. 2000, Loffredo and DeSantis 2014).

Mesowear variables have been suggested to be correlated with environmental variables in extant equids (Kaiser and Schulz 2006), but only through the effect of climate on vegetation and thus diet abrasiveness, not by climatic variables as such (Schulz and Kaiser 2012). Several authors have been able to associate mesowear analyses of fossil mammals with the characteristics of their palaeoenvironments. Kaiser (2004) compared the mesowear signals of fossil populations of the early Late Miocene hipparionine horse *Hippotherium primigenium* from the localities of Höwenegg and Eppelsheim, Germany, and found significant differences between them. The fossil population of *H. primigenium* from Höwenegg shows very attrition dominated mesowear signal which indicates browsing diet, whereas the population from Eppelsheim shows rather abrasion dominated signal indicating “moderate grazing” diet. Following these results, based on the association of available resources and diets of herbivorous mammals, Kaiser (2004) suggested that the palaeoenvironment of Höwenegg was likely subtropical mesophytic forest, which is supported by the overall composition of the mammal fauna, whereas Eppelsheim would likely have included at least seasonally abundant grassy vegetation, which is supported by palaeobotanic finds. Similarly, Kaiser and Croitor (2004) suggested based mostly on the rather abrasion-dominated mesowear signal of the dominant species of deer (*Eucladoceros ctenoides*,

Praemegaceros obscurus and *Metacervocerus rhenanus*) that the palaeoenvironment of the Early Pleistocene locality of Ceysseguet, France, would have likely been open grassland with wooded areas near a lake. Kaiser and Kahlke (2011) found that the fossil population of the rhinoceros *Stephanorhinus hundsheimensis* from the glacial, probably relatively open vegetated, locality of Süssenborn was significantly more abrasion-dominated (indicating mixed-feeding diet) than the very attrition-dominated signal (indicating browsing diet) of the population from the forested interglacial locality of Voigtstedt in the early Middle Pleistocene of Germany. Croft and Weinstein (2008) used the mesowear method for palaeodietary analyses of endemic South-American ungulates from the Late Oligocene locality of Salla, Bolivia, and suggested based on the results that although the mesowear of the ungulates alone does not answer the question of the habitat in Salla, it indicates that the ungulates spent most of their time feeding in open habitats, and a semi-open environment is thus more likely than forest. The mesowear signals of the ungulate fauna from the Early Pliocene of Laetoli, Tanzania, are in general quite attrition-dominated, which does not indicate open grassland environment, but rather more woodland-type of vegetation (Kaiser 2011). Muhlbachler and Solounias (2006) analysed the evolution and dietary variations of oreodont artiodactyls (Merycoidodontidae) through their evolutionary history from Late Eocene to Late Miocene in North America, and found out that long-term changes in climate and vegetation patterns had shifted the mesowear signals of the oreodonts from relatively abrasion-dominated (probably fruit seed browsing in forests) to extremely attrition-dominated (leaf browsing, probably in more seasonal forests or woodlands) and finally to increasingly abrasion-dominated again (increasingly mixed-feeding in increasingly open habitats). A very similar pattern

was observed by Muhlbachler et al. (2011) for horses (Equidae) throughout their evolutionary history from Early Eocene to present times in North America. The earliest horses show a rather generalized, not purely attrition-dominated, mesowear signal which probably reflects rather generalistic fruit and leaf browsing diet. In the Oligocene to Early Miocene the anchitheriine horses of North America probably had shifted towards more specialized herbivorous diets based on dicotyledonous leaves, which is reflected as very attrition-dominated mesowear signals. From the later Miocene on, the mesowear signals of horses started to shift towards increasingly abrasion-dominated, probably as the result of the spread of grassland habitats and the increasing specialization of equine horses to utilizing grass as their diet. Yet another similar case of early generalism followed by increasingly specialised browsing diets was revealed by the mesowear analyses of Miocene deer (Cervidae) by DeMiguel et al. (2008).

More recently Bernor et al. (2014) analysed palaeodiets from the ungulate assemblage of the Late Miocene locality of Maragheh, Iran, and discussed how the dietary signals reflect what has been interpreted about the Maragheh palaeoenvironment based on the taxonomic composition of the fauna. The results are consistent with the taxon-based interpretation of a woodland habitat in the Late Miocene Maragheh. Eronen et al. (2014) did a complete mesowear analysis of the Late Miocene “*Hipparion* fauna” from several localities from Baode, China, which together with stable carbon isotopes mostly confirmed previous environmental interpretations but highlighted temporal and spatial differences within the localities. The mesowear analysis was applied by Viranta and Mannermaa (2014) for comparing the dietary signal of medieval domesticated horses from the archaeological site of Levänluhta, Finland, with the mesowear

signals of medieval horses from Estonia. The results indicate interesting differences between the medieval Finnish and Estonian horses, which are probably due to differences in the available fodder and could be caused by seasonal variations in the available plant material.

I suggest that any attempt to reconstruct environmental conditions in the past by analysing dietary signals of mammals should ideally include all the large herbivorous mammal species in the community (but not necessarily small mammals of less than ca. 1 kg of body mass, because their resource use does not necessarily reflect the large-scale vegetation patterns in the environments because they are able to utilize microhabitats which the larger species cannot). The term “community” is used here in the sense of a closely associated fossil assemblage of mammal species from a locality (palaeocommunity). I recognize that this type of community includes some time-averaging and does not strictly speaking correspond with extant communities (see e.g. Raia and Rook 2014). On the other hand, Pleistocene stratigraphy is often rather precise due to the rapidly changing conditions, and the mammal assemblages are often quite well associated. Moreover, the spatiotemporal averaging associated with fossil communities may in fact be beneficial for understanding the wider regional environmental conditions on which the processes of climatic and environmental changes operate. Dietary adaptations of species, competition (both within and between species) and dietary preferences (the food chosen by individuals depending on the quality and availability of food resources) are the underlying factors behind local variations in mammal diets. Different species behave differently under similar resource conditions. Some of the species may be very flexible and actively shift their diet according to available resources (generalists) whereas others may be

unable to shift to more abundant resources and rely on the less common elements of the available vegetation (specialists). The structure of the herbivore community is an important factor as well because of interspecific competition and even resource facilitation by other species can significantly affect local dietary preferences of a population of a species (see paper III).

