The Functional Morphology of British Cattle: Biomechanical and Shape Analysis of Aurochs and Domestic Cattle

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Archaeology

January 2024

Abstract.

This study focused on the morphological changes associated with the domestication of *Bos primigenius* to *Bos taurus*, particularly changes to the morphology of the skull. The domestication of cattle from aurochs is integral to and entwined in the human story. Given the economic and cultural significance of cattle to humans, it is vital to understand fully this relationship and how it shaped development of humans and cattle. This was investigated using state-of-the-art 3D statistical shape analysis methods, geometric morphometric methods (GMM) and finite element analysis. The first aim of this project was to undercover shape change within and between *Bos primigenius* and *Bos taurus*, and to determine whether domestication has altered the relationship between size and shape in bovine skulls. Secondly, the project assessed whether changes to cranial shape have functional implications, principally regarding feeding and mastication, but also other cranial functions such as the impact of different horn sizes. The results of this research address many important questions surrounding differences between aurochs and the *Bos taurus*. Most notably showing differences in the cranial form between wild and domestic species that have previously not been identified. Furthermore, it is shown morphological differences have biomechanical implications for the living animals, with wild cattle having greater functional ability with regard to diet but also the headgear they can physically support. This research supports novel findings with regards to aurochs and domestic cattle, along with the application of techniques not previously applied to this area of research.

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Acknowledgements.

Foremost, I would like to thank my supervisor, Dr Phil Cox, for introducing me to virtual morphology and functional anatomy and especially for his support, patience and guidance in the research of this thesis and for always being available to offer assistance.

I am grateful to staff at HYMS and the Department of Archaeology, York, (particularly Paul O'Higgins, Steve Roskams, Sam Cobb, Laura Fitton and Emily Hunter) for their interest in my research topic and always being gracious in offering advice.

To my friends and colleagues who encouraged and distracted me as required.

Finally, and especially to my parents and family for their unwavering support across the years this research took to conclude.

Declaration.

I declare that this thesis is a presentation of original work, and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references.

1. Chapter One: Introduction.

1.1. Introduction.

This thesis investigates the relationship and differences between the cranial morphology of aurochs (*Bos primigenius*) and domestic cattle (*Bos taurus*). The main purpose is to examine the extent to which aurochs and cattle differ in features of morphological shape and to a certain extent size and allometry, or if they are more disparate than the close association previously supposed (Grigson, 1978; Bohlken, 1962). The functional implications of differing shapes is also tested. This research addresses two main questions: is the cranial morphology of aurochs and cattle different? How do morphological differences influence cranial function (or biomechanics)? By asking these questions it is hoped a previously unexplored area of cattle evolution might be illuminated, with particular regard being paid to the skull but also morphology more generally. The results will have broader implications for our understanding of domestication, as the parameters within which this research takes place directly compare wild and domesticated variants. This first chapter sets the parameters of the research and establishes the terms, context and variables against which the wider scope of the results can be assessed.

1.2. Topic and aims.

This thesis is concerned with two types of cattle that are of importance to human-animal interactions, the most familiar are domestic cattle (*Bos taurus*), our modern-day cows, prevalent across Britain, and indeed the world. However, *Bos taurus* are the modern-day descendants of their progenitor, *Bos primigenius* (the aurochs) (Park *et al.*, 2015; Bollongino *et al.*, 2012; Teasdale and Bradley, 2012; Ajmone-Marsan *et al.*, 2010; Edwards *et al.*, 2007). Aurochs once enjoyed a wide distribution in Britain inhabiting the island from the retreat of the last Ice Age around 10,000 years ago. While it was often a key species in prehistoric contexts with aurochs and domestic cattle living contemporaneously for approximately two thousand years, aurochs eventually became extinct in Britain during the late Bronze Age but persisted in Europe until 1627 (Evans, 2015; van Vuure, 2002). The uncertain relationship between humans and cattle, particularly the further back in the past we look, allows for the possibility of fresh research in this area to elucidate further knowledge about early husbandry practices and particularly the domestication process. While the centres of cattle domestication that initiated the integration of cattle into human husbandry are located at some distance from the UK, in the Near East (Pitt *e al.*, 2019; Scheu *et al.*, 2015; Beja-Pereira *et al.*, 2006), the impacts can readily be seen in our local cattle. Indeed, Britain presents the opportunity for an interesting case study as there is less interference from other early forms of cattle domestication. By the time domestic cattle arrived in Britain it was several thousand years after their appearance in the initial epicentre of domestication (Cummings and Morris, 2022).

This thesis places the morphological and anatomical study of cows into context, by giving special consideration to specific cranial features that may be linked to evolution in the wider remit of functional morphology. The aim is to examine which aspects of cattle cranial morphology have been altered via the process of artificial selection and whether these have improved or inhibited feeding performance and masticatory efficiency. This research examines the impact of human exploitation on wild and domestic cattle from Britain, and the resultant changes in morphology and biomechanical differences. Previous studies have been successful in categorising general patterns of size change using traditional zooarchaeological methods (Schmoelcke and Gross, 2021; Wright, 2013), but it is theorised usual methods are not appropriate to detect the subtle changes anticipated. The purpose of this study is to use novel methods in the application of morphological and biomechanical research to investigate the disparity between aurochs and domestic cattle resulting from human husbandry. By the use of geometric morphometrics and finite element analysis this research aims to:

- Verify the methods as appropriate to the study of cattle.
- Identify differences in the cranial shape between aurochs and domestic cattle that suggest the impact of domestication.
- Assess the importance of size and its contribution to shape to establish if aurochs are to put it simply, very large cows.
- Use fragmentary material to investigate if differentiation of cranial shape is still valid in reduced data sets.

- Investigate if cranial shape differences influence feeding biomechanics in aurochs and domestic cattle.
- Assess the contribution of headgear (horns) in determining cranial shape.

1.3. Terms and scope.

In order to create some clarity and continuity when discussing often complex ideas throughout the research it is necessary to describe some precise meanings for various words, whether scientific and/or colloquial. The first term is aurochs, widely accepted as the name for the wild ancestor of domestic cattle. However, there are some variants of spelling particularly in older texts and while suitable for plural and singular, aurochsen is also commonly used for plural (here, the word aurochs will be used throughout to represent the species *Bos primigenius)*. In a similar manner, their domestic descendants have a variety of names, most common is simply cow, referring to the whole group of *Bos taurus*. However, cow is also specifically the female, with bull being the male so it is possible this could create confusion although in most cases the context would nullify this. The term 'cattle' is also widely used referring to a group or herd of cows, but again cattle can also refer to any group or herd of other livestock in the yak, bison, and buffalo taxa. Here we settle for 'domestic cattle' as a sex-neutral term, in this case representing specifically *Bos taurus*. Where discussion of sex is necessary, the convention in human anatomy is followed using male and female rather than bull and cow. 'Domestic' is used to mean resulting from human husbandry, and similarly 'wild' being the absence of human intervention or domestication. In this case wild cattle also include some breeds (the Chillingham cattle) that have been rewilded, and so despite technically being domestic cattle the herd are now absent from significant human interaction. As a final note two common acronyms used in this research are 'GMM' for 'geometric morphometrics' and 'FEA' for 'finite element analysis', full descriptions of these methods are given later in this chapter and in Chapter Two.

In terms of scope, it is necessary to apply several parameters to confine many of the potential possibilities into a strong data set resulting in a strong research focus. Limiting the geographical study area to include only UK material provides a convenient and distinct location in terms of practical considerations (both time-constraints and financial-constraints), whilst also representing the physical barrier provided by the sea, in the formation of post-Ice Age Britain. Furthermore, rather than looking for initial markers of domestication we can directly compare the wild morphology in aurochs to the morphology of cattle once domestication has been firmly established. This is obviously assuming no local domestication of British aurochs creating the aforementioned proto-domestic morphologies overlapping with aurochs. The evidence for local domestication in Britain, and the European continent more widely, is at present uncertain (see Götherström et al, 2005 and more recently Edwards et al, 2007), if further clarified in the future local domestication could have an impact on this research. This is also the case in the date range of specimens, being primarily late Pleistocene and early Holocene for aurochs, and post-medieval and modern for domestic cattle. Comparison will therefore be between the undomesticated aurochs and the most recent domestic cattle. While comparison of changes in morphology for each time-period is not possible, the most recent forms of domestic cattle can be compared to understand any potential changes up to the present day. Typically for archaeology many of the older specimens were also incomplete suffering, taphonomic and post-excavation fragmentation, further limiting the kinds of analysis possible on material from archaeological contexts. A wide number of specimens were available and sourced from multiple institutions, in total 84 aurochs and 144 cattle crania were accessed from 22 institutions. For the aurochs only 10 were complete enough to use in the full analysis, with a further 20 aurochs being used for partial analysis. Similarly for domestic cattle, 65 were complete with an additional 26 being included in partial analysis. This unfortunately meant 107 crania of aurochs and cattle were too fragmentary to use in this research. The domestic cattle crania available of sufficient completeness were primarily from modern periods being reference specimens, this obviously has clear implications for conclusions as comparison is between aurochs and the most recent modern cattle. The full details and specimen list can be seen in appendix 1 showing all meta-data for the specimens used and those collected but not included.

1.4. Contribution of the research to the wider field.

To date knowledge gained into aurochs and domestic cattle has generally been from biometric comparative studies looking at various aspects of morphology but prominently featuring size variation as a major research theme (Wright and Viner-Daniels, 2015; Guintard, 1999; Cerilli and Petronio, 1992; Grigson, 1969). With recent methodological advances and the adoption of newer techniques into archaeology and zooarchaeology (Spyrou *et al.*, 2022), this offers the potential to review and advance the traditionally accepted limits of data. This is particularly relevant to 3D shape-based analysis and biomechanical analysis for which the validity has already been established in similar studies of other species (e.g. Gaastra, 2023; Haruda *et al.*, 2019; Seetah *et al.*, 2014; Owen *et al.*, 2014). There are some obvious research clusters which primarily focus on improving understanding of living organisms emanating primarily from the biosciences (Polly *et al.*, 2016; Lawing and Polly, 2010; Panagiotopoulou, 2009; Rayfield, 2007). Naturally archaeological research is firmly based in biological findings; however, it adds the time depth not always found in other scientific disciplines which focus on living or recently dead animals. Therefore, scientific disciplines like anatomy have given good descriptions of the morphology of cows whilst the humanities have considered the historical development and socio-economic value.

Specifically, this thesis aims to uncover differences in the form and function of aurochs and cattle and how these were affected by domestication and husbandry. Using virtual reconstruction, biomechanical simulation and statistical shape analysis methods, the variations between cattle and aurochs in response to human exploitation will be quantified. This is an attempt at novel research by utilising techniques from other disciplines together with new technologies. Through this, new insights of past peoples' husbandry practices, attitudes towards wildlife and the place that cows occupied in this changing world will be elucidated to address long held questions such as why do cows remain part of our modern environment, but aurochs have become extinct? Non-destructive techniques, new to the application of archaeological material, will be used to investigate early human-bovine interactions and how they shaped aurochs and cattle in Britain. It is becoming clear that traditional techniques in archaeology cannot reveal the full picture of domestication, so methodologies from other disciplines (e.g., engineering) via the use of photogrammetry and surface scanning will be harnessed in order to create virtual models of skulls.

1.5. Research questions and hypothesis.

Taking into consideration the wider context and scope, research questions were developed for this thesis to address specific areas where there was the potential for new results to provide significant conclusions. This was particularly the case given the application of novel methods (not extensively used on cattle species in the past) to address some of the previously held views about cattle morphology and domestication. There are two primary overarching research questions this thesis will address, which are:

1. Are there morphological changes between aurochs and domestic cattle and is shape change important compared to size?
2. How do morphological differences in the crania of aurochs and domestic cattle impact skull performance?

These research questions are formulated to be broad thematic questions running through the thesis and addressed in each of the results chapters. While these questions seem wide in scope, they are further broken down into sub-questions in each chapter to make analysis and results more manageable. In general, it is hoped that the difficulties in evaluating the size and shape in aurochs and cattle overlapped in terms of their morphology, can be reviewed. Size has always been at the forefront of research into aurochs and cited as a major distinguishing factor although often seen as being allometric between aurochs and domestic cattle. New methods in research carried out on other species have shown that there are often much greater changes in shape (Alarcón-Ríos *et al.*, 2017) often overlooked due to the difficulties in defining shape. Shape in cattle has received little attention and has to date not been addressed, thus the need to ask why changes might be occurring and the mechanisms that underpin morphological changes. Bearing this in mind, two hypotheses are proposed:

HYPOTHESIS 1: Wild and domestic cattle are morphologically distinct not just in size but in shape, and this is likely related to the differing environments they lived in and breeding selection, particularly related to human animal husbandry.

HYPOTHESIS 2: The differences in cranial shape are predicted to have a marked impact on the biomechanical performance of aurochs and domestic cattle, with human husbandry reducing the resistance to stress from both feeding and horn mass.

In light of this, geometric morphometrics (GMM) and finite element analysis (FEA) were proposed as suitable tools to investigate if shape change is important in cattle, and to evaluate the biomechanical differences that could drive morphology. Wild and domestic will be considered to see how did human husbandry alter the evolution of cattle and in which ways this influences form.

1.6. Layout of the thesis.

1.6.1. Chapter Two: Literature review.

To begin, a review of published literature on aurochs and cattle is necessary to highlight the research context and established knowledge on the topic. The key themes in literature published on aurochs, cattle and morphology will be highlighted to give an indication of why there is scope for this study. Aurochs have had a long history of research with often contentious strands of evidence. A brief history of this will be outlined along with some of the potential problems misinformation has caused. The wider ecological habitat is also worthy of consideration, as it is known to impact evolution, with a consideration of how cattle husbandry practices may be a driving force in skeletal variation. This will inform the establishment of what is currently known of the skeletal anatomy of the aurochs and the cow, with specific reference to the cranium in terms of form, function, and variation. It will also look at the study methods proposed for use by this research and why they are considered suitable for a study of this nature.

Given the scope of this research it is acknowledged that there will be inevitable omissions. Most notable is any critical review of the time and location of domestication events in the Near East as this is not central to the themes and scope of this research, the geographical focus being maintained upon Britain. However as this is an important event in understanding why morphological changes occurred, consequently a brief review of the current theory on this topic of domestication with regards morphological change is provided. It must be stressed that this research is not concerned with the formulation of a general principle on the effects of domestication, but with the distinction between cranial morphology of aurochs and cattle. Britain provides a good case study for this giving us a pre and post snapshot study of cattle domestication.

1.6.2. Chapter Three: Sensitivity.

It is necessary to establish the validity and the inclusion of any potential problems of the proposed methods with specific focus on cattle. The main technique that requires consistency is GMM and there are a number of tests to ensure results can be replicated, are repeatable and are reliable. Chapter Three establishes the methodology for collecting 3D scans via photogrammetry testing for different parameters. This includes making models of the same specimen on three consecutive days to test user consistency in terms of photography technique and software usage. The models were also exported as unscaled and scaled to identify if this has an impact on results, and if there is consistency in the way the software exports models. The final sensitivity test was of user error in landmarking, by repeatedly placing landmarks on five consecutive days to test for individual user variability. This chapter also establishes the data set and landmarks used in the shape analysis in chapter four, establishing user variability as low and model variability as a negligible impact. Potential pitfalls and limitations will be discussed alongside the advantages of these methods. In particular, the level of user and equipment error will be assessed on a specific specimen and data set to investigate the accuracy and precision of data collection at the imaging and landmarking stages.

1.6.3. Chapter Four: Shape variation in wild and domestic cattle.

In this chapter, GMM will be applied to a data set of aurochs and cow specimens in order to determine the level of morphological variation. This chapter uses the landmarks established in the previous chapter applying them to a larger data set. This will allow examination of the changes in the shape of the skull that may not be readily perceived or not easily quantifiable via traditional osteometric methods. It is known that skull shape can adapt rapidly to external stimuli, e.g., selective breeding or environmental pressures (Young and Badyaev, 2010; Klingenberg, 2010; González-José *et al.*, 2005). The first analysis undertaken is a general comparison of skull shape between aurochs and domestic cattle in order to quantify the overall shapes of the groups and to establish any peculiarities and differences. Following this, several other traits are tested to examine their influence on cranial shape; this includes sexual dimorphism and breed. Different breeds will be considered to determine recent ‘improvements’ developed via selective breeding that have increased morphological disparity in cows disproportionately than that between cows and aurochs. The degree of sexual dimorphism will also be tested as cattle are known to exhibit strong male-female size and appearance variations. GMM was also undertaken on fragmentary material by reducing the number of landmarks so it could be applied to a larger number of fragmentary specimens to see if the shape differences were still apparent, and if this could be a viable method in assessing more typical archaeological material. The contribution of size was also tested, using regression analysis to plot the size-shape trajectory of aurochs and cattle to enable the investigation of the allometric trends of each group.

1.6.4. Chapter Five: Feeding biomechanics.

Following the shape analysis in Chapter Four, one specific area of the cranium is tested for its potential contribution to shape difference: the feeding apparatus. Here FEA is used in an attempt to establish if cranial form is related to function. Clearly, a large portion of the cranium in cattle is occupied by the feeding apparatus and is used extensively in the ingesting and processing of large quantities of food materials. This chapter seeks to establish if domestication has influenced the ability of cattle to process specific kinds of herbaceous material. It is a generally held view that domestication and control of diet by humans will have reduced the ability of domestic cattle to feed as efficiently as in previous times, particularly on tough or fibrous foods. This is due to the more limited diet including a smaller range of foraging options available than aurochs, and indeed other wild cattle, where foraging and feeding on tough material like tree branches occurred commonly, particularly in winter. FEA models of domestic cattle, Chillingham cattle and aurochs are compared as representative of domestic and wild cattle species to see how loading in a bilateral and unilateral bite results in stress across the cranium. Furthermore, the bite force and mechanical efficiency of biting is estimated to their feeding strategy.

1.6.5. Chapter Six: Cranial response to headgear.

This results chapter will explore another aspect critical to the functioning of cattle, the horns, thought to have a marked impact on the posterior aspect of the cranium. The frontal and occipital region was noted as a key area of shape change in previous analysis, so here a preliminary study is conducted to begin quantification of the role of horns in driving cranial morphology. FEA is used to see if having large horns, as seen in aurochs, is accompanied by specific biomechanical requirements in the skull to support large headgear. Similarly, if smaller horns have led to a reduction in robustness in domestic cattle. In addition, the functional morphology of domestic cattle, Chillingham cattle and aurochs is compared using proportionally sized horns to review their impact on the cranium, and to determine whether domestic and Chillingham cattle could support similarly sized horns to aurochs.

1.6.6. Chapter Seven: Discussion and conclusion.

The final chapter will synthesise of all the available results into an overarching statement regarding the morphological disparity between aurochs and domestic cattle. Some suggestions will be offered relating to these differences observed and as to why they are occurring. This will be related to the initial research questions to establish the relevant success of the research. In addition, the limitations will be highlighted along with the potential for future research and suggestions for promising areas of study.

1.7. Conclusion.

This chapter has set out the core aims and hypotheses for this thesis, establishing the parameters within which research into aurochs and domestic cattle shall be undertaken. In summary, research presented in this thesis investigates if there are shape based morphological changes between aurochs and domestic cattle and how differences in the crania relate to skull performance. To do this only material from British institutions shall be used, incorporating all available aurochs at the time of data collection along with a representative sample of domestic cattle. All specimens are included into analysis of shape and then further explored with regards to functional performance using novel methods. The potential significance of the topic has also been established, with no comparable studies having been undertaken previously utilising the methodological approach with GMM and FEA. It is therefore proffered that this thesis could have potential impact further understanding of the morphology and biomechanical situation in aurochs and domestic cattle. The background to this research is established in more detail in Chapter Two, where a review of the most relevant literature is undertaken. The relevant methodological framework is also established, from a theoretical perspective in Chapter Two and then practical in Chapter Three.

2. Chapter Two: Literature review.

2.1. Introduction.

This chapter has several functions following on from Chapter One in establishing background knowledge and why the research presented later in this thesis is important. This chapter's purpose is to provide a theoretical baseline on the study of wild and domestic cattle from the published literature and establish the methodological background of this research. In this chapter first reviewed is the study of size and shape in aurochs and domestic cattle to present the currently accepted research. A large part of this chapter is dedicated to review of previous research of aurochs and cattle, initially from an historical perspective to give research context and then to critically review previous studies. In addition, the factors which influence size and shape will be considered, these factors include chronological age, geographic location and human interventions such as domestication. Many of the existing studies into domestication highlight the complicated nature of this topic, involving both biological and human mediated processes that have directly and indirectly influenced cattle size and shape. The second half of this chapter examines the methods used to investigate and answer research problems related to size and shape in aurochs and domestic cattle. Understanding the development of the methods and their implementation is important to validate the choice of methods (GMM and FEA) and how they have been previously applied. Some general understanding of the establishment of GMM and FEA in (zoo)archaeology and other disciplines is necessary to appreciate the questions that can be addressed, and from which data can be generated. This is relevant in understanding the results in Chapters Three to Six. Overall, this chapter has a broad scope covering many topics, related to aurochs and cattle which have been the subjects of study for a long period of time. This thesis offers a new approach and methodology, focusing on current understanding of the skeletal morphology, particularly cranial, in aurochs and domestic cattle and how this can relate to biomechanics. To provide sufficient scope for discussion in this chapter it is necessary to include review of material from outside the core geographical study area of this thesis, the, as research solely within Britain does not support the required background synthesis.

2.2. A concise history of aurochs and cattle.

The aurochs was a large species of wild cattle. The precise origins of the aurochs are somewhat unclear as its evolutionary history is complex and spans a significant period through time. Fossil evidence suggests that the ancestors of the aurochs existed in Eurasia as early as the Late Pleistocene, around two million years ago (van Vuure, 2005), these early bovine species gradually evolved and diversified. By the time of the Late Pleistocene, there were several different species and subspecies of wild cattle present in Eurasia, and indeed represented today by the diverse tribe Bovini comprising (depending on classification) four to seven genera and between 14 and 18 species (Robinson and Ropiquet, 2011). The specific lineage leading to the aurochs likely emerged during the Late Pleistocene, with the species *Bos primigenius* eventually becoming dominant. The species name '*primigenius*' refers to its ancient or so-called primitive nature, distinguishing it from other extant species within the *Bos* genus. The aurochs belong to the same genus (*Bos*) as modern domesticated cattle (*Bos taurus*), indicating their close evolutionary relationship. Over thousands of years, the aurochs evolved and adapted to different regional conditions, resulting in the development of various subspecies and regional populations. By the beginning of the Holocene epoch, approximately 11,700 years ago, aurochs' populations were relatively widespread (Mona *et al.*, 2010; Sommer, 2020). The aurochs spread across various habitats in Europe, Asia, and North Africa and thrived in a variety of environments, including grasslands, forests, and wetlands (van Vuure, 2005). They coexisted with early human societies and had a significant role in the cultural and ecological landscapes of many regions (Ajmone-Marsan *et al.*, 2010).

Aurochs were important game animals and were hunted by early human communities for food and other resources. Throughout prehistory, aurochs were hunted for their meat, horns, hides, sinews, and probably other useful products not preserved in the archaeological record (Wright, 2013). The hunting of an aurochs would have been a formidable task, especially bulls, which were estimated to weigh upwards of 1,000 kg (van Vuure, 2005). As human societies transitioned from hunting and gathering to agriculture, the aurochs became increasingly significant. During the Neolithic period, which began around 10,000 years ago, the aurochs played a significant role in the lives of early human societies. The transition in subsistence strategy from hunting and gathering to agriculture and animal husbandry marked a crucial turning point in human history (Diamond and Bellwood, 2003), and the aurochs was one of the primary animals involved in this process. As humans began to settle and establish agricultural communities, they started domesticating plants and animals (Larson and Fuller, 2014; Ucko and Dimbleby, 2007; Zeder, 2006b). The aurochs was one of the first large animals to be domesticated (MacHugh *et al.*, 2017), indeed possibly on multiple occasions and in different locations giving rise to the taurine (*Bos taurus*) and indicine (*Bos indicus*) species (Pitt *et al.*, 2019). Whilst the range of aurochs covered Europe and Asia, zooarchaeologists generally agree the first domestication centres were in the Near East (Crabtree, 1993; Payne, 1991), in the Fertile Crescent from *Bos primigenius primigenius* in the Neolithic producing taurine cattle (Bruford *et al.*, 2003). Around 1,500 years after taurine cattle, a second domestication event took place in the Indus Valley, where *Bos primigenius namadicus* gave rise to indicine cattle or zebu cattle (*Bos indicus*) (Loftus *et al.*, 1994). There may have also been suggestions of independent domestication in several other locations such as northern Africa (Pitt *et al.*, 2019; Grigson, 2000), and even hybridisation in Europe (Götherström *et al.*, 2005) although these claims are less well substantiated (Edwards *et al.*, 2007).

Domestication of aurochs into cattle had clear benefits for humans, as it allowed for a more stable and controlled supply of not just food but many secondary products. Domesticated cattle provided a source of meat, milk, hides and traction for early farmers (Kamjan *et al.*, 2022; Greenfield, 2014; Halstead and Isaakidou, 2011). The importance of these attributes can be seen in the rapid expansion of cattle following domestication, following routes northwest into Turkey, Balkans, Northern Italy through the Mediterranean and along the Danube River (Pellecchia *et al.*, 2007). Eventually cattle reached all areas of the world, and differing climates and geographies, with location significantly influencing as to what humans considered beneficial attributes in cattle. Breeding, sometimes human mediated (so-called selective breeding), in different parts of the world created a wide variety of cattle typology (Manning *et al*., 2013; Bovine HapMap Consortium, 2009). While the domestication of cattle was underway during the early Holocene, there were still wild aurochs populations persisting in certain areas, though these became increasingly fragmented and reduced. These populations faced various challenges, including habitat loss, competition with domesticated cattle, and hunting pressure (Augustyn and Perzanowski, 2022; Hall, 2008). Over time, the wild aurochs populations declined, and the last known wild individual died in the 17th century (van Vuure, 2005). However, domestication marked the beginning of the process that ultimately transformed the aurochs into the various breeds of domesticated cattle we have today.

From the late prehistoric periods, cattle were a mainstay species that underwent phases of improvement and alteration. This is most notably seen in the Roman period, where, by the late Roman period, the bones of large cattle are seen at sites across Europe (MacKinnon, 2010). Such remains suggest the possible replacing of a smaller, earlier variant of cattle, and this is often seen as the first evidence for the agricultural improvement of cattle or exportation of new larger breeds (Groot and Albarella, 2022; Colominas *et al.*, 2014; Murphy *et al.*, 2000; Teichert, 1984). This follows a general pattern of size decrease in the subsequent centuries, possibly indicating social or economic alterations to cattle herds and husbandry practices (Grau-Sologestoa *et al.*, 2021; Pigière and Goffette, 2019; Albarella *et al*., 2008; Schlumbaum *et al*, 2003). From the late Medieval period and particularly into the post-Medieval period, there are again size shifts seeming to be dictated by agricultural improvement (Cussans, 2013). While the trend had been for cattle of smaller stature, the post-Medieval agricultural revolution saw cattle increase in size (Grau-Sologestoa and Albarella, 2019; Thomas *et al.*, 2013). It is also in this period that we have the first recorded evidence of distinct cattle breeds with established characteristics and lineages (Felius *et al.*, 2014), although these were likely in existence before this time even if informally. Cattle in more recent times have undergone many husbandry processes, with the aim of specialisation to suit a particular purpose, being of benefit to humans. The main roles of cattle in modern society are in dairy and beef production, but historically traction would have also been important (Thornton, 2010). By products of cattle carcass processing culminated in products of secondary importance, such as hide for leather, hard tissue structures such as the horn used in a way comparable to modern day plastic, and the use of bones for glue and even as a building material (Leoci, 2014). The importance of cattle is certainly a worldwide phenomenon with various breeds being exported around the globe. In the modern period and with the rise of mechanised agriculture, husbandry increased to industrial proportions and the management of herds was expanded to a monumental scale.

As it can be seen, aurochs and cattle have had a long and varied path with several critical steps. The aurochs continued to be a vital animal in human societies throughout the Neolithic and beyond, with its influence extending into subsequent historical eras but its importance was certainly diminished by the wholescale uptake of domestic cattle (Conolly *et al.*, 2011; Troy *et al.*, 2001; Bökönyi, 1974). It should be added that the briefly discussed background presented here is not without complexities, even the definition of what is considered 'wild' and 'domestic' are much contested (Purugganan, 2022; Bökönyi, 2014). The reality is that there are a multitude of processes that have resulted in the varied relationship between aurochs and cattle that is mediated by humans, though further interrogation of this history is outside the focus of this thesis. This background frames the general understanding of both species and how they are related but also gives some indication of their differences particularly in terms of treatment by humans. Indeed, the close control of animal husbandry marked the pivotal turning point in terms of change, not just in treatment, but the influence this has on morphology as seen not just in cattle but through numerous and varied species such as trout, dogs, and ducks (Duggan *et al.*, 2015; Pulcini *et al.*, 2013; Wayne, 2001). This is in addition to the more general factors that all have the potential to induce morphological changes. Specific changes are reviewed with more focus in the next section.

2.3. Morphology: what is known from past research.

Aurochs and domestic cattle have been extensively studied for decades, from the very inception of early modern zooarchaeology. To maintain relevancy and to avoid repetition of the more popular threads of aurochs and cattle research, the parameters of the major part of this literature review have been established to look at skeletal morphology. A review of all literature related to cattle morphology would be a formidable task as the subject has been active in a research sense for hundreds of years in multiple subject fields. Aurochs and cattle skeletal morphology has been primarily researched through traditional zooarchaeological methods, primarily biometry; this area will be presented in two sections. These will first cover postcranial and then cranial material, reviewing the major contributions in each area. Research has been more prevalent in the former of these areas seemingly for preservation reasons, with crania receiving less attention. However cranial morphology is of a particular relevance to this thesis, especially considering the specifics of morphological differences between aurochs and domestic cattle for which past studies have been infrequent. Crania seldom survive taphonomic processes intact and are some of the least explored bones in zooarchaeology. Undoubtedly crania are important to animals, housing various sensory organs, along with feeding apparatus. In this instance both cranial and postcranial adaptations are important in understanding the changing evolutionary and morphological response in aurochs and domesticates.

2.3.1. Summary of research on postcranial morphology.

The postcranial morphology of aurochs and domesticates has received the greater share of attention, compared to crania. As mentioned previously, this is largely for taphonomic reasons as the material exists in reasonable quantity and quality, but also methodological reasons, as the questions that can be answered have more utility to zooarchaeology. Themes in this work include size change, distinguishing aurochs from domestic cattle, sexual dimorphism, and temporal variation. Postcranial bones lend themselves to size analysis, being primarily robust long bones that preserve with reasonable reliability making linear measurements achievable. This section therefore provides a review of the diversity of work undertaken over a long time span to give a general impression of the state of research, rather than a critical review, as postcranial material is considered quite different to cranial with different biological functions. For this review primary consideration is given to two key topics that are most prevalent in research related to morphology in postcranial material, these are species identification and size. In research terms, identification and size are closely linked, with size often being the distinguishing factor in determining aurochs from domestic cattle.

Identification is of primary importance for zooarchaeologists seeking to differentiate species based on their bone content, to understand exactly what is being examined, and how it relates to past populations, and indeed the animal itself. Identification based on skeletal morphology and the discrimination of wild and domestic forms of animals derived from comparative anatomy underpins much of what is known about aurochs and domestic cattle. It should however be mentioned that identification is closely related to the work regarding size as a key distinguishing feature (Schmoelcke and Gross, 2021). At the core of this topic is how to differentiate between species of bovid, particularly aurochs and domestic cattle that are closely related, especially when presented with a fragment of bone that is seemingly morphologically indeterminate. This problem dates to the 18th century and the early history of archaeological research, where there were two schools of thought on the origin of bovine remains. Some believed one wild cattle existed in Europe, being *Bison bonasus*, others proposed there were several including the bison and aurochs (Von Leithner, 1927). While providing the basis of modern research on the topic, early studies introduced some confusion that later academics spent much time investigating.

To the present day it is common to see aurochs and other similar bovids confused with one another because of early innocence. It was even proposed that two species of aurochs existed, a suggestion based on two identifiable aurochs size groups (La Baume, 1909; Adametz, 1898; Nehring, 1889). Leithner (1927) was the first to describe the size difference as resulting from sexual dimorphism, calling both large and small forms male and female as *Bos primigenius*. It is reasonable to suggest that these early accounts were hampered by unreliable data, dubious verbal and written reports, and ignorance born of obscurity concerning aurochs. However, from this moment research intensified, and coupled with an increase in skeletal finds data, authors attempted to link skeletal morphology of aurochs to their way of living (Lehmann, 1949; Von Leithner, 1927; Nehring, 1900). Unfortunately, the initial results were unconvincing. What emerged from early scholars was an interest in looking at the physical size of aurochs in relation to domestic cattle. Even into the 1950s and 1960s, researchers (e.g. Grigson, 1969, 1978; Jewell, 1963) were debating the possibility of identifying various groups of aurochs and taurine cattle based on size divisions. This line of enquiry has prevailed almost as long as bones of aurochs began to be recovered and is certainly the most common form of study on aurochs. What becomes apparent is how many authors described size as a determin of species. Linked to this was an attempt to reconstruct past characteristics of aurochs, particularly height at withers, based on standard osteological measurements usually comprising length and width. Early studies differed greatly, citing heights ranging from 130 cm to 220 cm (Von den Driesch and Bossneck, 1976; Lengerken, 1957; Astre, 1937). Matolcsi (1970) proposed using conversion factors to determine height from certain bones. Vuure (2005) combined results from Matolcsi (1970) and Degerbol and Fredskild (1970) to suggest a credible figure for the aurochs' height, specifically 160-180 cm in bulls and 150 cm for cows. While many of these studies were important in establishing aspects regarding aurochs, the use of size may have been detrimental, creating some confusion regarding exact classifications.

From the 1960s a more detailed approach to skeletal morphology began to be applied to problems concerning aurochs and domesticates. Skeletal elements were subjected to more rigorous biometric analysis and comparisons with an increasing dataset. Consequential to the number of measurements being taken in relation to aurochs, other uses for the data were initiated. Aurochs and cattle have been shown to exhibit a size overlap. Grigson (1965) used metric data to separate aurochs from domestic cattle at archaeological sites such as Windmill Hill. For example, by plotting scattergrams of the length and breadth of skeletal elements it was shown that the measurement for cattle and aurochs overlap when plotted. Research by Jewell (1963) on measurements of the distal width of the metacarpal and humerus further demonstrated the aurochs remains from Star Carr had a great overlap with domestic cattle from later periods in Britain. Degerbol and Fredskild (1970) produced a comprehensive work on Danish aurochs that was seen as seminal and significantly advanced the data available for future comparative studies. This provided an assessment of all known material of aurochs and a large number of cattle with resulting biometric information. Much of the information was based on postcranial material, although there was, significantly some assessment of skulls looking at sexual dimorphism, as discussed in the section below. One of the main outcomes was highlighting the degree of sexual dimorphism that exists both in aurochs and domesticates. Despite this several overlaps were seen, both between males and females of each species but also between domestic males and aurochs females, noted universally in nearly all bone measurements. It was suggested there is a likelihood of overlapping groups comprising a combination of wild and domestic cattle, which is noted by early researchers (Grigson, 1978). However, it is now believed the distinct groups starting with the smallest measurements represent domestic female cattle, next domestic males and female aurochs and the largest showing male aurochs. However as stated by Wright (2016), these biometric studies were restricted by overlapping measurements of the two species causing a lack of resolution, compounded by a paucity of comparative data, and the lack of an in-depth study on *Bos* material.

More recently, several large-scale studies have looked at aurochs skeletal morphology on a broad geographic scope with many specimens (Wright, 2016; Viner-Daniels, 2014; Guintard, 1999). These studies in particular investigated some of the long-held views regarding aurochs, but with the largest data set compiled to date, taking into account factors such as geographic location that had previously only been tentatively investigated. Viner-Daniels (2014) investigated the size variation across the Mesolithic-Neolithic transition in Britain, suggesting a highly complex local situation. This established a synthesis of large amounts of the biometric data for aurochs creating a key baseline for future studies. From this it was suggested that while a size decrease was present in the Pleistocene, it was not so apparent in the Holocene and changes seemed to mostly impact teeth (Viner-Daniels, 2014). Expanding on this to look at aurochs' morphological variation on a large scale, Wright (2016) used osteometric data from numerous aurochs taken from several geographical areas in Europe spanning a large time period. In this research a number of broad scale patterns were identified relating to size and shape differences in aurochs, including a south-north gradation in body size during the Pleistocene and Early Holocene, and lesser indication of a west-east cline during later periods. However, when looking at later periods, patterns in size and shape become more difficult to ascertain, due to issues of distinction between wild and domestic animals, it is noted there is some indication of a size and shape change between wild and domestic cattle. A number of bones tend to have a more slender appearance in domestic cattle compared to aurochs, and this pattern becomes especially clear in the latest periods, when selective breeding became common. It was noted that this pattern of change could be mistaken for many other processes, and that other factors, including geographic/climatic discrepancies may result in indistinguishable impacts on the shape of bones as the domestication process (Wright, 2016).

From these topics other outputs for morphological variation were developed, particularly in domestic cattle where wider considerations regarding morphology can answer questions about human society and husbandry. These were centred on what could be determined from the physical appearance of bones regarding the life of the animal. To this end work on morphological differences has been used to answer questions regarding sexual dimorphism, breeds, time-period and site differences, and even wider environmental change (Kamjan *et al.*, 2022; Schmoelcke and Gross, 2021; Khan *et al.*, 2018; Meier *et al.*, 2017; Grigson, 1969). Similarly, to work already discussed, many of these factors have been established via biometry and comparison of size. Indeed, differentiation on the basis of morphology is a common practice in zooarchaeology, and the development of osteometric criteria based on morphology has been key.

From the literature on postcranial skeletal morphology, two observations become apparent. First is that, while the study of morphology has enjoyed a longevity of research, the volume of evidence until recently is sparse. Indeed, research is seemingly limited to linear measurements on bones, investigating questions of size and by using size identification. Second, a consensus existed in research early on, that aurochs and cattle are the same in all but size, which prevails to a certain extent to the present. Furthermore, the morphological investigations undertaken until quite recently were generally brief, and often focused on the same skeletal elements (metapodials). In recent studies of morphology there has been the potential to look at much more than merely size comparisons, but this has not yet been significantly undertaken. Indeed, a large part of this thesis is invested in showing that the morphological make up of a bone is greater than a summarising measurement to length and width. It may be that to date we have simply failed to identify the more subtle aspects of skeletal morphology due to the complexity in presenting multiple dimensions simultaneously. This is always the problem in dealing with biological material with intricate shapes. This is particularly the case when we consider crania, being very complicated in shape, which are considered next.

2.3.2. Summary of research on cranial morphology.

Interest in skulls dates to the roots of early zoology, and indeed in antiquity skulls were probably more coveted than other skeletal material. Much of the early research from the later 18th century investigated classifying cattle skulls into different types, particularly with regards to domestication and breeds (Schafberg and Swalve, 2015). Categorisation began in earnest from the early 19th century particularly with the introduction of Linnaean taxonomy (Felius *et al.*, 2011), that emphasised morphological differences as the basis for classification such as visible differences in cranial shapes but predominantly horn dimensions. In this early system the different cranial forms seen in the Neolithic were considered the best examples of domestic cattle. Divisions were primarily based on horn orientation and length, for example

Youatt (1834) who proposed five classifications; long-horns, middle-horns, short-horns, polled and Irish Cattle. These classifications were altered and refined by various early scholars, for example work from Rütimeyer (1867) and Nilsson (1849) looked at groups of skulls to develop classifications of the most characteristic skulls. Wilckens (1876) grouped cattle into several separate breeds using measurements of skulls to suggest similarity. By 1899, Dürst looked more closely at the variation in the skull and the possibility of horns to influence this proposing; longhorns with great weight were associated with skulls that are stretched and flat across the frontal, while short horns accompanied a domed cranial vault, in polled cattle the convex skull shape was seen as being even greater (Felius *et al.*, 2011). While much of this early research collated and described the state of archaeological finds and organised them, there were problems with overlapping characteristics that did not fit, or indeed overlapped several classifications.

Following this early research, the cranial measurement of aurochs and cattle began to be analysed and the identifiable characteristics led Bohlken (1962) to argue they were so similar he saw no reason for their classification as separate species. Based on this reasoning, it was proposed that the only effect domestication had on cattle was a reduction in size with implicit allometry. This view seems to have largely prevailed in archaeology as the study of aurochs is still based on using traditional analysis techniques, though these may not be suited to measuring fine scale morphological change. Other osteological observations of the cranium were also made, of note is Grigson's (1969) suggestion that the aurochs was a particularly variable animal especially with regards to the skull. This variability was suggested to be exacerbated by sexual dimorphism, however when osteometric data is plotted for males and females separately they are normally distributed. There is no suggestion that either male or female group could be subdivided based on size, suggesting variation is merely an expression of sexual dimorphism. If this is correct it would suggest that Bohlkan's (1962) recommendation, that there is no quantifiable difference beyond physical size, might be true. However, it is well established (e.g. Aristide *et al.*, 2018; Goswami, 2006; Hanken and Hall, 1993b) that many factors influence morphological traits (for example geological age, geographic isolation, ecology) to different extents.

While already discussed with regards to post-cranial material, Degerbol and Fredskild (1970) also provided a summary of several aurochs and cattle skulls. This provided a large amount of detailed analysis on how size varies in aurochs. Basal length of skulls was used as an indicator of size and sexual dimorphism, noting that “length is most affected by the developmental age and sex of the animals” (p.64). Furthermore, the temporal variation was also noted with older specimens generally being considered larger, suggesting a size reduction across time. This was caveated by the indication of outliers known from all periods. Beyond just basal length other measurements were also compared, such as width dimensions. These, along with lengths, were noted to overlap in range with large domestic cattle, “being coextensive with the range of variation in domestic males” (Degerbol and Fredskild, 1970, p.69). Many other comprehensive measurements were obtained and compared individually between aurochs and domestic cattle, but the results generally indicated the same pattern that the lower measurements of aurochs overlapped with the upper dimensions of domesticates. This is a specific issue of comparing single measurements along an allometric size overlap. Qualitative observations were also proffered regarding the overall character of crania, it was indicated aurochs had a more concave frontal bone in profile as viewed behind the orbits compared to domesticated cattle. Indeed, domestic cattle exhibited a more dome shaped frontal bone and a projecting occipital crest between the horns, and this shape was not seen in aurochs. Such differences have also been noted while collecting data for this thesis, but this observation has not been investigated through a zooarchaeological lens due to the methodological difficulty in quantifying more complex shapes.

In one important paper, Grigson (1978) specifically investigated aurochs and cattle craniology to examine relationships between size, proportions, angles and non-metric characteristics. Grigson concluded that aurochs and domestic cattle have a cranial morphology “so similar that they form a continuum and should be considered as the same taxon” (p.123). Interestingly, however, *Bos taurus* differ in some aspects. Two specific observations were noted; in aurochs the frontal bone was extremely concave emphasising the intercornual ridge’s prominence, and the intercornual ridge formed a greater acute angle in aurochs. These were listed as some of the main features in which domestication changed morphology. While not all these features had to be present in all domesticates, domestic morphologies included: overall smaller skull size, relatively broader skulls in bulls, relatively more narrow skulls in cattle, reduction of horn length in bulls, out of proportion horn length compared to cranium, rounded intercornual ridges, relatively concave and convex craniofacial regions and lower face and palate taking a forward rotation. Moving beyond just domestication, Grigson (1978) ascribed these differences as a consequence of breeds, something she termed specialisation. It was therefore argued that Bohlken's (1962) original proffering was correct, that aurochs and cattle do form one species with the overlapping reduction in size accounting for many of the differences between the species. This premise is one of the key assertions that seems to still exist to a certain extent in zooarchaeology, without any significant works on aurochs and cattle crania having been undertaken in recent times. It therefore remains to be explored if this assumption around size is still accurate, and this provides one of the major points of inquiry for this thesis.

Despite early classification attempts in cattle almost exclusively looking at the cranium, in research terms the cranium has received relatively little attention beyond this. This is with a few exceptions, a single paper has been published with direct relevance to this thesis that used GMM and FEA to examine Niata cattle (Veitschegger *et al.*, 2018), a full review is undertaken in section 2.4.3. A separate study by Balcarcel *et al.* (2021b) using some of the same data as Veitschegger *et al.* (2018) examined the brain size in aurochs and different domestic cattle breeds. This study measured characteristics related to the cranial vault to show a reduced brain size compared to aurochs, and that brain size was quite variable depending on breed. It was indicated that this could be due to husbandry practices and the amount of human interaction relating to docility of cattle breed (Balcarcel *et al.*, 2021b). More generally recent publications on aurochs' morphology have described isolated finds of crania, detailing measurements, and contextual information. While this has added more data to the general background in this area (Brudnicki *et al.*, 2011), few have opened further discussion on morphological relationships. One of the main problems has been the availability of material and its completeness (or lack of). Undoubtedly crania are fragile bones and seldom survive the taphonomic rigour of archaeological sites and recovery. It is also suspected that the kinds of information that can be gained from a cranium might be of less use and the data harder to obtain. Skulls are one of the most complex shaped collections of bones and have a range of functions combined into a single functional unit. This includes multiple sensory organs such as the brain, eyes, ears but also uses such as food procurement and even combat. These functions are quite different to postcranial long bones where the primary function is locomotion. Despite this, it was not until the 1960s that recovered crania of cattle began being described with proper scientific formality. Results from predominantly metric analysis have generally suggested that while there are some morphological differences, most measurements are normally distributed and overlapping between aurochs and domestic cattle. Any other observable differences were attributed to an increase in variability of domestic species compared to wild ones as expected from highly selective breeding (Grigson, 1978).

2.3.3. Factors influencing morphology.

While the cranial morphology of aurochs and cattle has been discussed, this has up to this point been absent of any consideration as to why morphology might be different, and indeed how skeletal alterations come to pass. As is evident, the cranium is complex in terms of its function serving several roles, protecting various important sensory organs (Lieberman *et al.*, 2000; Hanken and Hall, 1993a), and a functional basis for oral processes like breathing, procuring food and vocalisation (Marroig and Cheverud, 2001; Wake and Roth, 1989). This section could be extremely broad as skeletal form is controlled ontogenetically and evolutionarily which can be influenced by a multitude of factors (Dumont *et al.*, 2016; Hanken and Hall, 1993a). One of the key influences is the immediate surroundings in which an organism lives, and how changes to this environment can create the conditions for morphological adaptations. Such a phenomenon had been recorded for decades, with Darwin noting the composition of an animal can be influenced by the environment in which it lives (Darwin, 1875). This section considers the influence of environmental factors on morphology, and is divided into climate and interaction with the environment, followed by human specific mediation. As this thesis is focused on cranial morphological changes, some factors, such as the impact of the genetic composition of different populations and the contribution this makes to a specific morphology, while important, cannot be measured. With regards to this, the impacts of time, locations and genetics have already been alluded to and are not discussed in detail being outside the focus of this thesis. However, specific factors of population ecology and environment and specialised forms of control by humans are covered with more relevance in each individual results chapter in this thesis, along with a general overview presented below.

The natural environment in which an animal lives provides the best baseline for its morphology. Environmental change can be short term, creating a genetic isolation that suddenly makes a certain trait more prevalent, or on wider scales such as climatic fluctuations over thousands of years (Gilg *et al.*, 2012; Smit *et al.*, 2000). Evolution of a species within a specific climate and the ways in which the animal can interact with its environment is known to have an impact on the form of bones, reflecting the various selection pressures of the area leading to population developments (Hall, 2009; Lamb and Bauer, 2006). The interaction between an animal and its environment is directly related to its morphological capabilities in procuring resources to survive (Vitt *et al.*, 2003). Such a pattern has been shown in species where ecology is integrated into feeding behaviour, as this can produce pressures on selection and drive skull shape evolution (Jiangzuo *et al.*, 2023; Dumont *et al.*, 2016). Selection pressures can vary, and different morphologies can co-evolve to provide a different solution to the same problem, along with the functional requirements of the cranium being related to multiple purposes resulting in evolutionary trade-offs (Herrel *et al.*, 2009, 2007). While morphology could be considered quite adaptive, there are constraints by phylogenetic and developmental factors (Fabre, 2016).

The cranium is crucial in the concept of morphological differentiation in response to the environment, due to the relationship between the animal performing certain behaviours and the impact this has on bone. When an animal performs a task, for example feeding, muscles are activated to allow movement and generate force (Fabre *et al.*, 2014; Herrel *et al.*, 2008). Many of the main large muscles in the cranium are related to feeding, so it has been suggested diet plays a large role in influencing areas where these masticatory muscles attach (Cox, 2008; Herrel *et al.*, 2008). Indeed, the tougher the diet, the more robust the skull will be (Dumont *et al*, 2016). One of the key concepts about this is habitual loading and how an animal's attributes and behaviours can influence morphology. Under systems of naturally induced stress during use, bones can adapt and remodel to better resist stresses, termed Wolff’s Law (1986). While subsequent research has significantly revised this concept to improve its accuracy, the basic concept that bones respond to mechanical loading over time remains generally accepted (Stock, 2018), instead referring to the process of adaptive remodelling or 'bone functional adaptation' (Ruff *et al.*, 2006). This relates to the general process of functional adaptation of bones as a dynamic tissue, and has been well established (Robling *et al.*, 2019; Carter *et al.*, 1991). In relation to aurochs and domestic cattle, this process could lead to differences if there was a substantial environmental difference in the way each species interacted with its surroundings. For example, bite performance could be altered by variation in cranial morphology resultant from feeding on foods of different toughness. This could include an overall increase in bite force resulting in features such as increased masticatory muscles, improvement in the biomechanical levers and head robusticity to accommodate bigger muscles (Barros *et al.*, 2011; Herrel *et al.*, 2001). This concept is explored more in Chapter Five investigating feeding and Chapter Six examining horns.

In cattle specifically, consideration of the influence of the environment on morphology has received little investigation. In aurochs this topic has generally been focused around proposing the kinds of locations they might have lived in and using morphology to evidence this. For example, the aurochs' preference for more open grassland has been indicated based on the characteristics of the skull and teeth, which were highly adapted to feed on grasses and graminoids (Grigson, 1978). The hypsodont dentition seen in aurochs and cattle has been cited as evidenced for this, being ideally adapted to grasses, rather than tougher forbs or tree foliage, possibly suggesting less time in wooded environments. The reliability of such observations can be questioned in any extinct species or environment, and the level in which this could have influenced their skeletal morphology. With regards to cattle, while often considered to be dietary restrained, they have occupied nearly all climates from very cold to warm. Climatic variation has been shown to produce a wide range of morphologies in closely related species (Dumont *et al.*, 2016). However, when contrasted with the wider group of modern Bovids, it seems the situation might not be as simple. The different cranial shapes in Bovids were investigated under the assumption that the range of cranial differences would equate to some kind of specialisation, however this was not the case. The various shapes of skulls were seen as insignificant when considered against dietary preferences and habitat, but size was strongly correlated (Bibi and Tyler, 2022). This is remarkably like the situation currently proposed by research in the morphology of domesticated cattle and aurochs, the process of environmental adaptation is reviewed next.

Adaptation of animals to specific environmental processes determined by humans is termed domestication, manifesting in animals as a domestic phenotype with the expression of certain traits enabled by domestic adaptation (Kohane and Parsons, 1988). Environmental control can also be human mediated and create strong selection pressures in short time frames known to influence morphology. Indeed, Price (1999) encapsulated the concept in the definition as "the process by which captive animals adapt to man and the environment he provides" (p.246). Animal domestication can be seen to comprise a spectrum of gradual differences which should be distinguished from simply rearing an animal in captivity, although this is often the first step. At one end, domestication can be seen as a co-evolution that was beneficial to both humans and animals (O'Connor, 1997). Alternatively, it could be defined anthropogenically as the collective control of animal groups by humans for their use and service. While both are possible, a definition between this is often opted for, viewing domestication as a fluid process taking a long time before selective breeding involving complex shifts in population levels, technology, and social conditions (Bogaard *et al.*, 2021). However, and importantly, it should be noted domestication required humans to assume responsibility for the breeding, care, and nutrition of animals (Mignon-Grasteau *et al.*, 2005). To this end, numerous definitions have been proposed for the process of domestication and the effects it has on animals. The issue is that over the past 40 years, there has been no consensus among researchers, due to the diverse array of relationships between humans and animals (Vigne *et al.*, 2005). For this reason, it is difficult to formulate a definitive definition of domestication that encompasses the multifaceted factors contributing to this process, yet that is specific enough to define the biological and evolutionary actions that occur. However, two reasonable assumptions for domestication may be that we recognise the captive 'domestic' environment is different to the wild environment of the species. In addition, we assume a level of general management and curation applied consistently over time in rearing and maintaining the species in captivity. These are both reasonable assumptions for domestication.

Domestication creates a unique situation for animals, where environmental differences created by husbandry practices allow evolutionary mechanisms to bring about direct morphological changes as the population adapts over generations. Newly domesticated animals will inevitably bear a strong resemblance to their predecessors with only subtle changes; this may stay constant even in significantly advanced stages of domestication

(Clutton-Brock, 1992a). However, consistently applied animal management practices allow ever increasing extension to the domestic phenotype, for example, reduced fear of humans. Future generations of the animal will be subjected to artificial selection by man for favourable economic, cultural, or aesthetic characteristics (Clutton-Brock, 1992a). There are some commonly seen cranial morphological traits that are seen across several domestic species (Belyaev and Trut, 1989; Trut, 1988). Overall changes in size are commonly seen as the major factor of domestication, with large animals reducing their size to make handling easier or adapt to limited space (Kohane and Parsons, 1988), and small animals increasing in size to produce more yield. However, it has been noted size modification is not consistent for example in domestic cattle fat reserves are redistributed to the muscles as opposed to wild counterparts which store fat in the skin and kidneys (Clutton-Brock, 1992b). In cranial morphology the typically described features are often termed 'brachycephalic', used to describe the shape of a skull that is shorter than normal for its species. Along with size, brain case volume has decreased in many domesticates (Diamond, 2002; Gross, 1998), which is often noted as being accompanied by reduction of the craniofacial region, smaller and fewer teeth, changes in the shape of horns, wider and shorter crania (Zeder, 2006a). All these specific characteristics would come under a general relaxing of size, resulting from removal of strong sexual selection pressures, which are seen in numerous species (Grigson, 1969) although there are also suggestions this could be driven by diet (Samuels, 2009). In combination with these specific changes, we see a general wider array of morphologies as classically seen in Darwin's 1859 (Darwin, 1859) study of pigeons but also any species where wide scale morphological study has occurred (Stange *et al.*, 2018; Trut *et al.*, 2009; Wayne, 1986).

