INTRODUCTION

The Natural History Museum of Denmark is part of the University of Copenhagen and can trace its roots back to the 17th century. The Museum comprises botanical, geological, and zoological collections; the latter contains some 10 million specimens representing an estimated 10% of the named multicellular animal species. The strength of the zoological collection lies in its unique diversity of particularly Danish, North Atlantic, Arctic, and marine specimens brought back from a great number of expeditions. These collections include specimens dating back several hundred years, enabling the study of temporal as well as spatial changes within populations, species, and communities.

To make specimen data more accessible to the global scientific community, an increasing number of natural history museums are planning or have already initiated large-scale digitization of their collections. In the coming years, these digital archives will allow researchers to access an unprecedented volume of historical, geographic, and taxonomic specimen data, mobilizing an as yet largely inaccessible trove of information spanning hundreds and even thousands of years.

The mammalogy collection at the Natural History Museum of Denmark comprises ~58,000 specimens. So far, only a small fraction has been digitized and is publicly accessible. The collection includes a unique assemblage of polar bear (Ursus maritimus) skulls (Fig. 1a). The associated specimen data have never been systematically assembled, and data associated with a large number of the samples, especially the older ones, have not previously been transcribed from their handwritten archives (Fig. 1b) into an electronic format.

To get a much-needed overview of the skull collection, and to provide an easily accessible, reliable, and up-to-date database to visiting researchers, we recently transcribed all the specimen data to an electronic database.

Here, we present a history and overview of the polar bear skull collection and provide a brief summary of its use in the scientific literature so far. Our motivation for presenting a synthesis to the readership of Arctic is to make this wonderful collection known to a wider audience, in the hopes that it will foster new synergistic research activities and collaborations. We hope that the use of...
new, additional, or complementary methods will allow specimens from the collection to provide the foundation for new scientific discoveries, leading to further insights into the ecology and evolution of polar bears.

COMPILING AN ELECTRONIC DATABASE

We transcribed all handwritten documents, comprising historical paper archives (Fig. 1b) and four bound books dated from 1830 to 2016, into an electronic format. The information was merged with any previously digitized accounts of the skulls into one database. A benefit of this exercise was that it has added a layer of security to the safeguarding of our specimen data; if our paper archives or books were to be damaged or misplaced, without digitization, the data would be forever lost.

For each specimen in the polar bear skull collection, we compiled data on date of sampling, name of collector, date of admission to the collection, sampling locality, and any other information documented in the handwritten records. We compiled information on the sex of each individual, although this information has not always been recorded, and on age, which has since been estimated for a large number of the specimens using cementum growth layer counts of the lower incisor (I3) (Fig. 2).

The majority of polar bear samples registered in the Museum collection since 1999 have been collected by researchers at the Arctic Research Centre, Aarhus University, in collaboration with the Greenland Institute of Natural Resources. The samples have been collected during research activities in Scoresby Sound (Ittoqqortoormiit) in East Greenland (1999 to present) and Thule in West Greenland (2009–11).

For the majority of skulls collected by Aarhus University, associated frozen organ and tissue samples, such as liver, kidney, muscle, adipose tissue, and sexual organs, as well as associated formaldehyde-preserved samples and histological slides, are stored at the Aarhus University campus in Roskilde, Denmark. Aarhus University furthermore has soft tissue collections of bears harvested from 1985 to 1999, although skulls were not collected from individuals during that time.

The polar bear samples in the Museum database have a unique Museum identifier (a three- to five-digit ZMUC-CN number; e.g., ZMUC-CN-583). However, for the skulls donated by Aarhus University, there is also a unique five-digit Aarhus University identifier (e.g., 21755). This last number is the identifier most often provided in related papers, most of which were published before the skulls were added to the Museum collection. We therefore made an effort to check, double-check, and merge data and unique Aarhus University identifiers from various versions of the university’s electronic data archives with the sparse handwritten information and Museum identifiers recorded for each specimen when it was added to the Museum collection.

OVERVIEW OF THE SCIENTIFIC LITERATURE

To compile an overview of the research that has been carried out using specimens in the skull collection, we reviewed the scientific literature using a variety of search terms related to the Museum and Aarhus University specimen identifiers and departments.

In the absence of specimen identifiers, the Museum and its staff are often mentioned in the acknowledgements section of a paper, and we therefore also ran a literature search in Google Scholar using these search terms: “Zoological Museum,” “ZMUC,” “Natural History Museum of Denmark,” “University of Copenhagen,” “polar
bear,” “Ursus maritimus,” and “Thalarctos maritimus.” The search terms reflect the fact that the Natural History Museum of Denmark was formed in 2003, when the Zoological Museum, the Botanical Museum, the Geological Museum, and the Botanical Gardens were merged into one department at the University of Copenhagen. We also included as search terms the names of Hans Baagøe, the recently retired curator emeritus, and Mogens Andersen, the collections manager of the mammalogy collection.

