Assessing primate skull shape variation in relation to habitat:
a 3D geometric morphometric approach

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ABSTRACT

The advancement of digital imaging and open-source geometric morphometric (GM) software is positively impacting the way we understand morphological adaptation as an evolutionary response. Shape-space data and multivariate statistics quantifies shape variation patterning and, therefore, consolidates hominoid systematic procedures.

This thesis identifies ecomorphological patterns of variation within extant primates. Through a comparative, multivariate and geometric morphometric approach, this research provides a better understanding of the effects of the environment on craniomandibular form in early hominins. In this study, 107 cranial and 108 mandible specimens of 9 modern primate species were 3D imaged, and geometric morphometrics statistics were used to quantify and assess the patterns of variation between intra- and interspecific datasets concerning habitat type. Results were visualised through Principal Component scatter plots and Thin-plate Spline deformation warps, which identified critical morphological high-to-low-energy bending areas. This application addressed the questions:

- to what extent does ecology influence craniomandibular morphology?
- what are the main environmental pressures that encourage morphological variance in hominins?

The main methodological aims sought to a) create accurate 3D digital renderings of primate skull specimens and b) define a reproducible geometric morphometric technique, which could be used as a valid and precise statistical procedure for future studies regarding hominin ecomorphology. This was achieved by pilot testing laser scanning hardware, digitising cranial and mandibular specimen, testing 3D scanning accuracy, and the best practice for capturing accurate 3D imagery, e.g. environment, lighting and meshing multiple scans. The pilot phase of this thesis also tested statistical programming toolkits capable of carrying out the finalised geometric morphometric methodology. This was achieved through trials of landmarking and statistical procedures on various data processing software, e.g. Checkpoint, TINA, and MeshLabs. Ultimately, the R Project software and accompanying IDE, R Studio, was used to collect, process and analyse the specimen shape data.

This thesis contributes to the study of hominin ecomorphological patterning through a comparative approach investigating primate skull adaptation. The main findings showed habitat type as having statistical significance on the cranium's morphology but quantifiably more so in the mandible, which reported 63.71% of the overall variance observed in the first two Principal Components. This was an increase of 10.44% compared to the interspecific cranial dataset and was supported by Two-block Partial Least Squares and Procrustes ANOVA analysis.

The geometric morphometric results showed significant environmental influence on the morphology of the primate cranium, most notably concerned with locomotive functions and visualises a distinction between primates who are more arboreally inclined versus those whose primary form of locomotion is terrestrial. The study also found that dietary specialisations are particularly distinguished by patterns of variation between highly folivorous versus more frugivorous species in both inter-and intraspecific groups.

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1 INTRODUCTION

This thesis seeks to identify patterns of ecomorphological variation within extant primates using a comparative and multivariate approach to 3D geometric morphometric analysis. The results from this study will further our understanding of the extent to which morphological evolution is affected by environmental variables, as well as the leading ecological pressures that influence morphological variance and encourage phenotypic plasticity in early hominins.

1.1 Limitations in current human evolution and morphological research

Luskin (2012) identifies three key challenges within human evolutionary study: 1) the fossil record is patchy and sparse; 2) the fossils themselves are often in poor condition and fragmented making conclusions regarding morphology, behaviour and systematics difficult; and 3) accurately reconstructing the behaviour and morphology of extinct organisms is challenging. This is echoed and exemplified by Frans de Waal (2001) who observed nearly identical morphology between chimpanzee and bonobos skeletons but also noted a dramatic difference in behaviour between the two conspecifics. This thesis addresses these issues through paleoanthropological and methodological aims.

1.1.1 Addressing these challenges through the study of shape

In response to a lack of hominin fossil evidence, this study examines the efficacy of comparative methodologies in palaeoanthropology by using extant primate specimen shape studies to draw conclusions regarding the morphological response in fossil hominins to contemporary environments. Secondly, a novel approach to 3D digital imaging and analytical software addresses the issue of incomplete specimen and replicability amongst peers. Finally, by assessing patterns of variation between extant primate species in varying and differing environments, comparative hypotheses can be made regarding diet and locomotive behaviour in early hominins, which can subsequently be used as speculative indicators towards social behaviours as evident in the living referential models (Thorpe, 2016).

As Elton (2008) argues, reconstructing palaeoenvironments is important to understanding hominin morphological and behavioural evolution. Studies of ecological morphology can be used to ascertain the relationship between an organism and its environment. (Reed, 2013; Losos and Miles, 1994; Weiskopf, 2020). Whilst Miocene-Pliocene environmental records are well documented (Steinthorsdottir *et al.,* 2021; Drury *et al.,* 2017; Drury *et al.*, 2018; Dekens *et al.*, 2007; Cerling *et al.*, 1997), early hominin fossils are few and far between. This thesis outlines a new methodology to understand the effects of habitat type, similar to that of late Miocene and early Pliocene hominins, on craniomandibular morphology. The variation that exists between extant primate species will show patterns of variation linked to ecology that can be used as a basis for early hominin evolutionary study.

1.1.2 A digital quantification of morphological variation

Replacing qualitative and traditional methods of data collection with landmark-based 3D geometric morphometric analysis will assist in this endeavour to understand hominin ecomorphology. This procedure ensures the dissemination of accurate and precise shape data information, which is scarce and often ambiguous when gathered through traditional morphometric methods (Zelditch *et al.,* 2012). 3D laser imaging and digitized landmarks will be used to effectively and accurately capture craniomandibular shape information minimizing observer error. Digitally capturing the complexities of the skull and using open source analytical software means that 3D specimen form and shape datasets can be shared easily and ensures the replicability of the study.

1.2 Research Aims

The primary aim of this thesis is to better understand the effects of environment on the shape of the primate skull. Through a 3D geometric morphometric approach, an analysis of extant primate crania and mandible specimens will uncover trend patterning between- and within-species in relation to habitat. By quantifying and visualising these ecomorphological patterns, this thesis will address the following research questions:

- to what extent does ecology influence the morphology of primate skull shape and,
- what are the main environmental pressures that encourage morphological variance in hominins?

1.2.1 A geometric morphometric approach to the research aims

As comparative 3D geometric morphometric studies of the entire primate cranium have yet to be fully explored in relation to shape patterning and habitat variables, the research in question provides a substantial methodological and paleoanthropological contribution towards the study of hominin ecomorphology. 107 cranial and 108 mandible specimens of 9 modern primate species are 3D imaged using the Matter and Form desktop scanner, standardised by General Procrustes analysis and put through multivariate statistical procedures in R Studio software (see **Figure 1.1**). Procrustes ANOVA and covariation Two-block Partial Least Squares methods assess the level of morphological variation existing in between- and within-species groups. Subsequently, Principal Component scatter plots and Thin-plate Spline warp grids visually report key areas of morphological variance and deformation between the specimen sets.

As researchers in the field of palaeoanthropology, we face a challenge in the paucity of fossil evidence, and therefore, small sample sizes, which are often deformed *in situ*

(Brown and Vavrek, 2015; Gould, 1980). Small sample sizes are a secondary issue to morphometric study which can have a dramatic effect on the validity of quantitative research through sampling error (Cardini, 2015). This thesis addresses the prevalent issue of insufficient fossil sample sizes in geometric morphometric analyses through a comparative approach to morphological study.

Great Ape genera (*Gorilla*, *Pongo* and *Pan*) and Hylobate specimen will be assessed for patterns of covariation between craniomandibular morphology and ecology. Subsequent comparative discussion will address early hominin morphological evolution based on the results of the present study. The virtual extant primate skulls created within this study can be easily disseminated for peer reviewed statistical testing and publicised for future anthropological research, whilst preserving the original specimen material. The validation of the 3D scanning process, using a widely available laser scanner, will be explored through comparative pilot study, as well as the open source coding software, R, used to conduct the geometric morphometric analyses (see **Chapter Four**). The results of these analyses will provide insights into the following statements:

- Quantitative GM analysis can be used to better understand the relationships between evolutionary adaptive response and environmental patterns
- Early hominin and extant hominid species, which live in comparable climates, will adapt similar craniomandibular morphological traits
- Facial morphology can be used as a predictor of environmental type and can therefore be used for comparative studies
- Specific environmental niche conditions will lead to retention of primitive traits from an ancestral lineage

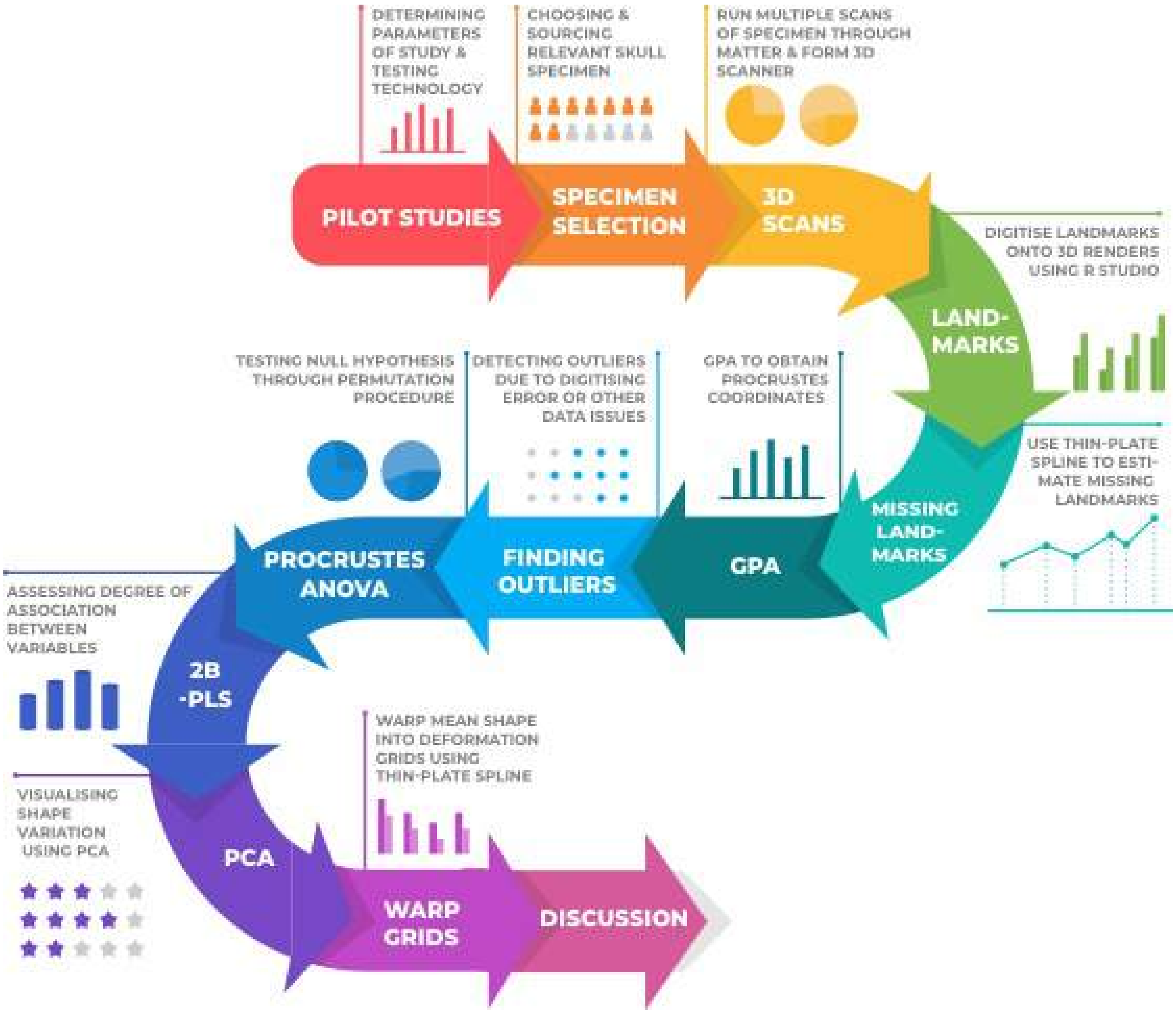


Figure 1.1: The geometric morphometric approach informed through pilot studies and literature review. Data collection is facilitated through 3D scanning and landmarking exercises and data analysis is conducted using Generalised Procrustes and multivariate statistics.

1.3 Research Roadmap

Following this section, **Chapter Two** investigates environmental hypotheses of human evolution and the importance of phenotypic attributes in systematics and species classification. This review synthesises the current understanding of hominin morphological evolution in relation to environmental change and habitat. Insufficient fossil material is a major pitfall to paleoanthropological study; therefore, this thesis uses a comparative methodology as a way to better understand the human past, whilst helping to preserve vital early hominin fossil remains.

Chapter Three reviews past and modern research using shape statistics and advanced geometric morphometric techniques to understand how palaeoanthropological study has hitherto utilised shape data and multivariate statistics to quantify variation. The strengths and weaknesses of this procedure are also identified. Subsequently, this review shows GM analysis as a strong analytical tool for studies pertaining to environmental and evolutionary morphology. This quantifying toolkit is shown to encompass both morphological data and environmental variables with a view to understand the relationships that exist and the extent to which habitat influences physical form. This chapter shows how this methodology can potentially broaden current understanding of early hominin ecomorphological patterning by way of comparative study.

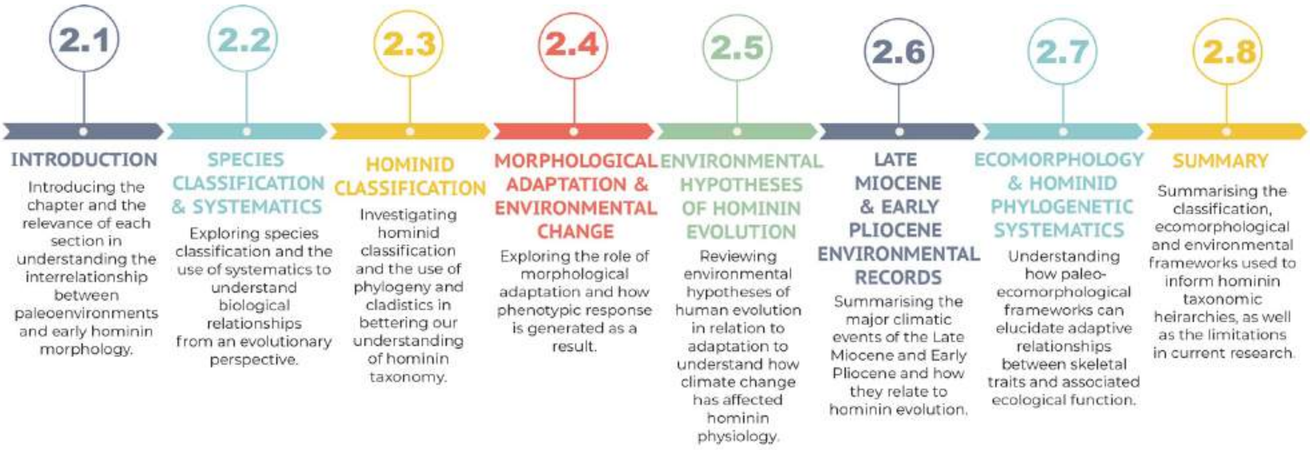
Chapter Four outlines the development of the quantitative methodology used in this study. Pilot studies are preformed to analyse and test the capability and validity of digital imaging and analytical software pertinent to the geometric morphometric analysis. This chapter also considers intra- and inter-observer error and details the finalised methodology, including 3D scanning of the bone specimen, preparatory data capture and shape standardisation. Digitised imagery of the specimen is created, and raw shape data collected from landmark constellations. A Generalised Procrustes analysis is preformed to standardise the shape information before further statistical testing can take place.

The results of the geometric morphometric analyses are visualised and reported in **Chapter Five** showing evidence of shape patterning existing between- and within-group species in relation to habitat. The effects of sexual dimorphism on the primate datasets are examined using ANOVA. Subsequently, habitat specific analyses are grouped by cranial and mandibular specimen and further split into interspecific and intraspecific results. ANOVA results, Two-block Partial Least Squares, Principal Components Analysis, and Thin-plate Spline warps are reported for all datasets.

Chapter Six contains the discussion section of the thesis which summarises the application of 3D geometric morphometrics on the primate craniomandibular specimen datasets. Examination of the datasets is presented with a focus on evidentiary variance patterning in relation to species and habitat variables. The impact of the comparative nature of the study is examined to understand the implications of the results towards human evolutionary study.

Chapter Seven focuses on the major findings of this thesis which showed 1) distinct patterns of variation grouping species of similar dietary behaviour; 2) morphological variation patterning informed by habitat type; 3) clear patterns of variation grouping species of similar locomotive behaviours, and 4) specific physical modules of the mandible and cranium that are highly influenced by ecology. This chapter also concludes whether the research aims are sufficiently met and identifies the limitations of the thesis, which are shown to be excellent opportunities of expansion in future related studies.

2 HUMAN EVOLUTION AND ECOLOGY



INTRODUCTION

Introducing the chapter and the relevance of each section in understanding the interrelationship between paleoenvironments and early hominin morphology.

SPECIES CLASSIFICATION & SYSTEMATICS

Exploring species classification and the use of systematics to understand biological relationships from an evolutionary perspective.

HOMINID CLASSIFICATION

Investigating hominid classification and the use of phylogeny and cladistics in bettering our understanding of hominin taxonomy.

MORPHOLOGICAL ADAPTATION & ENVIRONMENTAL CHANGE

Exploring the role of morphological adaptation and how phenotypic response is generated as a result.

ENVIRONMENTAL HYPOTHESES OF HOMININ EVOLUTION

Reviewing environmental hypotheses of human evolution in relation to adaptation to understand how climate change has affected hominin physiology.

LATE MIOCENE & EARLY PLIOCENE ENVIRONMENTAL RECORDS

Summarising the major climatic events of the Late Miocene and Early Pliocene and how they relate to hominin evolution.

ECOMORPHOLOGY & HOMINID PHYLOGENETIC SYSTEMATICS

Understanding how paleo-ecomorphological frameworks can elucidate adaptive relationships between skeletal traits and associated ecological function.

SUMMARY

Summarising the classification, ecomorphological and environmental frameworks used to inform hominin taxonomic heirarchies, as well as the limitations in current research.

Figure 2.1: Chapter Two roadmap summarising the utility of each section towards investigating the importance of the interrelationship between paleoenvironments and early hominin morphology.

2.1 Introduction

This chapter investigates the importance of the interrelationship between paleoenvironments and early hominin morphology. An examination of the main environmental hypotheses of human evolution provides a better understanding as to how ecology affects physical characteristics and how these defining features are subsequently used to support systematics and species classification. This chapter offers a synthesis of the current literature and identifies gaps in our current understanding of early hominin craniomandibular morphological study. An examination of comparative methodologies shows the benefits of this approach in supporting future paleoanthropological study, which is limited by a lack of fossil material.

2.2 Species Classification and Systematics

Discovering the relationships between taxa, and the diversity among them, is key to understanding how species have evolved and represents the genetic and morphological similarities and differences in nature. Systematics explores these biological relationships from an evolutionary perspective, describing hierarchies in taxon (a group of organisms), species, genera and families (Carlson, 1999). Traditionally, systematics uses taxonomy and phylogenetic relationships, the latter of which informs the classification of higher-order groups (Strait, 2013).

Species classification is important to the study of human evolution in determining the relationships between early hominin species. Hominin diversity is complicated and dramatic, as can be seen from frequent and unexpected fossil finds (Strait, 2013:37), and as such has resulted in contentious debate regarding the lineage of newly discovered fossil hominins (Jones, 2021; Nowaczewska, 2000). This is exemplified in the most recent interpretation of the Harbin cranium from north eastern China. This specimen presents a combination of features, such as a low cranial vault and face, large square orbits, flat cheekbones and a shallow palate, which differs from other local *Homo* species morphology. The analysis of the Harbin cranial fossil suggests that the diversification of the *Homo* genus must have a deeper timescale than previously thought (Ni *et al.,* 2021) and exemplifies the changeable nature of hominin classification.

2.2.1 Morphological Approaches to Systematics

Consistency is key to communicating early hominin species' classification to prevent unambiguity and misperception in species lineage. Research has typically relied on morphological variables and inter-and intraspecific patterns of variation to define a species (Tattersall and Schwartz, 1998). Phenetic and cladistics methods are morphological-based approaches to systematics and are used to understand the relationships between organism groupings through character similarity or synapomorphic traits (Hall, 1988).

2.2.1.1 Identifying species-status through morphological features

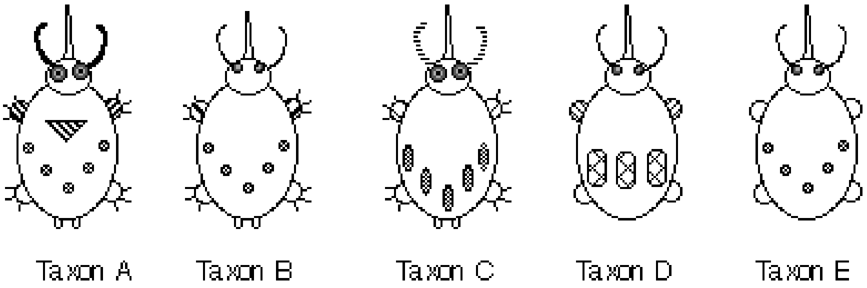
Unique or characteristic primitive and derived morphological features are used as species-status indicators (Strait, 2013:38). A derived, or primitive, character is a newly developed innovation passed through ancestral lineage (Cavalier-Smith, 2010). Cladistics, a method of hypothesising taxonomic relationships, relies on the assumption that derived characters will be evident in every group member (Senut *et al.,* 2001; Brunet *et al.*, 2002). The class Reptilia, for example, encompasses multiple clades, including birds, crocodiles, lizards and snakes (Wiens *et al.,* 2006). The legless derived characteristic of snakes has created the Serpentis clade within which multiple species of legless reptiles are classed (Papenfuss and Parham, 2009, 2013).

Once species-status has been identified, systematists endeavour to reconstruct the phylogenetic relationships in question, recording lineage divergence and transformations. It is generally agreed (e.g. Adrain *et al.,* 2002; Lipo *et al.,* 2006; Strait, 2013; McNulty, 2016; Kitching *et al.,* 2017) that species which are considered as closely related will exhibit similar, novel (primitive) morphological traits that are phylogenetically derived (known as synapomorphies,) and inherited from a recent common ancestor (Strait, 2013:38). Classification subsequently organises the newly discovered species into the hierarchy of nested taxa using similarity matrices, grade-based (assigning based on recent common ancestor descendants and similar adaptive responses) or clade-based approaches (assigning species based on phylogeny and single common ancestors excluding adaptive information) (Senut *et al.,* 2001; Brunet *et al.*, 2002; McNulty, 2016; Strait, 2013).

2.2.1.2 Phenetics

The phenetic approach to classification, or numerical taxonomy, distinguishes the taxonomic relationship between groups of organisms based on the degree of similarity in one group of organisms to another, either phenotypically or anatomically, and without evolutionary assumption (Sokal, 1986; Oxford Ref, 2020). These defining characteristics are used to create a similarity coefficient grouped within a matrix between 0-1, i.e. no similarity to highest similarity, and the phenetic relationships are described using a branching diagrammatic phenogram tree (Choudhuri, 2014) (see **Figure 2.2)**

a)



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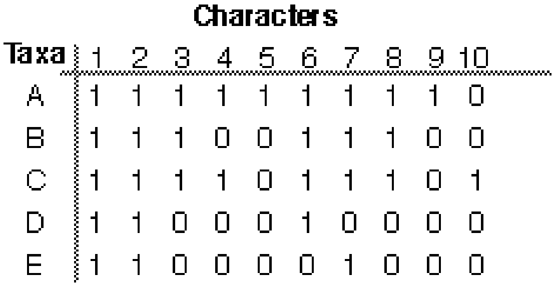
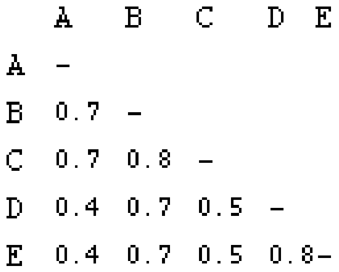


Taxa	1	2	3	4	5	6	7	8	9	10
	Characters									
A	1	1	1	1	1	1	1	1	1	0
B	1	1	1	0	0	1	1	1	0	0
C	1	1	1	1	0	1	1	1	0	1
D	1	1	0	0	0	1	0	0	0	0
E	1	1	0	0	0	0	1	0	0	0



	A	B	C	D	E
A	-				
B	0.7	-			
C	0.7	0.8	-		
D	0.4	0.7	0.5	-	
E	0.4	0.7	0.5	0.8	-

c)

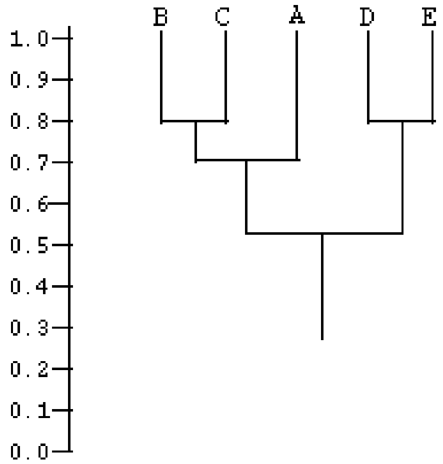


Figure 2.2. Phenetic process of classifying organism groups based on similarities. A) represents the four organisms with differing physical characteristics. B) shows the configuration of similarity coefficients and matrix which assign each organism group into a rank system of low-high similarities (1-10). C) depicts the final phenogram showing the defined relationships between groups based on the level of physical similarity (image source GWU, 2006).

Whilst Lewens (2012) supports this approach to classification, stating its particular use in microbiology and botany, the underlying principles of proposed phenetic relationships are inherently flawed. As such, this method of systematics is heavily criticised by scholars such as Sneath (1971), Jensen (2009) and Fenton *et al.* (2014). The main drawback to phenetic classification is the issue of homology and homoplasy (Erdelen, 1989; Torres-Montúfar *et al.,* 2018). Characterising groups of organisms due to overall similarity can be misleading as there are two reasons why different species could display similar features (Van der Steen and Boontje, 1973; De Queiroz and Good, 1997). Firstly, when two species present a similar characteristic, it could be explained through inheritance by both groups from a common ancestor, i.e. a homologous feature or homology (Williams, 2004). However, unrelated species who adopt a similar way of life can also produce similar physical characteristics, i.e. dietary specialisation or locomotive behaviour. These analogous features (homoplasy) subsequently produces a resemblance between species due to convergent evolution (Speed and Arbuckle, 2017; Hanboonsong, 1994). As the phenetic method fails to consider homology or homoplasy, the cladistics approach has become the most commonly used method to classify organism taxonomy (Guralnik and Smith, 2005).

2.2.1.3 Cladistics

Cladistics has played an essential role in the reshuffling of hominid classification using both molecular and morphological data to support the current monophyletic clade between gorillas, chimpanzees and humans, with orangutans as the most distantly related species within the clade (McNulty, 2016). Cladistics works under the premise that members within a group will share a common evolutionary history and be more closely related to one another than to organisms outside of this group (Guralnik and Smith, 2005). Groups are characterised through uniquely shared features, or synapomorphies, inherited from the most recent common ancestor who derived such traits through evolutionary processes. These characterised groups are subsequently used to establish phylogenies between species (Novick *et al.,* 2010) and visualised through a cladogram (see **Figure 2.3**)

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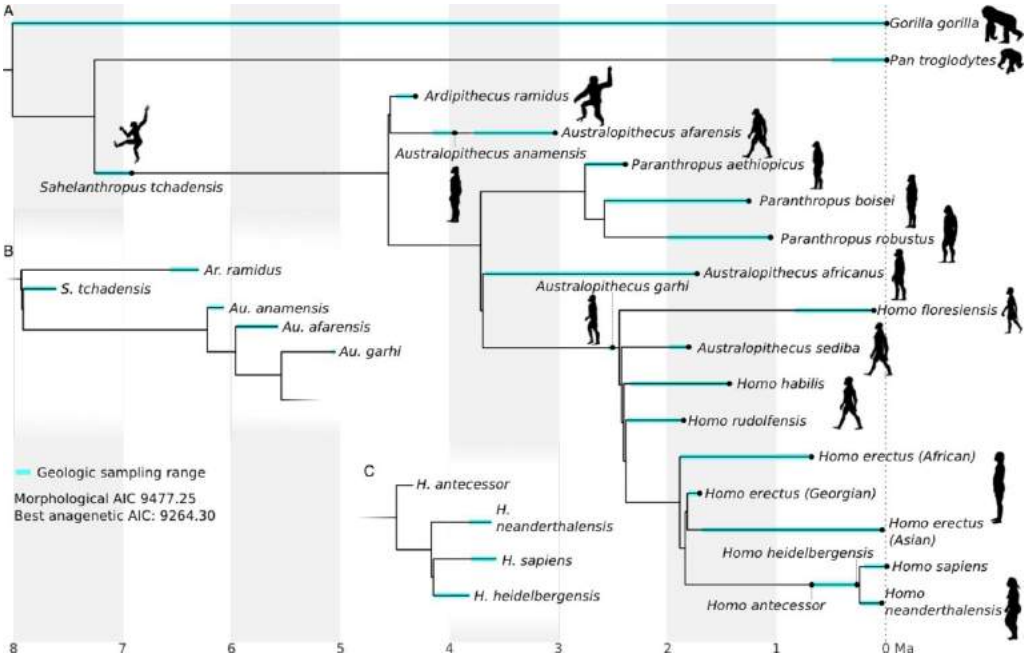

Figure 2.3: The cladistic graph exemplifies probabilistic approaches to hominid phylogenetic inference. A) exemplifies phylogenetic relationships between hominid species with approximated age ranges. Connective lines indicate possible relationships showing the earliest hominin species as obvious points of contention due to small sample sizes. Considering this, B) shows a reconstruction of time-scaled phylogeny considering morphological data and accommodated anagenesis and C) shows possible earliest hominin relationships when morphology is the sole consideration (image source Parins-Fukuchi *et al.,* 2019).

