Climate-Related Adaptations in the Human Skull: A Review of the Different Contemporary Theoretical Models and Methods

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Abstract

Questions regarding our ancestral species have always appealed to our curious side. Our first ancestral species lived in arboreal settings before gradually adapting to a more open, terrestrial environment. It can be observed in the fossil record that hominins began to show a greater degree of adaptations towards anatomical traits that would be beneficial in such environments. Significant changes can be seen as hominins migrated out of Africa and were subsequently exposed to different climates and ecological niches. Accordingly, gaining further knowledge about these climate-related adaptations is of prime interest for understanding the context from which our ancestors emerged and evolved. However, to understand these events it is important to develop useful theoretical frameworks which can aid researchers in tying such links between human morphological variation and climate. Theoretical frameworks are used to make sense of data and more focus must be on developing such frameworks. The conclusion of this thesis is that there are only two theoretical frameworks that can be useful to climate adaptation research: modern evolutionary theory and the ecological rules of Bergmann and Allen. However, more in-depth theoretical models are needed to bridge the gap between morphological variation and climate. This study will present theoretical models and methods, compare and discuss these theoretical frameworks and methodologies, and investigate any consistencies in the use of theories within the field. This thesis also aims to critically analyse and highlight the limitations of the discipline by addressing present issues. The final aim and purpose of this thesis is to better understand the need and significance of well-built theoretical frameworks and methods in achieving a better understanding of the links between climate and morphological variation.

I dedicate this thesis to my mother and my grandmother who both passed away from cancer during the writing of my master’s thesis.

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Chapter 1 – Introduction

1.1. Thesis outline

Chapter 1 introduces the reader to the topic of modern human climate adaptation research. A brief description of the significance of using a theoretical framework as well as the topic of direct and indirect effects of climate will be given before moving on to an overview of the terminology to prepare the reader for the rest of the thesis. The research problem statement, aim, objective and rationale will be provided at the end of the chapter. Chapter 2 will review the development of theoretical frameworks within physical anthropology. The chapter begins with a definition of evolution before discussing what lead up to the discovery of biological evolutionary theory and the contribution made by Darwin and Wallace. The following subchapters will describe Mendel's genetic principles, evolution by mutation or natural selection, modern evolutionary theory, and the ecological rules of Allen and Bergmann. Chapter 3 is a full overview of methodologies used within modern human climate adaptation research. It begins with describing how to create a sample and collecting climate data before it moves on to quantitative methods used within the discipline. The following subchapter introduces an important tool used within the discipline, geometric morphometrics. The reader is then introduced to the most common statistical analyses used within the field. Chapter 4 critically analyses, compares, and discusses the major topics. It presents competing conceptual frameworks and criticism against the modern evolutionary synthesis and discusses the applicability of Bergmann's rule and Allen's rule as well as modern evolutionary theory in terms of climate adaptation research. This chapter also investigates whether the theoretical models are universally used, and what issues and other explanations climate adaptation research faces.

1.2. The significance of a theoretical framework

The last common ancestor shared between chimpanzees and humans existed about six to eight million years ago and that ancestor gave rise to two separate lineages. These two lineages eventually led us to our species, *Homo sapiens* and our cousin species, the chimpanzee (Jurmain et al., 2014, p. 25). Many changes have taken place since the divergence between the two lineages. When describing these changes, we must look at data. We use theoretical frameworks to interpret these data and to make better sense of the results we are left with. This is particularly useful in a situation where all you have are skeletal elements, some easily identifiable and others not.

The theory of evolution is a theory in the scientific sense of the word, which means that it can be tested empirically. Evolutionary theory is supported by a vast amount of evidence, accumulated over decades and across biological organisms, and has also been observed directly in multiple instances both in the laboratory and in the field (Sniegowski et al., 1997; Waclaw, 2016; Maino et al., 2018; Petrova and Russell, 2018). It is the most well-established scientific theory in biological sciences. Furthermore, the theoretical framework is constantly updated with new knowledge regarding evolutionary processes (Jurmain et al., 2014, p. 26).

There is a general demand for theoretical frameworks and models connecting the effects of climate on hominin cranial variation. A theoretical framework provides the foundation on which later hypotheses can be built, like the question of what drives brain size variation within and among extant species, before moving on to more complex questions regarding the role of climate in brain size variation (Faith et al., 2021, p. 804).

1.3. Direct and indirect effects of climate

The human face has been suggested to reflect climate signatures, e.g., mandibular shape, facial height and/or breadth (Guglielmino-Matessi et al., 1979; Harvati and Weaver, 2006; Hubbe et al., 2009; von Cramon-Taubadel, 2009). The human nose has particularly been of interest to many researchers (Carey and Steegmann, 1981; Beals et al., 1984; Franciscus and Long, 1991; Roseman, 2004; Hubbe et al., 2009; Betti et al., 2010; Noback et al., 2011; Katz et al., 2015; de Azevedo et al., 2017; Buck et al., 2019; Stansfield et al., 2021). There is a general agreement that the human nose has adapted to different environments, e.g., cold/dry, and hot/humid. Studies have shown that populations living in cold and dry climates display narrower and taller nasal cavities while those living in hot and humid climates exhibit wider, shorter, and lower nasal cavities (Noback et al., 2011; Evteev et al., 2014).

The neurocranium has also been suggested to reflect climate adaptation, specifically the overall shape or breadth of the neurocrania (Hubbe et al., 2009; Katz et al., 2015) as well as the cranial base (Beals et al., 1984; Roseman, 2004; Nowaczewska et al., 2011; also see Caldwell, 2014 for cold-adapted effects on Neanderthal cranial base).

Indirect effects of climate are difficult to verify and therefore remain speculative. However, the elements presented here could be related to a changing Pleistocene climate, where hominins must adapt to new environmental settings. For example, rainfall became more seasonal, leading to less tree cover, and at this point, the hominins were still relying on the forests. It is impossible to argue that climate change directly led to bipedalism. However, perhaps the changes observed in the climate could have forced the hominins to explore a more open, terrestrial habitat (Jurmain et al., 2014, pp. 271-272), causing significant evolutionary advances. It also seems likely that a more challenging climate called for behavioural responses, such as controlling fire, creating tools, hunting, making shelters and clothing, trading, developing complex communication skills, and so on. This cannot be directly observed on the skeleton but is hypothesised to be connected to a larger brain and more complex cognition in the later stages of human evolution.

Another point worth highlighting is that geographic isolation brought about by recurring glaciations in the Pleistocene could have led to speciation events. This is based on the isolation-by-distance model (Relethford, 2004a), which predicts that as one introduces geographic distance, the genetic similarities between two isolated populations will decrease due to minimal or no gene flow. In addition, the Pleistocene climate fluctuated between glacials and interglacials, which may have led specific populations to become isolated.

1.4. Terminology

This section will provide an overview of the most commonly used terms regarding the human skull. The term skull refers to the entire skeletal body of the head, including the lower jaw. Researchers often work with either the whole skull containing all elements, a skull excluding certain elements, or isolated elements. The isolated lower jaw is called mandible, and the skull without the mandible is called cranium. The face of the skull (facial skeleton) by itself is called splanchnocranium. Calotte is the crania excluding the mandible, face, and cranial base. The braincase is known as the neurocranium. The internal aspect of the cranium is the endocranium, and the internal aspect of the cranial base can be separated into anterior, middle, and posterior cranial fossae which holds the different parts of the brain, e.g., temporal lobes, frontal lobes, and cerebellum (White and Folkens, 2005, p. 77).

In anatomy, the view of the skull is often referred to as anterior, lateral, posterior, superior and inferior. These views refer to how the skull is facing the observer. The anterior (see left image in figure 1) refers to the skull facing towards the observer. A lateral view is when the skull is viewed from either side (see the left image in figure 1). Posterior view refers to when the back of the skull is facing the observer. The superior view represents the top of the skull, where the observer looks down at the skull from above. Finally, the inferior view describes a bottom view looking up, e.g., at the lower part of the skull or base (see figure 2) (White and Folkens, 2005, p. 75). The bones making up the skull are the frontal, parietals, temporals, palatines, occipital, vomer, maxillae, lacrimals, inferior nasal conchae, nasals, ethmoid, zygomatics, mandible and sphenoid (see figure 1 and 2).

The shape of the human nose is a distinctive and derived element of *Homo*. The nasal structure forces air to take a 90° angle when inhaling and exhaling. The external nose comprises five pairs of cartilage and nasal bones, forming the bridge of the nose. The cartilage can be divided into the dorsal, lateral and midline. The midline cartilage works as an extension of the nasal septum (Lieberman, 2011, p. 135).

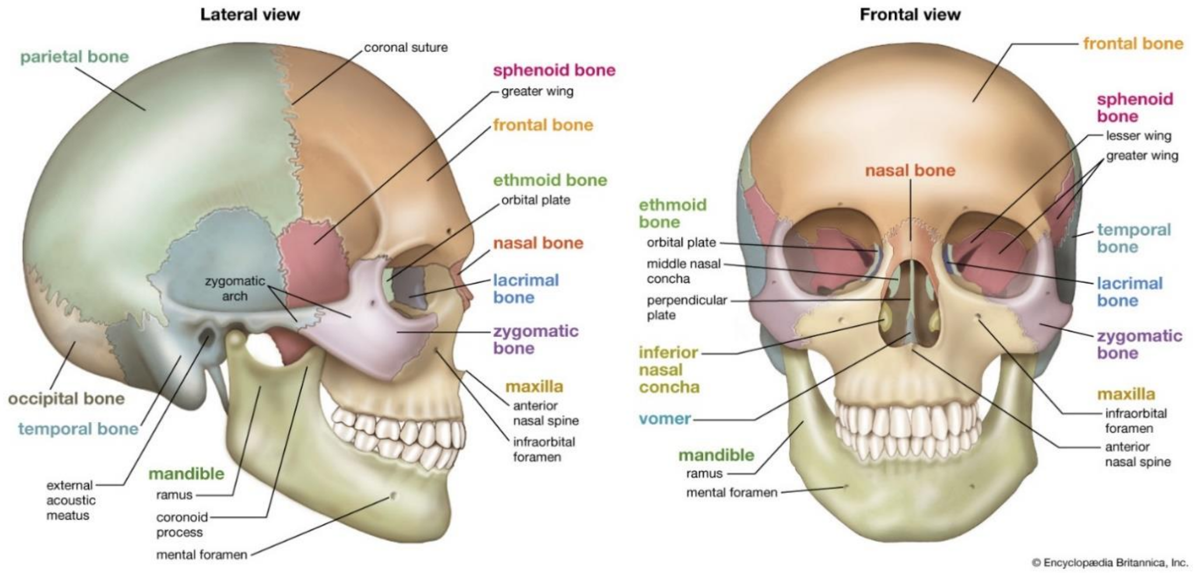

Figure 1: The lateral and frontal view of a human skull (Britannica.com/science/skull).

The nose (see figures 3 and 4) is a complex tube-like system enclosed by different bones: the sphenoid, nasal conchae, ethmoid, vomer, maxilla and palatine. The tube carries inhaled and exhaled air which, after a complex route through the nasal cavities, ends up in the lungs or leaving the nostrils (Lieberman, 2011, pp. 130-131). During an inhale, the air travels first through the nostrils and into the nasal vestibule inside the nasal opening. The air then passes through the nasal valve and then the turbinates (conchae), consisting of three meatuses, or small passageways, before entering the nasal cavity. When the air passes through the two lower meatuses, the air is humidified, filtered, and heated up before travelling to the lungs through the nasopharynx (Lieberman, 2011, p. 401).

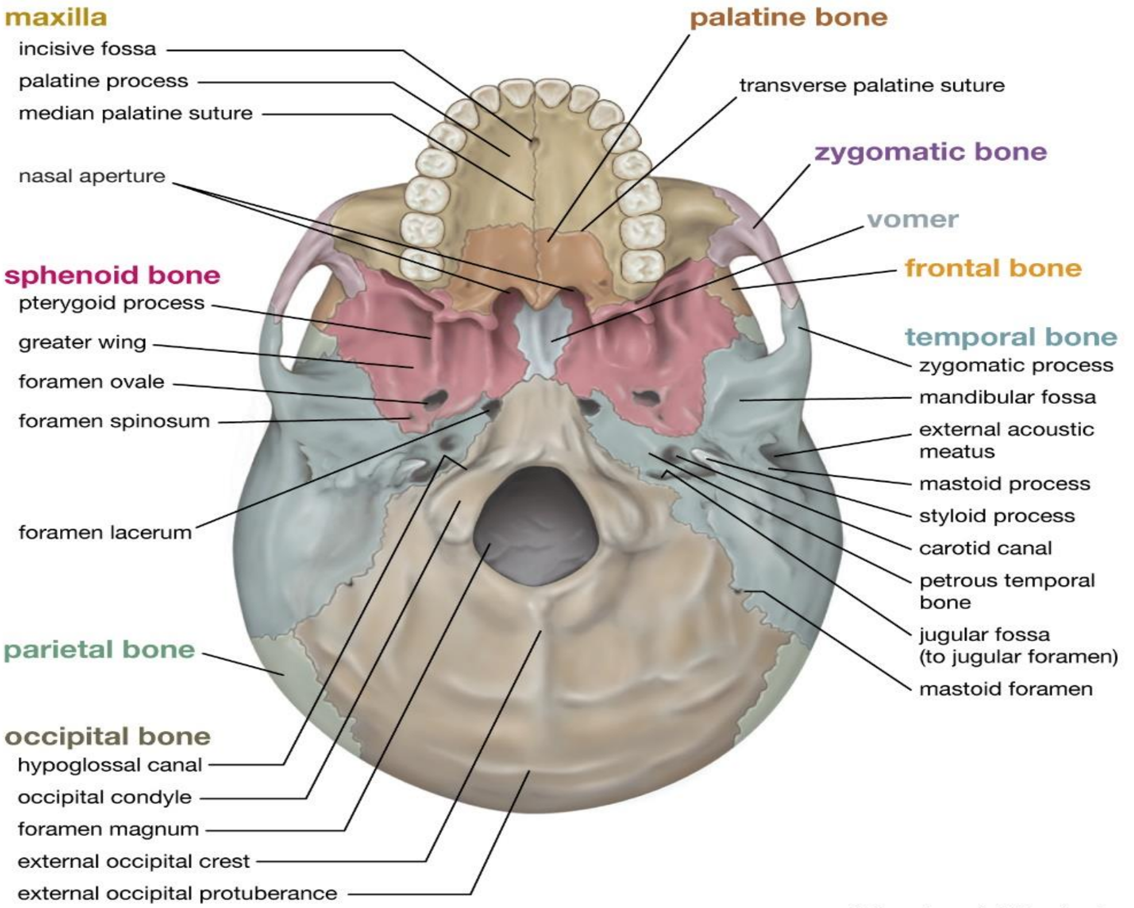

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Figure 2: Inferior view of the human skull (Britannica.com/science/skull). Note the central position of the foramen magnum, which is one of the characteristics of the human lineage. As you can see, there are a several smaller bones and cartilages supporting the major bones.

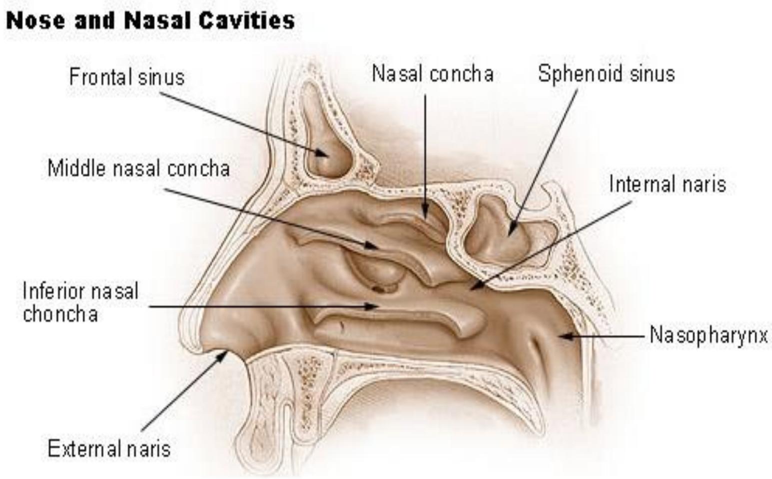

Figure 3: Image shows the lateral view of the nasal complex including internal and external naris, nasopharynx, internal naris, sinuses and nasal concha (https://training.seer.cancer.gov/anatomy/respiratory/passages/nose.html).

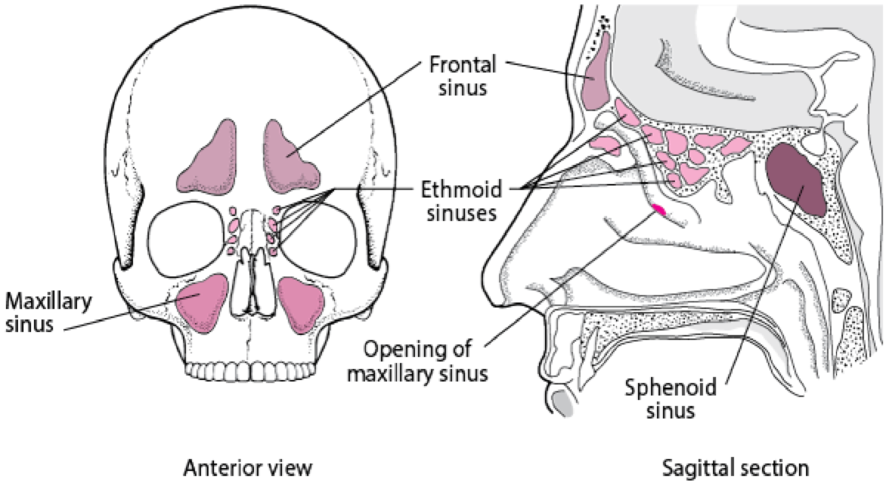

Figure 4: Anterior and lateral view with emphasis on frontal, maxillary and sphenoid sinuses (msdmanuals.com).

1.5. Research problem statement

Although there are many studies exploring the topic of climate-related adaptations in hominins, the discipline still has a long way to go before confidently connecting climate to hominin evolution. Introducing more in-depth theoretical frameworks might contribute to establishing such links.

The lack of large datasets makes it difficult to test hypotheses regarding which region of the human skull has been influenced by climate or population history. There are also ethical issues regarding the recording of extant human skulls, making it difficult to create several larger datasets. The discussion of ethics also incorporates the general handling of human remains.

This thesis aims to provide a full overview of the different theoretical models and methods used within modern human climate-adaptation research. This thesis will thus also aid those who wish to better understand this line of research.

1.6. Research question

What are the criticisms of the modern evolutionary synthesis? What theoretical frameworks can be applied to climate adaptation research and how efficient are these at explaining the effects of climate on human cranial morphology? Are there any consistencies in the type of theories used? What issues do researchers face when looking for climate signatures in modern and fossil human crania?

