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Hunting Ancient Walrus Genomes

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PhD Thesis

Hunting Ancient Walrus Genomes

Uncovering the hidden past of Atlantic walruses
(*Odobenus rosmarus rosmarus*)

This thesis has been submitted to the PhD School of The Faculty of Science,
University of Copenhagen on 30th October 2020

by

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Name of departments: The GLOBE Institute & The Arctic Centre

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Title and subtitle: Hunting Ancient Walrus Genomes: uncovering the hidden past of Atlantic walruses (*Odobenus rosmarus rosmarus*)

Topic description: Ancient genomic analyses into the past population structure of Atlantic walruses, and the nature of human-walrus interactions across the North Atlantic.

Submitted on: 30th October 2020

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university of
 groningen

Hunting Ancient Walrus Genomes

Uncovering the hidden past of Atlantic walruses
(*Odobenus rosmarus rosmarus*)

PhD thesis

to obtain the degree of PhD at the
University of Groningen
on the authority of the
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and in accordance with
the decision by the College of Deans

and

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on the authority of the
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and in the accordance with
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Double PhD degree

This thesis will be defended in public on

Thursday 28 January 2021 at 09:00 hours

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***"In salty ice, in frost and blubber...
The endless glory"***

D.D. Dumbo, lyrics to 'Walrus'

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Abstracts

English Abstract

The human experience is fundamentally tied to the natural world. Our survival, society and cultural development are shaped by our surroundings; the climatic conditions; the geology of the terrestrial and aquatic environments around us; and the plants and animals that we eat, use, keep and avoid. However, the relationship is not uni-directional, rather there are innumerable inter-connected and reciprocal interactions. Our presence and activities in the natural world leave a mark; altering the distribution, diversity and ecology of other species, changing the landscapes we pass through or live in and, most fundamentally, altering the climate of our planet. Developing an understanding of how we impact, and are affected by, the various parts of the natural world is essential for knowing how our choices have led us to where we are today, predicting what our futures hold and how we construct our own identities as human.

Traditionally, this understanding of our interactions with the natural world has been studied from an academic perspective within the confines of distinct disciplines. There is a growing need, and appreciation for, a more integrated, interdisciplinary approach as we learn more about the complexities and connections inherent in our world and cultures. This thesis bridges the divide between archaeology and biology by using ancient DNA to reveal new insights into human-walrus (*Odobenus rosmarus rosmarus*) interactions. The main aims were to characterise past genetic structure within Atlantic walruses to understand the fate of extinct populations (chapter five), generate a series of baselines for future comparison with modern genetic data that are sensitive to time and space (chapter six) and to identify how broad climatic conditions may have shaped the evolution of walruses (chapter six). These aims were generated after identifying key knowledge gaps across and between disciplines within the existing academic literature (chapter one and two). Additionally, on a more technical note, this thesis also aimed to identify predictors of DNA preservation to inform sample selection prior to destructive analyses (chapter three) and to develop a methodology for the sex identification of ancient pinniped remains (chapter four).

A total of 177 walrus bones, teeth and tusks were sampled for genetic analyses. Of these, 164 were successfully shot-gun sequenced, 74 provided mitochondrial genomes and 28 provided nuclear genomes of sufficient coverage to allow for further bioinformatic

analyses. These samples formed the foundation for the methodological and analytical chapters of the thesis. Additional information and data were gained from literature reviews of existing academic publications, collaborations with other biologists and archaeologists, as well as previously published genetic sequences.

The combined work presented in this thesis offers new insights into the evolution, past population structure and cultural significance of walruses in the North Atlantic. The timing of major divergence events between the Pacific and Atlantic walruses, as well as between the 'mixed' and 'western' clade of Atlantic walruses, coincides with the onset and end of the Last Glacial Maximum respectively. The current population structure seen in Atlantic walrus mitochondria seems to have remained relatively consistent over recent millennia.