Unlike phenetics, the cladistics approach to systematics is explicitly evolutionary. This method makes it possible to examine developing characteristics within a group of organisms over time and the relative frequency within which those traits have developed (Guralnik and Smith, 2005; Ridley, 2004). Traditional cladistic and morphometric research has relied on the quantitative analysis of distance and angles to understand variation among taxa (Marcus, 1993). Geometric morphometric techniques allow for the specific analysis of homologous landmark coordinates and for the partitioning of size and shape, i.e. non-morphometric variables, and therefore, is a powerful tool for investigating cladistics and hominin classification (Goswami, *et al.,* 2019; Rohlf and Marcus, 1993; Bogdanowicz *et al.*, 2005).

2.3 Hominoidea

Within this study, the two families encompassing the superfamily, Hominoidea (Hominidae and Hylobatidae), will be used as comparative indicators of ecomorphological variance patterning. Hominidae members include the great ape genera (*Gorilla*, *Pan*, *Pongo* and *Homo*), and Hylobatidae includes the 'lesser ape' gibbon and siamang species. The term 'hominid' assigns a species as a primate of the family Hominidae and 'hominin' refers to a taxonomic tribe consisting of *Homo sapiens* and extinct species that are considered ancestral to, or closely related, to humans (Almécija *et al.,* 2021).

It is important to include the two families of Hominoidea in this research as they are united by similar features. Hominid species possess such features as habitual orthograde posture, relatively large brains, wider anterior palates and delayed maturation within an extended lifespan (MacLatchy *et al.,* 2015). Though hylobatids are much smaller and possess a unique postcranial skeleton in comparison to hominids (due to habitual ricochetal brachiation) (Harrison, 2016), their inclusion within comparative human evolutionary study is important. Hylobatids make strong analogues to early hominin species due to their taxonomic diversity, the hybridisation that exists between species, the similar timings of their diversification and their reduced sexual dimorphism (Zichello, 2018).

The following section synthesises the hominoid fossil record, discusses the classifying factors of hominid taxonomy and phylogeny and explores the crucial features that make up hominid cranial diversity.

2.3.1 Hominid Classification

McNulty (2016) argues that hominid taxonomy should reflect phylogeny and shows how this methodology can inform systemic classification of new fossil discoveries through a shuffling of data, i.e. the change in the usage of the term ‘hominid’ to encompass all species of great apes and humans in the single-family Hominidae (Underdown, 2006:680). Currently, there is no consensus as to the phylogenetic relationships of hominid taxa due to sparsity in the fossil record (Aiello and Dean, 2002) though **Figure 2.4** depicts the most widely accepted model. Utilising a cladistics approach alongside quantitative morphometric and reconstructive landmark-based technologies will provide a more accurate examination of the fossil record and enhance the current understanding of hominid evolutionary relationships.

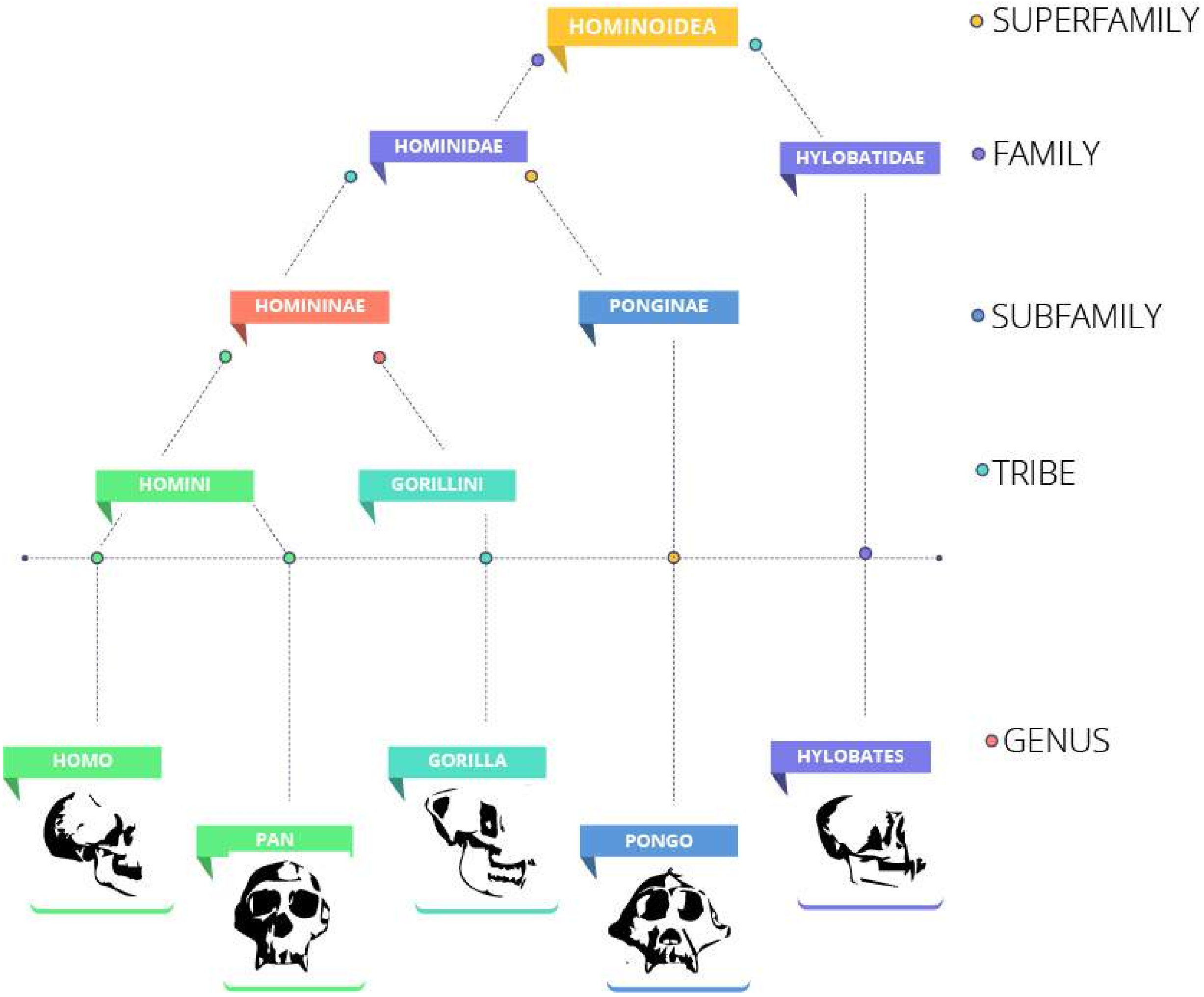

Figure 2.4: Taxonomic classification of Hominoidea superfamily detailing split between Hominidae and Hylobatidae families (adapted from Hunt, 2020).

2.3.2 Hominoid Taxonomy and Phylogeny

The Hominidae family includes the two branching families: hominids (great apes and hominins) and hylobatids (lesser apes or gibbons) (Underdown, 2006; Groves, 2005). One of the main goals in human evolutionary research is to deduce the common ancestry between these families, the origins of which are known to have lived during the Miocene epoch in both African and Eurasian locales (Koufos, 2007).

The hominoid fossil records extend from the Oligocene (25 Ma) to the late Miocene (5 Ma) and are scattered throughout southern Africa, China, Germany, and Spain (Begun, 2015). The first known hominoids originate in Africa, the earliest known as *Kamoyapithecus*, dating to the latest Oligocene from 27.8-23.9 Ma and located in Kenya (Koufos, 2007; Leakey *et al.,* 1995; Steiper *et al.,* 2004). Early Miocene proconsulids represent a large number of fragmented fossil hominoids in Africa, varying in size from approximately 3-8kg and displaying various levels of frugivory and folivory, as well as quadrupedal and arboreal locomotion (Andrews and Kelley, 2007).

Subsequently, the early to middle Miocene brings the arrival of *Ardipithecus*, *Orrorin* and *Sahelanthropus* in the fossil record (Koufos, 2007:1348-1349). The early Miocene taxon *Proconsul* is widely considered a stem taxon, which could be the origin of the ape-human lineage (McNulty, 2010; Begun, 2007; Kunimatsu, 2007). Towards the end of the middle Miocene, hominoids migrate to Eurasia and are represented by the taxon, *Griphopithecus*, who diversified into several taxa, including *Dryopithecus*, *Oreopithecus*, *Sivapithecus,* approximately 9-13 Ma (Casanovas-Vilar *et al.,* 2011).

During the Pliocene, approximately 4.2 Ma, the earliest members of the genus, *Australopithecus,* appear in the hominin fossil record in South Africa (Pontzer, 2012; Dart, 1925; Andrews, 2020). This species was named *A. africanus* based on the juvenile skull fossil and brain endocast from Taung (Kimbel, 2007). During the 1950s, Broom (1950) hypothesised a partitioning between the more robust *Paranthropus* genus, a specialised herbivore based on morphology, and *Australopithecus,* thought to be a tool making, generalised omnivore (Kimbel, 2007:1541).

The earliest Homo species, *Homo habilis,* is found in East Africa during the early Pleistocene, approximately 2.3 Ma (Kimbel *et al.,* 1997). This species displayed similar brain and body size to the australopiths (McHenry, 1992); however, it also showed a difference in the morphology of the molar teeth suggesting a change in dietary subsistence (Pontzer, 2012). *Homo erectus* is found in the fossil record from 1.9 Ma to 100 Kya throughout Africa and Eurasia. During this time, the fossil record shows significant encephalisation, with later Asian *H. erectus* specimen displaying a brain size of up to 1,250cc (Anton, 2003). Approximately 700 Kya, *H. erectus* gives rise to the socially complex *H. heidelbergensis* species, an active tool maker and game hunter, who shows evidence of fire control around 400 Kya (Pontzer, 2012; Roebroeks and Villa, 2011). Subsequently, Neanderthals (*H. neanderthalensis*) evolved from *H. heidelbergensis* by 250 kya in Europe (Rightmire, 2008), with cold-adapted physiques and a similar brain size to *H. sapiens* (Hubblin, 2009).

With the advent of new fossil discoveries, such as *Homo luzonensis,* found on the Philippines' Luzon island (Detroit *et al.,* 2019) and the analysis of the Harbin cranium (Ni, 2021), the hominin taxonomic model is in a constant state of flux**.** Maslin *et al.* (2005) regard the ever-evolving fossil record as providing two significant improvements to the study of palaeoanthropology: firstly, it provides a greater understanding of the variation seen in the hominin phenotype, and also, through modern dating techniques, a more succinct chronology can be linked to these phenotypes also regarding the environments within which they evolved. Maslin *et al.* (2005) further stress that the fossil record is still limiting further advancement in this field as there is a significant lack of cranial fossil remains, particularly between 2 and 2.5 Ma. **Figures 2.5** and **2.6** visualise the phylogenetic taxonomy of the hominoid family as it pertains to the African, Eurasian and European fossil records.

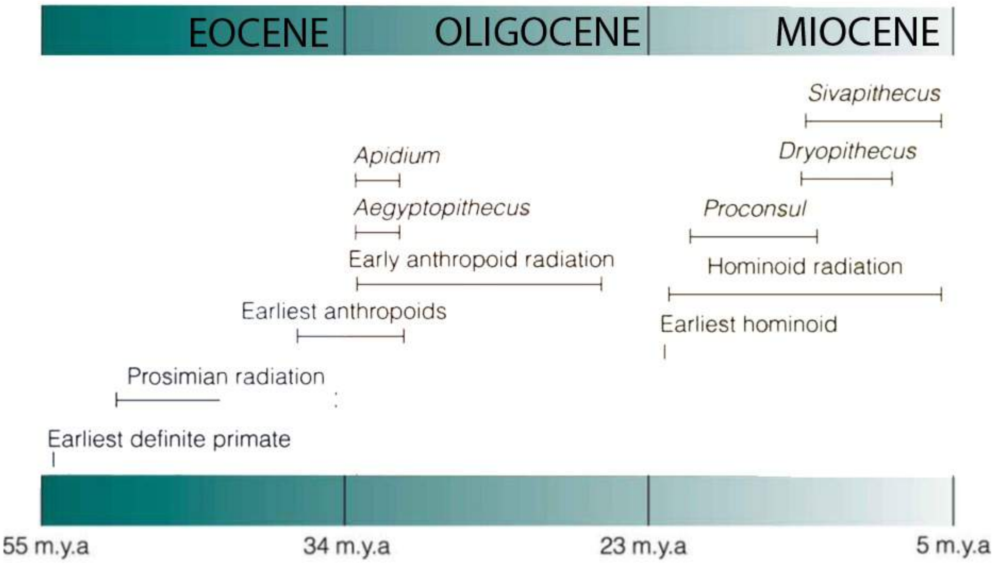

Figure 2.5: Oligocene anthropoid radiations (adapted from Jurmain *et al.,* 2017). This graph shows the evolutionary radiations between hominoid species with associated timelines from the earliest definite primate of the Eocene to the hominoid radiation of the Miocene**.**

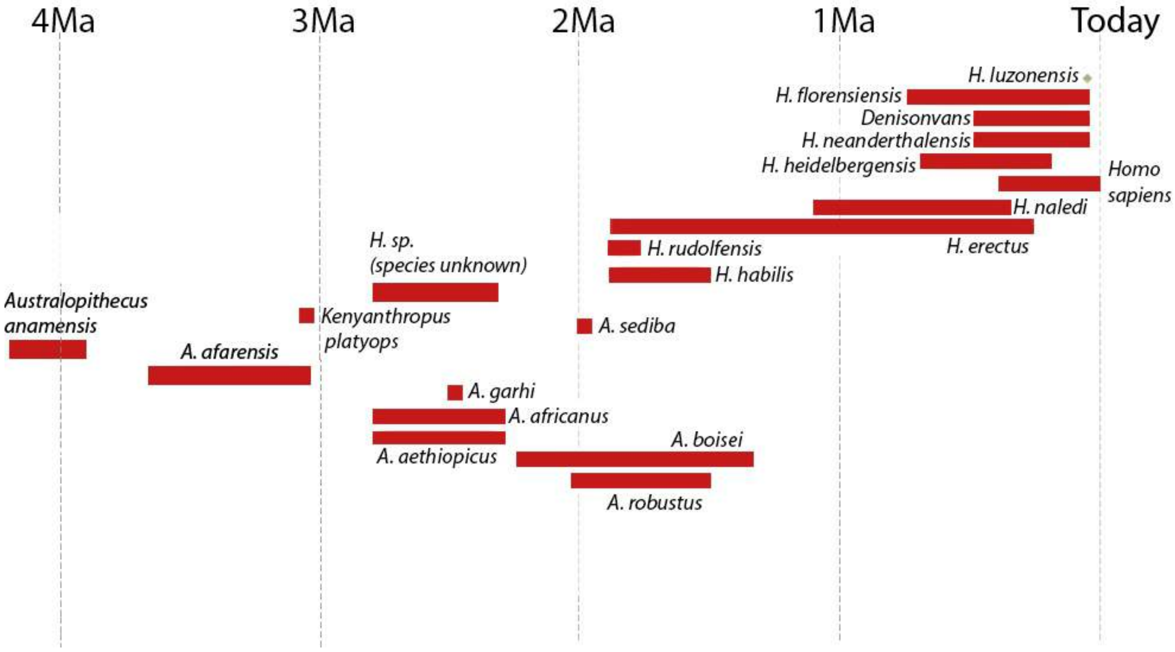

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Figure 2.6: Taxonomy of hominin species through phylogenetic analysis including more recent finds, e.g. *H. naledi* and *H. luzonensis* (adapted from Gresko and Haas, 2019).

Hominid skull characteristics have played an essential role in the classification of fossil hominin species and creating hypothesis regarding phylogenetic relationships between taxa (Shultz, Nelson and Dunbar, 2012). Understanding the defining skull traits that extinct within the hominoid family is essential to identifying patterns of covariation that arise in a geometric morphometric analysis.

2.3.3 Classifying Hominid Skull Characteristics

Hominids exhibit considerable craniomandibular morphological variation, both within-species and across the major taxonomic groups (Bilsborough, 2004). The hominid skull has been subject to evolutionary pressures over time, resulting in a complex developmentally and phenotypically integrated structure, which is distinctly responsive to environmental changes and habitats (Shea, 2013:119). Natural selection has served to produce morphological and functional comprises throughout primate skull evolution (Weaver *et al.,* 2008), including developmental and architectural diversification in mastication (Singleton, 2013), vocal and visual communication (Cheney and Seyfarth, 2018) and the protection of the brain and soft tissue appendages, i.e. the eyes. (Caygan *et al.,* 2016). Cranial evolution in apes is generally discussed in relatively established phylogenetic relationships (Taylor, 2008; Biegert, 1963).

2.3.3.1 Distinguishing features of the hominid skull

Hominids share a broad cranial and dental covariation pattern (Klingenberg, 2013; Monson, 2020). Taylor (2018) defines the most distinguishing features of the primate skull in comparison to most mammals as: 1) the presence of a postorbital bar, 2) a decrease in cranial base angle, 3) an increase in cranial base flexion and, 4) orbital convergence and frontation.

The hominid skull is functionally adapted to house a large brain, as well as olfactory, visual and auditory organs (Mattson, 2014). Food acquisition and processing, respiratory and postural factors, have greatly influenced the morphology of the basicranium and external structures, such as the sagittal crest and tori (Bilsborough and Rae, 2007). The craniofacial structure is primarily associated with mastication, i.e. the zygomatic and oral regions are integrative influences, with the nasal region providing less contribution (Ackermann, 2002, 2005). This specific characteristic sets the hominid clade apart from Old World monkeys, whose primary contributor to the facial integration is the oral region (Bilsborough and Rae, 2007; Marquez, 2008).

Historically thought of as a liner and progressive evolutionary model, it was assumed that a morphological continuum extended from prosimians as smaller-brained and snouted ‘lesser primates’ to more sophisticated anthropoids and culminated as the large-brained, flat-faced *Homo sapiens* (Leibermann, 1995). However, morphometric and phylogenetic studies show the modern human cranial form to have been characterised through gradual and more complex adaptation models (Lesciotto and Richstmeier, 2019; Leibermann *et al.,* 2002). Key evolutionary trends are increased visual activity, deduction of jaw and dentition, encephalisation, decreased olfaction dependency, and an assumed orthograde head posture (Singleton, 2013; Fleagle *et al.,* 2010).

2.3.3.2 Orbital positioning

Primate orbital positioning and size, for example, defines a unique and acute binocular vision and is considered as a necessary adaption in the evolution of primates, i.e. the visual predation hypothesis (Singleton, 2013; Ravosa & Savakosa, 2004; Heesy, 2008). Through GM and Principal Components Analysis, Pereira-Pedro *et al.* (2017) found that orbital positioning in extant apes sits anteriorly to the braincase, inferiorly to the braincase in modern humans, and is positioned intermediately within fossil hominins. This change is suggested as directly influenced by the competition of surrounding soft tissue, temporal space and the orientation of the eye itself. The forward-facing aspect, orientation, size and structure of the orbitals, Singleton (2013) states, signals an ecological and phylogenetic divergence within hominid groups (Kirk, 2006; Ross & Kirk, 2007).

2.3.3.3 Facial kyphosis and cranial base angle

Larger-brained primates exhibit more flexed crania, whilst their smaller-brained counterparts display an extended cranium. The strength of this angle is also dependent on factors such as facial size (Leiberman *et al.,* 2008; Bastir *et al.,* 2010). The cranial base angle is an important and telling feature as it determines the spatial relationships between major functional modules such as the braincase, pharynx, and orbits (Leiberman *et al.,* 2000; Singleton, 2013).

Kyphosis, or the angular orientation of the facial form relative to the neurobasicranium, is influenced by the cranial base form (Singleton *et al.,* 2013). In primates, the anterior cranial base is strongly integrated with the orbital region (the upper face) and contributes significantly to the orbital roof (Leiberman *et al.,* 2008, 2000). The upper face and the posterior maxillary plane create a structure which ventrally and posteriorly rotates as the cranial base flexes. This decreases the angle in between the palate and the base and brings the upper face beneath the braincase. This is referred to as 'klinorhynchy', which can be described as greater kyphosis (Leibermann *et al.,* 2000; Singleton *et al.,* 2013).

Kyphosis is limited by the positioning of the nasopharynx between the cranial base and palate, which in turn, indirectly constrains the cranial base angle (Jeffery, 2005; Singleton *et al.,* 2013). Circumnavigating this constraint, the great ape species possess more dorsally oriented faces than expected for their powerfully flexed cranial bases; however, orangutans are more airorhynch in comparison (Leibermann *et al.* 2002). Interestingly, this is also true of male howler monkeys who display the same specialised, enlarged laryngeal sacs as Pongo (Biegert, 1963; Singleton *et al.,* 2013).

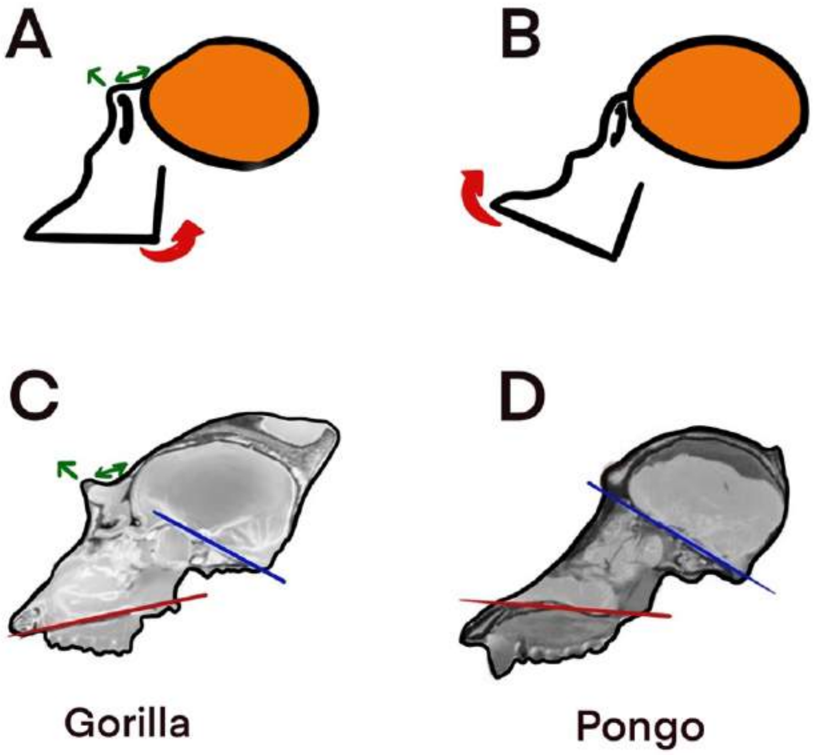


Figure 2.7: Brow ridge and facial kyphosis development in apes. In more klinorhynch apes (A), the face is rotated counterclockwise, ventrally and posteriorly, relative to the neurobasicranium (depicted in orange). In more airorhynch primates (B), the face is rotated clockwise, dorsally and anteriorly relative to the neurobasicranium. Larger-bodied apes (C) display relatively long brow ridges, spatial separation between the anterior neurocranium and the orbit, and neuro-orbital disjunction as a result of klinorhynchy. Figure (D) illustrates the ventrally oriented lower face of the relatively klinorhynch gorilla with widely separated orbital apertures and prominent brow ridge. Figure (E) demonstrates the dorsally oriented lower face in the airorhynch orangutan with absent neuro-orbital disjunction, less restricted nasopharynx and no true brow ridge (adapted from Singleton *et al.,* 2013).

Bilsborough and Rae (2015) consider kyphosis and facial prognathism as reflections of divergent functional adaptation to body size and dietary specialisation. Folivorous primates that consume harder, tougher foods, e.g. capuchins, exhibit comparatively broader faces and shorter jaws, which retract beneath the midface on an orthognathic facial configuration (Singleton, 2013; Koyabu and Endo, 2010). This formation increases masticatory muscle leverage and maximises bite force; however, it limits the size of the food that is easily ingested. Primates that exhibit pronounced facial prognathism, e.g. baboons, have large bodies and considerable canine sexual dimorphism. These species have decreased masticatory efficiency; however, their facial structure accommodates larger, projecting male canines and produces a large gape (Singleton, 2013: Ravosa & Profant, 2000; Wright, 2005).

2.3.3.4 Brow ridge development

Brow ridge development is also related to facial kyphosis. More klinorhynch and larger-bodied apes display ventral and posterior facial rotation relative to the neurobasicranium, relatively long supraorbital ridges, neuro-orbital disjunction and pronounced separation between the anterior cranium and orbit (Singleton *et al.,* 2013). There are currently two leading hypotheses to explain the evolution in brow ridge size: the spatial hypothesis and the mechanical hypothesis (Godhino *et al.*, 2018).

The spatial hypothesis suggests that brow ridge size decreased as the brain case grew larger and is a reflection of the spatial relationship between these two unrelated cephalic components (Moss *et al.,* 1960; Godhino *et al.*, 2018). For example, chimpanzee's eyes are protected by a pronounced brow ridge as the orbits sit in front of their brain case. However, humans' eyes sit under a broad forehead, which accommodates the frontal lobes (Daley, 2018).

The mechanical hypothesis argues that bigger brow ridges are a form of resistance to masticatory loading, protecting the skull by distributing stress from powerful chewing and biting muscles, which is less necessary in humans as we pre-prepare our food (Onyen, 1979; Godhino, 2018; Daley, 2018; Spikins, 2018). Hylander *et al.* (1991) tested this theory of well-developed primate brow ridges and masticatory stress on macaque and baboon specimen. They measured and analysed the patterns of *in vivo* bone strain recorded in the supraorbital region during incision and mastication. Their data showed that principal strain forces tend to bend the supraorbital region in the front plane (after Endo, 1966). However, the researchers note that this strain is minimal in nonhuman catarrhines during mastication and indicates that there is more supraorbital bone than is necessary to counter masticatory loads. Hylander *et al's* experiment could provide no support towards a direct link between masticatory stress and brow ridge morphology.

Godhin *et al.* (2018) tested the main competing hypothesis of brow ridge development using computed tomography (CT) scans of the Kabwe 1 fossil skull, belonging to the Middle Pleistocene hominin *Homo heidelbergensis* (dated from 125-300 kyr). The team created digitised models from the scans, producing 3D images of the original skull and two subsequent models with reduced brow ridge size. By virtually decreasing the brow ridge form, Godinho *et al.* were able to test the impact of the brow ridge on the eye sockets. The researchers found that more bone is needed in the development of the brow ridge than is suggested by the spatial hypothesis (Daley, 2018; Spikins, 2018). Godinho *et al.* (2018) also tested the mechanical hypothesis by modelling various brow ridge sizes and their effects of the skulls biting ability and different levels of strain. The results showed no marked difference between the various cranial models suggesting the size of the brow ridge did not affect the masticatory function of the 3D simulation (Daley, 2018).

Subsequently, Godinho *et al.,* (2018) conclude that the prominent facial swellings such as the brow ridge may be used for social signalling and displays when they aren't directly related to spatial or mechanical processes. Godinho and his colleagues argue that the hominin lineage evolved communicative foreheads as a result of encephalisation. The face became smaller and retracted underneath the braincase exposing a more vertical forehead and more visible eyebrows to convey subtle and emotive messages (Daley, 2018). Godinho *et al's* results suggest non-verbal communication as an advantageous by-product of brow ridge reduction but does not explain the evolutionary trigger for this adaptive characteristic.