1.7. Aims and Objectives

There are three objectives (1.-3.) and one aim (4.) for this thesis:

1. Create a descriptive overview of the development of theoretical frameworks and present contemporary methodologies collected from the literature.

2. To critically examine and compare the theories and methods used in literature

3. To critically analyse the issues found within the discipline.

4. To better understand the significance of theory and method as applied to research.

1.8. Rationale

Adequate theoretical frameworks and methods are needed to understand the underlying factors behind how variation is created and distributed, and to bridge the gap between human skeletal data and ecological data. Researchers also use different methods to make sense of data and to either strengthen or reject hypotheses.

There are two main mechanisms known to cause evolutionary changes, and these are mutation, which occurs within the biological organism, and natural selection. Natural selection is a process where certain biological organisms successfully adapt to their ecological surroundings to survive and reproduce. There are also two additional evolutionary mechanisms known as genetic drift and gene flow which determine the distribution of trait variation (Jurmain et al., 2014).

The environment during the Pleistocene fluctuated considerably, including periods of drying and cooling. These climatic fluctuations have coincided with hominin evolution and, as in the case of any living organism, species adapt to different environments. Hominin species likely experienced external selective pressures that lead to specific anatomical changes for a particular environment, whether humid, dry, hot, or cold. Theoretical frameworks are important to understand how variation was created and to connect what we know of climate with modern human morphological variation to better understand adaptation and evolution.

Chapter 2 – The Development of Theoretical Frameworks Within Physical Anthropology

This chapter will review the development of the theoretical frameworks central to physical anthropology and climate adaptation research. This thesis will focus on two theoretical frameworks: modern evolutionary theory and the ecological rules of Bergmann and Allen. The ecological rules of Bergmann and Allen are not equivalent theoretical frameworks to modern evolutionary theory as they both represent different theories. However, Bergmann's and Allen's rules are connected to modern evolutionary theory as they describe a pattern of thermal adaptation to cold climates, which is a product of evolutionary adaptation through processes described by modern evolutionary theory.

This chapter will first introduce and define the topic of evolution, before briefly addressing the preceding time before the discovery of biological evolution. The following subchapters will describe Darwin and Wallace's theories, Mendel's genetic principles, evolution by mutation or natural selection, modern evolutionary theory and the ecological rules of Bergmann and Allen.

2.1. A definition of evolution

The term evolution is occasionally misunderstood as simply meaning the appearance of a new species, and although this is a significant part of evolution, it is not the only outcome. Evolution is an ongoing biological process that affects all organisms constantly. There are two ways of approaching evolution: micro or macro. Macroevolution is caused by genetic changes in populations over time, and speciation events can occur if the populations are isolated from one another over longer periods. Microevolution occurs from genetic changes within populations and does not typically lead to the appearance of new species. Instead, it leads to trait frequency differences between populations of the same species (Jurmain et al., 2014, p. 5). The most important difference between the two approaches is that macroevolution occurs over a vast period of time and microevolution takes place over a shorter period, e.g., changes seen between generations.

2.2. Before the discovery of biological evolution

The topic of evolution was mostly unheard of in Europe before the 19th century. Opinions at the time were influenced by religious principles which defined species as biblical creations. Living forms were viewed as incapable of changing as God only created perfection, later known as 'fixity of species'. It was also believed that the whole universe was created by 4004 B.C. according to God's plan, this was later known as 'argument from design'. However, events that took place in the 15th century, like the mapping of the globe, contradicted some of the preconceptions people held about the world. The discovery of new animal and plant species made people realise that the world's biodiversity was much more extensive than originally thought (Jurmain et al., 2014, pp. 26-28).

2.3. Darwin and Wallace

Scepticism against 'fixity of species' and 'argument by design' grew during the 19th century and scholars began to realise that natural processes were a better explanation for biological change. The interest in evolution peaked when Charles Darwin, in 1859, published his book *On the Origin of Species* (Jurmain et al., 2014, p. 12).

The idea of biological evolution was borrowed by Western science from other cultures, like the Arabs, Indians, Chinese and ancient Greeks. The existing knowledge of biological evolution was further developed by scholars in Britain and France, who also laid the groundwork for Darwin and Wallace. Charles Darwin was the first to officially develop the theory called 'natural selection' which applied to all organisms. According to Darwin, natural selection was the most fundamental mechanism behind evolutionary processes. Alfred R. Wallace arrived at the same conclusion more or less at the same time as Darwin (Jurmain et al., 2014, p. 26). Wallace and Darwin realised that there is a connection between population size and available resources, as the size of the population will depend on resource availability. Fewer resources leads to competition between individuals, which again leads to a reduction in population size (Jurmain et al., 2014, p. 32). Darwin understood that variation was increased by sexual reproduction, and favourable traits was preserved in those individuals that successfully survived the competition for resources. The fittest individuals would produce offspring that propagated these advantageous traits, and in time, this would result in the formation of a new species, i.e., speciation. Darwin also believed that geographical isolation could lead to speciation, as two isolated populations would have to adapt to different environments. Natural selection also only works on an individual level, and evolution works at a population-level (Jurmain et al., 2014, pp. 36-38).

2.4. Mendel’s genetic principles

In the 19th century, Gregor Mendel was the first to discover the basic rules of inheritance through experiments performed on garden peas. Although his experiments focused on garden peas, the principle can be applied to any living organism. One of Mendel’s genetic principles is the principle of segregation. The principle of segregation explores how the variation of pairs of units, later known as genes, are divided into reproductive cells through the cross-mating of pea plants resulting in hybrid offspring. He experimented with different traits, like the colour and shape of seeds, the shape and colour of pods, the colour and position of the flower and the length of the stem. Mendel chose two groups of pea plants: the first group contained tall plants and the second, short plants. These two groups are known as the parental generation. Mendel was curious about cross-mating tall plants from the one parental group with short plants from the other parental group, and how this action would be expressed in the offspring. The hybrid offspring generation, called $F_{1,}$ was, to Mendel’s surprise, all tall pea plants. A F_2 generation was created through the self-fertilization of the F_1 generation, which resulted in three quarters tall plants and one quarter short plants. The results of the second cross-mating were surprising, as the expression (short) was not visible in the F_1 generation, but suddenly appeared in the F_2 generation. The experiments revealed that the various expressions of a trait were controlled by discrete units. These units occurred in pairs and one unit from each parent was inherited by the offspring. A trait is controlled by members of a pair of units, and these members are divided into different sex cells. During mating, one member from each parent unites in the process of fertilizing the ‘egg’. This was initially known as Mendel’s first principle of inheritance (or principle of segregation), but today it is formally known as meiosis. When the ‘short’ trait reappeared in generation F_2 after being absent in generation F_1, Mendel understood that the unit, which expressed the short trait, was there all along. Hence, the trait short was lost as ‘recessive’ and the successful ‘tall’ trait was known as ‘dominant’ (Jurmain et al., 2014, pp. 78-79).

2.5. Evolution by mutation or natural selection?

An apparent dichotomy was visible between two theories in the 1920’s and 1930’s: evolution caused by mutation (Mendel’s rule of heredity), or evolution caused by natural selection. In the mid-30th century and onwards, evolutionary biologists filled the gap between the two theories and named it “the Modern Synthesis” (MS). According to the new and improved theoretical model, both mutation and natural selection can cause evolution in a two-stage process. Evolution is made possible by the production and the redistribution of variation, which is the differences between organisms that have been inherited. Natural selection will accordingly act on these variations within organisms. Inherited variations will consequently impact living organisms’ ability to survive and thus reproduce (Jurmain et al., 2014, p. 94).

The issues that Charles Darwin and other scholars faced at the time was that they did not understand the underlying mechanisms behind variation within species or how offspring inherited traits from their parents. The application of Mendel’s rules allowed for the filling of certain gaps in the theory of natural selection regarding the mechanism for inheritance, but without the full understanding of how genetics works (Jurmain et al., 2014, p. 42).

2.6. Modern evolutionary theory

The understanding of evolutionary theory has expanded considerably since the discoveries of Darwin, Wallace, and Mendel. The structure of DNA was uncovered in 1953 and the human genome was sequenced in 2001, which could be considered two of the most significant achievements in biological science (Jurmain et al., 2014, p. 42).

Technology has improved considerably, and researchers are now able to monitor small genetic changes in the allele frequency observed in populations of model organisms from one generation to the next, now fully recognised as microevolution. What is today known as macroevolution is the long-term effects of changes in the allele frequency (Jurmain et al., 2014, p. 95).

For a long time physical anthropology was restricted to nineteenth-century racial typology. A paradigm shift led to the replacement of this outdated mindset with new methods and evolutionary ecological approaches. These new methods and approaches embraced genetic variability and developmental plasticity through the adaptive and complex interactions between populations. This reorientation of the theoretical framework has resulted in new approaches that utilises biological, cultural, and palaeoenvironmental evidence to understand the complex process of adaptation. Boas (1912), the founder of American anthropology, was opposed to the simplistic hereditarian interpretations of human variation. Boas (1912) embraced the value of cultural and biological history of our species in his own anthropometric research, as well as the need for statistical analyses in understanding the variability within his samples (Lambert and Walker, 2018, pp. 9-10).

2.6.1. The production and redistribution of variation

Variation is created by mutation, which is caused by a change in the DNA. For evolutionary change to occur, mutation must take place in an individual's gametes, as this is the only way of transferring the mutation from one generation to the next (Jurmain et al., 2014, p. 95). Variation can then be redistributed by factors like gene flow and genetic drift.

Gene flow is the continuous exchange of genes by breeding between different groups or populations. Gene flow has been relevant to human evolution since the first dispersal of the genus *Homo* into other parts of the world. If a continuous flow of genes moves between populations, speciation events would not occur due to the genetic similarities between the groups. Genetic drift occurs when the population size is small, and there is a reduction in genetic variability. Specific alleles might disappear due to the chance effects of this allele within the population. The founder effect is a type of genetic drift and has also been observed in more recent times. A founder effect occurs when a group of 'founders' leave its current group to establish themselves in a different place, either to colonise or as isolated survivors of a disaster that killed off the rest of the population. If the group is isolated, intra-group breeding will occur and genetic variability will decrease over time. The populations succeeding the 'founder' will only be left with a small collection of all the alleles that existed in the original group (Jurmain et al., 2014, pp. 96-97).

2.6.2. Natural selection: the final factor needed for adaptation and evolution

Variation is created by mutation but distributed by factors like gene flow and genetic drift. However, these factors alone are considered directionless, which means that an additional mechanism must be in place for adaptation and evolution to take place. The reason why natural selection is described as a directional force is because it encourages certain directional changes in the genetic pool of a population. For example, favouring certain traits over others, which is deemed suitable for the surrounding environment, would enhance an individual's ability to survive and reproduce. A typical population have a set of alleles, and adding direction (natural selection) allows some alleles to become more frequent than others. If the population becomes exposed to a new environment, selection pressures will force a change in the allele frequency, which is known as adaptation (Jurmain et al., 2014, pp. 100-101).

Evolution, on the other hand, is caused by changes in the allele frequency of a population, transferred from generation to generation through reproduction. Hence, evolution takes place over time, and the term ‘adaptation’ can refer to an individual or a populations’ ability to survive a given environment. Evolution can happen without natural selection but is then due to random change. Natural selection acts through differential net reproductive success, and individuals who carry the selected beneficial allele, or combination of alleles, will successfully produce more offspring than others who do not. Natural selection will also act against alleles considered disadvantageous, so that individuals carrying this allele will produce less offspring or be less successful in producing offspring. In time, these changes will lead to extensive evolutionary changes. Evolution can therefore be considered as the result of a long process that works on a molecular, cellular, individual and population level (Jurmain et al., 2014, pp. 102-104).

2.7. The ecological rules of Allen and Bergmann

Allen’s rule and Bergmann’s rule have been fundamental in understanding how warm-blooded vertebrates adapt to their environment. However, applying these rules to humans was only attempted in the beginning of the 1900s. The ecological rules have since become significant to understanding how different human populations differ according to the climate in which they live in. At the core of both ecological rules lies the argument that, according to the reduction or the adding of radiation to the skin surface per unit of body mass, the body will react by retaining or dissipating the heat (Newman, 1953, p. 311).

According to Bergmann’s rule, a greater body size, or a more compact body, will increase the body mass/body surface ratio. Increasing the ratio between the body mass and body surface will, in turn, reduce body heat loss by radiation, which is a typical characteristic of populations living in colder climates. The larger the body mass, the smaller the skin surface compared to mass (Newman, 1953, p. 312). Consequently, a low body mass/body surface ratio in warmer climates will be more successful at dissipating body heat due to smaller body size (Newman, 1953, p. 324).

Allen’s rule states that a reduction in the size of the extremities and appendages will reduce the heat radiating body surfaces for populations living in cold environments. Another element observed in cold-adapted animals is how reducing such extremities increases the body mass/body surface ratio (Newman, 1953, p. 312). In summary, there should be an increase in body size but a reduction in extremities and appendages in individuals living in cold climates compared to individuals living in warmer, who exhibit an increase in extremities and appendages.

Chapter 3 – Methodology

The methods presented in this chapter have been chosen based on what is most commonly used by scientists within the discipline. This chapter will also critically look at, and compare, the different methods used by scientists and provide some case studies to better understand how the methods can be applied. The first subchapters will discuss the method of creating a sample and collecting climate data. The following subchapters will discuss quantitative methods, shape analysis and statistical analyses.

3.1. Creating a sample

The type of samples used in research can be crucial for the results, but when is a sample size large enough for reliable results? Why is it a problem if specimens are not of same age and sex? Any discrepancies in the samples can cause bias in the results. The case studies below will give an insight into the steps and criteria researchers follow when collecting samples.

Identifying sex and exact ages of individuals can prove challenging, like in the case of Harvati and Weaver's (2006, p. 1227) research on the population history and climate signatures in the human crania. Both 3D geometric morphometric and genetic data were included for thirteen global populations. Their method of identifying age was determined by the full eruption of the permanent dentition, as their samples were concentrated on adult specimens. An attempt was made to have an equal number of males and females, which proved difficult because in most cases sex was unknown, and consequently, sex had to be estimated morphologically. Harvati and Weaver (2006) used the method of 'matching' to preserve a large quantity of samples. 'Matching', in this setting, is a method that compares two different datasets to identify whether there is a common significant element shared between the two datasets. For example, if two samples are considered genetically similar and share a common ancestor, these samples can be matched to create a larger sample. If the matching is imperfect, the result will be biased and not provide significant connections between genetics and morphology. Harvati and Weaver (2006, p. 1227) faced some difficulties matching the morphological datasets with the genetic ones due to limitations in these datasets. This was most likely due to certain sample groups being underrepresented in terms of genetics, and the best way to solve this issue is to match geographically neighbouring populations which are thought to be genetically similar and share a common ancestor. Another example found in Harvati and Weaver’s (2006) research was the matching of a Greenland Inugsuk morphological sample with a Siberian sample. According to previous archaeological and genetic evidence, both the Greenland Inugsuk and Siberian population are thought to have a common recent population history. Another significant element allowing the matching between the Inuit and the Siberian group is because both groups reside within similar latitudes and climatic conditions. Since the objective of their research was to establish whether certain elements of the human cranial morphology reflect adaptation to climate, it was acceptable to match these two groups (Harvati and Weaver, 2006, pp. 1227-1228).

In another study done by Hubbe et al. (2009), a total of 7422 modern human male crania were selected from 135 global geographic locations in an attempt to look for phylogenetic and climatic information in cranial morphology. Hubbe et al. (2009) chose populations according to sample size and each sample had to contain a minimum of 15 individuals. The sample size matters in these types of studies and larger samples will lead to more accurate results. It is natural to have some variation between individuals, sexes and ethnic groups, which is why it is important to have large enough samples that cover most of these variations represented in and between populations. Females were excluded since not all population samples included measurements of female crania. Another decision was made to combine closely related populations to increase the sample sizes (Hubbe et al., 2009, p. 1721). Female and male cranial morphology is often different from one another. This is especially important to keep in mind if the objective is to locate climatic signals in cranial morphology. The samples must therefore be as similar as possible in both age and sex so that the sole focus of the research can be to identify variations relating to climate or population history, and not due to age or sex.

Datasets commonly used among researchers are either Howells’s craniometric dataset (1973; 1989; 1995) or Hanihara’s (1996; 1997). Howells, in the years from 1965 to 1980, collected 2524 craniometric measurements from 28 populations around the world. His dataset has allowed for extensive research into human cranial variation as researchers were able to compare datasets from populations worldwide. Hanihara (1996; 1997) collected recent and prehistoric craniometric measurements from populations in Australia, Melanesia, Southeast Asia, Polynesia, West Asia, and Europe. This was supplemented with measurements from his previous work (Hanihara, 1993 a,b). The issue concerning these datasets is that they only account for linear measurements describing the size of the different cranial regions. If the objective is to compare the relationship of each cranial region with neutral genetics, it is important to include the relative contribution of shape and size (Harvati and Weaver, 2006, p. 1226).

3.2. Collecting climate data

Climate data must be measured against morphological data to understand the relationship between climate and human cranial variation. Climate data is usually either based on other researchers' available climate data or from weather stations. Using climate data from the same geographic areas as the sample populations are generally preferred. Data used in this line of study typically consist of yearly average temperatures, precipitation and humidity from different parts of the world.

Roseman (2004) used Howells's dataset (1973; 1989; 1995) and compared the locations of the different populations in his dataset with weather stations from a global climate dataset (U.S. Federal Climate Complex, 1996). Based on Howells's dataset and data collected from the weather stations, he was able to build a selective pressure hypothesis regarding the geographic and ethnic connection between the cranial and genetic data, the geographic position of the weather stations and the temperature data gathered from these stations (Roseman, 2004, pp. 12825-12826).

Harvati and Weaver (2006) used available climate data and corrected for longitudes and latitudes estimated for each population where possible. Temperature, precipitation, and vapour pressure were included as climatic indicators for each population. Temperatures and vapour pressure (humidity) used in the study were the yearly means, minimum and maximum, and the yearly precipitation included was the total, minimum and maximum (Harvati and Weaver, 2006, p. 1228).

3.3. Quantitative methods

Collecting data on any cranial element is done by specifying what type of element is being measured, how it is measured, and the result of the measurements. The results of the measurements are numerical (quantitative), and the collection of measurements gathered is referred to as data. These data are then further analysed to better understand the significance of the measurements (Jurmain et al., 2014, p. 20). The method of measuring will depend on whether the research object is a full cranium, parts of the cranium or the nasal complex. The best way to measure the external cranium is by using landmarks. Measuring, for example, the external and internal nasal complex, the volume of the neurocranium (cranial capacity), or any of the sinuses can be more challenging. A few examples will be provided of how to measure certain cranial regions.