On a finer geographic scale, a unique genetic lineage of Icelandic walruses previously suggested by place names and historical sources was confirmed with both nuclear and mitochondrial genomic data. According to radiocarbon dating walruses were no longer found on Iceland within a few centuries of Norse (Viking age) settlement at the end of the 9th century. Comparison of ancient and modern mitochondrial data showed no evidence for the persistence of the lineage and suggests total extinction of Icelandic walruses.

A method of genetic sexing was developed for pinnipeds and was found to be highly successful on historic and ancient faunal material. In contrast, no simple relationship was found between a range of factors and the quality or quantity of DNA preserved across a large and diverse collection of zooarchaeological samples. There were some significant trends with respect to particular skeletal elements or the microenvironment of deposition (e.g. cave conditions), however other factors such as age and latitude were not found to be statistically significant.

Overall, this thesis contributes important new data, findings and methodologies to our understanding of past human-walrus interactions in the North Atlantic. There are exciting new opportunities for future research, particularly in generating modern genomes and comparing them against past baselines, examining the process of local extinction more closely for Iceland or the Maritimes, as well as creating detailed genetic chronologies for particular regions such as Foxe Basin.

Danish Abstract - Dansk resumé

Menneskets eksistens er på et fundamentalt plan bundet til naturen. Vor overlevelse, samfund og kulturelle udvikling er blevet formet af vores omgivelser; de klimatiske forhold; de geologiske forhold som påvirker det terrestriske og akvatiske miljø omkring os; de planter og dyr som vi spiser, anvender, holder som husdyr og prøver at undgå. Forholdet går ikke kun den ene vej, men består af utallige indbyrdes forbundne og gensidige interaktioner. Vores tilstedeværelse og aktivitet i naturen efterlader sig spor; ændring af andre arters udbredelse, diversitet og økologi, ændring af det landskab vi bevæger os i eller bebor, og af mest fundamentalt betydning ændring af vores klodes klima. Kendskab til hvordan vi påvirker, og bliver påvirket af, de forskellige dele af naturen er derfor vigtigt for at kunne forstå hvordan vores handlinger har ført os til det sted vi er i dag, samt forudsige hvad vores fremtid kan bringe og hvordan vi konstruerer vores egen identitet som mennesker.

Traditionelt er den forskning som omhandler vores interaktioner med naturen blevet belyst indenfor rammerne af separate fagområder. Der er imidlertid et voksende behov for, samt påskønnelse af, en mere integreret, tværfaglig tilgang sideløbende med at vi har fået større forståelse for den kompleksitet og de sammenhænge, der er tilstede i vores verden og blandt vores kulturer. Denne Ph.d. afhandling bygger bro mellem disciplinerne arkæologi og biologi ved at benytte sig af fossilt DNA til at belyse nye sider af interaktionen mellem mennesker og hvalros (*Odobenus rosmarus rosmarus*). Hovedformålet var at karakterisere fortidig genetisk populationsstruktur blandt atlantisk hvalros for at kunne forstå hvilken skæbne uddøde populationer led (kapitel 5), at generere genetisk data til brug som basis for fremtidige komparative analyser med moderne genetisk data, som dermed kan udvise større følsomhed overfor tid og rum (kapitel 6) og at identificere hvordan omfattende klimatiske ændringer var med til at forme evolutionen af hvalros. Disse mål blev sat efter at have opnået kendskab til den manglende viden der findes på tværs af discipliner i den eksisterende litteratur (kapitel 1 og 2). På et mere teknisk plan har denne Ph.d. afhandling også til formål at identificere forudsigelser for DNA bevaringsforhold til brug for prøveudvælgelse forud for destruktiv prøvetagning (kapitel 3) og at udvikle en metode til kønsbestemmelse af gamle prøver tilhørende underordenen Pinnipedia (kapitel 4).

I alt blev 177 knogler, tænder og stødtænder prøvetaget til genetisk analyse. Blandt disse blev 164 succesfuldt shotgun sekventeret, 74 gav mitokondrielle genomer og 27 gav nukleæregenomer, som var af tilstrækkelig kvalitet til videre bioinformatisk analyse. Disse prøver dannede grundlaget for Ph.d. afhandlingens metodologiske og analytiske kapitler. Yderligere information og data blev indsamlet ved studier af den eksisterende akademiske litteratur, samarbejde med andre biologer og arkæologer samt allerede offentliggjorte genetiske sekvenser.