THE COLLECTION

The polar bear skull collection at the Natural History Museum of Denmark comprises 683 specimens collected between 1830 and 2016 (Fig. 3). In addition, the Museum has various other material from the same or additional individuals, including bacula, whole skeletons, skins, and various soft tissues (Table 1), bringing the total number of bears that contributed specimens to this collection to 717 individuals.

The oldest skull specimen is from East Greenland and was collected in 1830 (Fig. 1b). A timeline of the samples therefore spans almost 190 years, and assuming an average generation time of 11.5 years (Liu et al., 2014), this time span represents ~15 polar bear generations. However, specimens are not evenly distributed in time (Fig. 3). Fifty-two specimens were collected during the 1800s, with subsequent bursts in the 1920s, 1960s, and 2000s, reflecting the timing of major Danish polar expeditions and recent large-scale Arctic research efforts.

Not all of the skulls in the collection are fully intact; some have been partly crushed (when they were shot) or are missing components such as teeth, and others have had their brain cases cut open during dissection. This damage limits their use in certain morphometric analyses.

The specimens have been procured by various means. Many were donated by polar expeditions, including the Thule expeditions led by Greenlandic/Danish polar explorer Knud Rasmussen in 1910–33. Others have been donated by private collectors or public institutions; for example, the ~300 skulls donated by Aarhus University, which also donated a number of bacula (Table 1). Two whole skeletons were donated by the Copenhagen Zoo following euthanization of the individuals because of old age. Other explanations are stated in the admission record entries, including “sailed down by a motorboat,” “killed in self-defense,” and “confiscated by the Greenland police, before being handed over to the Museum.” One memorable entry from 1907 reads “Killed with knife by Søren Nielsen (known as Solo). He was hunting far within the fjord when his dogs went after a polar bear. They attacked it and Solo tried to shoot it, but he had forgotten his cartridges. He then killed it with [his] knife.”

New specimens are continuously being added to the Museum collection (Fig. 4a). Recent samples have mostly been obtained from the Scoresby Sound/Litqoqportooormiit area, where polar bears are legally subsistence hunted by the local Inuit population within an annual quota of 35 (Fig. 4b). The bears are randomly harvested, and there is no bias towards sex selection by hunters or in the regulations (Sonne et al., 2012). The only change in the demography of harvested bears is linked to the Greenland Self Government’s protection of female polar bears.
accompanied by cubs up to the age of two years, and females hibernating in maternity dens.

**DEMOGRAPHY**

The polar bear skulls are from six of the 19 polar bear management units recognized by the International Union for Conservation of Nature (IUCN), including the Southern Beaufort (n = 12), Kane Basin (n = 63), Baffin Bay (n = 23), Davis Strait (n = 10), East Greenland (n = 512), and Barents Sea (n = 7) management units (Fig. 5). The provenance of 56 of the 683 skulls is not known. The majority of the specimens (75%) have been collected in East Greenland, reflecting the large number of polar expeditions and research activities in the region.

Where available, we compiled data on age (estimated using growth layer counts, Fig. 2) and sex of specimens, shown in Figure 5. Data were available for 382 of the specimens, representing 220 males and 162 females. Only a few specimens outside of East Greenland have been age determined, reflecting the limited research activities on these samples so far (Fig. 5). Specimens were grouped into subadults (< 6 years for males and < 5 years for females) and adults (≥ 6 years for males and ≥ 5 years for females). We found 129 adult and 91 subadult males in the collection, compared to 74 adult and 88 subadult females.

**USE IN THE SCIENTIFIC LITERATURE**

To date, the polar bear skull collection at the Natural History Museum of Denmark has been used in at least 116 scientific articles. When reporting results in scientific articles, reports, or dissertations, it is important to include the unique specimen identifiers of any material used in the study. A lack of information and transparency can lead to time wasted, duplicated efforts, and the potential repeat of projects, and specific data, findings, or a paper cannot be attributed to the specimen(s). Unclear or incomplete information also precludes any expansion of the study, and research cannot be replicated to check for reliability. As some articles published on the polar bear material may not have correctly referenced the material, our estimate of 116 articles should be taken as a minimum.

The most notable (and to our knowledge, the first) reference to specimens from the skull collection in the published literature was in Björn Kurtén’s seminal work on polar bear evolution (Kurtén, 1964). Kurtén writes in his Introduction that “...the most important recent comparative material available to me has been the large collection of *Ursus maritimus* from Greenland in the Zoological Museum of the University of Copenhagen” (Kurtén 1964:4).