3.3.1. Traditional tools vs. digital tools

Several measuring tools can be used for collecting measurements from osteological material. The sliding calliper, which is the most widely used tool for crania, has a set of jaws that can be adjusted according to the size of the object. A scale, or dial, is located on the shaft of the traditional sliding callipers which is used to collect measurements (White and Folkens, 2005, p. 341). Digital callipers are standard callipers with a digital reader which allow for measurements to be directly entered into Microsoft Excel.

Evteev et al. (2014) used coordinate, sliding or spreading callipers in their research on how climate affects mid-facial morphology, specifically the nasal morphology, amongst populations in northern Asia. In addition, another type of calliper was used with oblique jaws which are more suitable for the internal nose. Measurements included in the analysis were collected from sections of the external nose and nasal cavity which have been regarded as cold-adapted (Evteev et al., 2014, pp. 452-453).

3D surface scanning can also be used as a non-destructive method compared to callipers. This portable and accurate method scans the surface of the specimen and creates high-density point clouds. This method digitalises bones and crania and creates a three-dimensional model from which landmarks can be collected. Another popular method used within geometric morphometrics is a three-dimensional digitiser arm and the most common type is the MicroScribe Digitizer. In contrast to the 3D surface scanning method, the MicroScribe Digitizer collects landmarks directly from the specimen and not through a model (Messer et al., 2021, p. 2). The portable MicroScribe 3DX Digitizer has been used by several scholars to collect coordinates of craniofacial osteometric landmarks (e.g., Harvati and Weaver, 2006; Noback et al., 2011) in climate adaptation research. The only issue with the MicroScribe Digitizer is that it can only be applied on externally accessible landmarks (Noback et al., 2011, p. 602). Although using the MicroScribe Digitizer is a much faster method than other techniques, scanners can collect more information on internal structures. Using scanners also means handling the specimen less than with other techniques, which is preferable. There are also overall fewer errors documented using scanning techniques instead of digitisers, although the difference is minor (Robinson and Terhune, 2017, p. 70).

Advancements in 3D imaging technology have been beneficial to analyses on human remains. For example, within geometric morphometric analyses of evolutionary and adaptive variations, especially in cases where human remains are fragmentary, 3D digitising technology allows for the reconstruction of fragmentary human remains. Other beneficial areas include the creation of interactive 3D printed or digital displays, easier sharing of digital datasets, and the ability to create 3D printed or digital copies of human remains, especially in cases of repatriation, which allows for continued scientific analysis. Thus, 3D imaging technologies allow the production, visualisation, storage and sharing of data beyond what traditional methods are capable of (Squires et al., 2019, pp. 315-316). 3D technology has replaced traditional methods of using nails, resins, cocktail sticks, glue and plasticine which has been harmful for human remains. 3D imaging technology has not only allowed for a non-destructive virtual reconstruction of human remains, but also recreating missing portions or holes by interpolation, or reflecting across a plane of symmetry. This is a much more accurate process for reconstructing remains and it allows for a better understanding of skeletal material. Digital and 3D printed reconstructions can also reveal morphological and palaeopathological features not visible on the original remains (Squires et al., 2019, p. 324). However, as incredible as 3D technology may sound, there are some downsides in relying too much on it. Squires et al. (2019, p. 337) argue that an overreliance on the digital record could lead to the neglect and loss of physical remains. Although there are great advantages of using this type of technology, there are still certain types of research that require the presence and use of human remains. Therefore, it is important to not only rely on 3D digital data to the exclusion of physical human remains.

3.3.2. Endocranial volume

Neubauer et al. (2012) attempted to calculate the endocranial volume of several incomplete *Australopithecus africanus* crania by reconstructing missing elements and creating a virtual endocast (also see Gunz et al., 2009 for detailed description of virtual reconstruction of hominin crania). A modern reference sample was used including CT scans of 60 chimpanzees and 60 modern humans of all ages and sexes. The CT scans were segmented through both a 2D and 3D- semi-automated segmentation in a software known as Avizo. Avizo has a built-in tool that can measure volume which was used to measure the endocranial volume of the chimpanzees and humans (reference samples). The reconstruction of the incomplete fossil endocrania was done through different steps: (1) CT scans were taken of the partial endocast and segmented using the same method as with the reference sample. (2) A 'mirrored' copy of the endocasts was created using mirror-imaging techniques. The mirrored copy was employed to estimate the missing elements of the original specimen. (3) There were still missing elements after the mirror-imaging techniques was used and a geometric (thin-plate spline) method was utilised to fill in the missing elements. The method involved measuring 29 endocranial landmarks and 58 semilandmarks on the endocranial curves of the chimpanzee reference sample. 358 surface semilandmarks were also measured on the endocranial surface, which amounted to a total of 445 three-dimensional points for every chimpanzee cranium. Semilandmarks were measured on the preserved regions of the fossil specimen and thin-plate spline interpolation was performed by mapping the subsequent missing regions using the chimpanzee endocasts as reference. (4) When the entire virtual endocast of the fossil specimen had been created, the endocast volume was measured by mode, median, arithmetic mean and range (Neubauer et al., 2012, pp. 501-502). The method of creating virtual endocasts has also been performed to measure endocranial ontogenetic shape changes in humans (Neubauer et al., 2009) and to measure shape changes in human and chimpanzee endocrania during growth (Neubauer et al., 2010).

In some cases, mirror imaging techniques will not work if the same cranial elements are missing on both sides or in the symmetry "plane". In the absence of landmark coordinates, such coordinates can be estimated, or predicted, by collecting information from a complete reference specimen. There are two algorithmic approaches that can be used in reconstructing forms: statistical reconstruction and geometric reconstruction. Statistical reconstruction is done by using a multiple multivariate regression on a sample of a complete specimen to predict the location of every missing coordinate. Every variable containing missing values is regressed on all the other variables containing complete cases. A linear regression model is used to predict the missing values. Geometric reconstruction (as was done in Neubauer et al., 2012) can also be used to estimate missing coordinates by computing a thin-plate spline interpolation of the subsection of semilandmarks and landmarks on the complete reference specimen and on the incomplete target specimen (Gunz et al., 2009, pp. 50-51). The method of correcting for deformation is, according to Gunz et al. (2009), an almost perfect method of creating a match between the original specimen and the reconstruction. The only requirement is that the deformation must be somewhat uniform across the cranium (Gunz et al., 2009, p. 56; also see pp. 52-53 for correcting minor deformations).

3.3.3. External nose

The external nose can be measured in different ways. The nasal index can be calculated as the ratio between the width of the nasal aperture and height of the entire nasal skeleton multiplied by 100 (Franciscus and Long, 1991, p. 419).

Maddux et al. (2016) made an overview of measurements, including both the external and internal nose. The external nose, which can be referred to as the external pyramid, can be calculated in numerous ways, such as measuring the inferior nasal bone width, nasal bone height, least nasal breadth, piriform aperture height, interorbital width subtense at nasion, naso-dacryal subtense, naso-zygoorbital subtense and the mid-orbital breadth subtense at rhinion. The width of the inferior nasal bone at the piriform aperture is measured as the distance between the most inferior points of the nasomaxillary sutures. The interorbital width subtense at nasion is measured by the distance from nasion to the bi-frontomalare orbitale chord. The mid-orbital breadth subtense at rhinion is the distance from rhinion to the bi-zygoorbitale chord. The nasal bone height measures the distance from the superior endpoint to the inferior endpoint of the nasomaxillary suture. The naso-dacryal subtense is the distance from the innermost end of the nasal bone shape to the bi-dacryon chord. Naso-zygoorbital subtense is done the same way as with the naso-dacryal subtense, only measured from the most inner point of the nasal bone profile to the bi-zygoorbitale chord. The height of the piriform aperture is measured as the distance from the rhinion to the nasospinale. The minimum transverse distance between the two nasomaxillary sutures is known as the least nasal breadth. The nasal aperture breadth is measured as the length between the right and left alare. The height is measured as the distance between the nasion and nasospinale (Maddux et al., 2016, p. 5).

Another method of measuring the external nose is by creating landmarks on 3D cranial models rendered from CT scans. Butaric and Klocke (2018) placed 31 landmarks on the models and calculated the distance using x-y-z coordinated to compute the shape and size of the entire outer middle section of the face and the nasal area. The calculated distance between the coordinates and the geometric mean was then used to estimate three size measurements: a facial geometric average (not including nasal distances), a collective craniofacial geometric average (including all distances) and a geometric average including only nasal distances. A larger cumulative geometric mean for the entire sample was also created by incorporating all the cumulative means from the 17 distances for all individuals in the sample. The individual geometric mean was further divided by the larger geometric mean for the entire sample to provide a scaling model. The average size for the sample can then be created by multiplying the grand geometric mean with each of the individual distances (Butaric and Klocke, 2018, pp. 3-4). This method can also be quite helpful if dealing with a fossil skull and a small section is missing. In addition, if the sample contains well-preserved individuals of the same species and sex, average shape and size can be created for the total sample.

The use of landmarks and semilandmarks are important in capturing the changes in the shape of curves and surfaces as well as local features (Gunz et al., 2005, p. 96) which makes this method significant if the objective of the research is to document changes in the external nose according to ethnic groups.

Although measuring manually can be considered cost efficient, there are certain aspects that make the use of digital methods more beneficial. When measuring, e.g., a fossil specimen manually, there are two issues: the risk of overhandling the specimen and the risk of accidentally scratching the specimen with callipers. Digital methods, although more costly, allow for less handling of the specimen which is better for the conservation of the specimen itself as well as for future research. Another issue worth addressing is that linear measurements only measures size, and not the effect of shape and size. Measuring manually also comes with intra- and interobserver errors and these types of errors are often less prominent in digital methods.

3.3.4. Internal nose

Measuring the internal nose is a complex task as the nasal cavity is relatively narrow and certain areas are difficult to access. An article written by Maddux et al. (2016) includes methods of measuring aspects of the internal nose, like the internal nasal fossa and the nasopharynx. The internal nasal fossa can be measured in six ways: the interorbital breadth, inferior ethmoidal breadth, internal nasal fossa breadth, internal nasal fossa height, nasion-hormion length and superior ethmoidal breadth. The interorbital breadth is the distance between the left and right alare and the inferior ethmoidal breadth is the most significant distance between the left and right ethmoidomaxillary sutures. The breadth of the internal nasal fossa in the nasal cavity is the greater distance calculated between the lateral nasal walls at the inferior nasal turbinate level. The height is the mean score of the nasal height and choanal height. The distance between the nasion and hormion is known as the nasion-hormion length and the superior ethmoidal breadth is the largest distance between the left and right frontoethmoidal sutures. The nasopharynx can be calculated by measuring the basion-staphylion to hormion subtense, the basion-staphylion length, choanal breadth and choanal height. Choanal height is the distance from the furthest posterior point of the parallel plate of the palatine to the furthest point of the cranial base. The breadth of the choanae is the largest distance from one side of the choanae to the other based on internal points of the medial pterygoid processes. Basion-staphylion length is the distance between staphylion and nasion, and the basion-staphylion to hermion subtense is the subtense from the basion-staphylion chord to the hermion (Maddux et al., 2016, p. 5).

A different method of measuring the internal nose without using callipers is by running CT scans through a 3D slicer program. Linear measurements can be collected from each scan by using a slice tool (Marks et al., 2019, pp. 4-5).

Acoustic rhinometry is a method of measuring the geometry of the nasal cavity. Corey et al. (1998) applied this method on the nasal cavities of 106 healthy living individuals. The method consisted of using a two-microphone acoustic rhinometer carefully placed inside the individuals' nasal cavities. An AR computer software, Eccovision Software, recorded the average cross-sectional area, volume, and the measurements' standard deviations (Corey et al., 1998, pp. 389-390).

Inthavong et al. (2007) calculated the heating capability of the human nasal cavity by applying Computational Fluid Dynamics (CDF) techniques on a computational model created from CT scans. Fluid Flow Modelling is a complex method involving many steps. The general idea is that by creating a model of a human nasal cavity, it is possible to recreate and measure the effects of how each nasal cavity (left and right) process airflow and heat transfer of inhaled air (Inthavong et al., 2007, pp. 842-843).

3.3.5. Sinus volume

The seed technique was a common method of measuring sinus volume before being replaced by digital techniques. The seed technique was used by Shea (1977) to measure maxillary sinus volume, which was executed by using a thin funnel to transport seeds into the nasal cavity (Shea, 1977, p. 291). A more modern approach in measuring maxillary sinus volume was used by Butaric (2015) consisting of creating variables taken from CT scans. Since the

CT scans were grey scaled, it was difficult to observe the boundaries between bone and air. Butaric (2015) applied the half-measurement-height technique in ImageJ 1.45 to better observe the bone-to-air boundary. The half-measurement-height technique creates an average between the minimum and maximum numeric density values of the air and bone material through the boundary between the maxillary sinus and the nasal cavity wall. The following step was to view and process the CT scans in the freeware program Slicer 2.6. By using a colour-label map, the average value obtained from the half-measurement-height technique was used to distinguish the bone densities from air. The right and left maxillary was segmented using a semi-automated technique in Slicer 2.6. to colour-label across a stack of CT slices. The volume was obtained by creating digitally rendered models of the maxillary sinuses and using the Geomagic Studio program to create an average value (Butaric, 2015, pp. 1712-1713).

3.4. Shape analysis: geometric morphometrics

Geometric morphometrics (GM) is used for quantifying shape and form based on two-dimensional or three-dimensional coordinate data or landmarks. There are two methods of collecting landmarks, or coordinate data. The first method is done by recording the x, y and z coordinates from each landmark using 3D coordinate digitisers and digitising tablets. The second method is by using computed tomography (CT), surface scans or magnetic resonance imaging (MRI) to collect coordinates from the scans. There are strict requirements for placing landmarks to avoid errors. The landmarks must be placed so that they correspond with the original structure of the specimen. It is also important to be consistent with the number of landmarks being used on all specimens and place them in the same order on each specimen for correct results. There are two important terms in geometrics: shape and form. The shape of an object does not provide information regarding position, orientation or scale. Form provides information on the shape and size of an object. Before the GM analysis, the shape information is extracted from raw coordinates, including information on the object’s position within the coordinate system. The following steps are either done using Procrustes Superimposition or Euclidean distances between landmark coordinates (Schillaci and Gunz, 2013, p. 87).

3.4.1. Procrustes superimposition

By using matrix algebra, Procrustes superimposition extracts shape variables from raw coordinates by correcting (standardising) position, orientation and scaling so that all specimens are the same size. If data from a specimen are two-dimensional, the centroid is calculated by averaging all x and z coordinates. If these data are three-dimensional, additional z coordinates are averaged together with x and z. The position can be standardised by removing the centroid from the specimens' landmarks which translates it to the original coordinate. The absolute size differences between specimens can be removed by dividing specimens by their centroid size (CS). CS is the square root of the added squared distances of every landmark to the specimen's centroid. CS helps to scale the specimen to a unit centroid size. Information on the rotation of the specimen can be removed by creating a mean shape of the averaged superimposed homologous coordinates made from rotating all specimens to fit, e.g., the first specimen. Lessening the square root of the totalled squared distances amid homologous landmarks and creating a mean shape optimises the fit between specimens to the mean shape. The shape differences between the two landmark configurations can be visualised using a thin-plate spline deformation grid. The space between landmarks is interpolated based on the target shape and the reference landmarks. Thin-plate spline formalism is also functional regarding the semilandmark algorithm and estimating missing data. Semilandmarks can capture and analyse curves and surfaces based on coordinate statistics. The exact number of semilandmarks are positioned in homologous positions across all specimens, e.g., slide beside the tangent vectors to the planes or curve on the surface. The term "Procrustes distance" describes the measure of shape similarity, or dissimilarity, between two landmark configurations and produces a "shape space" metric. Procrustes form-space is created by augmenting the matrix of Procrustes shape variables with a column of the natural logarithm of centroid size (Schillaci and Gunz, 2013, pp. 87-89).

3.4.2. Analysing geometric morphometrics data

There are different statistical analyses used on geometric morphometrics data. Principal component analysis (PCA) is beneficial as it looks for large-scale trends in data and quickly detects outliers (Schillaci and Gunz, 2013, p. 89). Canonical variates analysis (CVA) or linear discriminant analysis (LDA) can also be used to look for dimensions in Procrustes form space or shape space that divides two or more groups. CVA, like any other discriminant analysis, is very much affected by the large number of variables compared to the number of specimens. If the number of specimens is higher than the number of variables, the CVA will be computed by reversing the sample covariance matrix. PCA can be used to reduce the number of variables, i.e., inverting the covariance matrix to perform a CVA. A small sample size can also be problematic when computing Mahalanobis distances for GM, like with PCA.

Regression analysis is a very reliable method used within multivariate statistics. It can predict how shape and size, or shape and climate, co-varies by using centroid size as an independent variable. This is done by regressing the Procrustes shape coordinates on one or several variables. The regression analysis results can be read as biological or ecological factors. Partial least squares can also be used to depict the relationship, or covariance, between a series of blocks containing variables based on linear combinations. The blocks can contain variables like environmental, functional or behavioural processes and help understand the association between shape and these different factors (Schillaci and Gunz, 2013, pp. 89-91).

Thin-plate spline (TPS) grids and surface morphs is another method that can be used to visualise and interpret the superimpositions and shape differences between forms. The other method uses principal components (PC) of the Procrustes shape, in which coordinates are visualised as PC scores and projected into PC axes or TPS deformations. As a result, TPS deformations will display shape differences related to every PC axis. Shape regression is another type of visualisation method similar to PC axes, and one can use TPS deformations to plot the impacts of an independent variable on a shape. The last method of visualising shape differences is by using mean differences. The mean shape for every group is calculated by computing an average of the Procrustes coordinates and by further calculating the TPS deformation grids or surface morphs between them (Schillaci and Gunz, 2013, pp. 92-93).

3.4.3. Estimating missing data using geometric morphometric methods

Estimating missing data must be done before further analyses as the exact amount and order of landmarks and semilandmarks must be used on every specimen. If possible, researchers can manually assemble isolated or segmented pieces on a computer, and missing parts on one side can be mirrored across the local midplane. Mirror-imaging techniques can be used to measure landmarks and semilandmarks on the surfaces, and missing data on both sides and along the midsaggital plane can be assessed by applying GM methods. A TPS method can be used to estimate missing data if there is a considerable number of landmarks and semilandmarks around the defect area. This method utilises a complete reference specimen to estimate data for an incomplete specimen by collecting the coordinates from the complete specimen and mapping them onto the incomplete specimen based on the subset of coordinates available on both. Any method of estimating missing data relies on using semilandmarks as the point is to capture information from dense measurements. Another way of estimating missing data is by using statistical methods, e.g., Procrustes mean shapes or multiple multivariate regression based on a reference sample. The requirement for reconstructing missing data using the latter method is that the unobservable coordinates must be predictable. The coordinates can be predictable due to the smoothness properties of the thin-plate spline or through the covariance matrix of a reference sample. Whether missing data can be reconstructed also depends on several factors, e.g., how integrated the missing parts are with the available parts, the type of reference specimen used, the density of measured coordinates and how these are spaced in the surrounding area of the defect, and whether the morphology of the incomplete specimen can be accurately captured by using landmarks and semilandmarks (Schillaci and Gunz, 2013, pp. 93-94).