As complete as possible dietary analyses of fossil mammal assemblages (and even extant communities) are challenging because of the lack of universally applicable, easy-to-use and, above all, consistent dietary analysis methods which could be used for all kinds of herbivorous mammal teeth. Microwear analysis (Walker et al. 1978) and microtexture analyses (Ungar et al. 2003, Scott et al. 2005) of fossil teeth offer a possible methodological frame for these kinds of extensive dietary analyses, but due perhaps to the relatively laborious procedures and the subsequent challenges in obtaining sufficient sample sizes, those methods have not yet been widely applied for studies covering whole mammal communities. Another approach would be stable isotope studies (Lee-Thorp & van der Merwe 1987, Cerling et al. 1997) and indeed they have been used for dietary analyses and comparisons of fossil populations and palaeocommunities (e.g. MacFadden and Cerling 1996, Cerling et al. 1997, Cerling et al. 1999, Nunez et al. 2010), but the limit of that method is that the results are not directly comparable with the extensive tooth-wear based analyses, and they are not globally comparable because they reflect plant photosynthesis types which in and around tropical latitudes include C4-photosynthesizing plants. The mesowear method (Fortelius and Solounias 2000), used in our studies for the dietary analyses of ungulates, would be a robust, rapid and highly consistent analysis method, but it has traditionally been limited for tooth morphologies from which the

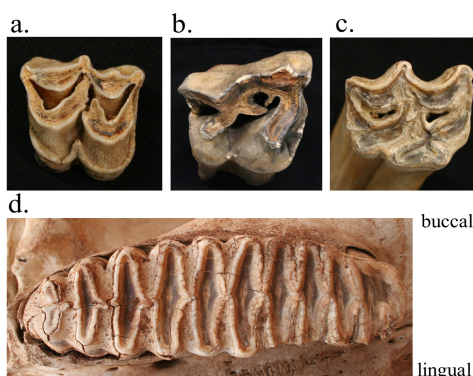


Figure 4. Molar tooth morphology types of some large herbivorous mammals. The photos show the occlusal surface (biting surface) of the teeth. **a.)** Selenodont morphology where the four cusps of the molar are elongated into crescent-shaped crests. This is the typical tooth morphology of ruminants. **b.)** (Ecto-) lophodont morphology where the anterior and posterior cusps are connected with transverse ridges (lophs) and an outer (buccal) loph forms a continuous enamel edge (ectoloph). This tooth morphology is typical e.g. for rhinoceroses and many archaic perissodactyls. **c.)** Plagiolophodont tooth morphology shows complex folding and fusing of the lophs but again there is a continuous outer enamel edge (ectoloph). This is the typical tooth morphology type of derived equine horses and some specialized rhinoceroses. **d.)** Loxodont or lamellar tooth morphology where the occlusal surface consists of multiple transverse lophs which form separate enamel loops when worn. This is the tooth morphology of derived proboscideans such as elephants. Note that the morphological types a.), b.), and c.) all have a continuous outer edge formed by enamel ridges, thus enabling wear facets to be observed in the traditional mesowear analysis (Fortelius and Solounias 2000), but in type d.) there is no continuous outer edge and wear facets cannot be observed visually as introduced for the traditional mesowear analysis. The example specimens are: **a.)** *Cervus elaphus* (SMNS 17010), **b.)** *Stephanorhinus kirchbergensis* (SMNS 6617.2), **c.)** *Equus ferus* (SMNS 880) and **d.)** *Loxodonta africana* (Tsavo Research Station, unlabelled skull). The photos are not in the same scale.

occlusal shape can be easily observed (molar teeth with continuous outer edge, such as the selenodont, ectolophodont and plagiolophodont teeth of ruminants and perissodactyls, see figure 4). The challenge of analysing diets from mammal teeth of different morphologies with a universally applicable and consistent way has led us to develop a method for Proboscidea, which I will introduce in this thesis. We developed a

macroscopic tooth wear -based dietary analysis method applicable for proboscidean molars (analogous to the mesowear analysis), which is based on measuring the occlusal relief of the molar teeth as an angle measured by placing the tips of the angles in the bottoms of worn dentine valleys and the sides of the angles as tangent to the top of the wear-resistant enamel ridges on the tooth surfaces.

1.2 Body size patterns of mammals and their connections with climate, environmental conditions and ecology

Body size is one of the most essential characteristics of all organisms and it has profound connections with most of their physiological characteristics and ecology, usually following allometric relations (e.g. Hemmingsen 1960, Peters 1983, Damuth and McFadden 1990, West et al. 1997, Gillooly et al. 2002, West et al. 2002). Understanding the patterns of body size evolution and the mechanisms which have driven those patterns are some of the most crucial questions for the understanding of mammal ecology and palaeoecology. The great challenge in understanding what ultimately drives body size evolution and fine-scale body size fluctuations in mammal species and populations is that body size is interconnected with several physiological and ecological variables, and the effects of these are often hard to separate in analyses.

Generalised “rules” based on empirically observed patterns form the basis for testing and refining hypotheses on the mechanisms behind mammal body size evolution. Metabolic rates increase with body size but less than proportional to the change in size following in general an approximately 0.75 power allometry (Hemmingsen 1960, Peters 1983). This basic physiological scaling of metabolism is reflected in energetic needs and means that the absolute energetic needs increase when body size

increases but the relative energetic needs per a unit of body mass decrease with increasing body mass. This leads to one of the significant benefits of large body size: increased fasting endurance (Lindstedt and Boyce 1985). Larger size also helps animals to survive shortages of water and to migrate more efficiently over larger distances and helps to avoid predation (Peters 1983). Diets and food processing of herbivorous mammals set limits on how large the species can grow. Larger mammal herbivores need relatively less energy and they have longer ingesta passage rates than smaller ones because of their large gastrointestinal tract capacity, and because of that large size is beneficial for utilizing large quantities of poor-quality food (Clauss et al. 2003). However, there are limits on how large the gastrointestinal tract can grow without resulting in too long passage times of food so that the energetic costs associated with food processing exceed the energy obtained from the plant food. Hindgut fermenting herbivores, such as perissodactyls and proboscideans, have larger maximum sizes than ruminants, because in ruminants, the specialized foregut-fermenting gastrointestinal tract limits the food passage rates and it would not be efficient above the probably ca. 2000 kg maximum size of ruminants (Clauss et al. 2003).