Det samlede arbejde præsenteret i denne Ph.d. afhandling giver ny indsigt i hvalrossens evolution, tidligere populationsstruktur og kulturelle betydning i Nordatlanten. Den genetiske opsplitning mellem stillehavshvalrossen og den atlantiske hvalros, så vel som mellem den "blandede" og den "vestlige" gren af den atlantiske hvalros, falder tidsmæssigt sammen med hhv. begyndelsen og slutningen af den sidste istid. Den nuværende mitokondrielle populationsstruktur i den atlantiske hvalros synes at have været nogenlunde stabil gennem de seneste årtusinder.

På et finere geografiske plan blev det bekræftet ved hjælp af både mitokondrielt og nukleæregenomisk data, hvad stednavne og historiske kilder tidligere havde antydnet, at der eksisterede en genetisk unik gruppe af hvalros på Island. Kulstof 14-datering viser at hvalros ikke længere var at finde på Island et par århundrede efter nordboerne bosatte sig fra slutningen af 800-tallet (Vikingetiden). Sammenligning mellem fossilt og moderne mitokondrielt data viser at der ikke er tegn på at denne unikke genetiske gruppe fortsatte med at eksistere, hvilket derfor tyder på en total udryddelse af den islandske hvalros.

En metode for genetisk kønsbestemmelse af Pinnipedia blev udviklet og viste sig yderst succesfuld til brug for såvel historiske som forhistoriske knogleprøver. Der blev derimod ikke fundet nogen entydig simpel sammenhæng mellem en række testede faktorer og kvaliteten eller kvantiteten af bevaret DNA blandt en stor samling af diverse knogleprøver. Der var nogle signifikante tendenser med hensyn til bestemte skeletelementer eller mikromiljøet for aflejringen (f.eks. grotteforhold), men andre faktorer så som alder og breddegrad viste sig ikke at være statistisk signifikante.

Overordnet set har denne Ph.d. afhandling bidraget med vigtig ny data, resultater og metodeudvikling til at forstå fortidens interaktioner mellem mennesker og hvalros i

Nordatlanten. Der er spændende nye muligheder for fremtidig forskning, i særdeleshed muligheden for at generere moderne genomer og sammenligne dem med den her genererede basislinje, at undersøge processerne for lokal uddøen nærmere på Island eller Maritime Provinsen i Canada, samt at skabe detaljerede genetiske kronologier for bestemte regioner såsom Foxe Basin.

Dutch Abstract - Nederlandse Samenvatting

De mensheid is fundamenteel verbonden met de natuur. Ons voortbestaan, onze samenleving en culturele ontwikkeling worden gevormd door onze omgeving; de klimaat omstandigheden; de geologie van de terrestrische en aquatische omgevingen om ons heen en de planten en dieren die we eten, gebruiken, houden, en vermijden. Deze verhouding is echter niet eenzijdig, er zijn ontelbare wederzijdse interacties tussen mens en dier. Onze aanwezigheid en activiteiten in de wereld laten hun sporen achter; ze veranderen de distributie, diversiteit, en ecologie van andere soorten, ze veranderen de landschappen waar we ons door bewegen of in leven, en het belangrijkste, ze veranderen het klimaat van onze planeet. Om te kunnen voorspellen hoe onze toekomst eruit zal zien en hoe we onze identiteit als mens vormen is het essentieel om te begrijpen hoe onze beslissingen ons hebben gebracht waar we nu zijn. Dit vereist inzicht in onze impact op verschillende onderdelen van de natuur en omgekeerd.