3.5. Statistical analysis

Choosing statistical analyses will vary depending on the research question being investigated and what type of data are included. Nevertheless, statistical analyses play a central role in the discipline as most of the methods used are based on statistics.

There are two statistical focus areas within mid-facial climatic adaptation: the differences in the among-population means and the between-individual variation. As climate and genetic data are available on a population level and not on an individual level, focusing on the variance between individuals can prove disadvantageous (Evteev et al., 2014, p. 455).

3.5.1. Data types and preparing for statistical analyses

Data can be divided into numerical and categorical variables. Numerical/scale variables can be further divided into either continuous or discrete variables and categorical can be divided into ordinal and nominal variables. Continuous data includes any complex numbers and data values measured over time, like height, weight or age. Discrete data are a type of count that involves integers and is limited in the number of values. The discrete data are numeric and finite. Ordinal data follows an apparent order, e.g., scale, and nominal data follow no apparent order, e.g., gender. Outliers and certain patterns within raw data can be identified by summarising data. If data are continuous and normally distributed, it can be summarised by calculating means and standard deviations. Creating a chart before analysing data can prove helpful in detecting any outliers or skewed data. If data are skewed, or any outliers are found in the chart, calculating the median and interquartile range can be useful (Marshall and Boggis, 2016, p. 7).

Raw data, like linear measurements, do not always make sense by themselves, which is why researchers often standardise data, or turn them into z-scores, before further analyses. Z-scores are the standard deviations from the means of the original score and the z-scores have a standard deviation of 1 and a mean of 0. Turning data into z-scores is beneficial when comparing a score relative to the average of the sample/population or comparing scores measured with various units or on several populations. This is particularly beneficial when not all variables have the same type of distribution because the z-scores will not look like the scores and are thus easier to compare. Calculating the z-score is done by subtracting the mean from the original score, which leaves the original scores' deviation from the mean. The original unit of measurement is removed by dividing the score deviation by the standard deviation. Z-scores effectively centres and normalises the distribution of the scores (Abdi, 2007, pp. 1-2).

3.5.2. Error test

The impact of within-observer or between-observers' reliability can be tested by what is known as "error tests". The way error tests are conducted depends on the type of research or the researchers. If more than one researcher has collected measurements, one must look for inter-observer error. When only one researcher has collected measurements and there is a lack of consistency in the measurements collected over time, it is referred to as intra-observer error. Intra-observer error can be controlled by calculating standard deviation in the different sets of measurements (and potentially units of measurements), and the quantiles can be compared in a table to estimate any deviations. An inter-observer error can be calculated using intraclass correlation coefficient for every measure and linear mixed models in which the observer is regarded as the independent variable and the subject is treated as the dependent variable. Any consistencies or inconsistencies can be observed by comparing the mean measurements between the two observers (Zaidi et al., 2017, p. 26). However, the best way to avoid inter-observer error is for one researcher to collect all measurements several times in the course of a few months between the two assessments and then calculate and compare the average difference between the measurements (Evteev and Grosheva, 2019, p. 2).

3.5.3. Most common statistical analyses

Choosing statistical methods depends on the type of data used, the research question, whether there are dependent and/or independent variables, how many variables there are, if the variable includes several repeated measurements for every subject, and so on. The independent variable, like binary, nominal or time/condition, is seen as the cause and the value is independent of other variables in the research. The dependent variable, like scale, is seen as the effect and will depend on the changes in the independent variable. When performing both single comparison tests and tests of association and the researcher is studying a population sample that follows a normal distribution, parametric tests like, t-tests, ANOVA tests, regression analyses and correlation coefficient tests can be used. However, in the case of ordinal data with less than seven categories, or if data are skewed, non-parametric tests like the Mann-Whitney test/Wilcoxon rank sum, Kruskal-Wallis test, Wilcoxon signed rank test and Friedman test is recommended. If data has a skewed distribution, there is always an option to transform these data or exclude the outliers (Marshall and Boggis, 2016, pp. 9-10).

T-tests and non-parametric equivalents

Comparing the means of two distinct groups is often a part of the statistical process. The type of test used for this is either an independent t-test or Mann-Whitney test, depending on the variables included in the research. The Mann-Whitney test is a non-parametric type of independent t-test. Two assumptions must be met when performing a t-test: there should be variance uniformity and the dependent variables within each group should be normally distributed. A non-parametric Mann-Whitney test can be used if these assumptions are not met (Marshall and Boggis, 2016, pp. 21-22).

If data are paired or matched, a paired sample t-test can be used to assess whether the mean of the paired difference is zero. A paired t-test should only be used if the paired differences are normally distributed and a non-parametric Wilcoxon signed rank test can be used if the paired differences are not normally distributed. The Wilcoxon signed rank test compares recurring measurements on a single sample, matched samples or two related samples to observe if the mean ranks differ between populations. The signs of the ranked difference are used to create positive and negative ranks (Marshall and Boggis, 2016, pp. 23-24).

ANOVA and non-parametric equivalents

The one-way ANOVA test can be used in cases where there are three or more independent groups, specifically when requiring the difference between means. Taking the ratio of the within- and between-group variance will detect either a statistically significant or non-significant difference between the groups. The residuals must be normally distributed or the variance must be identical to perform the test. If these assumptions are not met, it is recommended to perform a non-parametric Kruskall-Wallis test or a Welch test and Games-Howell post hoc instead. The Kruskall-Wallis test is a non-parametric test that determines whether the samples originate from different populations. There is no assumption of a normal distribution or an equal variance. The medians of the two or more samples are compared to detect significant or non-significant differences (Marshall and Boggis, 2016, pp. 25-26).

The one-way repeated measures ANOVA is a type of one-way ANOVA only with repeated samples. It can be performed when the residuals are normal by time point and there is equality in variance between each pair of repeated measures. The test looks for changes and differences in the mean score, differentiates the variance from the measures and the variance from people, and decreases the mean squared error. If the results show a significant difference between two or more time points, a Bonferroni post hoc should be used to investigate where the differences are. Alternatively, a two-way repeated measures ANOVA and a ‘mixed’ ANOVA can be used to observe the means plot with time/condition on a diagram. If the assumptions are not met, a non-parametric Friedman test can be used to observe variations in scores across several occasions or conditions. Each subject’s scores are ranked and the total sum of the ranks for every condition can be used to do a test statistic. The significance value will indicate differences in the distributions across time points or conditions. A Wilcoxon signed-rank test and the Bonferri adjustment can be performed to monitor where the differences occur (Marshall and Boggis, 2016, pp. 27-28).

A two-way ANOVA can be used when requiring the average for two independent categorical variables. The assumption for the two-way ANOVA follows the same assumptions as the one-way ANOVA. The test follows three hypotheses: 1. There must be no interaction between the factors, 2. The means of the population for the first factor must be identical, 3. The second factor for the population means must be equal. Tukey or Scheffe is typically used for post-hoc adjustments. Transforming data or comparing the p-values with a smaller significance level can help if the assumption of the test is not met (Marshall and Boggis, 2016, p. 29).

Chi-squared test

The non-parametric chi-squared test can be used depending on whether the null hypothesis expects no relationship or association between two categorical variables. A chi-square test is typically utilised to establish whether there is a statistically significant differentiation amid what is expected frequencies and what is observed frequencies in one or several categories. The result of the test is calculated by using percentages in a table to observe the between-group differences (Marshall and Boggis, 2016, p. 30).

Correlation analysis

Correlation analysis is utilised to calculate the strength of the association between two variables. The correlation coefficient value ranges between -1.0 to -0.9 or 0.9 to 1.0, which is a very strong association, -0.9 to -0.5 or 0.5 to 0.9, which is strong, -0.5 to -0.3 or 0.3 to 0.5 which is moderate and -0.3 to 0.3 which is considered weak. There are different correlation tests, but the most common is Pearson's correlation coefficient. To use Pearson's correlation coefficients, data from all variables must be continuous, linearly related or normally distributed for both variables. If there is a third continuous or binary variable to control for, a partial correlation test can be used to first remove variation due to control and then measure the association between the dependent and independent variables. The non-parametric Kendall's rank correlation coefficient or the non-parametric Spearman's rank correlation coefficient can be used if data are ordinal or the variables are not normally distributed. Spearman's rank correlation coefficient statistically quantifies the strength of a uniform relationship between paired data. Kendall's Tau is used for small datasets with copious quantities of tied ranks and can measure the rank correlation between two measured quantities. In other words, a series of data are ranked by each quantity and the similarities between these orders are measured (Marshall and Boggis, 2016, pp. 32-33).

Regression analysis

There are several regression analyses depending on the type of dependent variable. If the dependent variable is continuous, a linear regression can be used and logistic regression is preferable if a dependent variable is binary. The analysis reveals how variables relate and predicts the dependent variable. Whilst describing a relationship between two variables, it also controls for contradictory factors. Linear regression can be used on continuous dependent and any independent variables except for categorical variables. Before performing linear regression, categorical variables should be turned into binary dummy variables. Certain assumptions must be met to perform certain linear regression analyses: a normal distribution of residuals, a linear relationship between independent and dependent variables, there must be independent observations, which means no correlation between the successive values, and homoscedasticity, or observations, must not have a significant overall influence. Logistic regression can be used on binary dependent and independent variables, including categorical variables. It is recommended to use a Chi-squared test if the variables are categorical as it investigates whether there is a relationship between two categorical variables. When the variable has a continuous outcome and the researcher wishes to investigate the relation amongst a dependent variable and multiple independent variables, multiple regression analyses can be used to control other explanatory variables and predict the outcome of a dependent variable by providing a linear combination of explanatory (independent) variables. If the variable has a categorical outcome, logistic regression can be used to create a model that foresees the likelihood of an event taking place for an individual (Marshall and Boggis, 2016, pp. 34-36).

3.5.4. Multivariate techniques

Multivariate statistical techniques are commonly used within the discipline as these techniques allow for the analysis of multiple variables simultaneously. The most common multivariate techniques used to analyse angular and linear measurements are principal component analysis, canonical discriminant functions analysis, hierarchical cluster analysis, principal coordinate analysis and multidimensional scaling. There are also non-metric multivariate techniques which are used to analyse geometric morphometric data (Schillaci and Gunz, 2013, p. 75).

Principal component analysis

The most common multivariate statistical technique used by biological anthropologists is principal component analysis (PCA). The data used for analysis can be raw or standardised and it is recommended to include strongly correlated variables. PCA can either be used to observe group-specific patterns in data or for data reduction. Typically, the number of principal components (PC) depends on the number of variables and how strongly correlated these are. When data are raw or standardised, the variables will have a mean of 0 and a variance of 1 and PCA can be performed by using either a variance-covariance matrix or a correlation matrix. Interpreting data using PCA can be quite useful because each principal component represents different data dimensions. The variables are arranged into a linear combination so that the first PC has the most variation. The coefficients belonging to the different variables, called eigenvectors, provide information on the impact of each corresponding variable on a PC. The eigenvectors belonging to each variable can have high positive or negative eigenvector values. If this is the case for the first PC, the high positive or negative value often reflects variation in size. The overall variance in the dataset is demonstrated using PCs since the variance in each PC, called eigenvalue, reflects the variables’ variance. The PCs are arranged so that the first PC has the highest eigenvalue and the last PC has the lowest. The results from the PCA can be obtained in two ways: 1. By visually comparing the bivariate distribution of PC scores or 2. By using univariate and bivariate statistical tests such as linear regression and t-tests (Schillaci and Gunz, 2013, pp. 76-77).

Canonical discriminant functions analysis

Canonical discriminant functions analysis, or canonical variates analysis (CVA), identifies linear combinations of variables that distinguishes populations or species. The variations identified amongst groups are maximised and variations within groups are minimised. CVA is similar to PCA in different ways: it produces canonical discriminant functions (CAN) that are linear combinations of the variables, and the CANs are also arranged in a way so that the first CAN displays the most variation and variation following the first CAN decreases until the last, which shows the least variation. The CVA, like PCA, has eigenvectors. The CVA also differs from PCA in several ways. The eigenvectors are not derived from a variance-covariance matrix, like in PCA, but rather collected from a sum of squares matrix and cross-products which describes the variation within and among groups. The linear combination of the CANs is also differently constructed than in PCAs so that when investigating the variation within and among groups, a one-way analysis of variance of the CAN1 produces the most significant F-test among all possible linear combinations. Not correlated with CAN1, CAN2 produces the most significant F-test among all linear combinations. The process continues where CAN3 is not correlated with CAN1 and CAN2 and thus shows the most significant F-test among all linear combinations. While the PCA has almost no assumptions regarding the variables, the CVA requires a multivariate normal distribution and uniformity of covariance matrices among groups and there must be more observations per group than variables. A singular covariance matrix results from too few observations compared to variables and must be avoided. The results can be interpreted using graphs, like bivariate plots, of the scores from the first two canonical variates. The plots will demonstrate whether the groups can be distinguished using the chosen variables (Schillaci and Gunz, 2013, pp. 77-81).

Distance-based techniques

If a research question requires investigating relative phenotypic similarities among groups, different distance measures can be used to account for correlation in the phenotypic data. The most common distance-based methods are the Euclidian distance, the Mahalanobis distance and the Manhattan distance. The different methods have different requirements, e.g., to use the Mahalanobis distance method there must be more variables than observations for every group in the analysis. If there are outliers in the dataset, the Manhattan distance method is preferable to the Euclidian method. Several multivariate techniques can help illustrate the distance matrix: cluster analyses, principal coordinate analysis and multidimensional scaling (Schillaci and Gunz, 2013, p. 82).

Both principal coordinate analysis (PCO) and multidimensional scaling (MDS) are non-metric techniques that can be used to represent distance matrices graphically. MDS attempts to locate and recover absolute coordinates for observed distances between groups based on the number of dimensions. Sometimes the objects will not all be positioned on the same plane, and thus more than three dimensions will have to be included if the analysis is performed on more than three groups. The next step is calculating the Euclidian distances amongst groups and regressing the configuration distances on the true distances using linear or monotonic regression. The final step is to compare the regression model with the original distances. A set of coordinates that reduces the difference between the original distances and the fitted distances is chosen and used to create a two-dimensional or three-dimensional map built on the original distance matrix. How well the MDS map represents the original distance matrix is measured and expressed by stress values. The MDS plot is suitable if the stress values are low (0 - 0.10). PCO also graphically represents distance matrix by creating a type of map. The map is helpful as it creates an overview of the relationships among groups. PCO, like PCA, also uses eigenvectors and eigenvalues from a distance matrix (Schillaci and Gunz, 2013, pp. 82-84).

Hierarchical cluster analysis unites groups that are close, or related, to each other. The results of the cluster analysis are presented in a dendrogram, which is a tree-like diagram. If the dendrogram exhibits branching, it can reflect an ancestor-descendent relationship. The accuracy of the dendrogram compared to the original distance matrix can be observed through the range of the cophenetic correlation coefficient. If the cophenetic correlation coefficient is 0, there is no relation between the dendrogram and the original distance matrix.

If the cophenetic correlation coefficient is a minimum of 0.8 or 1, there is a positive or strong positive relationship between the original distance matrix and the dendrogram. The process of merging comparable groups relies on algorithms and dendrograms will differ depending on which algorithm is used in the analysis. The unweighted pair group method with arithmetic mean (UPGMA), single-linkage and Ward's technique are a few examples of standard algorithms used in the discipline. The UPGMA technique observes the average distance between groups in a cluster and connects algorithm groups based on these average distances. The single-linkage algorithm links groups based on the minimum distance between groups in a cluster. A bootstrap method can be used to assess the accuracy of the dendrogram. The bootstrap method calculates a new dendrogram based on *n* observations and any bootstrap value higher than 60 % will support any branching points on the dendrogram. The single-linkage algorithm, or neighbour-joining algorithm, is quite useful when estimating phylogenetic relationships as it allows for different branch lengths and does not assume uniformity regarding evolutionary rates across groups or taxa. Similar taxonomic groups are grouped as "neighbours" through a single branching point. The method will display an axis of divergence and a quantity of derived similarity and, depending on whether the morphometric variables exhibit phylogenetic signals, assume phylogenetic inferences (Schillaci and Gunz, 2013, pp. 84-85).

Chapter 4 – Critical Analysis, Comparison and Discussion of the Major Topics

This chapter will be the most extensive part of this thesis and will be delving deeper into the different theoretical models to better understand the shortcomings and successes of some of these theories in explaining human cranial variation. The first subchapter will critically discuss the competing conceptual frameworks and criticism against the modern evolutionary thesis. The following subchapters will critically analyse the applicability of Bergmann's rule and Allen's rule and modern evolutionary theory in climate adaptation research. The next subchapters will critically discuss whether these theoretical models are consistently used within the discipline, and present contemporary issues and other explanations within climate adaptation research.

4.1. Modern evolutionary theory: competing conceptual frameworks and criticism against the Modern Evolutionary Synthesis

The most recent and supported view within evolutionary theory today is “the Modern Synthesis” (MS) which owes its existence to the earlier work done by scholars like Darwin and Wallace (Jurmain et al., 2014, p. 94). The MS has developed these original theories in conjunction with advancing technology and updated knowledge of genetics and the role of natural selection in evolution. The difference between pre-modern and modern evolutionary theory is that modern evolutionary theory sees natural selection and genetics as two mechanisms working simultaneously and interchangeably. These two forces put together will encourage adaptation and evolution in living organisms. Modern evolutionary theory also explains the production and redistribution of variation on a cellular level, which Mendel’s genetic principles lacked (Jurmain et al., 2014, p. 42).

However, some scholars believe that the MS neglects to include some significant processes, like developmental biology, genomics and ecology (Gilbert et al., 1996; Wagner and Altenberg, 1996; Brakefield, 2006; Pigliucci et al., 2006; Müller, 2007; Badyaev, 2011; Brakefield, 2011; Laland et al., 2015). New conceptual frameworks, like “Evolutionary Developmental Biology”, informally known as Evo-devo, and “the Extended Evolutionary Synthesis” (EES), has recently been gaining support and the argument they both share is that the original MS overemphasises the role of genetics. Consequently, other vital processes are being ignored. It has proved challenging to understand whether Evo-devo and the EES represent two different conceptual frameworks, or if Evo-devo is a part of the EES. Regardless, this thesis will treat them separately. Supporters of Evo-devo and the EES argue that these conceptual frameworks should not be seen as separate, competing theories looking to replace the MS but instead seen as an extension. While some of these conceptual frameworks lack empirical support, some critical arguments are worth highlighting and will therefore be included in this thesis.