2.3.3.5 Summary

Understanding these crucial axes of primate skull morphology aids in the exploration of evolutionary and functional influences that have led to great hominin cranial diversity. In the fossil record, complete cranial specimens are unprecedented and sparse, so comparative study is often necessary to conclude taxonomic and phylogenetic relationships (Luskin, 2012). However, the jaws and teeth of hominin fossil specimens are more likely to be persevered in the fossil record due to the dense nature of the bone material, which allows fossilisation to occur over time. Dental and mandibular fossils can yield information regarding subsistence behaviours, dietary specialisations and phylogenetic positioning of extinct species (Lucas, Constantino and Wood, 2008) and, therefore, have been included in this study as a separate dataset in exploring primate morphospace and pattern variation.

Also, Shea (2013:119) argues that our understanding of hominoid evolution has been severely hindered by the lack of attention afforded to the ‘lesser apes’ (hylobatids), which they suggest has obfuscated the character novelties existing in ‘great ape’ skull patterning. The methodology proposed in this thesis will seek to include Hylobatidae as a dataset to assess the cranial size variation that is purportedly influential in the discussion regarding fossil taxa comparisons.

Foley (2016) argues that the overall pattern of primate evolution provides insight into increased brain size, locomotive behaviours, and social complexity, and those morphological traits observed in the fossil record are correlates of this patterning. They conclude that ecomorphological approaches to comparative perspectives of human evolution are powerful models and excellent predictors of variation patterning. Where an ecomorphological approach has identified anomalous variation and outliers, it has highlighted exceptions to the rule as a species exhibiting unique elements requiring specialised explanation. Therefore, studying primate skulls using an ecomorphological model can theoretically improve upon current knowledge of phylogenetic relationships through a proportional viewpoint towards hominin evolutionary history (Lewin and Foley, 2004; Foley, 2016).

2.3.4 Comparative Phylogenetics

The accepted phylogenetic positioning of *Homo* within the hominin family has led to the utilisation of extant apes as referential models towards determining evolutionary adaptation origins in humans (Kappeler and Silk, 2010; Whiten *et al.,* 2010; Duda and Zrzavy, 2013). Chimpanzees, in particular, have played an influential role in identifying shared homologies (behavioural and ecological) within the *Pan* and *Homo* clades, leading to in-depth research regarding the phylogenetic reconstruction of the chimpanzee-human last common ancestor (e.g. de Waal, 2001; Bradley, 2006; McBrearty *et al.,* 2005; Patterson *et al.,* 2006; Wakeley, 2008; Duda and Zrzavy, 2013).

Advancements in systematic processes and analytical technology triggered a revolution in how we understand primate diversity (Ellison, 2018). Singleton (2013), for example, discusses the importance and influence of modern multivariate and morphometric analysis in divulging the evolutionary reorganisation of the primate cranial structure, particularly in understanding the strepsirrhine-haplorrhine divergence, also known as the origin of modern apes.

Rocatti and Perez (2019) developed a comparative phylogenetic study using geometric morphometric analysis to create a morphometrically informed view of hominid evolutionary radiations. The team offer a complex and variable taxonomic scenario shifting along 10 million years rather than a gradual and continuous process. The authors show their results through a time-calibrated phylogenetic tree showing radiations fitting Foley's (2002) hypothesis of adaptive radiation, a data-driven hypothesis using the cranial-base size and a further hypothetical scenario using Principal Components Analysis scores (**Figure 2.8**).

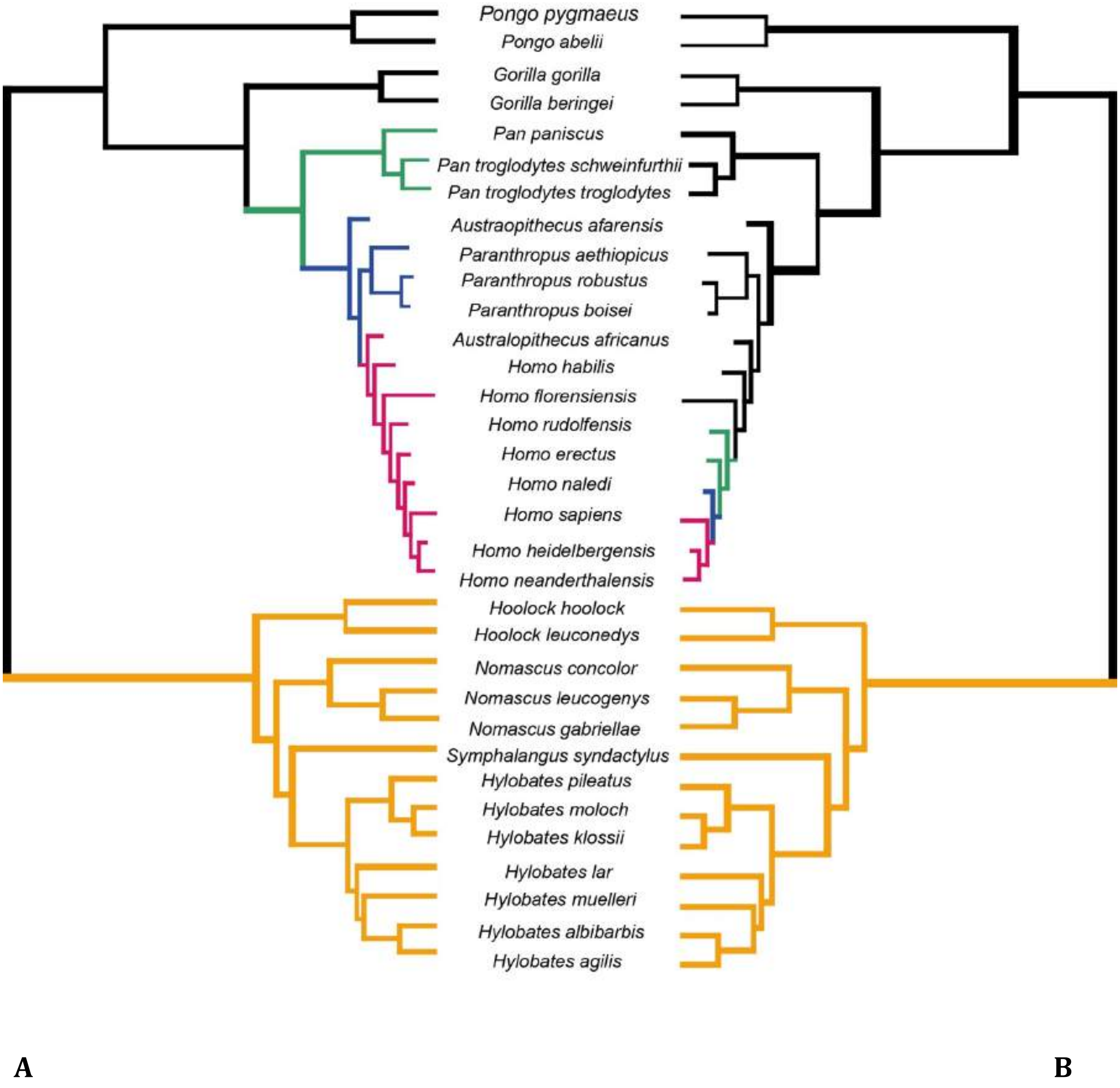


Figure 2.8: Rocatti and Perez's (2019) hominid evolutionary radiations informed by phylogenetic comparative and geometric morphometric applications. A) shows a phylogenetic model composed through Principal Component scores and B) shows the hypothetical model informed through craniometric data with the varied coloured lines representing adaptive radiation. Diversification in variance patterns shows gradual disparity through time and suggests a complex scenario. The authors suggest furthering

understanding of hominid taxonomy with the addition of extant species specimens and variables such as ecology and behavioural/morphological innovations (Rocatti and Perez, 2019:5-6).

Rocatti and Perez (2019) argue the importance of comparative phylogenetic methods, i.e. the addition of extant species data, to increase capabilities of understanding extinct clades and additional variables, e.g. climate shifts and behavioural adaptation (2002:5-6). Environmental change is a major influential factor in the evolution of the hominid skull (Elton, 2008). It is necessary to understand the effects of climatic driving forces on evolution and the hypotheses surrounding environmentally induced morphological adaptation to conduct comparative research utilising ecological variables (National Research Council, 2010).

2.4 Morphological Adaptation and Environmental Change

Why do organisms adapt to their environment, and how does this happen? The traditional Darwinian hypothesis assumes adaptation and speciation are driven by natural selection, i.e. organismal interaction (e.g. predation, competition) produces physical change under selective pressures causing speciation, which differs between groups and in between geographical location (Darwin, 1859; Costa, 2009; Burckhardt, 2013; Vrba, 2015).

As Fusco and Minelli (2010) state, this traditional hypothesis regarding the effects of the organic environment on biological evolution can be summarized as ‘environment proposes, natural selection disposes’. This statement implies a one-way relationship between adaptation and environment where the organism is seen as a passive object impacted by evolutionary forces (Lewontin, 2000). However, Fusco and Minelli (2010) argue that this linear approach to the question of environmentally induced adaptation is limiting in that the persuasiveness of phenotypic plasticity and inheritable or selectable epigenetic variation is ignored (Gilbert and Epel, 2009; Love, 2010). They argue that we only have a shallow understanding of the complexity of developmental and phenotypic determination and the evolutionary consequences of these processes.

Vrba (2015) echoes this sentiment stating that, to understand the complex dynamics of environmental stimuli in hominid origins, the causal linkages of physiology and environment should be considered at varying levels, i.e. during ontogeny to the macroevolutionary level of speciation and extinction. Vrba (2015:1442) argues that the separate and combined roles in the appearance of new phenotypes and species and the direct influence of physical environmental stimuli on evolution at each level of evolution should be investigated.

The hominid fossil record shows significant evolutionary events that defined key morphological, functional and behavioural traits characteristic of hominin species, e.g. encephalisation, bipedalism and the first use of stone tools (Foley and Lee, 1991). The geological record confirms these evolutionary events coincided with substantial shifts in contemporary Eurasian and African climates (Behrensmeyer, 1982; Boaz, 1983; Bromage and Schrenk, 1999; Foley, 1994; Ruddimann, 2001).

Due to the sparsity in the hominin fossil record and an incomplete record of past climates, environmental adaptation in human evolution is speculative (National Research Council, 2010). Improving the understanding of covariation patterning in morphology compared to ecological data will shed light on the climatic influences that force adaptation (Maestri *et al.,* 2017). Ultimately, in studying how climate affects an organism's morphology, we must first explore the role of adaptation and how phenotypic response is generated as a result (Fusco and Minelli, 2008, 2010).

2.4.1 The Concept of Adaptation

As a product of natural selection, adaptation, by definition, describes a change within an organism, providing improved function and overall survivability of the specimen within its environment. Adaptation can take on numerous forms, presenting as behavioural, physiological or morphological change (Fusco and Minelli, 2010; Schaffner and Sabeti, 2008; Frisancho, 1993; Stinson, 2000). The creosote bush, for example, is a plant specimen prosperous in a harsh desert climate that produces toxins to prevent other plants from growing nearby, thus reducing competition for water and available nutrients (Sharifi, 1999).

Defining what constitutes an adaptation is crucial to understanding how to view anatomical features from an evolutionary perspective (Gould and Lloyd, 1999). Vestigial structures, for example, are features that are considered adaptations specifically for the organism’s ancestor but evolved to be non-functional due to environmental change. Cave-dwelling fish, for example, have vestigial eyes, whose function became unnecessary when their sighted ancestors began to thrive in a darker habitat (Rétaux and Casane, 2013).

The key question in determining ecomorphological patterns of variance is how we can identify adaptive morphological features within the hominin fossil record. Natural selection is the driving mechanical force of evolution whereby positive adaptation improves an organisms' ability to survive and reproduce in a specific environment (Gregory, 2009). Positive natural selection is the tendency for beneficial traits, or advantageous genetic variants, to increase in frequency within a population and is considered the driving force behind adaptive evolution (Shcaffner and Sabeti, 2008).

The three principles of natural selection, as proposed by Darwin & Kebler (1859) and Wallace (1855, 1869, 1889), state that individuals within a species population will exhibit anatomical and trait variations, i.e. phenotype. Some of this variation is heritable due to genotype; and that variation, in general, will help individuals compete in the same environment. Organisms possessing heritable traits allowing them to better adapt to their environment, in comparison to other members of their species, will be more likely to survive and reproduce (Darwin & Kebler, 1859; Gregory, 2009).

Tingenberg (1963) strengthened the theory of causality through evolution by proposing four approaches to identifying novel morphological and behavioural variation. For example, if we were to ask Tingenberg's questions (see **Figure 2.9)** to understand the evolutionary explanation of speech, we would first address how the organism mechanically and functionally produces stable vocal sound. Next, we would endeavour to discover how the organism acquired language capabilities and the development of this trait. The third type of explanation addresses the advantageous selective and adaptive value of speech and finally attempt to discern the evolutionary antecedent of this trait, i.e. primitively derived, an adaptation from gestural language (Tingenberg, 1963; Mayr, 1982; Krebs and Davis, 1987; Lewin and Foley, 2004).

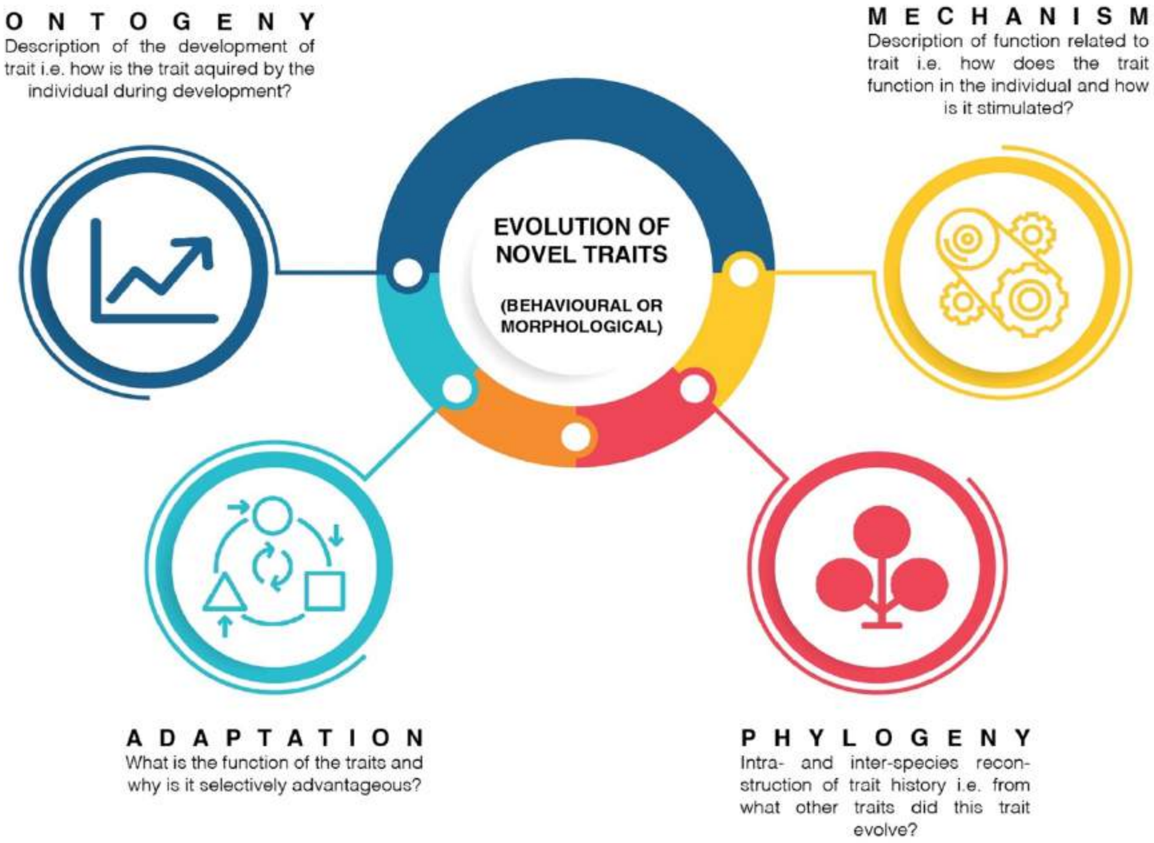


Figure 2.9: Four evolutionary questions as proposed by Tingenberg (1963) addressing issues of mechanics, selective advantage, ontogeny and phylogeny (adapted from Lewin and Foley, 2004:33).

Tingenbergs (1963) question of phylogeny as an evolutionary explanation is of particular interest to the study at hand, as it provides a framework for elucidating relationships between species using morphological traits in relation to habitat. In human evolution, phenotypic plasticity is considered a major mechanism in response to environmental change. Antón and Kuzawa (2017) argue that conclusions can be drawn regarding the causes and consequences of phenotypic variance for both inter-and intraspecific datasets by focusing on environmental means of morphological difference.

2.4.2 Phenotypic Plasticity

At an individual level, adaptation is driven by selection and partly driven by phenotypic plasticity, which encompasses all types of environmentally induced variation within an individual (Young *et al.,* 1989; Potts, 1998; Fusco and Minelli, 2010). Pigliucci *et al.* (2006) define phenotypic plasticity as 'the ability of individual genotypes to different environmental conditions' and represents a positive or negative influence on an individual's fitness.

Phenotypic plasticity can be considered as an adaptive evolutionary strategy to variable environments, exemplified in modern human populations as skeletal responses to climate variables, i.e. Bergmann and Allen's rule linking smaller body masses to warmer temperatures (Yom-Tov, Benjamini and Kark, 2006; Beal *et al.,* 2010). Holliday (1997) and Weaver (2003), for example, have drawn comparative conclusions regarding related skeletal patterns of variation, arguing Neanderthal long-term adaptation to colder European climates is non-existent in the earliest *Homo sapiens*.

Phenotypic responses allow for novel phenotypes to emerge in reaction to environmentally induced change, which informs a more gradual genetic adaptation model labelled as 'phenotype first' evolution (Kuzawa and Bragg, 2012). This is exemplified through genetic assimilation where, for example, the environmentally induced phenotype expresses throughout multiple generations in the absence of the initial stimulus (Waddington, 1953; Anton and Kuzawa, 2017).

The ‘flexible-stem’ model of species dispersal is an example of the climate forced phenotypic principle, which states that phenotypic plasticity patterns will be directionally and morphologically constrained in the ancestral stem populations when faced with ecological pressures (Wund *et al.,* 2010). The phenotypes induced in descendent populations will support short-term survival in novel climate conditions and guide longer-term genetic evolution by determining specific locally expressed phenotypes (Antón and Kuzawa, 2017).

Temperature, altitude and humidity are important environmental factors in developmental adaptation in hominins, e.g. adapting to low oxygen pressure at high altitude (Frisancho, 1977; Witt and Herta-Sanchez, 2019). Bergmann and Allen’s rule, for example, states that: 1) homoeothermic species will display larger body variants when inhabiting colder climates with smaller variants in warmer climates and, 2) the length of the homoeotherm appendages, e.g. legs and arms, will be comparatively shorter in colder climates than those living in warmer regions (Beal *et al.,* 2010; James, 2018). This ecomorphological rule is seen in modern human populations, and the fossil record, i.e. the broader body characteristic of Neanderthals, is an ecomorphological adaptation for retaining heat (Ruff, 1993; Holliday, 1995; Weaver, 2003; Weaver and Steudel-Numbers, 2005).

A further example of environmentally induced plasticity is hypothesised by Antón and Kuzawa (2017), who argue that the plasticity in body and brain size of *H. erectus* are pertinent clues to the local variation and dispersal of this hominin. Approximately 1.8 Ma, the Homo genus is represented by this singular taxon for a considerable length of time until the advent of *H. naledi* in the fossil record. Antón and Kuzawa suggest that plasticity allowed for environmentally optimal phenotypes to be advantageous to *H. erectus'* survival in disparaging habitats. They exemplify this through dental signals of nutritional stress and taphonomic predator activity signals with the smallest bodied *H. erectus* specimens found in the Dmanisi palaeodeme. The team note that nutritional stressors, in particular, favour reduced metabolic expenditure of the brain, signalling how environmental factors of deprivation, i.e. low subsistence seasons, or enrichment can influence allometry and brain development (Antón and Kuzawa, 2017:11).

Antón and Kuzawa's (2017) study shows the relevance of environmental adaptation in hominin species, identified as phenotypic plasticity in the fossil record. A significant issue in human evolutionary study is the lack of evidentiary material relating to the earliest hominins of the late Miocene and early Pliocene. For this reason, a comparative perspective is best utilised, using evidence of extant environmentally induced phenotypic plasticity and morphological variation to draw conclusions relating to extinct hominin populations.

Dietary intervention is a further example of environmentally induced plasticity which is evident in the hominid brain. The hippocampus, related to memory, learning and temperament, is a particular region in the brain known to be highly sensitive to environmental pressures (Murphy *et al.,* 2014). Menegaz *et al.* (2010) utilised a comparative morphometric and statistical analysis to investigate the effects of dietary properties and mastication on the morphological plasticity of the hominid neurocranium.

The results showed that masticatory stress influences the growth and plasticity of the neurocranium. Menegaz *et al.* report long-term increases in masticatory loads, i.e. harder, tougher diets, resulting in a thickening of the bones that form the neurocranial vault and altering the wall curvature. As diet is directly related to habitat and the subsistence found in a particular region, morphological adaptation associated with masticatory function can act as a signal towards the type of habitat in which a species lived (Luca, Perry and Rienzo, 2014).

2.5 Environmental Hypotheses of Human Evolution

Understanding the sensitivities of environmental factors on physiological adaptation is paramount as the key features of human evolution, i.e. bipedalism, encephalisation, tool creation and enhanced social functioning, can all be thought of as reflecting adaptations to changing environments (Luca *et al.,* 2010; NRC, 2010). The effects of unstable ecological shifts on hominin evolution are expressed as a series of hypothetical models (Vrba, 2015).

Potts (1998) describes the main hypotheses used to create assumptions regarding climate and evolution of hominin species: 1) the savannah hypothesis or aridity hypothesis, which is associated with hominin bipedalism (Potts; 1998); 2) the turnover pulse hypothesis suggested to explain adaptation as a result of acute climate shifts (Vrba, 1980); and 3) the variability selection hypothesis, which advocates the role of environmental unpredictability in selecting ecological or behavioural flexibility (Potts, 1998). Stable environments are also hypothesised as equally strong influential drivers of hominin evolution (Maslin *et al.,* 2015). They are explained through sympatric evolution or the Red Queen hypothesis, which highlights the importance of continued adaptation for retained fitness amongst co-evolving systems (Papkou *et al.,* 2019).

The following sections will detail the leading environmental hypotheses of human evolution with a view to synthesise the effects of climate change and ecology on morphological adaptation in hominin species.

2.5.1 The Turnover Pulse Hypothesis

Vrba's Turnover Pulse hypothesis (1980, 1985, 1988) explains evolution through climatic forcing. The phylogenetic model of turnover pulses refers to brief periods of time that experience concentration of speciation and extinction events resulting from climate change. Thus, ecosystem stasis in terms of species composition must sit between pulses (Maslin *et al.,* 2015). According to Vrba's model, a shift in warm and moist conditions towards a drier, cooler and more open habitat (forced by global cooling) manifested a sharp ^{18}O isotope enrichment transition of the deep-sea, which allowed for a turnover episode of African mammalian clades around 2.5mya (Vrba, 1985; 1988). As the origins of robust australopiths and early *Homo* are purported to coincide with this turnover pulse, a causal link can be posited between a global climatic event and hominin evolution (Potts, 1998).

Further turnover pulses are described by Vrba (1980, 1985, 1988), which include a speciation episode in bovid clades occurring during the same 2.5 Ma mark, and two further periods of cooling and continental drying approximately 5 Ma and 0.9 Ma. Closely correlated with these environmental events are the extinction of robust australopiths, the origin of the Hominini tribe and the dispersion of *H. erectus* into Eurasia (Potts, 1998; Menegaz *et al*., 2010; Maslin *et al.,* 2015).

Faith and Behrensmeyer (2013) tested the underlying mechanics of Vrba's model using south African Quaternary ungulate records. The team generated specific predictions concerning ungulate responses to changes in sea level, topographic barriers and vegetation based on different habitat preference and feeding habits. Faith and Behrensmeyer proposed Milankovitch-scale climate oscillations as a driving force of steady and moderate faunal turnover over 10^4-year time scales. A turnover pulse, they conclude, would require 'additional and temporally constrained climatic forces' to accelerate evolutionary change, e.g. biotic interaction.

Similar studies, such as Kerr (1996) and McKee (2001), have tested Vrba's Turnover Pulse hypothesis by examining temporal correlations between climatic events and turnover pulses. However, it is difficult in palaeoecological study to dissect these correlations and impossible to observe turnover or predict lineage response to climate change. Therefore, it is unclear whether faunal turnover is influenced by climate change in the same manner that the Turnover Pulse hypothesis predicts (Faith and Behrensmeyer, 2013).

2.5.2 Habitat-Specific Hypothesis

Adaptive evolutionary hypotheses differ from turnover models in that they attempt to detail how environmental context influences natural selection, survival and the emergence of significant adaptations. However, such hypotheses do not necessarily relate to the pattern of species turnover directly. The main narrative of hominin adaptive evolution is habitat-specific and explains the reasoning behind the advent of adaptations to meet that habitat's distinct requirement. (Potts, 1998).

The savannah hypothesis is an example of a habitat-specific narrative that has dominated human evolution research in its earliest phases, whereby adaptations to increasingly open and drier biomes are considered responsible for hominin evolution from the late Miocene to the early Pleistocene. Contemporary savannah environments are thought to have incited key human traits such as terrestrial bipedalism, encephalisation and behavioural adaptations in tool-making and dietary habits. (Potts, 1998; Klein, 1989; Wolpoff, 1980).

Although the savannah hypothesis has its supportive proponents (e.g. Vrba *et al.*, 1989, Prentice and Denton, 1988; Stanley, 1992), there are arguments which state that closed vegetation, by way of woodland/forest growth, has been more important to the evolution of early hominins (Potts, 1998:110). Early australopiths, for example, are closely associated with woodland habitat and display significantly amplified arboreal activity (Berger & Tobias, 1996). *Ardipithecus ramidus*, one of the earliest known hominins, is also associated with a tree-dominated habitat-setting (WoldeGabriel *et al.,* 1994; Potts, 1998:111). Potts (1998) regards habitat-specific hypotheses as being the most widely used explanation for adaption to the environment, but comments on alternative views having merit within this subject, i.e. the variability selection hypothesis.

2.5.3 The Variability Selection Hypothesis

The variability selection hypothesis states that human evolution's driving forces stem from environmental instability rather than single habitat and climate trends. Through this hypothesis, inconsistent selection eventually replaces habitat-specific adaptation with behaviours and structural functions responsive to complex changes in the environment (Potts, 1999). This is exemplified by the adaptive genus *Homo's* response to survive in a multitude of environment types rather than specializing within a single habitat (Potts, 1998, Borg & Channon, 2012, Grove, 2011).

It could be argued that this state of 'fluctuating selection' is already described by the development of phenotypic plasticity. Potts (1998), however, suggests that empirical studies focused on the fluctuating selection of extant organisms occur in relatively short timeframes, i.e. variation in harsher seasons, and that the variability selection hypothesis has a more complicated, long-term effect. Long periodicities of environmental change, in this hypothesis, are vital in the development of evolving adaptation (Potts, 1998). Grove (2011) furthered this hypothesis, modelling a position whereby climate variability is considered the driving force behind human evolution rather than climate change (Grove, 2011; Kingston, 2007; Maslin and Trauth, 2009).

Borg and Channon (2012) tested the variability selection hypothesis using binary strings of genotypes and phenotypes relating to individuals within a population exhibiting combinations of social and individual learning, as well as genetic evolution. Success was measured using the Hamming distance between phenotype and environment. This research assessed the feasibility of increasing variability in the environment influencing versatile behaviours and survival strategies, i.e. social learning. The team concluded that environments linked to high or increasing variability also show greater mortality rates when social learning is exhibited, unless individual innovation develops in isolation. Results showed that increasingly variable environments are sufficient but vital in creating evolutionary advantages for populations that exhibit extra-genetic learning behaviour (2012:317-324).