When considering morphological factors, there are suggestions that a great variability exists but also that the relatively slimmer bone proportion is the main difference between aurochs and domestic cattle, and some metric changes in segments of the limbs (Lasota-Moskalewska and Kobryn, 1989). The domestication process is key and likely presents the majority of changes between aurochs and domestic cattle. While this thesis is not measuring the actual process of domestication, this research is intrinsically bound to examine the outcome of such a process as a driver of morphological disparity. However, it has been suggested that even before domestication, and indeed in aurochs that were never domesticated, morphological changes were occurring from the late Pleistocene and early Holocene (Wright, 2013). When Pleistocene aurochs are compared to later Holocene aurochs, there has been noted a reduction in size, and this has been linked to environmental factors across this time span (Wright, 2013). Climatic warming from the Holocene allowed the aurochs to spread in range, with Bergmann's rule stating animals in cooler regions generally have larger size (Bergmann, 1848, 1847), although the validity of this has later been questioned (Bogin, 2022). This trend is seen widely in the morphological size studies of aurochs as mentioned previously in this chapter (Wright and Viner-Daniels, 2015). Indeed, one of the main issues has been that the anatomy of aurochs and domestic cattle is very similar with a lack of methodological resolution to differentiate them, as noted in several attempts at identification. Such issues have been widely discussed, with identification based primarily on size, with domesticates tending to be generally smaller than their wild progenitors (Noe-Nygaard *et al.*, 2005; Andersen, 1993; Brock, 1990). No clear metric has yet been devised to allow consistent and clear distinction however due to the size overlap in metrics of cattle and aurochs, especially between aurochs females and domestic males (Rowley-Conwy, 1995).

From the wider literature, environmental conditions of an animal have been shown to have an impact on morphology (Ryding *et al.*, 2021; Koehl, 1996). Indeed, when examining the morphology of captive versions of species, compared to their wild versions, a difference is noted in cranial form with causal factors particularly related to limited diet (Siciliano-Martina *et al.*, 2021; Parsons *et al.*, 2020;). This is particularly related to the relationship between form and function, where the more specialised an animal is in its adaptation to its environment, the more this will be reflected in its morphology (Jiangzuo *et al.*, 2023). Here I have discussed the possibility of the environment, both anthropogenic and natural, to influence the morphology of cattle. The skull as a highly complex system of integrated functional components has also been highlighted, including its role in a wide variety of activities be it food procurements, defence, sexual behaviour, or locomotion (Barros *et al.*, 2011). The question of size is an obvious one as aurochs are visibly much larger, and so this has been explored in postcranial material. There are many studies, both older and more recent, that tackle questions of size between aurochs and domesticates (e.g. Wright and Viner-Daniels, 2015; Wright, 2013; Ajmone-Marsan *et al.*, 2010; Kyselý, 2008; Linseele, 2004; Guintard, 1999; Lasota-Moskalewskaand and Kobryń, 1990; Kobryń and Lasota-Moskalewska, 1989; Grigson, 1969). Seldom explored is shape, that is in any comprehensive way beyond a measure of width on a skeletal element. Shape is more difficult to characterise as it deals with the holistic 3D characteristics of a bone which is hard to quantify through zooarchaeological methods.

2.4. Introduction and review of the methods.

This section is focused on the methodological aspects of this thesis, and in particular the rationale on which the methods will be applied and the context within which the results can be interpreted. Coverage of the practicalities of each particular method is contained within Chapter Three and in each results chapter. The methods, geometric morphometrics (GMM) and finite element analysis (FEA) are discussed below in terms of their development and applicability, but both are applied in the context of this thesis as part of a toolkit that is used to quantify bone and how differing conditions can impact response in bone, primarily in response to longer term evolutionary trends. To establish this observation more fully, we first need to consider the practical aspects of bone, its formation, its development and how it responds to pressures. Indeed, understanding bone and how it adapts is a key aspect of the shape and functional aspects of this thesis.

Before considering methodology, it is important to understand how bone functions and how we can measure differences in morphology. As Marks *et al.* (2002) indicated, bone is a type of connective tissue highly specialised in form, having a primary function of providing support and protection for the body and an attachment for muscles and connective tissues. It plays a significant role in the metabolic system but also biomechanics (Marks *et al.*, 2002; Rodan, 1992; Hancox, 1972). The bone is constantly being adapted by replacing and altering the matrix when looking at a cellular level (Freemont, 1998; Parfitt, 1994). This process is done through osteoblasts and osteoclasts, resorbing, and laying down new bone (Marks *et al.*, 2002). Under this process, osteoclasts, being large multinucleated cells found in the bone surface, control the resorption of bone tissue (Teitelbaum, 2000). The osteoclasts occupy specialised sections in the bone surface, a ruffed border, and a clear zone, acting as a location for bone resorption (Marks *et al.*, 2002). Working in contrast are bone forming cells termed osteoblasts, which are responsible for new formation of the bone matrix. The osteoblasts are formed from osteoprogenitor cells and synthesise the majority of proteins required to build the bone matrix. This is undertaken either in the plasma membrane for woven bone or between overlapped collagen molecules for lamellar bone (Marks *et al.*, 2002; Rodan, 1992).

The cellular process of bone formation and remodelling is important, as this thesis seeks to understand how the skeletal morphology of cattle differs and possible reasons for this. One key concept in this thesis is how bone remodels in response to long term external stresses. It is well established that bones subjected to heavier loads over time will reconstruct themselves to accommodate that weight (Cowin, 1983), also known as in vivo adaptation. The performance of any activity undertaken in everyday function will influence the process of bone adaptation, which in most cases, is the response to the major vectors of impact (loading) through bones (Pivonka *et al.*, 2018). This concept has been explored for decades, and the relationship between bone adaptation and its function was originally addressed in the 19th century under the concept of 'Wolff's Law' (Wolff, 1986), now commonly called bone functional adaptation (Ruff *et al.*, 2006). This is how bones typically respond to stress and describes the adaptive changes that bones can make internally to resist strain. Despite initially discussing bone remodelling as a short-term stress response, an advantageous morphology related to functional performance could then be selected during evolution if it facilitated the success of individuals. Indeed, plastic morphological change that occurs via bone remodelling can also be a component of evolutionary change, ultimately leading to heritable change via genetic assimilation (Campbell *et al.*, 2021; Anderson *et al.*, 2014). As already discussed, this could be the case through natural selection or processes like domestication. Regardless of the causal mechanisms behind remodelling of bone, and the physical process of this, how we measure and quantify morphological differences is important. There are various methods that have been used, as already mentioned earlier in this chapter, but osteometrics remains the primary method. Osteometrics makes the association between morphological differences in bones and their overall dimensions and sets this against the overall variation within a population. However, in more recent years, a suite of other techniques has been developed that might be more applicable to the study of morphological variables in biological populations.

2.4.1. Methods In the study of morphological variables.

Morphometrics (or osteometry or biometry) has a long history. Within certain disciplines, the need to categorise variation has driven development of various ways of communicating size and shape (Slice, 2007). The origins of modern morphometrics began in the 1960s and 1970s, when biometricians began investigating variables using multivariate statistics in order to analyse and describe shape variation and quantify shape patterns (Adams *et al.*, 2004). This method, now under the umbrella term 'traditional morphometrics', commonly utilised linear measurement combined with a subsequent suite of statistical analyses, including Principal Components Analysis (PCA) and discriminant function analysis, to quantify variation within and amongst groups. A large portion of research was dedicated to studies of allometry and for size correction, as it was noted that linear distance measurements are usually highly correlated with size (e.g. Bookstein *et al.*, 1985; Jolicoeur, 1963). Size correction was important if studies wanted to examine shape only, removing the size correction, allowing size-free shape variables to be deduced (e.g. Jungers *et al.*, 1995; Sundberg, 1989).

Zooarchaeologists investigating morphological change in species have relied on a range of morphological and non-morphological markers that are thought to reflect human attempts to manage animals (LeFebvre and Sharpe, 2018; Steele, 2015). The ability to recognise the advent of change in people's relationships with animals is important in understanding how and why certain animals rose to prominence. Furthermore, it provides the basis of archaeological study into what a wild and a domestic animal may look like. Some of the methods used in previous studies have already been alluded to in the literature discussed above, and the methods proposed for use in this research have also been mentioned. As can be seen from past research, one of the most common methods in zooarchaeology has been biometry (Albarella, 2002), this has been used in different ways to investigate aspects of size and shape in relation to the morphology of aurochs and cattle. Biometrics with regards to aurochs and domestic cattle post-cranial and cranial material has already been reviewed in a previous section. As a method, biometry clearly has good utility in investigating many aspects of skeletal differences, but is less suited to investigating fine scale or complex differences. High resolution of biometric data is one of the clear limitations with traditional measurements in the study of wild and domestic species that might be improved through application of new methods. To understand the current situation with additional clarity, and provide a more general overview of the present situation in zooarchaeology, biometry is briefly reviewed with its methodological relevance. As a widely used and popular method of analysis applied to wide ranging topics, the application of biometry has been well applied in a European context to include questions addressing around species identification, ecology, and cultural history.

As Albarella (2002) noted, modern applications of biometry are now benefiting greatly from computer analysis which has improved our understanding of factors affecting measurements, now being one of the most promising areas of zooarchaeology. This is particularly true considering the more recent adoption of geometric morphometrics, as one of the latest techniques to be applied. While the criteria discussed above are effective in many ways, they are generally strongest in looking at change in the broadest sense with discrete variables. Furthermore, several of the criteria (size, morphology, age, and sex) rely on linear measurements to draw conclusions. This also assumes enough measurements for the same skeletal element are obtainable in sufficient detail to characterise its metric properties. However, as argued by Vigne *et al.* (2005), surprisingly zooarchaeologists still rely heavily on the characteristics based on metric data. The issue is that traditional linear measurements do not retain their spatial information. Size is one of the most cited effects of domestication but can be a poor indicator as factors linked to domestication are genetically and environmentally derived. Size is resultant from isometric size and shape change, which are known to develop independently from each other. A decrease in size in skeletal elements observed in many domesticated animals, including cattle, can result from either isometric size decrease resulting from environmental pressures or bone modifications driven by genetically linked factors.

More recently, functional morphologists have looked at a variety of methods in the application of exploring the workings of skeletal form and function and its constraints. A large step forward has been the incorporation of models in various forms such as physical, mathematical, and direct experimentation (e.g. Fitton *et al.*, 2009; Wang *et al.*, 2006; Demes and Creel, 1988; Demes *et al.*, 1984; Greaves, 1978; Hylander, 1975). However, most recently and of greatest relevance are computational simulations (e.g. O'Higgins *et al.*, 2011; Curtis *et al.*, 2009; Strait *et al.*, 2009; Ross *et al.*, 2005; Sellers and Crompton, 2004). Digital based models are advantageous allowing exploration of complex variations in geometry and how these influences function along with structural shape-based constraints and evolutionary developmental pathways (O'Higgins *et al.*, 2011). This section looks more closely at how we can quantify morphology and functional changes in skulls, particularly using GMM and FEA as the main tools of analysis for this thesis.

2.4.2. Geometric morphometrics and the study of shape.

Geometric morphometrics (GMM) is a generic term for a set of procedures that emerged from research attempts to synthesise the various styles of morphometric analysis into a single coherent approach to the study of form (MacLeod, 2017), with 'geometric morphometrics' first being used to describe this methodological approach in the late 1970s (Bookstein, 1978). However, it was between the 1980s and 1990s that morphometrics experienced what Rohlf and Marcus (1993) termed a 'revolution'. A key aspect of this was shape based statistical theory, particularly coordinate-based methods, and computational use of deformations grids in analysis of shape (Mitteroecker and Gunz, 2009). The fundamental insights that made this revolution possible were contributions by Kendall (1989, 1984) who published a comprehensive description of geometric shape space. Based on Kendall's (1989, 1984) description, and in organisms, GMM statistically analyses geometric information regarding location, and where location is relative to other parts of the organism. These tools combine morphometrics, computer science, and modern engineering to analyse shape using 2D and 3D geometric coordinates representing landmarks, curves, outlines, or surfaces. The main aim of GMM is to study how shapes vary and their covariance with other variables (Cardini, 2020). To do this GMM methods examine shape rather than linear, areal, or volumetric variables (Polly and Motz, 2016), and these shapes can be expressed in space related to the developmental and evolutionary trajectories of an organism (Mitteroecker and Gunz, 2009).

In GMM, shape variables data is provided from mathematical location points established via a range of techniques in multiple dimensions (Zelditch *et al.*, 2012). Location points are called landmarks and data can simply be listed as a number of designated points, or complex parameters such as the outer surface of a form or curve (Bookstein, 1997a, 1997b). Geometric information is extracted from multivariate statistical methods and can be processed in accordance with the parameters of the research question (Monteiro, 1999). The most applied approach is to process landmark coordinates according to Procrustes Superimposition (Slice, 2001) whereby points are translated, rotated, and scaled to a common unit size depending on the landmark configuration (Ajayi, 2003). As part of this process, size can be removed from shape and treated as a separate analysis component, or included into the general allometry of morphology, and the analysis of covariation between size and shape can also be assessed (Klingenberg, 2016; Lleonart *et al.*, 2000). When the GMM is broken into its components, this follows the workflow of landmarks, standardisation, and analysis.

The development and the early adoption of GMM was within Bioscience, Medicine, and Statistics, these disciplines were a major driver for methodological innovation (Slice, 2007). GMM has since been employed across several other fields where quantification of variation is of interest, for example, palaeontology, anthropology, biology and most recently archaeology (e.g. Courtenay *et al.*, 2019; Pelletier, 2019; Seetah, 2014; Baab *et al.*, 2012; Cardini *et al.*, 2009; Gunz *et al.*, 2009). Importantly GMM presents several advantages that go beyond traditional morphometrics. This is primarily in the method's ability to identify important shape changes that might be marginal between individuals and groups of specimens in a data set (Haruda, 2014). This information is often lost in traditional quantitative and qualitative measurement methods. The retention of shape information, detached from or related to size, is key (Curran, 2012, Zelditch *et al.*, 2012), along with the ability to relate abstract, multivariate results to the physical structure of the original specimens (Toro-Ibacache *et al.*, 2016a). This allows researchers to quantify features using GMM that would otherwise be described qualitatively, as they are difficult to measure with traditional measurements. The visualisation capabilities of GMM combined with the large number of shape variables lend themselves to a particularly exploratory nature of data analysis, through which unknown shape features can be identified (Mitteroecker and Gunz, 2009). Here, I look at the principles and applications of GMM defining its development and how GMM has been adapted for use in a range of disciplines with specific reference to archaeology.

2.4.3. The successful application of GMM in studies of morphology.

With regards to archaeology and especially zooarchaeology the past 20 years has seen the ever-increasing adoption of GMM, initially this was primarily in 2D to explore identification of differences between individuals as well as population variation. Focus has often been on mandibles as they are most suited to 2D analysis being predominantly flat in profile along with teeth, plotting the outline shape. Such an approach has yielded important information into a variety of taxa from rabbits, mice, and rats (Cucchi *et al.*, 2020; Puckett *et al.*, 2020; Pelletier, 2019) to larger mammals such as pigs, horses, llama, and bears (Hernández *et al.*, 2021; Hanot *et al.*, 2017; Evin *et al.*, 2015a; Seetah *et al.*, 2013; Cucchi *et al.*, 2011b; Bignon *et al.*, 2005). These studies in combination with traditional metrics have used shape and size gradients to identify different respective species from their larger to smaller size. Problematically, 2D analysis still has inherent issues when looking at more complex bone shapes, suffering the loss of information regarding the full 3D shape (Cardini and Chiapelli, 2020; Buser *et al.*, 2018;). This has limited study somewhat to elements that are predisposed to 2D analysis, and it is only more recently that 3D application has become commonplace. The use of 3D GMM analysis of elements allows for a more accurate reconstruction incorporating the whole shape of an element and therefore comparison of shape will be more complete. Indeed, such an approach has already been shown to have great application in research into the species it has been applied to, such as looking at population variation and domestication. In such studies the morphology of skulls and teeth have generally been the focus of such GMM studies (Haruda *et al.*, 2019; Bopp-Ito *et al.*, 2018; Duval *et al.*, 2018; Drake *et al.*, 2017, 2015). Element choice in zooarchaeology is often limited however, due to taphonomic processes, and crania are quite fragile and seldom recovered intact. There is a much stronger emphasis in more traditional methods to examine robust post-cranial bones.

As mentioned in section 2.3.2, one study that is of particular relevance from a methodological and species perspective by Veitschegger *et al.* (2018) used GMM and FEA to examine the morphology and biomechanics of a particular cattle breed. This paper showcased the type of analysis proposed for use in this thesis and demonstrated its functionality and the possibilities when applied to cattle material. Veitschegger *et al.* (2018) analysed a wide variety of cattle cranial material with specific focus on establishing the parameters regarding Niata cattle. This is a now extinct breed of cattle exhibiting a peculiar morphology of extreme brachycephaly, the reason for which is relatively unknown including the morphological and biomechanical requirements of such a cranial shape. Comparison was made to other cattle crania of many breeds to establish how the cranial shape compared using GMM. From this it was suggested

Niata cattle cranial shape is clearly disparate from other cattle breeds exhibiting a different anatomy to other known chondrodysplastic forms. In addition, FEA was applied to evaluate the impacts on feeding biomechanics that the reduced craniofacial region produced. It was revealed that reduction of the face resulted in a lower magnitude of stress when biting in a more localised distribution. This study highlighted the relevance of virtual methods and data in providing novel information into the domestication process, although with specific focus on a single breed. Other recent studies have also looked at slightly different aspects of cattle cranial morphology, such as brain size change with domestication. Balcarcel *et al.* (2021) showed that on average brain size had decreased in domestic cattle by approximately one quarter, but this was also variable by breed. It was also suggested that brain size was related to different husbandry practices and the selection intensity for characteristics such as docility. This was evidenced by the genealogy of certain breeds and their use. For example, highly developed agricultural cattle like beef and dairy cattle had smaller brains than park cattle which were significantly absent from human improvement by selection processes.

While little has been undertaken with direct relevance to cattle specifically, related species in the wider taxonomy of ungulates has been investigated. A large contribution in this area has been made towards methods to separate closely related taxa and especially wild and domestic morphotypes and the domestication processes. Indeed, significant contributions have been made in a few general areas, this includes quantifying general population morphological variation and identification in species (Boessneck, 1969). But also, importantly the complex shape changes that occur in line with domestication and the determination of wild and domestic traits. While numerous studies have shown similar results in this area of research, the results of modern fox domestication and breeding perhaps display this most clearly in relation to human based husbandry (Lord *et al.*, 2020; Parsons *et al.*, 2020; Trut *et al.*, 2004). In one study (Kistner *et al.*, 2021) two farmed populations of foxes were compared, one group actively selected for domestication and the other group captive but unselected in comparison to completely wild counterparts. The two captive populations, domestic and unselected, showed minimal differences in cranial shape and size, but there were significant differences in captive groups compared to wild populations. This was seen in terms of the degree of cranial base flexion, size, and volume of cranial vaults (Kistner *et al.*, 2021), indeed being captive alone seems to have been enough of a selection pressure to drive morphological changes away from those characteristics seen in wild populations. Similar morphological changes have also been noted in multiple studies (e.g. Brassard *et al.*, 2023; Neaux *et al.*, 2021; Owen and Thomas, 2013) suggesting a common pattern of shape changes might occur as a result of the domestication process. These features are change in overall size particularly shortening of the facial region, so called brachycephalic or paedomorphic features, reduction in endocranial volume, wider skull relative to length, reduction in tooth size and overcrowding, general morphologies that might be considered disadvantageous in wild populations (Balcarcel *et al.*, 2021a; Zeder, 2006a). GMM was readily adopted in the study of pig domestication (Evin *et al.,* 2015b, 2013; Ottoni, *et al*., 2013; Cucchi *et al.*, 2011b), proving to be useful in measuring both size and shape changes over time and geographic location. Following this, the results of studies have detected phenotypic changes in tooth morphology linked to pig domestication, along with hybridisation and led to a re-interpretation of some of the established ideas of early pig domestication. These studies have shown shape can be a marker of phylogeny, however it is still less clear how these differences resulting from domestication can be extrapolated from other processes associated with morphology like habitat change that causes genetic isolation and reproductive differentiation (Zeder, 2015). From initial applications on Suidae, more recent applications of GMM have focused on other species and has expanded significantly on the existing data.

Closely related or morphologically similar species are often a serious problem for zooarchaeologists as they are difficult to distinguish, l*et al*one when considered alongside wild and domesticated variants. Methods facilitating identification of these differences are important given the difficulties inherent in wild and early domesticated populations and the use of size as the only criteria in this process. Of the more recent studies this is clearly seen in research on sheep and goat determination. Gaastra (2023) published a shape-based method for analysis of ovine/caprine astragali, aimed at providing an accurate differentiation between different taxa and morphotypes of the same taxon. It was also key that results were not influenced by differences in the age and/or sex composition of the comparison data. Importantly this research has confirmed GMM's ability to differentiate between wild and domestic population morphotypes of very closely related taxa, along with extracting early domestic population morphotypes from wild ones. This work built on similar earlier research where sheep populations were investigated in relation to trade, using the assumption that the different populations will have inherent morphological differences (Haruda *et al.*, 2019). Some of these morphological differences were already known through linear biometry (e.g. Salvagno and Albarella, 2017; Prummel and Frisch, 1986) and so while the conclusions might not be completely novel, the ability to clearly and statistically separate species through GMM adds great value. Such a trend has also been seen in South American camelids which, like sheep, also have a "low level of morphological variation in the skeleton and a significant overlap in their body size at population scale" (L'Heureux and Hernández, 2021, p.823). This made osteometric analysis difficult, but GMM initially tested on modern camelid populations and then archaeological material was able to differentiate the skeletal elements by species. Even in species considered early in their domestication process GMM has been shown to have great utility, where differences are hardly perceptible in comparison with traditional morphological markers.

While the body of evidence for successful application of GMM to various aspects of the archaeological record is still increasing, it clearly has great potential in the determination of closely related species and morphologies. It should be noted that many of these trends were known about from the substantial body of research undertaken via traditional biometry (as shown in section 2.3), and GMM is seen as complimentary to this rather than as a wholesale replacement. Regardless, GMM has been demonstrated as a valuable method of identification based on shape criteria that would not be possible with other methods and it has also helped establish some key patterns in the morphological changes associated with domestication. To summarise the changes in general terms, the impacts of domestication on skeletal morphology (especially the cranium) are most noticed through size and shape changes, particularly to morphologies not seen in wild populations. Chapters Three and Four establish the parameters for investigating these changes in aurochs and domestic cattle. These take a shape-based approach using GMM, however it is important to relate this back to the living animal. Any shape-based differences in crania could represent either long-term adaptation that influence how the skull performs. This will also be investigated and the methods for doing this are reviewed in the next section.

2.4.4. Methods used in the study of function.

As previously discussed, much morphological variation is related to specific aspects of functional demand in animals. To have a better understanding of the results of morphological analysis some analyses of functional skeletal demands are therefore made in conjunction with the GMM. This also helps recreate and assess some aspects of the living animal and how it performed tasks, something often overlooked in zooarchaeological studies. To achieve determination of functional demands, finite element analysis (FEA) will be used to provide some additional insight. This is based on the principle that form follows function (Wake, 1992; Lauder, 1981), in that adaptations in physical behaviour will result in morphological changes to better accommodate an action. While this principle of form and function is valid overall, there are constraints based on evolutionary history and developmental pathways (Smith, 1993). The general methodological concept of finite element analysis (FEA) is to provide a basic reconstruction of a task to visualise stress, strain, and deformations in a digital model. Such an approach has been reasonably common for some time in several disciplines, originally used in engineering and physics to solve complex problems related to the behaviour of structures, materials, and physical systems. At least 30 years ago FEA transitioned into orthopaedic medical science and later palaeo-sciences as recently as 15 years ago (Rayfield, 2007). It is therefore quite a recent adoption to zoological and paleontological sciences, particularly in relation to topics of morphology and functional evolution. FEA is noted as having “much potential in addressing questions of form-function relationships, providing appropriate questions are asked of the existing data” (Rayfield, 2007, p.541). This section provides background and review of the utility of the method and how it can be used to make a significant contribution to studies in morphology and function.

2.4.5. Finite element analysis and the study of function.

FEA, or finite-element modelling (FEM), is a method that uses numerical data to analyse the behaviour of structures under various simulated conditions and variables by breaking down a complex system into smaller elements examining how they interact and respond to forces. This could be, although not exclusively, stress, strain, deflections, heat transfer and fluid flow in structural models (Ross, 2005). While the mathematical foundation for FEA was established in the 1940s, the modern application can be achieved computationally with relatively low-cost

PCs and most steps are automated (Gokhale, 2008). In general, there are several steps that all FEA progresses through to build and analyse a model. These include geometry modelling, mesh generation, assigning material properties and boundary conditions, solving equations and post-processing results (Srirekha and Bashetty, 2010). At its core FEA involves breaking down a complex solution region into a smaller number of discrete elements (finite elements) interconnected at specific points known as nodes (Rayfield, 2007). These elements can be triangles, quadrilaterals, tetrahedra, hexahedra, etc., and put together in a variety of ways depending on the dimensionality of the analysis (2D or 3D) and the complexity of the shape being studied (Jagota *et al.*, 2013). The nodes and elements make a mesh that can be programmed to contain material and structural properties, loads, and boundary conditions, which define how the model will react when software performs the calculations and generates results (Srirekha and Bashetty, 2010).

The basic idea behind FEA is to limit the number of calculations required to simulate and understand how the system behaves under various conditions by interpolating the results for the whole surface (Srirekha and Bashetty, 2010). At the same time, by having a set limited number of elements, this removes any continuous degree of freedom in the model that would make mathematical solving impossible. FEA software packages handle the complex mathematical computations involved in these steps using equations often derived from the governing physical principles, such as mechanics, heat transfer, fluid dynamics, and electromagnetics. This is depending on the type of analysis being performed, stress and strain being most relevant to this thesis, with results often simplified into the different properties along X, Y, and Z axes. Through this complex process a method for addressing a range of inaccessible questions is available that would otherwise be too difficult to solve and visualise (Richmond *et al*., 2005). Indeed, Ross (2005) noted it could be “one of the most powerful tools in the methodological arsenal of vertebrate biomechanics” (p.253).

2.4.6. The successful application of FEA in studies of function.

FEA has numerous applications across various fields, as already mentioned primarily in physics and engineering but also including mechanical, civil, aerospace, and biomedical science. Overall, FEA is a versatile tool that enables engineers and researchers to simulate and analyse a wide variety of physical phenomena, leading to more informed design decisions, reduced development time, and improved safety and performance of products and systems (Srirekha and Bashetty, 2010). Engineers and researchers use FEA to optimise designs, test different scenarios, and gain insights into the behaviour of complex systems without the need for physical prototypes, which can save time and resources in the product development process (Reddy, 2019). This has been readily adopted into studies of comparative anatomy and morphology having great utility in answering questions about past and now extinct animal populations. Within this research sphere a lot of work has been done validating the method for application to fossil and extant species (Bright, 2014; Panagiotopoulou, 2009; Rayfield, 2007). Primarily researchers have focused on FEA's applications to stress and strain analysis, FEA can predict how structures deform and experience stress and strain under various loads. This has typically stemmed from designing safe and reliable structures like bridges, buildings, and mechanical components but can also be used in biomechanical settings.

One area of research where FEA has seen the greatest impact is palaeoanthropology, with the methods being readily adapted from biosciences. In terms of studies of palaeo-science, research has focused on establishing a link between form and function or research to test the shape and use relationship (Rayfield, 2007). This has also included a large amount of validation work to show the appropriateness of conclusions generated from FEA, and indeed developing the methodology surrounding the analysis (Panagiotopoulou *et al.*, 2012; Tseng *et al.*, 2011; Kupczik *et al.*, 2007). This development has firmly established FEA as a viable and useful tool in the reconstruction of mechanical behaviour that allows researchers to gain insights into the biomechanics and functional morphology. FEA has been used to simulate how the muscle and skeletal system in extinct and fossilised remains would have functioned under different parameters, dealing with the complex geometries and load conditions associated with crania (Thilmany, 2012). It also has the advantage of being non-invasive, particularly when dealing with fragile specimens, and can provide clues about their behaviours, diet, locomotion, and adaptations by reconstructing stress at multiple sites and depths throughout the model. With particular regard to this thesis two areas provide the closest analogy: cranial biomechanics and facial morphology. FEA can model the skulls to study bite forces, feeding behaviours, and the ability to process different types of foods (e.g. O'Higgins *et al.*, 2019; Godinho *et al.*, 2018; Fitton *et al.*, 2012; O'Higgins *et al.*, 2012). Different cranial shapes, tooth size, muscle forces and toughness of food have all been explored as potential parameters (Toro-Ibacache *et al.*, 2016b; Wright, 2005), morphological results have also been used in conjunction with functional findings suggesting that the morphometric findings are functionally significant (O'Higgins *et al.*, 2011). This can provide insights into their dietary preferences, ecological niches, and social behaviours.

Whilst only some of the most relevant studies to cattle, in terms of phylogenetic proximity, have been discussed, FEA has also been applied in many other extant and extinct species (Bright, 2014; Rayfield, 2007). The increasing frequency of use of FEA is in part related to the method's potential in interpretation of structure and its relation to functional performance (O'Higgins *et al.*, 2011). The ability to estimate and visualise the impacts of loading has been critical in the way researchers can explore biomechanical implications of particular components of skeletal forms (Thilmany, 2012; O'Higgins *et al*, 2011). In animals FEA predominantly has been used to quantify masticatory stress in various vertebrate taxa using 3D and 2D models (Serrano-Fochs *et al.*, 2015; Neenan *et al.*, 2014; Gill *et al.*, 2014; Piras *et al.*, 2013). FEA provides an effective analytical tool through which to investigate the biomechanical capabilities of the feeding apparatus in relation to challenging foods and adaptations to cope. This is particularly the case for extinct animals where exact feeding methods are unknown. In a comparative anatomy context, FEA studies have used both qualitative and quantitative approaches in the interpretation of results (Zhou *et al.*, 2019). Both have merit and can be used in conjunction, with qualitative approaches visually assessing stress distribution plots, while quantitative methods focus on stress values at particular points, or mean values of the model as a whole often paired with GMM to assess model distortion (O'Higgins *et al.*, 2011). Looking at general stress patterns of the whole model and seeing quantification of stress at specific points have proven instrumental in ecomorphological studies (Figueirido *et al.*, 2014; Parr *et al.*, 2012; Farke, 2008). This helps researchers simulate and understand cranial adaptations of extinct species in response to biting, chewing, and other biomechanical forces.

While the masticatory applications have been highlighted, FEA has a wider range of applications, indeed any biomechanical aspect can be investigated. This has implications involved in locomotion where studies have used locomotory function and adaptation to stress in movement to infer habitat (Stein *et al.*, 2020; Püschel *et al.*, 2018). Of more relevance to this thesis are studies of headgear, a term used to describe horns and antlers seen particularly in artiodactyla. There are a number of FEA studies looking at cranial stress induced by fighting with headgear (e.g. Johnson *et al.*, 2021; Geramy, 2019; Klinkhamer *et al.*, 2019; Drake *et al.*, 2016; Maity and Tekalur, 2011), these are explored in more depth in Chapter Five. To date FEA has not been applied with regards to zooarchaeological application on cattle, nor any species. This is likely due to the specific requirements of FEA and the traditions of zooarchaeological analysis, being group based while FEA looks at single specimens. It has however been successfully and more extensively used in paleoarchaeology studies of human evolution to show many differences in physical performance between species of hominids with regards to cranial shape.

As shown, FEA adds an additional and important analytical tool by which we can explore potential differences between closely related species, to deduce if form differences related to functional adaptations. FEA has proven to be a powerful tool for simulating the behaviours of structures and systems, with the main advantage that parameters and variables can be easily adjusted and standardised. This has aided design optimisation and reduced the need for physical prototypes and laboratory testing although some real-world validation might be required (Srirekha and Bashetty, 2010). Along with this however is the limitation that the models developed are seldom accurate enough to convey every biological detail and system, indeed it has been suggested simpler models might prove more beneficial in looking at general patterns and trends (Clarke *et al.*, 2013). Pertaining to this thesis, FEA remains previously under-utilised as a method of highlighting potential biomechanical implications of differing morphologies, no prior evidence can be found for it having been undertaken to directly compare aurochs and domestic cattle.

2.5. Conclusion.

This chapter has focused on establishing the background context for the research presented as a continuum in this thesis, building on the aims established in Chapter One. The purpose was to contextualise the current trend in aurochs and cattle research, and why the application of new methods could significantly progress understanding. This is particularly regarding size and shape that is an area already receiving much attention through traditional zooarchaeological methods. It is apparent that research into the cranium of aurochs and domestic cattle specifically is underrepresented in the literature, and previous studies have tended to adopt an osteometric method of data collection. This highlights the possibilities for expansion of novel methods to this area of research, with GMM and FEA being discussed as to their suitability in examining complex morphologies and biomechanical applications. The application of digital methods for comparisons of cranial shape and functional simulation in aurochs and domestic cattle has great potential in questions of form–function relationships and evolutionary investigations. Key to this research will be the ability to visualise shape-based differences via GMM, and further investigation into the variation of crania when loaded with forces in FEA, predicting biomechanical performance. As demonstrated throughout this chapter, such techniques have been extensively used in research related to form and function in the biosciences. More recently they have been developed to aid biomechanical modelling to measure shape variation, comparing performance statistically and relate this to form. The subsequent chapters in this thesis will use these techniques to understand the morphological variation between aurochs and domestic cattle and the functional consequences of that variation.

3. Chapter Three: Testing methodological validity, variation and error.

3.1. Introduction.

In archaeology the ability to make digital models of artefacts, sites and landscapes has instant utility, considering archaeologists strive to document the process of excavation and discovery as completely as possible (e.g. McPherron *et al.*, 2008; Sumner and Riddle 2008; Weniger *et al.*, 2007; Borderie *et al.*, 2004). While the methods and techniques for the construction of such models have been available for more than 40 years (Lanjouw, 2016), it is only since the early 2000s that archaeology has deployed any widespread application of digital modelling, and this was mostly carried out by specific trained professionals due to the nature of data and processing (Vozikis *et al.*, 2004). Models have only become really feasible to produce in an everyday context since the mid-2000s not only due to the reduction in cost and size of equipment, but also because of an increase in computer power, revolutionising archaeology with the ability to capture likenesses with increasing ease. The obvious advantage with model-based methods is that the inherently three-dimensional primary data of archaeology can be captured without the conventional methods of recording and visualising through which information can be lost through (e.g. drawings and 2D photography) (Lanjouw, 2016).

3.1.1. Establishing the most viable imaging modality.

The application of 3D scanning in archaeology tends to be divided into two broad approaches which also define the technology type that is employed. A large-scale category typically investigates buildings and structures or even whole landscapes (e.g. Yastikli, 2007; El-Hakim *et al*, 2004). The other category is more concerned with smaller objects (e.g. Karasik and Smilansky, 2008). As this research is focused on such objects, specifically crania, large scale digital capture methods such as aerial-based laser scanning are not considered here; instead I will look at techniques that can be used to capture the surface of objects in high detail. Digital imaging techniques have become a necessity in research fields that study anatomical variation such as archaeology, comparative anatomy, palaeontology and anthropology (e.g. Luhmann *et al.*, 2006; Weber *et al.*, 2001), with developments and applications increasing exponentially. Despite these technological and methodological advances the overall outcome, however, remains the same: to create a digital representation of an object's topology to enable us to analyse and assess variation between objects with a high degree of accuracy.

There are many different imaging modalities available, and the choice of modality depends very much on the research question, time and funding available, specimen size and other practical constraints. To this end, several techniques have been developed specifically within archaeology and biological anthropology intended to accurately describe 2D and 3D shapes (O'Higgins, 2000; Rohlf and Marcus, 1993). While we are mostly interested in digital methods it should also be said there are physical methods of capturing morphology which involve extracting coordinates from the actual physical object. These methods are exemplified by 3D digitizers (e.g. Microscribe®) which take 3D coordinates via a mechanical pen placed on the physical specimen. Obviously taking data directly from the specimen can be advantageous as the object can be physically examined by the data collector and the best place to take a coordinate located, although this can be difficult in the case of very fragile objects. However, it has the downside that post-data collection manipulation or addition to the landmark set is very difficult thus limiting the use of the data for secondary studies.

In contrast, virtual methods capture the surface of an object and recreate it in virtual space, often involving an extra step of processing or rendering. Virtual methods are seen as advantageous, as digital reconstructions can obviously be more easily manipulated than physical objects and rotated, zoomed and moved as the user wishes, possibly allowing analysis and data to be more easily undertaken, especially for very small specimens. There are two very commonly used techniques to digitally acquire a virtual based representation of an object: Computerized Tomography (CT) and surface scanning. CT scanning can be done on micro or medical scanners suitable for producing detailed models of very small to medium objects through the combination of many X-rays from varying positions to produce cross-sectional slices of a scanned object. Surface scanning, by definition, only records external details, but can record colour and texture unlike CT. There are various models of surface scanners but they are generally based on laser or structured light (usually based on a moving camera, or a stereo array of stationary cameras) (Weber, 2014). The obtained datasets comprising many images are collated into a model's points calculated based on the triangulation between the camera's known position and the light source (Weber, 2014). The major disadvantage is that objects (or scanners) have to be moved many times to obtain full coverage of the entire surface of an object.

The validity of both CT and surface scanning has been assessed many times and is briefly summarised here. CT scanners are often considered the ‘ideal’ modality as they can easily cope with dense and very dense objects like bones or teeth and can deliver submillimetre (or even submicrometre in some cases) resolution (Weber, 2014). However, it has been shown that surface scanners although obviously lacking internal details can produce similar surface models to CT scanners, but also that different scanners will produce models of various accuracy (Slizewski and Semal, 2010). The resolution of a surface scan (ranging from c. 0.05mm to 0.15mm best case) is generally less than that of CT but this is quite often sufficient for the research question being asked. Given the cost of CT scanning, which is more expensive than surface scanning, and the large size of CT scans (frequently in excess of 1 GB), a lower resolution maybe actually be preferable. Clearly there are differences to CT and surface scanning but, as Friess (2012) has suggested, rather than considering the two technologies as alternatives, they should be seen as complementary means of archiving and measuring samples. Therefore, in advance of data collection, projects should consider which imaging modality would be best for their particular samples and the questions being asked.

Advances in digital cameras and computing technology have also promoted an older method into new applications. Photogrammetry is now a compact and viable method of creating 3D models, in which digital information in 2D photographs can be used to generate models based on pixels and camera distance to the object (Powlesland, 2016). Photogrammetry or 3D photography has increased in popularity dramatically recently with the adoption applied widely in archaeology and palaeontology in large part due to advances in dedicated software. Structure from Motion photogrammetry is increasingly used in archaeological studies from excavation recording to object analysis. It works similarly to certain surface scanning methods in which software uses several overlapping 2D photographs and calculates the precise location of a target object from the data within the images. From each overlapping image individual pixels can be triangulated and this is used to build the object’s surface (Evin *et al*., 2016). The need for close range techniques of data acquisition that are especially portable and user friendly has meant photogrammetry as a tool is now widespread. Applications in 3D morphometric analysis are relatively new, and results are highly promising with models found to show a similar accuracy to surface scans (Evin *et al*., 2016; Kart and Friess, 2014). The obvious advantage is the ease of capture, requiring only a standard digital camera, making it a very rapid and affordable method (Habib *et al*., 2004). Furthermore, there are a variety of software packages available ranging from open-source freeware to expensive commercial packages.

Photogrammetry has often been considered a technique with a lower resolution of 3D capture; however this seems to be dependent on numerous factors briefly summarised here. One of the major factors seems to be regarding the geometry accuracy of objects created through photogrammetry, with some distortion of models noted (Mathys *et al.*, 2013). Several publications have since investigated the surfaces produced via photogrammetry with other methods and recorded a low degree of deviation (Evin *et al.*, 2016). Most importantly it has been shown that differences between individual skulls were more pronounced than between the specific method/device used to make the models (Katz and Friess, 2014). More recent studies have embraced the adoption of the technique and applied it in a range of research questions looking at very large and small specimens to evaluate its overall performance (e.g. Giacomini *et al.*, 2019; Buzi *et al.*, 2018; Fahlke, 2014).

There remain some questions over the ability to standardise the methodology of photogrammetry. Until recently this was unaddressed in the literature, when Morgan *et al.* (2019) published an attempt to provide a standard guide to making digital skeletal models from SfM photogrammetry using perhaps the most common market software, Agisoft PhotoScan. This study explored many of the settings such as number of photographs used, running resolution and similarity to physical specimen. Following this a number of recommendations were made: to use approximately 150 photographs and running software on the most detailed settings would result in digital models that are most comparable in appearance and proportion to their physical counterparts. Furthermore, Historic England (2017) produced a very focused document concerning the practicalities on how to undertake photogrammetry in archaeology, setting out the necessary steps and explaining how good results might be achieved. The results presented by Morgan *et al.* (2019) validated photogrammetry as being extremely reliable, producing models similar to the objects and akin to other scanning methods, although it was recommended nonetheless to avoid mixing different scan types in the same analysis to avoid potential problems.

As briefly discussed, it seems the three commonly used modalities each have slightly different applications and the best modality depends strongly on the research to be conducted (Dixit *et al.*, 2019). For this study, comparing the morphology of aurochs to cattle, it was decided that a single modality would be used to maintain consistency and to develop an adeptness in operating procedure, especially to avoid any potential problems with mixing models made in different modalities. Other considerations regarding time and the location of specimens in different museums meant it would not be feasible to transport the number of specimens to a CT scanner, and that using a surface scanner would often be difficult especially given its need for a power source. Another consideration was specimen size - a complete aurochs skull is too large to fit into a regular medical CT scanner, and many scans would be required on a surface scanner making it a slower process. Considering these limitations, photogrammetry was chosen being lightweight in equipment requiring only a camera as a minimum but also relatively fast to capture the required images for the subsequent building of digital models. Furthermore, the large size of the specimens actually seems to lend itself to photogrammetry allowing photographs to be taken easily and to high quality, but also being too big to fit in most conventional CT scanners and requiring multiple rotations with a microscribe due to the limitations of the range of stylus. The technical aspects of photogrammetry are considered in more detail below.

3.1.2. Potential problems.

The model making process requires significant user input in making decisions regarding how a scan is made along with the digital processes that are applied post surface collection. The diversity of imaging modalities, scanning methods and software not to mention transparency of procedure can make assessing model error difficult. With regard to photogrammetry, model error has been assessed several times in a variety of applications (e.g. Titmus *et al.*, 2023; Morgan *et al.*, 2019; Agüera-Vega *et al.*, 2017; Barbero-García *et al.*, 2017; Muñoz-Muñoz *et al.*, 2016; Sapirstein, 2016), but these studies compare photogrammetric models with another model made with a different imaging modality, usually a CT scan, which is often seen as the ‘ideal’ in model attainment. Comparison of surfaces is usually assessed from comparison of the polygon mesh, the vertices, edges, and faces that define the shape and contour of 3D objects. Another common approach is also through geometric morphometrics (GMM), a collective name for methods using a mathematical description of shape forms according to geometric definitions of their size and shape. In GMM landmarks, 2D or 3D cartesian coordinates, can be pinpointed precisely on the surfaces of a structure from one specimen to another representing the model’s surface architecture. As with any measurement-based analysis, the accurate identification and quantification of landmarks is essential in GMM to successfully categorise biological specimens with precision, accuracy, and repeatability. This can be influenced by model creation where much work has been undertaken to establish the impact of this. Methodological problems are possibly compounded by a further number of variables surrounding model creation and landmark sets. Therefore, two most obvious sources of error are suggested, model creation and landmark placement. At these stages there is the highest potential for user and computational error with the two factors being closely related.

One of the major potentials of model error seems to revolve around merging data obtained from multiple surface collection devices and/or collected by different operators. As shown by Fruciano *et al.* (2017) significant measurement error can be seen when combining models produced by different surface scanner devices, and particularly among landmarks created by different operators. It was suggested error could be reduced when combining existing surface scans by having a single person place landmarks, rather than combining existing sets of landmarks, even if obtained from the same device. Furthermore, measurement error could be greatly reduced by reducing the number of landmarks that were challenging to digitise. The use of different methods of landmark collection are possible but depend on the quality of models and the accuracy of the person collecting points (Boldt *et al.*, 2009). However, in other studies it has also been suggested that aside from user variability devices can be more variable than users (Evin *et al.*, 2016). It can therefore be surmised that multiple sources of variation will be present in the final dataset when combining surface scans made from several methods, compounded further if landmark sets were also acquired by multiple operators.

Turning to landmarks, the process of obtaining landmark coordinates is inherently correlated with at least some level of measurement error being a user-based process. From early studies on error in GMM it was recognised that not all landmarks are equally identifiable or easy to place on a specimen. Bookstein (1991) provided a typology of landmarks that recognised the extent to which each landmark represents a distinctive and easily identifiable position. Type 1 are landmarks identified on three different structures at a discrete location, type 2 are points on a maximum or minimum of a feature, and type 3 are placed relative to other identifiable features or landmarks. It is natural that the most reliable in placement accuracy are type 1, but often landmark sets use a combination of all three. Therefore, it is common procedure to undertake a sensitivity analysis in which imaging and/or digitising of specimens is replicated and the within-specimen measurement error compared to the between-specimen shape differences (Webster and Sheets, 2010). It is at this stage that reflection can be made on potential error beginning with the user and their ability to place landmarks. Error can then be assessed by repeated placement of landmarks on a single specimen to examine observer error through the individual landmark variance (e.g. Valeri *et al.*, 1998; Corner *et al.*, 1992). O'Higgins and Jones (1998) showed that repeated placement of landmarks on one specimen grouped closely when compared to the shape variation seen in the sample as whole. Through testing intra-observer error, it was suggested that it was unlikely to confuse the overall variation of individuals in the sample provided landmark placement was precise. Although landmark placement and model user error cannot provide details about the difference in precision of a single landmark, it has become a standard approach to check the overall effect of observer error on "individual specimen affinity" (Lockwood *et al.*, 2002, p.451).

To summarise, it seems there are some considerations to be made in landmark choice, placement and the user. As mixing different digitisation methods and users within the same study seems to increase the potential for introduced error, in this study this will be minimised through only one user undertaking the analysis via the same collection procedure. Virtual digital methods are preferable as these can be reinterpreted, with landmarks logged digitally allowing for editing and modification. The ability to review landmarks will also ensure the placement of landmarks is as accurate as possible. While sources of error can never completely be eliminated, the potential can be reduced by precise photography and landmark choice. To explore this in more detail imaging methods and digitising of specimens will be the focus of this chapter: looking at the results of specimen shape comparison with respect to measurement error. Therefore, many of the problems can be mitigated in the project design stage with potential error measured to see if present and acceptable.

3.2. Analysing Feasibility.

3.2.1. Applications to this study: aims, objectives and hypothesis.

The cranium can be challenging for surface reconstruction methods due to its anatomical complexity possessing significant topological detail of a diverse scale and nature. These include distinctive biological features of various kinds such as concavities and openings. The purpose of this chapter is to analyse the sensitivity of the data acquisition methods with specific regard to this thesis to ensure the validity of data and results prior to wholesale application. This seems logical to be undertaken in two stages; the first looking at initial model creation via photogrammetry to ensure there are no user or software anomalies and that models can be produced consistently. The second is ensuring landmark placement is consistent and minimises user error. The initial step has already been taken to standardise data acquisition as just a single user will be making models and placing landmarks. It is expected there will be little difference in model accuracy or landmark accuracy, and that potential sources of error highlighted in other published studies can be mitigated.

As crania would not be available apart from at the institutions visited it was imperative to be able to create accurate models in situ or this could have led to inaccurate landmark placement. In this context, we wish to explore the day-to-day ability to generate models with photogrammetry and place landmarks with accuracy and consistency. Observer landmark error has been commonly tested (Timbrell *et al.*, 2022; Fox *et al.*, 2020; Shearer *et al.*, 2017) and is readily screened with a simple test, detailed below. To test inter-model variability however was more challenging as we are dealing with more unknown variables, particularly in the reconstruction ability of the software Agisoft Photoscan. The issue of using photogrammetry under varying environmental conditions is less tested. As the models are made from the pixels in the photograph's variations and distortion through camera position and in/out of focus could all impact the surface of the model in aligning, dense point creation and meshing.

The aims of the sensitivity analysis are to assess if photogrammetry can be used consistently to produce reliable models of cattle crania and if user error during landmarking acquisition across time is present. Therefore, this chapter has two objectives:

1) To assess user reliability in landmark data collection and analysis.

2) To determine whether photogrammetry is a viable and accurate image capture tool.

It is predicted that there will be minor differences in user landmarking and photogrammetry will exhibit slight differences in models, but this will not impact the accuracy of such models and any model differences will be lower than the effect of a single observer landmarking on separate days. It is hypothesised that:

HYPOTHESIS 1: There will be no difference in accuracy of landmark placement on the same model made on different days. This will be achieved through GMM by landmarking the same skull model five times on successive days to evaluate precision of landmark placement and the ability to identify anatomical features consistently.

HYPOTHESIS 2: There will be no difference in models made on different days. This will be achieved by making a model of the same skull on three consecutive days via photogrammetry to assess if day to day operation of the equipment and slight changes in conditions impact model creation and accuracy. This will be tested through comparison of mesh distance.

3.3. Methods.

3.3.1. Sample.

For the sensitivity study the primary analysis was restricted to a single domestic cattle cranium, from the University of York Zooarchaeology reference collection (project ID 111). The same specimen was used for all sensitivity testing both inter-model error and landmark error. It was important to keep the same specimen as it was the repeatability of methods that is in question. However, in addition 12 other cattle crania (project ID: 91, 124, 109, 140, 112, 125, 110, 106, 105, 102, 120, 119) were selected at random using a number generator from the wider project data set (see appendix 1) to provide control and context.

3.3.2. Photogrammetry model creation.

Where possible the method was standardised, but this was subject to the specific conditions at the institutions visited, for example lighting, space, ability to manipulate specimens. The conditions were very similar for the repeated model making of specimen project ID 111 but differed for all other specimens listed in section 3.3.1 depending on resources at the various institutions. The basic equipment used was a Nikon D5300 digital camera producing 24.3 megapixels, mounted with a Nikon AF-P 18-55 mm f/5.6 lens. A tripod was used for all scans with camera lens zoom at a minimum of 18x. In addition, two scale bars were placed in each photo, 5cm and 10cm, with the longer positioned along the length of the skull, and the other across the front of the frame. These were retained throughout all captured images, and where necessary a black cloth was also used as a background to eliminate unusual surfaces and reduce background interference.

A table was used with the cranium placed in approximately the centre. Photos were then taken walking around the skull in three views of decreasing height until a complete 360° rotation had been obtained providing 30-40 images per height although no exact image target was adhered to. Each height or ‘chunk’ varied by 20° in height to produce a set of three chunks with overlapping images. The skull was then turned over (frontal bone down), and the process repeated to attempt to capture the full morphology. While taking images, camera settings were changed slightly as appropriate given the light condition of the specific working environment; this often involved changing the ISO and aperture to produce a good clear image with no extremes of colour or shadow. Focus was automatically set but manually adjusted where necessary to ensure as much of the skull as possible was in sharp focus.

Images were imported into Agisoft Photoscan Professional Edition v1.3.2 (2016) with all images from each skull orientation placed in a single chunk, meaning approximately 100 photos per chunk with usually two chunks to represent the top and base of cranium. The standard Agisoft workflow was then followed in batch process mode to align the photos and build the dense point cloud with consistent settings used. Alignment was run on ‘high’ accuracy with a ‘key point limit’ of 80,000 and ‘tie point limit’ of 4,000. ‘Generic preselection’ and ‘adaptive camera model fitting’ were both on. The dense cloud was generated on ‘high’ accuracy. Once this was complete the dense cloud was checked visually and markers added to the two chunks on identifiable aspects of the skulls which overlapped in each chunk. The chunks were aligned by markers, and then were merged to produce one model combined from the two chunks. From this model the mesh was generated on ‘high’.

From here the models were scaled using the markers tool to place points on the two scale bars, ensuring these were automatically placed correctly in each picture and moving them manually if not. The scale bar tool was then selected, and the measurements inputted for each distance between the two markers on the scale bars. By using two scale bars it ensured the measurements were taken in at least two directions and were on different sides of the objects. Scaling was double checked with measurements taken during visits via callipers to two decimal places. While a small degree of error was allowed for variation in real and digital measuring, measurements were accurate to one decimal place. After scaling the models were exported as .stl files, unscaled models were also exported by simply missing out the steps detailed.

3.3.3. Visual observation of models.

An initial comparison of the models was conducted to include a visual observation of the models through data taken directly from Agisoft recording information including number of photos taken, number of points generated and the measurements from the digital models. Digital measurements were also compared to calliper measurements taken between landmarks 4 and 5 (see figure 3.1). Following this, a mesh-to-mesh deviation map (Schlager *et al*, 2018) was generated by an analysis performed in the R statistical environment (R Core Team, 2016), package ‘Morpho’ (Schlager, 2017), see appendix 2.1. For this package the distance is surmised to be an average of the least distances between every triangle of a mesh and the nearest triangle of the other (Bærentzen and Henrik, 2002). The mesh distance function therefore determines the distance from the reference model surface to the target. This is done through projection of each vertex of the reference mesh to the target mesh (in this case one photogrammetry model to another). It returns a coloured heatmap that is a visual representation of the average distance so the differences between each pair of meshes can be visualised. As only a single mesh can be compared to another at one time, each model was compared to the other two in turn. The pairs of models were spatially aligned to a common axis in Avizo by a landmark translation based on three landmarks placed on the left rear M3, right rear M3 and right front of tooth row. The landmark coordinates were then translated so the left rear M3 landmark was on the origin axis at 0,0,0 with the other landmarks also correspondingly moved. This was only done for scaled models as mesh distance would be too great and meaningless for unscaled models.

3.3.4. Geometric morphometrics.

A second analysis based on GMM assessed the accuracy of surface geometry of the models, and precision in observer landmark placement. A landmark set was developed to capture key anatomical components of the cranium in order to measure the models' accuracy and user error. The specimen chosen was a modern reference specimen (project ID 111) in excellent preservation, with the advantage of all landmarks being able to be placed covering the cranium as evenly as possible. A set of 48 points was selected, designed to define the overall shape of the domestic cattle skull, and specifically to capture changes in cranial morphology. The landmark set comprised as many type 1 landmarks as possible although some type 2 and 3 were used. Landmarks were added systematically following the reference guide shown in figure 3.1.