4.1.1. The Extended Evolutionary Synthesis

The EES is defined by Laland et al. (2015) as a developing line of contemporary evolutionary thought within evolutionary biology. It does not deny the MS as a whole or prior knowledge of evolution in biology. Instead, Laland et al. (2015, p. 3) argue that although EES is a different theoretical framework than the MS, it can be used alongside other traditional frameworks within evolutionary biology. EES has four focus areas: developmental plasticity, niche construction theory, evolutionary developmental biology and inclusive inheritance.

Central to the EES is developmental plasticity, also known as phenotypic plasticity, which refers to the capability of an organism to alter its phenotype to better adapt to its surrounding environment. The evolution of plasticity is not a phenomenon monopolised by EES, instead it is a process that has been well-studied within the discipline. Traditional beliefs argue that plasticity is a consequence of phenotypic evolution, while EES believe plasticity is also a cause of phenotypic evolution. According to Laland et al. (2015, pp. 3-4), plasticity has several roles in which it serves to assist or to facilitate: the occupation of novel environments, helping in the way populations connect and gene flow. Plasticity affects selection by providing spatial and temporal variation, it might encourage adaptive peak shifts, speciation events and radiations, and lastly, it contributes to evolution through genetic and phenotypic accommodation. It is believed that phenotypic accommodation occurs during development and in parts of an organism where functional and mutual adjustments arise. It does not necessarily involve genetic mutation. While the environment stimulates and selects for different phenotypes, genetic accommodation can supply a tool for fast adaptation to such new environments. Phenotypic accommodation can encourage genetic accommodation only when phenotypes that are stimulated by the environment are stabilised and finely adjusted through generations. This can be done by selecting earlier cryptic genetic variation, standing genetic variation or new mutations. Inclusive inheritance refers to a broader definition of heredity in which inheritance can occur at any level from germ cell to the external environment.

The traditional definition of inheritance is the transference of genes from one generation to the next. Thus, inclusive inheritance is the inclusion of several more levels. Niche construction theory entails the idea that organisms play a more active role in selection through activities, metabolism and the choice of modifying and stabilizing environmental states. Species of animals create nests, burrows and webs which can alter and generate stable and directional changes in the environmental conditions. Supporters of this theory believe that constructing niches influences ontogeny where the environment plays a considerable role during normal development (Laland et al., 2015, pp. 3-4).

4.1.2. The Extended Evolutionary Synthesis vs. the Modern Evolutionary Synthesis: using a comparative model produced by Laland et al. (2015)

Laland et al. (2015) produced an overview of the main assumptions of the MS and EES. The first assumption relates to the relationship between an organism and its environmental adaptation. Supporters of the MS believe that natural selection is the significant directing force in evolution and is evidenced by how the properties of an organism match the properties of the surrounding environment, known as adaptation. On the other hand, EES argues that there is a reciprocal causational relationship between an organism and its environment. This means that an organism shapes and is shaped by developmental and selective environments. Natural selection is not the only directing force but operates with developmental processes, such as niche construction and developmental bias. The second assumption concerns inheritance and supporters of the MS firmly believe that only genes constitute the general inheritance system. EES believe that the term inheritance can be expanded to include ecological inheritance, cultural inheritance, social or behavioural transmission, epigenetic inheritance and physiological inheritance. The third assumption relates to variation and the classical MS assumes that there is no connection between the direction in which mutation takes place, which also includes the supply of phenotypic variants, and the path leading to better fitness. EES argues for non-random phenotypic variation, which means that developmental bias, occurring from phenotypic accommodation or non-random mutation, implies that specific phenotypic variants are more probable than others. These are functional phenotypic responses to environmental stimulation or mutation and are facilitated by developmental systems. The MS argues that evolution happens gradually. Phenotypic changes occur over several stages, gradually resulting in evolutionary change. This is because mutations have disruptive pleiotropic effects (Laland et al., 2015, p. 2). Pleiotropic effects, or pleiotropy, is when a single gene affects more than one trait (Jurmain et al., 2014, p. 93). On the other hand, EES assumes that the rates of change are variable, and contrary to the MS, they believe that rapid evolutionary change can happen through variants of significant effects. Evolutionary "jumps" can take place via mutations in central governing control genes, demonstrated in module, compartment, tissue, or tissue specific ways. Evolutionary jumps can also occur as a response to environmental challenges through developmental processes. The MS is also preoccupied with the idea that changes in gene frequencies are the key to evolution, with assistance from natural selection, drift, gene flow and mutation. The EES prefers an organism-centred view for describing how evolution occurs. According to EES, developmental systems facilitate adaptive variations that alter selective environments. Evolution is seen as an intergenerational alteration in the supply of a population’s transmissible traits. Macroevolution, according to the MS, is explained by microevolutionary processes, e.g., selection, drift, gene flow and mutation. EES, however, believes that macroevolutionary patterns and evolvability can be explained by other evolutionary processes, e.g., ecological inheritance and developmental bias (Laland et al., 2015, p. 2).

Another overview created by Laland et al. (2015) compares ten predictions between the two conceptual frameworks: (1) Adaptive evolution: the traditional prediction (MS) is that genetic change comes before, and thus causes, phenotypic change while EES believe that phenotypic accommodation can occur before genetic change. (2) Directionality of novel phenotypic variants: the MS predicts that genetic mutation and novel phenotypes have a random, neutral or slightly disadvantageous direction. Contrary to this, EES argues that novel phenotypic variants are functional and directional. (3) Mutations or variants in single or multiple individuals: The MS believes that isolated mutations generate novel phenotypes which will only occur in one individual. In contrast, EES believe that the environment stimulates novel phenotypic variants that will occur in several individuals. (4) How adaptive evolution occurs: The MS believe that adaptive evolution results from a selection of mutations with minor effects. EES argues that several novel phenotypes can occur due to a major regulatory control gene mutation or through assisted variation. (5) Repeated evolution in an isolated population: The MS predicts that repeated evolution is due to convergent selection and EES predicts repeated evolution as either due to developmental bias or convergent selection. (6) How adaptive variants are reproduced: The MS argues that adaptive variants are reproduced through selection. EES claims that adaptive variants are reproduced through learning, selection, non-genetic heritage, repeated environmental stimulation and cultural transmission. (7) Rapid phenotypic evolution: The MS describes rapid phenotypic evolution as dependent on whether there is a substantial selection on abundant genetic variation. Contrastingly, the EES believes that rapid phenotypic evolution can occur more frequently than the traditional belief states. It is the result of concurrent stimulations and the selection for functional variants. (8) Taxonomic diversity: The MS argue that diversity in the selective environments will lead to taxonomic diversity and EES claim that taxonomic diversity is instead the result of features of developmental systems, like constraints and evolvability. (9) Heritable variation: There is a disagreement on whether heritable variation is biased or unbiased, where the MS believes that heritable variation is unbiased and the EES considers it systematically biased. The EES further argues that it is inclined towards variations that are adaptive and unified with current facets of the phenotype. (10) Niche construction: The term is not typically used within the MS but is described as environmental states modified by organisms. Supporters of the MS do not consider niche construction any different than other non-organism processes that change the environment. In contrast, the EES describes niche construction as systematically biased toward changes in the environment that reflect the constructors' or descendants' phenotype and, in turn, the fitness of the constructor or descendant (Laland et al., 2015, p. 10).

4.1.3. Evo-devo vs. the Modern Evolutionary Synthesis

At the core of modern evolutionary developmental biology (Evo-devo) is molecular genetics of embryogenesis and developmental genetics. Evo-devo investigates the evolution of developmental pathways, how development can be linked to the evolution of form and whether similar types of pathways and changes are involved at different phylogenetic levels. One of the objectives of Evo-devo is to establish whether there is a link between changes in developmental pathways and the evolution of different forms, or body plans, in distantly and closely related taxa (Brakefield, 2011, pp. 2070-2071).

Brakefield (2006, p. 362) points out the general interest in how developmental processes change during the evolution of morphologies. Morphological variation can, through developmental mechanisms, pattern formation and morphogenesis, be mapped onto genetic variation. He argues that the variation observed in complex morphological traits is not due to the presence or absence of specific genes, but rather the consequence of changes in the mechanism of gene regulation. This gene-regulating mechanism decides when and where a gene is expressed. He further suggests that the morphological diversity in evolution is not due to new genes but instead reflects a limited genetic tool kit where old genes are 'recycled' into performing new 'tricks'. There are, however, two central issues worth mentioning: how patterns of allometric growth change during evolution and to what extent the process that produces variation in morphology bias evolution (Brakefield, 2011, p. 362). Another issue is whether developmental bias and genetic channelling are the same or represent different processes. Developmental bias is the potential of developmental systems to bias evolution, e.g., pace and direction, and genetic channelling leads to the clustering of species or populations along axes or lines of least resistance. Brakefield (2011) argues that a more comprehensive term, such as generative constraints, would encompass both terms describing the process of producing variation in phenotype relating to evolution (Brakefield, 2011, p. 363).

Another interesting point made by Brakefield (2011) is whether the observed pattern of parallel evolution is due to developmental bias/genetic channelling or whether the parallel evolution of two similar species reflect a shared environment and modes of natural selection. The way phenotypic variation is created encourages adaptive evolution to be organised along specific pathways. He further believes that parallel evolution occurring in similar ecological surroundings can be predictable once developmental processes have been better researched (Brakefield, 2011, p. 364).

Love (2006), another supporter of Evo-devo, is particularly critical of how morphology or comparative anatomy is presented in the MS. Love (2006) argues that the valuable contribution of morphology is not openly acknowledged or displayed by the MS. Furthermore, there is a potential to contribute but without contributing. Love (2006) describes it as follows:

"…It preserves the sense of exclusion experienced by morphological researchers without imputing intentionality for this result to other biologists" (Love, 2006, pp. 318-319).

Lastly, because morphology is descriptive, there is a theoretical inability to contribute (Love, 2006, pp. 318-319).

Love (2006) also points out that the MS neglects the higher levels of organisation, which is witnessed by the exclusion of researchers specialising in morphology. Love (2006) explains that the focal research area within Evo-devo is to explain the inception of specific evolutionary novelties, e.g., neural crest cells, feathers or bone. Distinctive morphological features, like vertebrate jaw, occur at higher levels of organisation. The MS has also received criticism from philosophers of biology (Moss, 2003 and Robert, 2004 in Love, 2006) who believe that the narrow focus on genetics alone means that no attention is given to the developmental relationship between gene and phenotype. Evo-devo aims to recover the neglected topic of ontogeny as a prerequisite for evolutionary explanations. The role of embryological processes must be recognised as it works at several complex hierarchies of structures. It is only through understanding development and its evolution that researchers can attempt to comprehend the diversity of these processes, including those taking place at higher levels of organisation. The focus must also be directed towards the hierarchical organisation of organisms and populations to identify and explain evolutionary innovations and novelties. This means addressing where these activities occur and how relevant variation is generated. Several hierarchies must be explored, ranging from genes to cells, cells to entire organisms and organisms to ecosystems. There is no need to focus only on the primary or natural levels (e.g., gene, cell, tissue, organ, organism, and species) (Love, 2006, pp. 321-323).

Badyaev (2011) recommends that the roles of natural selection and inheritance must be updated concerning the functioning of organisms and development. The mechanisms that create diversity amongst organisms differ from those responsible for modification and maintenance. The MS should incorporate the causal relationship between development, natural selection, phenotypic variation and inheritance. These components must exist together with variability and plasticity, where the role of natural selection is to "show up" due to changes in ecological contexts and developmental resources between generations. Badyaev (2011) mentions only two conceptual frameworks that successfully explain evolution: the theory of evolution by natural selection and the MS. However, both only proved successful after removing some of these components (Badyaev, 2011, pp. 1921-1922).

Gilbert et al. (1996) believes that there are three topics neglected by MS: macroevolution, embryology and homology. The MS typically extrapolates the role of macroevolution and the evolution of species and higher taxa. According to the MS, macroevolution results from microevolution and the origin of higher taxa is due to population genetics. Gilbert et al. (1996) claim that embryology was initially a part of evolutionary theory but was later replaced with genetics as no other mechanism for evolution was available. Concepts like macroevolution, which are large-scale evolutionary processes (Jurmain et al., 2014, p. 107), and homology, which is the similar structures shared between organisms based on descent from a common ancestor (Jurmain et al., 2014, p. 110), lost their significance during this process, which were both processes that Darwin embraced fully (Gilbert et al., 1996, pp. 357-358). While genetics is sufficient in explaining microevolution, there are other questions neglected regarding macroevolutionary processes, such as how mammals evolved from reptiles or amphibians from fish? (Gilbert et al., 1996, p. 361).

4.1.4. A delve into the discussion on re-evaluating evolutionary theory

Laland and colleagues in Laland et al. (2014) proposes that evolutionary theory should be re-evaluated, arguing that a change is required. Wray, Hoekstra and colleagues (in Laland et al.

(2014) argue for the continuation of the MS as the main conceptual framework describing evolution. Supporters of EES believe that the MS views organisms as "programmed" to develop because of their genes and that these organisms evolve to fit into already existing environments. According to the supporters of EES, many biologists who, with support from other disciplines like genomics, social science, developmental biology, epigenetics and ecology, argue that the way evolution is currently theorised should be changed. Supporters of the EES claim that variation should not be seen as random and that there is more to inheritance than just genetics. Multiple routes link the fit between organisms and the environment and, in the case of speciation events and adaptation, development is the direct cause of how and why these events occur. Development is also a direct cause of the patterns and rate of evolutionary change (Laland et al., 2014, pp. 161-164).

In Laland et al. (2014), Wray, Hoekstra and colleagues are proponents of MS who believe that the current synthesis accommodates the evidence well. The MS is not a static conceptual framework incapable of change, but has been extended, modified and corrected by generations of evolutionary biologists. After the discovery of «selfish DNA», there was reason to believe that selection occurs at a genetic level and not at the level of traits. However, this does not mean that the focus is only on genetics to the exclusion of other processes. The cornerstones of EES, developmental bias, niche construction, inclusive inheritance and phenotypic plasticity, are also significant to the MS. These processes have been a part of evolutionary biology since Darwin. Niche construction theory has also been a well-known concept described as the feedback between organisms and their environment. None of these ideas within EES are new and they still need to prove their value through theory, empirical evidence and discussions. Laland and colleagues are not the only evolutionary biologists who request specific topics to receive more attention. There are other topics, like epistasis, cryptic genetic variation, extinction, climate change adaptation, the evolution of behaviour, etc., which, according to several evolutionary biologists, urgently needs more attention. When asked whether the MS places too much emphasis on genes, Wray, Hoekstra and colleagues argue that genes are, in fact, essential. Changes in hereditary material are vital for adaptation and speciation events, and the significance of genetics is well backed up by empirical evidence and theory. This does not mean that the MS is dismissive to other non-genetic processes. Phenotypic plasticity plays a significant role in an individual's adaptiveness, which is well-known and documented within the current synthesis. However, more focus could be placed on whether plasticity can direct genetic variation during adaptation. What is important is the transmissible variations in traits, especially those that are selectively beneficial. The term “inclusive inheritance” in adaptation has also not been sufficiently backed up by evidence. The processes mentioned by Laland and colleagues are merely additional processes that can alter the evolutionary process under particular conditions but not cause evolution (Laland et al., 2014, pp. 161-164).

4.2. The applicability of Bergmann's rule and Allen's rule

The ecological rules of Bergmann and Allen have been used by many scientists because they describe patterns that are products of evolutionary forces of adaptation as defined by modern evolutionary theory. This section will investigate the issues of applying the ecological rules to climate adaptation research.

4.2.1. Bergmann’s rule

Bergmann’s rule states that a larger body size will increase the body mass/body surface ratio. Increasing the ratio between the body mass and body surface will reduce body heat loss by radiation. The larger the body mass, the smaller the skin surface when compared to body mass (Newman, 1953, p. 312). Bergmann's rule was written in 1847 by Karl Georg Lucas Christian Bergmann. There are disagreements and confusion relating to the taxonomic levels, taxa and mechanisms to which the rule is meant to be applied. There are issues mentioned by Meiri (2011) that prevent modern researchers from reading it, such as it being difficult to access, being 114 pages long and being published exclusively in German. The first attempt at translating his work was in 1970 (James, 1970 in Meiri, 2011), but only one page out of 114 pages was translated. The translation was criticised by other scholars because it neglected the full context of the paper. Another effort was made to translate Bergmann's work (Watt et al., 2010 in Meiri, 2011), and the objective this time was to improve the clarity of his rule by directly translating his manuscript. The translation proved less useful than the previous one, but it did provide one previously neglected insight: Bergmann tested his rule "among races of domestic animals". The discussion pertaining to Bergmann's rule concentrates on several questions: can Bergmann's rule be regarded as a pattern or a process? Which taxa and taxonomic level should it be applied to? Do the different mechanisms, patterns, taxa and taxonomic levels need different names? (Meiri, 2011, p. 203).

Several scholars have criticized Bergmann's heat retention mechanism over the years, however, Bergmann's rule merely describes a pattern observed by Bergmann himself. It has been proven that populations of the same species living in cold environments are larger than those living in warmer environments, irrespective of whether the hypothesis of heat retention is correct. In the latter translation, it is believed that Bergmann originally applied his rule to within-species. He did not focus on the mechanism behind these changes, but rather what he found empirical support for. Bergmann's size clines have been interpreted as such: different populations belonging to the same species have been under various governing selections that encouraged size clines. Size variations thus result from climate adaptation. Meiri (2011) argues that Bergmann's rule can also be applied to between-species that have been split from one species, as well as between-populations within a lumped species. Vast climatic variation is necessary for size clines to evolve. Meiri (2011) deems Bergmann's rule valuable when applied to research on size variation combined with temperature or latitude in any taxon. He further recommends that temperature-size should be seen as a pattern. The mechanism behind this pattern could be heat retention or other mechanisms related to metabolic rate. A size cline could result from animals living in warm climates obtaining less food and are thus smaller than those living in cold climates where food is more crucial. Meiri (2011) concludes that the temperature-size pattern would be more potent at a population level than between closely related species (Meiri, 2011, pp. 204-205). Regardless of what direct mechanism lies behind these patterns, evolutionary adaptation appears to be the governing mechanism that causes these changes.

There have been discussions regarding which environmental factors should be correlated with latitude, e.g., humidity, temperature, precipitation, seasonality, primary productivity, resource availability, competition, species range size or species richness (Gutiérrez-Pinto et al., 2014, p. 851). If climate (humidity, temperature and precipitation) is the variable used in correlation with latitude, how do we know that size cline is entirely caused by climate and not, e.g., related to resources or productivity?