Much of the work that refers to the collection has been published since 2004. These papers largely use the Aarhus University specimen identifiers, and our electronic database now enables easy referencing of the specimens with the Museum collection. The majority of these papers have been driven by the extensive monitoring of long-range transported contaminant exposure in polar bears by researchers at Aarhus University. Their primary focus has been on the East Greenland region, where samples are being collected as part the Arctic Monitoring and Assessment Programme (AMAP, www.amap.no) to monitor the contaminant loads and health of the East Greenland polar bear subpopulation. Polar bears of this subpopulation carry some of the highest persistent organic pollutant loads in the Arctic, and the bears are killed and eaten by local subsistence hunters (Letcher et al., 2010; Sonne, 2010; Sonne et al., 2012). Skulls and bacula samples are being collected in the Baffin Bay, Kane Basin, and Davis Strait regions and are used to monitor the contaminant loads and health of the East Greenland polar bear subpopulation. Polar bears of this subpopulation carry some of the highest persistent organic pollutant loads in the Arctic, and the bears are killed and eaten by local subsistence hunters (Letcher et al., 2010; Sonne, 2010; Sonne et al., 2012). Although most of the studies focus on analyses of various associated soft tissues, the skulls have formed a fundamental part of the work, as the age estimations using tooth growth layers of the lower incisor (I$_3$, Fig. 3) have provided essential demographic information.

The Aarhus University sampling, which started in 1983, initially focused on levels of heavy metals. The testing has expanded to cover persistent organic pollutants, a group of chemicals that encompass, for example, PCBs, DDT, and dioxins. In 1999, the work was further expanded to cover histopathology, brain biomarkers, and skull and bacula morphometrics and composition (Letcher et al., 2010; Sonne, 2010; Sonne et al., 2012). Skulls and bacula have also been used to detect effects from exposure to...
organochlorines and climate change (Sonne et al., 2004, 2013, 2015), and these studies suggest that exposure to environmental contaminants and climate change may affect bone composition over time. From 1983 to today, hair has been used to detect mercury exposure, as well as temporal and spatial (geographic) trends. In 2006, hair was used to establish ancient temporal trends of mercury back to the preindustrial time and later also its linkage to health effects and the stress hormone cortisol (Dietz et al., 2013). In 2011, the researchers began to study cortisol levels in the hair in relation to chemicals (both mercury and persistent organic pollutants) and climate change (Bechshøft et al., 2015). Teeth, hair, and bone have also been analyzed using stable isotopes to study temporal trends in food preferences, in addition to mercury (Dietz et al., 2013). Extensive research on persistent organic pollutants has also recently been conducted using pharmacokinetic and individual-based modeling and dose response work to identify temporal trends, climate-change driven changes in ecosystems, and effects on the immune system (Jenssen et al., 2015; Desforges et al., 2016, 2017).

The unique temporal aspect of the skull collection has been used to investigate morphometric change within the East Greenland population over the past two centuries, and morphometric variation has been surveyed between the East Greenland and Barents Sea populations (Fig. 5). Similarities between East Greenland and Svalbard bears suggest an exchange of individuals between these two populations (Pertoldi et al., 2012). The skulls have also been used in comparative studies with other bear species, investigating behavioural differences or evolutionary adaptations within the Ursidae, such as the evolutionary implications of bite mechanics and feeding ecology in bears (Christiansen, 2007).
Finally, nuclear genomes have been generated from soft tissues associated with 89 skulls from Kane Basin, Baffin Bay, and East Greenland (Fig. 5). A comparative analysis using these data and the genomes of brown bear estimated that the two species diverged ~400,000 years ago (Liu et al., 2014).

**FUTURE WORK**

Because of the large number of specimens and the unique temporal (Fig. 3) and geographic (Fig. 5) range of the samples, the polar bear skull collection provides an important assemblage of voucher specimens that documents variation across space and through time. As Arctic ecosystems continue to change, natural history collections will become increasingly relevant, allowing us to investigate and understand how species and communities are responding.

A large body of research has already been published on the polar bear skull specimens from East Greenland. However, relatively little work has been carried out on the specimens from other regions (Fig. 5), providing ample space and opportunity for new avenues of research; our own ongoing research on the skulls includes spatial and temporal stable isotope and geometric morphometric analyses.

We hope that this introduction to the collection will inspire novel research ideas, and we welcome the application of new or complementary methods and analyses to the specimens. Further research on the material will undoubtedly provide fascinating new insights into the ecology and evolution of the polar bear, a flagship species of Arctic ecosystems.

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