Van oudsher worden onze interacties met de natuur bestudeerd vanuit een academisch perspectief binnen verschillende zelfstandig-werkende disciplines. Er is echter een groeiende behoefte aan, en waardering voor, een meer geïntegreerde, interdisciplinaire aanpak naarmate we meer leren over de complexiteit en talloze connecties die zo eigen zijn aan onze wereld en culturen. Dit proefschrift is erop gericht om de twee verschillende disciplines van de archeologie en biologie samen te brengen door oeroud DNA (ancient DNA) te bestuderen om nieuwe inzichten te verkrijgen in de interactie tussen mens en walrus (*Odobenus rosmarus rosmarus*). De belangrijkste doelstellingen van dit onderzoek waren om het lot van uitgestorven populaties te begrijpen door het in kaart brengen van de genetische structuur van vroegere Atlantische walrussen (hoofdstuk 5), referentiekaders te genereren voor toekomstige vergelijkingen met moderne genetische gegevens die gevoelig zijn voor tijd en ruimte (hoofdstuk 6) en om te onderzoeken hoe algemene klimatologische omstandigheden de evolutie van walrussen kunnen hebben beïnvloed (hoofdstuk 6). Deze doelstellingen werden vastgesteld aan de hand van belangrijke kennislacunes in de wetenschappelijke literatuur binnen en tussen disciplines (hoofdstuk 1 en 2). Hiernaast had dit proefschrift ook twee technische doelstellingen, namelijk om voorspellende factoren van de kwaliteit van DNA-preservatie te identificeren om de selectie van monsters voorafgaand aan destructieve analyses te vergemakelijken

(hoofdstuk 3), en om een methode te ontwikkelen voor geslachtsidentificatie van resten van oeroude vinpotige dieren (hoofdstuk 4).

In totaal werden 177 walrus botten, tanden, en slagstanden bemonsterd voor genetische analyses. Hiervan werden 164 succesvol gesequenced met de 'shot-gun' methode, 74 van de monsters leverden mitochondriale genomen op en 28 leverden nucleaire genomen op met een dusdanige goede kwaliteit dat verdere bioinformatische analyse mogelijk was. Deze monsters vormden de basis voor de methodologische en onderzoekshoofdstukken van dit proefschrift. Aanvullende informatie en data werden verkregen door het kritisch doorzoeken van bestaande wetenschappelijke publicaties, samenwerkingen met andere biologen en archeologen, en eerder gepubliceerde genetische sequenties.

Het werk dat in dit proefschrift wordt gepresenteerd biedt nieuwe inzichten in de evolutie, de vroegere populatiestructuur, en de culturele betekenis van walrussen in de Noord-Atlantische Oceaan. De timing van divergentie tussen walrus populaties uit de Grote Oceaan en de Atlantische Oceaan, en tussen de 'gemengde' en 'westelijke' clade van Atlantische walrussen, valt samen met het respectievelijke begin en einde van het Laatste Glaciale Maximum. De huidige populatiestructuur, zoals waargenomen op basis van mitochondriale data van Atlantische walrussen, lijkt relatief onveranderd te zijn gebleven over de recente millenia.

Op een fijnere geografische schaal werd een unieke genetische tak van IJslandse walrussen aangetoond op basis van zowel nucleaire als mitochondriale genomische data. Deze vondst was in lijn met eerdere vermoedens op basis van plaatsnamen en historische bronnen. Uit radiokoolstofdatering bleek dat er zich op IJsland geen walrussen meer bevonden binnen een paar eeuwen na aanvang van de Noorse kolonisatie (Vikingtijd) aan het einde van de 9e eeuw. Een vergelijking van oeroude en hedentendaagse mitochondriale data leverde geen bewijs op voor het voortbestaan van deze IJslandse lijn en duidt daarmee op totale lokale uitsterving van IJslandse walrussen.

Een methode voor genetische geslachtsbepaling werd ontwikkeld voor vinpotigen en deze bleek zeer succesvol te werken met historisch en oeroud dierlijk materiaal. Daarentegen, werd er geen eenduidig verband gevonden tussen verschillende factoren en de kwaliteit of kwantiteit van het bewaard gebleven DNA in een grote en diverse verzameling van

zoöarchologische monsters. Een aantal significante trends werden waargenomen met betrekking tot bepaalde skeletelementen of de micro-omgeving waarin het monster had gelegen (bijv. een grot omgeving), maar andere factoren zoals leeftijd en breedtegraad bleken niet statistisch significant te zijn.