4.2.2. Allen's rule

Allen's rule represents an empirical observation of latitudinal patterns in homeotherm morphology. Allen's rule states that populations within a species or closely related species have larger-sized limbs and appendages relative to body size in warmer climates, and smaller limbs and appendages relative to body size in colder climates. An increase in temperature would alter the allometric relationship between the size of the body and the length of appendages and limbs. Several studies have observed a positive relationship between climate warming and Allen’s rule (Ryding et al., 2022 in Santoro and Calzada, 2022). However, Santoro and Calzada (2022) argue that none of these studies focuses on the disproportionate change in appendage length relative to body size, even with body size as a control variable. According to Allen's prediction, there should be a disproportionate relationship between the length of the appendage relative to body size, which means a change in the allometric relationship. Santoro and Calzada (2022) believe that only concentrating on appendage size, and neglecting allometric differences, will lead to false results regarding how temperature affects the size and shape of animals, including the ecological consequences. Thus, previous research has not captured the essence of Allen's predictions. Another issue concerning Allen's rule is the type of measurement used in quantifying body size, whether it is body length or body mass. Different measurements have different implications for determining whether the relationship is isometric or allometric. An isometric relationship predicts the trait and body size growing at the same rate, while an allometric relationship predicts a different growth rate between the trait and body size. Another matter worth mentioning is how the variations in allometry explain changes in heat dissipation. Allen's rule states that an organism can dissipate more heat when the allometric slope of appendage length according to body size is steep. Santoro and Calzada (2022) claim that, in determining animal morphology, various adaptive and non-adaptive mechanisms work together with environmental conditions. It is challenging to separate only one of these processes, like heat dissipation, to measure its effects when many other processes work simultaneously. However, experimental evidence suggests that temperature can have a direct impact on bone growth and thus has the potential to generate different phenotypes at different latitudes. Whether physiological responses to temperature can be passed from parental generation to offspring and are subject to selection remains unclear (Santoro and Calzada, 2022, p. 475).

Similar issues present in Bergmann's rule can also be found in Allen's rule regarding whether it should only be applied to entire collections of species at higher latitudes, closely related groups of species or different populations within a species. There have also been disagreements on which environmental factors associated with latitude promote changes in morphology and whether the underlying reason for needing evolutionary change is heat conservation or other physiological requirements. Allen's rule has also received very little attention compared to Bergmann's rule due to the contradictory patterns found in different studies. Gutiérrez-Pinto et al. (2014) criticizes previous research for focusing on the correlation between morphology and latitude, and therefore assumes that temperature is the driving force behind any positive relationship between the two. Instead, a direct emphasis on the relationship between temperature and morphology would be more correct. They further imply that most studies on birds have focused on latitude, and not the effects of elevational gradients in temperature, and how this affects morphological variation. There is also a narrow focus on whether single traits are proxies for body size (length of wing or tarsus) or the reduction of morphological variation in several characters utilizing multivariate statistical methods. This is without the knowledge that each trait might be under different selection pressures of which some of these traits could represent the effects of locomotion or foraging, and not the effects of climate (Gutiérrez-Pinto et al., 2014, p. 851).

4.3. How useful are theoretical models when applied to modern human climate adaptation research?

Modern evolutionary theory does not specifically touch upon the impact of climate on morphology, except for what is mentioned as the effects of natural selection or the environment. While the environment and natural selection encompass much more than just climate, it is the effects of climate specifically that is essential to this topic. The lack of conceptual frameworks describing the impact of climate on morphological variation could be due to the scarcity of robust empirical evidence. However, recent progress has been made towards the gathering of more evidence, specifically on how some aspects of the human cranium reflect climate adaptation (Carey and Steegmann, 1981; Franciscus and Long, 1991; Keck et al., 2000; Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Noback et al., 2011; Evteev et al., 2014; Caldwell, 2014; Jaskulska, 2014; Katz et al., 2015; de Azevedo et al., 2017; Butaric and Klocke, 2018; Marks et al., 2019; Stansfield et al., 2021). Another reason for a lack of conceptual frameworks linking climate to morphological variation may be due to the neglect of effort in producing specific theories relating to climate adaptation. For now, natural selection is considered one of the most important mechanisms for variation, and thus climate adaptation falls within the theory of natural selection.

4.3.1. Natural selection and climate adaptation research

Some of the basic principles of natural selection are: (1) There is biological variation in all species. (2) Species produce offspring faster than the environment can replenish necessary resources. (3) The birth rate in a population is higher than the natal mortality rate leading to an increase in population, which in turn creates increased competition for limited resources.

(4) Individuals with a favourable variation or traits that best match the environment have an advantage over others in survival. (5) The environmental context decides whether a trait is beneficial. (6) Those with favourable traits are more likely to produce more offspring than others. Traits are thus inherited and passed on. As time passes, the favourable trait becomes more common and less favourable traits are "cleared out". Those producing the most offspring have the best fitness or reproductive success. (7) A new species will appear when successful variations in a population have accumulated over time, making that population distinct from their ancestral population. (8) Geographical isolation also leads to speciation. For example, populations A and B are separated due to distance or natural barriers. Population A and Population B will, in time, adapt to their respective environments and the mechanism known to initiate these adaptations is known as selective pressure. Selective pressures are different ecological situations that these populations are exposed to, and in time this separation and exposure to different environments may lead to separate species (Jurmain et al., 2014, pp. 38-39).

Climate is one of the selective pressures that hominins have been exposed to in the Pleistocene. Hominins likely suffered from different stressors, such as harsh climates or limited resources, depending on what selective pressure was acting on them. Different skeletal parts might adapt differently to such selective pressures and constraints (Buck et al., 2018, p. 157). Many researchers believe that the differences between Neanderthals and modern humans are due to natural selection acting differently on the two species, and thus both adapted to different environmental scenarios. However, Pearson (2013, p. S222) argues that these adaptive hypotheses lack experimental support. There is a way of observing whether selection or drift is the mechanism behind changes in the lineages of Neanderthals or modern humans. If drift were the primary mechanism diverging the two species, then the changes in morphology would appear right after or during periods of low population numbers, as genetic drift operates strongest on small populations. If selection were the key mechanism, there would be evolutionary or morphological changes during periods favouring large population numbers, e.g., during periods of climatic stability. However, testing this hypothesis is difficult due to, e.g., a limited fossil record and inadequate dating of fossils (Pearson, 2013, p. S227).

The main environmental stressors experienced by hominins were likely extreme environments, like dry and arid conditions, unpredictable environments where habitats were unstable or fragmented and resources fluctuated. These environmental challenges were met by directional adaptations in brain and body size in hominins and occurred both over short-term scales (during a lifespan or across several generations) or long-term scales (many millennia). The hypotheses used to explain these changes are often phenotypic plasticity or natural selection (Will et al., 2021, p. 2).

Franciscus and Long (1991, pp. 424-425) describe a method used to test natural selection by linking variation in a particular trait, such as nasal morphology, and environmental factors, such as climate. This is known as the correlational method and two hypotheses were presented for this method. The first hypothesis is the null hypothesis, which states that the trait will vary independently of the relevant climatic variables. The other hypothesis dictates that geographically varying selection results in a relationship between the trait's variation and climate. The association between the trait in question, e.g., nasal index and climatic variables, can be tested statistically and the results will either be statistically significant, strong statistically significant or non-significant. The climatic variables used in the correlation test can be mean annual temperature, mean annual absolute humidity and mean annual relative humidity. However, the correlational method does not demonstrate that natural selection has led to the variation in the trait. Another method used to detect natural selection is the ‘equilibrium prediction of the outcome of natural selection’ method. This method deals with the outcome of natural selection by using the first principles of biology to predict an optimal functional design.

Climate adaptation research divide the effects of selective pressures on populations in cold climates and those in hot climates. What is particularly interesting to anthropologists is what drives populations to differ from one another and what this means for our species' ability to adapt to environments. Modern humans living in different climatic zones possess different features that best match the environment. Specifically, populations living in northern latitudes express cold-adaptive features and populations in southern latitudes express warm-adaptive features (Caldwell, 2014, pp. 17-18). These features can be found in both post-cranial and cranial elements. Caldwell (2014, p. 70) observed a lengthening of the face and cranial base in both Neanderthals and anatomically modern humans and linked it to an expansion of the mid-face due to the adaptive need for increased space for air turbination, moisture absorption and warming in the nasal complex. This can be connected to climatic pressures on adaptive processes and the selection for a better cold-adapted face.

Roseman (2004, pp. 12827-12828) argues that the role of natural selection is to shape between-population differences, which is reflected in cranial morphology. He states there is a strong link between variations in average temperature during the coldest month of the year and morphological variation, but only when population history is removed. However, the positive correlation is only apparent when the Siberian sample is included in the tests. Two cranial elements appear to have been selected for in colder environments: thermoregulatory capacity leading to brachycephalisation (increasing value of the cephalic index) and a tall narrow nose consistent with thermoregulatory breathing.

Several scientists have argued that natural selection (climate) has acted on facial shape and, specifically, external and internal mid-facial shape (including nasal morphology) (Carey and Steegmann, 1981; Franciscus and Trinkaus, 1988; Keck et al., 2000; Roseman, 2004; Churchill et al., 2004; Harvati and Weaver, 2006; Márquez and Laitman, 2008; Hubbe et al., 2009; Noback et al., 2011; Evteev et al., 2014; Jaskulska, 2014; Butaric, 2015; Maddux et al., 2016; Evteev et al., 2017; Butaric and Klocke, 2018; Evteev and Grosheva, 2019; Marks et al., 2019; Stansfield et al., 2021; also see Baab, 2021 for *Homo erectus*). The vast amount of evidence suggests natural selection has explicitly acted on the mid-face in specific populations of *Homo sapiens*. However, the results of most of these studies are greatly influenced by the inclusion of populations living in cold environments (Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Evteev et al., 2014).

Interestingly, Weaver et al. (2007, p. 143) suggests that diversifying natural selection did not play an active role in the differences between the cranial morphologies of Neanderthals and modern humans. They further argue that natural selection did perhaps not play a significant factor in hominin cranial heterogeneity after the emergence of the genus *Homo*. This does not mean that natural selection did not play a role in shaping cranial morphology intrinsically after the emergence of *Homo*, but merely in the shaping of cranial shape differences between Neanderthals and *Homo sapiens*.

4.3.2. The ecological rules of Bergmann and Allen applied to modern human climate adaptation research

The ecological rules of Bergmann and Allen are commonly used within modern human climate adaptation research. Research has shown that the neurocranial shape and size appear to vary with climate, following both ecological rules. In cold climates, crania appear larger and more brachycephalic (Beals et al., 1984; Nowaczewska et al., 2011). According to Allen's rule, cold adaptation can also be visible in facial breadth and decreased facial projection (Hubbe et al., 2009; Betti et al., 2010; Evteev et al., 2014; Evteev et al., 2017) as well as the shape of nasal morphology (Carey and Steegmann, 1981; Franciscus and Long, 1991; Noback et al., 2011) which is narrower in colder climates.

Although the ecological rules of Bergmann and Allen were not originally applied to modern humans, it has become more common to do so. The application of Bergmann and Allen's ecological rules to humans was made in 1953 by both Newman and Roberts, although Newman (1953, p. 311) mentions Ridgeway as the first to officially apply the ecological rules to humans in 1908.

Newman (1953) applied the ecological rules on the natives in the New World, which consisted of measuring body size clines (Bergmann's rule) and limb proportions (Allen's rule) to look for adaptive responses in humans. He found that the native populations in the New World follow both ecological rules, indicating adaptive changes. However, he also acknowledges that the underlying mechanism behind these adaptive changes is uncertain, whether natural selection or plasticity, but most likely a combination of both (Newman, 1953, p. 325). Roberts (1953) published an article on whether mean body weight differs following average annual temperature and if it is influenced by ethnicity. His study was performed on global Indigenous populations (Roberts, 1953, p. 533). He does not refer to Allen's rule and appears to only have tested for Bergmann's rule in his research. He argues that Bergmann's rule can be applied to humans because his samples followed a weight/temperature relationship according to Bergmann's rule. He chose weight as a measure of body size, but criticized the rule for neglecting to define "body size", which could incorporate either body stature or weight. Roberts (1953) suggests that the rule needs redefining to include postulated variation in size amongst subspecies and within species. He further points out that his research do not indicate a direct or indirect relationship between weight and temperature, but simply demonstrates a pattern (Roberts, 1953, pp. 551-552).

Guglielmino-Matessi et al. (1979) conducted a study on climate and the human skull, and used Howells' skull measurement data from 17 different populations spread across the world (Guglielmino-Matessi et al., 1979, pp. 549-551). They hypothesised that anatomically modern *Homo sapiens* split into two branches: a branch migrating west and a branch migrating east. The former group occupied Europe and Africa, while the latter group further divided into two groups. The first group from the eastern branch migrated through Southeast Asia to Australia and Melanesia and the other group migrated north to America through the Bering Strait. Accordingly, two groups inhabited cold climates and two occupied warm climates. They further explain that these groups adapted similarly to their respective environments: populations living in the North became cold-adapted and populations in the South became warm-adapted. This is evidenced by the overall size (from all linear measurements) and trunk/appendices ratios (skull/face ratios), which increases in lower temperatures according to the ecological rules of Allen and Bergmann. These rules can thus be applied to the evolution of cranial metrics in humans. However, Guglielmino-Matessi et al. (1979) also understood the issues regarding an incomplete fossil record, phylogenetic history, the quality of climatic data, techniques of correction or if other parameters than climate plays a role in creating variations (Guglielmino-Matessi et al., 1979, pp. 562-563).

Beals et al. (1984, pp. 325-326) observed that populations living in cold environments express more globular crania according to a combination of both Bergmann's rule and Allen's rule as observed in the variation in both shape and size of the crania. However, Beals et al. (1984) point out that the rules should be applied to global variation and not local cases because climatic variation within a small area is minor and would not lead to regional variations.

Relethford (2004b) built on research done by Boas (1912) on how migration affects craniometric variation, but he additionally controlled for natural selection, gene flow and plasticity. When examining the influence of climate, he included the relationship between geography and craniometric variation to investigate whether regressions were negative or positive. He observed that the individual regressions were negative regarding certain cranial traits, which supports both ecological rules. This means that some cranial traits were positively correlated with temperature, but the average pattern was low (Relethford, 2004b, p. 384). Similar observations were made by Hubbe et al. (2009) and Nowaczewska et al. (2011), who observed distinct pathways towards wider braincases or cranial bases in populations living in extremely cold climates, following both ecological rules. More recent studies done by Will et al. (2021, p. 8) also confirm that the body size of Mid-Pleistocene *Homo* correlates with the expectations of Bergmann's rule.

4.4. Are these theoretical models universally used?

The question in the heading will be dealt with in two sub-questions: do researchers similarly test for natural selection? Do all researchers within the discipline rely entirely on natural selection to explain morphological variation?

Most researchers agree that natural selection is challenging to test for and that some, but not all, methods can detect it. One of the most common methods of testing for natural selection is the correlational method. It seeks to explain natural selection by providing a link between variation in a specific trait and environmental variables. The correlational method can be used to test two hypotheses: the null hypothesis and the alternative hypothesis. The null hypothesis assumes that the dimensions of a trait will vary independently of the climatic variables. The alternative hypothesis states that geographically varying selection will lead to a correlation between a trait and climate. The correlation between a trait and climatic variables must be either statistically significant or strong to prove natural selection. This type of method is still used today by many scholars to establish links between morphological variation and climatic variables (Franciscus and Long, 1991, pp. 424-425).

Another approach called "the neutral theory of phenotypic evolution" has been gaining support over time, which, regardless of its name, does not reject natural selection. Instead, the neutral theory accepts that the direct testing for natural selection is difficult, and the best way of doing this would be to eliminate any non-selective forces of evolution, e.g., gene flow, mutation and random genetic drift. The neutral theory of evolution provides a simple set of predictions manageable to test for and can more efficiently be used to form hypotheses. The prediction of the neutral theory of evolution is presented by Roseman and Weaver (2007) as follows:

…The rates of evolution of characteristics given population sizes and mutation rates and, perhaps most useful for our purposes here, a set of expected relationships between molecular genetic variation and phenotypic variation within a species. Genetic distances and phenotypic distances are expected to be similar, or at least proportional, if the phenotype in question is neutral (Roseman and Weaver, 2007, p. 1186).

Thus, any deviations from these expectations would be either due to natural selection or a non-randomly dispersed impact from the environment (Roseman and Weaver, 2007, pp. 1185-1186). Scholars like Roseman (2004), Relethford (2004a), Harvati and Weaver (2006), Nicholson and Harvati (2006), Roseman and Weaver (2007), Weaver et al. (2007), Hubbe et al. (2009), von Cramon-Taubadel (2009), Pearson (2013), Evteev et al. (2014), Katz et al. (2015), Zaidi et al. (2017), Evteev and Grosheva (2019) and Baab (2021) have tested for, not only, climatic distances but also other non-selective forces like neutral and/or phenotypic distances.

Do researchers rely primarily on natural selection to explain questions regarding morphological variation? In modern evolutionary theory, natural selection is one of many mechanisms that can cause variation. If we imagine modern evolutionary theory as a spectrum and natural selection is at the far left and genetics at the far right, there are researchers within the far-left side of the spectrum who put too much emphasis on natural selection. According to Roseman and Weaver (2007, p. 1185), these are called "adaptationists" and they view selection as the only explanation for most evolutionary phenomena. Researchers on the other side of the spectrum argue only for genetics and completely disregard, or put less emphasis on, natural selection. In the middle of the spectrum are those who embrace the value of both natural selection and genetics (Roseman and Weaver, 2007, pp. 1185-1186). However, other common explanations for morphological variations are phenotypic plasticity, mutation, gene flow, random genetic drift and population history.

To summarise, several forces cause morphological variation and most scholars do not only rely on the theory of natural selection to explain morphological variation. There are different methods used to investigate what causes variation where some focus, specifically, on natural selection and others combine and test for mechanisms other than just natural selection.

4.5. Climate adaptation research: contemporary issues and other explanations

4.5.1. Material and datasets

Human skeletal material is often limited due to taphonomic processes taking place post-burial and during excavation. Incomplete skeletal remains restrict scientists from extrapolating information, and poor preservation limits sample sizes and research capabilities (Squires et al., 2019, pp. 323-324). In such cases where the material is not well preserved, missing elements of fossil material can sometimes be reconstructed using methods such as semilandmarks and mirror imaging techniques (Harvati, 2003; Gunz et al., 2005; Nicholson and Harvati, 2006; Gunz et al., 2009; Bastir et al., 2011; Neubauer et al., 2012).

Different types of datasets are used within the discipline, such as genetic data, climate data and metric data from skeletal material. Climate data can be easily uploaded from weather stations worldwide. However, collecting genetic data or measurements from human skeletal material becomes a little more complicated.