The variability selection process requires long periods of unpredictable climate conditions whereby adaptive genes can advance and proliferate in the gene pool (Potts, 1999). Potts and Faith (2012) show how African hominin adaptation is consistent with this model of variability selection exemplified by larger evolutionary and phylogenetic events, dispersal and migration, as well as behavioural milestones. East African hominins, for example, encountered substantial climate variability between 350-50 kya (McDougall *et al.* 2005; Behrensmeyer *et al.,* 2002). Combined with critical evolutionary markers of increased adaptability, i.e. migration, development of symbolic culture and technological innovation, variability selection provides evidentiary support towards a link between climate instability and key evolutionary events (Potts and Faith, 2012).

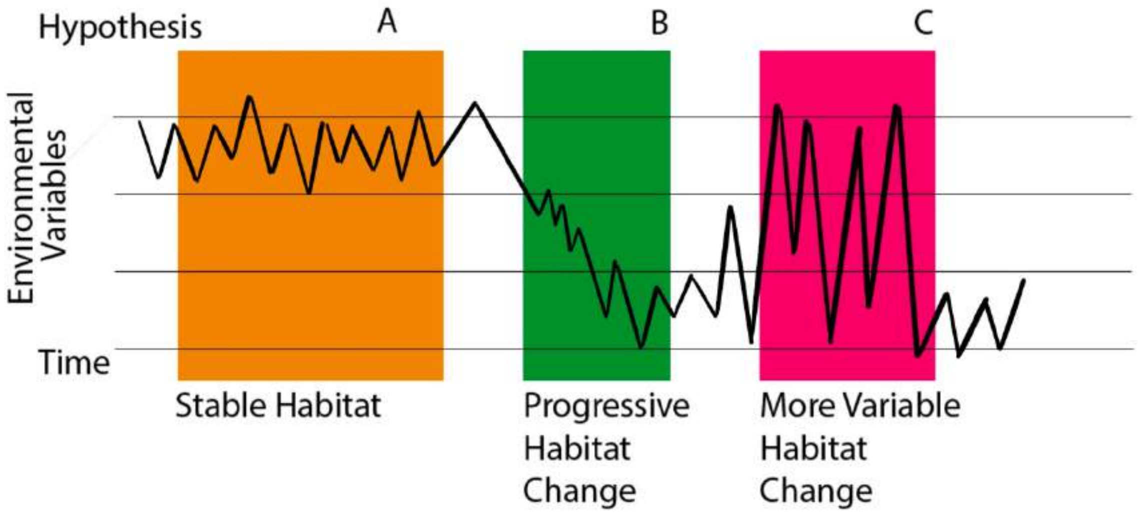


Figure 2.10: Graphical depiction of stable, progressive and more variable habitat changes in response to time and environmental factors. New adaptations may evolve during periods of A) relatively stable habitats, B) periods of progressive or directional change e.g. wet to dry environments and C) highly variable climates as predicted by the variability selection hypothesis (adapted from SMNH, 2020).

The variability selection hypothesis requires long periods of highly volatile environmental variability however, Van Valen (1973) suggests climate stability as being equally important to adaptation and evolution. This theory is known as the Red Queen hypothesis and emphasises the role of biotic divergence over abiotic forces in driving selection (Brockhurst *et al.,* 2014).

2.5.4 The Red Queen Hypothesis

The Red Queen hypothesis states that relatively long periods of climate stability has an equally significant effect on hominin morphological evolution compared to periods of climate shift (Van Valen, 1973; Papkou *et al.,* 2019). In this view, continued adaptation is required for species to maintain necessary fitness levels compared to co-evolving ecological surroundings. This hypothesis suggests that biotic interactions, rather than climate change, are evolutionary driving forces (Stotz *et al.,* 2018). Maslin *et al.* (2015) argue that, for this to occur, a relatively highly productive environment is needed so that competition is the dominant adaptive control rather than environmental resources.

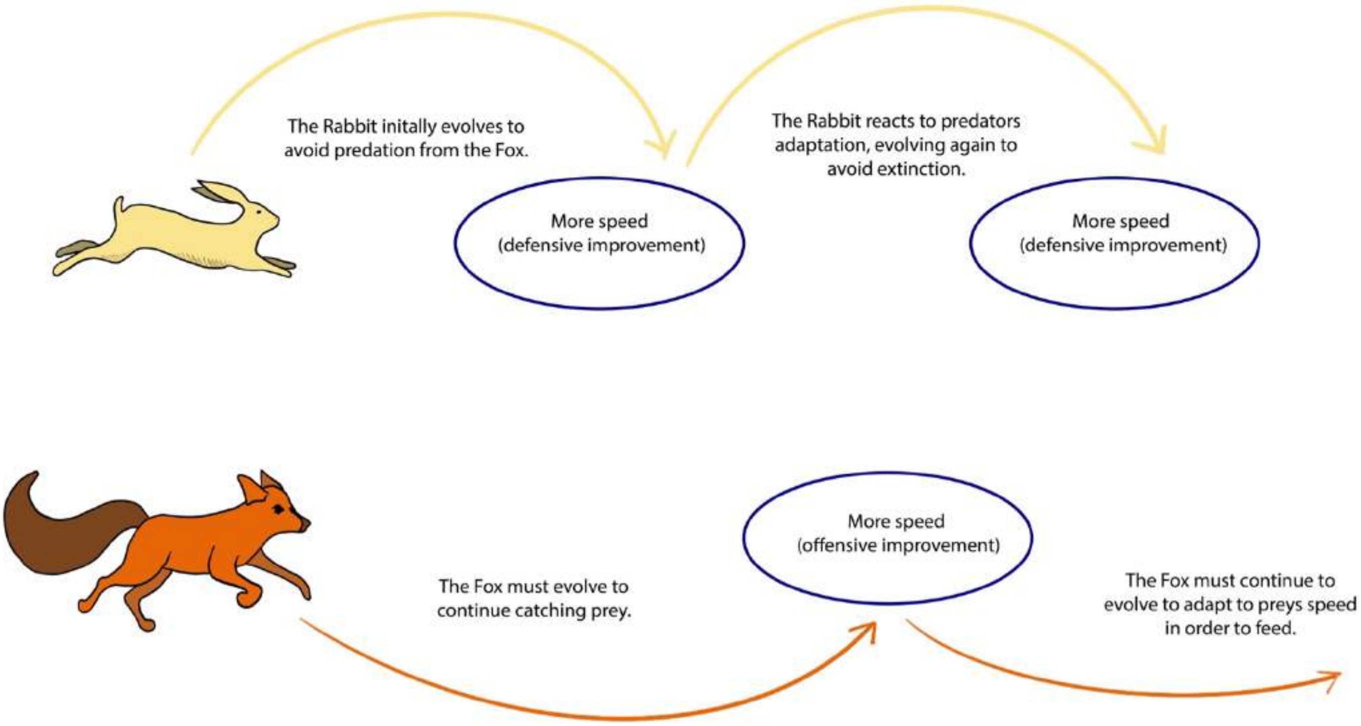


Figure 2.11: The Red Queen hypothesis exemplified through the predator-prey relationship. The fox and rabbit analogy show the prey animal evolving faster speeds (a defensive improvement) in response to the predator. The fox subsequently evolves to increase its speed to be able to catch its prey. This example shows the predator and the prey must be constantly and continuously evolving to avoid extinction.

Possible evidence supporting the Red Queen hypothesis can be found in the Koobi Fora, Northern Kenya, hominin fossil record, approximately 1.8-1.9 Ma. Geological records show a period of maximal lake coverage during this period (Rogers, 2010; Braun *et al.,* 2010) convergent with fossil evidence of numerous hominin species, including *H. rudolfensis*, *H. erectus*, *H. habilis* and *P. boisei* (Mana *et al.,* 2019). It is suggested that high levels of resource availability, afforded by quality water sources, drove the evolution of these hominins as a direct result of resource competition (Maslin *et al.,* 2015).

2.5.5 Summary

Environmental hypotheses linking climate change and human evolution are primarily based on evidence that large-scale climate shifts or variability altered the ecological landscape leading to speciation pressures which forced genetic selection. Limitations in testing these hypotheses are due to lack of data in the archaeological and fossil record, variable fossil density from various timescales and regions, and inconsistent fossil assemblages (NAC, 2010; Potts, 1998).

Understanding environmental stressors on morphological adaptation are vital to understanding the taxonomic and phylogenetic relationships between hominins. The effects of contemporary paleoecology on East African hominin evolution between the late Miocene and early Pliocene epochs is of particular interest due to the advent of key evolutionary characteristics, e.g. bipedalism and encephalisation (Cuddahee, 2017), which reflect adaptations to an ever-changing environment (Luca *et al.,* 2010; NRC, 2010). In the following section, the palaeoecological history of the Miocene and Pliocene epochs is discussed in relation to the converging hominin fossil record.

2.6 Late Miocene and Early Pliocene Environmental Records

Speciation, extinction and dispersal events have characterised human adaptation and have been linked to paleoclimate records, both regionally and globally. (e.g. Vrba, 1980, 1985, 1988; Vrba *et al.*, 1989, Prentice and Denton, 1988; Stanley, 1992; Kingston, 2007; Kingston and Harrison, 2007; Maslin and Trauth, 2009). Shultz *et al.* (2013), for example, suggest the precession-forced appearance and disappearance of deep lakes in East Africa have fundamentally changed the local environment through periods of aridity and moisture, which in turn significantly influenced the speciation, migration and encephalisation of *Homo* 1.9 Ma (Mana *et al.,* 2019; Maslin *et al.,* 2015). The late Miocene and early Pliocene epochs, in particular, are characterised by major global climatic changes which also coincide with major evolutionary events throughout the hominid fossil record (Andrews, 2020; Blumenthal *et al.,* 2017).

The Earth's climate is determined by intricate and circulating heat and moisture systems, which strongly influence the distribution of biomes, linking the atmosphere, oceans and landmasses (Bailey, 2009). This system is influenced by volcanic activity, uplift of the Earth's crust and orbital cycles affecting the planet's daily solar radiation dose. Atmosphere, landmasses, and oceans are all linked by this system that is strongly influenced by volcanic and tectonic activity, as well as Milankovitch orbital and axial cycles, determining the Earth's distance and positioning in relation to the Sun, ultimately affecting the overall amount and annual pattern of solar radiation (Potts, 1998).

Evidence of palaeoecological shifts, particularly in relation to late Miocene and early Pliocene timeframes, is deduced through many techniques that work to provide a comprehensive and precise view of the way the world looked millions of years ago (Begun, 2002). Combining fossil records with geological records of past climates demonstrates that organism reaction to change in the Earth's ecosystems has contributed to the evolution of life throughout several billion years. However, the fossil record has also shown that such efforts were not born from superficial cause-and-effect relationships, instead representing a more tumultuous and sporadic story of causative linkages (Agusti *et al*. 2003; Harrison, 2010; Kelly, 2002; McNulty, 2010).

2.6.1 Paleoclimatology and the Fossil Record

Understanding past climates provides a better understanding of the environmental pressures and constraints hominids experienced and, therefore, can provide insight into how habitat and climate potentially impacted their morphological evolution (Sih, Ferrari and Harris, 2011). Paleoenvironmental data is sourced through biotic and abiotic (non-living) components, including pollen, fossilised plants, faunal remains, sediments and soils. These components can indicate the climate structure and environmental shifts at a global, regional or local (NRC, 2010) level to create historical (and projected) environmental models (Reed, 2013).

2.6.1.1 Paleotemperature and marine oxygen isotope analysis

Paleotemperature research is one of the main factors determining what the climate looked like within a timescale greater than a hundred years (Potts, 1998). Understanding oceanic temperature evolution is critical to a study such as this, as water mass is a determining and influential factor to the Earths internal climate system. Scientists can establish the oceans historical temperature through isotopic and elemental proxies that are found preserved in marine sediment (Bradley, 1999; Imbrie & Imbrie, 1979; McManus, 2004).

Marine Oxygen Isotope analysis exemplifies the interaction between the Earth's oceans and atmosphere by analysing oxygen isotope ratios within the carbonate skeletons of benthic foraminifera, ultimately providing a proxy of evaporation and temperature (Pearson, 2012). Where evaporation occurs, the stable isotope ^{18}O becomes enriched within ocean water, whilst it's lighter counterpart, ^{16}O, is released into the atmosphere. Subsequently, marine micro-organisms with carbonate skeletons, such as forams, absorb the oxygen isotopes directly proportional to the surrounding water. So, it stands that an ocean enriched with ^{18}O results in a higher ratio of ^{18}O to ^{16}O in the microscopic shells of marine life (Jaffres, Sheild and Wallmann, 2007). This ratio is also indicative of temperature and evaporation – for every 1°C drop in water temperature, there is an increase in ^{18}O to ^{16}O proportions by approximately 0.22 parts per mil (‰) (Potts, 1998; Pearson, 2012).

Similarly, during glacial periods, the lighter ^{16}O released into the atmosphere becomes locked within ice sheets through precipitation (Lhomme, 2004). Ttherefore, studies of foram $\delta^{18}O$ provide a record of glacial ice volumes and temperatures (Oerlemans, 2004). However, proportions of $\delta^{18}O$ are used to determine global climate measures referring to ocean temperatures and ice volumes in particular and, therefore, may be distinguished from the contemporary environments on land (e.g., deMenocal et al., 1993; Potts, 1998, Lea, 2014).

2.6.1.2 Loess Deposits and Paleosols

Soils are products of environmental influences, such as topographic setting, climate, vegetation and formation time. Fossil soils, or paleosols, can provide insight into the climate change experienced by early hominins (Retallack, 2007; Beverly *et al.*, 2018). The traditional narrative of human evolution in East Africa suggests climate and vegetation transformed from a primaeval forest setting to dry and open grasslands in a single transition (Maslin *et al.,* 2015). Paleosol evidence contradicts this view, instead suggesting dramatic climate oscillations between wet, dry and alternating woodland and grassland expansions since approximately 18 Ma (Retallack, 2007). The fossil record reflects dry grassland adaptations, e.g. thick enamel (Udurawane, 2018) and adducted hallux (Crompton, 2008), punctuated by alternating woodland adaptations, e.g. erect stance (Niemitz 2010; Crompton, 2008), flat face and short, stiff back (Andrews, 2020; Retallack, 2007).

This 'first-family' Hadar site, in Ethiopia, provides a paleosol matrix that offers insight into the ecosystem in which *Australopithecus afarensis* lived. The 13 *Australopithecus afarensis* individuals near Hadar, Ethiopia (Johanson *et al*., 1982), were interred in flood deposits shortly after death and fossilised in a grassy and streamside woodland soil

(Retallack, 2007). The dominant environment at Hadar around 3.4-2.9 Ma was the vegetated and flat floodplain of the Awash River. $\delta^{13}C$ values in the paleosols of clay deposits suggest a majority 70% vegetative cover of C_3 plants and 30% C_4 grasses (Aronson *et al.,* 2008). The heavier $\delta^{18}O$ carbonates found in the soil indicate highly seasonal paleo-rainfall, approximately twice as much as modern rainfall in the same region (Hailemichael *et al.*, 2002). These values mean that the C_4 plants in the area would have been predominately large trees and that the *A. afarensis* fossils discovered in the area, would have lived in a grassy woodland biome (Aronson *et al.,* 2008).

Loess-soil deposits offer a valuable source of information across vast continental areas that can potentially exemplify environmental sequences and climate change experienced by early hominins in temperate latitudes (Schaetzl *et al.*, 2018; Potts, 1998; Ferring, 1986). Throughout vast areas of Europe and Asia, dynamic sequences of loess (windblown sand) and paleosol (soil) layers represent the quantity and quality of vegetation cover within specific periods of history. Loess layers, in particular, signify ealion material build aided by low vegetation cover, whereas organic-rich soil formations indicate an abundantly vegetated environment (Kemp *et al.,* 1995; Li *et al.,* 2008; Komar *et al.*, 2009; Juvigne *et al.*, 1996).

Loess accumulations require aeolian material and the ideal trap for deposition, which has been argued, is a sparse vegetation cover or topographic barrier (Mason *et al.,* 1999; Iriondo and Krohling, 2007). Loess deposits exist around the world with the Quaternary deposits in China being the thickest and most preserving record of paleoecology (Hao and Guo, 2007). Loess deposits are also found in the Indian Kashmir Valley (Dar and Zeedan, 2020), in several valleys in the western and Central Himalayas (Pant *et al.,* 2005), and in the Deccan Plateau and Indo-Gangetic Plain (Liu *et al.,* 2017, 2019). Loess soils that are intercalated with paleosols indicate relative landscape stability and provide valuable insight into paleoclimate dynamics, as soil properties depend on climatic conditions at the time of formation (Dar and Zeedan, 2020).

Further interpretations of the environment can be derived from loess-soil layers by studying the fossil pollen and fauna present in the samples, the carbonate content and the magnetic susceptibility of the material (Deng, 2004). The latter technique measures the concentration of magnetic grains in the layers. This component is found in high concentration in fine dust transported by wind from distant sources and is found abundant in warm, wet periods, whereas a coarser grain will be found in local sources, deposited during cold and dry periods (Tsoar and Pye, 1987). Therefore, high magnetic susceptibility measurements will be found in soil and low concentrations in loess layers. This analysis can determine the record of oscillation in climate and vegetation from specific periods in prehistory (Panaiotu *et al.,* 2001).

Analysis of marine oxygen isotopes, loess-soil layers and glacial cores have provided a view to the abrupt climate effects that coincide with the earliest hominin evolution (see **Figure 2.12**). Changeable seasonality ensured higher variability through fluctuating environmental over long periods of time (Potts, 1998). Following the variability selection hypothesis, variable climate has influenced the encephalisation, bipedalism, tool-making behaviours and complex social structures that emerge as a result of hominin evolution (Zachos, 2001; Begun, 2002; Harrison, 2010; Kelly, 2002; McNulty, 2010).

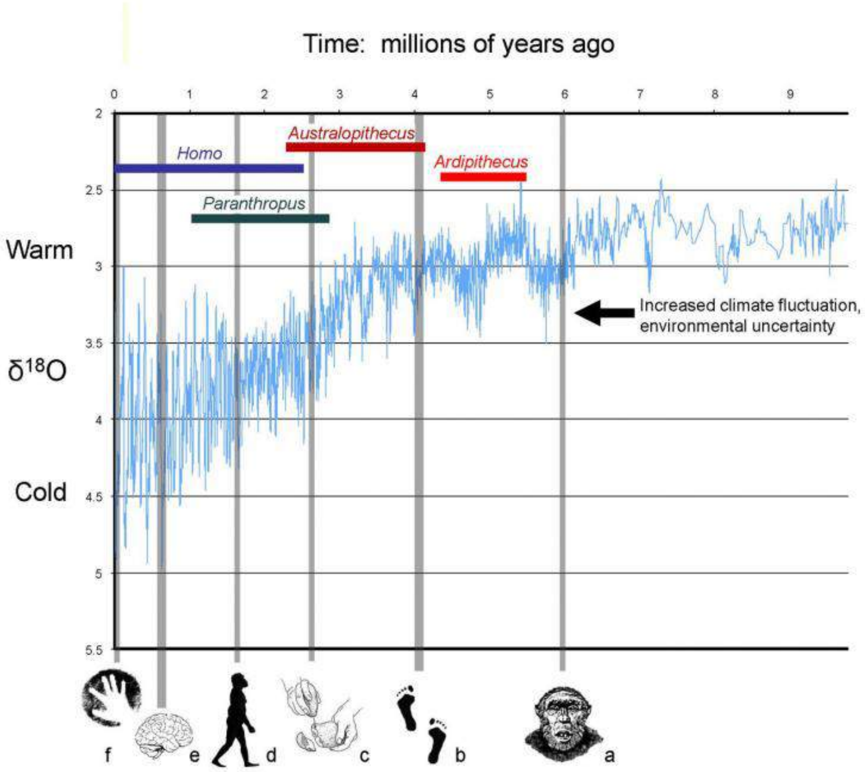


Figure 2.12: Ten-million-year record of oxygen isotope levels indicating increased climate fluctuation and environmental uncertainty during earliest hominin evolution during the late Miocene and early Pliocene. The $\delta^{18}O$ measurement reports a ratio of heavier ^{18}O and lighter ^{16}O isotopes, the latter of which is more easily evaporated from the ocean and sequestered into land-based glacial ice. The graph shows ocean temperature and glacial ice periods to be varied and unstable during a 6-million-year period that coincides with human evolutionary events such as: (a) approximated hominin origins, (b) habitual bipedality, (c) evidence of the first stone-tool production, (d) onset of long-endurance mobility, (e) rapid encephalisation, and (f) cultural diversity and behaviour evidenced by symbolic expression and innovation (Zachos, 2001; SMNH, 2020).

2.6.1.3 Floral data and pollen analysis

Plant remains in the form of macrofossils (e.g. seeds, leaves, and wood), pollen and phytoliths are fossils that can be taxonomically identified and assist in the reconstruction of the surround habitat (Reed, 2013:214; Andrews and Bamford, 2008). Macrofossils reveal local vegetation as this form of plant-life fossilise where they fall. Leaf sizes and drip tips, for example, have even been used to estimate rainfall levels in the tropics of Africa (Jacobs, 1999). Pollen describes representational vegetation over a larger geographical area due to its ability to be widely dispersed. Bonnefille *et al.,* (2004) utilised palynological study to understand the vegetation changes experience in the region inhabited by *Australopithecus afarensis* in Ethiopia. Lastly, phytoliths are microscopic bodies that are plant-part and taxon-specific depending on their size and shape (Reed, 2013). Phytoliths have been discovered in the hearths of early hominins providing evidence as to plant materials as fuel sources (Albert *et al.,* 2000), and are also recovered from tooth calculus providing multiproxy evidence of food-type consumption (Reinhard and Danielson, 2005).

Scott *et al.* (2019) utilised floral evidence to reconstruct the environment pertaining to a rare hominin bearing spring mound associated with Middle Stone Age tools and fauna in the central Free State grassland, South Africa. From historical palynological research of the spring mound, Scott *et al*. reviewed the pollen sequence evidence considering taphonomy and site geomorphology. The pollen stratigraphy associated with various parts of the site suggested that the lower levels which contained the Florisbad hominin (259Ka) and Middle Pleistocene fauna, experienced moist and grassy conditions. Overlying Middle Stone Age layers were correlated to the Last Interglacial period (124-

119Ka) and pollen evidence of fynbos shrubs in these layers support prevailing cool conditions throughout this period.

2.6.1.4 Taphonomy and fossil data

Temporal variation in species abundance and diversity can be attributed to climate-driven evolutionary change (Reed, 2013:207), and contemporary faunal data can help to elucidate local environmental changes through time (Bobe and Eck, 2001; Reed, 2013; Behrensmeyer *et al.,* 1997). Vrba's global aridification hypothesis, thought to have caused massive species turnover around 2.6 Ma in Africa, has been used as the prototype to test fossil data as an indicator of ecology (Vrba, 1988; Vrba *et al.,* 1995). Eronen *et al*. (2010), for example, discovered a correlation between tooth crown height in groups of extant mammals and annual precipitation levels. This pattern can be applied to animals within hominin localities which exhibit turnover to better understand if species change is similarly equated with environmental changes as signified by tooth crown height (Reed, 2013:207).

Paleoclimate models developed from sources other than fossil data can be compared with faunal patterns to test climate-driven species hypotheses. For example, Herbert *et al's* (2010) investigation on sea surface temperatures showed a strong CO^2 feedback around 2.7 Ma, which connected northern hemisphere icesheets with global ocean temperatures. This fundamental change in overall global climate may be correlated with faunal turnover in the tropics of Africa around 2.6 Ma, strengthening Vrba's hypothesis (1988, Vrba *et al.,* 1995; Reed, 2013).

McGee and Martin (1995:325) argue that taphonomy links fossil assemblages to their contemporary ecosystems and it can also shed light on missing information relating to that species and help towards behavioural reconstruction, e.g. predatorial behaviours (Reed, 2013:208). Researchers, such as Behensmeyer and Hill (1980) and Andrew (2007), emphasize the importance of determining taphonomic histories before attempting palaeoecological reconstruction, i.e. understanding the accumulation of an assemblage before other palaeoecological analysis (Reed, 2013). Soligo and Andrews (2005) further this by noting the usefulness of selecting an extant comparative sample representative of the fossil assemblage to help in the further understanding of habitat reconstruction (Reed, 2013: 208).

Behrensmeyer and Reed's (2013) comprehensive reconstruction of Australopithecine habitats (based on palaeoecological, taphonomic and faunal evidence) aimed to identify species-specific habitat preference and whether more than one of these species shared an ecosystem. The team concluded that the *Australopithecus* genus was possibly eurytopic based on the range of habitat types in which the fossil assemblages were discovered. However, they could only confidently confirm this through *Australopithecus afarensis* and *Australopithecus anamensis* fossil material, which spanned enough time range to support their eurytopic interpretation. Microwear analyses supported dietary differences between species although carbon isotope data were found to be similar (Behrensmeyer and Reed, 2013).

Faunal analysis is used for habitat reconstruction, understanding species interaction and recreating hominin subsistence patterns (Reed, 2013:209). An example of comparative fossil record and paleoclimate evidence towards environmentally induced adaptation is the advent of increased encephalisation, particularly within the last 800,000 years. This adaptation is especially pertinent to the present study as increased brain size directly affects integrated aspects of the skull, e.g. globular cranial vault, flexed cranial base and retracted craniofacial skeleton (Lesciotto and Richtsmeier (2019). **Figure 2.13** shows an extended length of time whereby the most significant climate fluctuation of the last 3 Ma is shown to have fluctuated with intense cooling and warming periods. The fossil record also shows the morphological evolution of the skull within the same period of time, shown here as a marked increase in braincase volume measurements (Pontzer, 2012; Su, 2013).

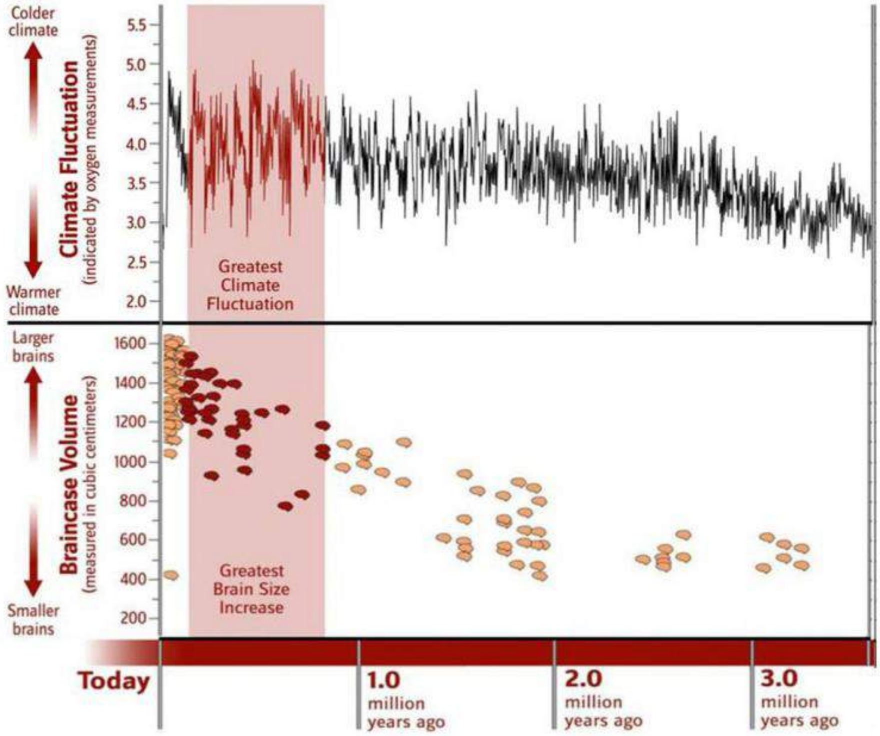


Figure 2.13: Climate fluctuation linked to increased encephalisation in hominin evolution (SMNH, 2020). Brain enlargement increases gradually during the first four million years after the approximated origins of hominin species. The greatest increase in brain size relative to body size is seen within the last 800,000

years coinciding with a period of great climate fluctuation evidenced through deep sea core oxygen measurements (Shultz, Nelson and Dunbar, 2012).

Hominin remains are rare in the fossil record likely due to small population sizes and preservation constraints. The few discovered Miocene-Pleistocene fossils, faunal and palaeoecological remains indicate that the ancestral lineage of humankind is concentrated in Africa. Three geological megastructures, in particular, have yielded the majority of all fossil remains relating to early hominins: the Lake Chad basin, the East African Rift Valley and the cave deposits in South Africa (Kullmer, 2007: 357). To gain better insight into the ecomorphology of late Miocene and early Pliocene hominids, knowledge of the contemporary geological framework is essential. This is demonstrated through the palaeoecological record and associated fossil assemblages.