Cope’s rule, attributed to E. D. Cope (1887, 1896) and discussed e.g. by Rensch (1954), Alroy (1998), Polly (1998) and Raia et al. (2012) is based on the empirical observation that there has mostly been a tendency of increasing body size in clades throughout their evolution. The pattern is supported by statistical analyses for most mammal lineages (Alroy 1998, Raia et al. 2012). The suggested mechanism behind Cope’s rule is that mammals have expanded into the niches of large sized terrestrial vertebrates left vacant by the extinction of large non-avian dinosaurs at the Late Cretaceous mass extinction. However, it has

been debated whether the increasing size trends in mammals were caused by active selection towards larger sizes or whether they were more of a by-product of ecological specialization. Raia et al. (2012) suggested that ecological specialization and the subsequent clade-level niche expansion explains Cope's rule rather than active selection of larger size, but on the other hand they recognise that adaptation to changing climatic and environmental conditions during the Cenozoic has had a significant role in shaping the fine-scale evolutionary changes in mammal body size. Raia and Fortelius (2013) further emphasized that larger body sizes tend to evolve as a result of specialisation, and they connected Cope's rule with the wider idea of the "Law of the Unspecialised" (Cope 1896), which notes that evolutionary novelties are in general more likely to originate from a generalised rather than a specialised ancestor. Evans et al. (2012) showed that decrease in the body size has happened much faster in mammal evolution than increase in maximum size, which suggests that it would be easier for large mammals to evolve into smaller than into larger size. However, increase in body size has been the dominating trend in most lineages. This suggests that the evolution of larger sizes has to have significant benefits for mammals.

The hypothesis known as "Bergmann's rule", formulated by Bergmann (1847), which states that endothermic animal species tend to be larger at higher latitudes and colder climates than their closest relatives at lower latitudes and warmer temperatures, is one of the most well-defined ecogeographic rules, and it was the first one to suggest a well-defined mechanism behind the observed body size variations in endothermic animals. The original mechanism suggested by Bergmann (1847) is heat conservation: larger animals have smaller surface area in relation to their body volume, which prevents loss of heat

from the body under low ambient temperatures. The original, interspecific, endotherm-based form of the rule (Bergmann 1847) was extended by Rensch (1938) and Mayr (1956) to include intraspecific body size variations and ectothermic animals, thus stating that the rule is rather a universal phenomenon regardless of the mechanism behind it (see also Blackburn et al. 1999). If the mechanism were heat conservation, it would have to apply only for endothermic animals which are able to actively regulate their body temperature. It has been suggested that global climatic cooling has driven, or at least affected, the large-scale patterns of body size evolution in mammals after the initial burst in body size increase after the Late Cretaceous mass extinction (paper I, Raia et al. 2012, 2013, paper II).

Since the origins of the Bergmann's rule it has been tested by several authors with the special emphasis on what the actual mechanism behind the rule is. Already Scholander (1955, 1956), Irving (1957) and Hayward (1965) criticised the idea of heat conservation as the mechanism explaining the tendency of mammals to be larger in higher latitudes and colder climates, saying that body size increase alone would not give sufficient benefit in heat conservation, and instead mammals living under cold climatic conditions have far more efficient ways to adapt to coldness (insulation and behavioural adaptations). Since then most of the tests on Bergmann's rule, and spatial as well as temporal variations in body size, have agreed that although there is a tendency of closely related species (or populations) of mammals and most other animals to be larger in high latitudes (e.g. Blackburn et al. 1999, Ashton et al. 2000, Meiri and Dayan 2003, Freckleton et al. 2003, Blackburn and Hawkins 2004, Clauss et al. 2013), this tendency is not at all conclusive and the heat conservation mechanism alone does not explain the variation in mammal body sizes

(e.g. Rosenzweig 1968, McNab 1971, Geist 1987, Dayan et al. 1991, Lister 1992, Meiri et al. 2004, Meiri et al. 2007, Wolverton et al. 2009, McNab 2010, Ho et al. 2010, Clauss et al. 2013). Not only coldness but also other kinds of “harshness” of the climate (such as increased aridity and seasonality) could explain why mammals tend to be large under such conditions. Large body size can increase resistance to seasonal lack of resources. It has been suggested that large size increases fasting endurance in large mammals, because it increases possibilities to store energy reserves in the body and is thus beneficial under climatic conditions where there are seasonal shortages of food (e.g. cold or dry seasons) (Lindstedt and Boyce 1985, Millar and Hickling 1990). Moreover, bovid species feeding unselectively on food items which are widely distributed and of relatively poor but constant quality (mostly grazers) tend to be larger than the species feeding selectively on more scattered plant items with more variable quality (mostly browsers) (Jarman 1974). Harsh (low temperature and low precipitation) climatic conditions, which have favoured grassland environments (see Guthrie 2001, Fortelius et al. 2002) could thus have favoured large sized, unselective feeders, which can partly explain the occurrence of particularly large species in the Pleistocene. Large size can also help mammals to survive under shortages of water, because the relatively small surface area in relation to body volume helps prevent evaporation of water from the body (Peters 1983). Furthermore, larger mammals can migrate relatively more efficiently over larger distances, which may help them to avoid local resource shortages (Peters 1983).

Despite the complexity of potential mechanisms affecting mammal body size, we are finally close to understanding what has mainly regulated the body size variations during mammal evolution, and the research

presented in this thesis has brought new support and insight into this understanding. Several authors have noted that it is most likely not temperature or any other climatic variable as such, but resource availability regulated by climate, seasonality, population densities of the species and competition between species, which explain most of the individual body size variation in mammal species (Rosenzweig 1968, McNab 1971, Geist 1987, Dayan et al. 1991, Meiri et al. 2007, Wolverton et al. 2009, McNab 2010, Clauss et al. 2013). The cold climates of the Pleistocene paradoxically created at least seasonally highly productive plant communities (e.g. because of the fertile soils created by glacial erosion and enhanced by the activity of the large mammals, see Zimov et al. 1995 and Geist 1998) and improved the digestibility of the plants reducing their morphological and chemical defences (Langvatn and Albon 1986, Geist 1998, Ho et al. 2010), which would have provided enough energy and nutrients for the large herbivores to grow into large sizes. Geist (1987) noted that the body size of large mammals increases towards higher latitudes up to 53° – 65° N but north from that it rapidly declines so that the smallest individuals of a species tend to live at the lowest and the highest latitudes. This does not make sense for the heat conservation hypothesis, but instead it can be explained by the availability of energy and nutrients during annual growth seasons. Meiri et al. (2007) supported this interpretation noting that in North American carnivores the body size patterns clearly follow the patterns of food availability and quality: body size of the brown bear (*Ursus arctos*) is not correlated with latitude but with the distance to the nearest salmon spawning area, whereas the body size of the wolf (*Canis lupus*) does increase with latitude up to ca. 60° – 65° N because the size and availability of its prey is similarly correlated with latitude. McNab (2010)

made a thorough summary demonstrating how resource availability ultimately could explain all the major “rules” associated with mammal body size patterns, including Cope’s rule (tendency to increase in size throughout evolution), Bergmann’s rule (tendency of being larger at higher latitudes and colder climates), Dehnell’s phenomenon (tendency of some small mammals to prepare for resource shortages during winter by reducing their body size), the “Island rule” (tendency of small mammals to get larger and large mammals to get smaller on islands) and the tendency of some mammals to be small in desert habitats. Small mammals can only utilize energy rich resources (e.g. insects, meet or seeds) for maintaining their high mass-specific metabolic rates, but these resources can be relatively hard and possibly dangerous to obtain. Larger size is required for herbivorous mammals, because they need to have low enough mass-specific metabolic rates in order to take advantage of the low-quality, digestively challenging plant material such as dicotyledonous leaves and grass, which provide an easily accessible, relatively abundant and stable food resource.