Over het geheel genomen draagt dit proefschrift met belangrijke nieuwe methodes, data en bevindingen bij aan onze kennis over vroegere interacties tussen mens en walrus in de Noord-Atlantische Oceaan. Voor toekomstig onderzoek liggen er spannende nieuwe kansen, met name in het genereren van moderne genomen en deze te vergelijken met vroegere referentiekaders, het nader onderzoeken van de processen van uitsterving van lokale populaties rond IJsland of de Maritieme Provincies en het creëren van gedetailleerde genetische chronologieën voor specifieke regio's zoals Foxe Basin (Canada).

Summary

Objectives

This PhD thesis represents the culmination of three years of research into historic and ancient human-walrus interactions across the Atlantic Arctic. The overall aim of this PhD was to use ancient genetic approaches to reveal past population structure and diversity of Atlantic walruses (*Odobenus rosmarus rosmarus*) to reveal the importance and potential impacts of human-walrus interactions. Within this overarching objective were several specific aims:

- To research and synthesise the current body of literature from both natural and social science on Atlantic walruses (Chapter 1, 2 & Appendices 1, 2).
- To identify existing knowledge, future areas of interest and suitable methods to answer ongoing questions relating to human-walrus interactions across the North Atlantic (Chapter 1 & 2).
- To investigate which sample characteristics, environmental factors or collection practices influence DNA degradation in order to predict whether a sample might be successfully sequenced (Chapter 3).
- To develop a method of identifying using only genetic methods the correct sex of a pinniped from skeletal material, allowing future work to characterise any sex bias in hunting or use of walruses (Chapter 4).
- To reveal the fate of Icelandic walruses following Norse Settlement as a case study into the impact of hunting driven by international trade and commercial markets (Chapter 5).
- To explore broad patterns in past population structure and diversity in Atlantic walruses with potential links to climatic events or human activities (Chapter 6).

Description of Research & Thesis Outline

In order to achieve the aforementioned objectives a combination of literary review, method development, novel data generation and genomic analyses were undertaken. The outcomes of this work are presented in this thesis as six chapters, two of which have already been accepted and published in peer-review journals, one of which has been published in an editor-reviewed journal, two more are in the second round of review with peer-reviewed journals, and the final one is a pre-submission manuscript. Across this thesis the majority of the research, lab-work, bioinformatics, data presentation and writing was completed by the author (detailed statements of author contributions can be found in the accompanying documentation).

The first, introductory, chapter (pages 29-44) provides a broad overview intended for a generalist academic audience explaining the current state, methodology and future prospects of paleogenetics (or ancient DNA, aDNA) in understanding past human-marine mammal interactions. This article presents a simplified summary of existing literature and knowledge, while also drawing upon some preliminary data (generated for this PhD) to provide specific examples.

The second chapter (pages 45-78) takes topics first presented in the introduction much deeper into the academic literature. It provides a detailed review of literature relating to Atlantic walrus drawn from both the natural and social sciences and highlights the need for interdisciplinary research. The article then poses and explores four key unanswered questions concerning human-walrus interactions, outlining how a variety of emerging methods can contribute to the answers. In particular, this second half of the chapter focuses on ancient genomic, stable isotope, trace element and hormonal analyses of archaeological material. The second chapter therefore provides the justification and context for the remainder of the thesis which focuses on the methods and results of aDNA analyses.

The following four chapters in the thesis draw upon results from the screening of 177 ancient walrus, completed for this thesis. Samples were selected from across Canada, Greenland, Iceland and smaller North Atlantic islands, spanning six thousand years. Additional data on other pinnipeds was gathered from collaborators. In total 154 samples

were successfully sequenced, 103 mitochondrial genomes and 29 nuclear genomes of sufficient quality for bioinformatic analyses.

The third chapter (pages 79-104) in this thesis discusses the challenge of sample selection in aDNA studies and draws upon a large and novel dataset to explore which factors or sample characteristics are most important in influencing DNA preservation. This paper highlights the importance of bone type, collection practices and depositional environment, while also confirming how complex and unpredictable much of the process of DNA degradation is in the real-world. It serves to help inform sample selection for other aDNA studies on zooarchaeological remains.