2.6.2 The Environments of Late Miocene and early Pliocene Hominids

The Late Miocene epoch, between 11.6-5Ma, was a particularly crucial period in hominid evolution. During this time, pervading laurophyllous evergreen woodlands were replaced by more seasonal and drier ecosystems, including savannahs and steppes (Yao *et al.,* 2011; Andrews, 2020). Researchers such as Lovejoy (1980) and Coppens (1983) argue that this transition played a significant role in the morphological evolution hominids by influencing new locomotive behaviours, e.g. bipedalism.

Agusti (2007) states that this transition was by no means a sudden one but rather was punctuated by periods of environmental and faunal events, e.g. the uplift of the Himalayas and Tibetan Plateau (Yang, 2012), and the closure of the Atlantic-Indian seaway in the

Mediterranean. These paleogeographic events, Agusti (2007) argues, affected the continent-ocean symbiotic relationship, leading to altered circulation patterns, the formation of the first Arctic glacials and dramatically enhanced monsoonal dynamics (Zhisheng *et al.,* 2001).

During the late Miocene, hominoids, including Hylobatidae and hominins, or great apes (Grove, 2001), had reached a significant level of diversity, and the earliest fossils proposed as possible human ancestors are thought to have originated in the human lineage during this time (Hardt *et al.,* 2007). Early fossil hominid remains have been discovered in a variety of habitats, particularly within regions known to have experienced climatic change during the late Miocene and early Pliocene epochs (Pontzer, 2012). Carbon isotope distribution associated with fossil hominid fragments in Africa show an abundance of C_3 plants, which indicate an environment of closed or wooded forest (Kingston *et al.,* 2002; Andrews, 2020).

Late Miocene apes are also found in eastern Europe and western Asia whose skull morphology was similar to that of the orangutan (Andrews, 2020; Begun, 2007), i.e. rounded cranial vaults, gracile brow ridges, deep jaws and enlarged, thickly enamelled molar teeth (Alpagut *et al.,* 1996; Begun and Gulec, 1998). Postcranially, these late Miocene apes are distinct from extant great apes and monkeys. For example, *Ankarapithecus* and *Sivapithecus* display evidence of terrestrial adaptation and pronograde and quadrupedal adaptations respectively (Kappelman *et al.,* 2003; Rose, 1994; Andrews, 2020).

Although their taxonomic attribution is uncertain, a second group of European fossil apes share morphological similarities with the skulls of African apes but have distinct postcranial skeletons, e.g. *Ouranopithecus* and *Graecopithecus,* are quadrupedal, pronograde and mainly terrestrial (Andrews, 2020). These apes have robust skulls, low-crowned canines, enlarged molar teeth and relatively slender jaws, and evidence suggests that their contemporary environment was deciduous woodland (de Bonis *et al.,* 1992; de Bonas and Koufos, 2014).

It has been suggested by researchers such as Andrews (1992) and Begun (1992, 2009) that a single late Miocene African fossil ape evolved in Europe (e.g. *Ouranopithecus* or *Graecopithecus*) and migrated back to Africa. This is understood on the basis of assumed shared derived characteristics that link some European fossil apes with the African ape and human clades (Andrews, 2020). Fuss *et al.* (2017) suggest that there are characteristics which link the European *Graecopithecus* with hominins; however, whether these characters are homologues or homoplasies, is unclear. Andrews (2020:135) makes it clear that the only certainty we can glean from the fossil record at this time, is that characteristics were evolving in a mosaic fashion before the divergence of the great ape species (Begun *et al.,* 2012; Begun, 2013).

2.6.2.1 Early hominin species in the late Miocene and early Pliocene

There are four late Miocene species found in Africa which are attributed to the hominin ancestral line and appear to offer insight into the last common ancestor of humans and chimpanzees (Andrews, 2020). These fossils belong to *Ardipithecus ramidus* (Ethiopia, approx. 5.2-4.4 Ma) (White *et al.,* 1994), *Ardipithecus kadabba* (Middle Awash region, Ethiopia, approx..5-6 Ma) (Andrews, 2020; Haile Selassie, 2004); *Sahelanthropus tchadensis* (Chad, approx. 6-7 Ma) (Brunet *et al.,* 2002) and *Orrorin tugenensis* (Kenya, approx. 6 Ma) (Senut *et al.,* 2001; Hardt *et al.,* 2007).

Sahelanthropus tchadensis remains are associated with a highly diverse mosaic of vegetation within a relatively small geographic area. The distorted cranial fossil associated with *Sahelanthropus* is dated to approximately 7 Ma and was recovered amongst faunal remains indicative of a wooded grassland environment near a lake (Brunet *et al*., 2002; Vignaud *et al.,* 2002). Associated fossil content includes fish remains, semi-aquatic mammals, like Hippos, and crocodiles, providing evidence of a rich water source during the time when *S. tchadensis* roamed the nearby gallery forest (Vignaud *et al.,* 2002; Kulmer, 2002).

This cranial fossils of *S*. *tchadensis* may indicate a gradual and slow evolutionary change to more prominent teeth, thicker enamel and a reduction in canine size along a 5 million yearlong lineage, i.e. *Sahelanthropus*, *Orrorin*, *Ardipithecus* and *Paranthropus*. However, recent analysis of the postcranial remains of *Sahelanthropus tchadensis* indicate that this late Miocene hominid is not a member of the hominin tribe; rather a related but non-direct ancestor to modern humans (Machiarelli *et al.,* 2020). A partial femur recovered next to the *S*. *tchadensis* cranium suggests that this species was not a habitual biped as previously suggested by Brunet *et al.* (2002). Machiarelli *et al* (2020) argue that, if we are to accept *S*. *tchadensis* as a stem hominin, then we must also accept terrestrial bipedalism as no longer a defining requirement of the hominin clade.

Contemporary fossil material belonging to the hominin species, *Orrorin tugenensis* and *Ardipithecus ramidus,* were discovered in areas associated with wooded forests (Andrews, 2020). Both species are known to represent the hallmark of hominin evolution, i.e. the adoption of habitual bipedal terrestrialism through morphological adaptation associated with the proximal femur and pelvic and foot morphology, respectively (Almecija *et al.,* 2013). Postcranial analysis of *Orrorin tugenesis* remains, dated approximately 6 Ma in Kenya, show this species to have been a habitual biped with arboreal capabilities (Senut *et al.,* 2001). Pickford *et al*. (2002) found several apomorphic features shared between *O*. *tugenesis*, australopithecines and *Homo* but none associated with *Pan* or *Gorilla* (Hardt *et al*., 2007). Reconstruction of *Orrorin's* habitat from faunal remains (colobines, carnivores and ungulates) and geological analysis, indicate a mosaic of open forest and woodland formed around a lake (Pickford and Senut, 2001). Sussman and Hart (2007) describe *Orrorin* as a typical 'edge species' living on the partition between habitats (Hardt *et al.,* 2007).

The late Miocene *O. tugenensis* BAR 1002'0'0 fossils are particularly interesting as Richmond and Jungers (2008) statistical analyses suggest an early evolution of hip biomechanics resembling later australopiths morphology, i.e. an anteroposteriorly compressed neck, wide proximal shaft and a small head. Congruent with *Orrorin tugenesis'* novel locomotive behaviour (Senut *et al.,* 2004) is the advent of widespread expansion of grassy woodland to a grass-dominated savannah biome (Jacobs, 2004; Feakins *et al.,* 2013). Late Miocene/early Pliocene aridification supported faunal and vegetative changes from a C_3 dominated to a mixed C_3/C_4 or solely C_4 dominated environment (Uno *et al.*, 2011). The convergence of ecomorphological variables suggests highly variable and dry conditions to have altered biotic communities in east Africa and ultimately driving the evolution of contemporary hominins (Wichura, 2015).

Ardipithecus ramidus lived between 5.2-4.4 Ma in the Middle Awash region of Ethiopia (Haile-Selassie, 2001; White *et al.,* 1994; Hardt *et al.,* 2007). Haile-Selassie (2001:178) argues that *Ardipithecus* postdates the divergence between lineages that gave rise to extant chimpanzees and humans. The *Ardipithecus* fossils are associated with a wet and wooded environment that WoldeGabriel *et al.* (2001) suggest are similar to the habitats found in the case of *Orrorin*, i.e. woodland and forest habitats with small open grasslands around lake margins (Hardt *et al.,* 2007). *Ardipithecus* skeletal characteristics have been described as the 'smoking guns' of habitat choice (White *et al.,* 2015) as the craniofacial structure, dentition, masticatory apparatus and locomotor adaptations, are considered direct lines of evidence for their wooded habitat. This species was adapted to chew softer foods and much better adapted to arborealism that any other hominin (Moore, 2009).

Palaeoecological and faunal evidence indicate that the late Miocene and early Pliocene African climates were marked by a shift from tropical, closed habitats to more arid and wooded, open land (Fortelius *et al.,* 2006) (see **Table 2.1**). This period also sees the adventof *Ardipithecus ramidus*, *Orrorin tugenensis* and *Sahelanthropus tchadensis* specie s showing increasing levels of habitual bipedalism and terrestrialism within an open, vegetated environment, canvassed by a mix of C_3 and C_4 plant life (Wichura, 2015). Although postcranial fossils have been useful in determining the locomotive behaviour of early hominins in relation to their habitat (e.g. Almecija *et al.,* 2013), hominin skull fossils are rarely found past 3 Ma, as can be seen in **Figure 2.13** (Haile-Selassie *et al.,* 2016)**.** Due to this sparsity in the late Miocene/early Pliocene record, a comparative ecomorphological approach is necessary in order to draw conclusions regarding hominin craniofacial evolution during this time.

Family taxon	**Fossil ape genera**	**Environmental evidence**	**Environmental reconstruction**
Hominidae	*Dryopithecus* *Anoiapithecus* *Pierolapithecus* *Rudapithecus* *Hispanopithecus*	Fossil mammals and plants, sediment and soils	Deciduous woodland and lauroid evergreen wood
Undetermined	*Graecopithecus* *Ouranopithecus* *Oreopithecus*	Palynology, fossil mammals, sediments, isotopes	Open deciduous woodland lauroid evergreen wood
Pongidae	*Sivapithecus* *Ankarapithecus* *Indopithecus* *Gigantopithecus* *Lufengpithecus*	Isotopes, sediments, fossil plants and mammals	Open deciduous woodland, subtropical forest
Hominini	*Sahelanthropus* *Orrorin* *Ardipithecus* *Australopithecus*	Sediments, soils, isotopes, fossil mammals and plants	Deciduous woodland, open woodland savannah

Table 2.1: Summary of late Miocene and early Pliocene hominids with genera, environmental evidence and reconstruction showing a trend from deciduous woodland and lauroid evergreen wood to open deciduous woodland and savannah. Adapted from Andrews (2020:128).

2.7 Ecomorphology and Hominid Phylogenetic Systematics

The aim of ecomorphological study is to identify morphological variation related to habitat (Barr, 2018) with the goal to elucidate adaptive relationships between skeletal traits and associated ecological function (Soligo and Smaers, 2016). As the study of early hominin skulls is constrained by the absence of data and the sparse fossil record, it is necessary to adopt a comparative approach to infer extant hominid ecomorphology, leading to hypotheses regarding hominin craniomandibular evolution and the phylogenetic relationships between early hominin species.

As discussed in **Section 2.3.2**, the most distinguishing characteristics of the primate skull is a decrease in cranial base angle, reduced relative snout length, the presence of a postorbital bar, an increase in cranial base flexion, orbital frontation and an increased relative brain size (Taylor, 2018; Cartmill, 2012; Sussman *et al.,* 2013; Fleagle, 2013). These traits are integral to understanding primate origins and have become the focus of prominent hypotheses emphasising the importance of diet (Cartmill, 1992; Sussman *et al.,* 2013) and locomotive behaviour (Crompton, 1995; Dagosto, 2007; Soligo and Smaers, 2016).

Soligo and Smaers (2016) formulated a paleo-ecomorphological framework that details a hierarchical and multi-levelled approach to environmental and evolutionary study (**Figure 2.14**). With the environment as an overarching variable, the framework is summarised as: 1) a description of morphology; 2) the functional capacity of morphology; 3) an interpretation of potential consequences of morphology on organisms' performance; 4) observation of organisms' actual performance, and 5) determination of fitness consequences of performance. This procedure questions how morphological adaptation reflects the environment (i.e. the functional and biological implications facilitated by that trait) and the evolutionary feedback and effect of these traits on the organism's environment (Odling-Smee *et al.,* 2003). Through this ecomorphological framework, Soligo and Smaers (2016) highlight the importance of considering variation and behavioural significance of anatomical traits.

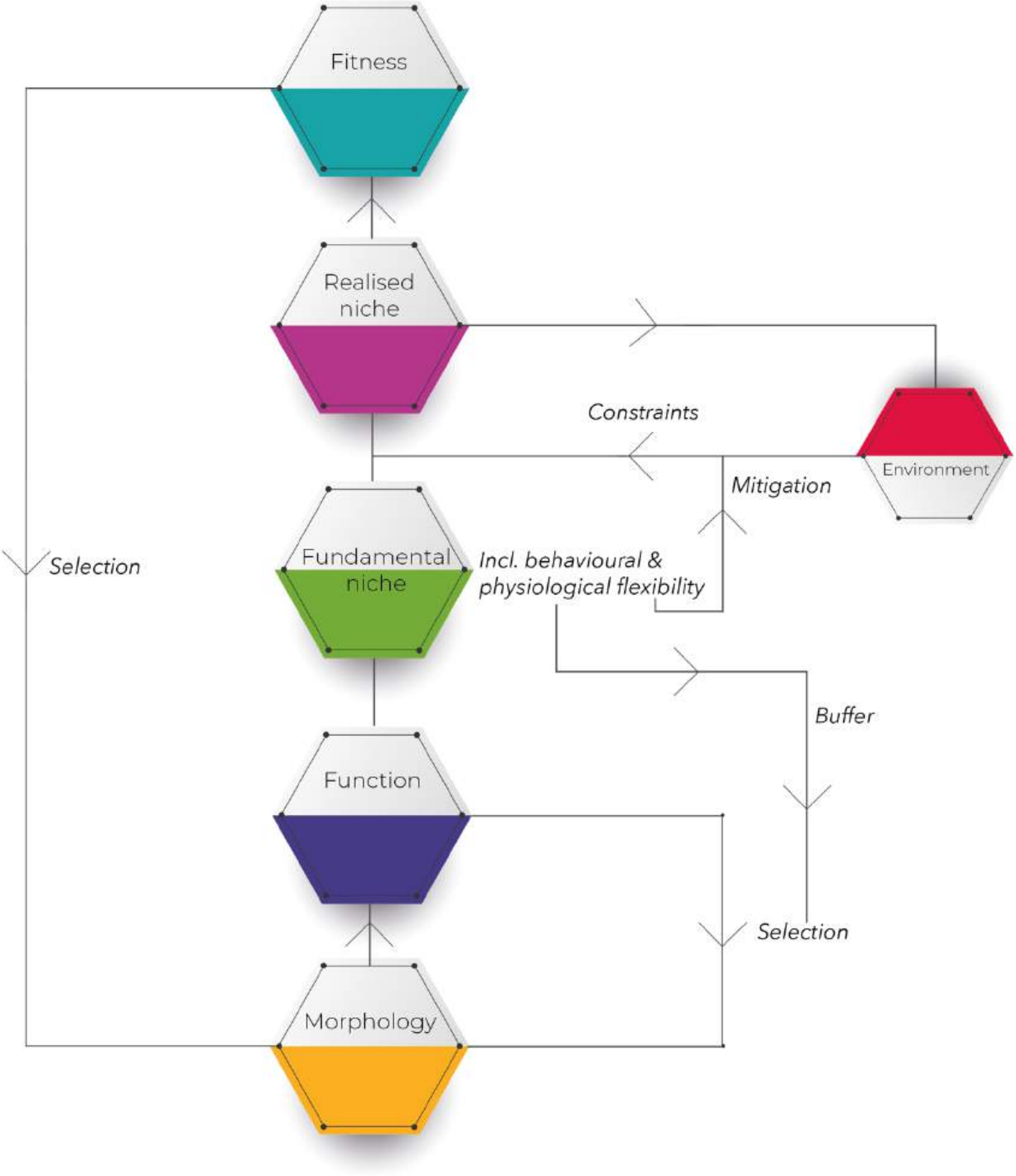


Figure 2.14: Ecomorphological framework adapted from Soligo and Smaers (2016) and Reilly and Wainwright (1994). The ecomorphological framework is summarised in five hierarchical levels: 1) description of morphology; 2) functional capacity of morphology; 3) interpretation of potential consequences on organisms' performance; 4) observation of organisms' actual performance; and 5) determination of fitness consequences of performance.

Elton *et al.* (2016) utilised a similar ecomorphological framework to explore the morphological generality in Old World monkey postcranium specimen. Using discriminant function analysis, this research investigated to what extent ancestral cercopithecid 'bauplan' is modified to incorporate terrestrialism and navigate distinct arboreal substrates. Results showed considerable similarity in specimen emphasising the importance of generality in the postcranium sample and considerable modifications for terrestriality. Elton *et al.* highlight the importance of including phylogenetic data as, like allometry (form size), it can contain significant ecomorphological information.

Westneat (1995) similarly states that ecomorphological studies should frame their analysis with the context of phylogenetic hierarchies rather than considering each taxon as an independent unit. Morphological and ecological data analysed in the framework of phylogeny can shed light on environmentally induced characteristics congruent with the cladistics hierarchy. This argument is echoed by Scott and Barr (2014), whose paleohabitat reconstruction study on fossil bovids utilised multivariate statistics to determine the level of 'phylogenetic risk' attached to ecomorphological study. They suggest that the most advantageous methodology in the ecomorphological study is based on functionally relevant observation and consideration of phylogeny used to appropriately bracket probable habitat preferences.

The study of hominid ecomorphology should be conducted as an interdisciplinary study, combining phylogenetic, functional and morphological data with careful consideration of behavioural and evolutionary feedback scenarios. Westneat (1995), Scott and Barr (2014), and Elton *et al.* (2016) stress the importance of phylogenetic reflection in a study designed to elucidate patterns of evolution in morphology and habitat. In utilising a comparative approach using extant ape species of known phylogenetic relation, this thesis will be able to comment on the phylogeny of early hominin species in relation to craniomandibular morphology and contemporary known habitats.

2.7.1 Hominin locomotive behaviour

Postural and locomotive behaviour signifies the interaction between an organism and its habitat. Such behaviour dictates the way an animal escapes their predators, competes for mates and acquires food in seasonal environments (Saunders, 2016). Primates are particularly unique amongst mammals as they exhibit a wide range of locomotive and non-locomotive strategies allowing for exploitation of arboreal and terrestrial environments (Schmidt, 2011).

Reconstruction of motion capacity in fossil hominins shows great flexibility and adaptability to an ever-changing environment, supported by a 'relatively unspecialised musculoskeletal system' (Schmidt, 2011:23). In order to compare positional behaviour, i.e. posture and locomotion, in early hominins, morphological form and function must be considered within an ecological context. Also known as 'ecomorphology', this approach defines and quantifies the mechanisms that link behaviour, environment and morphology to provide better insight into the evolution of positional behaviours (Saunders *et al.,* 2017).

Hominid locomotive behaviours are linked to selective pressures in the environment. The selective advantages which underpin this evolution has been a greatly contested topic of palaeoanthropological debate, e.g. hominin bipedality and arborealism in extant large-bodied apes. However, Saunders *et al*. (2017:2) argues that positional capabilities in primates are not solely facilitated through the evolution of particular positional behaviours, but also through behavioural flexibility, which allows the animal to quickly and effectively adapt its behaviour in response to the environmental pressure.

Inferring locomotive behaviour from cranial specimens has been the focus of ongoing debate in palaeoanthropological study. The basicranium is a significant feature of the skull as it is morphological designed to serve varied functions between the head and the post-cranium. It is clear from the fossil record that the hominin basicranium underwent significant reorganisation most drastically in its orientation and relationship to the facial skeleton (Villamil, 2017; Kimbel *et al*., 2014).

The foramen magnum, in particular, is argued to indicate positional behaviours such as posture and locomotion. In bipeds, for example, the foramen magnum is suggested to be more anteriorly located and inferiorly orientated compared to quadrupeds (Russo and Kirk, 2013, 2017; Villamil, 2017). Anteriorly positioned foramen magna has been linked by Dean (1985) and Luboga and Wood (1990) to differences in neck musculature and balance. This positioning is argued to be mechanically advantageous to orthograde taxa (Schultz, 1955) as anteriorly placed foramen magnum shifts the centre of gravity in the skull and reducing the amount of nuchal musculature needed to keep the head in an upright position (Şenyürek, 1938; Villamil, 2017).

Investigations of foramen magnum positioning in *Sahelanthropus tchadensis* (Brunet *et al.,* 2002; Zollikofer *et al.,* 2005; Guy *et al.,* 2005) and *Ardipithecus ramidus* (White *et al.,* 1994; Kimbel *et al.,* 2014) show that an anteriorly positioned foramen magnum conformation was acquired at least by the late Miocene period (Neuax *et al.,*2017).

When the postcranial elements of fossil remains are missing, the basicranium and foramen magnum specifically are used to assess the locomotive behaviours of the extinct species in question. Such was the case for the 7 million-year-old *Sahelanthropus tchadensis* fossil discovered in Chad (TM 266-01-60-1) (Brunet *et al.,* 2002). Three mandibular fragments accompanied a nearly complete cranium which was highly deformed and fractured *in situ*. A 3D digitised reconstruction of the skull, completed by Zollikofer *et al.* (2005), helped to correct these distortions and allowed for investigation into the locomotive behaviour of this species.

Analysis of the reconstructed skull suggested that *S. tchadensis* is part of the hominin family and further investigation of the basicranium indicated that this species may have been an upright biped, though this is contested by Macchiarelli *et al's* (2020) postcranial analysis. The cranial reconstruction displays widely recognised hominin synapomorphies such as a long, flat and more horizontally oriented nuchal plan in comparison to African apes; a shortened basioccipital and a more anteriorly positioned foramen magnum (Guy, 2005). These features suggest that bipedalism was a present characteristic in the earliest known hominins. Zollikofer *et al.* (2005:755) propose that bipedalism most likely developed subsequent to the divergence of the human and chimpanzee lineages.

As previously discussed, *Sahelanthropus tchadensis* remains are associated with faunal remains indicative of a woodland grassland environment. The presence of a large lake is evidenced by contemporary fossil assemblages, which included fish and semi-aquatic mammal remains (Vignaud *et al.,* 2002; Kulmer, 2002; Brunet *et al.,* 2002). Advocates of the 'savannah hypothesis' suggest habitual bipedalism to have been directly adapted in response to a more open environment (Ko, 2015). However, *S. tchadensis* was by no means an obligate biped and would have practised many postural behaviours in the mosaic environment in which it lived (Harcourt-Smith, 2010). *S. tchadensis'* primary form of locomotion and whether its locomotive characteristics can be gleaned from basicranial morphology is a focus of debate (Harcourt-Smith and Aiello, 2004; Wayman, 2012; Macchiarelli *et al.,* 2020).

Kimbel *et al.* (2014) investigated the locomotive behaviours of the Pliocene hominin *Ardipithecus ramidus* based on basicranial morphology to better understand this species' phylogenetic position with reference to *Australopithecus*, humans and extant African apes. ARA-VP 1/500 is the best preserved basicranial specimen of *A. ramidus* and includes two temporo-occipital portions that span the midline of the skull. From this specimen, Kimbel *et al*. reconstructed the distances between bilateral landmarks, including lateral margins of the tympanic elements and the carotid canal. As this particular specimen to insufficiently complete to collect direct estimates of the cranial base length, the team used breadth and length estimates that were size-standardised.

Based on the basicranial estimates, the ARA-VP 1/500 specimen is reported to have an anteroposteriorly short cranial base and a broad central basicranium, consequently abbreviating the tympanic element of the skull. This patterning is fundamentally similar to that of *Australopithecus* and 'derived in the direction of modern humans' (Kimbel *et al.,* 2014:952). Combined with postcranial evidence, *Ardipithecus ramidus'* basicranial morphology represents an evolutionary precursor to hominin bipedalism, i.e. an ape-like terrestrial quadrupedalism and climbing behaviours suited to a wet wooded and forested open habitat (White *et al.,* 1994, 2015; Prang, 2019).

Reconstructions of locomotive function in fossil hominins can only be achieved through a detailed understanding of the relationships between morphology, behaviour and the environment in extant apes (Saunders, 2016). Though geometric morphometric analysis of the ape cranium, this thesis will attempt to glean the morphological variance patterning in relation to contemporary primate habitats. This will improve current understanding as to how various levels of arborealism and terrestrialism are related to the shape of the cranium and if this is directly influenced by ecology, e.g. foramen magnum positioning reflecting habitual bipedalism, rather than arborealism, in a more open habitat.

2.7.2 Hominin dietary specialisation

The evolutionary history of hominin dietary specialisation has been punctuated by major anatomical adaptation (e.g. brain size increase and differing dental morphologies) and cultural innovation (e.g. agriculture and cooking) (Luca, 2010). Due to fossil sparsity, it is difficult to reconstruct the diets of late Miocene and early Pliocene hominins. Therefore, multiproxy data is used to provide insight into the levels of frugivory and folivory that characterise these early hominid species.

Section 2.6.2 of this thesis detailed the gradual ecological shift in late Miocene Africa from evergreen woodlands to more seasonal and mosaic open habitats. This change in climate would have forced alternations in diet composition as a response to food availability. This would have created strong selective pressures on early hominin morphology, particularly to the cranium and mandible (Luca *et al.,* 2010), which is evident in the fossil record as a suite of diet-adapted derived craniodental traits (Marcé-Nogué *et al.*, 2020).

2.7.2.1 Nongenetic and adaptive methods of investigation

There are two distinct lines of direct evidence when investigating dietary specialisations in fossil hominins: nongenetic and adaptive. Nongenetic evidence includes tooth wear, chemistry and evidence of bone remodelling as a result of masticatory strain. Adaptive evidence includes size, shape and structure of the teeth, the mandible and parts of the cranium associated with chewing (Ungar and Sponheimer, 2007). A multitude of multi-proxy techniques have been used to investigate the relationships between ingesta and morphology in early hominins, including biomechanics, comparative morphology, stable isotope analysis and allometry (Marcé-Nogué *et al.*, 2020). Geometric morphometric analysis in particular has been used extensively to investigate the functional craniomandibular morphology in extant primates and hominins (e.g. Smith *et al.*, 2015: Fitton *et al.,* 2012; Toro-Ibacache, 2016).

Mandible shape evolution is one way in which we can understand the role of ecology and diet specialisation on morpho-function (Alvarez *et al.,* 2021). Hominins, including 'australopiths' and members of the genus *Homo,* possess deep and short mandibles with relatively small canines and incisors compared to early hominids. These characteristics are through to have evolved in early clade members in response to variable environmental conditions and increased consumption of tough food items (Raia *et al*., 2018).

Dental allometry investigates tooth size and has played an important role in the reconstruction of early hominid diets. *Australopiths,* for example, display a distinctive trend towards megadontia, or large cheek teeth, in comparison to members of the *Homo* genus (Strait, 2007). Traditionally, tooth size has been directly related to use, e.g. large cheek teeth suggest the extensive mastication of low-quality foods ingested in large amounts (Hylander, 1975). However, the relationship between tooth size and diet is more complicated than mere functionality, as dental allometry also reflects phylogeny (Ungar and Sponheimer, 2007:166; Ungar, 1996).

Ungar's (2012) review of early *Homo* diet reconstruction based on fossil evidence showed tooth size, shape and structure to be particularly important. Differences in dental topographies were identified between *Homo* species and earlier australopiths as well as between *H. habilis* and *H. erectus*. Ungar (2012:318) suggests varying microwear patterns and changes in incisor shape and molar occlusal relief as probable evidence towards a diet shift, which included a 'broader subsistence base with a wider range of fracture properties.' Ungar suggests that these lines of evidence are consistent with increased meat-eating and food preparation tool-use (2012:327) at a time of increased climate variability (Potts, 2012:300).

Early hominins also differ from one another in craniomandibular morphology and masticatory muscle attachment sites. Biomechanical variation is thought to reflect the magnitude and direction of force needed for chewing (Strait *et al.,* 2009) and may also provide indirect evidence to the type of diet a particular specimen habitually consumed (Daegling and Grine, 1991; Ungar and Sponheimer, 2007).

The sagittal crest is one such site of attachment used to anchor the large temporalis muscle. This bone structure projects superiorly along the cranium midline and its presence usually indicates strong chewing abilities. The sagittal crest not only enlarges the area of temporalis attachment but also improves the power of the premolar teeth. This is caused by an increase in relative length of the muscle insertion axis in comparison to the load. The sagittal crest also increases the height of the neurocranium and enhances its resistance to the vertical forces of mastication (Davis 1964; Ungar and Sponheimer, 2007). The sagittal crest is also associated with sexual dimporhism particularly in gorilla and orangutan species and may play a role in social signalling (Balolia *et al.,* 2017).