To examine model error three models were made on consecutive days as per the photogrammetry method detailed in section 3.2.2 and exported as scaled and unscaled models (for a total of six models), landmarks were then applied in one event to all six models. To examine user landmark error a single model was used (a scaled models made on day 1), with landmarks being applied on five consecutive days to generate five repeats of the landmark set on the same model. The 12 other cattle crania were also landmarked to act as background data representative of the general cattle group. The surface files made via photogrammetry were uploaded and landmarks were recorded in Avizo v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). The collected raw landmark Cartesian coordinate data were compiled separately for user error and model error and saved as a .landmarkASCII file and edited into a Morphologika file using Notepad++. This allowed details of their spatial arrangement to be preserved for comparative analysis using geometric morphometric methods (Slice, 2007). The Morphologika file was opened in Morphologika V.2.5 (O'Higgins and Jones, 2006) to make a rapid check for general accuracy of the data. However, full analysis was undertaken in R statistical environment (R Core Team, 2016), see appendix 2.2.

Through a Generalized Procrustes Analysis (GPA), the landmarks were registered to minimise the full Procrustes distances (sum of squared distances) between corresponding landmarks via translating, rotating, and scaling to centroid size and remove size (O'Higgins, 2000). A Principal Component Analysis was then performed to places all landmark configurations of the repeats in a common coordinate system and allows differences between the landmark coordinate values to express differences in shape. PCA is commonly used in exploratory multivariate analysis (Zelditch *et al.*, 2012), and it summarises the data distribution in multidimensional space via a number of principal components which represent different axes of variation. For this reason, it can graphically describe the major trends of shape variation in a data set.

These results are a 'size free' shape space visually displaying shape differences through a number of principal components (Klingenberg and Monteiro, 2005; Adams et al., 2004; Rosas and Bastir, 2002). Size and shape was also assessed through a similar process. PCA was used to as a means of exploring the distribution of models based on their landmark discrepancy through the shape space to interpret any obvious patterns as a result of user landmark error or model error. In addition a test of disparity was undertaken for landmark placement (appendix 2.3), and centroid size was compared for model error evaluating scaled and unscaled models (appendix 2.4).

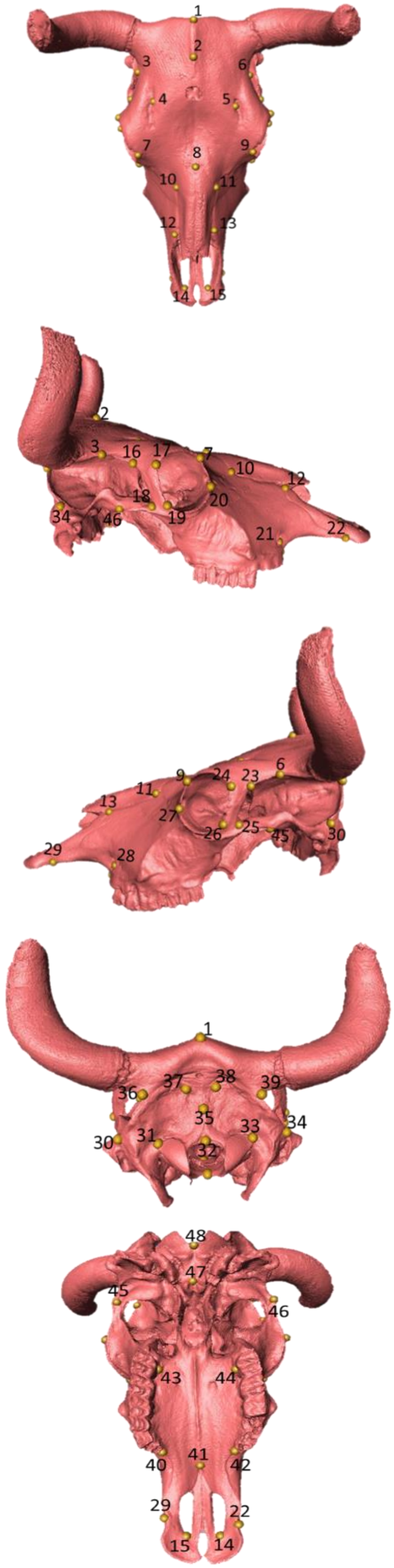
Landmark No. and side	Landmark anatomical description	Landmark locations on cranium
1	Intercornual protuberance	
2	Least point on distal frontal suture	
3(R) and 6 (L)	Parietal bone meets temporal line	
4(R) and 5(L)	Supraorbital foramen	
7(R) and 9(L)	Least confluence of frontal and lacrimal	
8	Central point between frontal and nasal	
10(R) and 11(L)	Anterior most point between lacrimal and nasal	
12(R) and 13(L)	Point between maxilla and premaxilla	
14(R) and 15(L)	Centre point of posterior premaxilla	
16(R) and 23(L)	Proximal of temporal line	
17(R) and 24(L)	Posterior proximal point on orbit	
18(R) and 25(L)	Posterior most point on zygomatic	
19(R) and 26(L)	Posterior distal point on orbit	
20(R) and 27(L)	Point on orbit between lacrimal and malar	
21(R) and 28(L)	Infraorbital foramen	
22(R) and 29(L)	Proximal junction between premaxilla and maxilla	
34(R) and 30(L)	Proximal of temporal bone / mastoid process	
33(R) and 31(L)	Lateral most point of occipital condyle	
32	Proximal median of foramen magnum	
35	Distal of external occipital protuberance	
39(R) and 36(L)	Least point on parietal	
38(R) and 37(L)	Greatest point between median and superior nuchal line	
42(R) and 40(L)	Most anterior point of maxillary tooth row	
41	Most posterior point of premaxilla and maxilla on upper palate	
44(R) and 43(L)	Lingual median point on rear most molar	
46(R) and 45(L)	Distal junction of zygomatic arch and squamous temporal bone	
47	Distal of basisphenoid bone	
48	Distal median point on occipital condyle	

Figure 3.1: Anatomical location and description of landmarks.

3.4. Results.

3.4.1. Visual assessment.

From the analysis 6 models were created; two for each day comprising a scaled and unscaled exported model from Agisoft. Initial basic comparative data was retained to assess if and where model creation variation may occur and if this was noticeable in Agisoft itself (table 3.1). From this it can be seen that generally similar numbers of photographs were taken across the three days which generated a broadly similar point density. This is with the exception of day 3 chunk 1, where a much smaller point cloud, with nearly half the number of points, was generated despite a nearly equal number of photos being used. Despite this no quality reduction (i.e. grainy, patchy, and uneven surfaces) was noted in the visual look of the model in Agisoft Photoscan software.

	DAY 1	DAY 2	DAY 3
Chunk 1	60 camera, 45,471 points	61 camera, 48,490 points	57 camera, 26,238 points
Chunk 2	55 camera, 45,371 points	56 camera, 43,305 points	55 camera, 42,895 points
Merged	115 camera, 90,842 points	117 camera, 91,795 points	112 camera, 72,133 points

Table 3.1: Comparison of model data from Agisoft Photoscan.

Additionally, the accuracy of scaling was tested across the three models with digital measurements taken in MeshLab (table 3.2) and compared to calliper measurements on the actual specimen. It can be seen that simply exporting the unscaled models led to some differences as days 1 and 2 were similar but day 3 much larger. This highlights the importance of scaling as Agisoft appears to apply a semi-random scale factor if not set by the user. In addition the models were created at a greatly inflated scale, so while the morphology may be correct the size certainly is not. On the other hand, the scaled measurements were very consistent with 1 mm difference on day three, imperceptible in reality. This was compared with the real life measurement of 100.1 mm, suggesting a 2-3 mm overestimation on digital models. This was considered acceptable as this level of variation would be less than any inter-user error taken via calliper measurements.

	DAY 1	DAY 2	DAY 3
Scaled model	102	102	103
Unscaled model	809	809	1246

Table 3.2: Digital measurements of models (in mm).

In addition, the mesh distance was calculated between models, to compare if surface meshes could be reproduced consistently (figure 3.2). Cranial models were shown to exhibit only the smallest amount of deviation from each other being approximately +/- 3mm variation. Model 1 compared to 2 showed some differences around the maxilla and premaxilla of around 2mm difference and along the posterior left side of the cranium approximately 1mm difference. Model 1 compared to model 3 showed a similar but more exaggerated pattern being approximately 2-3mm difference in models. Model 2 compared to model 3 were the congruent showing some minor variance of c.1mm in the occipital and premaxillary regions.

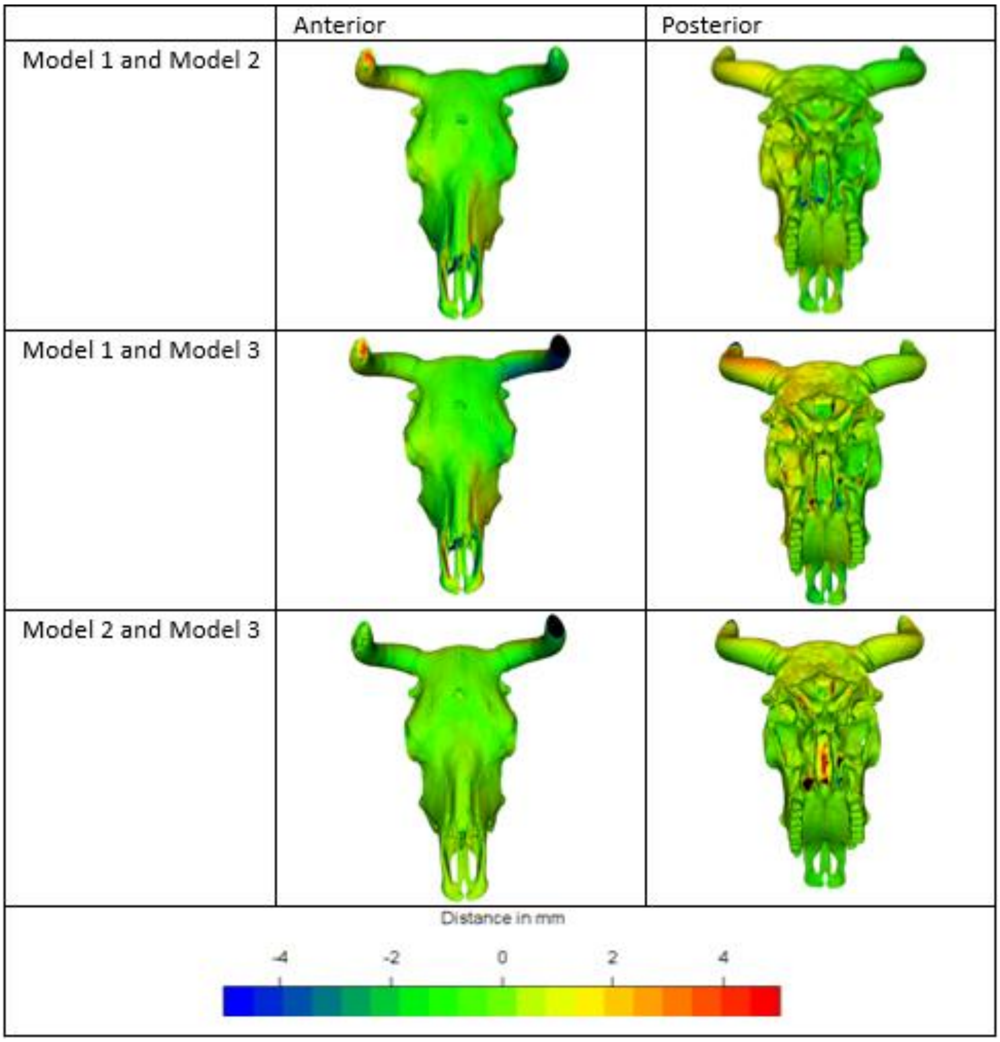


Figure 3.2: Mesh distance comparisons heat map in mm, ranging from blue-5 to red +5mm.

3.4.2. Landmark placement error.

The GMM results of the five days user variation landmark set showed some small differences between each day repeat. Assessment of placement error can only be properly visualised in the context of other data, doing this showed a clustering of the 5 repeats data in the bottom left of the shape morphospace (figure 3.3). The five repeated landmark sets all grouped at approximately -0.04 on PC1 and -0.02 on PC2. It was noted that each repeated day moved slightly more negatively along PC2 for each successive day but the repeats were more closely related than the other background data. The other data spread to occupy the whole x and y axes. To test this further morphological disparity was calculated between the day repeats group and the other background specimen data. The other group was randomly sub-sampled from 12 individuals down to 5 to match the number of day repeats providing a more balanced assessment of disparity. The result of this morphological disparity indicated that the day repeats were significantly different to the other data with a P-Value of 0.005 (table 3.3). Therefore, landmarking error on behalf of the user is smaller than shape differences between groups, especially considering the small sample numbers used here.

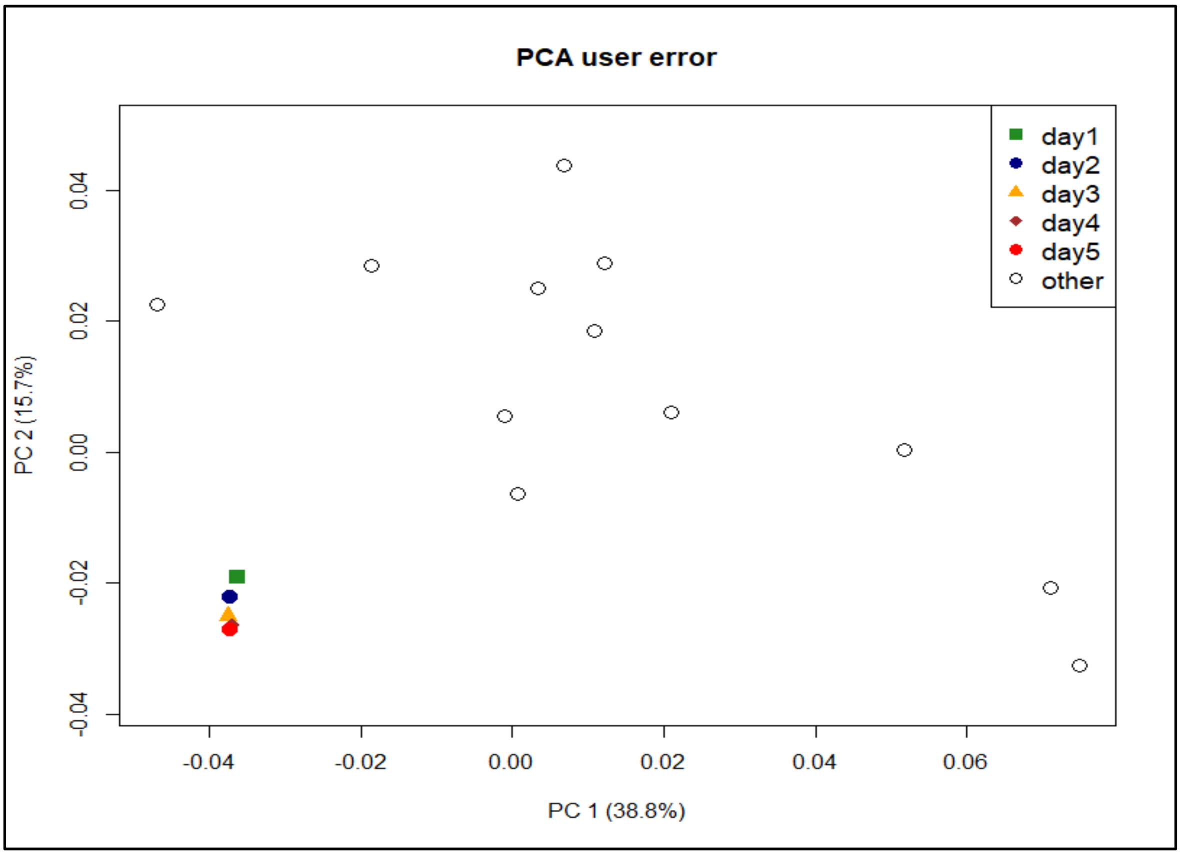


Figure 3.3: PCA plot of user error by landmark day repeats including wider data set.

Procrustes variance for defined groups		
	Model repeats	Other
	0.00114364	0.00519401
Pairwise absolute differences between variances		
	Model repeats	Other
Model repeats	0.00000000	0.00405037
Other	0.00405037	0.00000000
P-Values		
	Model repeats	Other
Model repeat	1.000	0.005
Other	0.005	1.000

Table 3.3: Morphological disparity between day repeats and subset of other data.

3.3.3 Model error.

The results of the model creation in GMM showed each model repeat to cluster closely within the morphospace. Similarly, to landmark variation the model error assessment saw a group in the bottom left corner, at approximately -0.04 on PC1 and -0.02 on PC2 (figure 3.4). The scaled and unscaled model variants were near identical in shape. From this it is apparent that the overall variation in model repeats is small set against individual variation of crania. PC 1 accounted for 40% of the total vitiation and PC 2 for 17.4%, while the first ten PC's cumulatively explained 97.1% of the variation. This is obviously regarding shape only, but size is also a consideration. Centroid size was therefore plotted on a bar chart (figure 3.5) showing the identical size of the scaled models and much larger more inconsistent size of unscaled models. As shape was only of interest here this would not necessarily be an issue but if size was also a factor any such specimens would need to be removed before continuing any analysis.

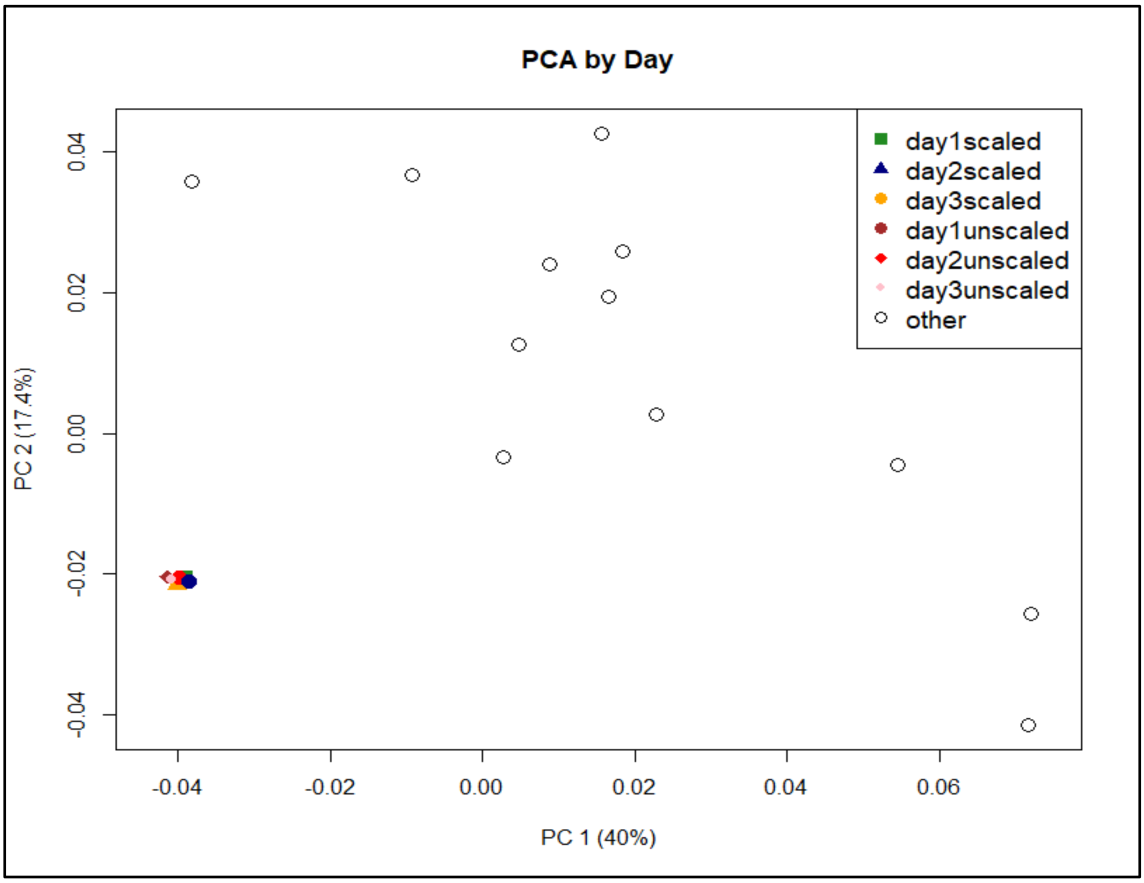


Figure 3.4: PCA plot of model error via model repeats models including wider data.

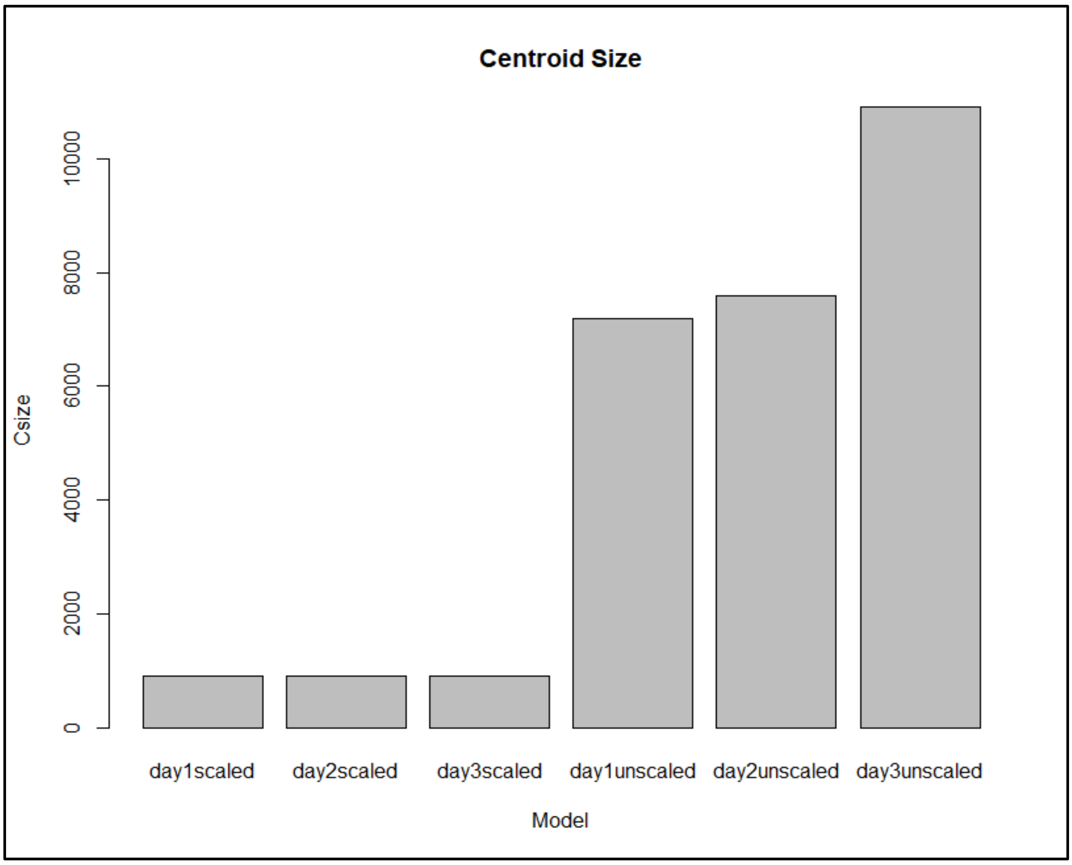


Figure 3.5: Comparison of scaled and unscaled model centroid size.

3.5. Discussion.

While the applicability of 3D model based GMM is established, this sensitivity analysis sought to validate some more variable aspects of the process specifically in relation to model generation via photogrammetry. This area is becoming increasingly transparent as more published data is available and standardisation of data acquisition or at least awareness of how data might be affected by varying methodological practices. Such standardisation has already been acknowledged with other imaging modalities such as CT and structured light scanning. We know photogrammetry data can be of equal quality to other methods, so it is hoped that with increasing scrutiny photogrammetry can develop methodologically. This chapter developed this body of knowledge by aiming to assess if photogrammetry can be used consistently to produce reliable models of cattle crania.

3.5.1. Visual assessment.

While seemingly less sophisticated than the other assessment methods deployed, the visual assessment provided some interesting details about the models. Generally speaking the models were successful in terms of providing a satisfactory level of detail and capturing morphology. Factors such as number of photos remained reasonably consistent and generated point clouds of comparable size, apart from the day 3 model chunk 1 where it was approximately half the number of points. It is interesting to note that this seemed to have little impact on the resulting model, and possibly could have been rectified by re-running some steps in Agisoft.

From the measurements taken on models, the importance of scaling was instantly highlighted. The scaled models were all very similar in size and produced a nearly exact match of the calliper measurement taken from the physical specimen with a slight over estimation of c.2mm. On the other hand, the unscaled models were all much larger with two being the same and one even larger still. This suggests that when not scaling Agisoft does not apply a uniform size; it is not certain what factors might influence this but it could relate to camera position, focal length and other camera or image file attributes. That being said, although no specific standardisation was applied, the same generic data gathering workflow was adhered to and no obviously different parameter was implemented to warrant generation of a differently sized unscaled model. When looking at shape only, the scaling factor was not seen as a problem; however, if size and shape were considered this obviously becomes highly problematic. If size and shape are highly correlated in specimens, lack of scaling could also be challenging, although this was not tested.

Mesh distance was also useful for visualising any potential differences, and, as could be seen, these were minimal with model to model comparisons mostly falling within the green to yellow range (+/-1mm). Some areas of the cranium exhibited more variation in mesh than others, notably the very proximal (premaxilla/maxilla) and distal (occipital). It is thought this could be related to image capture, with camera focus generally centralised, these portions of the skull have the most potential for being out of focus in image capture and result in a poorer accuracy mesh model. Alternatively, or additionally, when taking photos in certain orientations areas of the skull could also be in shadow creating darker areas with less contrast in the images. Agisoft often struggles to generate accurate surfaces if photos are too dark. However this should have been combatted when the skull was turned over as that portion would have then been in full light. Therefore, care is suggested when taking photos and modelling the rear or any portion of the skull that may be in partial shadow. Photography lights can be used, but placement can be difficult with the 'walk around' method as this often creates shadows elsewhere. However, limitations of this method cannot be ruled out requiring models to be aligned, in this case via landmarks and a common axis meaning any small variation in alignment will affect mesh distance results. That said the less than 4mm variation shown in models is considered acceptable. It has been shown that such measurement differences are not uncommon between experienced archaeologists taking calliper measurements (Dorland, 2017; Orton, 2014; Lyman and VanPool, 2009).

It is considered that a highly standardised photogrammetry method could potentially solve some of the small variations as recommended in Morgan *et al.* (2019). But this is limited by what is practically possible, for example very large specimens do not fit in most available photo booths or turntables. As this methodology had to be applied in a range of settings depending what facilities are available at museums it was more important to make sure any model creation was repeatable rather than as perfect as possible. Furthermore, the results of the mesh variation were similar to other studies that looked at mesh distance (e.g. Profico *et* *al.*, 2018; Schlager *et al.*, 2018) with results suggesting models could vary by a few millimetres. It is therefore considered that the level of model variation seen in the visual assessment is acceptable to undertake a GMM based methodological approach.

3.5.2. Landmark placement error.

Landmark placement was assessed using GMM. This was to ensure that landmarks could be consistently located and that user precision was high. By completing this step it also removed the potential for any model variation observed to be resultant from poor landmark placement. User ability to place landmarks is routinely screened in GMM studies (Shearer *et al.*, 2017) by multiple repeats of landmarking the same specimen. Therefore, landmarking the same skull five times on successive days was undertaken to evaluate precision of landmark placement and the ability to identify anatomical features consistently. The results of this showed a slight variation over the five repeats with landmarks becoming progressively more negative in PC2, possibly representing familiarity with the landmark set and the ability of the user to identify anatomical features and where to place landmarks. Despite this small variation, the landmark repeats still clustered more closely than the other background data that occupied the rest of the morphospace showing the full shape variation exhibited by this landmark and specimen data set. This was further confirmed by the test of morphological disparity between the 5 repeats and a subset of the other background data (reduced to 5 specimens to form an even comparison). This showed a significant difference between the groups again confirming any landmarking variation was much smaller than overall group variation.

The results of this sensitivity were consistent with results from previous studies (e.g. Valeri *et al*., 1998; Corner *et al*., 1992), finding that user error in landmark placement was considerably less than variation between different specimens. This was consistent with hypothesis 2 that there will be no difference in accuracy of landmark placement on models. This is consistent with the aim to ensure user validity, and the hypothesis that there would be no difference in placing landmarks on different days. It was expected there would be little difference as the digital nature of the landmarking method chosen allows very precise application of landmark points. It is also worth considering the experience of the user and familiarity with the landmark set; the latter days of landmarking seem to cluster more closely than days 1 and 2.

Despite this the overall error in day repeats is still less than the overall variation seen in the contextualised data.

3.5.3. Model error.

To test the results of the data collection method and model creation process, GMM was undertaken to determine whether photogrammetry is a viable and accurate image capture tool. To ensure this method was viable the method was tested across three days creating six models, three scaled and three unscaled models. The results of the tests were similar to that of landmark user error. The scaled and unscaled day repeats plotted close together and were almost indistinguishable when viewed against the background data of other models in a PCA. When considering shape no observable differences were noted and all day repeats, scaled and unscaled, plotted as expected on the PCA. This showed any model error to be substantially smaller than the overall variation seen in the wider analysis. This suggested that the individual morphological topology of models is consistent and photogrammetry accurately represents the physical specimens.

However, when considering size an obvious problem emerges regarding unscaled models exported from agisoft not shown in the shape only PCA. This was already highlighted in the visual assessment already undertaken that showed much larger measurements taken on unscaled models, unsurprisingly the centroid size of these models was also greatly exaggerated. Furthermore, lack of scaling was not applied uniformly with each unscaled model having a slightly different centroid size, all much larger than the actual real specimen size. Consequentially it is recommended that while unscaled models could be used for a shape analysis, caution should be used in any analysis where size is an important variable. In addition, shape analysis are often heavily impacted by size and some component of size if often displayed on PC1 of a shape analysis PCA, therefore the use of unscaled models would not be recommended unless there was no alternative.

This analysis also showed photogrammetry and processing of models to be consistent across three days. While it was predicted that there would be slight differences in models over the three days, there were almost no differences and all showed almost negligible size and shape differences when exported as scaled models. As predicted this did not impact the accuracy of such models and any model differences were much lower than the variation between specimens. Hypothesis 1 is therefore confirmed and that the model of the same skull made on three consecutive days via photogrammetry was a viable test to assess if day to day operation of the equipment and slight changes in conditions impact model creation and accuracy. This has highlighted the importance of scaling in models intended for GMM research as Agisoft does not apply a uniform measurement to unscaled models being in this case much larger than the real specimen. While this would not be problematic for some shape only analysis depending on the nature of research questions, this could lead to highly inaccurate results in analysis of size and shape.

Although no similar studies have been undertaken to investigate day to day variance of model creation in a single modality other studies investigating inter-modality variance did find some small differences but that models were generally similar (e.g. Evin *et al.*, 2016; Kart and Friess, 2014; Slizewski and Semal*,* 2010). This study has perhaps emphasised the findings of Friess (2012) in validating the use of a method that is most complementary to the research questions, specimens and project requirements rather than combining multiple modalities. Furthermore that standardising the methodology as much as practically possible as suggested by Morgan *et al.* (2019) would lead to more consistent results, or at least make errors more apparent. Taking into account the findings here photogrammetry was considered an appropriate method capable of producing models of a suitable resolution for analysis of the research scope of this thesis.

3.6. Conclusion.

This sensitivity study sought to elucidate two potential methodological problems 1) the impact of user error on landmark placement, and 2) variability in model creation. This thesis was dependent on both factors being manageable to provide valid applicable results for the study. For the user error study it was found there was little discrepancy in landmarks placement across the five days, with user error being much lower than the overall variation shown in the wider morphology of some control specimens. For the model error, it is apparent that there is no issue with photogrammetry models made under slightly varying day-to-day conditions. The actual variance was shown to be minimal when compared to the wider species variation in domestic cattle, with the model points clustering tightly together in shape space. Any difference between models was relatively small and is clearly much less pronounced than shape differences with other individuals in the wider group. The results of this sensitivity study have therefore achieved the aim of assessing if photogrammetry can be used consistently to produce reliable models of cattle crania and to determine if user error during landmarking acquisition across time is present. This is beneficial for this thesis showing surface collection and landmarks obtained were repeatable and comparable. It is essential methods could produce reliable, accurate data to ensure standardisation between analyses in the landmarks to be measured.

4. Chapter Four: Shape variation between wild and domestic cattle.

4.1. Introduction.

This chapter is concerned with the size and shape differences between aurochs (*Bos primigenius*) and domestic cattle (*Bos taurus*). The intention is to elucidate the complex relationship between the closely related morphologies in aurochs and cattle, separated significantly in lifestyle by human influence through domestication. Here the relationship between the species and their cranial morphology is examined with the intention of investigating the long-established idea that the major change from aurochs to domesticates is size (Götherström *et al.*, 2005). This research trend has been established in numerous osteometric studies between aurochs and domestic cattle in various skeletal elements (van Vuure, 2005; Guintard 1999). The traditional way of looking at morphological variation in zooarchaeology has been through size changes of bones (e.g. Albarella, 2002, Ervynck *et al.*, 2001, Mayer *et al.*, 1998; Payne and Bull, 1988) and while many of these have provided important information, they still have limitations. Such problems are particularly around quantification of size and shape variation, as traditional analysis is only able to accurately account for shape in a simplistic way and is unable to preserve 3D structures and measurements (Adams *et al.*, 2004; Rohlf and Marcus, 1993). This is further compounded due to the potential size overlap between species (Wright and Daniels, 2015), the fragmentary nature of many specimens and earlier publications conflating the species (van Vuure, 2005; Kobryń and Lasota-Moskalewska, 1989).

The field of research around aurochs and cattle crania has generally highlighted two factors; that there is an overlap between the two when compared osteometrically (Wright and Daniels, 2015; Grigson 1978; Bohlken 1964) and furthermore domestic cattle exhibit a wider range of size variation (Grigson, 1974b; Jewell, 1962), although this has not been tackled in detail or recently investigated with more contemporary analytical techniques within the past 50 years (e.g. Grigson 1978, 1974a). Through the application of novel analysis to this debate it is hoped understanding will advance regarding the relationship between the species. Geometric morphometrics (GMM) has already been introduced in Chapter Three, and so it is sufficient to recall that it is now a commonplace set of techniques used in many fields of biological and palaeontological study. GMM has been used to investigate various taxonomic and morphological questions in groups such as murids (Cucchi *et al*., 2011a; Valenzuela-Lamas *et al*., 2011; Cucchi, 2008), equids (Bignon *et al*., 2005) and cave bears (Seetah *et al*., 2012). Its application to zooarchaeology is increasingly being employed to answer similar questions of past animal populations. In addition, methodologies such as GMM that study shape as well as size can provide an approach which is able to better discriminate between wild and domestic species (Evin *et al*., 2013; Vigne *et al*., 2005). However, care must still be taken to not over state conclusion from any analysis especially given the complexities of the data and possibility for misinterpretation (see Rowley-Conwy, and Zeder, 2014). Interestingly the cranium remains one of the least explored skeletal structures of the focal species of this chapter.

4.2. Factors influencing the crania of aurochs and domestic cattle.

4.2.1. Domestication.

Domestication is recognised as the process in which animals are bred under non-natural conditions, isolating them from their pre-domestic forms (e.g. Zeder, 2015; Driscoll *et al*, 2009; Zeder, 2005; Clutton-Brock, 1999; Hemmer, 1990). The underlying process of morphological change resulting from domestication is not clearly understood. Hormonal changes triggered by fluctuating environmental conditions and the stress of captivity may influence some aspects of morphology (Arbuckle, 2005; Künzl *et al*., 2003). It is also highly possible that epigenetic or developmental change might be purposefully selected for in human husbandry (Vigne, 2011; Price, 1999, 1984). The most commonly observed difference in the archaeological record is a size reduction seen in many domesticated animals. Causes of size reduction in the context of domestication are complex as they include genetic, ontogenetic and ecological factors, combined with human-mediated selection (Grigson, 1969). Human selection for various traits is undoubtedly a reason for changes in morphology. The breeding of less aggressive animals and the moderation of natural selection allows previously non-adaptive characteristics to emerge (Ajmone-Marsan *et al.*, 2010). As domestication is influenced by multiple factors it makes understanding the drivers of the observed morphological changes highly complex. Furthermore, the relative impact of these factors seems to differ depending on species and their interaction with humans.

The artificial selection of advantageous natural variation is arguably the mechanism by which most domestic species evolved and, in this way, were moulded to suit human needs (Driscoll *et al.*, 2009). To this end humans have become formidable agents of mediated selection, over thousands of years promoting the survival of some variants and limiting the success of others. Such domestication commonly causes morphological deviation in size and shape from wild predecessors. In the archaeological record the primary indicators for domestication are the observable skeletal changes in relative proportions (e.g. Clutton-Brock, 1995, 1987; Epstein, 1971; Zuener, 1963). In many cases, the domestication process seems to have been quite gradual, and the newly created animals would have initially held a strong resemblance to their wild counterparts. It seems to have taken several thousand years before specific identifiable differences emerged (Vigne, 2011). While domestication was undoubtedly a major driver in morphological change, that is not to say there were not changes pre-domestication.

It is suggested that, under domestication, morphological change follows 'regular rules' that are an expression of the fundamental complexity of genetic and developmental systems expressed through changes in body proportions and in overall size (Wayne, 2001). Morphological 'markers' have been suggested like a decrease in brain size, snout shortening and concavity of the face, tooth crowding and tooth length reduction, and most cited, body size reduction (Albarella, 2002; Ervynck *et al.*, 2001; Dayan, 1994; Morey, 1992; Morey and Wiant, 1992; Payne and Bull, 1988; Flannery, 1982). The latter is often recognised as the most significant factor of domestication with discussion of body size dominating literature related to this topic. This has typically been documented through size measurements using linear distances of bones to deduce the status of archaeological remains as wild or domestic (Vigne *et al.*, 2005), and has been performed on a range of common mammalian species (e.g. Zeder, 2012; Hongo *et al.*, 2009; Zeder *et al.*, 2006a; Albarella *et al.*, 2005; Peters *et al.*, 1999; Morey, 1994, 1992; Clutton-Brock, 1988; Coppinger *et al.*, 1987; Davis, 1981). In the archaeological record reduction in size is traditionally accepted to be the primary indicator of the progression from wild to domestic (e.g., Vigne *et al.*, 2005; Meadow, 1989; Boessneck and von den Driesch, 1978; Bökönyi, 1974). The size criterion used places small individuals as 'domestic' and large ones as 'wild', but it can be noted that the ranges of measurements often show significant overlap between the two groups (Rowley-Conwy *et al*., 2012; Albarella *et al*., 2006; Albarella and Payne, 2005; Mayer *et al*., 1998; Payne and Bull, 1988).

All of those markers previously mentioned could be the result of an evolutionary response to human mediated domestication (Morey, 1992) but through different pathways dependent on the exact causal mechanism (Zohary *et al*., 1998; Morey, 1994). This makes the topic of morphological variation complex, although the outcomes of processes like domestication are well known, they are highly dependent on a plethora of factors that can influence and drive morphology. Besides, fundamental questions of domestication remain largely unanswered with much uncertainty still surrounding the biological and cultural processes involved in producing morphological transformations (Dobney and Larson, 2006; Vigne *et al*., 2005). It is thought contributing factors can include the environment, and temporal and chronological spacing, alongside the domestication process itself. Reduction in body size also being influenced by non-genetically driven factors makes separating the process of domestication and natural taxonomic or even spatial variation difficult (Zeder, 2006b). Changes in shape with size occur at a variety of stages and can be seen during development (ontogenetic), among adults of different groups including breed (intraspecific) and among adults of different species (interspecific) (Wayne, 2001), thus making the exact timing and trajectory of any morphological changes to be often uncertain. It is acknowledged that by the time there is any influence on morphology, animals may be far along the path of domestication (Arbuckle, 2006).

Taking the conditions of domestication into further consideration, morphological changes are also known to occur swiftly under the right conditions. Such changes can mimic the evolutionary change experienced by isolated populations which can lead to phenotypic divergence (Clutton-Brock, 1999). It has also been shown that isolated populations can be very interesting from an evolutionary perspective sometimes exhibiting rapid or unexpected morphological adaptations (e.g. Grant and Grant, 2006; Millien, 2006; Kinnison and Hendry, 2001). But while some changes can be significant, the majority in natural populations occur on a relatively small scale. Several large-scale evolutionary changes have been noted for many domestic species (such as size and shape reduction) but in most cases involved considerable human input to achieve this. Recent studies involving geometric morphometrics (Evin *et al.*, 2015b, 2013; Cucchi *et al.*, 2011b) have questioned the use of traditional size criteria that have typically been used in the distinction of domestic from wild, suggesting that looking at shape might provide more insight in addressing this. This is due to the changes seen in domestic animals resulting in a morphological diversity exceeding that which has been observed in wild populations (Drake and Klingenberg, 2010). That is not to say traditional use of size is unimportant in the research of domestication, having made a foundational contribution to our understanding.

While the general trends of morphological change in mammals subject to domestication are generally understood (Price, 2002), they have not been extensively explored in cattle compared to other species, for example wolves in comparison to dogs (Hansen Wheat *et al.*, 2018; Drake *et al.*, 2015; Power, 2012; Udell *et al.*, 2010). Many of the varied morphologies seen in cattle today were created through persistent artificial selection to promote desired traits through selective breeding. As domestication became more prolonged, cattle characteristics became more derived, with selection for increasingly different characteristics from the wild counterparts. Changes were not only focused on tameness and docility but also bodily characteristics like colour and physiological traits such as milk production (van Vuure, 2005). The exact circumstances regarding the timing and location of domestication have been key topics debated in archaeology for many years. Much of the previous work on aurochs has looked at the differences from domestic cattle, particularly using osteometric analysis to investigate size change (Grigson, 1978, 1969; Jewell, 1963). It is clear that aurochs are generally larger, with size shifts in the Holocene being attributed to the onset of domestication (Davis, 1981). However, there was also an earlier shift in size likely due to changing climatic factors (Wright and Viner-Daniels, 2015) and caution must be applied when using size reduction to identify domestication particularly in archaeological material. There are also some suggestions of shape changes associated with climatic variation (Cussans, 2017). The post-cranial skeleton has been foremost in leading conclusions using length and width measurements of limb bones to show wild-domestic differences but also change through time. Only a small amount of work has included skull measurements, for example Grigson (1974a, 1974b) showing aurochs craniobasal length to far exceed that of Neolithic cattle. The limited scope of cranial study is for good reason, being an element that seldom survives deposition and recovery.

In recent times, cattle have been intensively bred for specific characteristics, meat, milk, and traction, effectively restricting further the population size (Taberlet *et al*., 2008). This selection produced small changes that accumulated over time into diverse subtypes from a single ancestral stock. To that end, many breeds were achieved by selecting limited numbers of individuals for breeding from larger populations or by cross-breeding existing breeds for new desired attributes equivalent to new lineages from founder events and hybridisation (Sampson and Binns, 2006; Parker *et al.*, 2004). However, the notion of breeds in the modern sense was thought to be established about 200 years ago, over a relatively small number of generations biologically speaking, from narrow populations (Felius *et al*., 2014). While the desired phenotypic factors may be exhibited, reproductive isolation and limited population sizes also give rise to extensive opportunity for genetic drift (Wayne and Ostrander, 2007). In addition, the exact impact of this is not fully known. For example, as Zeder (2001, 2003) showed in goats, domestication had a limited impact on size, with factors such as sex and geographic location seeming to be more influential.

Through the processes of selection as described above, specific traits can yield sustained and substantial changes in skull shape. The most obvious example of this in cattle is the desire for hornless, or polled, animals (Schafberg and Swalve, 2015; Cozzi *et al*., 2009), but because of this cattle now exhibit a range of head shapes and sizes. The theme of decreased skull length is a common pattern noticed in the domestication of many species (e.g., Parés -Casanova, 2018; Geiger *et al.*, 2017; Wilkins *et al.*, 2014). In domestic cattle, a size decrease and change in shape of the skull relative to aurochs is generally seen (e.g. Grigson, 1974b; Bohlken, 1962). Typically, depending on the level of selection, this can lead to extreme flattening of the skull (so called bulldog features) that is also seen in Niata cattle (Veitschegger *et al.*, 2018). Decreasing size also resulted in smaller brain volume with aurochs having an estimated brain size of 650-830 cm^3, while domesticates reduced by approximately one third in comparison (Balcarcel *et al*., 2021b; Nickel *et al.*, 1975). Aside from just proportionate scaling, brain reduction was also in quality, with other domestic animals having been shown to have changed their behaviours compared to wild counterparts (Clutton-Brock, 1994). This includes poorer sensory perception (sight, smell, hearing) compared to animals in the wild which require larger brains, and therefore larger skulls, to fully use their senses. However, there are also constraints to morphological variation, such as integration of different parts of the cranium, acting as opposing selection regimes.

4.2.2. Other factors.

While domestication undoubtedly accounts for many morphological differences between aurochs and domestic cattle there are also other factors that influence this. The main factor observable in cranial morphology is sexual dimorphism, the difference between males and females, as seen in many groups of mammals. Selection for highly diagnostic dimorphism is the consequence of complex reproductive, environmental, and cultural factors and can have a marked effect on individual animals. This makes it a highly variable influence on cranial morphology. Species are highly dimorphic within Bovinae, with males displaying a marked increase in physical size over females (Polak and Frynta, 2010). This dimorphism is often attributed to sexual selection through male-to-male competition (Andersson, 1994), but it has also been suggested that there are more constraints on female body size than males (Fairbairn 1997), possibly related to differing growth trajectories for successful reproductive success (Hewison *et al.*, 2011). As mentioned above, domestication can remove many of these constraints compared to wild populations; however, as predicted by Rensch's rule, domestic cattle still demonstrate positive allometry between male to female body mass (Polak and Frynta, 2010). This sexual dimorphism has formed a key component of research on aurochs and domesticates involving osteometric analyses (Wright, 2013). In the early studies of aurochs and cattle, this created several problems as researchers attempted to explain different size groups observed in archaeological assemblages, initially suggesting two forms of aurochs or the process of domestication in action (van Vuure, 2005). More recent studies, particularly after considering sexual dimorphism in domestic cattle, then identified that male and female aurochs have quite a size separation, being almost distinct groups (Grigson, 1969; Jewell, 1962).

The climate in which an animal lives can have a large impact on its morphology. Temperature is a key consideration in this and is considered a major factor in size variation in mammals. It is suggested that populations of a species living in cooler climates will be larger than those in warmer areas, a hypothesis known as Bergmann's rule (Gohli and Voje, 2016; Meiri, 2011; Rodríguez *et al.*, 2008; Blackburn *et al.*, 1999). This is due to the theory that a larger body size in cold weather is better able to retain heat due to having a smaller surface area relative to body mass (Schmidt-Nielsen, 1984). However, this has been somewhat disputed when considering other factors such as coat fur thickness or body fat reserve level (Freckleton *et al*., 2003) and is likely also highly related to other factors such as food availability and resistance to starvation. In aurochs, as the climate warmed during the transition to the Holocene, body size is suggested to have decreased, a trend noted in numerous locations across Europe (Wright, 2013). Regional variation has also been identified as potentially indicating a north to south size difference, with aurochs being larger towards northern latitudes (Wright and Viner-Daniels, 2015). Exact effects of temperature on aurochs specifically have been difficult to understand completely due to the many climatic fluctuations and the partial archaeological record, limiting studies to specific areas and skeletal elements.

Food availability and seasonality is often considered one of the major driving factors in morphological diversification, particularly regarding the skull. The diet of aurochs is still debated but likely comprised grasses and leaves, with possible seasonal movements to take advantage of various new plant growth or to avoid shortages (Noe-Nygaard *et al.,* 2005). It has been suggested that body size is correlated with the amount of time an animal can survive without food and dietary preferences, with large size therefore seen as conferring an advantage (Demment and Van Soest, 1985). Furthermore, it is suggested that an environment's productivity is directly correlated with animal size and food availability per animal. A highly resourced environment will be able to support larger animals, but population density will also influence this. Population density is complex, and the implications of herd size, resources and individual size are difficult to disentangle being interlinked with multiple external factors. This is additionally complicated for extinct populations where density is unknown. It is nearly impossible to assume population density from archaeological material containing just a subset of bones, which reflects the decisions of past humans rather than the wild animal and if a natural population outstrips resources available it often leads to a reduction in numbers which only the most resilient animals will survive. However, this is a little more complex as temperature will likely influence plant resource availability and so there are multiple interlinked factors to consider before reaching a conclusion about this.

4.3. Aims and objectives.

This chapter explores shape and size differences between the crania of British aurochs and cattle, to assess if they are similar or if measurable differences actually exist. The purpose of this is to clarify the morphological relationship between aurochs and cattle that has often been unclear and based on a size division observed in measurement studies of mostly post-cranial skeletal elements. Particularly it is predicted the contribution of shape differences will be highlighted in the distinction of aurochs and cattle, as this factor has not yet been significantly investigated.

This chapter has two main aims:

1) To assess differences in shape and size between crania of aurochs and domestic cattle.
2) To assess if aurochs and cattle crania share a common allometric trajectory i.e., are domestic cattle simply smaller versions of their wild counterparts?

There are also two lesser-aims that will be investigated as they potentially influence shape and size factors in aurochs and cattle.

3) To investigate the impact of sexual dimorphism on cranial morphology.
4) To determine the extent to which inter- and intra-specific differences can be recovered from fragmentary specimens.

It is hypothesised that:

HYPOTHESIS 1: Shape differences will be apparent between aurochs and cattle crania. This will be tested with GMM. Predicted shape differences will be due to the substantial impact of domestication.

HYPOTHYSIS 2: Domestic cattle will be less constrained in terms of shape. This will be because of the removal of natural selection constraints through human selective breeding. This will also be apparent through disparity in the morphospace.

HYPOTHESIS 3: Cranial shape differences between cattle and aurochs will be more than just the product of static allometry. This will be tested by comparing the allometric trajectories through regression analysis.

HYPOTHESIS 4: Sex will have a significant impact on the cranial shape of cattle.

HYPOTHESIS 5: Shape differences between aurochs and domestic cattle will be recoverable from fragmentary specimens, although potentially with less clarity of separation between the species.

4.4. Methods.

4.4.1. Sample.

The sample comprised 65 complete crania belonging to domestic cattle (*Bos taurus*) and 10 complete crania of aurochs (*Bos primigenius*). All specimens were from Britain and were obtained from museum collections (see appendix 1 for further details). Classifiers were recorded including species, sex, breed, and time-period. Sex was only known for some domesticated cattle. Breed was recorded for some of the domesticates but only in low numbers, often two or three numbers per breed; it was therefore decided to only highlight one breed specifically, namely Chillingham, as there were 17 individuals in the dataset. Time period was not known for the majority of the sample but where possible was recorded textually, for example Neolithic or Roman. The core analysis was undertaken on the 75 complete specimens.

Due to the nature of archaeological material, there were also many fragmentary skulls in various states of preservation. To improve the sample size, these fragmentary skulls were included in a separate shape analysis but with a reduced landmark set. The fragmentary sample added an additional 46 partial crania (20 aurochs and 26 cattle) to the dataset (see Appendix 1 for details of these specimens). A shape-only analysis was undertaken on the fragmentary data set as a preliminary test to explore the application of the method to a reduced landmark set.

4.4.2. Geometric morphometrics.

To quantify differences between cranial morphologies, a landmark based GMM approach was applied. Skull surfaces were captured using 3D photography and exported as scaled digital models using Agisoft Photoscan (Agisoft LLC, St Petersburg, Russia). Analyses were undertaken in the R statistical environment (R Core Team, 2017), using the packages *geomorph* version 3.2.1 (Adams *et al.*, 2020) and *Morpho* (Schlager, 2017). 3D surface reconstructions of all crania were created using photogrammetry via the method outlined in Chapter Three. The same set of 48 landmarks (see Figure 3.1) were then placed on each cranium using Avizo v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). Using R studio, a generalized Procrustes analysis was performed to register the landmarks and finally a principal components analysis (PCA) was implemented to view the shape distribution. The same landmark-based method was applied to the dataset including fragmentary skulls, using a subset of 9 landmarks (numbers 1, 2, 3, 4, 5, 6, 35, 37, 38) focused around the frontal and occipital regions to suit the majority of fragmentary remains (Figure 4.1).

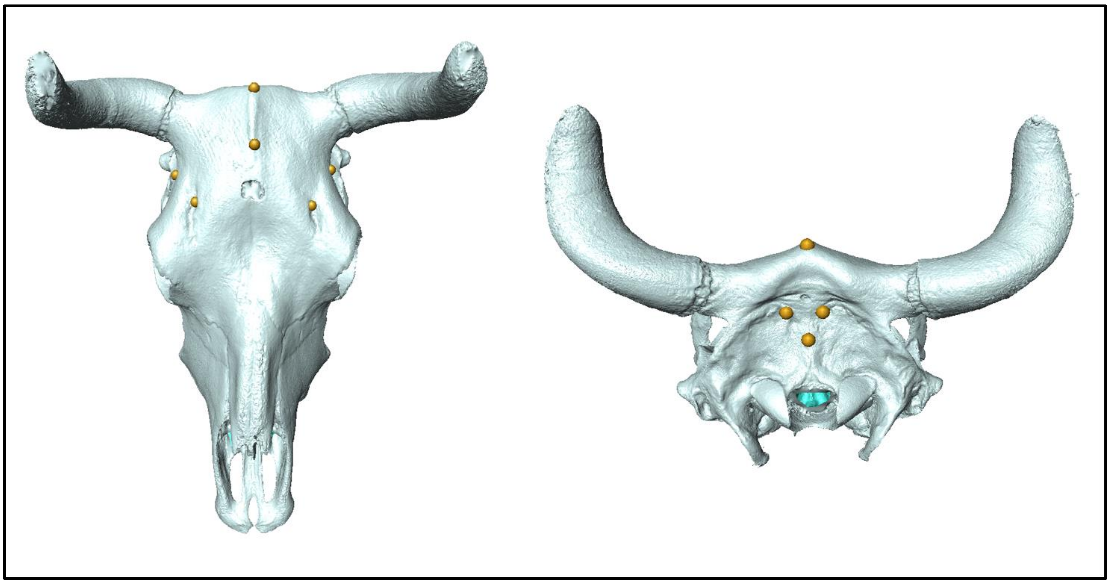


Figure 4.1: Landmark locations for analysis of fragmentary material.