The quality of plant food of herbivorous mammals (e.g. chemical defences and protein contents) varies across latitudes and tends to be better under cold, seasonal conditions (Bolser and Hay 1996, Siska et al. 2002, Wright et al. 2004). Langvatn and Albon (1986) suggested that increasing quality (energy contents) of plant food with decreasing temperature and precipitation, could alone explain the body size pattern of Norwegian red deer (*Cervus elaphus*), which shows increase in size from south to north and from coast to inland. Further support for this hypothesis was provided by Ho et al. (2010), who were able to show that plants consumed by herbivorous invertebrates collected from high latitudes tend to provide better energy and nutrient supplies for the growth of the species.

Furthermore, it seems to be diet quality, not latitude as such, which explains the body size variations in the species, because exceptions to the latitude-body size correlation were explained by latitude-independent differences in the nutritional quality of the plant food.

Not only productivity and quality of available plant food, but also population densities of herbivorous mammals are an important factor regulating resource availability and thus body size patterns of the mammals. High population densities may limit the amount of resources available for each individual, which can restrict individual body sizes. This has been demonstrated to be the case for several extant ungulate populations, including reindeer (Skogland 1983), feral donkeys in Australia (Choquenot 1991) and roe deer (Toïgo et al. 2006), and for temporal changes in the population density and body size of white-tailed deer in Fort Hood, Texas (Wolverton et al. 2009).

Another factor which could significantly affect body size is interspecific competition. Several authors, e.g. McNab (1971), Dayan et al. (1991) and Clauss (2013) have suggested that competition between ecologically similar species, leading to character displacements in body size, would affect body size patterns of carnivorous mammals, which could explain why Bergmann’s rule does not explain the body size variation of all species. The term “character displacement” (Brown and Wilson 1956) refers to the tendency of ecologically similar sympatric species to avoid competition by differentiating in one or more ecomorphological features through evolution or plastic changes in morphology.

In this work I analyse the patterns of long-term body size evolution of mammals as well as local variation of body size and diet of Pleistocene European ungulates in relation to climatic, environmental and vegetation changes, and discuss the mechanisms behind the patterns.

2. Overview of the original publications

2.1 Paper I: The evolution of maximum body size of terrestrial mammals (Smith et al. 2010)

In this study a dataset of maximum body mass estimates of terrestrial mammal orders per each subepoch time bin of the Cenozoic was used to analyse the evolution of total maximum body size in terrestrial mammals throughout the Cenozoic globally and on continents separately. The results showed an exponential increase in the maximum body size at the early phase of the Cenozoic following the Late Cretaceous mass extinction. After ca. 40 Ma (Middle Eocene) the increase in maximum size levelled off and started fluctuating. The early burst in maximum size evolution was driven by the diversification of mammals to the niches of large terrestrial vertebrates left vacant by the extinction of large non-avian dinosaurs. The fluctuations in maximum size since ca. 40 Ma correlate with fluctuations in global temperatures and land area, suggesting that phases of climatic deterioration have favoured the evolution of especially large sized terrestrial mammals. The patterns of maximum size evolution and the upper limits of maximum size are highly congruent on different continents and between different orders and trophic groups of mammals. These findings suggest that the factors driving the maximum size evolution of mammals have been global.

2.2 Paper II: Patterns of maximum size evolution in Cenozoic land mammals: intrinsic biological processes and extrinsic forcing (Saarinen et al. 2014)

This study follows the Smith et al. (2010) study (paper I) on maximum body size evolution of terrestrial mammals during the Cenozoic, which

already pointed at highly congruent patterns of maximum size evolution on each continent and between different mammal groups. In this study the evolutionary patterns and the temporal occurrence of maximum size in terrestrial mammal orders were studied globally and on continents separately. They were compared with global changes in abiotic conditions such as temperature, land area and atmospheric oxygen percentages. This was done in order to analyse whether the large-scale, global drivers of maximum size evolution have been extrinsic forcing by changing abiotic conditions or basic biological processes such as the filling of the niches of large terrestrial animals at similar pace in different groups.

2.3 Paper III: Patterns of body mass and diet of large ungulates from Middle and Late Pleistocene of Western Europe and their connections with vegetation openness (Saarinen et al., in review)

In this study variation in diets and body sizes of key ungulate species and assemblages from Middle and Late Pleistocene localities were compared against vegetation proxies (pollen records). The questions to be answered were how local vegetation patterns (particularly vegetation openness) are connected with dietary preferences and body size of the ungulate species, and what ultimately regulates body size and diet in different ungulates species. Mesowear analysis was used as the dietary analysis method and univariate mesowear values were calculated for the comparing of dietary signals and vegetation openness (non-arboreal pollen percentages in pollen samples associated with the mammal assemblages). Regression equations based on linear measurements of postcranial bones were used for body mass estimates of the ungulate species.

Averaged mesowear values of all key

species combined in the ungulate communities are significantly correlated with vegetation openness (non-arboreal pollen percentages) of the palaeoenvironments of the localities. This indicates that average diets in ungulate communities reflect available resources, and to a certain extent the structure and average dietary signals of ungulate communities can be used as proxies of vegetation structure. There are, however, significant differences in the dietary adaptations of different ungulate species. Whereas most of the species show positive correlations between mesowear values and non-arboreal pollen percentages, some species, particularly the red deer (*Cervus elaphus*), do not show any correlation between mesowear and non-arboreal pollen percentages of their habitats. This probably points at the role of interspecific competition affecting the local dietary preferences of ecologically flexible species.

Body masses of the key ungulate species are highly variable and their connections with the vegetation structure are not uniform. This reflects differences in basic ecological strategies of the species. Species which tend to have small group sizes, such as deer and rhinoceroses tend to have larger mean body masses in open than in closed habitats, whereas gregarious species which tend to form large groups in open habitats, such as horses, tend to be smaller in open than in closed habitats. This result supports the idea that resource availability, affected by population densities, is the most important factor regulating mammal body sizes. Increased diet quality and availability, easy manoeuvrability and possibly better ability to avoid predation are the most likely factors favouring larger body size in open habitats in species which retain relatively small group sizes in open habitats (such as deer), whereas open-adapted gregarious species such as horses may increase their group sizes and population densities in open habitats resulting

in reduced resource availability for an individual, thus decreasing individual body masses through these resource limitations.