Paranthropus robustus is an example of robust australopithecine with a pronounced sagittal crest formation. Thought as a specialist hard-object feeder, the *P. robustus* diet consisted of foods that required peak masticatory loads. Analysis of *Paranthropus* morphology shows low-cusped and large postcanine dentition, powerful muscles for mastication and thick mandibular corpora. Indirect evidence also supported this dietary inference as dental microwear on the molars of *P. robustus* fossils were consistent with ingestion of hard food items (Cerling *et al.,* 2011). Vrba (1974, 2013) suggests that robust australopithecines were more specialised to live in open and arid habitats than more generalised *Homo* species due to their specialist feeding characteristics. Wood and Strait

(2014) argue that the adaptive masticatory characters of *Paranthropus* actually broaden the range of consumable food items, rather than limiting them. Therefore *P. robustus* should be seen as an ecological generalist; able to thrive in a multitude of varying environments (Vrba, 2013).

Strait *et al.* (2009) tested the hypothesis that dietary adaptation had significant influence on the evolution of australopiths craniofacial morphology using comparative imaging and finite element analysis. The team found that *Australopithecus africanus* facial skeleton was particularly adept at withstanding heavy premolars loads. Strait *et al.* also concluded that australopiths craniofacial morphology was most likely influenced primarily by the ingestion and incisor preparation of large nuts and seeds, which are more mechanically protected by hard husks or shells.

The ecomorphological relationship between diet-related adaptation in *Australopithecus* is well-documented by Teaford and Ungar (2000). Their synthesis of cranial and dental morphological structure and mandibular biomechanics shows how the skull can inform researchers as to the dietary habits of hominids. Australopithecines represent a split between prehistoric apes and the earliest members of the *Homo* genus. From *Ardipithecus ramidus* to *Australopithecus africanus*, this taxon is generally viewed within a roughly linear sequence spanning 4.4-2.5 Ma and, therefore, offers the rare opportunity of fossil assemblages spanning nearly 2 million years in which to examine any changes in dietary adaptations.

Least-squares regression plots formulated by Teaford and Ungar (2000) show that relative incisor sizes for the gracile australopithecines are very similar to one another and fell close to the regression line like the extant gorilla species in the study. They conclud that australopithecines probably consumed less foods that required substantial incisal preparation such as fleshy foods with large, hard seeds or thick husks. The australopithecine hallmark molars are large and relatively flat compared to extant primates. Teaford and Ungar demonstrate trophic differences between robust and gracile australopiths based on variances in the amount of occlusal relief (data published by Grine, 1981).

Describing tooth structure capabilities helps to elucidate the types of foods that an early hominin could have consumed. Tough foods, for example, require shearing between the edges of sharp dental crests, and brittle foods are easily crushed between planar surfaces as they are easy to fracture but more challenging to penetrate. Frugivores will display rounder and flatter cusped teeth and omnivores will have reciprocally concave and high-crested dentition (Rodman *et al.,* 1984; Teaford and Ungar, 2000). Coined as Kay's 'shearing quotient' (Kay, 1985), the measurement of the relative shearing potential of a primate's molar teeth will suggest the level of frugivory or folivory demonstrated by that species.

Concerning Pliocene-Pleistocene hominins, *A. africanus* displays more occlusal relief than robust Paranthropus species suggesting trophic variability. Shearing quotient studies conducted by Teaford and Ungar (2000) affirm that australopithecines lacked the long shearing crests seen in many extant hominoids. The team conclude that changes in diet-related adaptation in *A. anamensis* to *A. africanus* suggests that harder, more abrasive foods became a necessary dietary requirement throughout the Pliocene. This time period, between 3.4 and 2.9 Ma, coincides with ecological data that suggests substantial environmental variability (Bonfille *et al.,* 2004).

Investigating the form and function relationship between diet, teeth and cranial morphology is vital to understanding the implications of ecological change and evolutionary adaptation. There are numerous techniques that can help in the understanding of diet-adapted morphology, however there are currently no comparative studies that investigate the ecomorphology of both the hominid cranium and the mandible using geometric morphometric techniques. This research will help to better our understanding of the patterns that exist in morphological form and habitat type. Intraspecific data will provide more insight into regional differences between species and their specific dietary preferences.

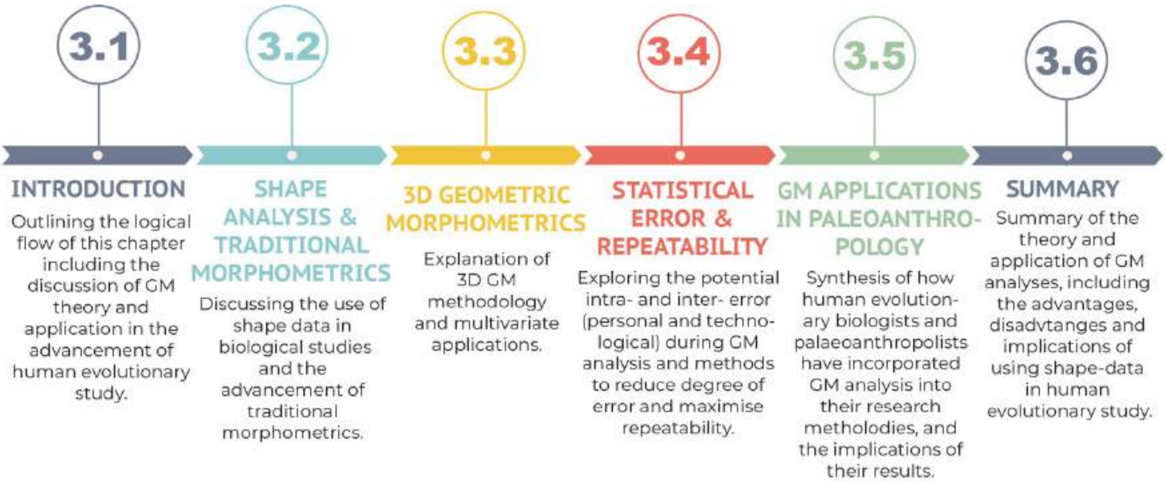
2.8 Summary

This chapter has shown the development of the ecomorphological hypothesis through turnover, habitat-specific adaptation, and climate variability. It has been shown how the primate skull's functionality has been evolved to better suit its environment through adapted cranial modules, which can be used as indicators of systematic diversity, i.e. separating species taxonomically and phylogenetically.

This chapter has also shown how palaeoecological methods are being used to better understand the nature of the global environment at the advent of hominid evolution. The environmental data that exists, comprising of terrestrial, marine and glacial components, shows an impressive view of the conditions our early ancestors lived within. The limitations of current paleoanthropological research exist primarily due to a lack of fossil material, particularly past 3 Ma (Luskin, 2012).

Chapter Three will discuss shape analysis and the theory and methodology behind biological 3D geometric morphometric applications to understand how this procedure has been used to advance palaeoanthropological study.

3 SHAPE ANALYSIS AND GEOMETRIC MORPHOMETRICS



Outlining the logical flow of this chapter including the discussion of GM theory and application in the advancement of human evolutionary study.

Discussing the use of shape data in biological studies and the advancement of traditional morphometrics.

Explanation of 3D GM methodology and multivariate applications.

Exploring the potential intra- and inter- error (personal and techno-logical) during GM analysis and methods to reduce degree of error and maximise repeatability.

Synthesis of how human evolution-ary biologists and palaeoanthropolists have incorporated GM analysis into their research metholodies, and the implications of their results.

Summary of the theory and application of GM analyses, including the advantages, disadvtanges and implications of using shape-data in human evolutionary study.

Figure 3.1: Chapter Three roadmap summarising the utility of each section in understanding the benefits of 3D geometric morphometric analysis in human evolutionary study.

3.1 Introduction

Chapter Three offers a review of a geometric morphometric technique in human evolutionary study and begins with a synthesis of the theory and methodology behind GM analyses, the significance of revealed variation patterning, and how it has been used in the advancement of paleoanthropological studies.

3.2 Shape Analysis and Traditional Morphometrics

Morphometrics is a way of addressing shape variation through quantitative analysis. Whereas visual, qualitative procedures can be used to create detailed, often heavily analogy-based descriptions of morphological shape, quantitative approaches allow for shape comparison, which does not rely on lengthy word accounts that can be interpreted differently depending on the researcher (Zelditch *et al.* 2012; Gelsvartes, 2016).

Before the advancement of statistical analysis methods, 'traditional morphology' provided shape data from measurements of length, width and depth. Biometricians of the 1960's used these traditional morphometric methods to apply multivariate statistics to draw comparative conclusions regarding shape data within and between groups of variables (Reyment 1991; Stark 2018). Jolicoeur (1963:499), for example, emphasises the use of traditional morphometrics for studies regarding allometry (the study of biological specimen growth) during the 1960's advent of the multivariate, quantitative approach (Stark, 2018:40).

The earliest physical anthropologists using traditional morphometric methods relied on the qualitative descriptions of linear measurements and anatomical features in assessing variation within hominin clades (Woods *et al.,* 2017; Baab *et al.,* 2012). However, through Howells and Oxnard's pioneering multivariate techniques (1969), a quantitative approach became the forefront of evolutionary research. They recognised that variations and covariations within complex shapes are often 'difficult to evaluate by eye' and that an accurate description of shape components offers clear advantages in quantifying anatomical geometry (Baab *et al*. 2012; Oxnard, 1983; Howells, 1969).

Zelditch *et al.* (2012) argue that traditional methods provide scarce and ambiguous information regarding form as morphometric data measurements of length, width and depth record relatively little shape data. As measurements of linear distance, this captured data makes it difficult to report size or shape differences in specific regions of the form. Additionally, this form of measurement may not sample the organism's homologous features, making comparative interpretation a difficult task (Zelditch *et al.,* 2012:3). In repeat tests, a researcher unable to locate the same points used for measuring will result in unusable data and creating graphical representations from these measurements is not possible (Gelsvartes, 2016).

Slice (2014) comments that traditional morphometric methods fail to capture and portray the spatial arrangement of the anatomical landmarks and instead results in data culminated from a 'limited set of distances, ratios or angles. Considering these limitations, the amount of shape variation collected through traditional morphological procedures was often vastly overestimated by the number of measurements initially taken (Zelditch *et al.*, 2012).

Strauss and Bookstein (1982; Bookstein *et al.,* 1985) improved upon this classical measurement scheme using a box truss system, shown in **Figure 3.2.** This measurement protocol samples more of the organism shape in comparison to earlier approaches, as there are more evenly spaced points of reference. The box truss method's main advantage is that the endpoints are biologically homologous anatomical loci, i.e. landmarks, meaning that they are visually identifiable and therefore easily replicable across the varying specimen in the same dataset (Zelditch *et al.,* 2012).

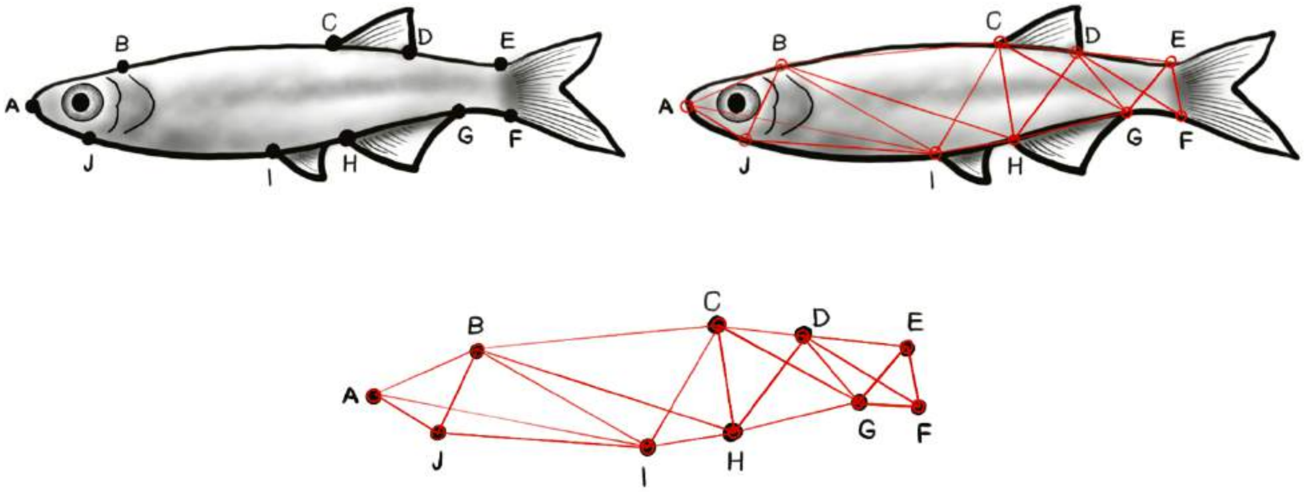


Figure 3.2: A box truss measurement scheme of the external body form of the river sardine, *Mesobola brevianalis,* adapted from Ridden, Bills and Villet (2016). This truss network, defined by ten landmarks (A-J), was used as the method of shape data capture in a morphometric analysis revaluating this species' phylogeny and taxonomy.

A prominent issue of both traditional and box truss methods is that they fail to capture information regarding shape differences and report a long list of numbers which lacks the visual communication needed for shape analysis reporting (Zelditch *et al.,* 2012:4). As morphometric relationships are not always contained in traditional morphometric data, a new approach was developed which captured the geometry of morphological structures and retained this data information for comparative analysis (Adams *et al.,* 2004). This conversion from traditional morphometry was coined 'geometric morphometrics' (Corti, 1993) and revolutionised the conceptual and statistical foundations of the field of biological shape analysis (Adams, Rohlf and Slice, 2013).

3.3 3D Geometric Morphometrics

Geometric morphometric analysis was created to improve upon the traditional methods that failed to capture geometric relationships in morphometry and visual representation of analysis (Baab et al., 2012; Woods et al., 2017). Adams, Rohlf and Slice (2013) define geometric morphometrics as' the statistical analysis of shape variation and its covariation with other variables.' After the effects of non-shape variables have been held mathematically constant, this progressive 'landmark-based geometric morphometry' uses tightly defined Cartesian coordinates of 3D homologous, anatomical points as the basis of statistical analysis (Bookstein, 1992; Adams, Rohlf and Slice, 2013).

Geometric morphometric research is conducted through a 'Procrustes paradigm' where the spatial configuration born from defined landmark placement is subjected to Generalised Procrustes Analyses, separating size from the shape, orientation and position (Rohlf, 1999; Adams, Rohlf and Slice, 2013; Zelditch, 2012). The resulting Procrustes shape coordinates are then used for further statistical testing (Mitteroecker and Gunz, 2009). The typical geometric morphometric process is outlined in **Figure 3.3,** the steps of which are explained in more detail in the following sections.

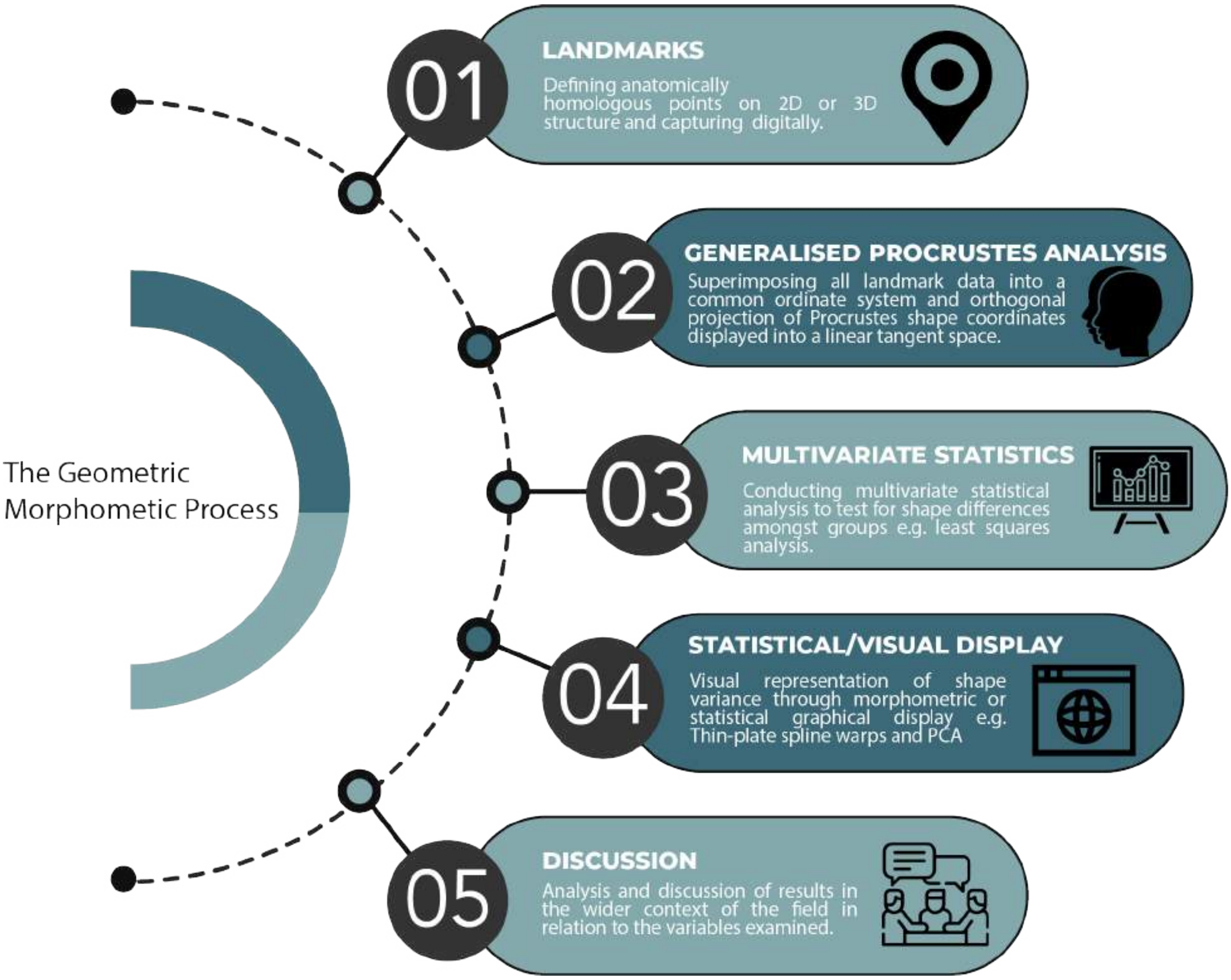


Figure 3.3: A typical geometric morphometric study including obtaining landmark data from anatomically-defined loci (Zelditch *et al.,* 2012); conducting a Generalised Procrustes Analysis (GPA) to superimpose all landmark data into a common coordinate system (Rohlf and Slice, 1990); orthogonal

projection of Procrustes shape coordinates (Slice, 2001) displayed into a linear tangent space providing Kendall tangent space coordinates (Kent and Mardia, 2011); conducting multivariate statistical analysis to test for shape differences amongst groups and the visual representation of this shape variance as morphometric or statistical graphical displays (Adams, Rohlf and Slice, 2013).

3.3.1 Landmarks

In a geometric morphometric study, landmarks are used as homologous anatomical loci that are recognisable and replicable within the shape of all specimens in a study (Bookstein, 1991). The advantage of this is that 'true' landmarks will always be of biological significance and will be present on every fossil in the study. Semi-landmarks can then be used to further define features along a curve (Zelditch *et al.*, 2012:23).

Macleod (2013) describes semi-landmarks as the more 'intuitive and useful' morphometric objects as they can capture critical information contained in complex structures where fixed landmark points do not exist. These points are not discrete and are less homologous but are significantly valuable for a study such as this where the specimen is complex in shape, e.g. primate crania and mandible.

Defined along a Cartesian system (X, Y, Z-axis), computerised landmarks are placed onto the 2D or 3D digital image, representing the specimen's spatial shape in the automated GM software chosen for application (Stark, 2018:43). Bookstein (1991) defines three types of landmarks used in a morphometric study:

Type I: A topologically homologous point defined by biologically specific areas on the specimen shape, e.g. located between different tissue structures.

Type II: A landmark that is geometrically located along the specimen outline boundary at the point of maximum curvature (Stark, 2018).

Type III: Commonly referred to as semi-landmarks, these points are topologically and geometrically miscellaneous and are logically dependent on other landmark locations, i.e. a tracing following the specimen's outline or shape boundary (MacLeod, 2013).

Several factors must be considered when deciding how many and which specific landmarks to include within a landmark-based geometric morphometric study. Firstly, by definition, the Cartesian landmark must be anatomically homologous loci that is recognisable on each specimen in the data set (Klingenberg, 2013). Secondly, landmark configurations should offer an adequate summary of the organism's overall form (Collyer *et al.,* 2020). Semi-landmarks can be included on curves of perimeters of more complex structures to preserve the outline of the form. Alternatively, hypotheses regarding shape, which include a particular region of interest, can be mapped out specifically rather than using the entire organism (Mitteroecker and Gunz, 2013). Being able to reliably digitise the landmarks is also a major factor or, as Webster and Sheets (2010:166) describe, 'should be consistently replicable with a high degree of accuracy' to avoid intra-/inter-observer error.

Landmark-based geometric morphometric analyses are common practice in modern paleoanthropological studies. For example, Gunz *et al.* (2009:48) implemented the use of

29 anatomical landmarks and 400 semi-landmarks in their virtual reconstruction of a hominin skull. The landmarks chosen on the skull's complete side were digitised onto a mirror-imaged reflection of the missing portion of the specimen. Thin-plate Splines algebra was used to distort the estimated shape to fit the target form's configuration, i.e., the completed side of the cranium (Gunz *et al.*, 2009:50). The team emphasises the importance of placing sufficient numbers of semi-landmarks around the specimen's curves and surfaces so that the most amount of data is collected. This is crucial as missing semi-landmarks can negatively alter the research outcome where the test has not accounted for the morphology of the curve (Gunz *et al.*, 2009:60).

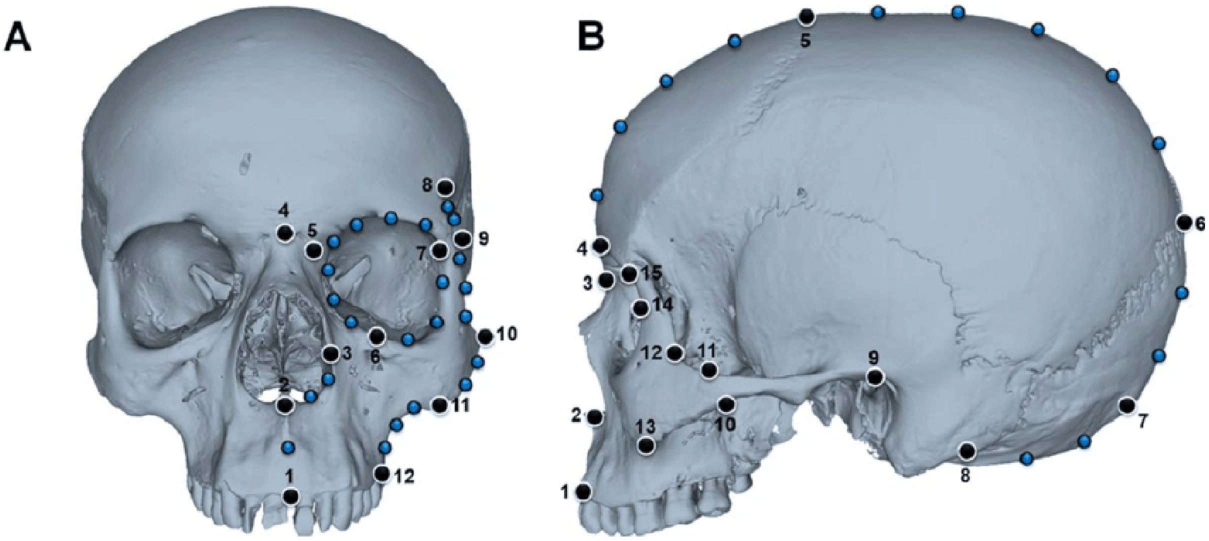


Figure 3.4: Facial and cranial landmarks (black circles) and semi-landmarks (blue circles) superimposed onto fixed anatomical points and along complex curves of a digitally imaged human skull (Delgado, 2016).

Landmark digitisation technology ensures that geometric morphometric studies can be completed using a suite of software to enhance accuracy, replicability and easier dissemination of shape information (Herzlinger and Grosman, 2018). Following landmark data collection, a Generalised Procrustes Analysis is performed to standardised the datasets for subsequent statistical processing (Gower, 2011; McWhinnie and Parsons, 2019).

3.3.2 Generalised Procrustes Analysis

Kendall (1977) defines shape as "all the geometric information that remains when location, scale and rotational effects are filtered out from an object" (Zelditch *et al.* 2012: 11). If the form is the figure without location or orientation, then two figures will have the same form if they are congruent or related by a rigid body transformation (Goodall, 1991). The shape is considered a form without size (Bookstein, 1984). The configuration created from Cartesian landmark coordinates is an inappropriate form of shape data in their raw state, as size, location and orientation will still exist as 'background noise' (McWhinnie and Parsons, 2019). As Geometric morphometric analysis solely explores spatial statistics, it is essential to remove these redundant data variables through Generalised Procrustes Analysis so that only data regarding shape remains (Rohlf and Slice, 1990; Gower, 1975).

Hurley and Cattell (1962) coined the term 'Procrustes Analysis' with reference to the nickname of a murderous thief in Greek mythology. Procrustes is said to have lived by the side of the road from Eleusis to Athens. He would offer travellers hospitality by way of a good night's rest on a magical bed that could fit any guest. Morosely, Procrustes would then stretch the unlucky travellers who were too short for the bed, or cut the limbs from those who were too tall, in order to make them short enough to fit.

The analogous name sake relates directly to the process of aligning shapes within a dataset to bring them into the 'shape space', which Stegmann and Gomez (2002) further describe as 'the set of all possible shapes of the object in question.' The Procrustes method is a least-squares type shape metric where two aligned shapes correspond within a one-to-one point, i.e. the shape space. This process involves four steps as defined by Stegmann and Gomez (2002:4):

1. Compute the centroid of each shape, i.e. the central point of the organism form
2. Re-scale all shapes to equal size
3. Align the shapes at their centroids w.r.t position
4. Align w.r.t orientation by rotation

Expanding on Hurley and Cattell's earlier work (1962), Gower (1975) introduced Generalised Procrustes Analysis (GPA) as a multivariate statistical technique used to analyse matrices of 3D datasets (Grice & Assad, 2009:93). This iterative approach chooses an initial estimation of the mean shape, i.e. the first shape in the data set, and aligns all the remaining forms in the set to this mean shape. The estimate of the aligned shape mean is recalculated, and convergence is declared when the mean shape does not significantly change within an iteration (Stegmann and Gomez, 2002:6).

To perform an iterative GPA on 3D data, an array containing the raw landmark coordinates for a set of specimen is used to establish the coordinate reference, or 'pose', to which all shapes in the dataset are aligned through rotation using the least-squares criterion, translation and scaling to a unit-centroid size (see **Figure 3.5**) (Zelditch *et al.* 2012:12). Sliding semi-landmarks are also slid along the tangent direction/plane of the curves they occupy, ensuring all corresponding coordinates in the dataset are aligned as closely as possible (Sherratt, 2015a:19; Bookstein, 1997).