4.4.3. Regression analysis.

To examine the association between size and shape in cattle and aurochs' crania, static allometry was considered. Separate regressions of the two species were performed, and the angle between the regression lines in multi-dimensional space (all the shape PCs against centroid size) was calculated. This was undertaken using the methods set out in Smith *et al.* (2021), where comparison of regression vectors between species groups was performed via a permutation test on the divergence of angles between vectors. In addition, to visualise differences in allometric trajectories between species, a template surface mesh was warped along the regression vectors to summarise the major differences in size and shape between groups. Changes were visually displayed as a colour map representing changes in area of each triangle of the mesh compared to the reference specimen. The displacement between target and reference mesh was shown as expanding in red and reducing in green. This was created in the R package *Arothron* using the localmeshdiff function (Piras *et al*., 2020; Profico *et al*., 2020).

4.4.4. Size and horns.

To measure horns, two measurements were taken according to the standard set in von den Driesch (1976). These are shown in Figure 4.2 as the greatest oro-aboral diameter (measurement code 45) and least dorso-basal diameter (measurement code 46). Measurements were obtained digitally from models using four new landmarks placed to represent calliper measurement positions, specifically for the purpose of extracting linear measurements and were not included in previous shape analyses.

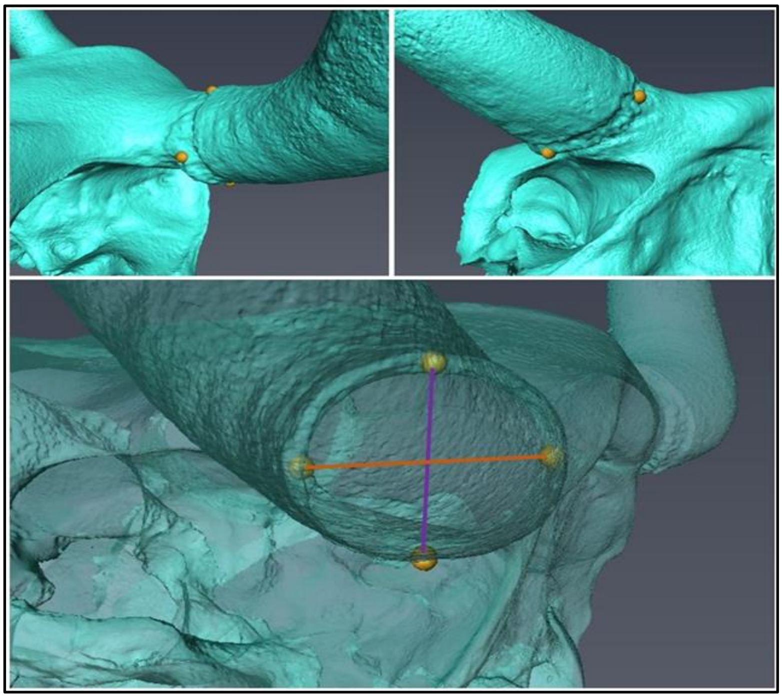


Figure 4.2: Landmark positions based on von den Driesch codes to obtain basal horncore dimensions.

Linear distances were extracted between the points in R to obtain the necessary dimensions using package *geomorph* version 3.2.1 (Adams *et al.*, 2020). Hornless specimens were excluded from this analysis, so 12 specimens were discounted bringing the total number analysed to 63. Centroid size was calculated in the previous GMM analysis and used here to represent absolute cranial size. Scatter plots were made in R using centroid size against basal horn width, basal horn height and the ratio of width to height. In this analysis length of horn was not assessed due to the fragmentary nature of archaeological material. It is suggested by Bartosiewicz (1997) that horn core diameters are highly correlated with length. The final horn measurement was of horn cross-sectional area, estimated by the following formula:

$$Area = width\ radius \times height\ radius \times \pi.$$

4.5. Results.

4.5.1. Shape analysis.

For the analysis of complete skulls, 89.93% of the cumulative variance is explained by the first 20 principal components, with the first 3 principal components explaining just over half (54%) of the variance (table 4.1). The first two PCs account for 27.7% and 18.3% respectively of the percentage variance explained along these axes. PC2 (figure 4.3) can be seen to separate aurochs and cattle into two distinct groups. The cattle group can be seen to have a much larger morphological disparity having a wide distribution across PC1 and the lower portion of PC2. The aurochs' group is more restricted in shape space, possibly relating to the smaller sample size or the less diverse skull shapes. In terms of shape, PC1 represents the relative length and breadth of the skull moving from narrow and long in the positive values to broad and short in the negative values. PC2 shows the concavity and convexity of crania from most convex in the positive values through to most concave in the negative. Aurochs and cattle are clearly separated on the basis of shape, with aurochs' crania being relatively longer, thinner and more convex. In figure 4.4, it is shown that PC3 relates to the location of the nasal bone and parietal/intercornual protuberance along the antero-posterior axis. This gives a long angular shaped skull in the positive values and a shorter, more rounded skull in the negative values but accounts for only 7.9% of the total variance.

PC number	eigenvalues	% Variance	Cumulative %
1	0.001331	27.69	27.69
2	0.000882	18.36	46.05
3	0.000383	7.97	54.02
4	0.000284	5.90	59.92
5	0.000232	4.83	64.76
6	0.000171	3.55	68.31
7	0.000165	3.44	71.75
8	0.000129	2.69	74.43
9	0.000109	2.27	76.71
10	0.000097	2.02	78.73
11	0.000082	1.70	80.42
12	0.000072	1.49	81.92
13	0.000062	1.30	83.22
14	0.000060	1.24	84.45
15	0.000052	1.07	85.53
16	0.000051	1.06	86.59
17	0.000044	0.91	87.50
18	0.000041	0.84	88.34
19	0.000039	0.80	89.14
20	0.000038	0.79	89.94

Table 4.1: Eigenvalues and variance along the first 20 principal components of the analysis of complete crania.

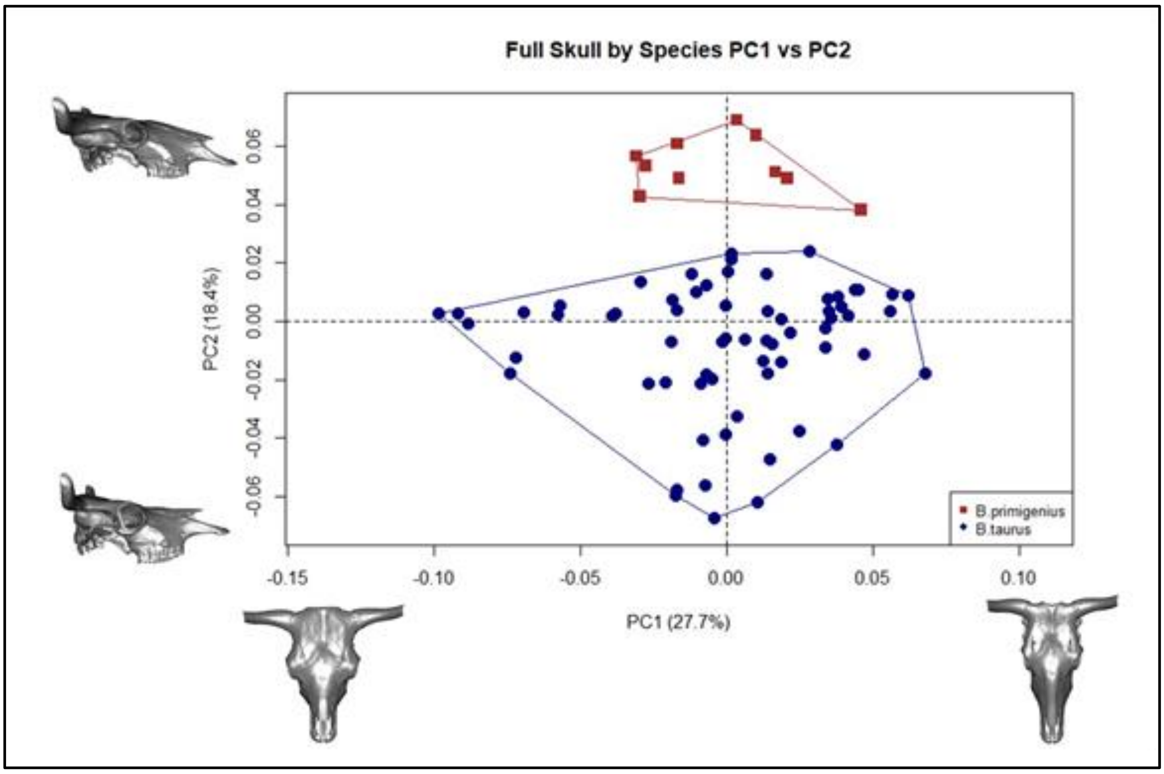


Figure 4.3: Plot of PC1 and PC2 from GMM analysis of complete crania by species. Blue circles = domestic cattle; red squares = aurochs. Surface warps represent cranial shape changes along principal components, omitting horncores as not landmarked.

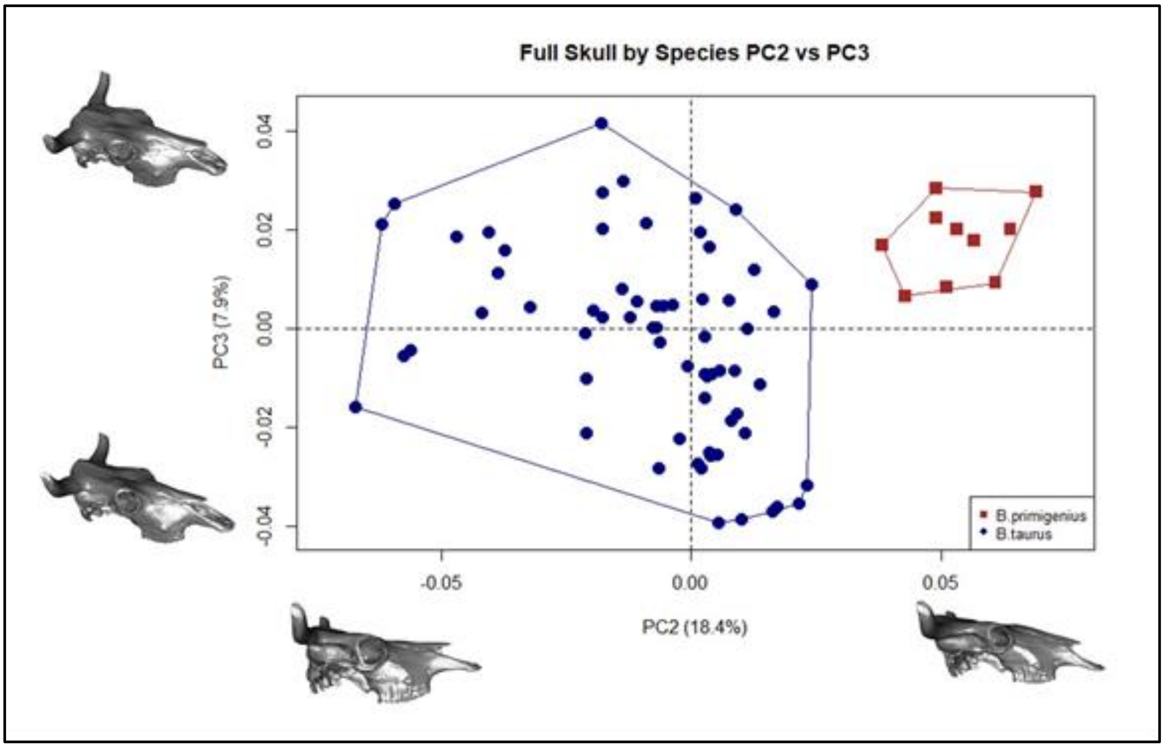


Figure 4.4: Plot of PC2 and PC3 from GMM analysis of complete crania by species. Blue circles = domestic cattle; red squares = aurochs. Surface warps represent cranial shape changes along principal components, omitting horncores as not landmarked.

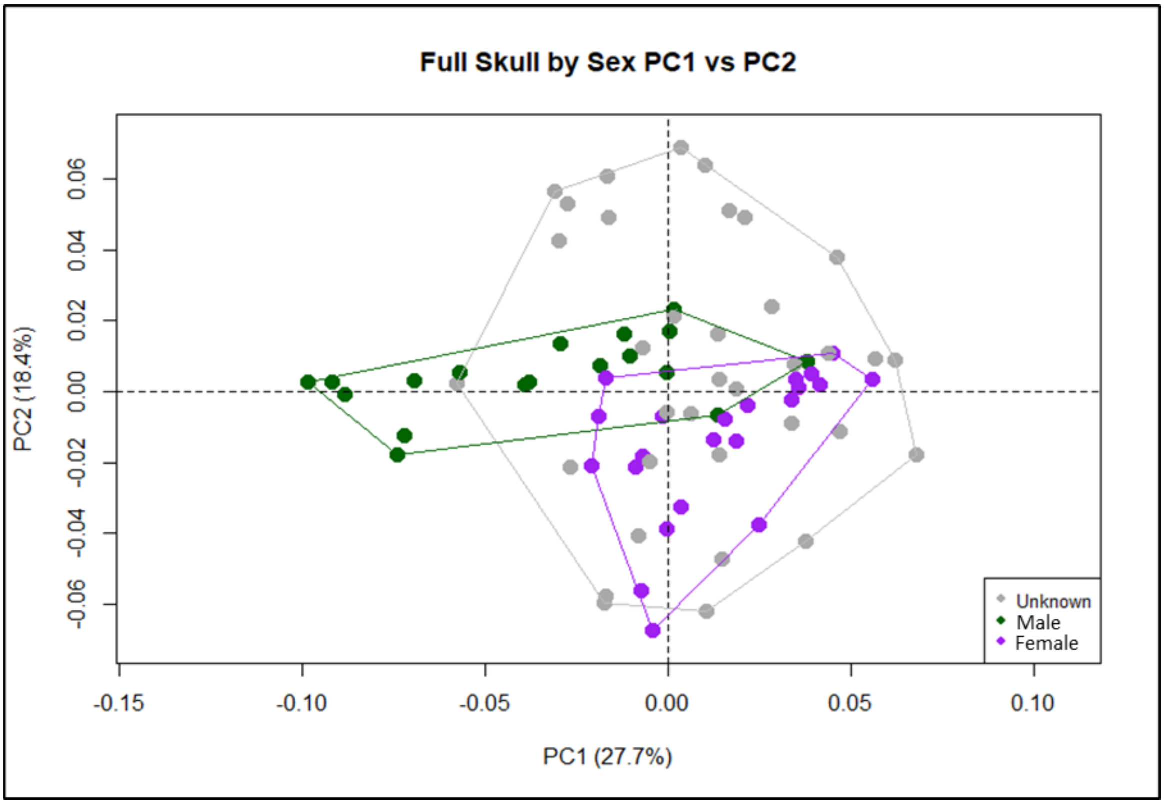


Figure 4.5: Plot of PC1 and PC2 from GMM analysis of complete crania by sex. Green circles = males; purple circles = females, grey circles = unknown.

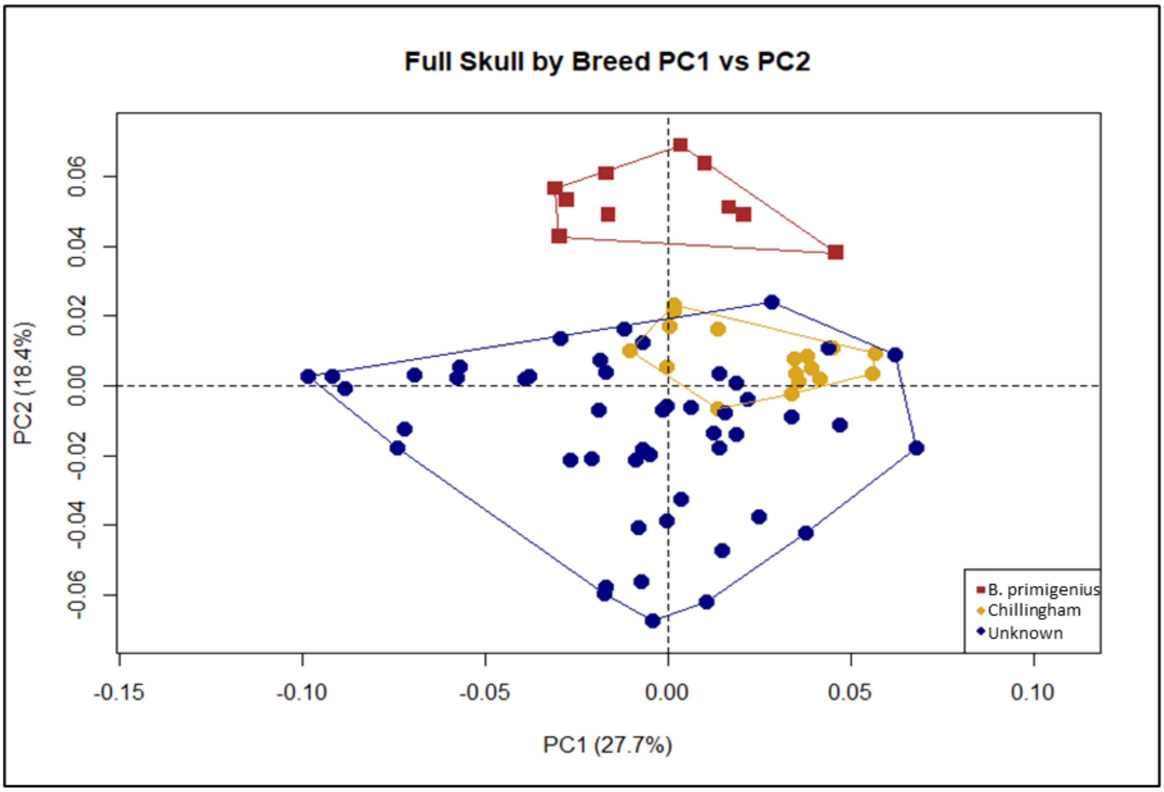


Figure 4.6: Plot of PC1 and PC2 from GMM analysis of complete crania by breed. Red squares = aurochs; yellow circles = Chillingham, blue circles = unknown.

Although many of the specimens are of unknown sex, some differentiation in skull shape between male and female cattle can be seen in figure 4.5. Bulls tend to be found towards the more negative end of PC1 but are positioned slightly more positively along PC2, which represents a broader distal cranium and reduced facial region. Domestic cattle are slightly more positive along PC1 and negative along PC2, being generally slender and longer in shape. Bulls have a wide range along PC1 but narrow along PC2. Domestic cattle seem to generally exhibit more variation across PC1 and PC2. The shape variation seen here is almost certainly influenced by the presence of a large number of Chillingham specimens drawing the shape distribution to the more positive quadrant of the PC plot. As no sex data was available for aurochs this can only be retrospectively surmised from their positions on the PCA, leading to the possibility of a male group of five specimens and a female group of five specimens divided along PC1.

When looking at breeds the shape representation is more limited due to the low numbers of specimens for some breeds, but a representative idea can be obtained if breed is significantly represented by shape differences (figure 4.6). For example, Chillingham cattle separate from other cattle suggesting there are fundamental shape differences in the crania that define the appearance of this breed. It also seems that low number in the breed groups is further affected by sexual dimorphism as this has quite a marked shape impact. The difference between males and females may be more pronounced than differences between breeds.

Partial crania were also plotted using a reduced subset of the landmarks (figure 4.7) but an increased sample number. This shows some separation of the species on PC1 which accounted for 34.3% of the variation although there was some overlap between aurochs and cattle. PC1 represents the angle at the fronto-occipital junction with negative values being acute while positive values represent a more rounded rear skull. PC2 represents 23% of the shape variance, indicating shape change from broad rounded skulls in the positive values to more slender and angular skulls in the negative values. Aurochs cluster in the upper left portion of the morphospace suggesting a thinner more angular shaped distal cranium. Domestic cattle occupy a larger area of shape space, particularly related to a rounded, broader distal cranium.

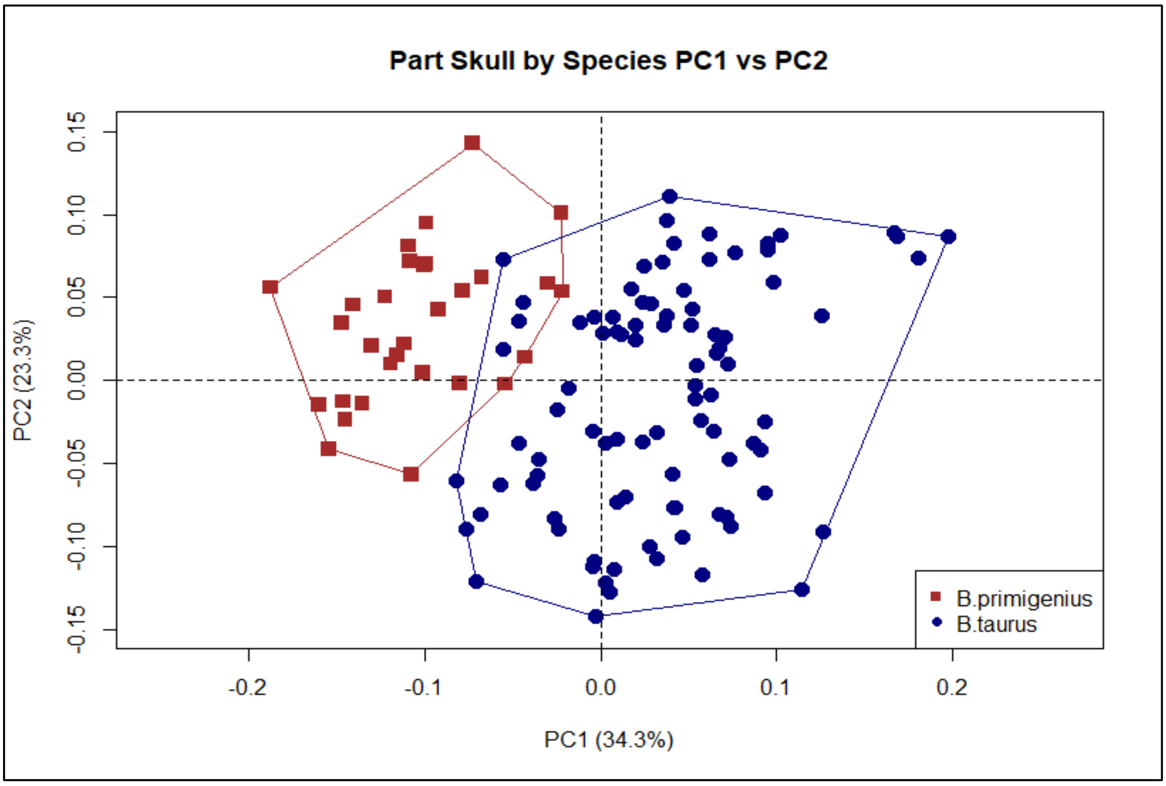


Figure 4.7: Plot of PC1 and PC2 from GMM analysis of partial (fragmentary) crania. Red squares = aurochs; Blue circles = cattle. This was undertaken on a reduced landmark set to previous analysis.

4.5.2. Regression analysis.

The results of the multiple regression analysis between centroid size and shape indicate that the allometric trajectories of aurochs and domestic cattle are divergent, with a 60.02° angle of separation (figure 4.8). A permutation test on 1000 random permutations demonstrated that the size-shape relationships of aurochs and cattle crania are significantly different, with a p-value of 0.001. The differences between the groups can be seen in the visualisations of warps along the regression lines within each species (figure 4.9). Variation is shown on maximum predicted values where red indicates expansion and green reduction. From this visualisation, the variation in aurochs' size and shape is shown to be in the facial region (maxillia, nasal, and premaxilla) indicating expansion in large specimens compared to small, but also in the frontal, occipital and basicranial regions that are reduced in large specimens.

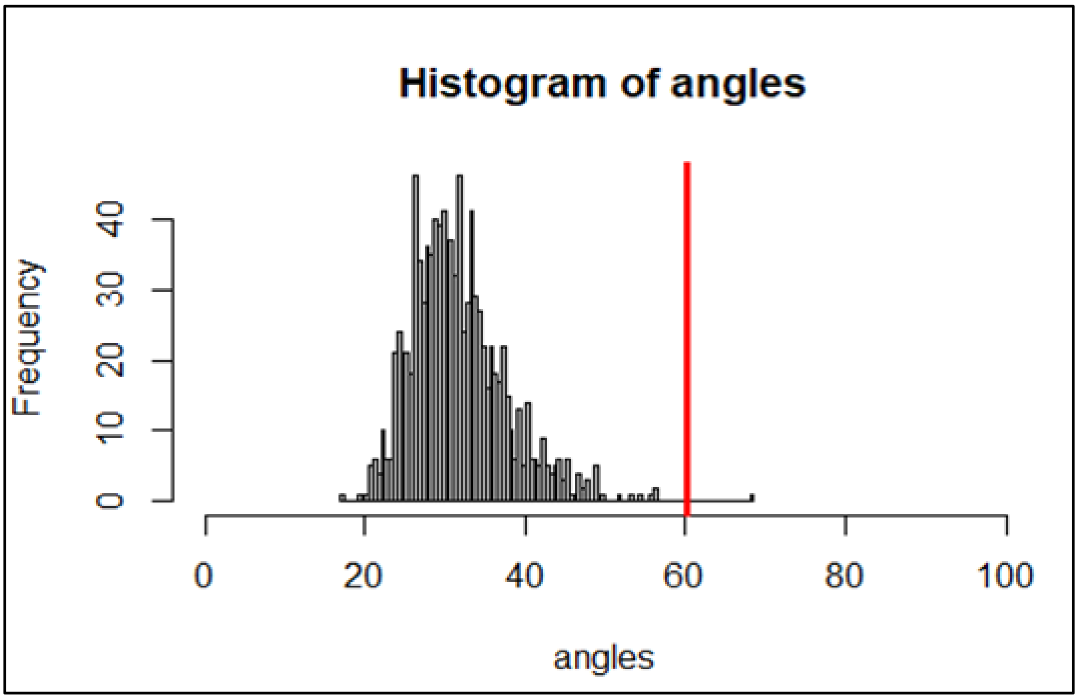


Figure 4.8: Histogram of angles between trajectories generated by permutation analysis. Red line represents angle between aurochs and cattle dataset.

In domestic cattle a similar pattern is noted regarding facial and frontal size and shape. However, the region just posterior to the orbit and the basicranium are different. In specimens at the maximum size along the regression line, the basicranium and occipital regions are expanding along with the area posterior of the orbit, whereas the opposite is observed in minimum size specimens. It is important to note that the colour maps do not show shape differences between species but simply shape change along the allometric trajectory. To further aid the comparison between size and shape differences, the diverging regression lines, translated to a common mean minimum sized specimen, were plotted in figure 4.10. This clearly shows each species' regression line and where they separate, aurochs along PC1 and domestic cattle along PC2. The shape changes between the mean small specimen and the large aurochs and domestic cattle specimen were again visualised with red-green colour maps. These shows that aurochs are more expansive in the frontal, lateral nasal and proximalmost pre-maxillary regions, whereas cattle are more expansive in the maxilla/distal pre-maxilla and most aspects of the basicranium/occipital regions.

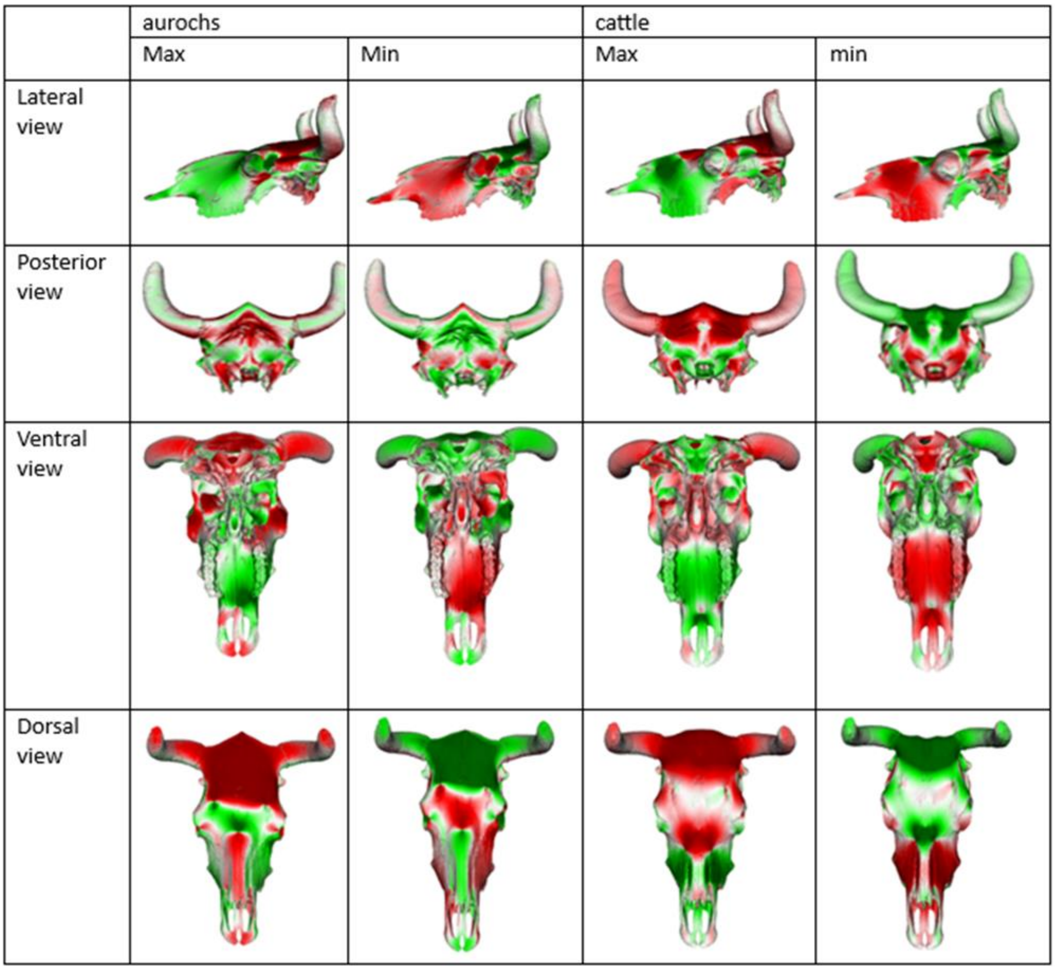


Figure 4.9: Warps along PCs showing maximum and minimum size and shape; red = expansion, green = reduction. Note that horns were not landmarked so any shape change shown in the horns is not supported by the data and should be ignored.

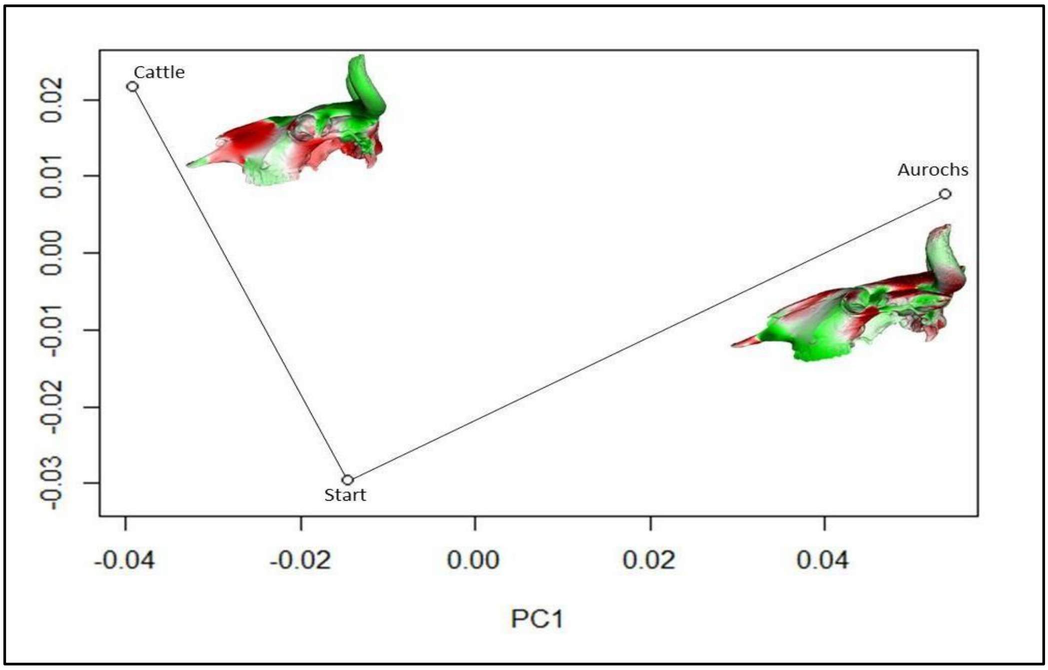


Figure 4.10: Allometric trajectories of aurochs and cattle crania translated to a common mean specimen ('Start').

4.5.3. Size and Horns.

Measurements of horn width and height showed that horns are correlated with centroid size. The general pattern indicated that, as skulls become larger, so too do horn width and height, and thus so does horn area (figure 4.11). It was clear aurochs were always larger in horn width, height, and area than domestic cattle, but still some variation was observed; for example, the aurochs with the largest cranium did not have the largest horn area although it was nonetheless very large. In the domesticate group, a larger variation was exhibited in the horn measurements. Size was then plotted against the ratio of width to height. This represented the relative 'circularity' of horns, with very circular horns having values close to 1, and more flattened and oval horns having larger values (figure 4.12). The ratio of horn circularity for aurochs was within the range seen for domestic cattle. There was no clear correlation between these variables, with larger sized specimens not always having the greatest width to height horn ratio, i.e., there was no clear trend between size and circularity.

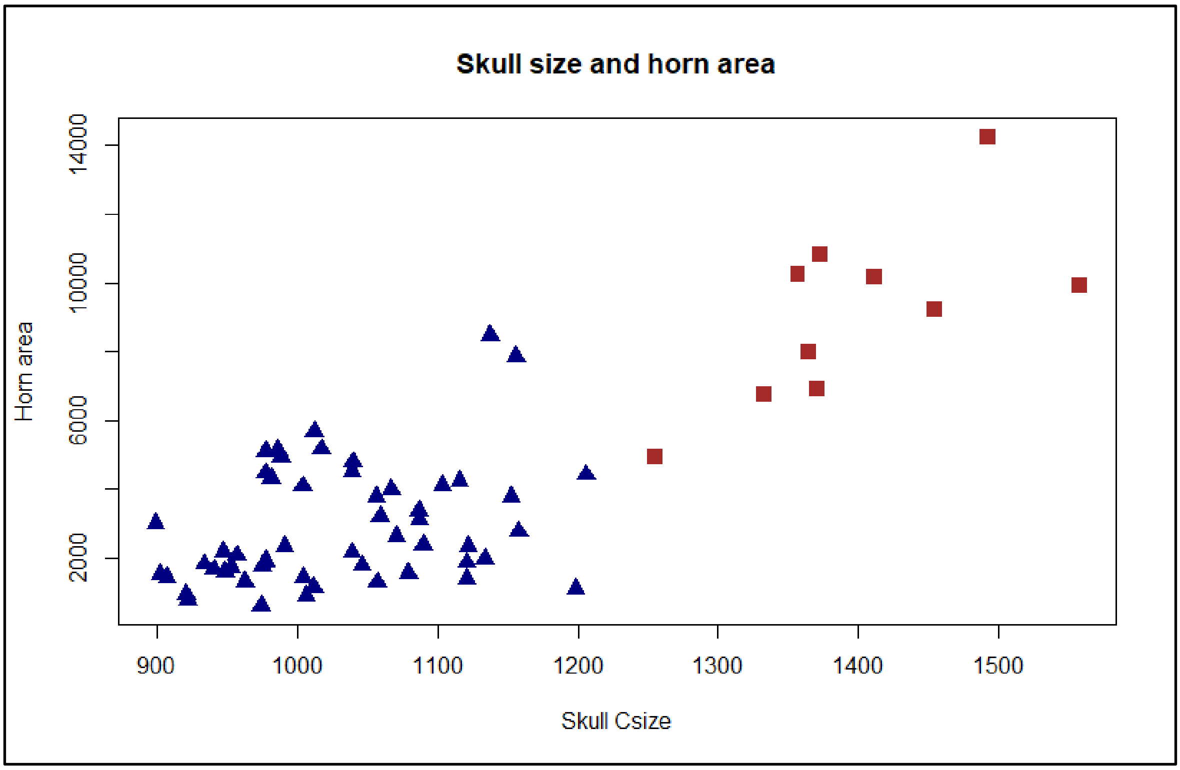


Figure 4.11: Plot of cranium centroid size and horn area. Red square = Aurochs, blue triangle = cattle.

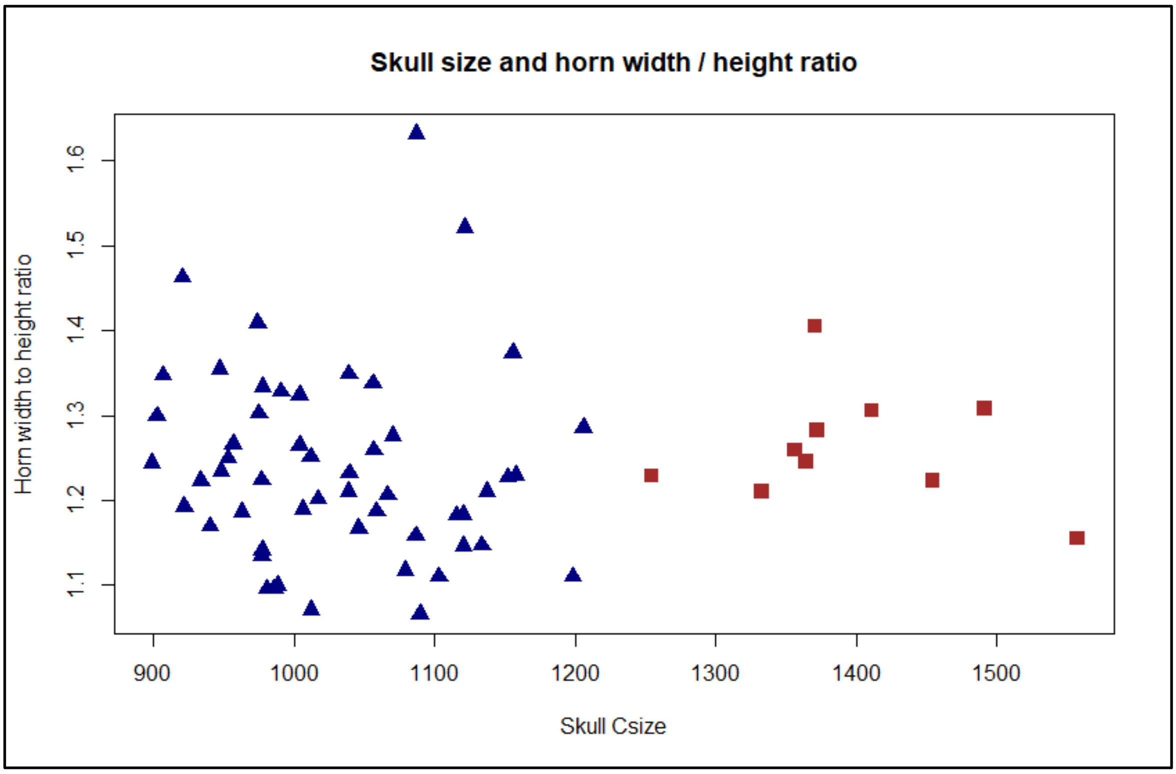


Figure 4.12: Plot of cranium centroid size and width to height ratio of horns. Red square = Aurochs, blue triangle = cattle.

4.6. Discussion.

4.6.1. Summary of results.

The results of the morphometric analyses showed some interesting patterns in the relationship between aurochs and domestic cattle crania. To summarise, the major differences in shape were the relative robustness and flexion of the cranium. Aurochs were shown to have quite a gracile and convex shaped skull when compared to their domestic descendants. In the domesticate group there was a wide range of cranial morphology. Even when fragmentary material was included this pattern seemed to be consistent. Aurochs crania were found to be significantly larger than those of domestic cattle, and moreover showed a significantly different relationship between size and shape. The horns of aurochs were relatively larger in cross-sectional area than those of domestic cattle, but there was no specific pattern identified in the circularity of the horn cross-section.

4.6.2. Shape differences between domestic cattle and aurochs.

Shape differences were apparent in the data, aurochs and cattle were clearly separated based on the morphology of their crania (figure 4.3 and 4.4). This is significant as previous studies have always indicated a morphological overlap between the species, although only based on linear size measurements (Wright and Viner-Daniels, 2015). The overall variation generally indicates aurochs occupied a smaller volume of shape space than domestic cattle. In terms of skull shape, aurochs were more elongated, slender, and convexly flexed while domesticates tended to be the opposite. This provides a novel indication that the cranial shape of aurochs and the domestic cattle group used here occupy a different shape space, likely based on the highly derived nature of the domestic cattle sample being predominantly modern specimens. This puts the results quite outside the scope of many previous studies that have tended to focus on comparisons between aurochs and neolithic (or prehistoric) cattle (Wright, 2013; Grigson, 1978, 1974a, 1969) making comparison with other research difficult.

The shape variation represented along PC1 and PC2 in this study was similar to that observed in the only other study of cattle cranial shape using GMM (Veitschegger *et al.*, 2018). This showed PC1 shape variation was defined by the transformation between short skulls and the elongated ones, PC2 related to differences concerning the angle between the nasal and frontal bones as well as the relative broadness of the cranium. Two aurochs skulls included by Veitschegger *et al.* (2018) were not separate to the general taurine group, and more specifically the shape variation did not separate aurochs from domesticates, unlike in this analysis. However, as that study was looking specifically at Niata cattle, the highly derived morphology of these unique cattle likely altered the morphospace significantly.

The results of this analysis do however also align with GMM shape-based studies of other wild and domestic ungulate species where similar work has been undertaken. In a paper examining wild, domestic and hybrid pigs Owen *et al*. (2014) recorded highly significant shape differences between wild and domestic pigs. The morphologies associated with wild and domestic pigs were distinct: wild pig crania were noted as having a more slender appearance, exhibiting straighter snouts, whereas, domestic pigs had deeply concave snouts and were overall more robust relatively. The domesticated pigs also exhibited greater morphological disparity occupying a wider area of shape space than wild pigs. This differs from the results of this chapter, particularly regarding relative flexion of the skulls around the frontal and maxilla. But similarities are noted between the shape differences in straightening of the snout and more slender elements in wild variants and the wider morphological variation in domesticates.

The pattern mentioned above is not an isolated case and seems to be part of a universal trend that occurs in wild and domestic related taxa. This is seen most clearly in studies of dogs which show highly derived and wide-ranging variations when in the domestic form compared to the wild that effectively cluster distinctly into groups (Selba *et al.*, 2019; Wayne, 1986). Analyses of wild canids compared to domestic dogs indicate that cranial shape includes an expansion of the orbital region, a compression of the rostrum, and an overall warping in the shape and orientation of the skull. In contrast, cranial morphology in domestic species shows an anterior shift in the frontal portion of the skull accompanied by the braincase assuming a more superior position (Schmitt and Wallace, 2012). It would therefore suggest that the results seen here in the analysis of aurochs and domesticates are not unexpected or different to trends seen in other mammals. To refer to the shape analysis, in a standard PCA including a multi-species sample, PC1 is often likely to represent combined size-shape correlated differences and shape differences among taxa unrelated to size (Cooke and Terhune, 2014). There appear to be similar trends in the ways that skull shape changes and this is likely related to and constrained by certain factors resultant from the domestication process where the major change is often size; this is discussed later in this section.

4.6.3. Size and shape differences between domestic cattle and aurochs.

In the previous section it has been discussed that cranial shape is different between cattle and aurochs. However, size is also considered important in the distinction between aurochs and cattle, particularly the relationship between size and shape, given the visible difference between the two species. Nonetheless, the results of the size-shape analysis (section 4.5.1) were counter to what was expected. The static allometry of each species was analysed to assess if domesticates are simply smaller variants of their wild form. Regression analysis showed size to be significant but also indicated that, far from being similar, aurochs and cattle have significantly different allometric trajectories in terms of morphology. As size changes so too does shape but in a diverging trajectory suggesting a separate size to shape relationship. From the colour maps (figure 4.9), the major size related shape changes can be assessed. For aurochs the largest specimens have an enlarged frontal and occipital region along with the palate area of the maxilla compared to aurochs at the minimum spectrum of the regression. Similar findings were seen in domestic cattle but with even stronger changes in the frontal and occipital region. The most pronounced changes are seen to occur moving from maximum size exhibiting a wide broad cranium to minimum having a narrow slender cranium. The reduction of the cranio-facial region is also more apparent in domesticates. It is of note that there are also many small differences between aurochs and domesticates, the most obvious being the intensity of expansion and reduction of the frontal and occipitals, and cranio-facial regions, with differences in cattle being much more acutely expressed. The visualisation of this in the heat maps indicated that specific portions of the cranium might be changing more along the size and shape component for each species. It indicates a pattern of size and shape change that cannot simply be described with size scaling alone, domesticates cannot be said to be smaller counterparts of aurochs.

Contextualisation of the size analysis undertaken here is difficult as no studies using comparable methods have been undertaken focusing on aurochs and cattle. Size is covered widely in zooarchaeological literature but using different methodological approaches (Grigson 1969, 1978; Jewell 1963; Bohlken, 1962), this makes the significant assessment of allometry with particular regards to shape in this thesis not comparable to previous literature. In addition, previous works have predominantly focused on post-cranial elements due to their frequency in the archaeological record compared to crania (Wright and Viner-Daniels, 2015). One common theme has been to establish that domestic cattle are in most cases smaller than the aurochs (Wright, 2013) but also form an overlapping data set of measurements between larger domestic cattle and smaller aurochs when plotted together (Grigson, 1975).

Grigson (1978) compared linear measurements of cranial bones from several European countries of aurochs and early domestic cattle and provided some useful information for size comparison. Even in crania it was demonstrated that aurochs are much larger than the domestic cattle, but that measurement overlaps apart from in basal length where a clear distinction was found. More significantly measurements have lower variability in aurochs than in domesticates, a pattern also noted in this chapter's analysis of shape (figure 4.3). Grigson (1978) concluded that the size proportional differences between species were no greater than between sexes dimorphism within each species and even of the same degree, allometrically. This supported earlier work on size that argued aurochs and domestic cattle are actually the same species with proportion differences between them the product of allometric relationships among the various skull measurements (Bohlken, 1962). However, the results here point to a contradiction of that viewpoint. The regression analysis (section 4.5.3) revealed sharply diverging size-shape trajectories in cattle and aurochs. This is likely a result of a more nuanced approach taken here, using geometric morphometrics, that considered cranial shape as a whole, rather than looking at individual linear measurements.

4.6.4. Do the changes observed match current understanding of domestication?

The results of this chapter seem to follow a similar pattern seen more broadly in the wider literature, particularly relating in some way to domestication. The morphological separation of wild from domestic relies upon the occurrence of transformed characteristics in the domestic forms and on them being observable relative to their wild ancestors. Changed characters of the cranium in domesticates include proposed increased concavity and shortening of the face, braincase reduction, tooth crowding and tooth length reduction, all of which can be linked to overall size reduction in many species, including pigs and dogs (Zeder, 2012; Morey, 1994, 1992; Clutton-Brock, 1988; Coppinger *et al.*, 1987). More generally, reduction in size and the appearance of other so called paedomorphic or neotenic features have been recognised for a long time as a product of the domestication process (Peters *et al.*, 1999; Price, 1984; Bökönyi, 1969). Many of these specific changes were noted in this analysis when domestic skull shape was compared to aurochs, with facial shortening and concavity of the face seen as the major observable shape differences. But also, clearly aurochs are seen to be more than just larger domesticates. It has been noted that domesticated animals in general often have a wider range of shape variation compared to their wild counterparts (Drake and Klingenberg, 2010). Many of these morphological differences likely relate to the relaxing of certain selection pressures (because animals are cared for, fed, sheltered, etc.) but domestication may also impose new pressures via artificial selection for certain phenotypes.

The drivers of morphological change brought about by domestication are not well understood. Size changes have been shown to correlate with various ecological factors including environmental pressure like temperature or resource availability, but size is also reliant on hormonal modifications that can occur from the stress of captivity, even without human intent (Arbuckle, 2005; Künzl *et al*., 2003). In addition, epigenetic/developmental changes or expressions of genetic mutations may also account for morphological changes which can be directly selected for by humans (Vigne, 2011; Price, 1999, 1984). Under domestication changes can be intensely selected for over a short period of time effecting changes in as little as a few generations and even deviate from established evolutionary trends (Manning *et al.*, 2015). Reduction in cattle body size has been explained by a number of different hypotheses which include reduced mobility and nutritional levels (Boessneck and von den Driesch 1978) and reduced sexual dimorphism (Helmer *et al.*, 2005; Trut 1999). Even within domestic cattle, long recognised patterns of size reduction occurring at different time scales and regional areas are difficult to explain (Schibler *et al.*, 2007; Tresset, 2000; Lasota-Moskalewska, 1980; Boessneck and von den Driesch 1978; Boessneck *et al.,* 1971).

Due to human husbandry, only domestic cattle underwent sustained and persistent evolutionary pressures that resulted in significant morphological change. It is worth considering human control possibly being the most important factor in triggering cranial morphological changes. It is safe to assume the diet of modern domestic cattle is significantly different to that of their wild ancestors, and while it may be grass based it is also supplemented by grains, soy, and maize to increase nutrition and therefore milk and meat output (Drakley *et al*., 2006). The change to a softer food diet under human control would have some physiological implications as "masticatory muscle activation and coordination determine the direction of the jaw movement, control occlusal force, and deform the skull in a variety of ways" (Herring, 2006, p.296). Bone is known to be quite receptive to biomechanical stress and differing pressures can result in shape adaptation of skeletal elements (Dinu, 2009). It is however of interest that one of the regions of change noted between aurochs and domesticates is in the distal portion on the skull being relatively wider and shorter in depth in domesticates (Figure 4.8). This is the region where the temporalis muscle inserts running down to the mandible. The orientation and elongated nature of wild skulls seems to allow a more optimum angle for higher bite force possibly suggesting a more fibrous diet that could include harder plant matter. The reshaping of the skull in relation to feeding would be a side-effect of domestication and could occur independently of human intentions. For example, in mink a shortening of the muzzle (Kruska and Sidorovich 2003; Lynch and Hayden 1995) may be a breeding/domestication effect, or this may be a dietary/environmental adaptation reflecting a change in prey and hunting (Bruner *et al.*, 2005).

4.6.5. Morphological differences explained by sexual dimorphism.

Sexual dimorphism is considered a major source of variation in cattle, being expressed strongly in wild and domestic varieties. While much of the data was of unknown sex, including all the aurochs' specimens, a reasonable proportion of the domestic material was plotted as male or female. From this it was clear there are pertinent trends in the domesticate data that hold some profound insights into possible causes of morphological variation. The males had a long spread along PC1 but narrow along PC2 suggesting most of the shape variation was related to the relative robusticity of the skull. Males also exhibited some of the more extreme forms in the shape space and were larger in size. Females showed more disparity in shape variation and were generally smaller in size. While the size element is well known, the variation in morphology is not. There is some overlap between males and females towards the centre of the PCA indicating there is not a clear shape difference but a morphologically overlapping shape trajectory that moves from females to males.

In modern cattle of known sex, it has been suggested that the main change between different sexes occurs along the same regression line, indicating that males are simply larger allometrically scaled than females (Albarella, 1997). This seems to be supported by the results here, the wide sexual variation in domestic cattle observed in this analysis might be explained partly because of the broad number of breeds available but also due to the absence of equal numbers of breeds of specific sizes (i.e., no very small or large breed). Moreover, it may also be partly because of the over-representation of narrow crania in the data due to relatively large numbers of Chillingham cattle. High variability in bulls occurs in characters that are particularly affected by shape (Grigson, 1974a). A similar pattern to domestic cattle can be seen in the aurochs' data where there are two distinct groups in the shape space, possibly representing male and female forms. These seem to fall on a tight trajectory in the subsequent size analysis and certainly seems to fit Albarella's (1997) argument relating to sexual dimorphism and allometry.

4.6.6. Morphological differences explained by breed.

Chillingham cattle are well represented in the sample and seem to exhibit a particular morphology. While other breeds were also recorded these were never in significant enough numbers to be certain of any trends, often with uneven number of males and females further casting doubts on their validity. The Chillingham group comprised 17 individuals of approximately equal numbers of specimens of each sex. This group plotted tightly within the cattle group towards the positive end of PC1 and in the approximate middle of PC2. Whilst not being completely distinct cattle, the Chillingham breed is clearly a little more distinctive in terms of shape. Chillingham cattle are unique among domesticates in that they have received no improvement or undergone husbandry for several hundred years, being left to roam a large parkland (Hall *et al.*, 2005; Visscher *et al.,* 2001). It is therefore of interest that they form a more discrete grouping and even seem to follow some of the trends seen in the wild group. While they could be considered feral or even wild in behaviour, their morphology is still most closely aligned with their more closely managed domesticated relatives.

The changes in morphology observed in domestics resulted in a diversification far beyond anything seen in wild animals (Drake and Klingenberg, 2010), through intense artificial selection many of these morphologies are now recognised today as domestic breeds (Owen *et al.*, 2014). It is suggested the differences in shape between different breeds can be even larger than between sexes (Albarella, 1997). From the data in this chapter this seems to be more complicated as both breed and sex exhibited a large continuum in the shape space (figures 4.5 and 4.6). This is slightly limited by only one breed being represented, but sexual dimorphism was distinctly apparent within the Chillingham group. The differences reflect selective pressures imposed on breeds by humans over many generations. Differences may also be due to variation in terrain and environmental conditions that play a role in the development of the bone morphology of each breed group (O'Regan and Kitchener, 2005). This may also have arisen through a combination of domestication and environmental pressures, so that phenotypic differences may have occurred because of the differences in both animal management and the geographical regions in which cattle have been herded. As a result, different geographical regions that have different climatic conditions having thus determined the cattle management strategies.

Any determination of breed in this analysis is limited by group size, along with wider consideration of any such determination from skeletal remains. Evidence for deliberate human breed improvement has relied on skeletal size (Davis, 2008), however this method is problematic suffering from similar problems of any size analysis in zooarchaeology, namely measurement overlap. Human selection can also lead to unintended consequences when selected traits are genetically linked to other unselected traits (Tamlin *et al.*, 2009); for example, tameness may also come with hair colour changes. Increasing intensification in breeding and specific selection for certain characters has resulted in a far wider variety of morphotypes in domestic animals than exists in their wild ancestors (Owen *et al.*, 2014), for example polled cattle (Schafberg and Swalve, 2015). The relaxation of selection pressure seen in the wild such as survival or productivity leads domesticated animals to altered morphology, behaviour and reproduction (Araki *et al*., 2007; Frankham *et al*., 1986; Price 1984). Commonly noted is a reduction in sexual dimorphism due to relaxed sexual selection (Lynch and Hayden, 1995).