2.4 Paper IV: A new tooth wear-based dietary analysis method for Proboscidea (Mammalia) (Saarinen et al., in press)

In this study we introduced a new approach for palaeodiet analyses of lamellar toothed proboscideans, such as elephants, based on macroscopic wear-induced morphology of the occlusal surfaces of molar teeth. The method is in principle similar to the mesowear analysis where relief and shape of the cusps of worn molars are used for analysing the abrasiveness of plant material consumed by the herbivorous mammals. Abrasive plants such as grasses cause lower reliefs and increasingly blunted cusp shapes. In its original form the mesowear method is based on simple visual scoring of cusp relief and sharpness, and it can only be used as such for selenodont, ectolophodont and plagiolophodont molars. Proboscidean molars have specialized lophodont and lamellar tooth morphologies unsuitable for traditional mesowear scoring. However, abrasive plant matter and tooth on tooth occlusion should result in different occlusal relief in proboscidean molars as well.

We decided to measure occlusal relief of the proboscidean molars as angles measured by placing the tip of the angle at the bottoms of worn dentine valleys within the central lamellae of the molars when the sides of the angles are placed as tangent to the top of the enamel ridges surrounding the worn dentine valleys. The larger the angles are the lower is the occlusal relief indicating presence of abrasive plant material (mainly grass) in the diet. We tested the new method by comparing the results with results from stable carbon isotope analyses from tooth enamel in fossil and extant East African and

Asian tropical proboscidean populations. In tropical areas the stable carbon isotope ratios are a proxy of abrasive C4 grasses in diet. The results indicate that averaged mesowear angle values in the proboscidean populations are strongly and significantly correlated with the isotope values, giving support to the method.

The main motives for this approach are that it is the first easy-to-do method which does not require expensive laboratory equipment (only an angle meter is needed), it can be easily and instantly applied to any fossil or extant molar tooth sample, it is highly robust and enables consistent comparing with tooth wear -based dietary analyses from populations across the world and from other large herbivorous mammals.

3. Discussion

In this thesis I examine mammal body size evolution before and during the Pleistocene and go deeper in to analysing spatiotemporal variations in body size and dietary preferences of Pleistocene ungulates in Europe. I seek to answer the questions of how climate has affected diets and body sizes of mammals in the Pleistocene, and whether it is climatic factors as such or environmental changes launched by climate changes that have had the most drastic effects on mammal diets and body sizes.

3.1 Diets of Pleistocene ungulates and their connections with the structures of vegetation and mammal communities

Local variations in ungulate diets reflect dietary adaptations of the species but also environmental conditions through the availability of resources and competition with other herbivore species.

Vegetation structure in various environments is profoundly affected by climatic conditions, and characteristics of ungulate communities (such as species composition and dietary signals of the species) reflect climatic conditions via the link between the vegetation and climate (paper III). Strong and often rapid cyclic fluctuations in global climate are characteristic for the Pleistocene Ice Ages. Plant and animal communities were constantly changing and shifting their distributions. Dietary analyses of ungulates from the Pleistocene localities in Europe, and their comparisons with associated vegetation (analysed from pollen records) give valuable information on how average dietary signals in the ungulate communities as well as dietary fluctuations within ungulates species reflect local vegetation patterns and, indirectly, climatic conditions (paper III).

3.1.1 Ungulate diets in relation to environmental conditions and structures of vegetation and mammal communities

For the analyses in paper III, univariate mesowear values were calculated based on the scored relief and sharpness of the tooth cusps in order to enable comparisons with non-arboreal pollen percentages from pollen samples associated with the ungulate assemblages. The higher the values are, the more there are abrasive components (primarily grass) in the diet of the ungulate species or population analysed. This approach of transferring mesowear scorings to univariate mesowear values from 1 (extremely attrition-dominated) to 3 (extremely abrasion-dominated) is similar to that of Rivals et al. (2007), but instead of counting the values as a numeric ranking of the combinations of relief and cusp shape, we calculated them as means of “mean relief values” and “mean shape values”, thus allowing all possible relief -cusp shape combinations to contribute to the mean value.

Other methodological extensions in mesowear scoring and measuring have been developed and successfully used for palaeodietary analyses (e.g. Mihlbachler et al. 2011, Loffredo and DeSantis 2014, Solounias et al. 2014), but we decided to retain the original mesowear scoring methodology of Fortelius and Solounias (2000) because of its simplicity and because it has been shown to give quite robust results and to resolve diets consistently for extant ungulate species and communities (e.g. Fortelius and Solounias 2000, Kaiser et al. 2000, Clauss et al. 2007, Louys et al. 2012, Schulz and Kaiser 2012).

The results of paper III show that the averaged mesowear values in the Middle and Late Pleistocene European ungulate communities are significantly positively correlated with the non-arboreal pollen percentages of the pollen records associated with the fossil ungulate assemblages. This indicates that the average dietary signal of the community reflects local vegetation openness in the past environments. The comparisons of ungulate diets with habitat openness must be interpreted with some caution, because it is often difficult to find representative fossil pollen samples which can be directly associated with fossil mammal assemblages (paper III). However, we considered this approach worth trying and managed to assemble a reasonable data set of non-arboreal pollen percentages associated with the fossil mammal assemblages, although the data are heavily biased towards interglacial assemblages which may in fact reduce some of the variation in the signal.

Despite the generally positive correlation between the mesowear values of the ungulates and environmental openness, there are drastic differences in the feeding adaptations and ecological strategies of ungulate species. This is clearly shown by the results of paper III. The mesowear signals of the key species in Middle and Late Pleistocene of Europe are highly

consistent with what is known of the diet of those species in extant populations, or of probably ecologically similar species. This is reassuring and demonstrates the robustness of mesowear analysis as a dietary analysis method applicable for fossil mammal populations. Most of the key species analysed show positive correlations between mesowear values and the non-arboreal pollen percentages of the environments. This indicates that ungulates tend to shift their diets according to available resources. However, there are generally too few data points, too little variation in the associated pollen data available or too much random variation in the mesowear values for these intraspecific correlations to be statistically significant. There are important exceptions which are clearly due to differences in ecological strategies. The reindeer (*Rangifer tarandus*) has altogether very low (attrition-dominated) mean mesowear values even if it occupied the most open environments of all the deer species, which demonstrates that it has been in the Pleistocene, like today, a specialized open-adapted browser. The wild horse (*Equus ferus*) represents a very different dietary strategy. Despite a weak positive correlation between mesowear values and habitat openness, *E. ferus* maintains a rather abrasion-dominated mesowear signal even in relatively closed, forested habitats, suggesting that it selected a significant amount of grassy vegetation even where such vegetation was scarce. Some key species, most notably the red deer (*Cervus elaphus*), do not show any evident correlation of its mesowear signal with vegetation structure even if it does show some variation in the mesowear values. Instead, the results suggest that the ecologically flexible *C. elaphus* could have shifted towards more abrasion-dominated diets under conditions where it had to compete with other ungulates with browse-dominated diets, especially the roe deer (*Capreolus capreolus*),