Scholars have different ways of collecting datasets, such as using other researchers' data, collecting data themselves or a combination of both. Unfortunately, there are few easily accessible datasets and those that are available are limited. Having large enough sample sizes with enough individuals to represent different global regions are important for conducting a thorough investigation linking climate to morphological variation. There are only two large craniometric datasets that contain large enough samples encompassing worldwide populations: Haniharas' (1993 a,b; 1996; 1997) and Howells' (1973; 1989; 1995). Thus, the discipline lacks larger datasets, and creating new ones is difficult. Working with smaller datasets or inadequate material can influence the research results. Roberts (1953) commented on the lack of genetic information of his samples in the 1950s:

"…It is when such a classification is attempted that the inadequacy of available material is most realized. Lack of genetic information of the samples precludes accurate genetic classification, an essential preliminary to the assessment of environmental influence. The small number of samples tends to lead to the use of too-inclusive categories, or categories containing too few results, both of which may well render indistinct any existing relationships" (Roberts, 1953, p. 546).

The situation has changed considerably since the 1950s and genetic information is more accessible to scientists today. Data processing was complicated until computers with large enough data storage and processing capabilities were introduced, and performing analyses thus became more straightforward (Lambert and Walker, 2018, p. 10).

Another issue voiced by Squires et al. (2019, p. 144) is that, before the 2000s, human remains were not always available for study and not all published data on human remains have been of reliable quality. Data were not comparable between authors and sites due to a lack of recording standards. In the UK, a guiding document was created by the working party BABAO which resulted in a recording standard. However, not all scientists were committed to these new universal methods of recording human remains, which is essential if scientists wish to compare data.

A concern worth discussing is the ownership of data and what that means for the availability of datasets for the scientific community. An example is digital data, in which the making of 3D models requires skill, funding and effort. It is thus understandable that these data belong to the researcher who produced it (Squires et al., 2019, p. 319). A survey conducted by Squires et al. (2019) targeted researchers and museum workers in the UK and North America. There was a general disagreement in terms of who owned data collected from skeletal collections. These mentioned data consisted of written, photographic/video and 3D data. When asking the collection managers/curators whether a scholar should be able to give their data to an associated scholar, 45% regarded this as either possibly or certainly not permitted for photographic or written data. For 3D data this increased to 57%. When asking the researchers who believed they owned these data, as to who owned the publication rights, there was considerable uncertainty. Furthermore, when asked about publishing or advertising data online, 8-40% regarded this as not allowed. Thus, this could result in inefficiency in the collection and management of data. Confusion regarding the ownership of data and whether it should be shared has resulted in repeated handling of human remains, which must be avoided due to the potential of damaging the remains (Squires et al., 2019, pp. 321-323).

The benefits of using and sharing digital data are many. These benefits include the easy accessibility it grants to multiple researchers, allowing them to work on larger global projects, as well as lessening or eliminating the physical handling of remains. Shared and cumulative digital data have been crucial in creating new databases to account for modern human morphological variation. Since 3D digital data have been found highly useful, it has become increasingly common for institutions to create 3D scans of their material and make data accessible for anyone to use. The amount of online stores containing digital 3D data of human remains is growing, making it easier for researchers to obtain and share data. As such, digital back-ups can be created of human remains, leading to less handling and potentially damaging the remains (Squires et al., 2019, pp. 334-335).

4.5.2. Ethical issues faced by the discipline

Human remains, especially the more recently deceased, do not exist in a vacuum. They where once living people with many social ties to the world around them, some of which may have endured into the present. It is thus pivotal that certain ethical questions and principals be asked and adhered to by scholars who wish to work on these remains. The deceased are often reduced to ‘things’ thought of as simply ‘specimens’, ‘data’ or ‘samples’. When working with larger datasets on human remains, it is simple to forget that data represents individuals who also once had a life, a personality, goals and accomplishments. Furthermore, whenever datasets are being borrowed from institutions or other researchers, what do we know about the consent of the individuals included in these data? The situation is much different when the remains are much older. Or is it? It is arguably important to know the background of a collection when gathering data from it. This section will discuss the ethical challenges faced by the discipline.

The past and the tensions that still exist today

Disciplines within the biological field continue to be impacted by the dark history of racist and nationalistic discourse. The work done by Samuel George Morton (1799-1851), a physician from the United States, was a typical example of the impact that past racial discourse had on the natural science as a discipline. He investigated whether skull shape corresponded to variations in brain shape and functioning. Morton had an extensive collection of human crania from different parts of the world, and created a hierarchy of racial types with ‘Black people’ at the bottom, ‘Native Americans’ in the middle and ‘White people’ at the top. His work proved to be seminal to the future research done by physical anthropologists during the rest of the 19th century. The essentialist idea at the time was that human variation was accommodated by different racial types, which corresponded with the racial inferiority and superiority that existed at the time and continues to do so in modern societies. As physical anthropologists wished to produce reconstructions of population movements and historical relationships, the idea of a positive relationship between cranial shape and genetic makeup was attractive to many (Lambert and Walker, 2018, p. 9). This seems to have persisted into the late 19th century to early 20th century when human remains were also collected and treated as ‘scientific’ specimens. Physical anthropologists were also particularly interested in eugenics and used human remains to study ‘racial typologies’. This was used as justification for later human right violations such as slavery and the Holocaust (Squires et al., 2019, p. 218).

Another dreadful part of the biological disciplines' history is grave robbing, which was mainly undertaken by, or on behalf of, medical schools and anatomists. Anatomists and their students were also known for showing great disrespect towards dissected human bodies as well as the families belonging to the dead. Murder has even been known to have been commissioned by anatomists to obtain more bodies (Squires et al., 2019, p. 74).

Ethical issues are evident in any situation involving human remains, e.g., the curation, collection and handling of them. Most of it stems from different value systems of how we perceive death, the afterlife, how the dead should be treated and the relationship between the dead and the living. Today the term multiculturalism is significant and most people live by moral principles of avoiding discrimination in terms of gender, ethnicity and religion. The issue is that with increased cultural diversity, the range of value systems and religions increases and what is considered socially acceptable thus changes. Consequently, social conflicts have become more common and ethics are important in solving some of these conflicts. Disciplines working on human remains are positioned between medicine, which focuses on preserving the generation of scientific knowledge that is helpful for patients, and anthropology, which concentrates on preserving our past and using cultural relativism to defeat ethnocentrism. It has become common for indigenous groups like Native Americans and Australian Aborigines to take back the moral authority of their ancestral land and the remains of their ancestors (Lambert and Walker, 2018, pp. 3-4). The issue becomes apparent when there is a conflict between scientific research and the beliefs of the descendants whose remains are the subject of said research. From a scientists' point of view, human remains are vital in understanding genetic, biocultural and physiological processes, and provide an important biological perspective on our collective past (Lambert and Walker, 2018, p. 14). However, conflicts become especially apparent in areas formerly colonised by Europeans where ancient human remains represent symbols of colonial persecution and cultural integrity. Thus, gaining control of their ancestors' human remains has become essential to indigenous people (Lambert and Walker, 2018, p. 17).

Who does the dead belong to?

On the one hand, there are issues concerning the recent dead and their descendants, but what if the remains are thousands or millions of years old? There is little agreement regarding old human remains that are distantly related to living people. Should living people be granted the moral authority of older human remains? There is an issue tracing existing, local populations, or groups, to ancestors who were mobile hunter-gatherers. Even in areas with stable gene pools, the likelihood of a person living hundreds of years ago being related to thousands of modern individuals is high. However, some might argue that ancestral relationships are more than just genetics but are based on a common culture, shared religious practices and language (Lambert and Walker, 2018, p. 24). On the other hand, it is important to remember the significance of studying our ancestors as they provide valuable information on our shared heritage. The issue is that there appears to be no global consensus as to where we draw the “cutoff” point between the dead individuals and their descendants, communities or groups that can lay claim to the individual. Is the “cutoff” point when the remains are five hundred years old? A thousand years old? If the remains are five hundred years old, there may be descendants who still feel they have a claim to the remains. The question is whether they then have a moral and legal claim to the remains when the remains are so distantly related to them? These are difficult questions which so far have not been adequately answered. Rather, it is an ongoing dialogue between the individual scientists, governing body and state laws. A generally accepted line is the division of species.

Lambert and Walker (2018, p. 14) argue that this sort of discussion between the scientific community and the descendants in relation to ancient human remains are often based on cultural issues from competing value systems. Lamber and Walker (2018, pp. 13-14) claim the discussion consists of simplistic dichotomies, which is science vs. religion and wrong vs. right. This can be difficult to navigate when the concerns of the descendant community and the scientific community differ so considerably. There is one matter that most agree on: if the dead individual can be identified and biologically traced to the descendants, the closest relatives will decide on the disposition of the remains. However, when the human remains are much older, e.g., several hundred or thousand years old, tracing immediate descendants becomes difficult. The older the remains are, the more problematic it becomes as more descendants share the same genetic relationship with the dead individual. Some argue that looking at genetic relationships is narrow-minded and misguided, and should instead look at cultural relationships, or links, instead. We can again ask the question: where do we draw the line? When an individual’s cultural links to the human remains are so weak that it is bordering into global cultural heritage? (Lambert and Walker, 2018, pp. 22-24). An example of this issue is the Kennewick site by Colombia River in Washington where 8400-year-old human remains were found. Scientists believe that the human remains contained morphological features deviating from modern Native Americans. Thus, conducting research would be of great value to better understand the reasons for these differences. Members of five different Native American tribes had claimed the remains and believed they culturally belonged to them as they had lived in the area since before creation. aDNA evidence demonstrated a genetic link between the five tribes and the Kennewick man, which essentially solved the issue (Lambert and Walker, 2018, p. 18). Interestingly, the human remains were claimed by not a few individuals, or one tribe, but by five tribes. This proves the point that the older the remains are, the more difficult it becomes for any individual or single group to lay claim to the ancient remains.

Dignifying the dead

Another issue faced by biological disciplines is the process of humanising, dignifying or providing a moral status to biological remains. Is it morally correct to manipulate a body once belonging to a subject with dignity? (Squires et al., 2019, p. 24). However, this issue seems to become less problematic when the human remains are old. Thus, the moral status of old remains would not be recognised like it would be with modern remains (Squires et al., 2019, p. 28). An archaeologist might argue that their practice can be justified because they make someone long forgotten known in the present. However, they have not received consent to do so from the dead. One solution would be to prevent excavation or handling of human remains, which would lead to the end of biological disciplines. The other solution would be to set limits and protocols that help protect the dignity of the dead (Squires et al., 2019, pp. 31-32). Human remains cannot speak for themselves, but they do represent the individuals and groups that the remains belong to (Squires et al., 2019, p. 60). This statement might not be applicable to ancient human remains whose cultures and groups no longer exist. However, some cultures may lay claim to ancient human remains who they consider to be ancestors. This topic is contentious as there is no clear argument for or against the claim of ancient human remains. It is essentially an eternal ethical debate between the scientific community and certain descendant communities.

In the UK, very few ethical protocols and regulations were in place in the 1980s for those wishing to analyse human remains. Instead, researchers were given free access. Luckily this has changed due to organisations like BABAO, who put forth ethics and practice guidance documents. Changes seen in the UK include, e.g., teaching about ethics, a better general awareness of ethics, dissertation proposals focusing on human remains must be approved from an ethical point of view, organisations like BABAO representing bioarchaeologists that have produced ethics and guidance documents (Squires et al., 2019, pp. 134-135). All these changes will help dignify the dead as scientists become more aware of the significance of ethics when working on human remains.

Digitising human remains

Ethical concerns exist about the sensitive nature of sharing digital data on ancient and recent human remains, especially when the remains belong to a different culture and are in the process of being repatriated. Before utilising images of the dead, the community in question should be consulted to prevent the misuse of images (Squires et al., 2019, p. 228). The issue is that there is little regulation regarding the 3D digitisation of human remains. While the original human remains might be protected, the 3D imaged remains are not. It is also essential to keep in mind that digital models are realistic and thus very similar to the original (Squires et al., 2019, p. 320). There have been cases where human remains have been scanned and/or printed without a community representative's consent, which has resulted in severe criticism. Creating 3D prints without consent have been considered as stealing cultural heritage material. It is not a given that communities will accept, or be comfortable with, their deceased ancestor being 3D scanned, printed and kept in a storage for later research (Squires et al., 2019, pp. 332-333).

Several ethical questions concerning the use and sharing of human remains data need to be addressed: who are authorised to share human remains data? How should data be shared? Who should be allowed to access data? How can other researchers use data? Some of these issues stem from the uncertainty regarding ownership of data. Online stores containing digital data need approval from the collection manager, or curator, in terms of publishing scans that belong to their collection. There are legal uncertainties about sharing 3D scans, and researchers can today create their own digital data stores and share them with colleagues and students without any legal consequences. This is especially problematic when it comes to human remains. Human remains belonging to Indigenous groups are perceived as culturally sensitive as they have a significant religious or cultural value. Potential unauthorised sharing and publishing of digital copies can disrupt the trust between the research community and the communities belonging to the remains (Squires et al., 2019, pp. 335-336).

Going forward

Certain recommendations can help the discipline manoeuvre ethical dilemmas. Anyone working on human remains should be mindful of the ethical considerations of working with the dead, whether recent or old. It is also essential to keep the topics of ethics and human remains relevant anywhere in the world through discussions, debates and mediation. Collections that are invisible to the public and collections that former scientists have inappropriately collected must be brought to attention and reflected on why they exist. Most importantly, one must treat human remains respectfully and with dignity, and teach students and the public to do the same (Squires et al., 2019, pp. 148-149). Another question worth addressing is whether it is respectful to refer to past living people as ‘specimen’, ‘data’ and ‘samples’. The most important thing is to keep updated on ethical guidelines and rules when working on human remains. It is also crucial to keep an open dialogue with descendant communities and to always show respect.

4.5.3. Is morphological variation caused by climate adaptation or other factors?

Whether the morphology of the human cranium displays developmental and adaptive changes connected to environmental factors or population history is an ongoing topic of discussion within anthropology. Cranial morphology has been used for research on, e.g., phylogenetic reconstruction, human geographic diversity and the effects of mastication and adaptation. Some scholars believe that modern human craniometric diversity follows a geographic pattern with genetic markers possibly resulting from evolutionary diversification, specifically isolation by distance. Relations between populations as observed in cranial morphology can also be matched with those collected from genetic data. Thus, modern human cranial morphology is likely shaped by population history, climate adaptation and possibly diet/mastication (Hubbe et al., 2009, pp. 1720-1721). However, most microevolutionary history is neutral due to processes like mutation, genetic drift and gene flow. Some variation in the modern human crania can be due to past diversifying selection through factors such as climate and diet. These factors appear to only affect certain cranial regions and these adaptations vary from population to population (von Cramon-Taubadel, 2014, p. 43). The human cranium is a complex mosaic-like structure that contains several anatomical regions from which the ossification patterns, functional attributes and embryological origins differ. It is thus important to understand the relative neutrality of each of these cranial regions before determining which regions are affected by non-neutral factors (von Cramon-Taubadel, 2014, pp. 49-52). Only a few examples will be discussed due to the limitations of this thesis.

Diet/mastication

Diet-related adaptation is one factor believed to have altered certain regions in the human skull (Thomson, 1903; Hubbe et al., 2009; Menegaz et al., 2010; von Cramon-Taubadel, 2014; Noback and Harvati, 2015; Buck et al., 2018). There are two focus areas of masticatory behaviour: the morphological effects of chewing behaviour and how the type of diet influences elements of cranial form amongst modern human populations. An example of the latter is the morphological differences between hunter-gatherer-forager and agricultural or pastoralist populations. The agriculturalist diet is known as being softer and more processed than the hunter-gatherer's diet. As the diets between these groups differ substantially, there should be systematic variations in cranial anatomy due to more/less mechanical stress on the masticatory apparatus. A hypothesis states that as humans transitioned from a lifestyle of hunting and gathering to becoming agriculturalists, less neuromuscular stress was applied to the masticatory apparatus, which changed the growth pattern in the jaw and lower face. Other accompanying changes occurred, like a less prognathic face and an alteration in the basicranium flexion, which resulted in a sharper angle of the basicranium and a more global-shaped neurocranium (von Cramon-Taubadel, 2014, p. 62).

A study on the influence of subsistence to worldwide human cranial variation done by Noback and Harvati (2015) found significant correlations between diet and cranial shape and the temporalis muscle. Interestingly, the study discovered a weak or no correlation between diet and the masseter muscle and dental arch. The masseter correlated instead with geographic distance and climate. In previous studies, the masseter muscle size has been found to correlate with the effects of masticatory stress on the zygomatic bone (fig. 1 and 2), bite force and diet-related shape changes in the zygomatic region. The dental arch is also the region directly in contact with food items and should be prone to high chewing stress. Although the shape of the dental arch did not correlate with diet, the Partial Least Squares regression (PLS) analysis showed that its relative positioning did. This implies that the relative positioning of the dental arch is more significant than its shape in diet-related adaptation. Different diets were included in the analyses (see Noback and Harvati, 2015, p. 8 for a complete overview of all diets), however, the diet that contributed the most to global cranial shape variation was the plant- versus animal-based diet. Noback and Harvati (2015) argue that these results show that the influence of diet on human cranial variation might have occurred before the Holocene. Noback and Harvati (2015) corrected for the effects of population history and climate before making explicit assumptions about the effects of diets on human crania (Noback and Harvati, 2015, pp. 9-14).

Menegaz et al. (2010) investigated the influence of diet on cranial robusticity and form. Weanling white rabbits were used as this species has several similarities in the form and function of the masticatory apparatus compared to general mammalian patterns. The study revealed that variation in masticatory loading affects facial structures as well as the growth of cranial regions relating to the generation and/or resistance of masticatory forces, like the cranial base and vault. In other words, the rabbits raised on tough/rigid foods experienced more stress on the masticatory apparatus, which directly or indirectly affected facial structures and neurocranial form. It was also observed that rabbits raised on hard/tough foods exhibited thicker outer tables of the frontal bone than those raised on soft foods. Rabbits raised on fracture-resistant diets also exhibited more globular cranial vaults and a more prominent curve of the lateral walls close to the caudal cranial fossa. Whether this is a direct or indirect effect of diet is unsure. This study illustrates that the skull is an integrated system and any changes to the facial skeleton will most likely affect other cranial regions, like the cranial vault and base shape. It was also observed that rabbits raised on a tough/hard diets exhibited a shorter basisphenoid and increased facial dimensions. These changes in the facial skeleton might have resulted in a shortening of the anterior basicranium and a larger retroflexion of the angle of the cranial base (Menegaz et al., 2010, pp. 635-638).

These studies illustrate that other factors besides climate and population history can affect cranial morphology in humans. It is difficult to differentiate what is due to genetic forces and what is due to climate or diet. As these studies illustrate, the cranium is a highly complex, integrated mosaic of regions that can be affected by numerous factors.