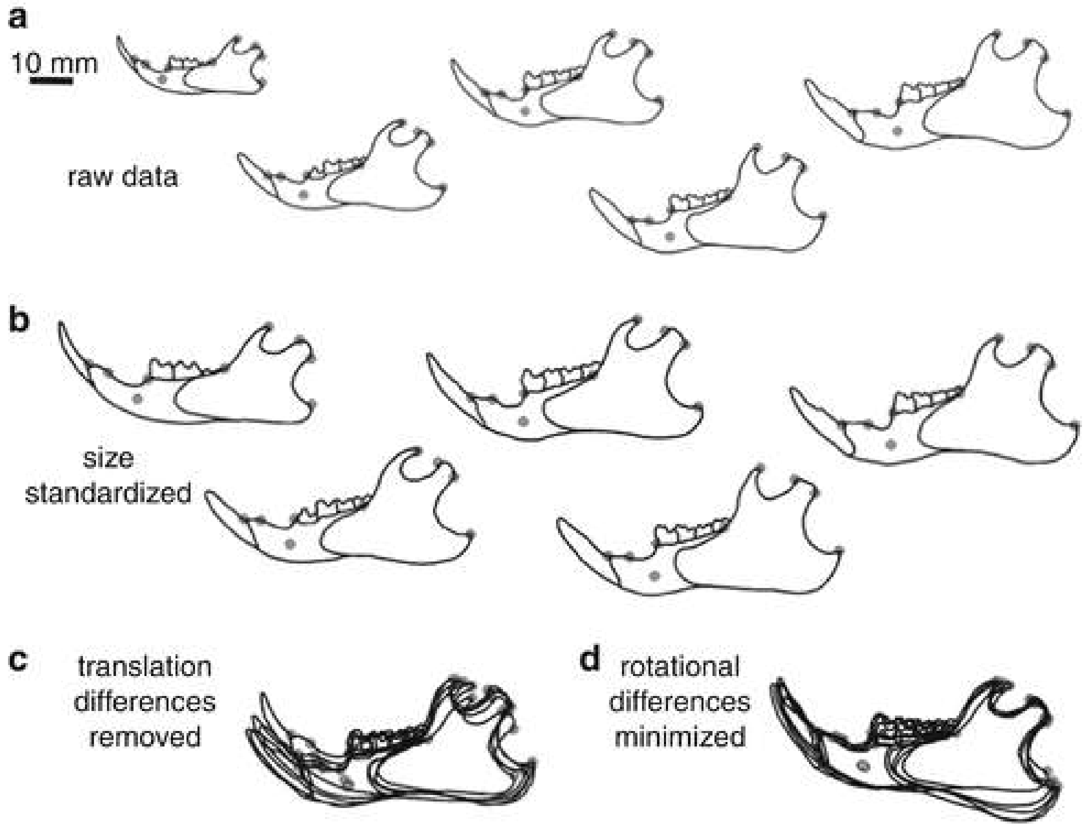


Figure 3.5: Example of Procrustes superimposition of five mandible specimen. a) shows mandible outline as described through raw landmark data. Size is standardized across all specimens as seen in b) row. Orientation and spatial location differences are removed and minimised as can be seen in images c) and d) where Procrustes coordinates now exist in an optimally comparable matrix (Sheetah, 2014).

3.3.3 Principal Components Analysis

In all geometric morphometric studies, superimposition of specimen shape data is the first procedure, conducted by way of Generalised Procrustes Analysis. Visualisation of covariation existing between variables is exemplified through ordination and projection tools, such as Principal Components Analysis.

Principal Components Analysis (PCA) is a descriptive ordination tool defined by Zelditch *et al.* (2012:464) as 'a method for reducing the dimensionality of multivariate data', which is achieved through the extraction of principal components of the variance-covariance matrix. The principal components have associated eigenvalues which is the existing variance within the dataset explained by each axis. Patterns of variation and covariation can be challenging to interpret depending on complexity - it is the role of the PCA to summarise these patterns for ease of understanding, with minimal loss of important information, and return a visually simplified graphical output (Zelditch *et al.* 2012:136).

Mathematically, a Principal Components Analysis organises the set using a 2-dimensional array of numbers or a correlating $m \times n$ matrix, where m is the number of measurements and n is the number of samples (Shlens, 2013). Standardising this range of continuous initial variables ensures that each variable contributes equally to the analysis. Transforming the data into comparable scales prevents the problem of biased results where a larger variable dominates those with smaller ranges. This is done by subtracting the mean and dividing the standard deviation for each value in each of the variables (Jaadi, 2019) which is expressed as:

$$Z = \frac{\text{value} - \text{mean}}{\text{standard deviation}}$$

Subsequently, the mean for each measurement type or row is subtracted, and the eigenvectors of the covariance (or SVD) calculated (Shlens, 2003). The principal components and eigenvectors of the covariances are best described visually in morphospace as they represent a deconstruction of the data points and valuable information found within a long string of numerical shape data.

Principal components are the underlying structure within a dataset. Visualising this structure is often more useful in terms of measuring data than within a normal x-y axis (Dallas, 2013; Firmin, 2019). To explain how the principal components are found within a data set, consider an oval made up of 11 irregular squares (**Figure 3.6),** which could be considered the points of data. To discover the directors of the most variance, a straight line is used to find the point at which the data is most spread out. The vertical straight line of point projection shows insignificant variance as the data points are not particularly spread apart from one another. When a horizontal line is used, the data is far more spread out, showing a larger proportion of variance (Dallas, 2013).

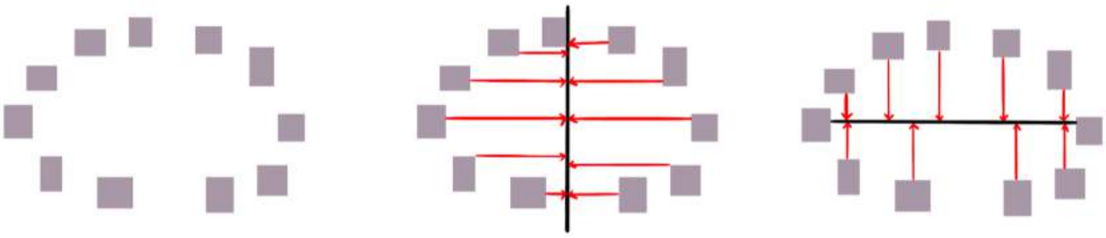


Figure 3.6: Finding the direction of variance using an oval of irregular squares. Projected vertical and horizontal lines are used to decipher areas of most variance which is reported here in the horizontal axis. This exemplifies the role of eigenvectors and eigenvalues in Principal Components Analysis.

A set of data points, such as the square example in **Figure 3.6**, can be deconstructed into eigenvectors and eigenvalues, which exist in pairs. An eigenvector is a direction, e.g. the orientation of the straight line in the example above, and an eigenvalue is a number that describes how spread apart the data is on the projected line (Dallas, 2013). The eigenvector showing the largest eigenvalue is the principal component. The number of variables in a data set reflects the number of eigenvectors/values, e.g. there are 3 eigenvectors and values within a 3D dataset with 3 variables (Alto, 2019).

Finding the principal components and eigenvectors helps reduce the dimensions of a dataset, reducing the data into basic components and essentially removing unnecessary information (Li, 2019). For example, the oval of squares in **Figure 3.7** is positioned on an x, y and z graph measuring width, depth and height. However, the points now sit within a plane on the 3D graph, which measures no height. There will be 2 large eigenvectors (ev1 and ev2) found in this dataset (width and depth), and the third will have an eigenvalue of 0 (**Figure 3.7**). Knowing the redundancy of the 3D eigenvector (ev3), the data set can now be displayed in 2 dimensions. This dimension reduction has simplified the data and made graphically visualising variance more accessible (Dallas, 2013)

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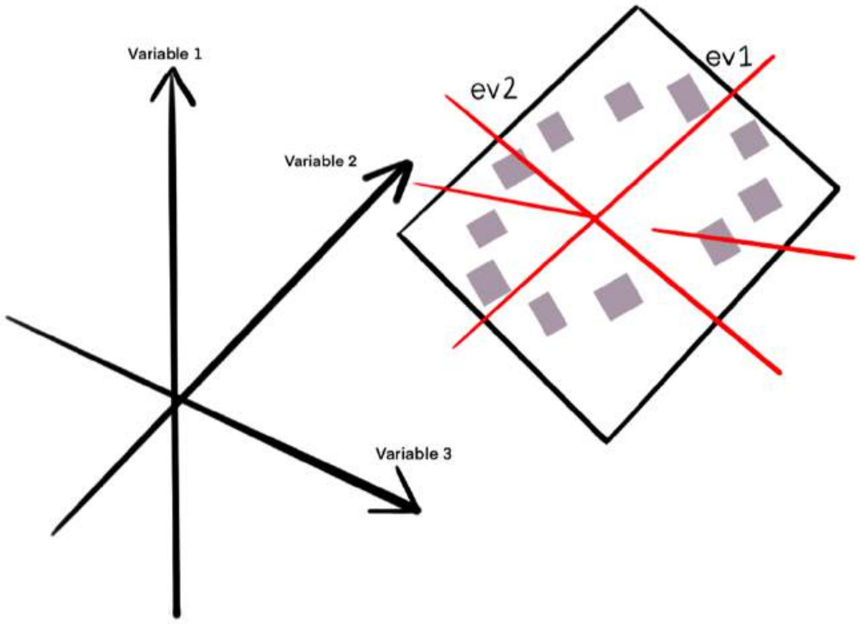


Figure 3.7: An example of dimension reduction in Principal Components Analysis. The oval projected onto a 3D x, y, z axis is reduced to 2 dimensions (ev1 and ev2) as the eigenvector returning for height (ev3) is considered redundant due to the plane within which the shape data sets sit. Dimension reduction is a benefit of Principal Components Analysis as it simplifies datasets and allows for clearer graphical visualisation (Cook, 2001: Dallas, 2013).

Most datasets will return 90% of variance described in the first two or three PCA's, which simplifies the presentation and dissemination of results. Graphical visualizations are used alongside Thin-plate Spline deformation grids to represent variation as clusters, or apparent groupings, within a scatter plot (Zelditch et al. 2012:146). The first principal component (PC1) represents the largest axis of variation, followed by the second component (PC2) and so on. Plotted specimen clusters represent more similarly shaped morphologies - the tighter the grouping, the more similar the shape is (Stark, 2018:45; Slice, 2007; Zelditch et al., 2012).

Schillaci and Gunz (2013) tested popular multivariate techniques used within palaeoanthropology through Principal Components Analysis to assess craniometric variation between fossil and recent human groupings. Visualizing their results through a bivariate scatter plot (**Figure 3.8**), the team showed 37% of the total variation in the first PC, with 22% appearing in PC2. The eigenvectors returned for PC1 fall within the plot's negative loadings, indicating that the component is explaining size variation. The PCA plot also shows an Upper Palaeolithic European grouping that falls within the recent human group range of variation and a large distinction between *H. heidelbergensis* and *H. neanderthalensis* in comparison to modern human populations (Schillaci and Gunz, 2013:77).

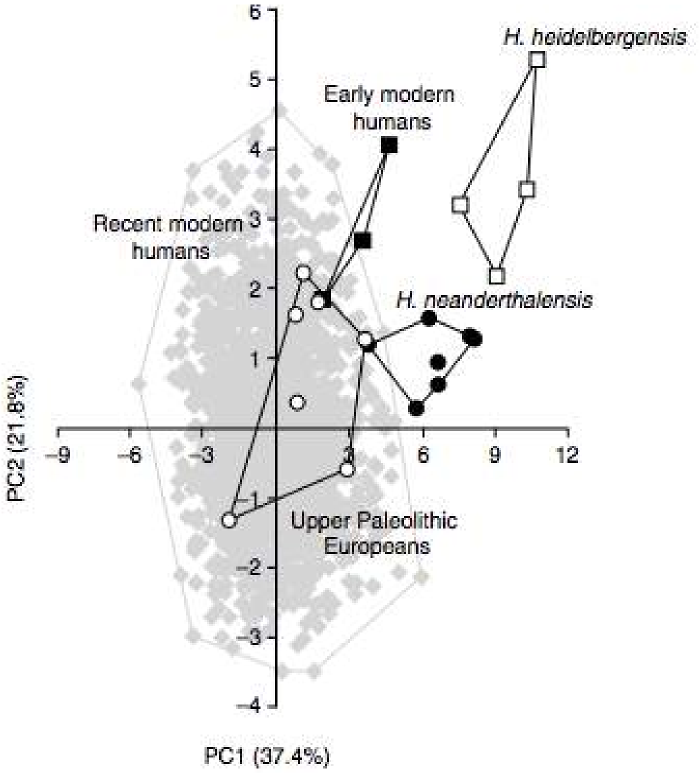


Figure 3.8: Bivariate Principal Components Analysis plot of scores depicting the first two PC's from craniometric shape data of *H. heidelbergensis, H. neanderthalensis*, Upper Palaeolithic Europeans, early modern and recent humans from 6 global regions. 37% of variation between fossil and recent human groups fall within the first PC (Schillaci and Gunz, 2013:79).

A strength of Principal Components Analysis is that it is a non-parametric analysis meaning there are no parameters or coefficients to adjust based on the user's experience or assumptions. Therefore, the results of the PCA are independent of the user (Jolliffe and Cadima, 2016). This can also be considered a weakness of PCA as the cost of fewer assumptions generally means a less powerful statistical test (Shlens, 2003).

Power is the probability of a test to correctly reject the null hypothesis (Riffenburgh, 2006). Therefore, Sullivan (2017) states that it is important to consider the possibility of

Type II error when a Principal Components Analysis rejects the null hypothesis as a non-parametric test can be subject to low power due to small sample size. Although this could be reporting a true effect, PCA's non-parametric aspect means it is underpowered to detect this accurately (Siegal and Castellan, 1988). **Table 3.1** details further limitations, as well as the advantages, of utilising the PCA method in a morphometric study.

Advantages of Principal Components Analysis	
1. Performance algorithm improvements	Speeds up machine learning algorithm, i.e. turning a data set into a model, through removal of correlated variables that do not contribute to any decision making (Heller, 2019).
2. Removal of correlated features	Reducing the number of features in the dataset allows for easy visualisation of results. Correlated variables are also more easily found in a large dataset which become Principal Components independent of one another after testing (Vidhya, 2016).
3. Better Visualisation of results	By transforming a data set of high dimensionalities to one of 2 dimensions, a scree plot can be used to see which PC results in high variance in comparison to other PCs in the study (O'Sullivan, 2020).

4. Reduces overfitting	In a study consisting of too many variables, overfitting can occur where noise variables are entered into the model by chance (Zhang, 2014). PCA eliminates this issue by reducing the number of features in the study and including only pertinent information (Lindgren, 2020).
Limitations of Principal Components Analysis	
1. Data standardisation is necessary	If the dataset is not standardized before testing, PCA will not be able to find the optimal Principal Components. Categorical variables must also be converted into numerical features before the PCA application (Patil, 2020).
2. Less interpretable independent variables	After PCA, the original dataset is converted into Principal Components which are not be as readable as the original features and must be visualised graphically for ease of interpretation (Patil, 2020).

Table 3.1: The advantages and limitations of Principal Components Analysis. Although PCA has many advantages including dimension reduction and graphical visualisation, the limitations of this method include less interpretable independent variables and necessary standardisation**.**

Results from a Principal Components Analysis are used as inputs of warping and shown visually as Thin-plate Spline warps. These deformation grids result from image warping using bending energy functions for a transformation over a set of landmark points (Whitbeck and Guo, 2006). The application and benefit of presenting Thin-plate Spine warps alongside Principal Components Analysis plots are discussed in the following section.

3.3.4 Thin-plate Spline Warps

As Klingenberg (2013:15) states, an essential aspect of geometric morphometric analysis is the visualisation of shape change within a dataset. A benefit of automated 3D GM analysis is the computerised illustration or animation that can be created to visually represent shape differences. This methodology can communicate complex morphological disparities or similarities more effectively than laborious tables of numerical coefficients used in traditional morphometric studies (Rolf and Marcus, 1993; Klingenberg, 2013).

Bookstein (1989, 1991) introduced Thin-plate Splines as a tool for shape difference visualisation, where an infinitely expansive and thin metal plate, or grid, covers the specimen shape form, causing warping to the points that return the most morphological variation in correspondence to the reference shape. The resulting graphical representation (e.g. **Figure 3.9**) provides a basis for interpreting shape variance along the PC1 and PC2 axis (Stark, 2018:45; Rohlf & Marcus, 1998; Bookstein, 1989:567).

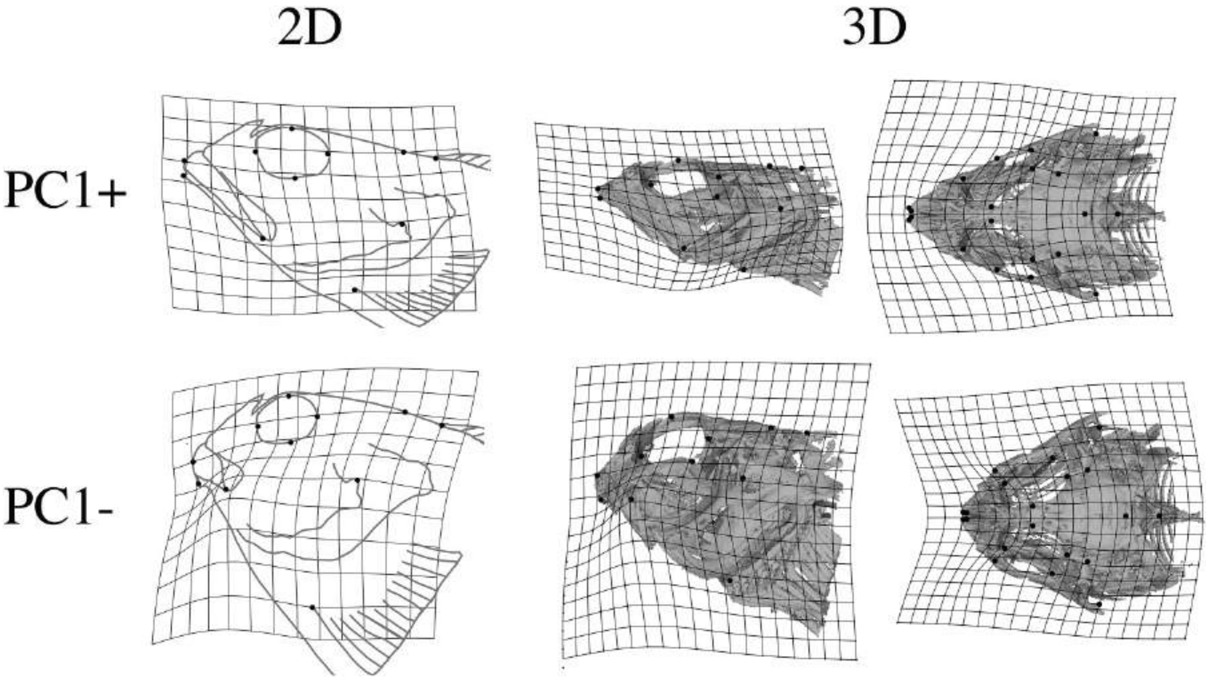


Figure 3.9: Comparison of 2D and 3D Thin-plate Spline deformation grids showing change in head shape among Oligocottinae (fish subfamily) specimen captured by PC1 values (Buser *et al.* 2018).

Belongie (1999) describes the Thin-plate Spline as 'a two-dimensional analogue of the cubic spline in one dimension'. Thin-plate Splines (TPS) are smoothing and visualise complex relationships between continuous predictors and response variables. Because of their multi-dimensional appearance, TPS grids are ideal for examining two continuous predictors on a single outcome. Each predictor is plotted onto the individual x-axis to create a 2-dimensional bivariate surface, and the outcomes are plotted onto the y-axis across the bivariate surface in 3-dimension (SAS, 2012).

Thin-plate Splines are fitted to the axes using a generalised additive model or GAM, which is expressed as:

$g(E(Y)) = \beta 0 + f(X) + \lambda$

$\beta 0$ is the constant and $f(X)$ denotes the flexible functions of x, i.e. the sum of the functions for more than one x, allowing for the flexibility of fitting a predictor to the outcome. λ is the error term which is described as the amount of pressure or tension needed to bend the 'thin plate of metal' (SAS, 2012). The error term acts as a built-in smoothing function based on a least-squares method (Clarman, 2014). Higher tension creates more resistance in the thin plate's bending or more resistance to the effects of X1 and X2 on the Y-axis. Consequently, the spline will appear smoother (SAS, 2012).

Generalised additive models do not require *a priori* knowledge of the relationship of interest or the functional form of the numerical data, which is an advantage of the Thin-plate Spline regression method (SAS, 2012; Wood, 2003). Also, general cubic splines can be challenging because of node placement determination; however, using the Thin-plate Spline method, this becomes automated as part of the smoothing function (SAS, 2012; Perperoglou *et al.*, 2019). This method's main benefit is the 3-dimensional nature of the Thin-plate Splines, which produce powerful visualisations pertaining to complex variable relationships (Klingenberg, 2013; SAS, 2012; Zeldtich *et al.,* 2012). When a heat map is applied to a Thin-plate Spline deformation grid, as in **Figure 3.10**, the surfaces' curvature is further emphasised (SAS, 2012).

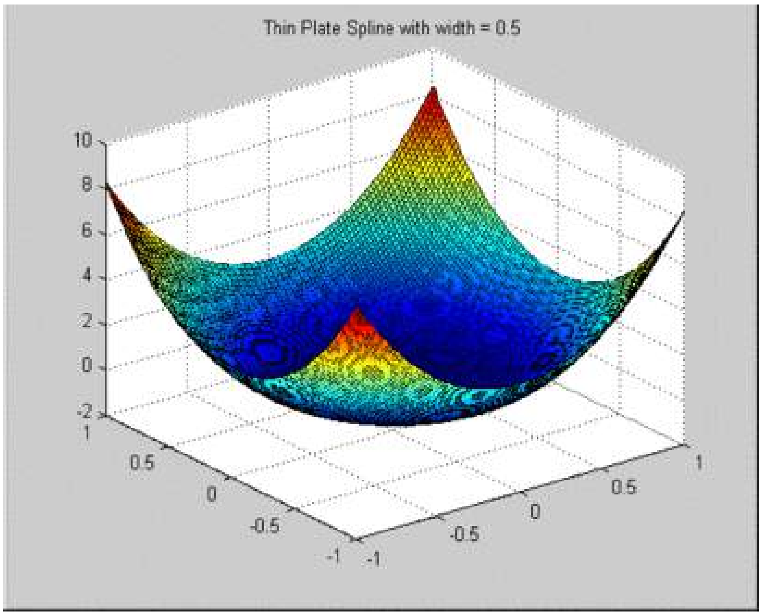


Figure 3.10: A Thin-plate Spline deformation grid showing high to low tension warping of a square plane based on the predictor and response relationship of the X-Y axes. The heat map shows red in the most tension of high-energy bending and deep blue in the least amount of bending pressure image (image sourced through SAS, 2012).

Yaroch (1996) successfully illustrates the Thin-plate Spline warp application in paleoanthropological research by applying this method to the problem of Neanderthal cranial shape characterization. Though the study was limited to 2-dimensions, geometric morphometric techniques were used extensively by first quantifying landmark configurations and subsequently separating size from shape.

Deformation grids were created to illustrate the transformation between the reference and target mean, as can be seen in **Figure 3.11.** From the grids, Yaroch (1996:66) highlighted shared primitive shape features comparable between unclassified hominin fossil specimen and known Neanderthal crania. Also, four distinct shape features out of the 18 tested were shown as significantly variable between Neanderthal and modern human skull specimen.

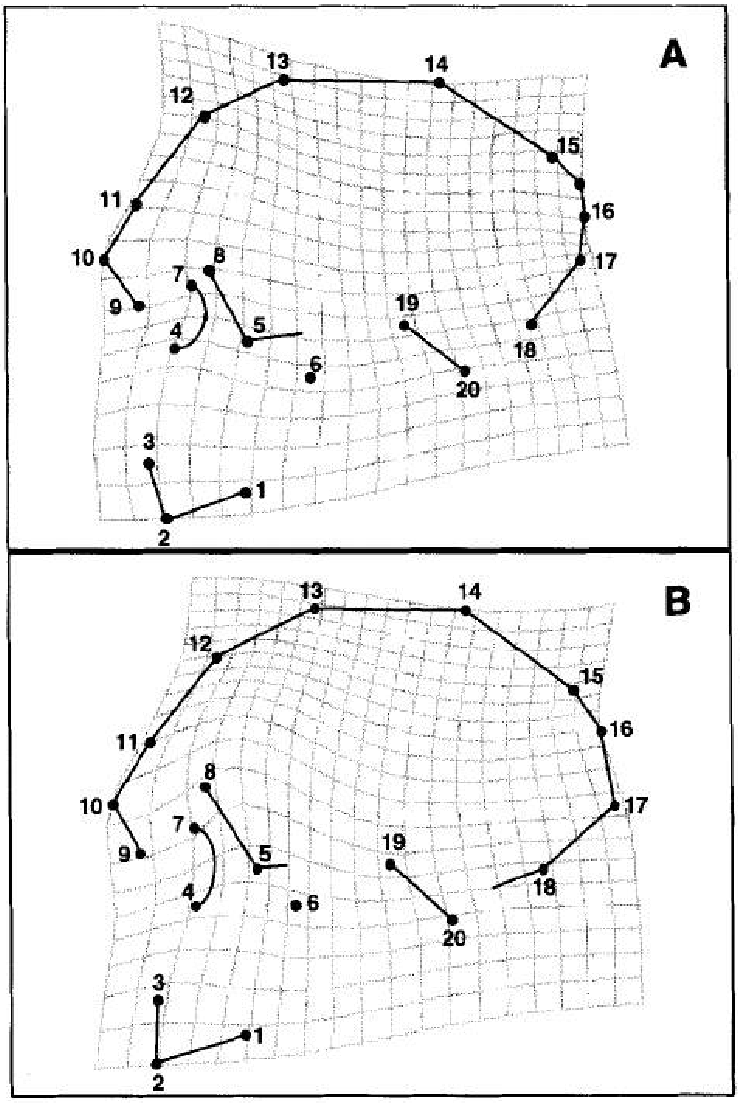


Figure 3.11: Deformation grids showing transformation between reference mean and two unknown hominin species' crania. In contrast to the mean shape form, the Thin-plate Spline grids show a reduction of the braincase, expansion of the brow region, a deepening of the zygomatic arch and enhancement to the maxilla (Yaroch, 1996:60).

Chiefly regarded as an advantage, complex data visualisation may also be a limitation of the Thin-plate Spline method as TPS-derived confidence intervals can be difficult to include within the 3-dimensionality of the warping grids. For this reason, SAS (2012) recommends plotting separate Thin-plate Spline grids for the upper and lower confidence intervals as well as the 'main effect' spline.

MacLeod (2010) also argues that the robustness of any Thin-plate Spline result is highly dependent on the experimental design; the visualised result is only valid for the specimens used in the calculation, in the landmark set used to quantify the shape variation and the reference form used as the basis of the spline. Alterations to these parameters will result in a different outcome of the spline's geometry. Therefore, Thin-plate Spline analysis should be thought of as a mathematical descriptor based on the analysts' goal of shape comparison between two or more forms (MacLeod, 2010).

3.4 Statistical Error and Repeatability

Developed extensively from traditional methods, geometric morphometric techniques are now computerised, mature methods of shape analysis and are routinely used in a broad range of biological studies. As with all scientific endeavours, the primary goal of any GM analysis is precision and repeatability of tests. Random measurement error can potentially inflate the amount shape variation and produce unreliable results and loss of statistical power (Fruciano, 2016). Digitised and automated geometric morphometric programs have greatly increased accuracy and reduced intra-observer error existing in traditional morphometric methods, though pitfalls do still exist that need to be addressed for replicability (Cramon-Taubadel, 2007).

Arnqvist and Martensson (1998) collated and defined the potential measurement error sources within a landmark-based geometric morphometric study where *Sm* is methodological error, *Si* represents instrumental error and *Sp* is personal error (Rabinovich, 1995).

S = Sm + Si + Sp

In landmark-based geometric morphometrics, erroneous landmark placement can result in a primary origin of error which feeds into the subsequent multivariate statistics and creates measurement error in the resulting shape variables (Arnqvist and Martensson, 1998:76). A major limitation of morphometric study is the accuracy and precision of recording data, i.e. the identification, precise placement and accurate quantification of landmarks, which have the ability to produce a great margin of error due to the manual nature of the procedure (Zelditch *et al.,* 2012; Arnqvist & Mårtensson, 1998).

Figure 3.12 shows the sequential portioning of the manual landmark collection procedure, including the main components of measurement error. Firstly, landmarks are collected from the specimen in the study. The potential error arising from this occurs as a result of slight variation in the preparation of the specimen for data collection, e.g. preservation of the specimen or mounting and presentation strategies (Arnqvist and Martensson, 1998). If data collection is being conducted on specimen with soft tissues, the source of error increases due to distortion in the state of which the specimens are presented (Carpenter, 1996).

Secondly, as 3D landmark configurations are reduced to 2D in landmark-based studies, dimensionality reduction error can arise as a result of ‘lack of perfect orthogonality between the major axes of the specimen (x,y) to that of the dimension being reduced (z) (Arnqvist and Martensson, 1998). In step 3 of the sequential error procedure (**Figure 3.12**), an error can occur as a result of unique methodological routines employed to prepare the collected data prior to analysis, i.e. recorded parts of a whole specimen separately in order to complete a configuration (Reig, 1998; Arnqvist and Mattensson, 1998).