which seems to retain very attrition-dominated, browsing dietary signal in all kinds of habitats. This interpretation is supported by observations of resource competition between *C. elaphus* and *C. capreolus* in extant populations (Gebert and Verheyden-Tixier 2001). The role of resource facilitation by other ungulate species is much less obvious, but it can have a role in the complex interspecific relationships as well. For example, it has been suggested based on observation from Scotland that grazing by cattle could improve forage availability for the red deer (*C. elaphus*) (Gordon 1988).

3.1.2 Proboscidean diets in the changing environments of the Pleistocene – introducing the mesowear angle method for dietary analyses of elephants and their relatives

Because of the different feeding strategies of different ungulate species, I suggest that averaged dietary signals of as complete herbivorous mammal communities as possible should be used when attempting to reconstruct palaeoenvironmental conditions based on dietary signals of mammals. The mesowear analysis method in its original form is limited to ungulates with selenodont, ectolophodont or plagiolophodont molar tooth morphologies (such as ruminants, horses and rhinoceroses, see figure 4), because they have continuous buccal margins and “ectolophs” from which the relief and shape of the macroscopic wear facets of the tooth cusps can be observed. This leaves some significant herbivorous mammal groups out of the scope of traditional mesowear analyses, such as bunodonts (e.g. pigs and primates) and bilophodont and other molar morphologies with transverse lophs (e.g. tapirs and elephants).

To open possibilities for including elephants and other proboscideans in the community-level palaeodietary analyses based on macroscopic tooth wear, we developed a new tooth wear

-based dietary analysis method for Proboscidea, which is similar in principle to the mesowear analysis (paper IV). Elephants particularly have specialized lamellar molars and fore-aft chewing, which makes it impossible to utilize anything like the traditional mesowear method where the wear-induced shape and relief of the occlusal surface of molars is visually inspected. However, elephant molars should follow the same mechanical principles of tooth wear as those of other herbivorous mammals, so the hypothesis is that increasingly abrasive plant material causes heavy wear on the wear-resistant enamel structures on the molar surfaces equalizing the wear rates of enamel and dentine, and thus lowering the relief (the relative height of the enamel ridges on the tooth surface). We measured the occlusal relief of the molars of elephants and other lamellar-toothed proboscideans as angles from the bottoms of worn dentine valleys as described in paper IV, and used the mean angles of the central lamellae as kinds of mesowear values. We then compared these mean mesowear angles with stable carbon isotope values sampled from tooth enamel from the same extant and fossil proboscidean populations from tropical Africa and Asia, and found a strong positive correlation between the mean angles and the isotope values at the level of populations. Because the stable carbon isotope values reflect the amounts of C4-photosynthesizing plants (mostly grasses which should cause heavy abrasion on teeth) in proboscidean diets in tropical zone (Cerling et al. 1997, Cerling et al. 1999), we conclude that the mesowear angles work as a proxy of diet abrasiveness in proboscideans. Comparison of mesowear analysis with stable isotopes was similarly used for testing the mesowear results of African ruminants (Louys et al. 2012) and the hipparionine equid *Cormohipparion emsliei* from Early Pliocene of Florida (Loffredo and DeSantis 2014), and also these studies found significant

correlations between the mesowear and isotope data. Interestingly, Loffredo and DeSantis (2014) noted that the results from mesowear analysis and isotopes are highly congruent at the level of populations, but not when individual specimens are compared. This is similar to our results of the comparison of mesowear angles and isotopes in the proboscideans: at the population-level the correlation is very strong, but it is much weaker and rather dubious when individual specimens are compared. The most likely explanation for this is simply that the isotope values and the mesowear signal are not formed simultaneously in the teeth, and thus they do not record exactly the same dietary signal for an individual because an individual's diet can vary during its lifetime and according to seasonal availability of resources. However, when the isotope data and the mesowear data are averaged over the populations, they both record the same average dietary signals.

The tooth wear data give much more consistent and globally comparable results than stable carbon isotopes, because they indicate abrasive diets (\approx grazing) independently of the signal of C4-photosynthesizing which only indicates grazing in the tropical zone where C4-grasses are dominant. Above ca. 40° N there are no C4-photosynthesizing plants, so north from that the carbon isotope ratios as such do not tell much about the characteristics of the plant diet. Also in the areas where C4-grasses do occur, tooth wear data can resolve abrasiveness caused by C3-grazing when the results are compared with the isotope data (C3-grazing is likely when the tooth wear data indicates abrasive diet but the carbon isotope values do not indicate the presence of significant C4-component in the diet).

Dietary analyses of extant and fossil Proboscidea have been done using stable carbon isotope analyses (Cerling et al. 1999,

Cerling et al. 2004, Nunez et al. 2010, Rivals et al. 2010, Pérez-Crespo et al. 2012) and dental microwear analyses (Capozza 2001, Filippi et al. 2001, Rivals et al. 2012), but altogether palaeodietary analyses for this group have yet been few, possibly because of the laboriousness of the available methods. The “mesowear angle” method introduced in paper IV is fast, easy-to-do, non-destructive and inexpensive, and it can be instantly applied to large samples of fossil proboscidean teeth. I believe this method will offer a great chance to expand the tooth wear-based dietary analyses of Proboscidea, and it also provides an opportunity to compare dietary signals based on macroscopic tooth wear with those of ruminants and perissodactyls for which a lot of mesowear analyses have been done.