For domestic cattle the breed of an animal can only very rarely be determined from skeletal remains especially as it is unlikely that there were well-defined and consistently maintained breeds until the agricultural revolution of the 18th century (Davis *et al*., 2012). This time has traditionally been associated with the appearance of most modern improved livestock breeds and when the concept of selective breeding began to be appreciated. However, the origin of other (more traditional) or so-called ‘rare breeds’ remains unknown, certainly this goes back well before the 18th century, perhaps the late Middle Ages (Felius *et al.*, 2011), selective breeding to improve domestic stock and promote desired traits has a long history. Despite this the only breed group investigated in this chapter, Chillingham cattle, do seem to form a distinct cluster within the morphospace of the domestic cattle group, possibly indicating the viability of GMM as a tool for investigation of subtle morphology of this nature if additional breed data was known. In this case the opposite is true for Chillingham cattle investigated here, they have been absent from selection pressures of agriculture for at least a several centuries (Hall, 1989) but still seem to exhibit distinctive breed characteristics linked with population size and isolation (Hall, 1988).

4.6.7. How does the fragmentary analysis compare to the full cranium analysis?

In addition to the analysis on complete crania, analyses were carried out on partial material. Very few complete crania are recovered from archaeological sites due to taphonomic factors. The fronto-occipital region of the cranium is a portion that seems to survive most often in archaeological assemblages. This analysis showed that discrimination between wild and domestic cattle was still possible using a reduced set of landmarks. The shape change towards the distal portion of the skull was focused around the fronto-occipital angle and robustness (PC1 and PC2 respectively). This was similar to the results of full skulls, although results showed more overlap. This was possibly due to the increased number of specimens available for analysis or more likely the reduction in number of landmarks. Previous research on crania (e.g. Grigson, 1974a, 1974b) has been limited due to the generally low occurrence of well-preserved examples in archaeological assemblages due to the element's susceptibility to taphonomy processes. This has made assessment of crania more limited in terms of its archaeological applicability. While including frontlets in the analysis increased the data, there are still few examples of aurochs and cattle frontlets recovered archaeologically. However, it can still provide validity to this area of study, that GMM methods could be applied to investigate a wider range of fragmentary material. This is further evidenced by a similar study on pigs that found a similar pattern (Owen *et al.*, 2014) when regions of the crania were artificially partitioned to simulate taphonomically reduced skulls. This reinforces the validity of using fragmentary data and has quite promising archaeological implications.

4.6.8. Horn shape differences between domestic cattle and aurochs.

The results of the analysis of basal horn dimensions show some clear trends. As the cranium gets larger, generally so too does horn cross-sectional area; that is horn width and height are both highly correlated with skull size. This is consistent with what might be expected: large animals have larger horns. Further analysis of more derived units of measurement (width/height ratio) was also undertaken and showed additional interesting trends. The width to height ratio represents the relative circularity of the horn base and demonstrated a large disparity within the domestic group. The basal aspect of horn cores ranges from very circular in the lower values to more oval in higher values. No correlation was noted between circular or oval horns and skull size. The results in the aurochs and domesticate sample were broadly comparable, with size being the major distinction.

Another point to note was the larger variation in horn measurements shown in the domesticate group, a theme common in all the results of this chapter. There are two significant factors that seems to explain this: sexual dimorphism and breed. To consider sexual dimorphism, the analysis showed both size and sex were found to be important, relating to area. This is consistent with previous studies that suggested there is sexual dimorphism expressed in horns with females being more slender and shorter compared to males (Bartosiewicz, 2006). This is of a similar finding to the results of this analysis; although only horn core basal dimensions were considered, some sexual dimorphism does seem to be expressed, although not investigated thoroughly due to sample size. Although it seems there may also be much variation, especially in horn length which is not a factor considered in this analysis. In domestic cattle the male cores tend to be either shorter than or as long as the female cores (Armitage and Clutton-Brock, 1976). This was primarily seen in the clustering of Chillingham cattle, but it is known that this population has an unusual history compared to most domesticated cattle. It is likely the isolated breeding conditions of Chillingham cattle, and the genetic homogeneity is responsible for their distinctive horns (Grigson, 1976, 1973).

4.6.9. How does this study compare to previous research using linear biometry?

This study shows that aurochs and cattle have differently shaped crania and that the allometric trajectories diverge significantly. The results presented here contrast with the techniques and approaches used in zooarchaeology that have indicated a overlap of size between the species. The potential overlap in size between the wild and domestic can at times be problematic in biometric distinction and this has been explored widely in zooarchaeological literature (Grigson, 1978, 1969; Jewell 1963) but always from the same perspective and not repeated in recent years. Such research has generally reiterated that domestic cattle are in most cases smaller than the aurochs, however there is also an overlap in the measurements of smaller aurochs and larger domestic cattle. Even within studies of modem cattle specimens only it has been demonstrated that a large amount of overlap can occur, especially when different populations, breeds and sex are considered (Fock, 1966). The determination of remains as wild or domestic is important for archaeologists to be able to draw inferences about the lifestyle and species utilization of animals by humans. Clearly there are developments to be made in shape and size, as aurochs and cattle were shown to be significantly different with regards to both.

By using GMM instead of traditional biometry we have been able to move away from the problem of overlapping data that has been a limitation in many past studies. Using linear measurements, as has typically been done previously, limits the ability to truly capture the shape variation of a sample (Bookstein, 1991). Using a GMM approach can potentially provide a more accurate representation of biological and morphological variation within a population (Zelditch *et al.*, 2012). In addition, size and shape components can be effectively separated, something not easily achieved with linear biometry, while preserving this information relative to spatial arrangements (Milenvić *et al.*, 2010; Swiderski *et al.*, 2000). The results have shown aurochs to have a uniquely differently shaped cranium from domestic cattle. This has been noticed in studies of other domestic animals such as pigs and dogs (Owen *et al.*, 2014; Schmitt and Wallace, 2012), where domestication can lead to a specific domesticated animal appearance, GMM usage might have the potential to differentiate between breeds, sexual dimorphism and even include fragmentary material. This has the potential to impact significantly on the study of domestication and the origins of animal husbandry, including development of improved livestock. However, very limited work has previously been undertaken of absolute shape differences between aurochs and domestic cattle so very few accurate comparisons can be made in this area.

4.6.10. Limitations of the study.

There were limitations to this study largely based on the sample available. There were many more domesticate skulls available than wild which created uneven sample groups. While this was not problematic in the shape analysis, some of the statistical tests would have benefited from a larger aurochs’ sample, unfortunately, this was not possible as the sample contained almost all known complete aurochs crania from Britain. The domestic group was similarly limited in the scope by numbers of known breeds and, to a lesser extent, known sex. Breeds were recorded for a number of skulls but these being in low numbers, often fewer than two, it was decided not to include breed as a covariate as it was not possible to establish how typical the measured individuals were of that breed. Similarly, sex was known for some specimens but not all, and was unknown for all aurochs. This situation is also problematic for breed, and makes assessment of shape and size more complex, especially when breed and sex are both known to influence morphology (Albarella, 1997; Lynch and Hayden 1995). This has the potential for results to favour specimens that are well represented in the study group. Over representation was only a problem in Chillingham cattle as they are extremely prevalent specimens in museum stores and readily available at the Chillingham Park. Having such a large group may have influenced the morphospace in the shape analysis and, being smaller domestic cattle, the size results too. But these disadvantages are offset by the known sex (and breed) making them an ideal case study.

4.6.11. Recommendations for further research.

This chapter has highlighted some interesting results that would benefit from further exploration and clarification. Namely the impact of sex and breed on shape and size in cattle as this potentially has quite a significant effect on results that at present remain relatively unquantified. This would require a larger sample size of known breeds and sex to test the various factors in morphospace. It would also be beneficial to expand the domestic sample to include more archaeological specimens of known time periods. Cranial material was chosen due to its significant role in evolution, but this restricted the direct archaeological viability of this study as whole skulls are seldom found in excavations. This then raises problems regarding how representative results might be of other post cranial elements, but this was offset by the usefulness of skulls in population morphological studies of this nature. Fortuitously the availability of aurochs and modern cattle skulls was more numerous in museums and reference collections than anticipated. Fragmentary crania also showed promise in differentiation between cranial shape through application of a reduced landmark set, potentially providing a solution to limited and partial data. Alternatively other skeletal elements could be explored, expanding to postcranial bones with similar methods to see if species, breed and sex could be derived for major skeletal elements likely to be encountered archaeologically. The results would have potentially important implications for the domestication, dispersal, and husbandry of cattle by humans.

The comparative morphology of wild and domestic cattle is of interest to the history of domestication and has been further elucidated in this chapter demonstrating that the species can be effectively classified on the basis of shape and size. It is hoped that future work in this area will develop the results presented here to include additional archaeological material particularly domestic skulls from older periods, but also known modern breeds, and that shape and size are not as morphologically similar as previously suggested in the archaeological literature. This has some quite profound implications for the study of aurochs and cattle and their relationship, particularly the causal mechanisms that impact shape and size development.

4.7. Conclusion.

This chapter suggested exciting and novel propositions regarding the shape and size of aurochs and domestic cattle. Shape analysis revealed a clear separation between the species, aurochs having relatively slender and convex crania compared to the generally broader and more concave shapes seen in domestic cattle. Most importantly, size analysis showed that aurochs and cattle are significantly divergent in their size-shape relationships, being on separate allometric trajectories. It was also shown that these methods can be applied to partial crania and results still seem to follow a similar pattern even on a much-reduced landmark set. Horns were also considered separately, suggesting that there is a possible correlation between skull size and horns, but this is not particularly clear or robust for this dataset. All these factors will be investigated further in the next chapters that look at the biomechanical implications of the observed morphologies.

5. Chapter Five: FEA Feeding performance.

5.1. Introduction.

This chapter investigates how the different morphologies of aurochs and cattle influence feeding performance through finite element analysis (FEA). Ungulates ancestrally have been browsers selecting leaves (Janis, 1976), but also initiated a specialisation to grazing (Williams, 1981) along with a range of adaptations to take advantage of most plants in the forms of browsers/mixed feeders (MacFadden, 1998). Such adaptation and selection for different food sources, particularly grazing softer leaves with less physical resistance will undoubtedly alter cranial morphology associated with feeding mechanics, seen most notably as loss of the upper incisors in cattle (Hongo and Akimoto, 2003). Even though related wild and domestic species often have similar dietary preferences, through human husbandry they often inhabit different niches (Lynch *et al.*, 2008). Cranial shape is well known to impact feeding efficiency (Metzger and Herrel, 2005; Perez-Barberia and Gordon, 1999), and it remains to be seen if aurochs and cattle skull shape is sufficiently divergent for feeding efficiency to be altered. The application of FEA is not considered a technique for largescale archaeological application, but to provide additional specific biomechanical information on the morphological shape of aurochs and cattle crania.

5.2. Feeding performance in aurochs and domestic cattle.

5.2.1. Biomechanics.

The actual process of how cattle, and ruminants more generally, eat grass has been established from a biological perspective, especially the process of digestion (Beauchemin, 1991; Welch and Hooper, 1988; Dulphy *et al.*, 1980). Here we are more concerned with the anatomical and biomechanical act of biting and chewing, which in cattle specifically has received little attention in academia. The general process initiates with the specific oral configuration of cattle. Cattle lack upper incisors but also have a relatively immobile upper lip (Orr, 2011), relying on the tongue to manipulate grass into the mouth and ripping it with the lower incisors against the upper dental pad by head motion (Hafez *et al.*, 1969). Food is then passed to the back of the mouth where it is shredded by the molar row in a lateral chewing motion. This initial chewing process is very short before material is swallowed, then later rumination can occur with more extensive chewing allowing complete digestion. Investigation into cattle feeding phases using pressure sensors has shown that during initial eating, chewing is very irregular, but during rumination chewing is very consistent (Braun *et al.*, 2014, 2013). This most likely represents the uniformity of material being chewed. Bite mechanics while grazing need to account for a non-constant food density, and even bite area and depth, which likely explains fluctuation in chewing (Hughes *et al.*, 1991). The exact bite force needed to bite and then chew seems to be predicted to be quite high (although seemingly there has never been an *in vivo* measurement of a cattle bite). One study predicted bite force based on measurements from the force of cattle removing feed from artificially constructed swards with loadcells at the base, estimating 3270–3280 N/min in cattle (Hongo and Akimoto, 2003). A higher bite force is considered somewhat necessary for grazing animals considering the multiple leaves taken by an animal during feeding exponentially increases toughness through volume (Vincent, 1982).

In feeding studies of similar ruminants, such as goats, bite force was not a limiting factor in feeding, even with tough food matter (Illius *et al.*, 1995). It is proposed that in varying the bite area, a consistent bite force can be maintained when feeding, taking in more, or less material depending on density (Laca *et al.*, 1992a, 1992b). The limiting factor would be biting efficiency given the long periods of chewing, a concept which has been termed ‘bite energy’ (Wight and Illius, 1995). Bite energy may be maintained by cattle, seeming to select softer vegetation, and even stripping softer leaves from plants and leaving tough ones (Dyce *et al.*, 1987). Such selective grazing is well known and usually dictated by the properties of plants, for example, with stiff stems creating a barrier to grazing. It is therefore more efficient for cattle to select soft materials requiring low bite forces (Illius and Jessop, 1996). Tough plant material is avoided due to the increased cost in time and energy to extract low nutritional value reward (Hongo and Akimoto, 2003), but also feeding and longer rumination time (Poppi *et al*., 1980; Janis, 1976; Allden and McDWittaker, 1970). Furthermore, the lack of upper incisors has been shown to give an advantage in selective grazing as animals can reduce intake of tough materials by stripping softer material off tough stems (Walker, 1994). When tough material is ingested, cattle may still have an advantage over other non-ruminating ungulates from reduced chewing times. It has been suggested that in horses, tougher material results in extended chewing periods to achieve similar digestion to ruminants (Janis *et al*., 2010).

5.2.2. Diet.

Differences between aurochs and cattle with regards to the specific differences in morphology and how these impact upon functional feeding performance have seemingly warranted little investigation. The most obvious initial necessity is to define the diets of aurochs and cattle and how they differ to inform why there might be differences in biomechanical advantage. Dietary preference in extinct species is difficult and complicated so it is a particular challenge for examination in aurochs, and often relies on observations of modern wild cattle for inference. For modern domesticates this diet is somewhat easier to deduce but has obvious husbandry-specific variations in feed.

5.2.3. Diet of cattle.

Following the industrialisation of agriculture after the Second World War, cattle feed was generally restricted to ryegrass, it being the predominant crop available (Roche *et al.*, 2017). While this trend has declined in recent years with the study of animal nutritional needs (Drackley *et al.*, 2006; Eastridge, 2006; Miller, 1979), it remains that the diet of most farmed cattle is tightly controlled. Modern agriculture and husbandry provide good information on what domestic herds are fed. Diets of cattle vary greatly but generally comprises ‘forage’ or material eaten while grazing (grasses and leaves) and concentrates including grains, beans, and meal (Kavanagh, 2016). The exact amounts of various feeds have been extensively studied in animal sciences, mostly regarding dairy cattle and with a view to maximising milk production (Reist *et al.*, 2003). When presented with choices, cattle have shown a preference for mixed diets of various herbage and grasses but also legumes (Rutter, 2006). However, preferred diet and that which is actively selected (or provided by humans) can be different based on access and location.

Unlike the highly managed domestic cattle on most modern farms, Chillingham cattle provide a unique juxtaposition in being unmanaged except to prevent total population extinction in the most severe circumstances (Yarwood and Evans, 1999). The herd lives in a 134-hectare park of mixed woodland and grassland. There is little documentation describing the exact food preferences of the Chillingham cattle, but inferences can be made from their environment and observations. In field observations in the late 1970s, the herd was observed using different areas of vegetation at different times of year (Hall, 1988). Bulls were noted to have specific set ranges, the size of which varied depending on the quality of grazing available. In such situations, it has been suggested that free-ranging cattle will have low selectivity and wide spacing during grazing (Hall and Bunce, 2019), which seems to be the opposite of domestic cattle in close husbandry. It is also important to note that for a time Chillingham cattle were living in conflict with a commercial sheep flock who were likely grazing much closer to the ground than cattle were able to, degrading the available grazing (Hall and Bunce, 2019).

5.2.4. Diet of aurochs.

Some deductions on the diet of aurochs have been made based on archaeological evidence, particularly considering the contextual information in which remains have been recovered, and from contemporary sources. Generally, such information seems to indicate aurochs were found in dense forests or more watery areas like marshes (van Vuure, 2005). Habitat descriptions from Poland, where the last population of aurochs existed until the 1620s, has suggested the aurochs inhabited wetlands and then forests in winter, looking for food and shelter (Anton Schneeberger 1602, in van Vuure, 2005). This contemporary evidence has also been compared to dental morphology, with aurochs described as grazers based on hypsodont teeth structure (Grigson, 1978). From these sources it is suggested aurochs were likely eating mainly grasses but also leaves branches and acorns. Parallels have been drawn with modern day wild cattle and the similarities in their food preference (Groot Bruinderink *et al.*, 1997).

This has been coupled with paleoenvironmental data to suggest the environments in which aurochs would have lived and therefore likely food sources. Palynology studies from the 20th century have been instrumental in suggesting an arboreal or non-arboreal habitat, essentially indicating how open or wooded the landscape was, showing a more closed forest in the early Holocene (Zoller and Haas, 1995; Aaby, 1994; Janssen, 1974). However, this is slightly in contrast to the suggestion that cattle, including aurochs, are specialist grazers. It has been suggested that their watery area and forest dwelling may have been influenced by competition with other species, such as horses and bison, in the search for open grass pasture. It is possible the aurochs were able to expand into marshy areas in ways horses were not able, and into forests, similarly to bison (van Vuure, 2005). Analogies with modern feral cattle have also been used to further reinforce the idea of aurochs inhabiting water-rich environments (Gander *et al*., 2003). In addition, aurochs were likely affected by the ever-increasing human expansion and colonisation of the landscape, forcing them to move into less natural ranges.

Microwear of large herbivore teeth has also been used to infer the diet of aurochs, suggesting they were variable grazers. Aurochs likely ingested fewer tough herbaceous monocots than other similar species, such as European Bison, although they still exploited a wider range of foods (Hofman-Kamińska *et al.*, 2018). Reflecting on microwear evidence through time, it has been suggested the diet of aurochs did not change greatly (Hofman-Kamińska *et al.*, 2018), and it may have been that aurochs always had a flexible feeding strategy, more similar to a mixed feeder or browser (Rivals and Lister, 2016). However, when this is considered along with the hypsodont dentition of aurochs being generally more suited to grasses than forbs or leaves, a dietary niche within a forested environment would not be considered optimal. This has also been compared with modern wild cattle that seem to avoid heavily wooded areas, particularly when feeding (Kohler *et al*., 2006; Hall, 1988).

In more recent analyses, investigation of diet has primarily used isotope evidence, particularly carbon and nitrogen. Such studies have focused on more widespread chronological changes and indicated some interesting patterns in the diet of aurochs and even in the role of similar large herbivores more generally. Looking at changes from the Pleistocene into the Holocene, it was shown that some animals responded quite significantly to climatic and habitat change. In Britain, a study of carbon and nitrogen isotopes (Lynch *et al.*, 2008) showed aurochs to be more depleted in carbon than cattle in Neolithic samples, but with no real variation in nitrogen. Two possible explanations were offered, the first of which is based around the canopy effect where some plants in the lower canopy are relatively depleted in carbon (Berry *et al*., 1997). The canopy effect associated aurochs with deep forest, and the shift from an open forest interspersed with open grasslands in this period to a denser forest by the late Boreal c.8000–5500 BC (Lynch *et al.*, 2008). The second idea could be a water-based environment, based on the water stress of plants in wetlands (Flexas and Medrano, 2002).

Availability of water to plants has been shown to be directly reflected in the depletion of carbon in cattle that feed on it (Schnyder *et al*., 2006). When this was considered with the dental anatomy of aurochs, along with modern cattle habitat preferences, a watery environment has often been preferred for aurochs (Lynch *et al.*, 2008). Similar patterns have been noted in work on aurochs from European material, for example in Denmark (Noe-Nygaard *et al.*, 2005) where it was suggested the Boreal transition also significantly altered the habitat and diet of aurochs. In fact, it was suggested that aurochs grazing in the more open Preboreal environment were more similar in diet to cattle grazing in the late Atlantic period when grasslands were re-established and managed by humans along the forest edges (Noe-Nygaard *et al.*, 2005). Aurochs of the later periods were more closely connected with deep forests, even more so than the red deer population that showed remarkably similar carbon results to early domestic cattle (Noe-Nygaard *et al.*, 2005).

The variability in suggested habitat and diet for aurochs is likely due to the temporal and geographic range of the species, spanning several climatic shifts but also responding to more local conditions. Developing forest into the Boreal would certainly emphasise a change from open grazing habitats to forest browsing, and then later to agricultural development and deforestation as the Holocene progressed (Hofman-Kamińska *et al.*, 2019). This adaptability has been suggested to be the reason why aurochs, and indeed other larger herbivores, were able to survive in response to climatic developments (Bocherens *et al.*, 2015). It should be noted that such habitats were likely not preferred, with the marginal habitats acting as refugia for aurochs (Kerley *et al.*, 2012) avoiding any human impacts that became increasingly persistent.

5.3. Measuring feeding performance.

As shown in Chapter Four, the cranial shape of aurochs and domestic cattle significantly differs. It is possible that any changes to skull morphology resulting from the domestication process could have had wider consequences, such as implications for feeding ability, and impacts on sensory structures such as the eyes and brain. It is suspected that if domestication led to a change in feeding ability, this could have been mitigated by human-mediated feeding. Therefore, analysis of the mechanical ability and performance differences in forms of cattle are key to further understanding of the impacts of domestication. Such differences can be measured using FEA.

Using FEA, we can simulate the behaviour of a three-dimensional object in a virtual environment, predicting the stress, strain and deformation resulting from a loading scenario (Rayfield, 2007). This is achieved by subdividing the structure into small discrete regularly shaped parts, called finite elements, with specific properties that can be solved to find structural and performance issues (Brodland, 1994). While FEA was developed for engineering (Zienkiewicz, 1971) it has gained traction with studies of biomechanics and musculoskeletal systems in questions of vertebrate morphology and evolution (Rayfield, 2007). There is good precedent in the published literature for studies of this nature, with investigations of the mechanical links between routine biting and cranial shape already being applied to many species (Lautenschlager, 2022; O'Higgins *et al.*, 2019; Marcé-Nogué *et al.*, 2017; McCurry *et al.*, 2015; Cox *et al.*, 2012; Dumont *et al.*, 2005; Preuschoft and Witzel, 2005). For example, in Tseng and Flynn (2015) broad scale links between Carnivora taxa were investigated in relation to dietary preferences and cranial biomechanical properties. The findings showed cranial biomechanical properties were linked with feeding preference in carnivoran, but the effect of phylogenetic and allometric factors might be stronger than diet. The emphasised link between cranial structure and diet, and the possibility of selection and evolution to dietary niches, is often central to research in this area. The skeleton, being a dynamic structure, responds to the ways strains are orientated and distributed by modifying and remodelling in a phenomenon known as Wolff’s law (Wolff, 1986). Wolff’s law describes bones as abiding to certain mathematical rules that optimise their strength and weight. However, while the concept of Wolff's Law remains generally valid, the application has been somewhat discredited and replaced with the concept of 'bone functional adaptation' (Ruff *et al.*, 2006). The important thing to note is that bone remodelling acts to keep strain at an optimum level with increased strain resulting in bone deposition, while decreased strain leads to bone resorption. This concept is applicable to aurochs and cattle as when an animal performs an action, in this case feeding (performing a bite or chewing), the resultant stress and strain distribution across the skull has the potential to influence morphology depending on the toughness of foods.

To date, few studies have investigated such problems in cattle specifically from a biomechanical perspective, considering how feeding might result in stress and strain and consequentially an osteological response. One study considering differences between digestion styles in foregut ruminants and hindgut perissodactyls using 2D FEA showed that mandibular robusticity was greater in species of hindgut fermenters (Fletcher *et al.*, 2010). It was suggested this was due to the need to chew food material more thoroughly pre-digestion. This finding tested previous assertions that feeding strategy plays an important role in morphology, such as grazers having larger masseter muscles (Clauss *et al*., 2009), to produce greater bite force, along with more robust mandibles to accommodate higher stress levels. Fletcher *et al.* (2010) ascertained no clear distinction in stress patterns between browsers and grazers. It was also noted that lower stresses were recorded in smaller forms, leading to the suggestion that allometric scaling may have a role in robustness, with increasing size leading to issues of how the muscles can activate larger heavier mandibles with relatively weaker mechanical advantage. In general, it was concluded that robustness of ungulate jaws show lower levels of stress in hindgut feeders compared to the relatively gracile jaws of ruminants, due to the higher food ingestion rate and mastication rate. This reinforces the notion that domestic cattle may actively avoid tough plant material. A more recent study also focused on ungulate mandibles using 3D FEA addressed whether the morphology of mandibles best reflected phylogenetic grouping or diet (Zhou *et al.*, 2019). The research indicated the ungulates phylogenetic signals had a strong association with mandible biomechanical performance. A clear difference in stress location and magnitude was seen particularly between Artiodactyla and Perissodactyla, but also Ruminantia and Tylopoda exhibited distinctive stress patterns. In ruminant species less emphasis was placed on initial ingestion to obtain sufficient digestion, compared to non-ruminating species like Perissodactyla relying on heavily chewing their food requiring increased bite forces and stress resistance. This trend was seen in the morphologies of the mandibles, reflecting the demands of specific food ingesta (Zhou *et al.*, 2019).

More specifically to cattle, FEA has only once been undertaken previously to this study, by Veitschegger *et al.* (2018); however, this paper had a very specific research focus to examine Niata cattle. Niata are a cattle breed that are unique in their cranial morphology being extremely brachycephalic compared to most other typical cattle. Two bites were simulated in three domesticate skull models: a Niata, a Simmentaler and a Zebu. Stress was compared between the models to examine how efficient the peculiar morphology of Niata cattle was compared to more commonplace domesticates. The stresses noted some common patterns in cattle breeds, such as a high stress along the zygomatic arch but also differences around the orbital and supraorbital regions. Most interesting however was that the short-faced Niata exhibited relatively lower stresses when performing both anterior bilateral and unilateral molar bites compared to other breeds, particularly Zebu cattle. The results were contextualised with beam theory to suggest "that under adduction of the jaws during biting, the rostrum will behave as a cantilevered beam loaded in the dorso-ventral direction" (Veitschegger *et al.*, 2018, p.9), therefore longer rostra would experience higher stress. In addition, the shortened cranium and reorientation of muscle fibres more vertically to accommodate this morphological change would create a greater vertical bite force generated from the molars, increasing ability to perform crushing bites. While an aurochs skull was not tested, we can extrapolate some possible interpretations, mainly that shorter and broader skulls might be better suited to dealing with stress.

5.4. Aims and hypotheses.

The purpose of this chapter is to investigate the premise that there is a biomechanical link between biting and cranial morphology in aurochs and domestic cattle. This is suggested to result from the difference in dietary preference indicated through the possible partition in niches and habitats the archaeological record has indicated. Furthermore, the aim is to explore whether over time evolutionary pressure, particularly domestication and human husbandry, influenced feeding ability in cattle enough through differences in skull geometry as seen in Chapter Four. Does cranial geometry relate to how cattle procure food and differences in food sizes, and therefore the bite force needed to break plant material? There are two hypotheses for this chapter:

HYPOTHESES 1: A wild type cranial morphology will be better suited to coping with the more varied and tougher diet necessary to survive year-round. This will be shown by aurochs exhibiting lower stress in FEA when performing the same simulated bite as domestic cattle. Chillingham cattle will be intermediary, being domestic type cattle but with wild ecology.

HYPOTHESIS 2: Domestic cattle will have a poorer feeding performance than aurochs, as domestication and human husbandry has removed evolutionary adaptations necessary for a tougher browser-style diet. This will be shown by a lower predicted biting efficiency (mechanical advantage) in aurochs compared to domestic cattle. Chillingham will have better feeding performance then other domestic cattle due to their unique husbandry.

5.5. Materials and methods.

5.5.1. Sample and model creation.

The cranium of a domestic cattle (*Bos taurus*, project ID 111) from the York Zooarchaeology Laboratory reference collection, was CT scanned at The York Hospital (York, UK). The resulting CT stack had a lattice info of 512 x 512 x 681. A 3D virtual reconstruction of the skull was created in Avizo v9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA), with cranial bone/teeth and horn keratin segmented separately to create a volume and resampled to an isometric voxel dimensions of 0.8 mm. A cranium of an adult female from the Chillingham herd was obtained from the collections of the Chillingham Wild Cattle Park and CT scanned at the University of Liverpool Small Animal Teaching Hospital. Due to the large size of the horns, scanning was undertaken in two orientations and the model was manually segmented in two sections and then merged in Avizo. The first scan had a lattice info of 512 x 512 x 1854 and voxel size of 0.824 x 0.824 x 0.3 mm. The second scan had the same size lattice info but voxel size of 0.976 x 0.976 x 0.3mm. These models were merged, and the voxel dimensions were resampled isometrically to 1.6 mm. Furthermore, the Chillingham cranium was missing several teeth, and to approximate these the closest next tooth was separately segmented and then resized and repositioned to act as a proxy. This recreated an M1 and M2 on the right side from the M3, and a M1 on the left side from the M2. Following this the area around the teeth was re-segmented to ensure no artefacts or gaps. As no aurochs CT scan was available (owing to the difficulty of finding a scanner large enough to accommodate an aurochs skull), the domestic cattle model was warped to conform to the size and shape of an aurochs surface model made at the Natural History Museum London (project ID: 5) using photogrammetry (see Chapter Three for methodology). This was done by placing 129 comparative landmarks on the domestic cattle volume model (figure 5.1) and the aurochs surface model, then performing a Bookstein warp. The accuracy of the warp was tested by performing a GMM analysis identical to Chapter Four but including the 'warped' aurochs' skull, to check it plotted within the aurochs group in shape space but also close to the target surface specimen (figure 5.2). The finished volume models were then saved separately as a bitmap stack and converted into a mesh of eight-noded cubic elements by direct voxel conversion in Vox2Vec.exe (Liu *et al.*, 2012). The resulting finite element models were then loaded into VOX-FE.

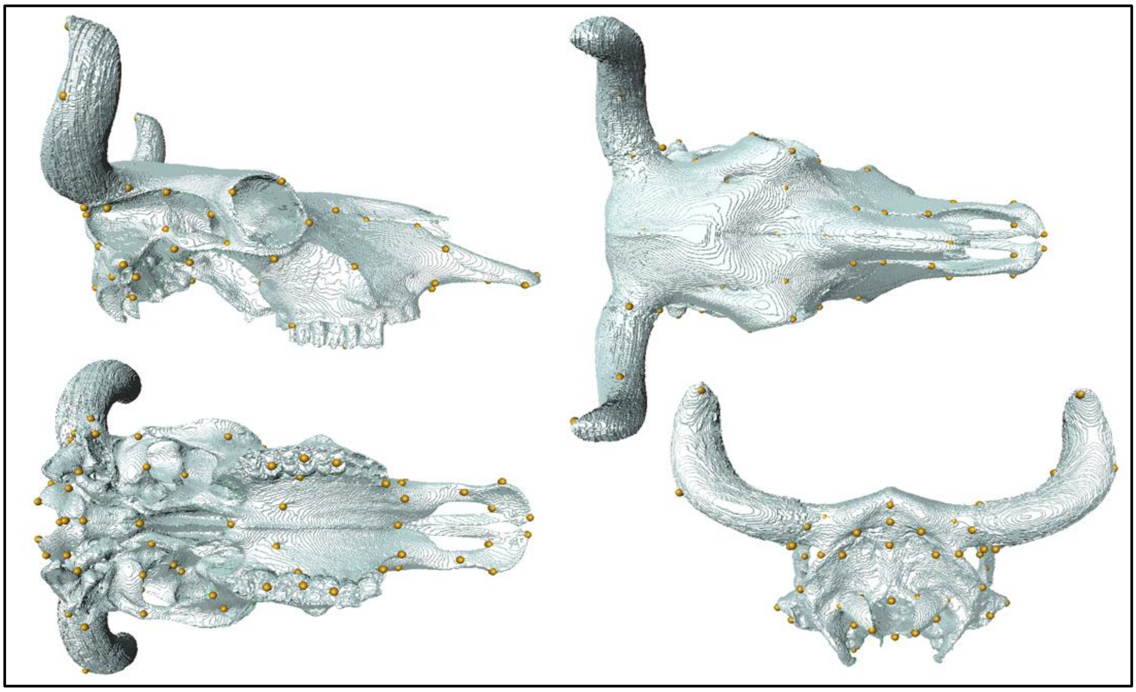


Figure 5.1: Landmarks placed on domestic cattle skull to warp to aurochs' shape.

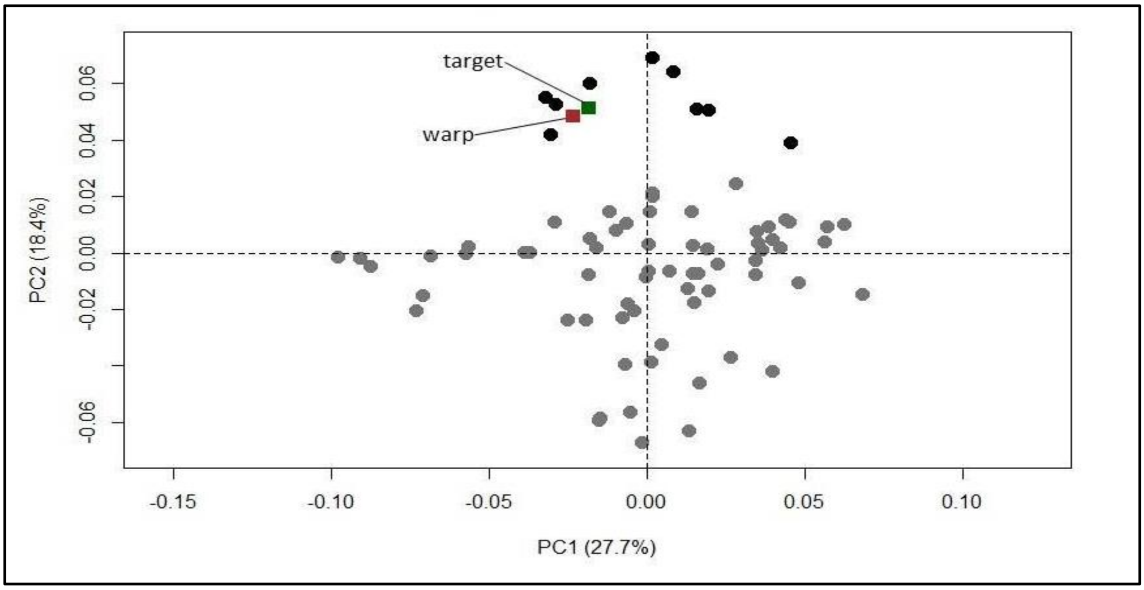


Figure 5.2: PCA showing the warped aurochs (red square) in relation to the target (green square) against the background data of aurochs (black circle) and cattle (grey circle).

5.5.2. Material properties.

In VOX-FE, all models were assigned the same material properties of bone, with a Young's modulus of 17 GPa, assuming that the skulls were composed entirely of cortical bone, and Poisson's ratio of 0.3, both of which lie within the published values (Schwartz-Dabney and Dechow, 2003). Validation for single material models has been well established (Godinho et al., 2017). Indeed, simplification of material properties has been shown to facilitate reconstruction and provide useful results about relative rather than absolute deformation along with a reducing effect on the magnitude of strain (Fitton et al., 2015). This would make models comparable in terms of the stress patterns although the absolute values should be treated with caution.

3.2.3. Forces.

For cattle no absolute masticatory muscle force data (for example *in vivo* measurements) exists so it was necessary to approximate it. The first step in this process was to calculate an approximate body mass for each specimen (aurochs, Chillingham, domestic cattle). Body mass can be approximated from cranial measurements (see table 5.1) using algorithm 4.1 in Mendoza *et al.* (2005):

$$\mathit{Body\ Mass} = 0.736*SUML + 0.606*SUMW + 0.530*MZW + 0.621*PAW + 0.741*SC - 0.157*SD + 0.603$$

Code	Description
SUML	Second upper molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
SUMW	Second upper molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protocone and the paracone
MZW	Muzzle width, measured at the outer junction of the boundary between the maxilla and premaxilla
PAW	Palatal width, measured as the distance between the upper second molars at the level of the protocones
SC	Length of the posterior portion of the skull, measured from the occipital condyles to the posterior border of the last molar
SD	Depth of the face under the orbit, measured from the boundary between premolar and molar tooth rows to the nearest point of the orbit

Table 5.1: Cranial measurements for body mass estimation, based on Mendoza et al. (2005).

Following this algorithm body masses were obtained of 816.823kg for the aurochs, 362.2965kg for domestic cattle and 346.7893kg for Chillingham. These body mass volumes were then used to scale muscle force data based on the dry skull method as introduced by Thomason (1991).

Here data obtained from Veitschegger *et al.* (2018) who used the dry skull method on a Niata specimen to create reference or 'ref' muscle forces (given as; masseter =1434.59g, pterygoid =889.87g and temporalis =957.98g). Similarly, muscle forces for aurochs, domestic cattle and Chillingham were scaled according to body mass, using Niata as given in Veitschegger *et al.* (2018) as the reference specimen.

Muscle forces are derived from physiological cross-sectional areas, whereas body mass is related to volume, so muscle force is proportional to body mass to the two-thirds (⅔) power (Fortuny *et al.,* 2015). The scaling equation (see table 5.2) is therefore:

$$MFtarget = MFreference * (BMtarget/BMref)^{2/3}$$

Code	Description
MFtarget	The muscle force of the target to be calculated
MFreference	The muscle force of the reference specimen
BMtarget	the body mass of the target specimen
BMref	the body mass of the reference specimen

Table 5.2: Codes for muscle forces and body mass, based on Veitschegger et al. (2018).

While this equation creates the closest approximation for cattle muscle forces, it is noted that this may not provide actual accurate muscle forces for each specimen. It does however keep the forces applied consistent so that evaluation of the impact of differences in cranial morphology (rather than size) can be compared consistently.

The muscles added to each of the models in these analyses were the superficial masseter, deep masseter, temporalis, and medial pterygoid. In Veitschegger *et al.* (2018) the masseter was treated as one muscle, but it was decided to model the deep and superficial masseter separately, owing to their distinct lines of action. Therefore, this muscle force was separated into a third for the superficial and two thirds for the deep masseter to approximate appropriate workloads. These forces are displayed in table 5.3.

	Aurochs	Domestic cattle	Chillingham
Deep Masseter	1466.9	853.2	828.6
Superficial Masseter	733.5	426.6	414.3
Medial pterygoid	1364.9	793.8	771.0
Temporalis	1469.4	854.6	830.0

Table 5.3: Estimated muscle forces (in N) for aurochs, Chillingham, and domestic cattle.

The attachment sites of the deep and superficial masseter, temporalis and medial pterygoid were added to each side of the model, using the bovine anatomical atlas (Budras *et al.*, 2003) to guide origin and insertion points. To assist with the orientation of muscle forces/fibres, the head of a Chillingham bull was obtained via a routine autopsy carried out on a single individual of the Chillingham herd annually (as required by DEFRA to check herd health, not specifically for the purposes of this research). Materials were collected on the 22nd of November 2021 with dissection taking place over the two days immediately following. Images can be seen in figure 5.3.

Initially the skin was removed on the left side to reveal the masseter, noting the attachment sites running along the ventral surface of the anterior section of the zygomatic arch (being the deep masseter), and between the orbit and the facial tuberosity (superficial masseter). The masseter was extracted as a single unit and subsequently separated into deep and superficial materials with weights of 165g and 252g respectively. From the muscle fibre orientation, it could be seen that the masseter muscles ran from their attachment sites on the cranium to the angle of the mandible. Following this, skin and small facial/neck muscles were removed to reveal the site of the temporalis. Due to some damage this was removed posterior to anterior, working from undamaged tissue towards more obliterated tissue, and once removed this weighed 143g. Due to damage to the mandible sustained during euthanasia it was difficult to locate exact attachment sites, but the temporalis appeared to wrap around and engulf the coronoid process. The medial pterygoid was significantly damaged and much of the muscle tissue was permeated with blood clots, which made clear extraction difficult. The mandible was fractured and so sections were removed, which allowed a clearer view of the anterior medial pterygoid attachment site. The distal aspect of the medial pterygoid was more uncertain and so estimated based on the more intact muscles surrounding it. When removed it weighed 274g. The attachment site seemed to be on the lingual aspect of the angle of the mandible.

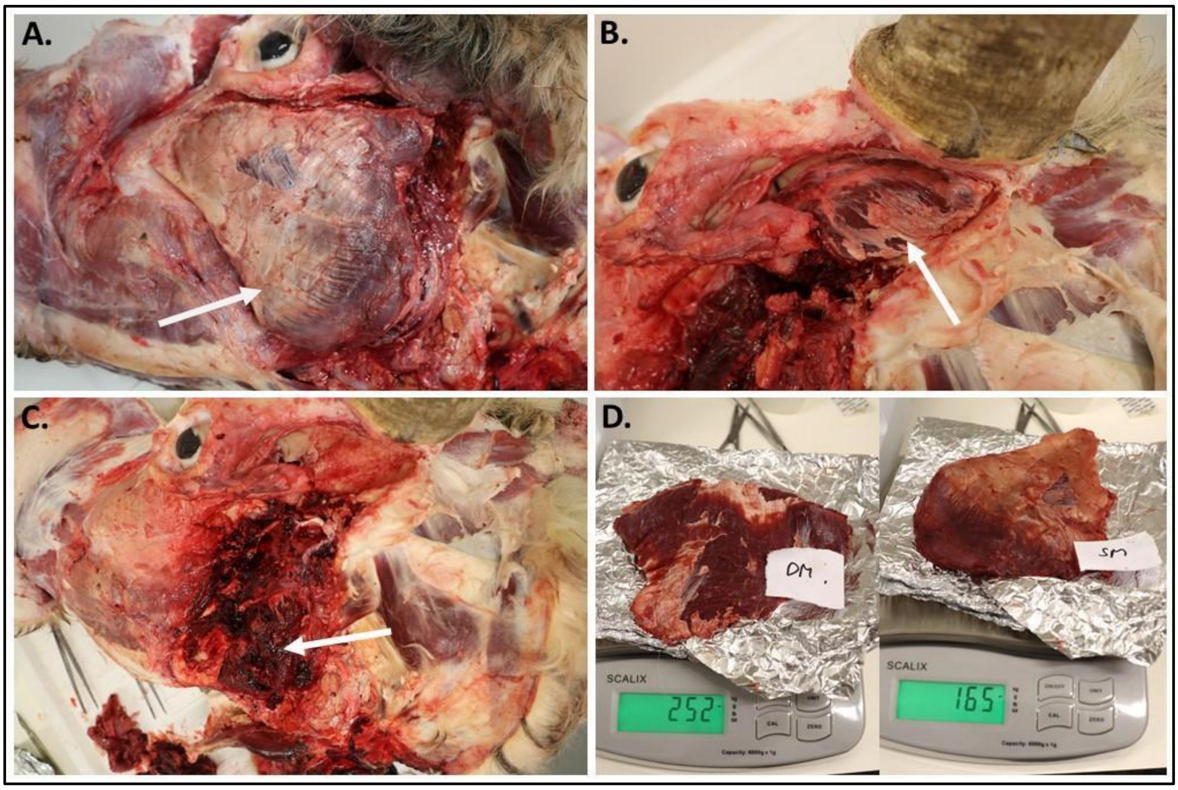


Figure 5.3: Dissection of Chillingham cattle head to show muscle locations. A. Masseter. B. Temporalis. C. Medial Pterygoid. D. Masseter divided into superficial (SM) and deep (DM).

3.2.4. Loading and constraints.

To help standardise repeatability between the muscle fibre orientation and force direction in VOX-FE, a mandible from the York Zooarchaeology reference collection was 3D modelled using Agisoft (see figure 5.4). As this was not the correct corresponding mandible to each specimen, it was aligned and scaled in Avizo using 5 landmarks and a rigid warp with scale. Being a hemi-mandible, it was also mirrored for the left and right side. Onto this mandible landmarks were added for each muscle to denote the central point of attachment site. These landmarks were then exported into VOX-FE and the muscle force vectors were oriented towards the landmarks. At the same time muscle forces were then added to the models from the estimated values, along with constraints at both temporo-mandibular joints in all three dimensions. To simulate two bites, the first molars (M1) were constrained in the orthogonally to the occlusal plane initially on both M1 to give a bilateral bite mid-tooth row, and then the left molar row (MR) only was constrained to simulate a more typical unilateral cattle chew. Once established with muscle forces and constraints, the models were solved by generating the displacement and forces files. These were added to the models in VOX-FE to calculate stress and strain at every element during the simulated bites.

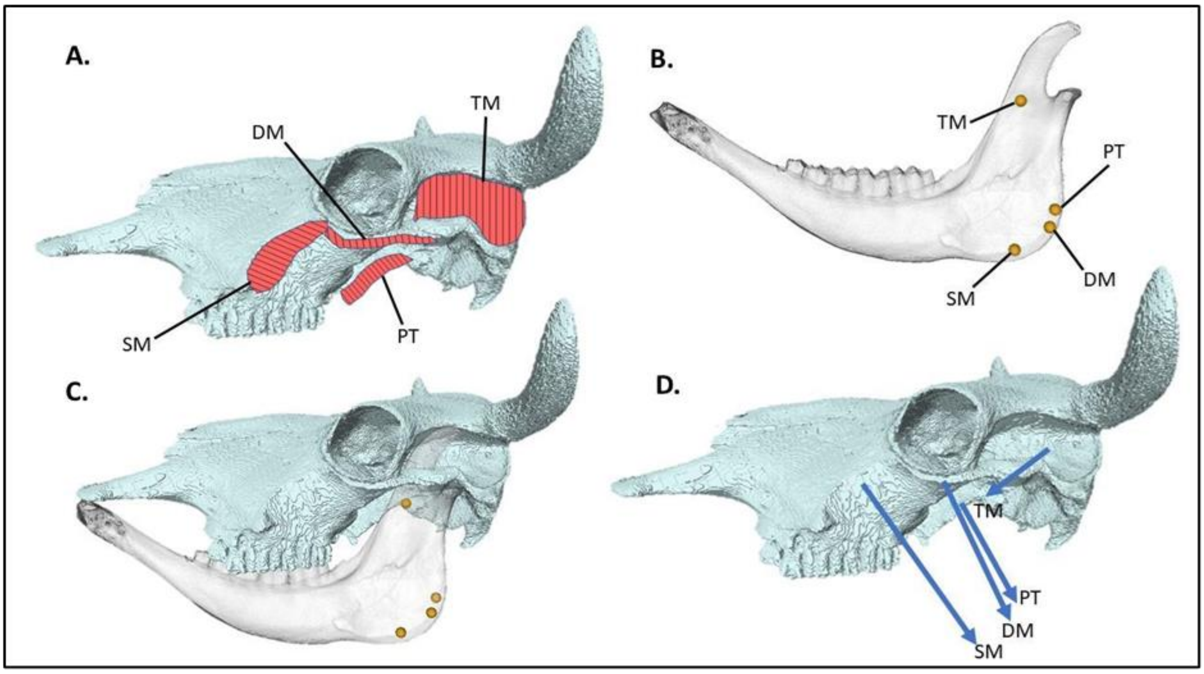


Figure 5.4: A. muscle locations added to FEA models. B. landmarks for muscle insertion on mandible. C. Cranium and mandible in occlusion. D. force directions from origin on cranium to end on mandible. (DM = deep masseter, SM = superficial masseter, TM = temporalis, PT = medial pterygoid).

3.2.5. Analysis.

For interpretation von Mises stress was visually examined, this metric being a combination of the principal stresses useful for indicating which regions of the skull are closer to their safety limit. Bite force and bite efficiency were also calculated. Bite force was calculated from the reaction force data generated in the FEA calculation for the bilateral first molar bite. All the forces from the bite constrained only in the Y axis were added together to produce a maximum muscle activation estimation of bite force. Mechanical efficiency of biting was calculated by dividing the bite force by the total muscle force (all the muscles in the model on both sides added together).

5.6. Results.

5.6.1. Model Deformation.

To assess the initial impact of the bite, model deformation was explored to make a quick assessment of the direction of forces bending the crania (figure 5.5). The visual implications of this were quite plain to see when deformation was exaggerated, with all three models showing a similar deformation pattern. Most notable was a concave bending of the anterior portion of the skull and particularly the stretching of the pterygoid muscle insertion region. The impact of other muscle groups used in this study was less pronounced but some distortion around the orbits, maxilla and zygomatic arch were also observed. This provided reassurance that the muscle forces and particularly directions were acting in a reasonable way.

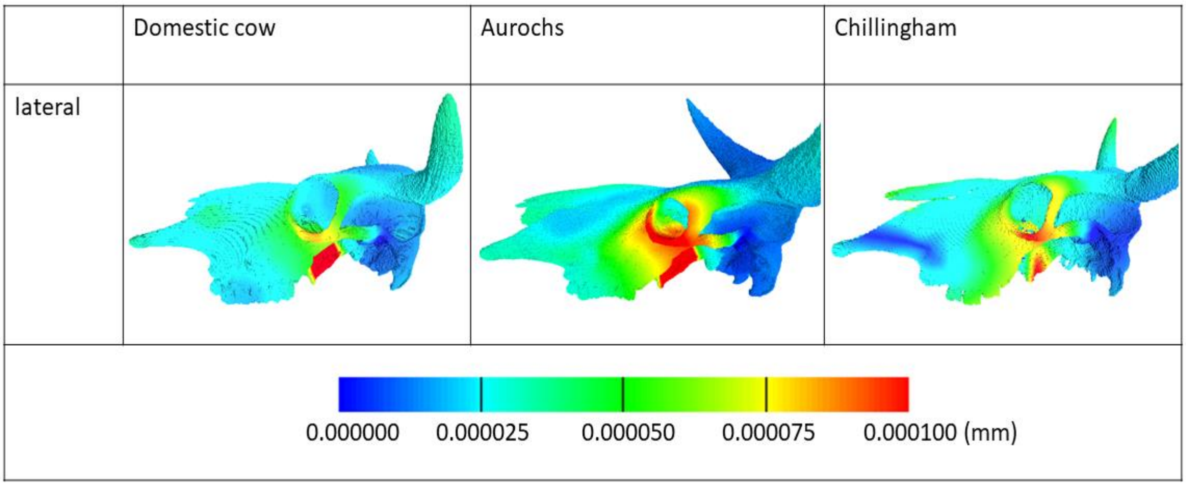


Figure 5.5: Deformations explored in VOX-FE.

5.6.2. Bilateral M1 bite.

A bilateral M1 bite was simulated first with the von Mises Stress examined. The results of this were visually assessed by a side-to-side comparison of the heat maps (figure 5.6), which showed that aurochs exhibited quite similar patterns of stress, but relatively lower magnitude across the cranium when performing the same bite as domestic cattle. This was particularly apparent in the posterior portion of the skull, around the occipital and parietal bones, and to some extent on the frontal bones. Areas of high stress were common to both models, being especially located on the pterygoid and palate bones, the jugal, orbits and zygomatic arch. Areas of higher stress were also seen on the premaxilla, maxilla, and palate of domestic cattle, particularly different from aurochs where stress seemed to be slightly lower. In all cases when performing a bilateral M1 bite both sides of the cranium exhibited a reasonable degree of symmetry.

5.6.3. Unilateral M Row Bite.

The unilateral molar row bite showed asymmetric strains across the cranium as might be expected (figure 5.7). The working side (left) performing the bite resulted in high stresses in the left palate, maxilla and between the orbit and zygomatic march. Stress in the palate was very similar in aurochs and cattle, but patterns around the orbit and zygomatic were more localised in aurochs compared to the widespread distribution seen in domestic cattle. On the balancing (non-loaded) right side of the skull, stress was observed to be more widespread and distributed more distally. High stress was seen in the pterygoid plate, orbit, zygomatic and parietal bones. More generally stress was also seen across the frontal area, not seen to such an extent when performing a bilateral bite. When performing a unilateral bite more torsion was exhibited in the cranium, fitting the pattern of stress seen in these models.

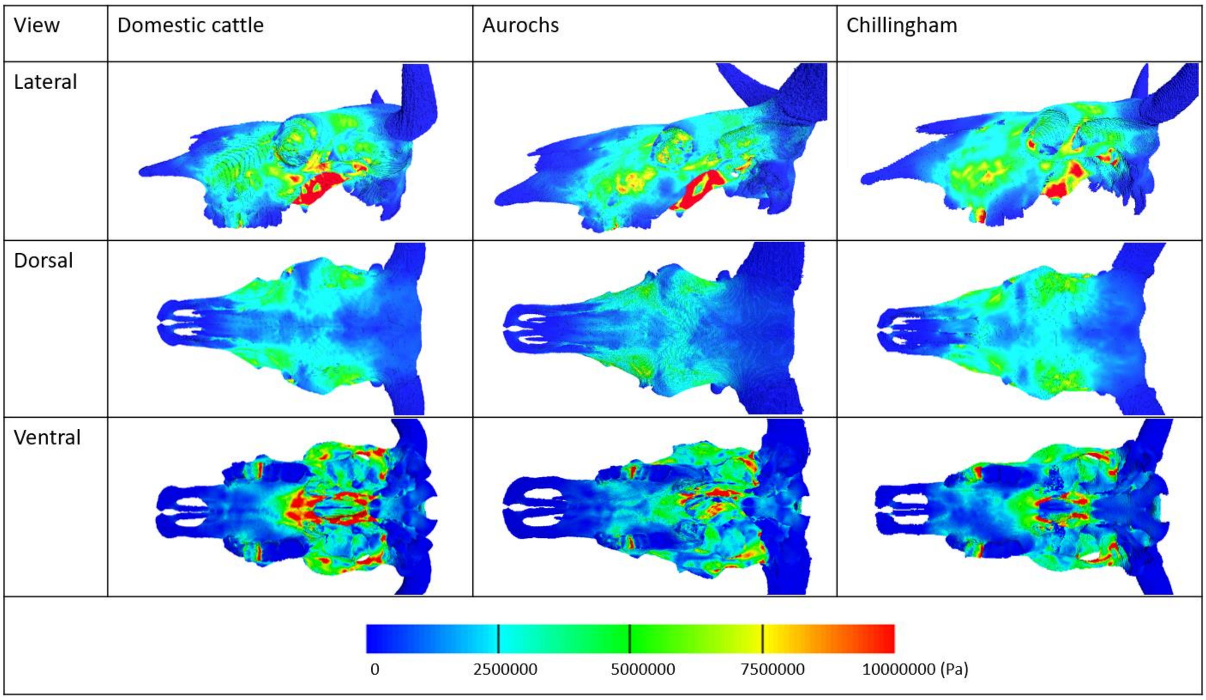


Figure 5.6: von Mises Stress in cranial models during a bilateral M1 bite.