Is craniometric variation caused by genetic forces? A discussion on approaches, results and different arguments

The most common neutral explanations researchers pursue are population structure, population history and phylogeny. Population history and structure are in some ways the equivalent of phylogeny, except the first terms include the effects of lateral gene exchange from population migrations. Phylogeny, on the other hand, has been recognised as the confounding force in the study of adaptation when comparing between species (although this is also relevant for populations within subdivided species). It is hypothesised that populations who share a recent common ancestor or exchange vast amounts of migrants should resemble each other. Populations that are geographically isolated from each other for a more extended period and are only distantly related to each other should not resemble each other (Roseman, 2004, p. 12824).

Variations in human crania are complicated to understand and growing knowledge of genetics shows that influences on cranial morphology are not straightforward. Several factors complicate the matter, e.g., genetic distances, development, integration, environmental variables and adaptive evolution. Studies have shown that variations in craniometrics typically correspond with molecular variations among groups (Roseman, 2004; Smith, 2009). Cranial morphology arguably reflects both population structure and microevolutionary history. Researching potential relations between morphological variation and molecular relationships can be done by using a population genetics framework. A null hypothesis of neutral evolution can be used when looking into the effects of microevolutionary forces on morphology. Populations separated from each other due to genetic drift will stray in allele frequency over time. According to the neutral evolution hypothesis, mutation will create a new variation and genetic drift will act on it to create patterns of variation. Two models explain the divergence between groups affected by neutral microevolutionary forces: the mutation-drift equilibrium and the constant-heritability model. According to the first model, a population is in a mutation-drift equilibrium when it reaches a balanced state where there is an increase in the rate of new genetic variation from new mutations, which is then decreased by genetic drift. The constant-heritability model assumes a neutral divergence among groups attributed to the degree of heritability of a relevant trait. One or both situations must occur for a morphological trait to reflect neutral molecular data. Both models expect the rate of neutral variance between groups to be shaped by the force of genetic drift, which is again determined by the heritability of the relevant morphological trait. If a morphological trait is evolving according to neutral evolutionary processes, and is thus selectively neutral, the distance among groups based on that trait would reflect fundamental genetic relationships. Suppose genetic drift and gene flow is the underlying reason behind a pattern of morphological variation in a particular morphological region. In that case, the population distances based on the morphological trait in question will correlate with the ones based on neutral molecular loci. Thus, populations sharing common ancestry would be more similar than those sharing distant common ancestry (Smith, 2009, pp. 36-37).

The discovery of new hominin species has led to the urgent need to create reliable hypotheses about human phylogeny to better understand how other hominin species relate to us. A reliable phylogeny can be used to create hypotheses about ancestry or link human evolutionary events with ecological and environmental influences. This sounds like an adequate tool for researchers to use, however, according to Collard and Wood (2000), hominin cladistic analyses have produced conflicting and inadequately supported hypotheses of relations. This has been argued to be because of a poor choice of character, flaws in the available analytical methods, taxonomic disagreements, or the type of quantitative and qualitative craniodental characters were not reliable for reconstructing phylogenetic relationships (Collard and Wood, 2000, p. 5003). Collard and Wood (2000) said:

"First, phylogenetic relationships are genetic relationships. Thus, in phylogenetics, morphology can never be more than a proxy for molecular data. Second, because osseous and other morphological characters can be highly influenced by external stimuli, such as the forces generated by habitual activities, they can be expected to provide misleading information about phylogeny more frequently than genetical characters…" (Collard and Wood, 2000, p. 5003).

To test the reliability of cladistic methods in reconstructing interspecific and intergeneric phylogenetic relationships in hominins, Collard and Wood (2000, p. 5003) used hominoids, which are closely related to fossil hominins, and papionins (baboons, mangabeys, and macaques). The results confirmed that cladistic analyses performed on craniodental traits are unreliable in reconstructing phylogenetic relations among hominoids and papionins, which can be extended to hominin relationships. They further argue that such analyses give false-positive results which can pass statistical tests used by researchers. Thus, phylogenetic hypotheses should not be relied upon when only based on craniodental evidence. This is because the hypothesis most likely reflects a combination of accurate phylogeny, but also the phylogenetically ambiguous consequence of parallelism, convergence, reversal, and/or behaviourally influenced morphogenesis (Collard and Wood, 2000, p. 5005). Hlusko (2004) explains that while cladistics is a powerful tool, it also relies on the number of independent characters accessible for analyses. This is problematic because researchers must often subdivide functionally and developmentally linked traits to analyse individual traits. According to the morphological integration or modularity hypothesis, it is impossible to subdivide such traits because they can be conceptualised as parts of sets that share a common developmental pathway or ultimate function. An organism is made of a unification of functionally, developmentally integrated and connected sets of correlated traits. Hlusko (2004) thus recommends that scientists use morphological sets instead of single traits in phylogenetic analyses (Hlusko, 2004, pp. 2653-2654).

The isolation-by-distance model explains how increasing geographic distance limits migration so that genetic similarity between populations decreases in tune with geographic distance. There is a connection between geographic distance and genetic variation, and when investigating genetic variation in global populations, it is important to examine whether contemporary genetic diversity reflects isolation by distance. Relethford (2004a) used the isolation-by-distance model to determine whether it can be successfully used on global patterns of human variations (Relethford, 2004a, pp. 499-500). His research suggested that isolation by distance has significantly affected average patterns of genetic similarity in global populations. This correlation is valid for both morphological and genetic data. Relethford (2004a) found it surprising that there was a strong correlation between geographic distance and craniometric traits, arguably affected by natural selection. There was also no significant difference in the rate of distance decay between the three datasets. The successful fit of the isolation-by-distance model also suggests that all datasets reflect the fundamental effects of gene flow among populations. He thus believes that the analyses of genetic variation and geography are forceful to the influence of other evolutionary forces. In conclusion, populations close to each other (within 5000-6000 km) will be more similar than those living further than 5000-6000 km away (Relethford, 2004a, pp. 505-507).

Manica et al. (2007) researched the effects of prehistoric population bottlenecks on human phenotypic variation and found that 19-25% of heritable variability in craniometric measurements can be connected to distance from Africa. There are two hypotheses regarding the origin of anatomically modern humans. The first is called the ‘single origin’ hypothesis, which states that all modern humans originated from a single location, which is generally accepted as Africa. Expanding out of Africa would lead to a loss of genetic diversity through a series of founder effects, also known as bottleneck events. The other hypothesis is the ’multiregional’ hypothesis, which is supported by studies of craniometric data that yielded archaic human-like traits in skulls from several continents that generally would be known as *Homo sapiens*, suggesting multiple origins. However, when Manica et al. (2007) tested both models, adding distance from other non-African countries did not improve the model for phenotypic or genetic traits, meaning they found no evidence of the ‘multiregional’ hypothesis. Instead, there is a steady cline from Africa, suggesting that Africa is the point of origin. It is, however, difficult to determine whether there were one or several exoduses from Africa because both scenarios would lead to a similar major cline from Africa. Thus, African populations exhibit the most phenotypic diversity, which gradually decreases when moving away from Africa. It is thus feasible that the human cranium strongly reflects ancient demography (Manica et al., 2007, pp. 346-348).

Harvati and Weaver (2006) are perhaps one of the first to match morphological and genetic data for as many as 13 populations compared to previous studies. Three-dimensional geometric morphometrics was used to investigate whether climate adaptation and population history has influenced human cranial size, shape and relative orientation/position of cranial regions (Harvati and Weaver, 2006, pp. 1225-1226). Roseman (2004, pp. 12824-12826) has also previously used a large, worldwide genetic dataset and morphological distances to calculate which region of the human cranium reflects climate adaptation or neutral genetic variation. Compared to Harvati and Weaver (2006), Roseman (2004) did not use a three-dimensional geometric morphometric method, but morphological distances calculated from linear measurements. He also used ten populations, compared to Harvati and Weaver (2006) who used 13. Roseman (2004, pp. 12826-12828) found evidence that some cranial measurements were highly correlated with neutral genetic distances. Specifically, most measurements, except facial measurements and the general shape of the cranial vault, reflected neutral genetic distances. Harvati and Weaver (2006, p. 1226) raised several crucial points when criticising the approach Roseman (2004) used. He did not specify which region has been influenced by population history. It is difficult to trace the individual contribution of each region in terms of neutral genetics when linearly measuring between landmarks on two different cranial regions. Roseman (2004) also focused primarily on size which makes it difficult to assess the relative contribution of shape and size. They further argue that using a three-dimensional geometric morphometrics method makes it much easier to account for, and differentiate between, the influence of centroid size and shape. Harvati and Weaver (2006, pp. 1231-1232) found evidence to suggest that cranial morphology, or parts of the crania, has been influenced by population history. Specifically, the temporal bone, neurocranial and total cranial shape distances were correlated with neutral genetic distances. They also found that the shape of each cranial region, and not the manner of integration, reflects population history.

Hubbe et al. (2009, pp. 1720-1721) investigated whether morphological variation reflect climate signatures or population/phylogenetic history in worldwide populations of modern humans. Compared to the populations used by Roseman (2004) and Harvati and Weaver (2006), the largest dataset yet was used containing 135 geographic human population samples. Hubbe et al. (2009, pp. 1728-1729) found a strong correlation between cranial morphology and geographic distance. They also found evidence suggesting that population history affects various cranial regions differently. Specifically, neurocranial variation correlate with geographic distances, and facial measurements appear to relate weakly with geographic distances, compared to the neurocranium.

Smith (2009, pp. 41-43) found evidence that several cranial regions preserve phylogenetic information differently. The shape of the basicranium, full cranium, temporal bone and upper face are phylogenetically informative. The results for the basicranium are not surprising as it is less vulnerable to external factors when compared to other cranial regions and is supposed to evolve neutrally. The morphological variation most likely reflects molecular relationships. This is also an endochondrally ossifying region which is typically highly correlated with molecular distances when compared to intramembranously ossifying regions. The temporal bone appears to evolve neutrally and reflect neutral relationships due to its partial endochondral ossification, which occurs relatively early in ontogeny.

Betti et al. (2009) researched what influences the global within-population phenotypic diversity. The results implied that distance plays a significant role, not climate. They argue that while selection can alter the mean size of specific traits, it does not mean that it affects variances. They discovered that sub-Saharan African populations contain the highest diversity and there is a smooth decline when moving away from the suggested place of origin. The most informative phenotypic traits chosen for this research could reveal 50% of within-population diversity without any input from climate. They further argue that while climate can be found to affect a single trait, merely measuring phenotypic diversity is not enough unless it can be shown that the same climatic variables were affecting many traits similarly. Climate has also not remained constant over the last thousands of years and measuring prehistoric climate is extremely difficult, if not impossible (Betti et al., 2009, pp. 811-813).

Betti et al. (2010) believe that the underlying issue that separates those who find correlations with climate from those who do not is due to the type of phenotypic metrics being used. These metrics refer to either size, shape or form, and those who prefer to look at size-related metrics have typically detected climate signatures. Contrastingly, those who focus on shape have found few correlations with climate. Another point worth considering is that populations affected by similar climatic conditions are often within close geographic proximity. Craniometric characteristics are shared between populations from similar climates, but this need not be because of natural selection. It could be due to recent common ancestry or genetic exchange. Recent research on global genetic datasets has shown that there is a strong correlation between geographic and genetic distance measured along landmasses where human migrations are thought to have occurred (Betti et al., 2010, pp. 76-77). An isolation-by-distance model was used which proved highly useful in indicating between-populations phenotypic variation. This model can be used to avoid overestimating the effects of climate. Surprisingly, they still found that climate had a role in driving between-population variation, but not within-population variation (Betti et al., 2010, pp. 79-81).

4.5.4. The extreme cold population

Climate has been an important factor in shaping parts of the human cranium. Several studies indicate that when analysing each cranial regions affected by climate, most differences appear to be driven by populations living in extremely cold regions (Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Betti et al., 2010; Relethford, 2010; see also Foster and Collard, 2013). When the extreme cold samples are removed from the analyses, the climate signal becomes significantly weaker or disappears. Do natural selective forces affect populations living in extreme cold climates to a greater extent than those living in extremely hot and arid environments? The inclusion or exclusion of extreme cold populations appears to greatly impact the outcome of analyses.

Roseman (2004) attempted to test a neutral hypothesis of cranial evolution by comparing the morphological and neutral genetic variation in 10 worldwide living and recent human populations. He also sought to explain detected deviations from neutrality, and natural selection is one example of deviation from neutrality (Roseman, 2004, p. 12824). Roseman (2004) calculated matrix correlation statistics ten times with the removal of one population each time without doing further tests. He did this to detect any outlier samples that contributed unevenly to deviations from neutrality. By using this method, he managed to identify the population that impacted the outcome of his analyses, the Siberian Buriat population. When the Buriat population was included in the analyses, a pattern emerged showing that natural selection has been essential in shaping among-population variations in cranial morphology and cranial breadth deviated from neutrality. Cranial length, on the other hand, did not vary much amongst regions. Roseman (2004) argued that natural selection has acted for a thermoregulatory capacity in cold climates, leading to brachycephalization. Interestingly, this association was eliminated when the Buriat sample was removed from the analysis. Interestingly, the other extreme cold population, the Greenland Inugsuk, do not have very broad crania. If he had included this population in the analysis, it would possibly have changed the outcome. He further argues that the effects of cold climates must be extreme to explain how much the Buriat population differs from the rest of the world. He further hypothesised whether there are limits of cultural buffering when faced with extreme environmental challenges (Roseman, 2004, pp. 12826-12828).

When Harvati and Weaver (2006) experienced a similar outcome when they removed the Greenland Inugsuk and Siberian paired samples from their research. There was a stronger correlation between the temporal bone, neurocranial shape and shape/positioning distances, and the shape of the entire cranium with neutral genetic distances after removing the outlier populations. According to Harvati and Weaver (2006), including the Inugsuk population led to the overall observation of climatic signal. When this population sample was removed from the analyses, there was no association with any of the climatic variables. However, the reduced-sample analysis still found some association between neurocranial shape, shape/positioning and facial shape/positioning with latitude. Although the extreme cold populations appear to be the most cold-adapted, there is still a general clinal trend in the morphology of the human face emphasising that climate has also affected other populations, albeit not as much as the extreme cold populations (Harvati and Weaver, 2006, pp. 1231-1232).

Hubbe et al. (2009) investigated climate signatures in morphological variations in worldwide human populations. They discovered an interesting pattern showing that northernmost populations, like northern Europeans, northeast Asians, and Americans living in the extreme North, affected variables differently. Specifically, Northeast Asia and American populations living in the extreme North contributed mainly to the between-group variation observed in facial breadth, biauricular breadth and nasal and facial height. The northern European population sample mostly affected the values for frontal breadth, nasal breadth and facial projection. The one variable all three populations affected similarly was the midfacial breadth, which did not correlate with climate (Hubbe et al., 2009, p. 1725). Hubbe et al. (2009) noticed that no correlations between climate and cranial morphology were found once the extreme northern populations were removed from the analyses. Thus, climate adaptation can only be observed in populations living in extremely cold environments. The variations observed between northern Europeans and the two other northern groups resulted from following distinct adaptive pathways matching their cold environments. All groups appear to exhibit short nasal cavities regarding height and/or breadth. However, the population showing the smallest average nasal breadth is northern Europeans, and the populations showing the most considerable average nasal height are northeast Asians and Americans living in the extreme North. This pattern can also be observed in facial height, possibly due to nasal height. There is also a differentiation in cranial breadth among the populations. While all groups exhibit wide neurocrania, the northern European populations mainly affect the maximum frontal breadth variable. Contrastingly, the other groups affect the variable for biauricular breadth. Either way, both pathways appear to lead towards a wider braincase which could be needed in extremely cold environments (Hubbe et al., 2009, p. 1728).

There could be different reasons why such extreme cold populations are affected so strongly by climate compared to other populations. Temperatures below a specific threshold could result in a plastic response in the crania's development, but scientists have not yet proved this. Previous studies have not confirmed any relationship between climate and cranial measurements during growth and development. A second option is that the climatic variables included in previous studies have been inaccurate, or limited, and have thus incorrectly picked up links with climate only for extreme temperatures. The third option is behavioural adaptation, most likely through cultural evolution, which shields the effect cold climate has up to a specific limit. When natural selection becomes powerful enough to outweigh the effects of behavioural adaptation, there will be climate-related changes in the phenotype (Betti et al., 2010, p. 81). Studies like these show that the extreme cold populations always appear to be outliers, while none of the other populations exhibits such strong links with climatic variables.

Conclusion

This thesis set out to answer questions relating to theoretical frameworks used within the discipline. In the absence of detailed outlines of theories and methods, this thesis attempts to provide a comprehensive overview.

What is the criticism against the modern evolutionary synthesis? The main criticism deriving from the extended evolutionary synthesis and evolutionary developmental biology is that the main conceptual framework overemphasise the role of genetics and neglects to include certain key elements. These are: developmental biology, genomics, ecology, embryology and macroevolution.

What theoretical frameworks can be applied to climate adaptation research and how efficient are these at explaining the effects of climate on human cranial morphology? The two theoretical frameworks chosen for this thesis were modern evolutionary theory and the ecological rules of Bergmann and Allen. Even though modern evolutionary theory does not mention the effects of climate in detail, but the environment in general, it is the mechanisms behind variation, adaptation and evolution that plays a key role within the theory. There has been confusion regarding the interpretation of both ecological rules, specifically how to apply them, which has proven to be problematic. The ecological rules were not originally meant to be applied to humans, but both have proven to be applicable.

Are there any consistencies in the types of theories used? Scientists appear to be divided as some put more effort into testing specifically for natural selection, while others prefer to test for other mechanisms, like genetic forces. However, it appears to be more common to test for neutral factors before making any assumptions regarding natural selection.

What issues do researchers face when looking for climate signatures in modern and fossil human crania? There is a general issue of limited/lack of datasets and fossil human skeletal material. Little can be done when it comes to lack of material but to hope for more being recovered from future excavations. I believe digital reconstructions and digitisation of material can help in some ways, and that researchers going forward must make available what datasets they have in digital stores. This leads to ethical issues, and there are arguments for and against the digitisation of human remains. However, by creating proper ethical protocols, such issues might be easier to manoeuvre. Students who works on human remains should be educated within ethics. This thesis also addressed what other factors, besides natural selection, can cause morphological variation. Since natural selection is difficult to test for, more researchers should seek out other explanations before confidently linking natural selection to morphological variation. Regarding the extreme cold sample, that appears to consistently be an outlier in most climate adaptation research, leads to the question of whether natural selection only has acted on these groups? What about those living in extremely hot environments? I believe more research is needed to understand the role of climate on modern human cranial morphology.

My thesis has shown that modern evolutionary theory puts too much emphasis on genetics and, although genetics are important, it would be imperative to better understand the role of climate on morphological variation. Although the ecological rules of Bergmann and Allen does explain a pattern between climate and size cline, which is ultimately a product of evolutionary adaptation, there appears to be inconsistencies and uncertainties in how to apply them correctly. I believe a new theoretical framework should be developed that explores the relationship between climate and morphological variation.

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