The fourth chapter (pages 105-120) presents a methodological development of genetic sexing in pinnipeds. It describes how the closely-related dog genome can be successfully used as a reference to determine sex genetically in modern seals and ancient pinnipeds. The method described uses the ratio of reads aligning to the X chromosome (females only), to that of one of the autosomes (male and female). This article also explores the quantity of data required to be able to perform such analyses, and hence the lower limit of sample quality that can still be sexed.

The fifth chapter (pages 121-142) is a multidisciplinary article that explores the fate of Icelandic walruses following Norse settlement at the end of the 9th century. Mitochondrial genomes and smaller mitochondrial target sequences provide evidence of a unique, genetic lineage of walruses found only on Iceland. The lack of shared haplotypes with existing modern mitochondrial sequences suggest that Icelandic walruses became locally extinct, within a few centuries of human arrival, as per radiocarbon dating. Additional discussion of place names, written records and the location of skeletal remains puts the biological results in a historical and cultural framework. The paper concludes that the loss of Icelandic walruses may be the earliest example of international trade driving the over-exploitation and eventual extinction of a marine species.

Finally, the final sixth chapter (pages 143-174) shows the most recent results utilising all successfully sequenced genomes of walruses captured in this research. It includes comparison of the phylogenetic relationships shown by nuclear and mitochondrial genomes, while also exploring patterns of genetic diversity and differentiation. It discusses

some of the past population trajectories of Atlantic walrus populations and the timing of key divergences. It presents several key conclusions, namely that the timing of key divergence events coincides with periods of glaciation and deglaciation, that finer-scale phylogeographic structure supports periodic dispersal of walruses from the east Atlantic to the west and that the mitochondrial affinity of some medieval walrus remains suggest that the Norse hunted or traded walruses from far beyond West Greenland.

This thesis concludes with the cover and introductory chapter from the edited book which I coordinated (Appendices 1 & 2). The book emerged from annual 'Walrus Research Days' Morten and I organised, and represents the academic network formed throughout the last four years. As lead-editor of the book, I was responsible for pitching the idea to Elsevier as a publisher, seeking the support of twenty chapter authors, coordinating their submissions and the reviews of their manuscripts and co-writing the introduction. I also supervised, and acted on the examination committee, of Elena Kakoshina, who completed beautiful illustrations for the book as part of her Master's in Scientific Illustration. Only the final chapter of the book is awaiting submission, and the volume is entering the final stages of production and copy-editing.

Conclusions and future perspectives

Overall, this thesis offers new insights into past human-walrus interactions across the North Atlantic over the last five millennia. Ancient DNA analyses allow us to bridge the disciplinary divide between archaeology, history and biology to improve our understanding of how climate and human activities can shape the evolution of a single species of marine mammal, while also revealing more about how, why, where and when humans hunted walruses. The sequencing of historic and ancient walrus samples uncovers genetic patterns that pre-date the arrival of humans in the Atlantic Arctic, as well as much of the last five thousand years, however, there remain critical gaps in our knowledge. Modern walrus genomes are required to understand the scale, nature and consequences of the most intensive period of commercial hunting between the 16-20th centuries. Additionally, obtaining more numerous nuclear genomes from Icelandic walruses should allow us to learn more about the processes and triggers of extinction. On the other side of the Atlantic, additional high-coverage nuclear genomes from Foxe Basin may offer the chance to recreate fine-scale genetic and cultural chronologies that characterise human-walrus interactions within a single locality.

The Atlantic walrus we know today has been shaped by growing and shrinking Arctic ice, human hunting driven by local demand and international markets, as well as the inherent biology and behaviour of these unique marine mammals. Humans across the North Atlantic have also been shaped by changing climatic conditions, human cultural developments and movements, as well as the inherent biology and behaviour of walruses. Walruses and humans have had a rich, diverse and complex past, and as we learn more about human-walrus interactions, we will have the best chance to improve our shared futures.

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