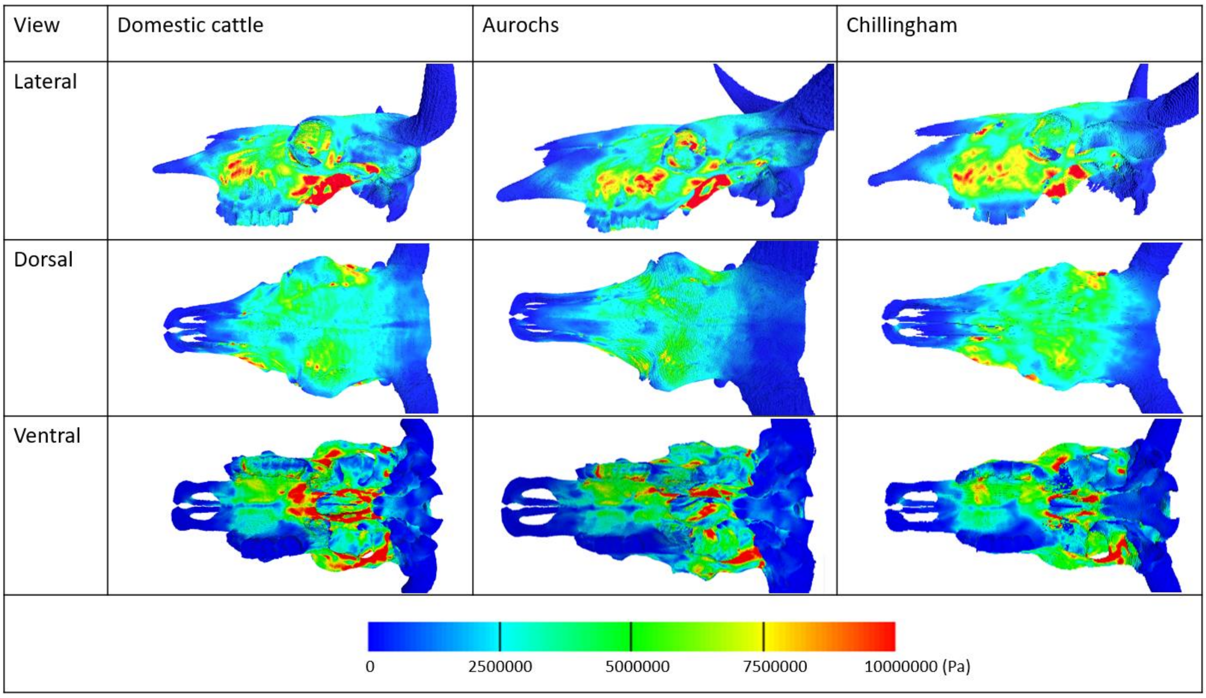


Figure 5.7: von Mises Stress in cranial models during a unilateral molar row bite.

5.6.4. Bite Force Estimation.

Estimated bite force was also calculated from the FEA analysis (table 5.4), indicating the maximum bite force the animal could produce in a single maximal bite. This was calculated at the bilateral M1 bite as an absolute force in newtons and indicated the domestic model at 1785.92N, Chillingham at 1645.49, and the aurochs 3500.53N. From this, the mechanical efficiency was then estimated by dividing the bite forces by the total muscle force in each model. The mechanical efficiency of biting in the domestic cattle was 0.28, Chillingham at 0.31 and for the aurochs 0.34.

	bite force (N)	total muscle force (N)	efficiency of bite
Aurochs	3500.5	10069.3	0.34
Domestic cattle	1645.4	5856.3	0.28
Chillingham	1785.9	5687.9	0.31

Table 5.4: Estimated bite force for all models, the total input muscles forces and mechanical efficiency of biting.

5.7. Discussion.

5.7.1. Are there differences in stress?

The results showed similar patterns of von Mises stress in all models but with some moderate differences. To first consider the bilateral M1 bite, the results showed some interesting patterns in the feeding performance between all models. Initially it was noted that muscle forces acted in similar ways when deforming the models, particularly around the pterygoid plate and posterior portion of the orbit. It was apparent the pterygoid muscle force was instrumental in this deformation and the subsequent stress heat maps. For all models, the heat maps showed stress to be principally present in the maxillary facial and posterior palate regions, posterior of the orbit on the frontal, through the zygomatic region and in the anterior occipital region. This could be related to the specific function of the muscle, pulling the mandibular ramus medially (Tuncer, 2020). The medial pterygoid in combination with the masseter also forms the major supporting muscles of the mandible, connecting at the mandibular angle to provide the power for bite force (Tuncer, 2020). For the specific models, domestic cattle had the highest stress, seen most acutely in the pterygoid region along with the posterior maxilla. The Chillingham model generally had slightly lower stress than the domestic cattle model but did have a more widespread distribution on the frontal and a higher magnitude in the facial/maxilla region. The aurochs model showed the lowest stress, and similarly to the Chillingham cattle the cranial facial/maxillary region was more stressed than seen in the domestic cattle. The von Mises stress patterns were broadly similar between the species in terms of the areas of stress located strongly in the central portions of the crania, with low stress anteriorly and posteriorly. This is as might be expected in closely related species from the same taxa performing a similar bite. However, domesticates did seem to have a higher overall stress pattern distributed symmetrically in the bilateral bite. This is particularly apparent in the ‘hot’ colours seen around the pterygoid plate and around the orbits. Furthermore, a highly strained area was seen in the distal zygomatic arch and TMJ.

The unilateral molar row bite also displayed some similar patterns of stress between species being predominantly focused around the maxilla, frontal and pterygoid/anterior occipital. The pterygoid was an obvious area of stress given the large forces working in this region to balance the hemi-mandibles when performing bites. This might also be because of the thinness of the bone at the medial pterygoid muscle attachment site on the cranium. The medial pterygoid was also the largest muscle by weight (274g), after dividing the masseter into deep (252g) and superficial (165g) portions. However, there were some clear differences to the pattern seen in the bilateral bite. The domestic cattle had the highest stress with the loaded side showing stress more anteriorly in the maxilla. The balancing side showed patterns of high stress from posterior to the orbit, along the zygomatic and across the parietal. In the Chillingham model, stress was noted as being overall slightly lower, but with very high stresses around the pterygoid, anterior frontal, zygomatic/orbit, and maxilla on the loading side and zygomatic/TMJ and posterior frontal on the balancing side. The maxillary/facial region showed a more widespread pattern of stress than the domestic cattle. The aurochs had the lowest stress of all unilateral bite models but exhibited similar patterns with a reduced magnitude. Stresses were highest in the pterygoid and maxillary region on the loaded side and around the zygomatic and TMJ on the balancing side. On the frontal an uneven pattern was seen being higher around the orbit and anterior frontal on the loaded side but located more posterior towards the horn core on the balancing side. A common trend was the highly stressed pterygoid and given that the medial pterygoid is instrumental in balancing lateral mandible action (Grujičić, 2023) this is not surprising. While the bilateral M1 and unilateral molar row did exhibit different stress patterns, they were not considered to be a function of the position of the bite, but rather a factor of loading all on one side or in parallel. The loading side exhibited more stain anteriorly compared to the balancing side shifting this posteriorly. This pattern of loading has been seen in other FEA studies (Dumont *et al.*, 2005), explained by the torsion created by the cranium bending and resisting such forces.

The patterns of stress and strain were similar in location across all the models, but the magnitude seemed to be lowest in aurochs, then Chillingham cattle, and highest in domestic cattle. As little work has been undertaken on biting in larger herbivores, wider comparison here is difficult but some general principles from other species apply. Mechanical studies have reiterated the link between bite force production and specific morphological features related to diet (Maestri *et al.*, 2016). It has been established that morphological shape reflects the "frequency and magnitude of muscle activation, bite force, and the properties of the food ingested, while ensuring structural integrity under all loads without dissipation or failure"

(Zhou *et al.*, 2019, p.2). So it is possible that aurochs skull morphology is simply better adapted to deal with stress and strain while biting. Or rather, changes in the crania resultant from domestication weakened the domestic cattle's ability to resist strain. This is an interesting pattern as aurochs' skulls were considered less robust in morphology from the shape analysis undertaken in the previous chapter, being longer and more slender. The pattern is also interesting when considering Chillingham cattle, as they are domestic cattle (*Bos taurus*) that have been rewilded over hundreds of years. This might suggest that diet and particularly a wide-ranging diet might be an important driver of cattle cranial shape. It has been suggested that different modes of specialisation to feeding have resulted in relatively stiffer bone structures. From FEA on mandibles of Perissodactyla and Artiodactyla (Zhou *et al.*, 2019), general browsers were shown to have stiffer mandibles than grazers and mixed feeders, while more specialist browsers were the least rigid. This could somewhat apply to the observations in aurochs, suggested to occupy a niche between general browsers and grazers. While cattle have become grazers and mixed feeders, this difference in dietary preference could explain the rigidity seen in aurochs compared to domestic descendants. As cattle are thought to derive from aurochs, any changes observed can be assumed to be related to the domestication process and the possible differences in diet created by husbandry.

The results seen in this study are also somewhat different to those seen in similar FEA research focused on cattle, specifically the result of extreme brachycephaly. It was suggested that the shortening of the craniofacial region resulted in a lowering of magnitudes of stress (Veitschegger *et al.*, 2018). This included the converse conclusion that a lengthening of the rostrum would result in greater magnitudes of stress particularly in the orbital and supraorbital region. The unique morphology of Niata cattle was interpreted to reorientate the muscles vertically increasing bite force and improving crushing ability (Veitschegger *et al.*, 2018). It therefore seems the Niata cattle had a unique advantage that allowed them to overcome any disadvantage of having brachycephalic features. Indeed, it was suggested as skulls get longer strains increase because of the cantilever effect with the bite point getting further from the temporomandibular joint (TMJ), creating more bending moment. In contrast, this chapter suggests that wild cattle, especially aurochs, had lower stresses, contrary to the suggestion that a longer rostrum increases the magnitudes of stress. This could be related to how skulls change shape, for example increased bending moment is only true if the middle of the skull lengthens so that the M1 is pulled away from the TMJ. If the anterior part of the rostrum extends, but the region from the tooth row to TMJ stays in proportion, then the overall stress remains similar. Under this scenario, it is even conceivable that stress in the model would decrease due to a larger unstressed region at the front of the skull. Aside from this, other factors could give aurochs models lower stresses, the bone could be more robust (thicker) which would give proportionally more bone volume for the muscle force to act on, leading to lower stress. It is possible that this is even related to size, domestication, and diet, in that the more robust aurochs have been domesticated, with domestic cattle and given a less tough diet resulting in less vigorous chewing, stress and strains in masticatory related bones is reduced, and by Wolff's Law bone is resorbed. When we apply proportionally scaled bite forces in FEA, the domestic cattle exhibits greater stresses compared to the aurochs. While this is very speculative, a similar pattern was also seen in Chillingham cattle, differences in magnitude of stress might be resultant from husbandry trajectory and the intensity of breeding (in relation to food choice), reflecting in the cranial masticatory morphology.

To summarise, wild forms of cattle and particularly aurochs seem better able to resist forces when biting, at least to a moderate extent. The pattern of stress was more generalised than seen in previous studies; in Veitschegger *et al.* (2018), strain although present in the anterior and posterior cranial regions, was more localised to the orbits and zygomatic arch. Furthermore, the interpretation of these results suggested shortening of the cranio-facial region. Beam theory was used to explain the advantage of Niata cattle; “that under adduction of the jaws during biting, the rostrum will behave as a cantilevered beam” (Veitschegger *et al.*, 2018, p.9). While this may have been advantageous in terms of the biomechanics of resisting strain and possibly producing relatively higher bite force, it seems to contrast with the aurochs results found in this research. In larger animals, such as aurochs, higher strain by having a longer rostrum might be overcome by the muscle location, bite location relative to the TMJ, force, and mechanical advantage. The specific morphology of the mandibles rather than the crania may also be more diagnostic of mechanical advantage, as the lengthened ramus as seen in aurochs would be thought to improve lever arm mechanics. In addition to this, the function of various parts of the cranium should also be considered when interpreting these results, as regions often exhibiting high strains (such as the orbitals) are more associated with sensory organ protection than masticatory apparatus.

5.7.2. Why are there differences in bite force?

As well as the variation in stress, there were marked discrepancies in bite force between aurochs and cattle. Bite force is often seen as a holistic measure for feeding performance, resulting from both cranial morphology and muscle orientation. In bite force alone, aurochs were estimated to produce a bite approximately double that of domestic cattle, around 3500N and 1645N respectively. This large difference is likely a product of size, with the larger aurochs simply having bigger muscles capable of producing more force, as exemplified by the estimated body masses of the animals used in initial muscle force calculations (aurochs 816kg, cattle 362kg). The Chillingham cattle had a slightly higher bite force than domestic cattle at 1785N despite having lower total muscle forces and being of approximately a similar size. Larger animals with bigger muscles have increased bite force. However, it has been noted that overall body and head size are not always directly related to diet, but longer in-levers are generally associated with tougher diets (Tan et al, 2021). The higher bite forces in Chillingham cattle suggest that their distinctive morphology provides greater mechanical advantage relative to domestic cattle.

When these forces were converted to mechanical efficiency of biting, aurochs were more efficient than domesticates. Chillingham cattle were also more efficient than their domestic counterparts, further suggesting a wild-type morphology is more advantageous in converting muscle force into an effective bite. As biting efficiency is a ratio, it can be inferred that these differences result from the shape of the crania and the orientation of the muscle force vectors, as shown particularly between domestic cattle and Chillingham cattle. However, while the relative pattern of results between specimens seems representative, the absolute bite forces may be overestimations as these models also assume that muscle activation is at full capacity when performing the simulated bites. This was exemplified by the high bite forces estimated, exceeding that of some carnivores. In herbivores, such as domestic cattle, this is very unlikely to be the case and the large muscle sizes are more likely needed for repetitive chewing rather than large force generation. All stresses experienced at muscle attachment sites would therefore be greatly reduced if it were possible to simulate a bite using an average domestic cattle bite. As there is limited published data on *in vivo* bite force in cattle, or other ungulates, the exact relationship between actual bite force and cranial stress remains hypothetical. It therefore seems there is great scope for in vivo work, obtaining EMG data on muscle activations during chewing in cattle, something seemingly not previously undertaken.

The relationship between bite force, size, and shape of the mandible in relation to ingesta has been studied previously in several mammalian clades including Artiodactyla. Morphologically, cattle have evolved to be highly adapted to the specialist type of diets based predominantly around grazing, although not exclusively. Such adaptation and selection for different food sources, particularly grazing softer leaves with less physical resistance, has undoubtedly altered cranial morphology associated with feeding mechanics, seen most notably as loss of upper incisors in cattle, including aurochs and other bovids (Hongo and Akimoto, 2003). During grazing, there is a non-constant food density and even variation in bite area and depth, which will lead to fluctuation in chewing mechanics. Depending on the volume of intake and its toughness, this will give varied amounts of resistance, constantly requiring adjustments in force required to break down plant material. This force could be low if only a few stems of fresh grass are bitten but would need to be considerably higher if browsing tree matter or acorns. This is further compounded by the digestive method of rumination and chewing the cud for long periods of time to extract maximum nutrients. Unfortunately, precise force data is not available for such variable feeding behaviour in cattle so it may be better to think of this in terms of bite energy (Wight and Illius, 1995).

Cattle do not perform maximum force bites but rather undertake repetitive chewing and so large muscles are a factor in resisting fatigue while chewing. The tougher the material the more fracture resistant it will be and therefore the more energy required to break it down (Sanson, 2006). In studies of cattle chewing frequency in relation to herbage density, it has been shown that in high density herbage, cattle perform significantly more bites in a day (Alvarez-Hess *et al.*, 2021). It has also been noted that it is therefore more efficient for cattle to select soft materials requiring low bite forces (Illius and Jessop, 1996). This is combined with avoiding tough plant material due to the increased cost in time and energy to extract low nutritional value reward (Hongo and Akimoto, 2003) and also longer rumination time (Poppi *et al.*, 1980; Janis 1976). This might particularly relate to wild cattle that have to procure their own food and are not fed any supplementary feed, so could potentially explain the more efficient bites seen in Chillingham cattle and particularly aurochs.

As aurochs and Chillingham cattle have a greater efficiency of biting, this might relate to lowering the energy expended in chewing to fracture foods. Bite energy can be maintained for longer periods of time and used to exploit more readily tougher plant materials, without sacrificing longer chewing and digestion and rumination times. It has been suggested that in ruminant Artiodactyla, reduced mechanical effort is needed in initial food processing, regardless of toughness of material ingested (Zhou *et al.*, 2019). Rumination allows a softening and rehydration of food, and an internal sorting of ingested material in the rumen to help remove hard substances from food. By splitting mastication into several cycles, this also reduces the masticatory load and mechanical demand, allowing a more roughly chewed food to be utilised (Zhou *et al.*, 2019). These adaptations would greatly reduce the necessity of high bite forces upon initial ingestion and relieve biomechanical demands and muscle fatigue.

In relation to cranial morphology seen in Chapter Four, aurochs were shown to have a distinctive cranial shape different from domestic cattle. Chillingham cattle were also shown to form a small group within the wider domestic cattle morphospace. Feeding and procurement of food could be related to, and a driver for, the morphologies seen, as wild species seemed to have more closely related cranial shapes. This could be due to the need, or ability, to produce higher bite force to take advantage of a wider range of tougher and more fibrous foods. In general, the greater the force required to fracture ingesta, and the more repeatedly such forces need to be produced, and the stiffer the bones must be to maintain structural integrity. Not only this, but aurochs also have an increased efficacy compared to their domestic counterparts so would be better adapted to break down plant materials in the mastication process.

5.7.3. Diets in aurochs and cattle and the relation to human husbandry.

From the results in this chapter, there are visible differences in the masticatory biomechanics in aurochs, Chillingham cattle and domestic cattle. As noted, the physical properties of foods have an important role in the development of cranial morphology. This principle has been noted in numerous diverse species with hard and soft diets being used to assess the result on anatomy (Law *et al.*, 2022; DeSantis *et al.*, 2020; Katz *et al.*, 2017; Santana *et al.*, 2012; Byron, 2009; Lieberman *et al*., 2004). It was interesting to note that cranial morphological differences seemed to be because of wild and domestic husbandry status, although in the case of the Chillingham cattle this is more complex. In general terms, wild cattle seem more able to resist stresses resulting from feeding processes. As already shown earlier in this chapter, extrapolating the diet of even extant cattle is difficult as it is highly varied. However, the results seem to indicate there are differences in mechanical advantage between aurochs and domesticates, and we can suggest this might be a result from diet and the domestication and evolution of domestic cattle. Generally, humans will both restrict the foods cattle have access to but also provide for them in winter to ensure cattle always have enough feed. This would create very different selection pressures on domestic cattle compared to those in the wild.

For modern domesticates, a lower bite force and mechanical efficiency of biting could result from two factors: domestication changing cranial shape via artificial selection and altering biting morphology, but also adaptation to a different diet. Diets vary greatly but generally comprise ‘forage’ or material eaten while grazing (grasses and leaves) and concentrates including grains, beans, and meal (Kavanagh, 2016). The exact amounts of various feeds have been extensively studied in animal sciences, mostly regarding dairy cattle and maximising milk production (Reist *et al.*, 2003). When presented with choices, cattle have shown a preference for mixed diets of various herbage and grasses but also legumes (Rutter, 2006); however preferred diet and that which is actively selected (or provided by humans) can be different, based on access and location, and probably most importantly in modern agriculture cost. It may be that diets are more closely monitored, and that necessary vitamins and minerals are supplied, so it is possible that domestic cattle have a better diet but also one that is readily supplied for them without the need for extensive foraging. The possibility of aurochs being better able to cope with stress, but also to generate higher bite force and mechanical efficiency of biting, might relate to their specific morphology and ecology. The diet of aurochs is more difficult to ascertain being an extinct species, but as previously discussed this has been contextualised through various sources of archaeological data. While this has already been explored previously in more detail in this chapter, it can be summarised to wetlands, open grassland and forests (Lynch *et al.*, 2008; Schnyder *et al.*, 2006; van Vuure, 2005).

The variation in the habitat suggested for aurochs perhaps provides an understanding of their mastication, their adaptability, and their long temporal chronology coupled with diverse spatial distribution of the species. Also, the impact of ever-increasing human expansion and colonisation of the landscape likely forced aurochs to move into less natural ranges (Kerley *et al.*, 2012). This, however, was probably advantageous to domestic cattle, increasing their available feeding range. As noted for aurochs, most of the suggested environments tend to comprise predominantly of harder and tougher herbaceous material and twigs. This would be the sedges, hardy grasses and reeds found near water and the woody plant matter of trees. If aurochs had diets high in these sorts of fibrous materials, it would certainly explain the stress resistance and greater mechanical advantage of biting seen in the results presented here. A higher bite force would be advantageous in processing tougher materials like branches, herbaceous plants, and other forage and increased biting efficiency would be important for the repetitive chewing that would be needed to process these tough foods. In addition, these natural foraged food sources are often more depleted in nutrients (O'Regan and Kitchener, 2005). Such foods also tend to contain higher quantities of abrasive particles, like sand, grit and phytoliths, that are necessary for wearing herbivore dentition at a normal rate and preventing abnormal tooth conditions (O'Regan and Kitchener, 2005). The impact of tough diets has been well documented (Menegaz *et al.*, 2010), particularly its importance in early life as skeletal morphology is developed (Ohlsson and Smith, 2001; Guthrie, 1984). If aurochs were living under such conditions, it would be difficult to distinguish a morphology perpetuated by feeding adaptation or environmental impact as they would be so closely linked, either way being suited to intake of tough fibrous plant materials.

Chillingham cattle provide a unique perspective being domestic cattle (*Bos taurus*) that have become feral or rewilded and survived several genetic bottlenecks in the wild. This creates the possibility that any morphological and therefore biomechanical differences are related, not only to their environment, but also genetic drivers. The uniqueness of Chillingham cattle has been well documented, being genetically homogeneous (Williams *et al.*, 2016; Hudson *et al.*, 2012). This also provides insight into their morphology, as they are essentially domestic cattle under free living conditions with autonomy regarding food choice. While the cranial morphology of Chillingham cattle is by no means the same as aurochs, the results here show them to have more resistance to stresses resulting from feeding than those seen in domestic cattle. As shown in field studies, Chillingham cattle do seek out certain types of food at different times of year (Hall, 1989), and are not always given the best food sources as in farmed domestic cattle. In comparisons of wild and captive animals, at least some of the differences compared to wild versions are related to the masticatory apparatus, and this could be related to the different mechanical properties of wild vs captive diets (McPhee, 2004). In terms of nutritional ecology, it is known that for wild mammals, diet changes through time and by necessity of location, with animals having to overcome seasonal variations by having a broad diet or migrating (Sanson, 2006). Chillingham cattle are an ideal control as they highlight the potential changes and differences between farm diets and wild diets in the same species, with differing evolutionary trajectories. It therefore seems very possible that, given the differences in cranial performance, diet is a factor in driving skull shape. The more nutritious and supplemented diet of farmed domestic cattle requires less biomechanical load, compared to Chillingham. While domestic traits, such as overall cranial morphology, persist in Chillingham cattle, as shown by the GMM study in Chapter Four, they also exhibit some wild characteristics, especially related to function, as shown by the FEA in this chapter.

In previous chapters it has been shown that morphological variation is apparent, with aurochs having a distinct cranial shape from their latter-day descendants. We are interested in how morphology and diet interact, and this has been well investigated. Many aspects of the results seen in aurochs and cattle are consistent with other species, in which similar research has been undertaken. The impact of feeding on the masticatory system and indeed cranial morphology generally seems well-established, particularly given the previous research on wild and captive animals of other species. In analysis of various zoo populations there seems to be a general trend that captive individuals have an altered cranial and mandibular morphology to wild counterparts (Crates *et al.*, 2023; Hartstone-Rose *et al.*, 2014; Groves, 1966). This has manifested as wider and broader crania and a change in mandibular angle in captives, remarkably similar to features seen in the shape analysis of domestic cattle in Chapter Four. However, while it seems the different foods could be a driver of morphological differences in cattle through their mechanical properties, it is uncertain to what extent other domestication traits have altered morphology inadvertently. The lack of competition in farmed species has been noted to change cranial morphology, including reduced sexual dimorphism (Lynch and Hayden, 1995), and even to alter the robustness of postcranial skeletal elements (Zohary *et al.*, 1998). Furthermore, adaptive changes seem to be able to occur rapidly with observable differences as seen between founder populations of American mink and their descendants after only c.40 years from being introduced into a new environment (Ulevièius *et al.*, 2001). The impact of any changes that occur can be reduced, however, in highly managed farmed species of cattle with changes to human husbandry and feeding practices. Indeed relaxation, or control of, breeding practices seen in domestic cattle could be one of the quickest ways to induce morphological change introducing features not typically seen in wild populations where the stronger males would control breeding. Humans can choose to positively select for traits that would not be naturally selected for (O'Regan and Kitchener, 2005). This was almost certainly the case with size and colour of cattle and may have introduced traits and indeed less advantageous adaptations at a much faster rate than would be possible in the wild.

5.7.4. Recommendations for further research.

This chapter while generating important results in terms of cattle feeding biomechanics has some limitations regarding the methodology. Specifically, there are three points that need addressing: (1) muscle data, (2) loading scenario; and (3) the significance of the results. All points are important in the interpretation of data and indeed the outcomes that can be deduced.

It has been mentioned previously in this chapter that muscle data (mass or force) pertaining to cattle is not readily available. After a review of available literature, it was clear that there were few examples of any specific values. In the rare case when muscle forces were stated, this was based on estimating the volume from cranial measurements (Veitschegger *et al.*, 2018), as done in this study. Here we based our estimation for muscle calculation by using equations and values given for Niata cattle. As Niata cattle have shown to be unique in terms of cattle morphology, it is uncertain how representative muscle data from this source can be. Related to this are muscle insertion and attachment points on the cranium and mandible. There is some veterinary guidance but not of the precision desired. The dissection of the Chillingham head has greatly augmented this area especially with regard to knowledge about muscle attachment points, orientation and mass. Dissection gave practical experience to the operator, but again there was some uncertainty due to tissue being damaged in some areas, meaning exact muscle insertions could not always be identified. Muscle mass estimation also still relies on imposition of data from domestic cattle to aurochs as it is obviously impossible to dissect an aurochs for species specific muscle data. It is hoped that future research can develop this by further dissections of less damaged specimens, augmented with muscle fibre length data to generate more accurate muscle masses and forces for Chillingham and domestic cattle. The topic of cattle mastication and muscle anatomy is generally an under-researched area, so any development would be a useful addition to the body of scientific knowledge, even in ungulates more generally. A limitation of the finite element method is that, as a static loading technique, it can only model a single bite happening at the moment of occlusion between tooth and food item. However, cattle process their food via low energy repetitive chewing, and so cattle feeding might be more accurately modelled using dynamic modelling (e.g., multibody dynamics analysis).

In terms of the significance of the results, while differences in patterns and magnitudes of stress were noted along with a large variation in estimated bite force, it remains unclear if these differences would have been problematic to cattle or significantly impacted feeding performance. For this study, the above points were minimised as realistic forces are not considered necessary, as we are simply comparing potential performance of the skull between wild and domestic cattle. Input parameters were kept consistent by scaling forces to body size and applying them in the same way to each model. Thus, any differences are a result of variation in cranial morphology. Similarly, although a single vertical bite does not represent the full range of cattle masticatory behaviour, by standardising the loading scenario, the analyses here were able to investigate the relative performance of the crania. In terms of the significance of the results, given that cattle feeding consists of repetitive chewing over a long time period, any reduction in stress is likely to be advantageous as its effect will be felt with every repetition of the chewing cycle. Similarly, small increases in mechanical efficiency will produce large reductions in the necessary input muscle force over a long period of mastication.

5.8. Conclusion.

This chapter investigated the differences between aurochs and cattle with regards to the specific difference in cranial morphology and how these impact feeding performance. Of the two hypotheses tested, both were shown to be supported by the results presented here. FEA showed wild cranial morphologies to be more able to cope with the stresses associated with a bilateral M1 and unilateral molar row bite. This was likely related to wild cattle being better adapted to take advantage of most plants with an increased feed range. This was reinforced through the differences in bite forces and mechanical efficiency of biting. The bite force of wild cattle, particularly aurochs, greatly exceeded that of domestic cattle and had higher efficiency due to their proposed ecology of having to forage and process a wider range of food materials more regularly. Human husbandry appears to have adapted domestic cattle to a different niche, particularly grazing softer leaves with less physical resistance. It should be noted that any causality is difficult to assign confidently, especially regarding which factors develop initially. Did humans select for a different cranial morphology which has reduced feeding performance, or did the less mechanically resistant food provided by humans drive remodelling of the skull? It seems that both could provide an equally valid reason and could occur simultaneously. It therefore seems domestication has an impact on feeding biomechanics as well as cranial shape.

6. Chapter Six: Horns and Morphology.

6.1. Introduction.

This chapter investigates another specific area of aurochs and cattle, and like the preceding chapter, explores the relationship between cranial form and functional demands of horns. The purpose it to establish a possible biomechanical and morphological link, rather than propose a method for the wide scale investigation of archaeological material. Horns can best be described as pointed projections found on the head of some animals. They are permanent structures and thus distinct from antlers which are shed and regrow periodically. Horns are found mainly in ruminant artiodactyls and are present in males of all species of Bovidae, with some females also bearing them (Castelló, 2016). In Bovidae, the horns are a composite of two parts, with an inner bone core wrapped by a keratin sheath joined with connective tissue (Zhu *et al.*, 2016; Bragulla and Homberger, 2009). The full nature of horns, their uses, and importance has not been previously investigated in its entirety, and their purpose seems to be wide ranging (Stankowich, 2011). Horns seem to take many shapes and orientations, fluctuating in size greatly between bovids and within specific species (Hall, 2005). In *Bos taurus*, the domestic cattle, horns are present in many breeds, and in their progenitor the aurochs. Through time and with the advent of domestic cattle breeds, the range of horn sizes and shapes has varied significantly, expanding far beyond that seen in wild cattle species. Domestication of horned bovids, particularly selective breeding but also other human activity such as hunting, seems to have placed a strong selection pressure on horns (Guo *et al.*, 2021; Pigeon *et al.*, 2016), seemingly in opposing directions depending on the breed. In some cattle the emphasis has been on removing horns, genetically through breeding selection or artificially through polling. In other breeds, horns form an integral part of what constitutes the characteristics of cattle typology, arising as the product of highly meticulous positive selective breeding (Bartosiewicz, 2006).

Research into horns has established their significance to the living animal (e.g. Algra *et al.*, 2023; Douhard *et al.*, 2020; Nasoori, 2020; Knierim *et al.*, 2015; Bonenfant *et al.*, 2009; Stankowich and Caro, 2009; Loehr *et al.*, 2007; Coltman *et al.*, 2002; Janis, 1982), but thus far there has been little exploration of the impact of horns on cranial morphology. In particular, research is lacking in how the skull adapts to the size or orientation of the horns and the pressure this places on bones of the cranium. Horns grow from, and are fused to, the cranium, so it is reasonable to suspect their size, orientation, and use would greatly influence their attachment site. Indeed, more generally it is well established that bone tissue responds to increased loads and strain within the lifetime of the individual, via bone remodelling (Wippert *et al.*, 2017). It is possible this is the case regarding horns, with horns themselves being remodelled but also contributing to the loading environment that can lead to bone remodelling in the cranium. In living bones, the mechanical load is constantly assessed, and adaptations made in response to increasing or decreasing strain (Haelterman and Lim, 2019). Remodelling is facilitated by bone resorbing osteoclasts and bone forming osteoblasts that remove fatigue related damage and allow adaptation of the bone mass and structure in a net gain or loss of bone (Klein-Nulend *et al.*, 2012). In regions of high strain bone deposition can strengthen the overall structure, while areas in low strain will experience resorption (You *et al.*, 2008; Vezerides *et al.*, 2006). Thus, via this process, bone reacts to the loading regime placed upon it. This could have significant implications for the evolution and development of horned cattle, and their ability to support headgear (an umbrella term for head protrusions including horns, antlers etc.) of varying sizes. The implications of large headgear include an increasingly robust cranium to support the associated weight of highly developed horns. This chapter considers the implications of horn size on the cranium along with their functionality, and the ability of the cranium to resist stresses resulting from horns.

6.2. Development and structure of horns.

In general terms, mammalian horns are extra-skeletal bony structures that grow from the dermal tissue on the cranium, permanently living and developing with the animal (Nasoori, 2020). For domestic cattle, the horn bud develops in the skin during the first two months of gestation (Wiener *et al.*, 2015). Pre-birth, the area of horn growth thickens, and nerve bundles appear in the dermis, although there is no ossification at this stage (Li *et al*, 2018). After birth, the horn buds continually develop with no connection to the frontal bone and seem to initially develop independently from underlying skeletal material (Nasoori, 2020). From two months old, the buds attach to the periosteum of the frontal bone and the horn begins to grow and ossifies. Around six months old, the frontal sinus connects with the horncore and extends into the horn for three to four years of growth (Reese *et al.*, 2007). The bone cores of the horn are supplied with blood from vessels and nerves, growing throughout the animal's life. As cattle continue to age, the sinuses extend deeper into the horncores, in a process known as pneumatization. In a fully adult animal, the sinus cavity fills the entire centre of the horncore, linking it to sinuses in the frontal cavity. It is uncertain when development of the core is complete. There are suggestions that pneumatization of the sinuses removes unnecessary bone that is non-structural, which reduces weight and optimised cranial architecture (Farke, 2010, 2008; Preuschoft *et al.*, 2002).

Around the horn is a covering of thick keratin that grows from a thick layer of germinative epithelium (Parsons and Jensen, 2006; Habel and Budras, 2003; O'Gara and Matson, 1975). It is attached to the bony horncore with longitudinal furrows, ensuring a large surface area over which to firmly attach the keratin to the core, through layers of skin and the corneum (see figure 6.1). In the horn region, the skin is highly specialised to produce dense horny tubules. Keratinization continues during the animal's development, growing into varying shapes, but the sheath is never usually shed (Janis and Scott, 1987). The keratin sheath is non-uniform in thickness along the length of the horn. At the base, closest to the skull and youngest point of growth, the keratin is thinnest and often roughest (Liu *et al.*, 2018). Here, the keratin sheath is marked with rings thought to be influenced by environmental stress (Castelló, 2016). Towards the end (tip) of the horn sheath, the final element of the horn has no bony core and is exclusively formed of thick and compact keratin.

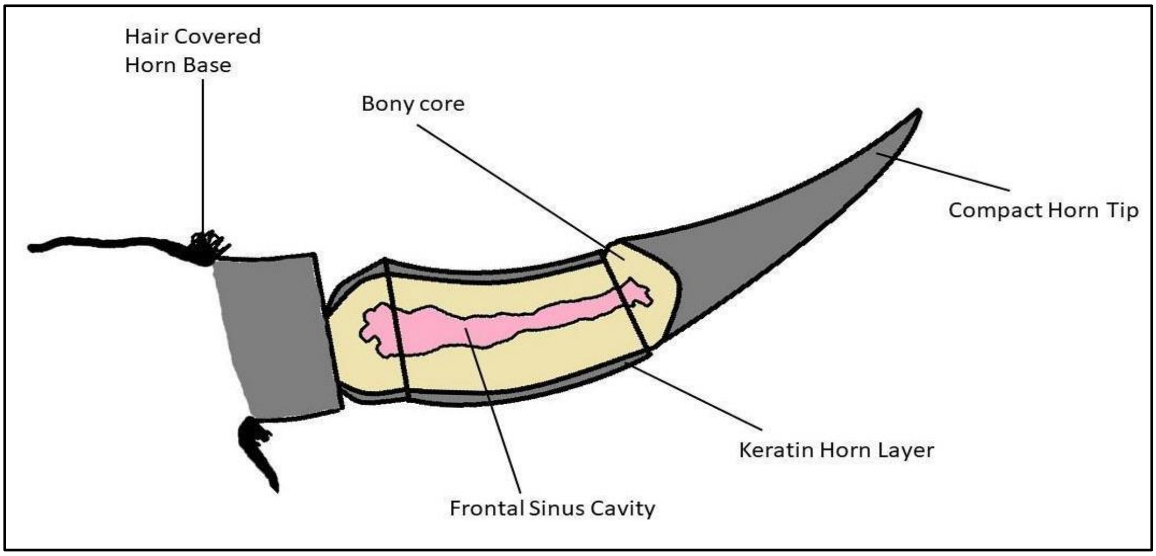


Figure 6.1: The basic structure of cattle horns.

Aside from the developmental growth of horns, the material and physical properties are also important in understanding horns. This starts with the structure of the horncore, comprised of trabecular bone (Drake *et al.*, 2016; Zhu *et al.*, 2016; Li *et al.*, 2011; Maity and Tekalur, 2011) of an approximate density of 0.9 g/cm^3 (Yu *et al.*, 2014). However, the horn also has a gradient of sponginess, from proximal to the distal end. This variation provides increased mechanical resistance through its porosity at the base, compared to the tip (Nasoori, 2020). Keratin has also been shown to be extremely tough and able to absorb high amounts of energy (McKittrick *et al.*, 2012). As keratin is very stress-resistant, this makes it ideal for horns, as throughout life, horns are subjected to repeated loads of variable magnitude (Zhang *et al.*, 2018). During defence, the slender distal part of the horn has the function of stabbing the opponent, thus it needs higher strength and stiffness, whereas the proximal part should be more flexible to absorb energy in wrestling (Li *et al.*, 2011). The mechanical properties are dependent on many factors, particularly moisture content, but also age, temperature, and loading direction (Li *et al.*, 2011; Kitchener, 1987;) and, like many biological structures, horns are not static and are constantly remodelling the bone core and adapting to environmental stimuli.

Horns can resist remarkably high forces with compression tests of cattle horn having recorded resistance of up to 7600 N (Li *et al.*, 2011). This force is far greater than that required to fracture most bones, and it is the combination of composite properties in horns that make them ideal for resisting fracture. In tests of the physical properties of horn, it has interestingly been shown that horns are progressively more flexible when running from proximal to distal. Hence, the very tip is the most flexible part of the horn (Li *et al.*, 2011). The gradient along the horn varies by species, and by use, and is suggested to functionally reduce mechanical stress (Nasoori, 2020). The horn sheath acts effectively as a load support element, withstanding large external loads without severe deformation or fracture. It is supported by the porous core and trabecular bone that is fused to the cranium, with the surrounding tissue adding additional support to the structure and dissipating forces (Cappelli *et al*, 2017; Drake *et al*., 2016). Forces can be transferred from keratin to the dermal underlayer and then, forces are transferred to the bony core in the radial direction, next to the skull along the longitudinal direction, and eventually to the neck and shoulder muscles of the animal (Maity and Tekalur, 2011).

6.3. Function of horns.

While this chapter is not specifically addressing the horns themselves, rather the morphological impact of having horns on the cranium, it is important to note the varied functions of horns. This is to gain an insight into the biomechanical demands on the cranium possessing horns poses and note some possible constraints of research based on morphology associated with headgear. As previously mentioned, horns are a complex component of cattle anatomy, serving wide ranging functionality. The traditional suggestion regarding headgear has been as offensive or defensive weapons in male competition and predator defence (Nasoori, 2020; Nasoori *et al*., 2016; Knierim *et al*., 2015; Schafberg and Swalve, 2015; Bro-Jørgensen, 2007). Indeed, a review of predator defence suggested that horn function in males is primarily intended for inter-male competition, with selection via intrasexual combat, evidenced by larger headgear on larger individuals (Clutton-Brock and Huchard, 2013). If used for defensive purposed against predators, this seems to be a secondary benefit developed in conjunction with other competition traits. Beyond this, however, horns also serve more passive processes being involved in metabolic heat exchange and function in social identification and interaction.

In bovids sexual selection pressure has often been evidenced with males generally possessing horns, while females largely lack them (Leslie and Sharma, 2009), indicating a higher necessity for males to compete. It has been suggested that the longer the horn length and the greater the body size, the better a male's ability to control reproductive access (Preston *et al.*, 2003). In wild populations, male reproduction is dependent on the animal's ability to contest, with horn size being a good indicator of general health (Ezenwa and Jolles, 2008). The function of horns in contests seems dependent on their morphology, with shape, structure, length, and orientation varying greatly, and possibly also dependent on fighting style (Calamari and Fossum, 2018; Lundrigan, 1996; Gentry, 1992; Modell, 1969). In males, both the shape and robustness of horns is suggested to relate to interspecific male combat, with horns being able to withstand butting or pushing forces in competition clashes with rivals (Packer, 1983). It is particularly noted that resistance to lateral forces is key, and where horn breakages are seen in male antelope, this is more prevalent in species with the thinnest horns in relation to body mass. Thus, horns need to be tough, strong, and able to withstand high pressure, to avoid breakage. Breakage is permanent and could impact the animal's health and ability to interact socially with a herd, or they could be more vulnerable to predation (Johnson *et al.*, 2021).

As previously mentioned, marked sexual dimorphism occurs, with males exhibiting larger headgear (Kiltie, 1985). This has however led researchers to question the function and purpose of horns in females (Stockley and Bro-Jørgensen, 2011), as sexual selection pressure is less evident. Furthermore, in bovids not all females possess horns, and where present differences are noted between males and females. For example, in male and female animals of the same body weight, horns were of similar length, but male horns were approximately twice the thickness at the base along with differing shapes (Packer, 1983). The variance in shapes between male and female horns led to the suggestion that they experience different selection pressures. In females, a longer, more slender horn is observed, with the suggestion that there is less need for behavioural inter-individual competition (Packer, 1983). Alongside this finding is also wide variation in female horns, which when present has led to questions about their functional capacity. It is proposed the horned characteristic in females arose from elevated competition levels for resources, but it could have been for defensive purposes or at least to act as a deterrent to predators (Knierim *et al.*, 2015; Clutton-Brock, 2009; Roberts, 1996). The broad shape of male horns has evolved to withstand head-on clashes, whereas female horns have evolved as spikes for displacing individuals (Lincoln, 1994). In observations of female sheep herds, horned females displaced others with less weaponry (Robinson and Kruuk, 2007). This finding was also closely linked to animal age, as older individuals were more likely to initiate dominating behaviours towards younger animals (Robinson and Kruuk, 2007), especially when herds were in high density populations with low resources (Festa-Bianchet, 1991).

For predator defence, much of the size and shape differences and indeed presence of horns, seemed at least partly related to the environment. In antelope species, it has been noted that open grassland species are more likely to have horns that are larger, compared to forest species in which horns are often absent (Packer, 1983). This trend was related to the higher visibility of species in the open, with animals being more easily detected by predators, in comparison to woodland species relying on camouflage instead of weaponry. Open grassland species also tended to be larger, with the suggestion that increased exposure to predation, due to larger body size or open environments, may be a good indicator of horns (Stankowich and Caro, 2009).

Aside from their physical use, horns also serve passive functions, many of which are poorly understood and likely have limited influence on the morphology of the cranium. It is however important to highlight that horns are not a distinct anatomical unit, but function closely with the animal's body. One of the best researched passive functions of horns is thermoregulation as a possible driver of horn size that is environmentally controlled particularly, when the animal's body is resistant to heat loss (Picard *et al.*, 1999; 1996; Blackshaw and Blackshaw, 1994). The general structure of horns makes them ideal for heat exchange having a double layer of highly vascularised periosteum adjacent to the core (Parès-Casanova and Caballero, 2014), allowing warm blood to transfer heat. This function has been noted in goats, where horns were shown to have variable temperatures and were fundamental in external heat loss and regulation of brain temperature (Taylor, 1966). Similarly, in sheep living in warm and cold climates, cranial measurements show that smaller horncores in relation to body mass were common in cool environments, and the opposite for warmer locations (Hoefs, 2000). This is likely related to the necessity for a large or small horn surface area required for heat exchange (Picard *et al.*, 1999). Indeed, thermoregulation control and metabolic restrictions have been suggested as limiting factors even for skull morphology and sexual selection in cold environments (Picard *et al.*, 1994).

In terms of social interaction cattle can use horns both as visual identifiers but also physical tools in interpersonal interactions. From a distance, horns help define the outline of an individual animal, helping the cattle identify each other and communicate with each other (Doyle and Moran, 2015). When in closer proximity, horns help define the herd hierarchy, and are part of the dominating behaviour that establishes this. Interpersonal space between cattle is strongly affected by horns (Irrgand, 2012; Oster, 1977), like a personal bubble. In horned animals, the distance between individuals can range from one to three metres depending on position in the herd. In addition to this, horns are used for grooming, being used by cattle to scratch themselves and others (Knierim *et al.*, 2015). It is apparent that each individual is acutely aware of the size and form of their own horns and the distance around them. In hornless cattle, interpersonal space reduces to as little as one metre.

In summary, both the physical and passive use of horns creates a dynamic tool that bovids, and cattle specifically, use in a variety of ways. While many of these functions do not relate specifically to the cranium, these various roles have created a great deal of unknown variables that are difficult to quantify for research purposes. It seems sexual dimorphism in horns is strong and could be one of the major biomechanical drivers for horns. However, factors such as environment cannot be eliminated and if suggestions are correct may have a greater influence on horns, then supposed. This is further compounded when also considering horns do not act independently but are intrinsically linked through soft tissue, skin, muscles and also affecting cattle behaviours. Unfortunately, in archaeologically we seldom have soft tissue, and for the purposes of studying anatomy only the bones can be considered with any certainty. For this reason, the impact of horn on skull morphology will be considered, regardless of functional use.

6.4. Cranial morphology and horns.

From a morphological perspective, the relationship between horns and crania is not well established. It seems that the highly derived functions and physiology of horns already discussed earlier in this chapter appear to have some influence on the cranium. This topic has not been explored particularly extensively in literature and seems to be a difficult question to answer, likely due to the high variability in headgear, its form and function. When referring to the literature, studies looking specifically at the interplay between horn size and cranial shape are limited and non-existent in cattle. This thesis has previously highlighted the potential for horns to have some influence on robustness of crania, as suggested in the shape analysis undertaken in Chapter Four. The results of this indicated some differences in the frontal and occipital regions seen between aurochs and domestic cattle, but also large cranial shape disparity within the cattle group itself. These differences were considered to possibly result from variation in horn size requiring a more robust cranial morphology. This would also fit the trend for inter-cattle cranial differences as horn variation (in terms of size and shape) is known to be great.

As discussed previously, horns seem to primarily serve as an indicator of fitness and in inter-male contests. In competition, cattle will hold their heads together and use their horns to push or wrestle, and stop themselves slipping (Sambraus, 1978). Cattle tend to adopt a more static push but also induce twisting and wrestling through the horns, which are important in remaining connected and stopping slipping. This obviously reduces the role horns seem to play in stress absorption from the initial impact of head butting, as those forces are concentrated on the cranium directly. In response to this direct stress, anatomical cranial adaptations have been suggested in studies of American bison. The interparietal bone was found to be of greater thickness then the frontal, and the increase in thickness might assist the stress absorption capabilities of the bone, while increasing its resistance to bending (Persons, 2019). It was hypothesised that skull adaptations could be in response to the forces associated with headbutting, and that American bison may have several different adaptations to mitigate stress, particularly the paranasal sinuses and bony septa separating them. The results showed interparietal-to-interparietal impacts resulted in lowest forces, compared to mid frontal-to-mid frontal and oblique collisions with higher, more localised stresses (Persons, 2019). It was also noted that under no conditions did stress extend beyond the threshold necessary to fracture bone. Strategic thickening of certain bones that receive the most stress was suggested as the most likely stress-reducing adaptation.

In other species, this cranial adaptation in relation to fighting behaviour has received more attention. Other studies have also looked at more fine scale localised mechanisms, particularly the ability of sheep to seemingly withstand high force head on head trauma (Ackermans *et al.*, 2021; Grimmelt *et al.*, 2011). When cattle are competing, impact tends to be head-to-head, rather than horn to horn like other bovids such as sheep. Sheep charge at speeds of around five metres per second into an impact with a rival (Kitchener, 1988), with suggestions around half the weight of the animal (c.2500 N) can be transferred in force during a contact (Li *et al.*, 2010). From this, a number of mechanisms were suggested to be involved in force absorption, including the cranial sutures allowing slight movement to dampen forces that travel through the skull, the horn keratin and sinuses (Johnson *et al.*, 2021). Horns are not static and receive a force but are a product of the dynamics behind speed of clash, angle of head, and readiness of the individuals to brace. Such processes involve tremendous forces but can be dissipated particularly by the neck and shoulder muscles. In fighting bovids, it has been shown that the neck and shoulders absorb forces rather than the horns (Kitchener, 1988). As noted in Klinkhamer *et al.* (2019), the various fluid processes involved in head-to-head clashes cannot be estimated with any certainty in FEA studies. The role of the vertebrae was also noted as a possible shock absorber in bison due to their robust nature (Persons, 2019; Kreutzer, 1992). In modelling of deer species (Klinkhamer *et al.*, 2019) suggested the constraints likely made models too rigid and artificially concentrated forces into the antlers. It would be difficult to account for the transfer of forces from horns into the body when looking at skeletal material and extinct species.

In cattle the most enigmatic evidence comes from cattle breeds that are genetically hornless or have the horn buds deliberately removed in early life. These are termed polled cattle, and in both cases the horn dermis does not grow (Schafberg and Swalve, 2015; Wiener *et al.*, 2015). In hornless animals, displays of dominance are less based around head-on pushing, as the animals slip from head-to-head. Instead, side tackles are more common, as indeed are instances of fighting (Menke *et al.*, 1999). This obviously has implications for the morphology of the cranium as the frontal sinus remains constrained, not extending into the horncore. This could make the absence of horns due to polling, the best evidence for the impact of horns in cattle specifically on the cranium. It is suggested that the dehorning process has a marked impact on the shape of the skull. The frontal bones of dehorned cattle seemed to be more concave in shape, drawn forward, and with a smaller distance between the eyes, which were more forward facing. In contrast, horned animals generally had flatter frontals and wider distances between the eyes (Spengler, 2016). In addition, personal observations indicate that dehorned animals have a marked bulge on their foreheads not seen in horned animals (noted in authors observations during data collection). This could be linked to the volume of the sinuses and compensation for the loss of space that horns would have otherwise provided. The extension of the sinus cavity into the horns has already been mentioned in a thermoregulatory function (Parés-Casanova and Kucherova, 2014; Taylor, 1966). This would increase surface area of the paranasal sinuses and could assist with nasal heat exchange. This seems to have several benefits in large mammals, particularly helping prevent lung damage from prolonged cold air exposure while maintaining body temperature and water loss during exhalation (Langman *et al.*, 1979).

More generally, it has also been indicated that pneumatized bone, as is the case with horns, develops in species that participate in some combat with their heads (Geist, 1966). The role of the sinuses has been explored with considerable debate regarding their specific contribution to the formation of the cranium possibly being related to animal size and sexual dimorphism (Blaney, 1986), but function being generally poorly understood. Sinus function in shock reduction relating to head trauma has been proposed and tested by Farke (2008) but it was suggested there was limited evidence for sinuses absorbing stress. Indeed, the morphology of the cranium was seen as more beneficial in dissipating stress, with a vaulted and pneumatized frontal bone being beneficial in dissipation of stress when headbutting in domestic goats. Furthering this work, it has later been indicated that even the size of sinus and arrangement of internal struts seems unrelated to headbutting (Farke, 2010). The sinus cavity is related more closely with area of frontal bone, possibly representing an evolutionary reduction in mass of biomechanically unnecessary bone rather than combat function (Witmer, 1999, 1997).

What remains unclear however is the impact of particularly large horns or small horns. For example, does the cranium exhibit features similar to polled cattle if horns are small, and do these features continually diminish as horns get larger? These questions are complicated and there is wide variation that might explain this. In the case of very large horned cattle, such as Zebu, the horns can be seen to protrude in an upright manner. However, this is not the case seen in aurochs where the horns grow, more laterally, curling out sideways. It is reasonable to suggest the forces placed on the cranium are different, as the angle and orientation of horns and mass change. As we know from Wolff's Law (1986) regarding bone functional adaptation (Ruff *et al.,* 2006), when bones, including in the cranium, are under high strain they adapt to combat this by increasing bone deposition. Hence, remodelling of the cranium to resist a particular weight of horn is a reasonable expectation. However, there are few studies that examine why some species of Bovidae have large horns and others small (Gerstenhaber and Knapp, 2022; Lundrigan, 1996). What makes horns grow large in some animals and small in others is not well understood and is likely the consequence of multiple complex factors interacting. In a study of the scaling of horns and their relationship with body size, and indeed species size, it was shown that allometry might have important implications (Packard, 2018). It was suggested there might be a minimum threshold in body mass for obtaining horns. A minimum size would not be problematic for cattle being at the larger end in body mass. However, there are constraints to horn size: horns do not necessarily scale as might be expected, particularly at large body sizes, a trend also noted in deer species. Once past a certain body size, larger males have smaller horns than predicted by statistical modelling and do not continue to scale allometrically (Packard, 2018; Lemaître *et al*., 2014).

Aside from cattle specifically, there are biomechanical studies of headgear in other artiodactyls, particularly sheep and deer species. One of the most relevant was an FEA study on *Megaloceros giganteus* to assess the impacts of large antlers and if they were functional in the same ways that modern deer species use their antlers (Klinkhamer *et al.*, 2019). While this study was focused primarily on the antlers, the cranial results are still of interest to this study. It was shown that the large headgear of the *Megaloceros giganteus* was functional, and the antlers could withstand the force load exerted from fighting behaviour, particularly rotational forces. However, other deer species were better adapted to pushing forces, to which *Megaloceros giganteus* showed less resistance. In all species tested, the highest stress levels in loading of antlers were found at the base where the antler joined the skull. This finding has potential implications for cattle, despite obvious differences in antler and horn as a material. The finding indicates that a large amount of force is accumulating at the connection site between headgear and cranium. If this is the case for cattle, and given the permanence of horns compared to antlers, the cranial attachment to horns must be very robust.