The most comprehensive palaeodietary analysis of fossil Pleistocene proboscideans from Northern Eurasia and North America was done by Rivals et al. (2012) based on dental microwear analyses. The results of that study demonstrate that there was considerable plasticity in the diets of the mammoths (*Mammuthus sp.*) and the straight-tusked elephant (*Palaeoloxodon antiquus*), and most of the species were able to shift their diets according to changing resources and competition with other proboscidean species. The American mastodont (*Mammuth americanum*) was an exclusive browser as shown by the microwear of its molars, which was expected based on features such as the relatively simple, brachydont molars of this species. Interestingly, in Europe the two lineages of Pleistocene elephants, the straight-tusked elephant (*Palaeoloxodon antiquus*) and mammoths (*Mammuthus trogontherii/primigenius*) show opposite temporal trends in their diets, which could indicate niche separation of these competing taxa. The mammoths seem to have started as browse-dominated feeders in the Early and Middle Pleistocene shifting towards increasingly grazing diets towards Late

Pleistocene, whereas *P. antiquus* seems to have been a graze-dominated mixed-feeder in the Middle Pleistocene and shifted to browsing in the Late Pleistocene. I believe it will be worthwhile in the future to integrate the new mesowear angle approach with the microwear analyses to get a more complete and extended picture of the dietary variation in the northern hemisphere high-latitude proboscidean populations during the Pleistocene.

The diet of the Columbian mammoth (*Mammuthus columbi*) in the Pleistocene of North America appears highly variable based on the microwear study of Rivals et al. (2012) ranging from browsing to grazing. Stable carbon isotope data of this species from Mexico (Nunez et al. 2010, Pérez-Crespo et al. 2010) indicate diets heavily dominated by C4-photosynthesizing grasses in these arid, southern populations of the species. Preserved gut contents and dung of *M. columbi* from Wasatch Mountains, Utah (Gillette and Madsen 1993), and from Bechan and Cowboy Caves, Colorado Plateau, Utah (Mead et al. 1986, Hansen 1980), show that the diet of those individuals was also heavily dominated by grasses and sedges although woody plants were taken as well. As a case study of an elephant species outside the tropical “C4-zone” we applied the new mesowear angle method for analysing the diet of the fossil population of *M. columbi* from the Late Pleistocene locality of Rancho la Brea, California (paper IV). The result indicated highly abrasive average diet for the Rancho la Brea mammoth, although there is considerable variation. Thus we suggest that *M. columbi* had very grass-dominated diet in Rancho la Brea, which is well in concert with the results from the populations of this species from Mexico and Utah.

3.2 What has driven body size evolution in mammals before and during the Pleistocene? – the roles of climate, resource availability, population density and competition

3.2.1 Climate and maximum body size evolution of mammals during the Cenozoic

At the long term, macroecological scale (globally throughout the Cenozoic), the main question in this thesis is what has driven body size evolution in mammals, and more precisely, has it simply been a continuing process of body size increase as a result of the species filling the niches of large sized terrestrial animals since the extinction of large non-avian dinosaurs (the “Cope’s rule” hypothesis), of whether global climatic and environmental changes have driven the patterns (the “Bergmann’s rule” hypothesis). The results of the papers I and II, as well as others (Raia et al. 2012, Raia et al. 2013) suggest that the initial exponential growth phase (ca. 65 Ma – 40 Ma) in maximum as well as mean body size of mammals was caused by rapid filling of niches (as suggested by Cope’s rule), but after that it starts to fluctuate following global changes in climate so that period of cooling have favoured particularly large body sizes in most of the lineages (as suggested by Bergmann’s rule). This result is robust as it has been reached by several studies using different approaches concerning both materials and methods. Paper II shows that the frequency of maximum body size in terrestrial mammal orders peaked significantly in Middle Eocene when several archaic orders reached their maximum size after the “early burst” phase in mammal body size evolution, and the next significant peaking does not occur until Late Pliocene and Pleistocene, which indicates that the largest species of the few surviving “modern” orders mostly evolved during the Plio-Pleistocene, after a long phase of relatively low

maximum size frequency. This result, which is highly congruent at each continent, suggests that the harsh climatic and environmental changes of the Pleistocene Ice Ages favoured the evolution of very large sizes in mammals. The climatic cooling and drying, and increased seasonality, had positive effects on plant productivity and quality, created extensive open habitats and caused strong seasonal variations in resource availability (e.g. Zimov et al. 1995, Geist 1998, Guthrie 2001). Ability to survive harsh climatic conditions, adaptation to seasonal variations in resource availability (from seasons of high productivity and resource quality to severe shortages of resources), relatively high overall plant productivity and improved manoeuvrability and gregariousness in open habitats could all partly explain the tendency of several terrestrial mammal groups to evolve into especially large forms during the Pleistocene.

3.2.2 Spatiotemporal variations in body mass in Pleistocene ungulate populations

Even if the large-scale, global and regional climatic and environmental changes had affected body size evolution at the long-term, macroevolutionary scale, short-term geographical variations in mammal body size at the level of populations and closely related species could have ultimately been regulated by much more complex sets of factors. It has become increasingly clear that the main mechanism driving the short-term variations in mammal body mass at the level of populations is resource availability, which depends on primary productivity and the quality (energy and nutrient contents) of plant food, but is also affected by population densities of the species (intraspecific competition), interspecific competition, predation and in some cases even by facilitation relationships between the mammal

species. Resource availability often correlates with climate (e.g. Geist 1987, Geist 1998) and this may explain why the correlations of body size and latitude (or cold climate) are relatively common but not enough to offer a conclusive explanation of the body size variations.

The results of paper III support the hypothesis of resource availability as the key factor which has driven local body size variations of the key ungulate species in the Middle and Late Pleistocene of Europe. Overall, none of the species analysed shows any clear indication that larger mean body masses in their populations would have been driven by cold climatic conditions, but instead there are connections between mean body size and vegetation structures of the localities, which probably reflect different ecological strategies and the effect of population densities and resource availability for the mean body size of the species. Of the species analysed in paper III, the abundant and ecologically quite flexible red deer (*Cervus elaphus*) especially shows on average larger body size in open than in closed habitats. This pattern is evidently not restricted to cold climate localities which usually had open vegetation, but it shows that large size *C. elaphus* also occurred at relatively warm but open-vegetated localities (e.g. Barrington and Gough's Cave in Britain). This finding certainly does not support the heat conservation hypothesis as the mechanism driving the body size pattern, but instead indicates that large body size has been beneficial for the species in open environments. Dietary analyses of *C. elaphus* indicate browse-dominated mixed-feeding (paper III). It is likely that this species was able to grow into large sizes in open environments by feeding unselectively on the abundant, equally distributed vegetation, and its population densities may have remained relatively low in the open habitats compared to more open-adapted species such as horses and bison. It is of course problematic to make

predictions of the role of population densities in the case of fossil populations, but it is reasonable to expect that open-adapted, gregarious species have higher population densities in open habitats than the more generalistic or close-adapted species. Langvatn and Albon (1986) suggested that body size in Norwegian red deer is positively correlated with food quality, which is high under climatic conditions where temperatures and precipitation are low. These kinds of conditions would also favour the development of relatively open habitats. The positive correlation between habitat openness and body size in *C. elaphus*, and possibly in other species with large sizes in open environments such as the giant deer (*Megaloceros giganteus*), may also simply be because of the benefit of large size for locomotion in open landscape where manoeuvrability is not restricted. In closed environments the benefit of smaller size for manoeuvrability among closed vegetation (as suggested by Bro-Jørgensen 2008) could have pressed the individual body sizes of this species smaller. Large size may also help to escape predators in open landscape, but for large ungulates (larger than ca. 150 kg) body size is more likely to be regulated by resource availability than predation (Sinclair et al. 2003).