Clearly when comparing horns of aurochs and domestic cattle, the horns of the latter are much diminished in stature. It seems likely the mere presence of such exaggerated headgear (as seen in aurochs) would have some implications for the cranium. However, this must be considered against the animal's body size, and while aurochs are larger than most cattle, there are modern breeds of cattle achieving similar body weights to aurochs that do not possess very large horns. Similarly in Klinkhamer *et al.,* (2019), the body mass of the *Megaloceros giganteus* and moose were seen as being approximately similar, but the antler size was greatly different. In this chapter we test if horns play a significant role in the morphology of the skull, as suggested by the results in Chapter Four. This is to test the biomechanical impact of having large horns and small horns, and the capabilities of wild and domestic crania in supporting the mass of the associated headgear.

6.5. Aims and objectives.

This chapter has one main objective, to investigate the stress placed on the cranium by the mass of horns, and to determine if this has impacted cranial morphology, particularly that of the frontal region, which was observed to be variable between domestic cattle and aurochs in Chapter Four.

It is hypothesised that:

HYPOTHESIS 1: Aurochs will experience higher stresses than Chillingham or domestic cattle owing to the size of their horns.

HYPOTHESIS 2: Aurochs crania will be able to resist the load imposed by large horns better than Chillingham or domestic cattle.

In order to answer the hypotheses, set out in the aims of this chapter, a number of decisions had to be made regarding representation of the living animal and the impact of horns on cranial morphology. Each hypothesis will be tested in turn using finite element analysis (FEA), similarly to Chapter Five. Three models will be tested: an aurochs, a domestic cattle, and a Chillingham cattle (feral domestic). It should be stated that primary interest is in the cranial morphology and its response to potentially different weights of horn, and not the loading response of the horns themselves. To standardise the impact and remove complications, the horns mass will be used as if the animal is static and simply resisting gravity. This research will be the first study to examine the impact of horns in cattle as a driver of morphological change, and how the cranium responds to the loading imposed by heavy headgear. The rationale for this study is to achieve better understanding of selection for large horns from the perspective of cranial adaptation, rather than through horns as an entity in themselves.

6.6. Methods.

6.6.1. Sample and model creation.

As an initial step, a series of FEA models needed to be developed, and for this, two crania were CT scanned. One skull was of a domestic cattle from the York Zooarchaeology Teaching collection, scanned at York teaching hospital, with a lattice info of 512 x 512 x 681. The scan had an original voxel size of 0.73 x 0.73 x 0.7 mm, but this was resampled to isometric voxel dimensions of 0.8 mm. The second cranium was from Chillingham Wild Cattle park scanned at the University of Liverpool. Owing to the large specimen size, it was scanned in two orientations. The first scan had a lattice info of 512 x 512 x 1854 and voxel size of 0.824 x 0.824 x 0.3 mm. The second scan had the same size lattice info but voxel size of 0.976 x 0.976 x 0.3mm. These models were merged, and the voxel dimensions were resampled isometrically to 1.6 mm.

These CT scans were manually segmented and aligned to a consistent orientation in Avizo 3D pro (Thermo Fisher Scientific, Waltham, MA, USA) to distinguish bone and teeth as one material from horn sheath keratin. As I was interested in the morphological impact of horns on the crania, rather than the material properties of horn, keratin was not considered to be significant to the models and was removed. Furthermore, as keratin sheaths were only present in the domestic and Chillingham cattle, and not the aurochs, removing keratin would also keep models consistent.

As no aurochs were available for CT scanning, the 3D reconstruction of the domestic cattle skull was warped, using Avizo 3D pro, to the size and shape of an aurochs skull, using a surface model obtained by photogrammetry as a guide (project ID: 5). The exact process is described in Chapter Five and validated via shape analysis to serve as a proxy (see section 5.5.1). This produced an aurochs model with a lattice info of 900 x 750 x 800 and isometric voxel size of 1 mm. The cranium models were then exported as bitmap image stacks and converted into finite element meshes using a bespoke software tool, vox2vec.exe (Liu *et al.*, 2012). This produced eight-node cubic finite element (FE) meshes via direct voxel conversion for use in VOX-FE (Liu *et al.*, 2012; Fagan *et al.*, 2007).

6.6.2. Material properties and constraints.

The material properties of bone were set in VOX-FE following the method described in section 5.5.2. The whole model was assigned a Young's modulus of 17 GPa and Poisson's ratio of 0.3 as per the published norms for bone (Schwartz-Dabney and Dechow, 2003). Models were constrained at both occipital condyles to simulate the head being articulated and fixed by the vertebra (Figure 6.2). Using the VOX-FE tool, constraints were hand painted onto the occipital condyle in all models and fixed in all dimensions (X, Y, Z) to prevent translation and rotation in space when the loads were applied.

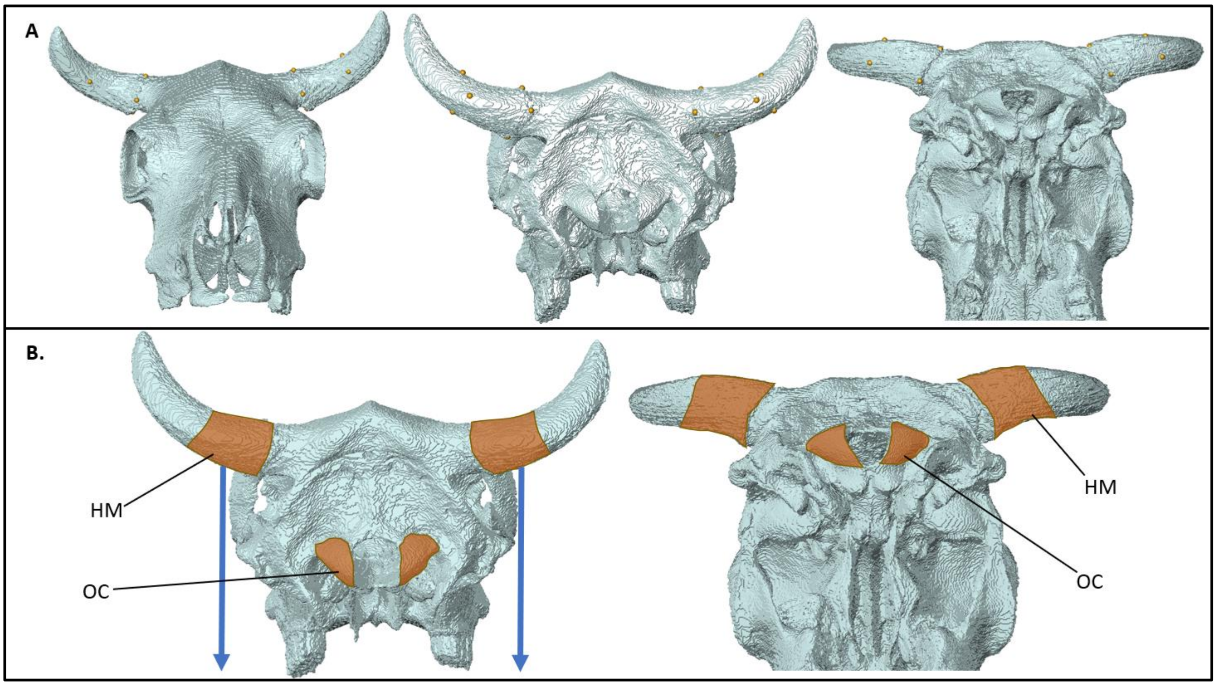


Figure 6.2: A. Location of guide landmarks 5cm from the horncore base. B. Location of horn mass (HM) force vector and constraints (OC) placed on the occipital condyles.

6.6.3. Forces.

The actual mass of horns was considered the most realistic starting point providing the nearest 'true to life' measure of horn impact on the cranium. To estimate the forces exerted by horns on crania, mass and density of horn were needed, this was taken following dissection of a Chillingham bull head (see Chapter Five). The left horn was removed from the Chillingham cattle head where the skin connected the horn keratin to the cranium. The mass of the whole freshly removed horn was recorded and a cylindrical section of horn was cut from the approximate middle of the horn. This was weighed, and calliper measurements taken of the height and diameter, using the average of two measurements taken on opposite sides across the cylinder to account for tapering of the horn. From this data the volume of the horn cylinder was calculated. Using the volume and mass, the density of the horn was then calculated, and overall horn volume estimated which is summarised in figure 6.3.

To check the comparability of physical volume and mass and digital volume and mass, the dissected horn was surface scanned using a structured light scanner (Artec Space Spider, Artec3D, Luxembourg). In Avizo the surface model was processed into a solid volume, and the volume measurement was calculated in Geomagic Wrap (Oqton, Ghent, Belgium) as 1047.91cm3. A mass calculation (using the density value calculated above) was performed to compare the known physical mass (1305g) to the digital model, which was 1278.45g. While mass and volume estimates varied between digital and physical calculations, this was only by 2% and considered within any potential sources of error, such as mass lost by cutting the cylinder from the middle of the horn. To measure the horn volume of other specimens, a horn was cropped from the CT models and segmented in Avizo into a solid volume, which was then converted into a surface model (.stl). These surface models were opened in Geomagic Wrap and the volume recorded (table 6.1).

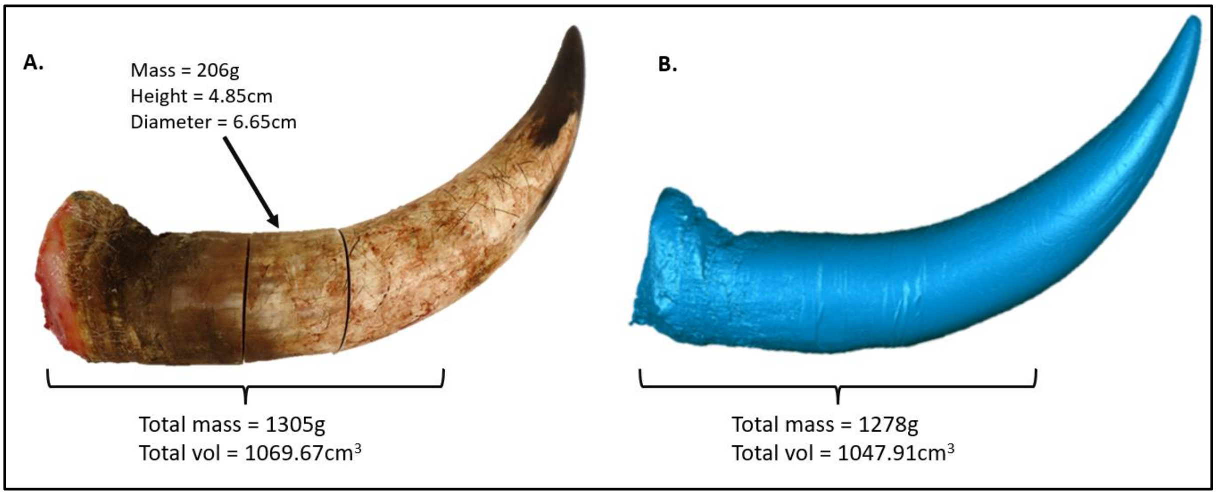


Figure 6.3: Method for calculating total horn volume and density.

Specimen	Model	Volume with horn sheath (cm^3)	Mass with horn sheath (g)	Volume without horn sheath (cm^3)	Mass without horn sheath (g)
Chillingham female CT		481.70	587.67	217.73	265.36
Domestic cattle CT		204.38	249.34	100.22	122.26
Aurochs surface models		8460.88	10322.27	2807.23	3424.82

Table 6.1: Summary of horn volume and mass for each model, with and without keratin sheath.

6.6.4. Loading.

Two sets of analyses were planned: first, to simulate the response to loading by a realistic horn mass; and second, with scaled loads to simulate all models having the same horn mass relative to cranial volume. The loads applied were painted directly onto the nodes of the voxel elements in the FE models representing the mass of static horns, including the keratin sheath. To remove the impact of different orientations of horns and look at morphological response in the cranium only, horns were loaded at the base over a region extending 5 cm from the cranium ('basal loading area'). To apply the basal loading consistently, guide landmarks were placed round the base of the horn and 5 cm along the length of the horn using the measure tool in Avizo (see figure 6.2). These landmarks were imported into VOX-FE and displayed on the models, and forces were painted using the landmarks as a boundary, so all models had a consistent loading area. Forces were set in a vertical orientation downwards. The force vector was established in VOX-FE using the coordinates of the force origin. To set the end of the force the X and Z values were replicated, while changing the Y coordinate value to 0.

For the loading values of absolute horn, the mass was calculated using volume and density of horn at 1.22 g/cm. Finally, force was calculated from mass using a conversion factor of 9.8 N/kg. However, the specimen used to create the aurochs' model was missing its keratin sheath. Thus, this was estimated by deriving the log-log relationship between horncore volume and full horn volume (including keratin) in the domestic cattle and Chillingham cattle model, and extrapolating to the horncore mass of the aurochs (table 6.2) The resulting volume of the aurochs horn was, of course, only an approximation as the relationship between bone and keratin masses found in domestic cattle does not necessarily persist at the large size of aurochs horns. Moreover, horn shape, age and sex could also affect the relative proportions of the component parts of the horns.

Model	Cranial volume (cm^3)	Horn mass (g)	Force (N)	Scaled force (N)
Aurochs	4029.8	10322.8	101.16	N/A
Chillingham	1332.3	595.9	5.83	33.45
Domestic	1084.3	249.3	2.44	27.22

Table 6.2: Forces applied to loaded models in absolute and unscaled force.

Following the analyses using actual horn masses, the impact of having larger horns on morphology was assessed. To do this, the forces applied to the domestic and Chillingham models were scaled to simulate the loading that would occur if their horns were in the same proportion to their crania as those of the aurochs. This was done using cranial volume calculated in Avizo 3D pro, removing horns to eliminate the discrepancy in horn size, and the horn masses already stated. This was calculated with the equation:

$$scaled\ cranial\ volume = \frac{actual\ cranial\ volume * aurochs\ horn\ mass}{aurochs\ cranial\ volume}$$

Similarly, force in Newtons was then also calculated as above. These forces (table 6.2) were then added to models in VOX-FE following the procedure already described. The scaling of forces and applying them to see the impact of loads from one individual in relation to another has a precedent set in the literature (Cox *et al.*, 2012).

6.6.5. Analysis.

The finite element models were solved using a high-performance computing cluster, (Viking), at the University of York, allowing for 10000 iterations and a maximum solving time of two hours. Von Mises stresses were viewed in VOX-FE to show the distribution of stress as a heat map across each skull. Heat maps were displayed using the same scale, so stress experienced by each element across all models was comparable. Heat maps of the surface stress were visually assessed for differences.

6.6.6. Sensitivity.

To test the validity of the method stated above, and particularly to understand some potential parameters, a brief sensitivity analysis was undertaken. The first test was of the validity of basal horn loading in comparison to loading the whole horn. For this, two models were created based on the domestic cattle model. One model was only loaded at the horn base via the method already described, and the other had the force applied across the whole horn. Both models were loaded with the same force vector, vertically downwards, and the force value for domestic cattle unscaled horn.

As already discussed, the rationale for using basal loading was to remove impacts of horn orientation and standardise what is a diverse trait in living cattle. It is however recognised that orientation and variation in force vectors will impact the loading on the cranium as seen in Godinho *et al.* (2018), so this was also tested. Additional models were created in which the orientation of the force vector was changed in VOX-FE. Changing the force vector can either represent horns that are re-oriented with respect to the skull, or a change in head posture with respect to gravity. Three head orientations were proposed, termed zero (also the vector models were loaded in as described above), 30 and 60 degrees. To simulate the head being in different orientations and the direction of forces acting on the cranium, the angle of the force was changed in the Y axis to 30 degrees and 60 degrees in an anterior direction in the sagittal plane recalculating the Y value with trigonometry, as in figure 6.4.

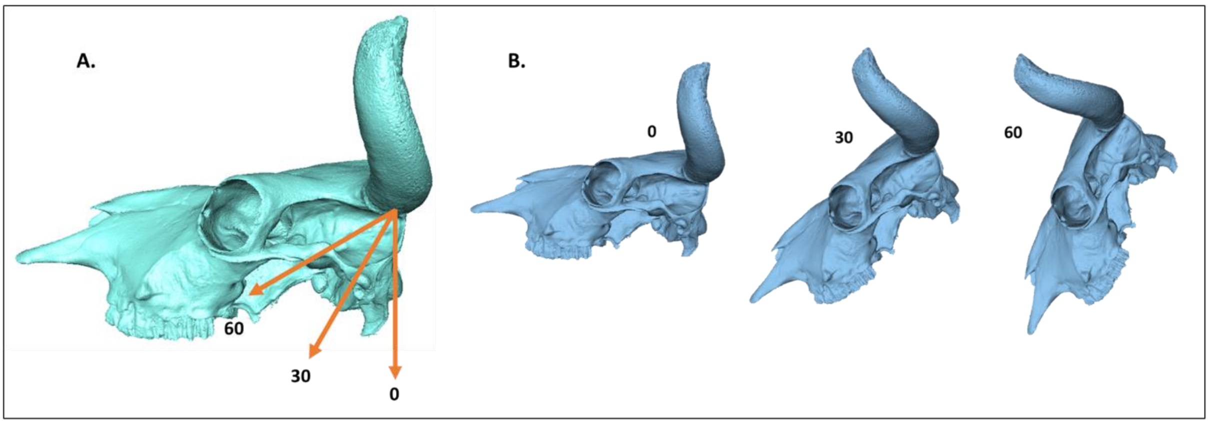


Figure 6.4: Head orientation at 0, 30 and 60 degrees, A. showing changing angle of force vector as applied in VOX-FE. B. showing a representation of different head angles of the cranium in standing position.

6.7. Results.

6.7.1. Sensitivity.

The results of the sensitivity analysis can be seen in figure 6.5, which shows that models loaded with the full horn have higher magnitudes of stress compared to models using basal loading. However, despite basal loading and full horn loading producing different stress magnitudes, the patterns of stress were consistent. Areas of high stress were observed in both models in the frontals, mid-occipitals, basal aspect of the horncores and under the horns in the parietals. The difference in magnitude between the models is thought to relate to how the loading was applied. The force magnitude added to the models was divided equally among all the loaded nodes. Therefore, in the full horn model force vectors nearer the horn tip were multiplied by a greater bending moment than those nearer the base. The full loading condition here is likely to be an overestimate because horn mass is not equally distributed along the horn. The conical geometry of the horn, being larger at the base than at the tip, means most of its mass is held close to the skull.

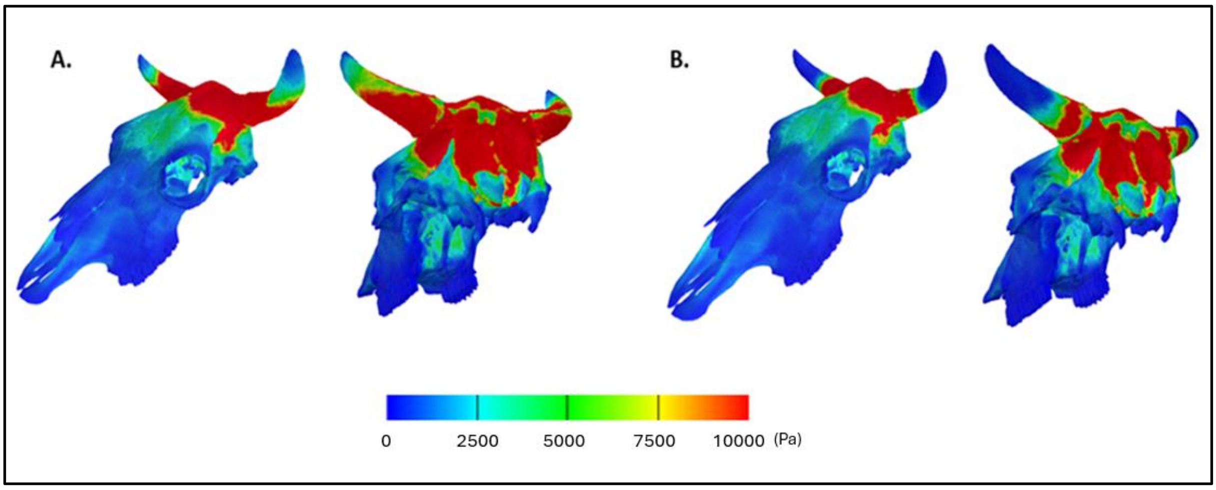


Figure 6.5: von Mises stress distributions across the domestic cattle skull resulting from two different loading scenarios. A. Forces applied across the whole horn. B. Forces applied at the base of the horn only.

In comparison, in the basal loading model there is a smaller bending moment as forces are divided over a smaller area near to the cranium. Basal loading is likely to be an underestimate for stress however because it ignores the bending moment of the parts of the horn further from the cranium. The exact contribution of force further from the cranium along the horn would be highly dependent on the horns' shape. The specific orientation, shape and size would impact the result of full loading more acutely than basal loading. Given the similar stress patterns, and nature of this study aiming to investigate the impact of horn mass in absence of other confounding factors like horn shape, basal loading was the most appropriate. It is therefore proposed that basal loading is an acceptable approximation of loading, which removes problems that could arise from very different shapes, orientation and sizes of horns that would significantly vary the locations of force vectors and induce other factors such as bending moment in models.

To preliminarily test the possible influence of different orientations of horns and to simulate changing head posture, the angle of force was adjusted in three models. The results (figure 6.6) show some minor fluctuations in pattern and magnitude of stress in different angles of force. The standard was the zero-degree model, where the force vector was applied vertically straight down. This loading showed stress across the frontals and mid-occipitals, and somewhat in the parietal. When the vector was moved anteriorly 30 degrees, some slight changes were noted. The magnitude of stress was slightly reduced, and the stress pattern remained similar although now located more posteriorly on the frontals and ventrally onto the central aspect of the cranium. This was seen most clearly in the parietal bone, where stress was shifted anteriorly towards the maxilla. The force vector was then moved anteriorly to 60 degrees and patterns of stress remained broadly similar to previous results. There were some minor differences, notably lower magnitudes of stress in the frontals than previous angles, but much higher stresses in the occipital condyle and ventral posterior area of the cranium.

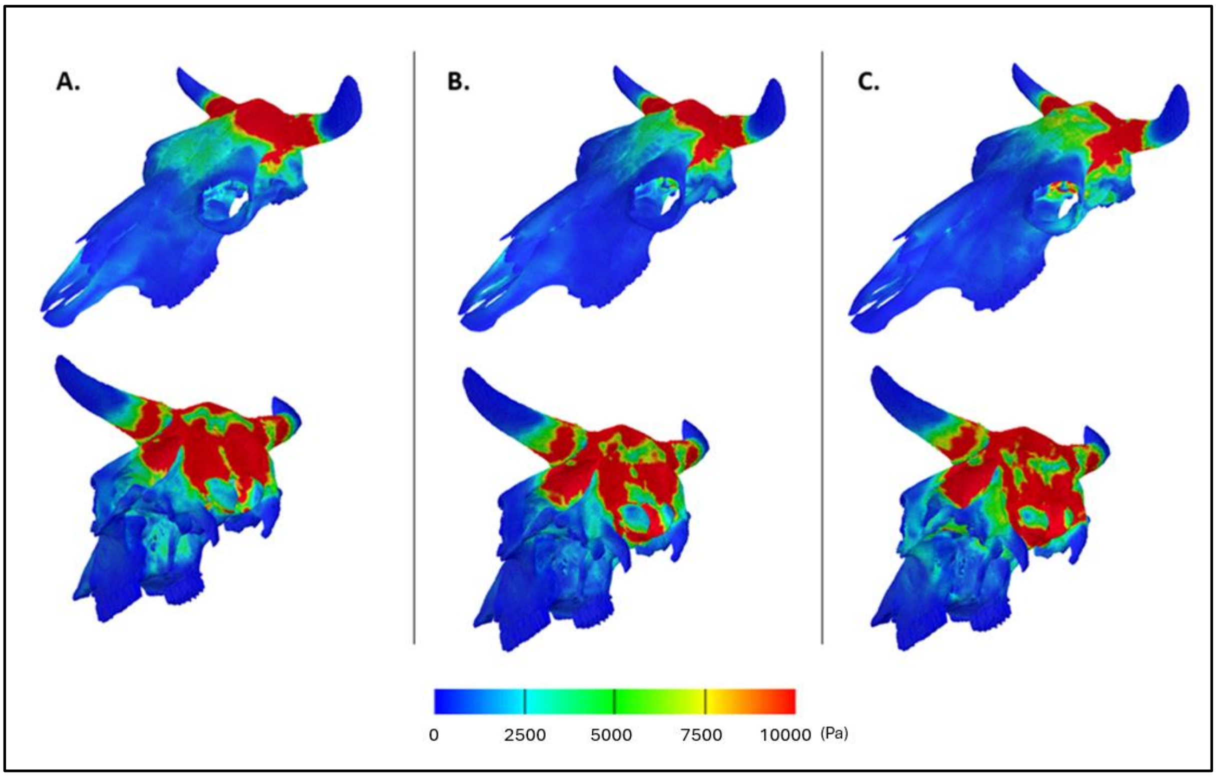


Figure 6.6: von Mises stress distributions for different angles of the force vector: A. 0 degrees; B. 30 degrees; C. 60 degrees.

6.7.2. Horn mass.

Absolute horn mass was tested with the force vector at a zero degrees angle straight downwards for each of the three models (figure 6.7). For all models, stress was concentrated around the posterior area of the cranium, particularly the frontal, occipital and parietal bones. In all models the mid-sagittal suture was an area that resisted stress relative to other parts of the cranial vault. Some high stresses were also seen in the horncore where forces were applied, this is common in FEA and considered a product of the direct loading on this area rather than actual stress distribution. There was a noticeable variation in the magnitude of stress present between the models. In domestic cattle, low stress was observed, and where stress was seen it was located laterally on the frontals and in the middle of the occipital. For

Chillingham cattle, the model showed a higher magnitude of stress than domestic cattle, but lower than aurochs. The Chillingham models exhibited highest stress laterally on the frontals, and more localised stress in the occipital being close to the nuchal line and above the occipital condyles. The aurochs exhibited the highest stress of all models. This was noted on most of the frontals (either side of the mid-sagittal suture), the majority of the occipital and the parietals. Stress also extended on the ventral aspect of the cranium.

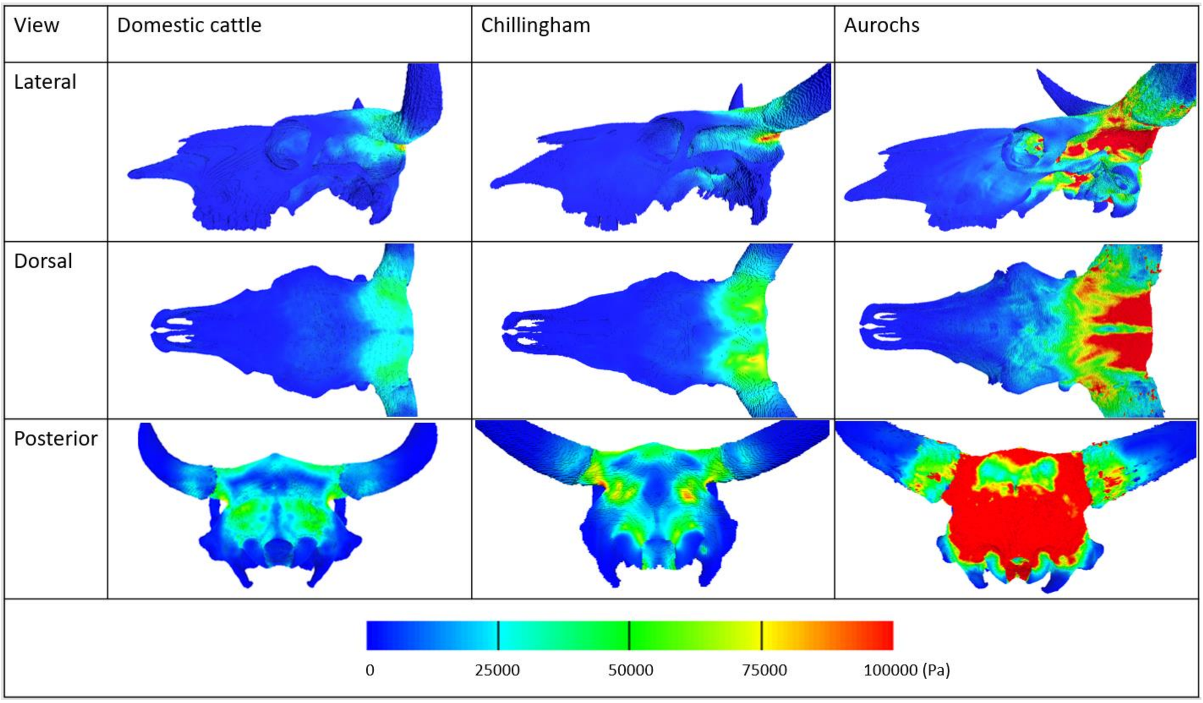


Figure 6.7: von Mises stress distributions across the cranium when loaded with absolute horn mass.

6.7.3. Scaled horn mass.

To further investigate the efficiency of cranial morphology in resisting stress, the domestic cattle and Chillingham models' horns were scaled to have the same relative horn mass (as detailed in section 6.6.4) as aurochs (figure 6.8). The aurochs' model did not need modifying but is included in the figures for ease of comparison. In general terms, the scaled horn mass results showed a marked increase in stress across both the domestic cattle and Chillingham models, which showed very similar trends in the heatmaps. Stress patterns were considered to be similar to those seen in the aurochs, being highly stressed in the frontals, parietals and occipitals. There seems to be some areas of lower stress along the frontal suture, seen most clearly in domestic cattle, and around the nuchal ligament attachment on the occipital. In comparison to the aurochs' model, all other models were more stressed in the frontals.

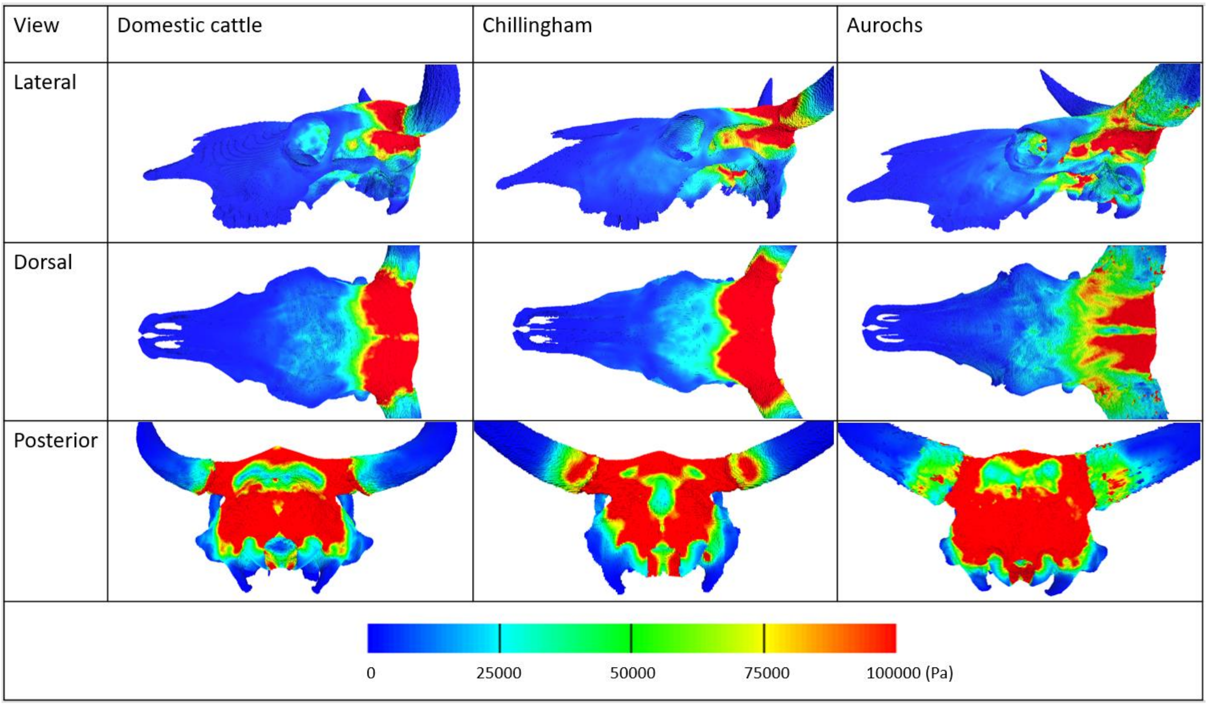


Figure 6.8: von Mises stress distributions across the cranium when loaded with scaled horn mass.

6.8. Discussion.

6.8.1. Role of horns in morphology.

The results of the unscaled models seem to clearly support hypothesis one, that larger horns will induce greater stress. Stresses in all models were seen in the bones that immediately connect to and support the horn architecture, including the frontals and occipitals. However, the magnitude of stress was considerably larger in the aurochs model compared to the domestic and Chillingham cattle models as seen in the heatmaps (figure 6.7). The domestic cattle model had the smallest horns and the lowest stresses, with the aurochs having larger horns and highest stress, and the Chillingham model fell in the middle. This is not surprising given the difference in input force, with aurochs horns being many times the mass of the domestic counterparts used in this research. The cattle model had particularly small horns, although not atypical of domestic cattle. The Chillingham model had larger horns than the domestic model but still only showed moderate stress. It is proposed that the slight difference in morphology at the rear of the skull in Chillingham cattle, meaning horns protrude more vertically, might reduce the stress induced in the cranium. Despite aurochs having high magnitudes of stress, they are clearly adapted to the large headgear they carry, and it certainly seems to place high functional and biomechanical demands on their cranium. One feature that was noted was the mid-sagittal suture as an area of low stress, present in all models but particularly in the aurochs. Sutures have been shown to effectively resist stress and respond to tension and compression being highly adaptable to loads and responding by modifying cranial development (Savoldi *et al.*, 2018; Balolia *et al*., 2017; Byron *et al*., 2004). Furthermore, forces acting on the sutures during development may help to stimulate growth and control osteogenesis of the sutures (Behrents *et al.*, 1978). In addition, sutures are recorded to provide some level of flexibility through having a viscoelastic property, as the nature of a specific suture is specifically adapted in response to the nature of loading (Herring, 2008). The mid-sagittal suture in aurochs is very pronounced and clearly visible as a robust line in the mid-frontal bones suggesting biomechanical significance. It is possibly a morphological adaptation, making the aurochs capable of bearing large headgear despite the high stresses observed.

The horn masses were then scaled in Chillingham and domestic cattle to be proportionally the same as in aurochs to assess the impact of cranial morphological variation. This alternatively could have been achieved by making all the models the same size and applying the same force. By doing this we can remove some of the impacts of size and focus more on the cranial morphology and its response to load. This produced a result that moderately supports hypothesis two, that aurochs seem to have a lower magnitude of stress than other models. This is most noticeable in comparison of the cranial vault, where both the domestic and Chillingham models show high stress while the aurochs has lower stress. However general patterns of stress across the rest of the cranium seem to be comparable between all models. It is therefore proposed that the morphology of aurochs has a mild advantage in dissipating stress across the frontals. Again, the role of the frontal suture must be highlighted as a possible explanation for the stress resistance seen in this area, with horn mass providing an impetus for thicker bone where the mid-sagittal suture has fused. The more concave shape of the aurochs' frontal bones might also play some role. While bone can fail due to fatigue or larger stresses (Alexander, 1984), it can also remodel to adapt to strain in order to resist it. As forces act on the bones within the range of normal activity, the strain in bone would lead to the formation of desirable morphology through adaptive remodelling of bone due to the mechanical loading (Biewener, 1991). However, if stress grew too large there would be bone failure, indeed in practice, stress and strain are very closely related, particularly in models with isotropic material properties as used here. Aurochs evidently have very large horns, so it is unsurprising that their crania are adapted to bearing the associated mass. The cranial shape of aurochs could assist in stress dissipation and reduction, having a broad and concave frontal bone with pronounced frontal suture that can resist the forces generated by gravity acting on the large horns. The angle of the frontal joining the nuchal arch/occipital might also play some role in this, being acute and the occipital being almost concave. This could possibly help resist tension and compression. In the shape analysis in Chapter Four, these were key areas that separated cattle from aurochs, and therefore shape and robusticity in the braincase region might be important in having larger horns. It may be that horns can act as effective drivers of cranial morphology, particularly in the posterior aspect of the cranium.

While differences might seem to be subtle, changes in the biomechanical ability of the cranium could be related to morphological differences because of domestication. Various traits in domestic cattle have been intensely selected for (Taberlet *et al.*, 2008; van Vuure, 2005), and this includes horn reduction and absence in many cattle species (Schafberg and Swalve, 2015). Size is often one of the most obvious and first documented changes (Albarella, 2002; Ervynck *et al.*, 2001; Dayan, 1994; Morey, 1992; Morey and Wiant, 1992; Payne and Bull, 1988; Flannery, 1982), and often contributes a major component of any shape change. In the domestic models used here, horns were significantly smaller than would be expected if cattle were simply scaled down versions of the aurochs. The horns associated with the domestic cranium used in this study were of small size, so it is possible that the capability to bear large headgear might also be breed or even individual specific. In domestic cattle cranial morphology might simply be adapted as required for the load, considering the low biomechanical demand of small horns. Bone is known to respond to stress and remodel to mitigate stress (Haelterman and Lim, 2019; Wippert *et al.*, 2017), so perhaps smaller horns only require minimal adaptation of the cranium. It might also be that having smaller horns is an efficient way to reduce mechanical load on the cranium, so this could have biomechanical advantages. Reducing the amount of force on the cranium from smaller horns might therefore be a valid strategy in stress reduction, although it is noted this was likely a by-product of selection for other traits. The Chillingham cattle model provides a juxtaposition to both the aurochs and domestic cattle, although a domestic cattle (*Bos taurus*) in taxonomic terms, has been rewilded and allowed to establish its own evolutionary (Hall *et al.*, 2005; Visscher *et al.,* 2001) and indeed morphological trajectory (as established in Chapter Four). In terms of the stress patterns seen in heatmaps, the Chillingham model was more consistent with the domestic cattle than aurochs. Chillingham skulls were noted in the shape analysis in Chapter Four to be quite gracile and slender, more similar in many regards to aurochs than some domesticates given the significant variation in domestic shape. In addition, from observation of Chillingham crania, they seem to be deficient in a well-defined sagittal suture, which is the opposite to aurochs where it can be seen clearly and robustly. It is possible that the present horn configuration in Chillingham cattle might be at the limit of their size potential for horns. As seen in the aurochs' model there might be a more specific morphology required to house large horns and the associated stress in the cranium. In the aurochs' model, the region that performed differently was the frontals, known to be an area of shape disparity compared to domesticates. Morphology in aurochs may be better adapted to stress as they had to support large headgear.

While size reduction linked to domestication likely accounted for much of the difference in stress seen in the absolute size models, the scaled domestic models did share many similar stress patterns with aurochs. This might be because domestic cattle have the potential to achieve very large horns, as seen in some modern breeds. In fact, the horns of some breeds are likely far larger than aurochs in proportion to their body mass, and indeed a wider range of shape variation is seen in domesticated animals than their wild counterparts (Drake and Klingenberg, 2010). It therefore seems that other morphological and biomechanical adaptations might be taking place in some domestic cattle to accommodate excessively large horns. With human mediated domestication, changes can be established over a few generations and even deviate from established evolutionary trends (Manning *et al.*, 2015). It is likely horns are particularly susceptible for this, as domestication would disrupt the normal sexual selection pressure in wild cattle, and reduced sexual dimorphism is well known in domestic cattle (Helmer *et al.*, 2005; Trut, 1999). While many of these concepts are too complex for the scope of this initial study, the potential was alluded to in the sensitivity analysis. It was indicated that changing the angle and orientation of the head can change the magnitude and location of stress. While not specifically tested in this analysis, it is thought re-orienting horns vertically would reduce the bending moment placed on the cranium from horn mass and allow larger horns, while also reducing stress. This would align the horn more closely with the resultant reaction force and help keep maximum forces lower, due to improved mechanical efficiency carrying weight closer or through the body. Such a morphological adaptation has been well documented in limbs where the more vertically aligned the greater the force reduction (Biewener, 1991). Reduction on bending moment has not been detected specifically in horns but it could be suggested bighorn sheep seem to adopt this arrangement. Bighorn sheep have the largest horns in proportion to body size in ruminants (Geist, 1966) so it seems reasonable this is possible through vertical orientation of horns to reduce stress. The more vertical orientation of horns is seen to an extent in Chillingham cattle can be seen. A vertical orientation would certainly be advantageous when the head is in a neutral position, however, as the animal lowers its head the angle of horns would extend away from the central axis and forces would increase as the mass shifts. The closer towards horizontal the horn is, i.e. the further the mass extends from the cranium, the greater the force would be, inducing a strong bending moment on the cranium. In contrast aurochs' horns are generally described as sweeping horizontally out and forwards, this would decrease the distance horns protrude from the cranium in all head orientations resulting in more consistent forces regardless of head and horn orientation. While this concept was not specifically tested it would provide a point for further analysis. It is therefore suggested the size and orientation of horns relative to the cranium could therefore significantly impact cranial shape and morphological skeletal adaptations can assist stress reduction.

The results presented here offer a small insight into the possibilities in this area of research. In an attempt to look at only cranial morphology many of the parameters have deliberately been simplified. One of the obvious areas that was indicated is the concept of horn shape and how this loads the cranium, rather than applying a basic gravitational force. This seems to be closely related to horn orientation. While it is tentatively suggested orientation might be important in domestic cattle with large horns, the specific angle of the head would also change force distribution significantly. The biomechanical constraints in the cranium resisting stress would be based around the bending moment, with large and laterally extending horns imposing high bending forces (Ceacero, 2016), placing the cranium across the frontals in tension and under the horns in compression. A larger applied load, and the greater the given distance from the point of axis, induces more torque. It is also acknowledged that many of the forces induced here are everyday occurrences for cattle, supporting their horns against gravity. We know cattle undertake far more rigorous ordeals that would generate magnitudes of force exceptionally higher than the loading applied in this research. In wild cattle, it is known that horns are an important part of social interaction and individuals that lose their horns through breakage are disadvantaged. There could also be strong selection pressure for large horns and associated cranial morphology to support them. Constraints have been removed in domestic cattle, sometimes by physically removing horns, and the social order is more closely maintained by humans.

Horns are still shown to be important but are either selected for as a breed trait or removed through breeding or polling. Domestication could have the ability to influence horns in selection for both large and small horned animals, depending on the requirements for that specific cattle group. Perhaps farming, selective breeding, and the specific evolutionary lineage of domestic cattle has created a disconnect between morphology and selection pressure. Domestication of animals is already documented to give rise to a range of characteristics unseen in the wild (Raghanti, 2019). Given farming's close control and selective breeding, the driving factors for the use of horns in establishing herd hierarchy would be somewhat lessened. Where horns are selected for, it seems to be a more aesthetic choice, to maintain a breed's distinctiveness, rather than to enable normal function of the animals as if under free living conditions. Indeed, even in wild environments, pressures such as inter-animal social interaction can influence horn selection as seen in wild bovids, but it is likely this is a much weaker selection pressure than deliberate and sustained selective breeding by humans. However, this should be treated as very preliminary findings moving beyond the core scope of the analysis undertaken here and would involve further work to fully understand and establish the parameters of this.

In summary, much of this work is preliminary, being the first of its kind to investigate cranial biomechanics in response to horn mass in cattle. Nonetheless, the results suggest a morphological basis for difference in biomechanical stress across the different crania. While the primary basis of this is suggested to result from a size reduction in domestic cattle compared to aurochs there are additional factors. These seem to be some shape differences in the frontal bone in aurochs making their crania slightly more resistant to loading from very large horns. Domestic crania are not so well adapted, possibly a consequence of sample choice in model building as in this study the domestic crania included do not have the functional demands of big headgear. The domestic crania have only responded to stress as required; this does not mean all domestic cattle would follow this pattern. Domestication is known to produce an altered morphology to the progenitor population, and this morphology seems less well-positioned to sustain very large headgear. This is shown most clearly in our results in the Chillingham cattle models, who, despite having the smallest body mass, exhibit large horns. It is possible the horns in Chillingham cattle are not capable of further increasing in size as this has already been highly selected for and achieved a maximum. Indeed, it is suggested horns are more important than body mass as an indicator of social stature (Bouissou, 1972), so in the absence of human selection large horns would be highly advantageous. However, as horns can be well selected for, it seems domestic crania have achieved morphology in response to biomechanical loading. This is seen in the vertical positioning of horns reducing bending moment and torque on the skull. It is therefore possible that while horn size is highly selected for, there are limits based on the anatomy and robusticity of the crania, for example, it would not be possible for Chillingham cattle to increase horn size to that proportionally seen in aurochs, however it would be possible in domestic cattle. From the great variation seen in cattle breeds large horns are possible and could form the starting point for future exploration on this topic.

6.8.2. Limitations and suggestions.

As this work is very preliminary and novel in scope, there are, to date, very few published studies available for comparison of methods and results. The impact of horns on cranial morphology seems as yet to be reasonably unestablished and so this research provides significant contribution to that area of study. There are identified some points that could progress this research further in the future and provide greater clarity on the results seen here. In the first instance, this would be regarding the specimens used to build FEA models. For this study we used the most representative domestic cattle model from the shape analysis in Chapter Four, but no aurochs specimen was available for CT scanning and so an approximation was made via landmark warp. This process has been discussed in the previous chapter and its validity established in addition to the precedent set in other literature for this (O'Higgins, *et al.*, 2011; Stayton, 2009). However, the horns were only landmarked sparsely due to their homogenous nature denying significant anatomical features for comparative landmarks. Moving beyond this, another limiting factor for both models was the lacking background data, particularly sex. As has been discussed, sexual dimorphism is significant in bovids, and it is unclear the extent this will have impacted results. An indication might be gained from the Chillingham model made from a female individual. From work in the methods section of this chapter, we can see the female Chillingham model used here had a volume of 481.1cm^3, while a Chillingham male has a horn volume of over double at 1047.91cm^3. While any size differences might be mitigated by differences in skeletal robustness and bone density, this remains to be investigated and is unsubstantiated in this research.

There are a few points of caution in the methods and application around FEA, notably regarding the force sites. In this research we used an arbitrary five-centimetre buffer from the base of the horncore, termed basal loading. While this standardised the force location somewhat between models, it does not actually represent the true distribution of the horn's weight. Indeed, on the domestic cattle model with small horns, the buffer incorporated most of the horn but only a small proportion on the aurochs. When applying the force vector, this has the potential to increase the loading moment, and it remains to be seen if moving the force location proximally or distally along the horn would also have an influence. In addition, clearly horn weight in a living animal is complicated and the forces acting will be constantly changing depending on the angle of the cranium as the animal moves. To attempt to combat this, the sensitivity did explore briefly zero, 30 degrees and 60 degrees which models were tested, and showed some differences. While these angles show a good range of motion, it does not cover all possibilities and gives a small insight into the potential horn stress for living cattle. Furthermore, the taper of horns and the specific shape may also help transfer weight along the horn to the cranium and so reduce mass away from the body. This would potentially change the lever arm mechanics and moment, particularly if moving the force along the horn away from the body. The force moving away from the skull potentially increases stress although it is uncertain to what extent this would be a significant factor.

It should also be mentioned that the various measurements from which horn masses and scaled horn masses were calculated have some assumptions. Firstly, the aurochs horn mass was estimated as keratin tends not to survive archaeologically. This was done based on the relationship between horncore and keratin in the domestic and Chillingham cattle models. Using the two data points, we were able to project the slope and intercept and assume the relationship is constant to predict aurochs horn keratin volume. With so few data points, it is very uncertain if the slide and intercept used is accurate, and more cattle data would be required to investigate this. Ideally this would be calculated from a larger sample of cattle but would require significantly more CT scans of cattle with complete horncores and keratin sheaths which are unfortunately at present unavailable. Alternatively, an aurochs skull with keratin sheath could have been used to estimate the total volume of an aurochs horn. There are also some considerations with the scaled models, when domestic cattle and Chillingham models were given forces to simulate the relationship aurochs have with their horns. This is based on the relationship between cranial volume and horns, assuming the two factors are related. Similarly, this needs further investigation to establish if there is a link requiring more CT scans of cattle and aurochs' crania.

6.9. Conclusion.

The FEA has shown some interesting and unexpected trends in terms of the horn's impact on skull morphology. Both hypotheses were supported, with larger horns producing more force inducing high stress in crania, and with wild cattle better adapted to resist high stress resulting from large horns. It is suggested that there is a strong selection pressure on domestic cattle horns, with smaller horns being a quick evolutionary adaptation to reducing stress. This is possibly related to a change in cranial morphology linked with domestication, in which the range of variation becomes great. Aurochs are likely more conserved in morphology given the biomechanical demands of large horns requiring some level of robustness. While much of this work is novel in scope, the relationship between morphology and horn size is suggested to be a topic that could provide a significant contribution to our understanding of drivers of morphology and horn size. The evolutionary potential for variation in domestic horns could be great, with the possibility of horn size even greater than aurochs when accounting for body mass. It may be that aurochs have achieved what might be considered the full potential of their horn size, but domestic cattle could have relatively larger horns in comparison. More work is needed to fully understand what is a complicated and under-researched area of cattle development.

7. Chapter Seven: Discussion and Conclusion.

7.1. Introduction.

The purpose of this thesis was to investigate the relationship between aurochs and domestic cattle and the influence of humans in this interaction. Building on previous studies, new methods were used to address some of the long-held views about how cattle changed through the process of domestication. The results presented in this thesis make a potentially significant contribution to our understanding of topics around cattle morphology and the impact humans can have on this. This final chapter will present all the evidence in the context of the original research questions. As stated in Chapter One, the objectives were: to investigate the morphological changes between aurochs and domestic cattle and to see if shape change is important compared to size change, and to investigate possible functional impacts of shape change in relation to feeding and the possession of horns.

These objectives were developed in response to the typical kinds of research that have previously been undertaken in the study of cattle. These predominantly perpetuated a specific idea, that aurochs and cattle were morphologically overlapping in terms of their size and shape. The key distinguishing factor in research was always size. However, when we look at similar work in other species, new methods have shown that there were often fine scale changes in shape (Alarcón-Ríos *et al.*, 2017) that were often missed in studies of cattle due to lack of available methodological subtlety. Indeed, the causes of shape changes particularly in cattle had not adequately been addressed to ask why changes might be occurring and the mechanisms that underpin morphological changes. Considering this, geometric morphometrics (GMM) and finite element analysis (FEA) were proposed as suitable tools to investigate if shape change occurs between aurochs and domestic cattle, and to evaluate the biomechanical differences that could be linked to morphological change.

7.2. Summary of key findings.

Resulting from the research questions, the findings of the shape analysis showed aurochs and cattle have different shape cranial morphology. This was established via GMM where aurochs and cattle crania clustered distinctly in shape space with no overlap (see Chapter Four).

Looking at the overall shapes, aurochs were seen to have relatively slender and convex crania compared to the generally broader and more concave shapes seen in domestic cattle. Along with this the cattle also occupied a larger shape space suggesting considerably more overall variation within the domestic group, compared to a more constrained aurochs morphospace. The differences in shape between aurochs and domestic cattle were noted as having similarities to those commonly found in other species where similar work has been undertaken in relation to wild and domestic variants (Selba *et al.*, 2019; Veitschegger *et al.*, 2018; Owen *et al.*, 2014). The trial analysis of fragmentary cranial material should also be noted, whilst still very preliminary, in which the analysis was rerun with a reduced landmark set that just covered the frontlets. Even when applying a reduced landmark set, results held validity and produced a similar result to the full landmark set, although with slightly less marked separation between cattle and aurochs. Being able to include incomplete crania also greatly increased the number of specimens available for inclusion into analysis. This should offer confidence to researchers wanting to include partial material in their analyses in the future.

Further to the findings of the shape analysis, size was also investigated, given the attention it has received in past research (Wright and Viner-Daniels, 2014; Linseele, 2004; Grigson, 1969). Indeed one of the major shape-based changes noted when looking at shape alone is often a combined factor of size-shape (Cooke and Terhune, 2015). Size can have a potentially significant contribution in determining shape, and from regression analysis on allometry of each species group this showed that aurochs and domestic cattle were on divergent size-to-shape (allometric) trajectories. Size changes were shown to be significant but also indicated far from simply being smaller, domestic cattle are on a very different morphological path, separate to the size and shape relationship of aurochs. However, shape and size differences were also noted as being marked within the domestic group itself, again highlighting the high internal variation in domestic cattle. Generally, the results of size and shape analysis revealed changes that cannot simply be described with size scaling alone, and that morphology is important in the differenced observed between domesticates and aurochs.

When considering the shape and size results, some areas of the cranium seem to be clearly responding in different ways between aurochs and domestic cattle, environment and feeding in conjunction with domestication, was considered to have the potential to drive specific aspects of cranial morphology (Lieberman *et al.*, 2004). Using a new method in the study of cattle husbandry, this was investigated through FEA. FE models of the skulls of an aurochs, domestic cattle and a Chillingham cattle were built and loaded to simulate biting on the molar teeth. The results indicated that aurochs' cranial morphology was better able to cope with the stresses caused by feeding. This was further evidenced by the higher mechanical efficiency of biting in aurochs compared to domestic cattle and the rewilded Chillingham cattle was also seen to have a greater efficiency then its domestic peer, suggesting much of the difference in result between wild and domesticated cattle might be highly related to diet and habitat. Wild cattle would by necessity need to forage and process a wider range of food materials more regularly and so bite force and efficiency needs to be better adapted (Sanson, 2006). It appears that domestication and human husbandry certainly have some influence on cattle feeding, but it is difficult to extrapolate the exact mechanisms. It seems plausible that both humans selecting for domestic traits might have created a different cranial morphology which reduced feeding performance, and feeding cattle less mechanically resistant food could drive remodelling of the skull.

Another aspect of the shape analysis was also considered, the area of the skull that supports horns. This was seen as an area of great shape difference both between aurochs and domestic cattle but also internally within the cattle group itself. A very preliminary study was therefore conducted to begin investigating this area as a possible region of morphological difference due to the biomechanical implications of headgear. These results showed when absolute mass was applied to the cranium, aurochs with very large horns had much greater magnitudes of stress compared to domesticates. However, when horn masses were scaled so proportionally similar forces were applied to all models, aurochs were considered marginally better adapted to cope with high loads. When the results are further considered, mechanical loading of larger horns could therefore help drive the formation of desirable morphology through adaptive remodelling of bone (Biewener, 1991). It is proposed aurochs have a more highly conserved morphology given the biomechanical demands of large horns requiring some level of robustness probably resulting from the high selection pressures horns provide in gaining and protecting resources (Johnson *et al.*, 2021; Nasoori, 2020; Preston *et al.*, 2003). Conversely, domestic cattle have undergone successive relaxation in factors that favour large horns, particularly sexual selection, which has led to small horns and a relaxing of the requirement for crania to be able biomechanically to support the associated large loads.

7.3. Interpretation of results.

When considered all together the results present a further step in aurochs and cattle research. Unlike much of the earlier research on aurochs (Grigson 1978; Bohlken 1964) and building on more recent large scale biometry analysis (Wright, 2016; Wright and Viner-Daniels, 2015; Viner-Daniels, 2014), it has been shown that the species are not as homogeneous as previously suggested (Grigson, 1978; Bohlkan, 1962). The results here provide strong evidence to suggest that since domestication, domestic cattle have been on their own morphological path. Furthermore, morphology is not considered to be similar between aurochs and domestic cattle, but divergent. This means if domestic cattle were to continue to follow their current trajectory, they would increasingly develop their own distinct morphology. A further key point is that the morphological analysis highlighted that domestic cattle showed great variation across the whole group, something not seen to such a great degree in the aurochs group. Here we have shown that some of the variation might be in part due to feeding ecology and horn size. Despite the results highlighting the shape diversification in the cattle cranium, distinguishing specific drivers of such evolution remains challenging. The underlying drivers of any morphological change can arise from multiple genetic and environmental factors concerned in this process (Stumpp *et al.*, 2018; Vidal-García and Scott, 2017; Marshall *et al*., 2014). This is of course in addition to the artificial selection of domestication that will have played an important role (Larson *et al.*, 2014).

With domestication in mind, humans' role in facilitating change cannot be understated. Domestication was the initial impetus that established cattle as a distinctive species, separate to the aurochs. Indeed, as noted by van Vuure (2005) the physical aspects of aurochs began to change from the moment of domestication when natural selection pressures were relaxed, and human selection implemented. It is also apparent that domestication and the consequent morpho-functional changes can occur extremely rapidly under human mediation, in as little as a few generations (Larson *et al.*, 2014; Wilkins *et al.*, 2014). Domestication of animals is known to produce the conditions for unique characteristics to develop that would not be prevalent in wild progenitor populations and domestic cattle seem to follow many of the common trends seen in other domestic species when compared to their progenitor (Albarella, 2002; Ervynck *et al.*, 2001; Dayan, 1994, Morey, 1992, Morey and Wiant, 1992; Payne and Bull, 1988; Flannery, 1982). These are often referred to as 'domestication syndrome' resulting in a suite of changes in response to the genetic and environmental conditions in the domestication process (Parsons *et al.*, 2020). Such changes include shortening of the craniofacial region, reduction in overall size, concavity of the skull, smaller cranial vault and indeed any deviation in morphology not seen in progenitor or wild counterpart populations (Diamond, 2002; Gross, 1998; Belyaev and Trut, 1989; Kohane and Parsons, 1988; Trut, 1988; Grigson, 1969). All these changes were noted in the domestic cattle crania analysed in this research, compared to aurochs. While definition or refinement of the markers and conditions of domestication was not within the scope of this study, some comments can be made. We have detected domestic traits in this research, initially in the wide variation seen in cranial morphologies of domestic specimens included in shape analysis. This extended to decreased feeding efficiency in domesticates, considered a product of humans providing food and decreased time spent foraging tougher vegetation. Furthermore, the decreased ability of crania to carry robust horns, again due to human selection for small sized horns and even absence of horns reducing the selection pressure that would normally be present for large headgear in wild populations.

In terms of the wider implications of the results, it seems aurochs might be more constrained in their morphology compared to their domestic descendants. While we have alluded to this in the previous discussion regarding domestication, the possible constraints and their impact are worth highlighting. Wild species have many selection pressures that maintain a generally stable population and eliminate unfavourable mutations (Allendorf and Hard, 2009). The results from this thesis seem to indicate a reduction in the ability of domestic cattle to thrive independently in the wild, particularly from feeding biomechanics but also their general fitness seen through the lack of traits which are important in wild populations such as, large horns. Although any potential disadvantage in domestic cattle would be marginal and not a significant impediment as evidenced by the Chillingham cattle. This research showed that in relatively little time, evolutionarily speaking, Chillingham cattle have established a viable wild cattle population that have improved characteristics compared to their associated domestic peers. Much of this is derived from competition in the wild for resources, i.e., food and reproduction. Contrast this with domestic cattle, particularly in more recent times where animal husbandry closely manages all aspects of an animal's life and removes many of the basic survival adaptations, instead placing pressure on different traits. It seems almost as quickly as cattle can be altered under human husbandry, so too can they adapt back to living wildly (van Vuure, 2005) and this has certainly been noticed here in the Chillingham cattle.

7.4. Limitations of this research.

While this research strives to make use of innovative methods and apply new techniques, highlighting many new findings, there are some general limitations to be noted. The primary consideration is the sample used and its composition and how it might have affected the results. The majority of the domesticates were from more recent periods (18th century to present) with many coming from comparative anatomy collections. It is therefore more difficult to make suggestions about historic, and even prehistoric, husbandry as we are predominantly measuring the most recent product of domestication. Indeed, GMM is reliant on a good sample to accurately define the shape space of a group. As such the specific specimens in the sample will define how morphological variation is displayed and interpreted. While group size was generally thought to be sufficient, the aurochs and cattle groups were uneven in number of specimens, with many more domesticates than aurochs. However, this was symptomatic of the wider specimen collections held by institutions, with every available near-complete aurochs' skull being included. So, while the aurochs' sample may be relatively fewer, it is exhaustive for the study area focus of Britain. Furthermore, to fully interpret the results it can be useful to define characteristics that might have an influence on morphology beyond species alone. Traits that are known to be diagnostic in cattle are sex and breed, both potentially having a marked impact (Albarella, 1997). Indeed, the morphological disparity between males and females in the domestic group was in some cases greater than the differences between domesticates and aurochs. No sex information was known for the aurochs' specimens so the impact of this factor could not be explored for this data set. Breed was also suggested to be distinctive as indicated by the Chillingham cattle clustering in shape space but again there was no comparative data for other breeds to assess this against. Similarly no chronological information for the domestic cattle, more specifically no groups representing prehistoric cattle makes the results of this thesis unlike the majority of previous studies, giving novel conclusions on the basis of the data set.

The other primary limitation was in the FEA analysis. Unlike many other zooarchaeological methods, FEA uses a single individual as representative of the sample. Clearly this creates room for outliers to influence FEA results if care is not taken with specimen selection, but FEA has generally been accepted as a valid and reliable method if it is understood the individual chosen is merely a proxy for the larger population or species group (Godinho *et al.*, 2017; Toro-Ibacache *et al.*, 2016a). To minimise the effects of this the domestic cattle specimen chosen for FEA was close to the mean of all domesticates in the shape space, thus representing an 'average' domestic cattle (at least of the sample assembled here). An aurochs cranium was not available to be CT scanned as a direct result of the Covid-19 pandemic, and so a warped model was created from the domestic cattle model. Again, there is good precedent for such a procedure in similar FEA studies on other species (Toro-Ibacache *et al.*, 2016b). The Chillingham model was generated from the availability of crania at Chillingham Wild cattle park, selecting the most complete cranium. The Chillingham FEA model does raise the important point of sexual dimorphism, as the model created was female and it is at present uncertain how much difference there is between male and female cattle. This research and some previous work on sexual dimorphism and size seems to indicate differences could be great (Ruckstuhl and Neuhaus, 2000). The data regarding the physical properties of cattle performing tasks in real life would have been of value but was surprisingly absent from the literature. Forces for muscles were needed so bite force could be investigated, and data surrounding horn mass and volume was also not commonly available. While this research has now produced values for these, further measurements of these values from other specimens would be beneficial to confirm their validity.

Finally, it should be noted that these are general considerations, based on factors that might have impacted on the research. They should be taken alongside specific recommendations for each particular research method given in the chapter pertaining to it. Despite the general limitations of this research, the data and results provide a strong starting point for future research in this area. As mentioned, many of the problems faced were due to the lack of suitable comparative studies and available data. The lack of data is not thought to undermine any of the conclusions as samples were still large enough for all tests and statistics to be valid. Furthermore, with a paucity of previous evidence against which to base many of the results this would in many cases provide useful preliminary research regarding aurochs and cattle.

7.5. Recommendations for further research.

While the key overall limitations of this research have been highlighted, this study does attempt to provide a significant contribution to the field of aurochs and cattle relationships and domestication. Future studies could continue this work building particularly on the data set. This study was based in the UK and was limited to specimen availability which obviously provides a limited geographical data set. While in the context of this initial research the UK was thought to be ideal, extension to more regions would increase the sample and allow further comparison. Expansion of the data could be possible by including European countries, particularly those where aurochs remains with a better-defined chronology are more numerous such as Denmark. It would also benefit by adding a geographical and temporal element to the research that is at present absent. Aurochs have previously been shown to be geographically variable and this could certainly be explored using shape-based methods to explore the full extent of morphologies. Part of this could be a better resolution of chronology, particularly radiocarbon dating of aurochs remains, but also inclusion of more intact domestic cattle remains from a variety of time periods, it would also be an opportunity to expand to other skeletal elements to evaluate if postcranial bones are also diagnostic. This would have several advantages, namely many elements being significantly more robust than the cranium, and which are more frequently recovered archaeologically. Morphologically speaking however, the research questions would differ as limb bones have a different biomechanical function to the skull.

Another area in which additional work would significantly improve our understanding of cattle would be with physical specimens and soft tissue. As discussed, data regarding the physical attributes of cattle is particularly lacking, likely in part due to the difficulty in obtaining such data. Further work would continue exploring cattle bite force, dissecting additional specimens, and measuring the muscle fibre length and cross-sectional area for more accurate muscle estimates. This could include in vivo work with force metres to gauge actual cattle bite force as the possibility of over-estimation via methods used in this research is high. This is due to the assumption that we are using full muscle activation, something cattle likely rarely do, instead having large masticatory muscles to resist fatigue associated with long periods of chewing. Ideally this could be done for a range of different size cattle to establish a range of possible and common bite forces. Obviously, such work can never be undertaken on aurochs, being extinct, but more dry skull work estimating the supposed bite force on additional specimens along with scaling of known in vivo or muscle dissection data would certainly assist refinement of our estimates.

The parameters around horns similarly need additional exploration, at a general level many of the mechanical properties of horns have been partially researched such as physical and material properties (McKittrick *et al.*, 2012; Li *et al.*, 2010; Kitchener, 1987). However, a lot more investigation could be undertaken regarding the range of variation of size and orientation on the skull. These two areas were the main problematic points in Chapter Six of this research as they are difficult to quantify. There is certainly scope for a large amount of research to be conducted, this could take the form of a GMM study with landmarks and semi-landmarks defining the horn shape and attachment angle to the cranium. Followed by further FEA work to investigate the ways different loadings can impact stress distribution. Furthermore, the resting gravitational mass of horn is the least force crania have to resist, and in use horns and the cranium experience magnitudes of stress hundreds of times higher. Further research could also look at the maximum limit of horns in terms of stresses before failure through mechanical testing and how these forces are transmitted down into the cranium to enable better understanding of the properties of horns that can impact the skull in a practical sense.

7.6. Conclusion.

To summarise, this research has used novel techniques and methods to advance the study of aurochs and domestic cattle being the first thorough study found after examination of the literature, of the species using shape-based analysis and biomechanical simulations. It has been demonstrated that aurochs are significantly different from their domestic descendants both in their overall cranial shape but also in the functional role the cranium has in living processes. Indeed, aurochs were seen to be much better adapted to life in the wild, absent from human influence. On the other hand, it is that very human husbandry that has led to the success of modern cattle across the world, being so highly adaptable. This work has highlighted some of the potential sources of such variation in cattle and the findings should be of use to zooarchaeologists and anatomists in looking at variation in species along with the impact of domestication and husbandry. It is hoped the data presented here will facilitate future researchers to build on the conclusions.

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Appendix One: Specimen List.

Project ID	Used in Analysis	Condition	Species	Breed	Sex	Period	Find Location	Institution Accession Number	Institution	Notes
1	Full set	Complete	Bos primigenius	N/A	N/A	N/A	N/A	1933.44.1	National Museums Scotland	
2	Full set	Complete	Bos primigenius	N/A	N/A	N/A	N/A	1933.160.002	National Museums Scotland	
3	Full set	Complete	Bos primigenius	N/A	N/A	N/A	Turbary, Kirkcudbrightshire	1972.5062	Natural History Museum London (Life Science)	Formerly palaeo M36405, presented earl of Selkirk 1859
4	Full set	Complete	Bos primigenius	N/A	N/A	Pleistocene	Near Athol, Perth	1972.5068	Natural History Museum London (Life Science)	Formerly palaeo M2245, presented D. Inglis Esq
5	Full set	Complete	Bos primigenius	N/A	N/A	Pleistocene	Lake District	1977.5012	Natural History Museum London (Life Science)	Formerly Palaeo M29481, presented by Miss M. G. leigh in 1971
6	Full set	Complete	Bos primigenius	N/A	N/A	Early Holocene?	N/A	N/A	Historic England	

7	Full set	Complete	Bos primigenius	N/A	N/A	N/A	N/A	475PVOR50086	Natural History Museum London (Palaeo)	On display in Museum of London
8	Full set	Complete	Bos primigenius	N/A	N/A	Pleistocene	N/A	Q.1878	Natural History Museum Oxford	
9	Full set	Complete	Bos primigenius	N/A	N/A	N/A	N/A	1998.77.1	National Museums Scotland	
10	Full set	Complete	Bos primigenius	N/A	N/A	N/A	N/A	1966.19	The McManus, Dundee	
11	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene to Neolithic?	Burwell Fen, Cambs	D33665a	Sedgwick Museum of Earth Sciences (Store)	1863
12	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Burwell Fen, Cambs	D33691a	Sedgwick Museum of Earth Sciences	1898
13	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Barrington	X50265	Sedgwick Museum of Earth Sciences	1900
14	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Barrington	X50266	Sedgwick Museum of Earth Sciences	1900, collected by C. E. Gray
15	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Barrington	X50267	Sedgwick Museum of Earth Sciences	1899

16	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	X50268	Sedgwick Museum of Earth Sciences	
17	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Isleham Fen	X50289	Sedgwick Museum of Earth Sciences	1898
18	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	AX5909	Newcastle Discovery Centre	
19	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	NEWHM 2016.H63	Newcastle Discovery Centre	
20	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	NEWHM HANM 3.359	Newcastle Discovery Centre	
21	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	H.29021	Cambridge Zoology Department	
22	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	H.29028	Cambridge Zoology Department	
23	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	H.29031	Cambridge Zoology Department	
24	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	HE1female	Historic England	

25	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Royal Holloway University London	
26	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Royal Holloway University London	
27	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1998.77.2	National Museums Scotland	
28	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1921.125	National Museums Scotland	
29	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1931.78.1	National Museums Scotland	
30	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	National Museums Scotland	Mounted skull
31	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1993.160.003	National Museums Scotland	
32	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1993.16.1	National Museums Scotland	
33	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	GSM53763	British Geological Survey	

34	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	GSM62589	British Geological Survey	
35	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Cotton collection	N/A	British Geological Survey	
36	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1986.5008	Natural History Museum London (Life Science)	
37	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	M385	Natural History Museum London (Palaeo)	Egerton collection
38	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Northwich?	M394	Natural History Museum London (Palaeo)	
39	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Twickenham	M5970	Natural History Museum London (Palaeo)	Dredged from the Thames at Twickenham, presented Leeson 1896
40	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Chingford, Essex	M10355	Natural History Museum London (Palaeo)	presented by metropolitan water board 1911
41	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Barrington, Cambs	M12241	Natural History Museum London (Palaeo)	Presented by Prof I McKenny Huges 1902
42	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Banbury	M17132	Natural History Museum London (Palaeo)	Frontlet and horn-cores of the urus. Discovered during the building of the Great Central

										Railway in 1899. Presented by F. Harding Esq. 1954
43	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	M21280	Natural History Museum London (Palaeo)	
44	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Osterley Park	M25192	Natural History Museum London (Palaeo)	From: K.J. Murphy Esq. Found eastside Osterley Park 100yrds back from Grand Union Canal - also a note saying: Willment's Pit 1958, received by museum 27.9.63
45	No	Fragmentary	Bos primigenius	N/A	N/A	late Pleistocene	Bournemouth, Dorset	M34868	Natural History Museum London (Palaeo)	18' deep nw corner of Kinson sewage works, castle lane Bournemouth. Present Wessex Water authority 22 sept 1977, through cooperation with Bournemouth Museum
46	No	Fragmentary	Bos primigenius	N/A	N/A	Pleistocene	Ilford, Essex	M45434	Natural History Museum London (Palaeo)	Purchased from Sir Antonio Brady Mar 1874
47	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Milton St Swanscombe, Kent	M5066	Natural History Museum London (Palaeo)	presented 1894

48	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Natural History Museum London (Palaeo)	
49	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Ilford, Essex	OR45425	Natural History Museum London (Palaeo)	Purchased from Sir Antonio Brady Mar 1874
50	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Ilford, Essex	OR45428	Natural History Museum London (Palaeo)	Purchased from Sir Antonio Brady Mar 1875
51	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Ilford, Essex	OR45432	Natural History Museum London (Palaeo)	Purchased from Sir Antonio Brady Mar 1876
52	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Ilford, Essex	OR45433	Natural History Museum London (Palaeo)	Purchased from Sir Antonio Brady Mar 1877
53	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	Twickenham	OR46881	Natural History Museum London (Palaeo)	
54	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Harris Museum, Preston	
55	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.1	Harris Museum, Preston	C14 dated to 1700BC
56	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.2	Harris Museum, Preston	C14 dated to 2880BC

57	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.4	Harris Museum, Preston	
58	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.5	Harris Museum, Preston	
59	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.6	Harris Museum, Preston	
60	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.7	Harris Museum, Preston	
61	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.12	Harris Museum, Preston	
62	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.13	Harris Museum, Preston	
63	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.19	Harris Museum, Preston	
64	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.22	Harris Museum, Preston	
65	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.23	Harris Museum, Preston	
66	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.24	Harris Museum, Preston	
67	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.25	Harris Museum, Preston	
68	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.26	Harris Museum, Preston	

69	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.27	Harris Museum, Preston	
70	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.30	Harris Museum, Preston	
71	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.31	Harris Museum, Preston	
72	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	PRSGM1997.54.15	Harris Museum, Preston	
73	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Harris Museum, Preston	
74	No	Fragmentary	Bos primigenius	N/A	N/A	Neolithic?	Goosemire Fen, Yorkshire	NA	Lower Winskill Farm, Tom Lord	
75	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	CB5542	Bristol Museums	
76	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	CC6635	Bristol Museums	
77	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	LL.144.A	Manchester Museum	
78	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	LL.144.B	Manchester Museum	
79	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	1981.923	Perth Museum and Art Gallery	

80	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Seacity, Southampton	
81	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	46.1995.506	Museum of Somerset	
82	Partial set	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	tthcm.784.1990.1	Museum of Somerset	
83	No	Fragmentary	Bos primigenius	N/A	N/A	N/A	N/A	N/A	Wessex Archaeology	
84	No	Fragmentary	Bos primigenius	N/A	N/A	Neolithic	N/A	N/A	AS Archaeology, Suffolk	
85	Full set	Complete	*Bos taurus*	Chillingham	Male	Modern	N/A	N/A	Chillingham Wild Cattle Park	
86	Full set	Complete	*Bos taurus*	Chillingham	Male	Modern	N/A	N/A	Chillingham Wild Cattle Park	
87	Full set	Complete	*Bos taurus*	Chillingham	Male	N/A	N/A	N/A	Chillingham Wild Cattle Park	
88	Full set	Complete	*Bos taurus*	Chillingham	Male	N/A	N/A	N/A	Chillingham Wild Cattle Park	
89	Full set	Complete	*Bos taurus*	Chillingham	Male	N/A	N/A	N/A	Chillingham Wild Cattle Park	

90	Full set	Complete	*Bos taurus*	Chillingham	Male	N/A	N/A	N/A	Chillingham Wild Cattle Park	
91	Full set	Complete	*Bos taurus*	Chillingham	Female	Modern	N/A	N/A	Chillingham Wild Cattle Park	
92	Full set	Complete	*Bos taurus*	Chillingham	Female	Modern	N/A	N/A	Chillingham Wild Cattle Park	
93	Full set	Complete	*Bos taurus*	Chillingham	Female	Modern	N/A	N/A	Chillingham Wild Cattle Park	
94	Full set	Complete	*Bos taurus*	Chillingham	Female	N/A	N/A	N/A	Chillingham Wild Cattle Park	
95	Full set	Complete	*Bos taurus*	Chillingham	Female	N/A	N/A	N/A	Chillingham Wild Cattle Park	
96	Full set	Complete	*Bos taurus*	Chillingham	Female	N/A	N/A	N/A	Chillingham Wild Cattle Park	
97	Full set	Complete	*Bos taurus*	Chillingham	Female	N/A	N/A	N/A	Chillingham Wild Cattle Park	

98	Full set	Complete	*Bos taurus*	Chillingham	N/A	Modern	N/A	N/A	Chillingham Wild Cattle Park	
99	Full set	Complete	*Bos taurus*	Chillingham	N/A	Modern	Chillingham	R625	University of Leicester	
100	Full set	Complete	*Bos taurus*	Chillingham	N/A	Modern	Chillingham	R748	University of Leicester	
101	Full set	Complete	*Bos taurus*	Chillingham	N/A	Modern	Chillingham	R749	University of Leicester	
102	Full set	Complete	*Bos taurus*	Chartley	Male	Modern	Chartley park, staff	0.46 - 1980.2665	Natural History Museum London (Life Science)	
103	Full set	Complete	*Bos taurus*	Chartley	Male	Modern	Skermer	1924.4.28.1	Natural History Museum London (Life Science)	
104	Full set	Complete	*Bos taurus*	Scottish Short Horn	Male	Modern	N/A	1952.8.15.3	Natural History Museum London (Life Science)	
105	Full set	Complete	*Bos taurus*	Longhorn	Female	Modern	Birmingham	1953.3.3.1	Natural History Museum London (Life Science)	
106	Full set	Complete	*Bos taurus*	Chartley	Female	Modern	Chartley park, staff	0.32	Natural History Museum London (Life Science)	

107	Full set	Complete	*Bos taurus*	Cadzow	Male	Modern	Hamilton and Kinneil Estate	1954.8.28.1	Natural History Museum London (Life Science)	c.4.5 years old
108	Full set	Complete	*Bos taurus*	Longhorn	Male	Modern	Birmingham	1953.3.16.1	Natural History Museum London (Life Science)	Bullock
109	Full set	Complete	*Bos taurus*	Welsh black	Male	Modern	Royal Holloway University London	1954.7.3.1	Natural History Museum London (Life Science)	
110	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	H28921	Cambridge Zoology Department	
111	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	University of York	
112	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	29	University of Southampton	
113	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	D528	University of Southampton	
114	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	2747	**Sheila Hamilton-Dyer**	
115	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	3750	**Sheila Hamilton-Dyer**	
116	Full set	Complete	*Bos taurus*	Highland	Male	Modern	N/A	4523	**Sheila Hamilton-Dyer**	

117	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	OC1328a	Natural History Museum Oxford	
118	Full set	Complete	*Bos taurus*	Kerry	Female	Modern	N/A	2410	Historic England	
119	Full set	Complete	*Bos taurus*	Short leg dexter	Female	Modern	N/A	2803	Historic England	
120	Full set	Complete	*Bos taurus*	Dexter	Female	Modern	N/A	2817	Historic England	
121	Full set	Complete	*Bos taurus*	Guernsey	Female	Modern	N/A	4091	Historic England	
122	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	Bournemouth University	
123	Full set	Complete	*Bos taurus* (Linne)	N/A	N/A	Medieval?	Bog of Allen, Ireland	D33730	Sedgwick Museum of Earth Sciences (Store)	Collected Mr. Murray, presented Prof Ridgeway 1901
124	Full set	Complete	*Bos taurus*	Gascon	Female	Modern	N/A	2711	Historic England	
125	Full set	Complete	*Bos taurus* (Bos longifrons)	N/A	N/A	N/A	Burwell Fen, Cambs	TN2080	Sedgwick Museum of Earth Sciences (Store)	

126	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	96H	National Museums Scotland	
127	Full set	Complete	*Bos taurus*	Hamilton	N/A	Modern	N/A	1876.21.2	National Museums Scotland	Modern Hamilton Ox
128	Full set	Complete	*Bos taurus*	Aberdeen angus	N/A	Modern	N/A	1929.40.118	National Museums Scotland	
129	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	1929.82.1	National Museums Scotland	Modern mature cow
130	Full set	Complete	*Bos taurus*	White park	Female	Modern	N/A	1965.39.1	National Museums Scotland	
131	Full set	Complete	*Bos taurus*	Heck	Male	Modern	N/A	1999.223	National Museums Scotland	
132	Full set	Complete	*Bos taurus*	Jersey	Female	Modern	N/A	2016.52.407	National Museums Scotland	
133	Full set	Complete	*Bos taurus*	Jersey	Female	Modern	Ashdown collection	2007.275	Natural History Museum London (Life Science)	

134	Full set	Complete	*Bos taurus*	Kerry	Female	Modern	N/A	0.24	Natural History Museum London (Life Science)	
135	Full set	Complete	*Bos taurus*	Chartley	Male	Modern	Chartley Park	1975.303	Natural History Museum London (Life Science)	
136	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	Natural History Museum London (Life Science)	
137	Full set	Complete	*Bos taurus*	Longhorn	N/A	Modern	Dersingham, Norfolk	0.23	Natural History Museum London (Life Science)	
138	Full set	Complete	*Bos taurus*	English polled	Female	Modern	N/A	1846.1.1.3	Natural History Museum London (Life Science)	
139	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	Portman Sq, London	1977.855	Natural History Museum London (Life Science)	
140	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	1062	National Museums Scotland	Modern ox
141	Full set	Complete	*Bos taurus*	Heck	Male	Modern	N/A	N/A	National Museums Scotland	

142	Full set	Complete	*Bos taurus*	Highland	Female	Modern	N/A	N/A	National Museums Scotland	
143	Full set	Complete	*Bos taurus*	Longhorn	N/A	Modern	N/A	N/A	National Museums Scotland	
144	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	Sk 14	National Museums Scotland	
145	Full set	Complete	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	National Museums Scotland	
146	Full set	Complete	*Bos taurus*	Ayrshire	Male	N/A	N/A	1952.8.15.1	Natural History Museum London (Life Science)	
147	Full set	Complete	*Bos taurus*	Ayrshire	Female	N/A	N/A	1952.8.15.2	Natural History Museum London (Life Science)	
148	Full set	Complete	*Bos taurus*	Welsh black	Male	N/A	N/A	1952.8.15.4	Natural History Museum London (Life Science)	
149	Full set	Complete	*Bos taurus*	Welsh black	Female	N/A	N/A	1953.4.21.1	Natural History Museum London (Life Science)	

150	Partial set	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	N/A	Burwell Fen, Cambs	D33695	Sedgwick Museum of Earth Sciences (Store)	1890
151	No	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	Medieval	Kings Ditch, Thompson Lane, Cambs	D33699	Sedgwick Museum of Earth Sciences (Store)	1896
152	No	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	Medieval?	Burwell Fen, Cambs	D33704	Sedgwick Museum of Earth Sciences (Store)	
153	Partial set	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	Medieval	Reach Fen, Cambs	D33705	Sedgwick Museum of Earth Sciences (Store)	1891, Longifrons crossed with Roman
154	Partial set	Fragmentary	Bos sp.	N/A	N/A	Roman to Medieval	Well in fissure, Mount Sorrel	D33712	Sedgwick Museum of Earth Sciences (Store)	1896
155	Partial set	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	Medieval	Reach Fen, Cambs	D33720	Sedgwick Museum of Earth Sciences (Store)	
156	Partial set	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	N/A	N/A	D33729	Sedgwick Museum of Earth Sciences (Store)	
157	Partial set	Fragmentary	*Bos taurus* (Bos longifrons)	N/A	N/A	N/A	Boltisham (Bottisham) Fen	TN2079	Sedgwick Museum of Earth Sciences (Store)	1890

158	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33706	Sedgwick Museum of Earth Sciences (Store)	
159	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33709	Sedgwick Museum of Earth Sciences (Store)	
160	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33710	Sedgwick Museum of Earth Sciences (Store)	
161	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33714	Sedgwick Museum of Earth Sciences (Store)	
162	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33715	Sedgwick Museum of Earth Sciences (Store)	
163	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33716	Sedgwick Museum of Earth Sciences (Store)	
164	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33740	Sedgwick Museum of Earth Sciences (Store)	
165	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	D33745	Sedgwick Museum of Earth Sciences (Store)	

166	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	H28752	Cambridge Zoology Department	
167	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	H28770	Cambridge Zoology Department	
168	Partial set	Fragmentary	*Bos taurus*	Ayrshire	Female	Modern	N/A	H28784	Cambridge Zoology Department	
169	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	H28904	Cambridge Zoology Department	
170	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	555	Bournemouth University	Half skull
171	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	FR:1994:202	Bournemouth University	Juvenile
172	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK from context 80	Bournemouth University	
173	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK from context 5131 (Annabelle)	Bournemouth University	
174	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK from context 5131 (Daisy)	Bournemouth University	

175	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK from context 11038	Bournemouth University	
176	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK31	Bournemouth University	
177	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK32	Bournemouth University	
178	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK36	Bournemouth University	
179	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK40	Bournemouth University	
180	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK49	Bournemouth University	
181	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK50	Bournemouth University	
182	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK60	Bournemouth University	
183	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK65	Bournemouth University	
184	No	Fragmentary	*Bos taurus*	N/A	N/A	BA/IA/Roman	N/A	SK66	Bournemouth University	
185	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	761	Historic England	half skull, juvenile

186	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	2024	Historic England	
187	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	2802	Historic England	
188	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	3495	Historic England	Juvenile
189	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	4007	Historic England	Juvenile
190	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	4092	Historic England	
191	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	4094	Historic England	Juvenile
192	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	19327	Natural History Museum Oxford	
193	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	OC1335	Natural History Museum Oxford	Skull in two halves
194	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	OC1338	Natural History Museum Oxford	Juvenile
195	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	OC1340	Natural History Museum Oxford	

196	No	Fragmentary	*Bos taurus* cross EU bison	N/A	N/A	Modern	N/A	2494	**Sheila Hamilton-Dyer**	
197	No	Fragmentary	*Bos taurus* cross EU bison	N/A	N/A	Modern	N/A	2495	**Sheila Hamilton-Dyer**	
198	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	2926	**Sheila Hamilton-Dyer**	
199	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	4232	**Sheila Hamilton-Dyer**	Juvenile
200	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	4234	**Sheila Hamilton-Dyer**	Juvenile
201	No	Fragmentary	*Bos taurus*	Zebu	Female	Modern	N/A	4436	**Sheila Hamilton-Dyer**	
202	Partial set	Fragmentary	*Bos taurus*	Ankole	Female	Modern	N/A	4474	**Sheila Hamilton-Dyer**	
203	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	DC45	University of Southampton	Most of posterior cranium missing
204	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	DC189	University of Southampton	
205	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	DC190	University of Southampton	
206	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	DC228	University of Southampton	

207	No	Fragmentary	*Bos taurus*	Friesian	N/A	Modern	Ballybot, Colgheen	2003.329	Natural History Museum London (Life Science)	Friesian cross calf - juvenile
208	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1920.53	National Museums Scotland	
209	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1929.40.64	National Museums Scotland	
210	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1929.40.65	National Museums Scotland	
211	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1929.40.69	National Museums Scotland	
212	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1929.40.70	National Museums Scotland	
213	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1993.160.15	National Museums Scotland	
214	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1993.160.16	National Museums Scotland	

215	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	N/A	National Museums Scotland	
216	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Roman	Newstead Roman Camp	1929.40.66	National Museums Scotland	
217	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	GSM625657	British Geological Survey	
218	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	N/A	British Geological Survey	
219	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	N/A	British Geological Survey	
220	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	N/A	British Geological Survey	
221	Partial set	Fragmentary	*Bos taurus*	N/A	N/A	Modern	Chillingham	R624	University of Leicester	
222	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	Chillingham	R747	University of Leicester	Juvenile
223	Partial set	Fragmentary	*Bos taurus*	Chillingham	N/A	Modern	Chillingham	N/A	University of Leicester	
224	No	Fragmentary	*Bos taurus*	N/A	N/A	N/A	N/A	1539	Bristol Museums	
225	No	Fragmentary	*Bos taurus*	N/A	N/A	Roman	N/A	N/A	AS Archaeology, Suffolk	

226	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	Chillingham Wild Cattle Park	
227	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	University of York	
228	No	Fragmentary	*Bos taurus*	N/A	N/A	Modern	N/A	N/A	University of York	

Appendix Two: R Code Used in Analysis.

Appendix 2.1 Mesh Distance Comparison

```
###Packages
library(rgl)
library(RRPP)
library(stringr)
library(Rvcg)
library(Morpho)
library(geomorph)
library(Arothron)
 #upload file and turn into R object mesh
mesh1<- file2mesh("Day1scaleAvScWarped.stl", clean = TRUE, readcol = FALSE)
mesh2<- file2mesh("day2scaleAvScWarped.stl", clean = TRUE, readcol = FALSE)
mesh3<- file2mesh("day3scaleAvScWarped.stl", clean = TRUE, readcol = FALSE)
 #run meshDist for each model comparison
mD1_2 <- meshDist(mesh1, mesh2, from = -5, to = 5, uprange = 0.9989,
    NAcol = "black", rampcolors = c("blue", "green","yellow","red"),
    shade = TRUE, scaleramp = TRUE, plot = TRUE, file = "dist1to2")
 mD1_3 <- meshDist(mesh1, mesh3, from = -5, to = 5, uprange = 0.9989,
    NAcol = "black", rampcolors = c("blue", "green","yellow","red"),
    shade = TRUE,scaleramp = TRUE)
 mD2_3 <- meshDist(mesh2, mesh3, from = -5, to = 5, uprange = 0.9989,
    NAcol = "black", rampcolors = c("blue", "green","yellow","red"),
    shade = TRUE,scaleramp = TRUE)
 dist(mesh1, mesh2)
 comp1<- render(mD1_2, from = -5, to = 5,
            uprange = 0.9989, tol = NULL, tolcol = NULL,
            rampcolors = c("blue", "green","yellow","red"), NAcol = NULL, displace = FALSE, shade = TRUE,
            sign = NULL, add = FALSE, scaleramp = NULL)
 export(comp1, file = "D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled data/MD1to2",
imagedim = "100x800")
```

Appendix 2.2: Principal Component Analysis

```
###Packages
library(Arothron)              #read.amira.dir
library(carData)               #car
library(car)                   #dataEllipse
library(ape)          #phylogenetics
library(phytools)              #phylogenetics
library(geiger)
library(rgl)
library(nlme)
library(geomorph)
library(scatterplot3d)
library(xlsx)        #opening .xlsx files
library(rlang)
library(abind)
library(stringr)
library(Rvcg)
library(RRPP)
library(Morpho)   #find.outliers
library(ggplot2)
```

```
 setwd("D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled data")
 # read in the data
Skull_data<-read.morphologika("user error.txt")
 #check data dimensions
dim(Skull_data$coords)
#should be correct number of landmarks, dimensions and individuals
#check the labels
Skull_data$labels
 #check the first 10 landmarks of first specimen
Skull_data$coords[1:10,,1]
 #set up labels for data
labels=substr(Skull_data$labels,1,5) #use 1 and 5 to denot the labels that is used?!
labels
day=factor(labels)
shapz=as.numeric(day)
 #plot PCA
#plot(PC_Skull$PCscores[,c(1,2)],main = "PCA by Species", col="black",pch=c(15:18)[shapz],cex=1.5) #pch is
point style
 ##Geomorph package
data=Skull_data
GPAS<-gpagen(Skull_data$coords)
 PCA<-plotTangentSpace(GPAS$coords,groups = day)
 #quick work around to label X and Y
#plot(PCA$pc.scores[,c(1,2)], main = "PCA by Day", xlab = "PC1 (27.7%)", ylab = "PC2 (18.4%)",
pch=c(15:18:21:30)[shapz], cex=1.5, asp=1)
#plot(PCA$pc.scores[,c(2,3)], main = "PCA by Species", xlab = "PC2 (18.4%)", ylab = "PC3
(7.9%)",pch=c(15:18)[shapz], cex=1.5,col=c("brown","navy")[species],asp=1)
 #Better plot with labels working
plot(PCA$pc.scores[,c(1,2)], main = "PCA user error",
            xlab =paste("PC 1 ", "(" , round(PCA$pc.summary$importance[2,1]*100, 1), "%)", sep=""),
            ylab =paste("PC 2 ", "(" , round(PCA$pc.summary$importance[2,2]*100, 1), "%)", sep=""),
  pch=c(15:19,21)[shapz], cex=1.5, asp=1, col=c("forest green","navy","orange","brown","red","black")[day])
 #set the legend
legend("topright", legend= unique(day),
  pch=unique(c(15:19,21)[shapz]),
  col=c("forest green","navy","orange","brown","red","black"), cex=1.2, bty="0")
 #write.csv(PCA$pc.scores, "D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled data/PCA data")
```

Appendix 2.3: Landmark Placement Disparity

```
###Packages
library(Arothron)           #read.amira.dir
library(carData)            #car
library(car)                #dataEllipse
library(ape)        #phylogenetics
library(phytools)           #phylogenetics
library(geiger)
library(rgl)
library(nlme)
library(geomorph)
library(scatterplot3d)
library(xlsx)       #opening .xlsx files
library(rlang)
```

```
library(abind)
library(stringr)
library(Rvcg)
library(RRPP)
library(Morpho)   #find.outliers
library(ggplot2)
 setwd("D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled data")
# read in the data
Skull_data<-read.morphologika("user error disparity.txt")
#check data dimensions
dim(Skull_data$coords)
#should be correct number of landmarks, dimensions and individuals
#check the labels
Skull_data$labels
#check the first 10 landmarks of first specimen
Skull_data$coords[1:10,,1]
#set up labels for data
labels=substr(Skull_data$labels,1,9) #use 1 and 5 to denote the labels that is used?!
labels
day=factor(labels)
shapz=as.numeric(day)
data=Skull_data
GPAS<-gpagen(Skull_data$coords)
# Morphological disparity for entire data set
gdf <- geomorph.data.frame(GPAS, day = data$labels)
distaprity=morphol.disparity(coords ~ 1, groups = day, data = gdf,
      iter = 999)
write.csv(distaprity$Procrustes.var, "D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled
data/disparity Proc V")
write.csv(distaprity$PV.dist, "D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled data/disparity
PV dist")
write.csv(distaprity$PV.dist.Pval, "D:/Chapter 3 - methods/sensitivity/real analysis/analysis/compiled
data/disparity P value")
```

Appendix 2.4 Centroid size

```
###Packages
library(Arothron)             #read.amira.dir
library(carData)              #car
library(car)                  #dataEllipse
library(ape)          #phylogenetics
library(phytools)              #phylogenetics
library(geiger)
library(rgl)
library(nlme)
library(geomorph)
library(scatterplot3d)
library(xlsx)         #opening .xlsx files
library(rlang)
library(abind)
library(stringr)
library(Rvcg)
library(RRPP)
```

```
library(Morpho)   #find.outliers
library(ggplot2)
 # read in the data
Skull_data<-read.morphologika("comparisonofbackgrounddata.txt")
#check data dimensions
dim(Skull_data$coords)
#should be correct number of landmarks, dimensions and individuals
#check the labels
Skull_data$labels
#check the first 10 landmarks of first specimen
Skull_data$coords[1:10,,1]
#set up labels for data
labels=substr(Skull_data$labels,1,12) #use 1 and 5 to denote the labels that is used?!
labels
day=factor(labels)
shapz=as.numeric(day)
#plot PCA
#plot(PC_Skull$PCscores[,c(1,2)],main = "PCA by Species", col="black",pch=c(15:18)[shapz],cex=1.5) #pch is
point style
##Geomorph package
data=Skull_data
GPAS<-gpagen(Skull_data$coords)
 PCA<-plotTangentSpace(GPAS$coords,groups = day)
 #quick work around to label X and Y
#plot(PCA$pc.scores[,c(1,2)], main = "PCA by Day", xlab = "PC1 (27.7%)", ylab = "PC2 (18.4%)",
pch=c(15:18:21:30)[shapz], cex=1.5, asp=1)
#plot(PCA$pc.scores[,c(2,3)], main = "PCA by Species", xlab = "PC2 (18.4%)", ylab = "PC3
(7.9%)",pch=c(15:18)[shapz], cex=1.5,col=c("brown","navy")[species],asp=1)
 #Better plot with labels working
plot(PCA$pc.scores[,c(1,2)], main = "PCA of Model Error",
	xlab =paste("PC 1 ", "(" , round(PCA$pc.summary$importance[2,1]*100, 1), "%)", sep=""),
	ylab =paste("PC 2 ", "(" , round(PCA$pc.summary$importance[2,2]*100, 1), "%)", sep=""),
  pch=c(15:17:18:30:31:35:40)[shapz], cex=1.5, asp=1, col=c("forest
green","navy","orange","brown","red","pink","black")[day])
#set the legend
legend("topright", legend= unique(day),
  pch=unique(c(15:17:18:30:31:35:40)[shapz]),
  col=c("forest green","navy","orange","brown","red","pink","black"), cex=1.2, bty="0")
 #create box plot showing centroid sizes
size=GPAS$Csize
barplot(size[1:6], main="Centroid Size",
  xlab="Model",ylab="Csize")
```

Appendix 2.5: Principal Component Analysis

```
###Packages
library(Arothron)        #read.amira.dir
library(carData)         #car
library(car)             #dataEllipse
library(rgl)
library(nlme)
library(geomorph)
library(rlang)
```

```
library(abind)
library(stringr)
library(Rvcg)
library(RRPP)
library(Morpho)   #find.outliers
 setwd("E:/Chapter 4- results 1/analysis 2020/data analysis/full skulls")
# read in the data
Skull_data<-read.morphologika("sizeshapeCompSet2020.txt")
 #check data dimensions
dim(Skull_data$coords)
#should be correct number of landmarks, dimensions and individuals
#check the first 10 landmarks of first specimen
Skull_data$coords[1:10,,1]
 #load classifiers from csv
classifier <- read.csv("CSV full skull clasifiers.csv", header=T,row.names = 1)
species <- factor(classifier$species)
is.factor(species) # check that it is a factor
ID<-factor(classifier$ID)
is.factor(ID)
 group<-factor(classifier$group)
sex<-factor(classifier$sex)
 ##Morpho package
 #create procrustes registration with landmark coordinates
PC_Skull=procSym(Skull_data$coords)
 #extract cumulative explained varience
PC_Skull$Variance
write.csv(PC_Skull$Variance, file="PC skull Variance.csv")
#make labeled bar plot showing varience for first 20 PCs
xlab1<-paste("Principal Components 1:20")
ylab1<-paste("% Variance Explained")
ylim<-c(0,30)
bars = barplot(PC_Skull$Variance[1:20,2],xlab = xlab1, ylab = ylab1, ylim = ylim, width = 20, space = 0.5,
main="Vairance along the first 20 Principal Components")
axis(1, at=bars, labels=c(1:20), pos=-1, cex=0.7)
#plot PCA
plot(PC_Skull$PCscores[,c(1,2)],main = "PCA by Species",
col=c("brown","navy")[species],pch=c(15:18)[species],cex=1.5) #pch is point style
legend("bottomright", legend=unique(species),
            pch=c(15,16),
  col=unique(c("brown","navy")[species]), cex=0.8, bty="0")
text(PC_Skull$PCscores, labels=ID,pos=1)
 #7.9% PC3
 ##Geomorph package
Y.gpa <- gpagen(Skull_data$coords)#GPA-alignment
### Traditional PCA
PCA <- gm.prcomp(Y.gpa$coords)
summary(PCA)
 #quick work around to label X and Y
#plot(PCA,axis1 = 1,axis2 = 3, main = "PCA by Species", xlab = "PC1 (27.7%)", ylab = "PC2 (18.4%)",
pch=c(15:18)[species], cex=1.5, asp=1)
#plot(PCA$pc.scores[,c(2,3)], main = "PCA by Species", xlab = "PC2 (18.4%)", ylab = "PC3
(7.9%)",pch=c(15:18)[shapz], cex=1.5,col=c("brown","navy")[species],asp=1)
 #Better plot with labels working
PC.plot<-plot(PCA,axis1 = 1,axis2 = 2, main = "Full Skull by Sex PC1 vs PC2",
  pch=c(16,16,16)[species], xlab = "PC1 (27.7%)", ylab = "PC2 (18.4%)",
            cex=1.5, asp=1, col=c("dark Green","purple","dark grey")[species])
#reset PCA margins if off
```

```
par(mar = c(5, 4, 4, 2) + 0.1)
#set the legend
legend("bottomright", legend=unique(sex),
  pch=c(16,16,16),
  col=unique(c("dark Green","purple","dark grey")[sex]), cex=0.8, bty="0")
#convex hulls
colour= c("grey","dark green","purple")
shapeHulls(PC.plot, groups = sex, group.cols = colour)
#set hull legend as below
#legend("topright", c("B.primigenius", "B.taurus"),
#            col = c("brown","navy"))
Csize<-Y.gpa$Csize
write.csv(Csize, "E:/endocranial test/Csize.txt")
 #export to new mophologika file
r2morphologika(data1, file="testnewdata.txt")
#export classifiers as CSV
write.csv(newlabels,file = "my classifier.CSV")
 PC.plot$PC.points
polygon()
 #visualise shape change on grids
ref <- mshape(Y.gpa$coords)# assign mean shape for use with plotRefToTarget below
# Item 2 to plot, the first TPS grid; here we use the outline option to add to the visualisation
par(mar = c(0,0,0,0)) # sets the margins
 plotRefToTarget(ref,PCA$shapes$min, outline=Skull_data$outline)
 plotRefToTarget(ref,PC.plot$shapes$PC1min,outline=Skull_data$outline)
# Item 3
plotRefToTarget(ref,PCA$pc.shapes$PC1max,outline=Skull_data$outline)
# Item 4
plotRefToTarget(ref,PCA$pc.shapes$PC2min,outline=Skull_data$outline)
# Item 5
plotRefToTarget(ref,PCA$pc.shapes$PC2max,outline=Skull_data$outline)
```

Appendix 2.6: Regression Analysis

```
library(geomorph)
library(Morpho)
library(stringr)
library(morphomap)
library(Arothron)
library(rgl)
totset<-morphomapReadMorphologika("sizeshapeCompSet2020.txt")
totset$variables
regress<-"size"
space<-"shapespace" #you can select also "shapespace""formspace"
Set1<-totset$array[,,totset$variables$species=="B.primigenius"]
Set2<-totset$array[,,totset$variables$species=="B.taurus"]
set1<-Set1
set2<-Set2
####
gpaTr<-procSym(sett,scale=FALSE,CSinit = FALSE) #same gpa
G1s<-gpaTr$rotated[,,which.min(gpaTr$size[c(1:dim(set1)[3])])] #shape minimum size B. pri
G2s<-gpaTr$rotated[,,which.min(gpaTr$size[c((dim(set1)[3]+1):dim(sett)[3])])] #shape minimum size B. tau
G12s<-arrMean3(bindArr(G1s,G2s,along=3)) #mean of the minimum shapes
```

```
G1f<-gpaTr$rotated[,,which.max(gpaTr$size[c(1:dim(set1)[3])])] #max shape B.pri
G2f<-gpaTr$rotated[,,which.max(gpaTr$size[c((dim(set1)[3]+1):dim(sett)[3])])] #max shape B.tau

ArrT<-bindArr(G12s,G1f,G2f,along = 3) #create an unique array
pca_arrT<-procSym(ArrT)
plot(pca_arrT$PCscores[,c(1,2)],asp=1)
text(pca_arrT$PCscores[,c(1,2)],labels=c("start","G1f","G2f"),pos=3)
(angleTest(PCscores[c(1,2),],PCscores[c(1,3),])$angle)*180/pi

refsur<-file2mesh("Sp111.ply")
commonOri<-tps3d(refsur,totset$array[,,37],pca_arrT$rotated[,,1])
BPrimax<-tps3d(refsur,totset$array[,,37],pca_arrT$rotated[,,2])
BTaumax<-tps3d(refsur,totset$array[,,37],pca_arrT$rotated[,,3])

localmeshdiff(BPrimax,commonOri,1,paltot = c("darkgreen","green","white","red","darkred"))
open3d()
localmeshdiff(BTaumax,commonOri,1,paltot = c("darkgreen","green","white","red","darkred"))
```

Appendix 2.7: Landmarks to Linear Measurements

```
library(geomorph)
setwd("E:/Chapter 4- results 1/analysis 2020/data analysis/full skulls")
# read in the data
Skull_data<-read.morphologika("sizeshapeCompSet2020.txt")

#load classifiers from csv
classifier <- read.csv("full skull classifiers.csv", header=T, row.names=1)
is.factor(classifier$sex) # check that it is a factor
#set classifiers as values
sex<- classifier$sex
breed<-classifier$breed
species<-classifier$species

# Make a matrix defining three interlandmark distances
lmks <- matrix(c(1,8,7,9,1,48), ncol=2, byrow=TRUE,
   dimnames = list(c("frontalL", "eyeW", "posteriorD"),c("start", "end")))
# where 8-9 is eye width; 6-12 is head length; 4-2 is mouth length
# or alternatively
lmks <- data.frame(frontalL = c(1,8), eyeW = c(7,9), posteriorD = c(1,48),
    row.names = c("start", "end"))
A <- Skull_data$coords
lineardists <- interlmkdist(A, lmks)

skull_dimensions<-as.data.frame(lineardists, row.names = NULL, optional = FALSE,
   make.names = TRUE,
   stringsAsFactors = default.stringsAsFactors())

plot(skull_dimensions[,c(1,3)], main = "skulls dimensions",xlab ="Skull length (mm)", ylab ="skull depth (mm)",
pch=c(15,17,16)[sex],
cex=1.5, asp=1, col=c("brown","navy","darkgoldenrod")[sex])

abline(lm(frontalL ~ posteriorD, data=skull_dimensions))
```

```
legend("bottomright", legend=unique(sex),
  pch=c(16,15,17),
  col=unique(c("brown","navy","darkgoldenrod")[sex]), cex=0.8, bty="0")
```

Appendix 2.8: Skull Size and Horn measurement Analysis

```
library(geomorph)
setwd("D:/Chapter 4- results 1/analysis 2020/data analysis/Horns")

# read in the data
Skull_data<-read.morphologika("newHorns.txt")
#load classifiers from csv
classifier <- read.csv("new classifier.csv", header=T, row.names=1)
#set classifiers as values
species <- factor(classifier$species)
is.factor(species) # check that it is a factor
ID<-factor(classifier$ID)
is.factor(ID)
group<-factor(classifier$group)
sex<-factor(classifier$sex)
breed<-factor(classifier$breed)
# Make a matrix defining three interlandmark distances
lmks <- matrix(c(1,2,3,4), ncol=2, byrow=TRUE,
    dimnames = list(c("max width", "min height"),c("start", "end")))
# where 8-9 is eye width; 6-12 is head length; 4-2 is mouth length
# or alternatively
lmks <- data.frame(frontalL = c(1,8), eyeW = c(7,9), posteriorD = c(1,48),
     row.names = c("start", "end"))
A <- Skull_data$coords
lineardists <- interlmkdist(A, lmks)

skull_dimensions<-as.data.frame(lineardists, row.names = NULL, optional = FALSE,
    make.names = TRUE,
    stringsAsFactors = default.stringsAsFactors())

write.csv(skull_dimensions, "D:/Chapter 4- results 1/analysis 2020/data analysis/Horns/linears")

data <- read.csv("horn analysis sex.csv", header=T, row.names=1)

width<-data$max.width
height<-data$min.height
size<-log10(data$Csize)
Ratio <- width / height
area<-log10(data$area)
cac<-data$cacscore

#plot width
plot(size,width, main = "Skull size and horn width",xlab ="Skull Csize", ylab ="Horn width (mm)",
  pch=c(15,17)[sex],
  cex=1.5, col=c("brown","navy")[sex])

#Then calculate the regression lines:
#set data for width and size groups of bulls and cows
widthbull<-width[1:18]
```

```
widthcow<-width[19:37]
sizebull<-size[1:18]
sizecow<-size[19:37]
#plot regression line for aurochs
abline(lm(widthbull ~ sizebull),col="brown")
#plot regression line for cattle
abline(lm(widthcow ~ sizecow),col="navy")

#plot height
plot(size,height, main = "Skull size and horn height",xlab ="Skull Csize", ylab ="Horn height (mm)",
  pch=c(15,17)[species],
  cex=1.5, col=c("brown","navy")[species])

#plot ratio
plot(size,Ratio, main = "Skull size and horn width / height ratio",xlab ="Skull Csize", ylab ="Horn width to height
ratio",
pch=c(15,17)[species],
cex=1.5, col=c("brown","navy")[species])

#plot area of ellipse
plot(size,area, main = "Skull size and horn area",xlab ="Skull Csize", ylab ="Horn area",
  pch=c(15,17)[sex],
  cex=1.5, col=c("brown","navy")[sex])
#add labels to plot
#text(size, area, labels=breed,pos=1)
#Then calculate the regression lines:
#set data for width and size groups of bulls and cows
areabull<-area[1:18]
areacow<-area[19:37]
sizebull<-size[1:18]
sizecow<-size[19:37]
#plot regression line for aurochs
abline(lm(areabull ~ sizebull),col="brown")
#plot regression line for cattle
abline(lm(areacow ~ sizecow),col="navy")

lmarea = lm(size ~ area, data = data)
summary(lmarea)
#na.rm=T removes rows where missing values appear

#one way ANCOVA
ANarea<-aov(area~size+sex,stack(data))
summary(ANarea)

#cac
plot(cac,Ratio, main = "CAC and ratio",xlab ="cac score", ylab ="Horn ratio",
  pch=c(15,17)[species],
  cex=1.5, col=c("brown","navy")[species])
#cac
plot(size,cac, main = "size and cac",xlab ="size", ylab ="cac score",
  pch=c(15,17)[species],
  cex=1.5, col=c("brown","navy")[species])

#add labels to plot
text(size, width, labels=sex,pos=1)

legend("bottomright", legend=unique(sex),
```

```
  pch=c(15,17),
  col=unique(c("navy","navy")[sex]), cex=0.8, bty="0")

#Then calculate the regression lines:
#set data for width and size groups of bulls and cows
widthbull<-width[1:18]
widthcow<-width[19:37]
sizebull<-size[1:18]
sizecow<-size[19:37]
#plot regression line for aurochs
abline(lm(widthbull ~ sizebull),col="brown")
#plot regression line for cattle
abline(lm(widthcow ~ sizecow),col="navy")
```