The wild horse (*Equus ferus*) shows an exactly opposite response of body size to vegetation structure to that of *C. elaphus*: it has on average smaller mean body sizes in open environments (paper III). Again this relationship is not explained by temperature, because small mean body sizes occur also in localities suggesting open vegetation but both relatively warm climate, such as Gough's Cave in Britain, and relatively cold climate, such as Kent's Cavern in Britain. I suggest the explanation to this is that *E. ferus* is ecologically a very different species than *C. elaphus*. Both of these species occupy a wide range of habitats from closed to open vegetated ones, but *E. ferus* is superbly adapted

for grazing and utilizing open habitats, and as a gregarious and social species horses tend to occur in large herds in open environments. Thus, in open environments the population density of *E. ferus* could have increased as a result of the optimal conditions for this species, and the high density would have driven the mean individual body size of *E. ferus* smaller in open habitats as a result of resource limitations caused by the high population densities. Similar results were reached by Skogland (1983) who noted that in reindeer (*Rangifer tarandus*), which is also a gregarious open habitat specialist, resource limitations caused by high densities in extant open-habitat populations drive individuals towards smaller body sizes. Also Geist (1998) noted that North American woodland caribou are able to live more sedentarily and to more freely select better forage areas, and thus to grow larger, than the barren landscape caribou. Unfortunately, there was not enough associated pollen data to show how body size and vegetation structure would be connected in the case of the Pleistocene European reindeer (paper III).

The rest of the large ungulate species of the Middle and Late Pleistocene of Europe do not show as clear connections of body size with vegetation structures as the abundant and ecologically flexible *C. elaphus* and *E. ferus* (paper III). This is unfortunately largely due to the fact that there was in most cases not enough associated pollen data to analyse the body size of the species in relation to the vegetation. Bisons (*Bison priscus* and *B. schoetensacki*) show some tendency towards negative correlations between vegetation openness and their mean body mass, which might suggest a similar limiting role of high population densities on body size as in the case of *E. ferus* and *R. tarandus*, but these correlations are not significant and remain inconclusive. The aurochs (*Bos primigenius*) shows quite a lot of variation in body size but

it is not at all correlated with the associated patterns of vegetation openness. However, the habitats of *B. primigenius* show quite little variation in vegetation structure altogether, so it may simply be that *B. primigenius* occupied rather specific kinds of habitats in which other factors unrelated to the structure of the vegetation would have caused the variation in body size. Rhinoceroses (*Stephanorhinus hundsheimensis*, *S. hemitoechus*, *S. kirchbergensis* and *Coelodonta antiquitatis*) show very little intraspecific variation in body size between localities, perhaps suggesting that their adaptation to specific environments has kept their body sizes rather constant. There are some cases where interspecific competition could have led to character displacement in the competing species. Such a case could be the opposite body size patterns of the reindeer (*Rangifer tarandus*) and steppe bison (*Bison priscus*) in some last glacial environments of England, where these two are the dominant ungulate species (paper III), but it is very hard to prove that in the case of fossil populations.

To conclude the discussion on body size patterns, I suggest that climatic cooling and the associated increase in seasonality and changes in vegetation (e.g. improved quality as forage for herbivores) has affected the long term evolution of maximum body size in mammals, ultimately leading to a major peak in maximum size frequency in the Pleistocene Ice Age. The actual mechanism regulating ungulate body sizes in the Pleistocene assemblages from Europe is likely to have been a combination of habitat structure (open vs. closed), resource quality and availability for an individual, and population densities (which are closely connected with the resource availability for individuals). Interspecific competition could also cause some of the fine-scale variations in body size observed in the Pleistocene ungulates.

4. Conclusions

The findings of this thesis can be summarised as follows:

- After the initial evolutionary burst in maximum body size of terrestrial mammals by filling the large size niches left vacant by the extinction of large non-avian dinosaurs at the end of Cretaceous (65 Ma), the trajectory of maximum size levelled off in the Middle Eocene (ca. 40 Ma) and started following fluctuations in global temperatures and land area. This indicates that periods of climatic deterioration have played a significant role in driving the evolution of particularly large forms among terrestrial mammals.

- The significance of the Late Pliocene to Pleistocene peak in maximum size frequency in major terrestrial mammal orders further indicates that the strong cooling and drastic fluctuations in climate in the Pleistocene ice age favoured the evolution of particularly large sizes in mammals. Temperature proxy alone explains much of the variation in the maximum size frequency, but other factors such as increased seasonality and open vegetation are actually more likely to have driven the evolution of particularly large species in the Pleistocene. Large size is beneficial under seasonally harsh conditions, e.g. because it increases fasting endurance and migration abilities. On the other hand, cold climate and good quality soils created by glacial erosion resulted in seasonally high productivity and food quality in Pleistocene environments providing sufficient resources for growing large bodies under favourable seasons.

- The more detailed comparisons of locality-based body size variations interspecifically and with vegetation proxies in Middle and Late Pleistocene European ungulate assemblages suggests that is not climate as such

which drives these population-level body size patterns. The main driving factor is resource availability, which is regulated by primary productivity (which can be seasonally high under cold climatic conditions), food quality (climatic cooling diminishes the chemical defences and increases energy contents of plants increasing food quality), population density (intraspecific competition limits the resources available for an individual when population density is high) and interspecific relationships (mostly competition causing character displacement in the body size of similar species) in the mammal communities. Also vegetation structure as such (open vs. closed) may have affected the body size patterns of some key species.

- Averaged dietary signals in large herbivorous mammal communities reflect local environmental conditions through the structure of the available vegetation. However, there are significant interspecific differences in the dietary strategies of individual ungulate species, and the structure of the ungulate community influences the dietary preferences of individual species through competition.

- Any interpretations of environmental conditions of fossil localities based on mammal ecometrics should be based on as complete analyses of the whole ungulate (or whole mammal) communities as possible, because individual species have different strategies and they may not represent the “general signal” of the environment. As part of this work, an easy to do, universally applicable and consistent tooth wear-based diet analysis method was developed for Proboscidea, which serves as a promising basis for extensive future analyses of proboscidean palaeodiets as part of the analyses of large mammal communities.

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