The final steps in Arnvist and Martenssons’ (1998:77) measurement error sequence show digital data acquisition and capture as a potential error source due to optical imperfection and digital distortion or misrepresentation (MacLeod, 1990). Computational image enhancement can also contribute to this error. Finally, the recording of the relative positioning of landmarks can result in inconsistent or imperfect localisation of the Cartesian points. This is greatly affected by the personal characteristics of the investigator, the resolution and quality of the imaging and the accuracy of the equipment (Arnqvist and Martensson, 1998).

Figure 3.12: Sequential partitioning of the main components of measurement in a landmark-based geometric morphometric analysis (adapted from Arnqvist and Martensson, 1998:77). *Sm* denotes methodological error, *Si* shows instrumental error and *Sp* represents personal error.

Cramon-Taubadel *et al.* (2007) demonstrate one such procedural error by way of the 'Pinocchio effect'. The 'Pinocchio effect' phenomenon occurs when the least-squares criterion is used to superimpose raw configurations, and the variance of the landmarks is displaced or 'smeared' across the rest of the points in the form (Zelditch *et al.* 2004; Cramon-Taubadel *et al.* 2007:26). This effect essentially describes the tendency of the

Procrustes superimposition method to distribute shape change over many landmarks even though different superimpositions might exist for the same landmark configurations that concentrate changes in one or a few landmark points (Klingenberg, 2020). The smearing of data hides the most influential landmarks' variance by allocating this information to other markers in the configuration (see **Figure 3.13**).

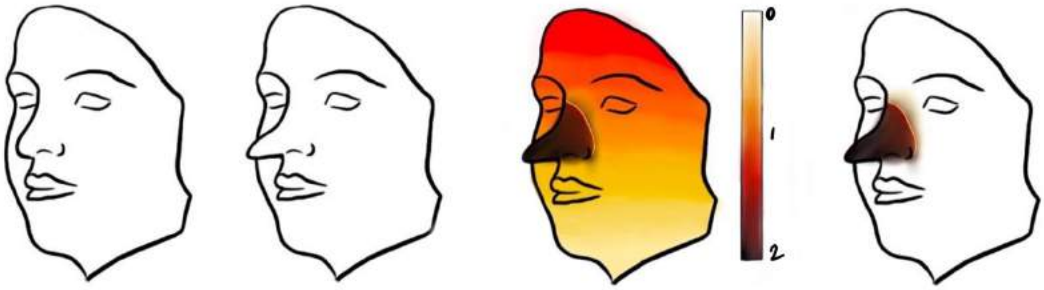


Figure 3.13: The Pinocchio effect, known in shape analysis as the large change of limited landmarks in a form, describes a flaw in the Procrustes superimposition method of smearing or hiding data and variance of the more influential landmark points by allocating information to other points in a configuration. Note the abnormal 'smearing effect' in the affected landmarks and the perfect alignment in the structure of the face or the unaffected landmarks. The fourth face depicts the dysmorphogram using a colour scale where the darker shades reflect the strongest outliers (adapted from Claes *et al.,* 2012).

Klingenbergs' (2020) critical review of the Pinocchio effect states that this abnormality stems from a widespread preference for superimpositions which involve a change in one or a small number of landmarks within a configuration rather than superimpositions where numerous landmarks change position in morphospace. The result of this review describes a difficulty in morphometric methods where the author states that 'it is not possible to assign shape changes unambiguously to individual landmarks or even a particular set of landmarks.' On the contrary, landmark-based geometric morphometric studies report the relative shape changes that encompass all of the landmarks in the configuration under investigation (Klingenberg, 2013; Klingenberg, 2020; Goswami *et al.*, 2019).

Addressing the issue of precise and replicable landmark placement, packages, such as *Auto3DGM* and *geomorph* in R, have been created to assess and reduce the impact of measurement error, i.e. users can use templates and automate the placement of landmarks and semi-landmarks (Stark, 2018:53). Error assessment should also be conducted through repeated digitisation to assess individual landmark placement variance as a result of observer error (Valeri *et al.*, 1998:113; Cramon-Taubadel *et al.*, 2007:25; Arnqvist and Martensson, 1998).

Registration methods, such as Generalised Procrustes Analysis, can be used to understand whether repeat measure variances successfully fall within a range suitable for the study at hand (Cramon-Taubadel *et al.*, 2007:26), as exemplified by Viðarsdóttir *et al.'s* (2002) study of human facial morphology and ontogeny. Fox *et al.* (2002) measured the degree of error and repeatability of GM analysis using the *geomorph* package in R and provided commentary for future studies toward the ideal procedure to minimise such risk. Whereas Fruciano (2016) argues that there are no procedures available that can eliminate error in GM analysis completely, Fox *et al.* (2020:3271) conclude several measures that can be taken to lessen the amount of introduced error. The team argue that using 3D data in a GM study works to avoid error created by 'dimensional loss' (Buser, 2018:815) in that modern digital imaging technology has greatly improved the data resolution of specimen form.

Fox *et al.* (2020) recommend avoidance of mixing observers in a geometric morphometric study, as this generates a considerable amount of digitisation error'. The team concludes that landmark data compiled from different sources will produce a high degree of measurement error that can obscure results of shape variation and negatively impact the repeatability of the study. Statistical evaluation and repeated measurements should be facilitated to discuss whether the amount of residual error can be deemed acceptable for the study objectives at hand (Fox *et al.* 2020:3271).

3.5 Geometric Morphometric Applications in Palaeoanthropology

Geometric morphometric techniques have become increasingly popular in the last 20 years, specifically among human evolutionary biologists and paleoanthropologists e.g. Loclwood *et al., (*2004); Grine *et al.* (2010); Groning *et al.* (2011); O'Higgens *et al,* (2011); Gómez-Robles *et al.* (2011). GM analysis can be applied to a variety of studies which can be characterized into three discerning categories: quantifying shape variation and covariation within a sample; testing significant variation between two or more groups for a targeted aspect of the shape; and identifying patterns between shape and one more additional variables (Baab *et al.* 2012:156).

Modern GM research has delved into many aspects of hominin evolution including phylogenetic comparative studies (Monteiro, 2013:25), analysis of allometry to determine ontogenetic evolution (Zelditch *et al*, 2012:297), and form and function of anatomical characters with a focus on disparity and variance (Laffont *et al.* 2011:133). Zelditch *et al.* (2012) comments that the vast majority of these studies involve inter/intraspecific comparisons of species' morphology.

3.5.1 Applications in the Hominin Fossil Record

Table 3.2 details the strengths and limitations of geometric morphometric applications in paleoanthropological study.

Author(s)	**Research Aim**	**GM Application**	**Strengths**	**Limitations**
Lockwood *et al.* (2004)	To better understand phylogenetic relationships between modern humans and great apes.	Neighbour-joining and ordinary least squares algorithm on 3D imaged temporal bone specimen.	Set a standard for landmark repeatability as well as exemplifying the positives of higher resolution landmark data.	Specimens limited to large bodied apes and it is unclear whether the methodology can be replicated using a larger dataset.
Groning *et al.* (2011) & O'Higgens *et al.* (2011)	Analysis of mandibular strain data influenced by the periodontal ligament.	Finite element model using analysis of coordinates and strain data.	Successfully combined 3D GM landmark and deformation methods with virtual functional simulation.	A small study intended to illustrate the possibility of a new GM application using too few landmarks and permutation tests not

				used to compare deformation.
Grine *et al.* (2010)	Virtual reconstruction of damaged and incomplete late Pleistocene Human skull from Hofmeyr, South Africa.	Thin-plate Spline interpolation method using reference and coordinate based estimations.	Utilised a comprehensive and extensive morphometric comparative method by way of clay modelling, CT scan, virtual reconstruction, 3D GM and previous estimates of the skull's morphology	Clay reconstruction used for mirror imaging could be replaced by 3D computational applications used for modelling i.e. Blender, making use of dynamic topology and multi-resolution for further accuracy
Cobb and Higgins (2004)	Examines hypothesis that postnatal trajectories in	3D GMA and principal components analysis	Using comparative species-specific PCAs,	Small sample size due to lack of fossil

	chimp, modern human and fossil hominins are parallel.	visualisation and comparison	found that the primary direction of *A. africanus* ontogenetic facial shape change is more closely related to chimps and gorillas than modern humans.	hominin specimen does not permit conclusive evidence towards ontogenetic facial shape change comparisons.
Gómez-Robles *et al.* (2011)	Analyses differences in hominin dental crown morphology.	3D GM, canonical variance analysis and 2B-PLS	Showed significant covariation in premolars of hominin species successfully reinforcing and expanding upon previous statements regarding European	Could not rule out possible continuity in Eurasian fossil record due to lack of comparable African fossils.

			fossil records and phylogenetic continuity.	
Morley *et al.* (2020)	Quantifies 3D morphology of metacarpal of extant African hominoids to facilitate an informed understanding of functional interpretation of fossil hominin morphology.	3D GM, PCA and Linear Discriminant Analysis	Reinforced the validity of 3DGM application as a method of quantifying MC1 morphology due to alignment with past functional interpretations.	Samples using mixed captive and wild specimen as well as those from unknown sources.

Table 3.2: A review of geometric morphometric applications in paleoanthropological study with strengths and limitations of methodology showing sample size and quality as a major weakness of fossil hominin morphometric analysis. GMA is identified as being particularly useful to specific research areas such as ontogeny, biomechanics, ecomorphology, systematics and phylogenetic study**.**

To provide a better understanding of how geometric morphometric techniques have been utilized in palaeoanthropology, specific application regarding ontogeny, systematics, biomechanics and ecomorphology is reviewed in the following sections.

3.5.1.1 Ontogeny

As Menke (2013) remarks, developmental information is a promising tool in aiding phylogenetic investigation into hominin morphological evolution, and central to this thought is ontogenetic trajectory as defined by Alberch *et al.* (1979). Geometric morphometric analysis can help to create a record of the physical development of an organism using shape and size, including age records where available (Zelditch *et al.* 2012: 298; Baab *et al.* 2012), and has also been a discerning tool for analysis between form and function, providing insight into the study of early hominin biomechanics (O'Higgens *et al.* 2012; Weber, 2013).

There have been numerous studies incorporating GM techniques to further our understanding of hominin ontogeny, often by way of comparative study (e.g. Baab *et al.* 2012; Zollikofer *et al,* 2005; Balzeau *et al.,* 2014; Schroeder *et al,* 2014; Carayon *et al.* 2015). The research undertaken by Balzeau *et al.* (2014) for example, shows how quantified structural asymmetries of the brain can reveal the anatomical functional asymmetries in extant hominin species, improving the understanding of form and function which previously relied upon qualitative techniques.

Using 3D landmark-based GM analysis and digital imaging, Balzeau *et al.* (2014:3) collected shape-form data from groups of fossil hominin, modern human and extant primate endocasts, which were subsequently tested through multivariate statistical analyses, i.e. linear regression, permutation t-tests and Bonferroni procedures. The results were visualized through bivariate plots where variations of shape and size of the third frontal convolution were reported during hominin evolution and, compared to the Great Ape groupings, found indications of a reorganisation of this area. To offer conclusions regarding Broca's area within the third frontal convolution of the brain (most notably a reflection of the origin of language capabilities within modern humans), Balzaeu *et al.* (2014:11) admits is difficult due to sparsity of physical record. However, their findings suggest that lateralization of the brain, an essential aspect of the onset of modern human language, is most likely shared by all hominins.

Another advantage of GM study is the use of deformation grids, which Mitteroecker *et al.* (2009) highlights as a powerful tool in visualizing shape and form variation. Rosas and Bastir (2002) explored the relationship between allometry and the ontogeny of sexual dimorphism in the human craniofacial complex. They used Thin-plate Spline warps to investigate the lateral profile of a dataset containing complete adult skulls of known sex. Their results confirmed both size and sex had significant influence of the facial shape form with 'marked allometric variation of the lower face' and a gradual prognathism of the alveolar region (Rosas and Bastir, 2002:240).

The Rosas and Bastir study utilized automated warping methods from the TpsREGR package (Rohlf, 1998; Rosas and Bastir, 2002:239) to visualise allometric and ontogenetic shape changes. The industry standard for the creation of computerised Thin-plate Spline methods, as noted by MacLeod (2010), are programs such as the PAST, MorphoJ, tpsSplin and tpsRelw packages, and in reviewing paleoanthropological literature concerning ontogeny and deformation warping, there are markedly few studies implementing the R packages *geomorph* or *Auto3DGM*.

These open-source packages are regularly evolved and expanded upon through researcher and statistician advancements in technique. They are freely available to any institution and research group and should be more commonly incorporated into morphological studies as a powerful and progressive tool of quantitative evolutionary research, due to their flexibility to mould to the demand of the investigative topic The digital imaging aspect of computerised GM analysis is a major benefit for studying ontogeny. Marfart *et al.* (2004) champion the use of 3D computer imaging techniques e.g. CT scanning, as a tool for studying fossil hominid shape variation due to the non-destructive and restorative application.

Carayon *et al.* (2015) exemplify the benefits of this digital approach in regard to ontogenetic study in their analysis of maturational patterns of the premastoid canal. The authors echo the effectiveness of modern 3D imaging approaches and conclude the digital application approach as a successful tool for use within osteological and anthropological studies. Their research makes use of numerous statistical tests, including the Spearman Test, Bonferroni Corrections, the Mann-Whitney test and the Breusch Pagan/Cook Weisberg test which were reported through PCA visualisations.

Neubauer *et al.* (2010) use CT scans followed by landmark-based geometric morphometric analysis to visualize the growth of aged chimpanzee and human endocasts. By analysing the ontogeny of these species, the team discovered, through a non-liner ontogenetic trajectory of analysis, that humans and chimpanzees do not share a similar endocranial shape at any point during postnatal growth, though they do share similar patterns of change. The authors comment on the data-limiting factor of using endocasts due to this structure being a highly localized area. Further additional patterns of variation could be revealed by using more defining homologous craniometric features of the skull e.g. facial shape, should the Neubauer *et al.* (2010) study be expanded upon in the future.

GM analysis has also been an insightful and powerful tool used in the study of the relationship between ontogenetic transformation and evolutionary biomechanics. Using a comparative combination of ontogenetic transformation, coupled with disparity analyses at varying developmental stages, morphometricians can test hypotheses regarding evolutionary development (Zelditch *et al*, 2012:297) and apply visual applications to better understand the functional morphology of early hominins (e.g. Baab *et al.* 2012; San Millán *et al.*, 2015; San Millán *et al.*, 2017).

In 2005, Zollikofer *et al.* analysed the incomplete skull of the *Sahelanthropus tchandensis* fossil specimen, TM 266-01-60-1. The team successfully virtually restored morphological continuity to the fossil specimen through computed tomography and virtual 3D reconstruction. Through comparative GM study of the cranium, the authors concluded that the *Sahelanthropus tchadensis* species were most likely bipedal without post-cranial evidentiary support furthering our understanding of early hominin biomechanics through GM techniques.

Geometric morphometric analysis can also be used to study measures of performance in skeletal form and function. Parr *et al. (*2012) outlined a new method of integrating geometric morphometrics and computational biomechanics through 3D virtual reconstruction and quantitative analysis of Finite Element Models. The warping methods and statistical procedures used to produce 3D mesh geometry of varanoid mandibles were successful in also providing landmark point strains and bending displacements proving GM approaches to be powerful techniques in the study of morphological function.

Using similar Finite Element Analysis (FEA), Smith *et al.* (2014) built a framework whereby mechanical correlates of intraspecific morphological variation are evaluated through GM. These tools were used to virtually visualize and reconstruct Chimpanzee crania and subsequently describe the reaction of the biomechanics of this species when exposed to various strains and loadings. A weakness of using such methods is shown in that, as the authors suggest, there is yet to be created a tool that efficiently and quantitatively assesses the strain patterns between the varying specimens. Because of this, the authors could not be confident within their results, concluding that their research provides a 'rough framework' for undertaking such an experiment.

The study conducted by Smith *et al.* (2014) shows how geometric morphometric analysis is a continuingly evolving technique that can be structured and reworked to benefit the testable specifics of a study. With the advent of open-source platforms such as R, researchers are able to provide technical, 'rough' frameworks, such as Smith *et al.* (2014), for other studies to improve upon so that the most accurate and relevant information is reported with minimal introduced observer error.

3.5.1.2 Systematics

Systematic procedure makes use of phenetic affinities based on traditional morphometric studies to assign fossils to hominin taxa. Landmark-based GM analysis is a superior tool for revealing taxonomic patterning between individual fossils that share morphological affinities, as this methodology can encompass size, sex and ontogeny as morphogenetic factors (Baab *et al.* 2012:156).

Baab and McNulty (2009; Baab *et al.* 2012) exemplify the use of GM analysis in systematic study through their exploration of static allometry, or the relationship between size and shape, of the Flores 'hobbit' fossils. The team used allometric and phenetic analyses to reveal strong affinities between *H. florensiensis* and the cranial fossils of Pleistocene hominin, such as *H. habilis* and *H. erectus.*

Similarly, Senut *et al.* (2001) used GM techniques in order to analyse the fossil remains of hominid species, *Orrorin tugenensis.* Differential diagnoses were used in order to compare the fossils in question with those associated with Australopithecus and Ardipithecus. From this, the authors were able to place the species *Orrorin* within the hominid lineage. This significant discovery through GM analysis validates the hypothesis that the divergence between apes and hominids took place prior to 6 Ma and more likely occurred between 9 and 7 Ma.

Comparative studies concerning genetic drift have also been used to comment on the study of hominin taxonomy. Schroeder *et al.* (2014) reported GM results that supports the notion of genetic drift playing a principal role in diversifying cranial morphology among hominin species, particularly between Australopithecus and Homo species. The team used 3D landmarks and laser scanners to visualize homologous structures across the varying fossil specimen.

Subsequently, these results were analysed by way of the hypothesis of proportionality, i.e. within-group variation and between-group variation, indicating diversification between taxa. The results led the team to argue that non-adaptive processes must be incorporated into models of evolutionary adaptation alongside adaptive processes. Schroeder *et al.* (2014) provides a valuable insight into the implementation of a conceptual framework in order to characterize evolutionary pathways. Also, this research shows how theoretical frameworks, such as the quantitative evolutionary theory, can be used successfully in conjunction with quantifying GM statistical testing.

Zichello *et al.* (2018) used GM analysis and extant ape cranial morphology to provide similar commentary regarding taxonomic classification and genetic diversity. The team's findings demonstrate that the enormity of genetic diversity within the extant ape study sample explains a large proportion of cranium shape variation, indicating that species which are more genetically diverse will often be also more cranially diverse. Their results suggest that genetic drift, as well as other neural evolutionary processes such as mutation and gene flow, can be seen genetically as well as in the cranial diversity among ape species.

Computerised geometric morphometric analysis is useful to evolutionary systematists as reconstruction of incomplete fossil specimen is possible through targeted digitisation of landmark estimation from an overall mean reference. Gomez-Robles *et al.* (2007) used this technique to reconstruct the mesial and distal borders of early hominin fossil tooth specimen which had been affected by wear. They were able to successfully demonstrate quantified variance in upper first molar morphology across early hominin taxa, most specifically between *H. sapiens* and *H. neanderthalensis.* Reconstructive landmark-based GM analysis allowed the team to report retained primitive dental morphology in modern humans.

Comparative geometric morphometric study is an insightful tool providing a better understanding of early hominin systematics which Robinson (2012) exemplifies through their use of 3D GM techniques studying intraspecies morphological variation of the mandibular corpus within the extant primate species, *Pan*. The author compared 3 species of *Pan* as well as various species of fossil hominins, using General Procrustes Analysis (GPA), Principal Component Analysis, MANOVA, Mean Square Errors and Discriminant Function Analysis as statistical tools to find variation patterning in the Procrustes-aligned dataset.

McNulty *et al.* (2006) utilized a similar comparative approach to assess the taxonomic similarities of the Taung Child fossils. Using developmental trajectories sourced from extant ape and human taxa, McNulty *et al.* (2006:288) predicted the juvenile specimen's adult morphology. The results suggested that the estimated Taung adult specimen is most similar to *Australopothecus africanus* of Sterkfontein and more specifically comparable to the STs 71 specimen of the same species (Baab *et al.* 2012:156).

Ackermann (2002) tested the validity and implication of comparative GM techniques by studying the patterns of covariation that exist within extant primates, used as living analogues, to allow for interpretation regarding early hominid facial variation. Through variation/covariation matrix correlations, a common principal component approach and plotted morphological distance distributions, Ackermann (2002:181) found that, although it is often comparable, phenotypic variation between apes and humans is not constant.

Ackermann does stress the use of cautious approach for studies using a similar, comparative methodology as we can only ‘assume consistency in variation structure between fossil and extant species. However, they conclude that variation patterns that do indicate phylogenetic relationships are a valuable source of data for understanding how evolutionary variation patterns change within the hominoid lineage (Ackermann, 2002:185).

3.5.1.3 Environment and Evolutionary Morphology

Most pertinent to the study at hand is research undertaken through the use of GM analysis with ecological variance in mind. Generally, geometric morphometric studies regarding ecology look to homologous comparative structures such as limbs (Young *et al.* 2010), teeth, mandibles and hominoid crania (Zelditch *et al.* 2009), in relation to known environmental niches and specialised diets, in support of evidence towards developmental, phylogenetic and functional constraints (Macho, 2013).

There are various statistical techniques suitable for superimposed landmark data, i.e. subsequent to Generalised Procrustes Analysis, that can help to explore patterning in shape, e.g. PCA, Group Comparison MANOVA, Phylogenetic Least Squares (Sherratt, 2016:11). MacLeod (2006) asserts that to explore morphology in relation to ecological variables associated with the assigned specimen taxa, the best approach is through multiple regression.

Multiple regression methods allow for a comparison of ‘linear patterns of variation in a dependent variable’ (e.g. morphology) to linear variation patterning within a set of independent variables (e.g. ecology type). From this, one can make assertions regarding the overall significance between independent and dependent variables, as well as detailing the structure of the existing variation patterns, i.e. the strongest or weakest patterns of covariation (MacLeod, 2006:36).

Casini (2013) exemplifies the successful use of ecomorphological analytical procedures using GM techniques and regression methods. Using known ecological biomes of extant ungulates in relation to craniomandibular morphology, Casini (2013:212) identified correlations between habitat type and morphological form and related morphology to feeding behaviour within the various ecological niches. PCA scatter plots and eigenvector tables were used to report and visualise results alongside Thin-plate Spline deformation grids to depict the degree of shape warping from the reference to target means.

Though comparative phylogenetic studies of hominid variation (e.g. Ackermann, 2002; Uchida, 1992) and ecomorphological studies exist for pre-historical fossil specimen (e.g. Martinez *et al.,* 2014; Casini, 2013; Anton *et al*., 2002), there are relatively few studies concerning specifically early hominin covariation between skull morphology and habitat type that adopt a comparative approach. Comparative approaches have been exemplified as useful ways of gleaning insight into trait evolution and morphological affinity patterning and, though should be used cautiously as Ackermann suggests (2002:185), is regarding by Monteiro (2013:25) as 'one of the most important parts of the morphometric toolkit for studies of morphological evolution'.

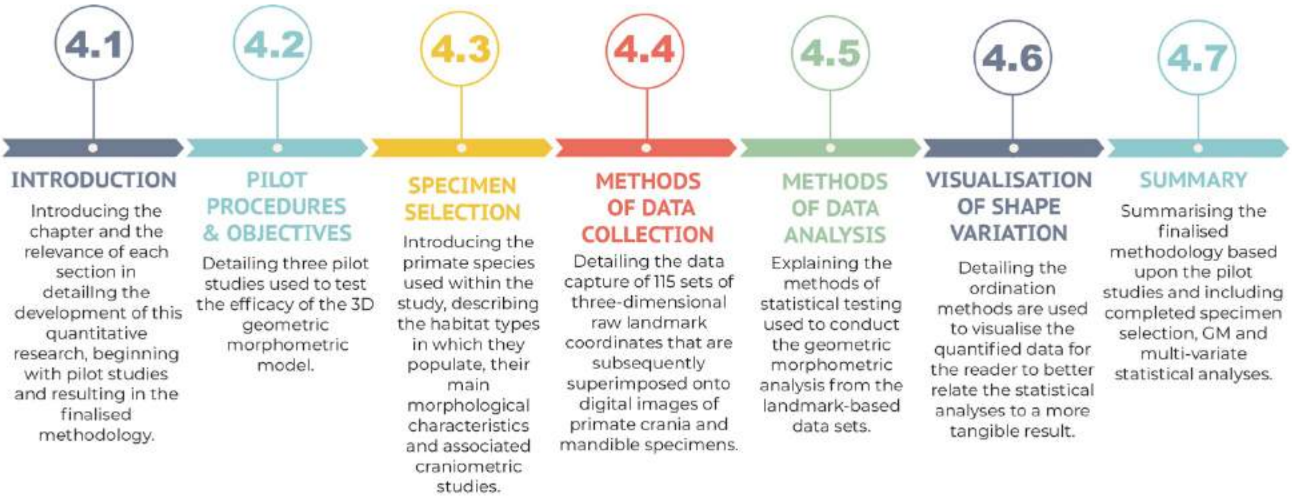
Correlative, phenotypic comparison of extant hominoid craniomandibular morphology would add quantifiable and replicable insight to the development of early hominins and will help to fill the gap within current literature regarding covariation of skull shape and habitat type.

3.6 Summary

This chapter has outlined the use of geometric morphometric techniques particularly within evolutionary studies, from the earliest form of traditional morphology to the modern, automated 3D morphometric analyses. The process of landmark positioning, superimposition by way of Generalised Procrustes Analysis and graphical visualization techniques, e.g. Principal Components Analysis and Thin-plate Spline deformation grids, are explained with examples of successful application in human evolutionary research. Weaknesses of geometric morphometric analysis are reported as introduced observer error and replicability of landmark placement, with an emphasis on how these limitations can be overcome in future studies.

A gap in the current paleoanthropological literature suggests a need for exploration of ecomorphological study of early hominins. **Chapter Four** shows the development of the GM methodology including digitisation of specimen imagery and selection of landmarking software used to collect shape data. The following chapter will also analyse the statistical methods relevant to this ecomorphological study, i.e. ANOVA, Two-block partial least squares, Principal Components Analysis and Thin-plate Spline grids, used subsequent to generalised Procrustes analysis to standardise shape information. A detailed plan of the methodology shows the steps taken in this GM study which is applied to extant primate species craniomandibular morphology with a view to understand inter/intra-species shape variation that exists in relation to contemporary habitats. This will allow for discussion regarding the bearing of ecology on the morphology of skull shape in early hominins.

4 MATERIALS AND METHODS



4.1 INTRODUCTION
Introducing the chapter and the relevance of each section in detailing the development of this quantitative research, beginning with pilot studies and resulting in the finalised methodology.

4.2 PILOT PROCEDURES & OBJECTIVES
Detailing three pilot studies used to test the efficacy of the 3D geometric morphometric model.

4.3 SPECIMEN SELECTION
Introducing the primate species used within the study, describing the habitat types in which they populate, their main morphological characteristics and associated craniometric studies.

4.4 METHODS OF DATA COLLECTION
Detailing the data capture of 115 sets of three-dimensional raw landmark coordinates that are subsequently superimposed onto digital images of primate crania and mandible specimens.

4.5 METHODS OF DATA ANALYSIS
Explaining the methods of statistical testing used to conduct the geometric morphometric analysis from the landmark-based data sets.

4.6 VISUALISATION OF SHAPE VARIATION
Detailing the ordination methods are used to visualise the quantified data for the reader to better relate the statistical analyses to a more tangible result.

4.7 SUMMARY
Summarising the finalised methodology based upon the pilot studies and including completed specimen selection, GM and multi-variate statistical analyses.

Figure 4.1: Chapter Four Materials and Methods roadmap summarising the utility of each section towards finalising the 3D geometric morphometric methodology.

4.1 Introduction

The previous chapters illustrate gaps within late Miocene and early Pliocene hominin paleoanthropological research due to lack of and/or incomplete fossil evidence. These chapters have also discussed a shift in fossil shape data collection, from historically qualitative-based methodologies to quantitative approaches, due to advances in image capture and analytical software. Geometric morphometric analysis has been introduced in the previous chapters as a particularly effective approach to quantifying shape variation in fossil specimens.

Drawing from these issues, and advancements in portable digital imaging and analytical technology, this chapter details the development of the quantitative research methodology, beginning with pilot studies that test 3D scanning technology and analytical software capable of performing GM analyses. The finalised methodology is used to collect raw landmark data and perform multivariate statistical testing to answer the main research questions.

4.1.1 Stating the null hypotheses

The null hypotheses tested in this study are:

- Interspecies Primate Crania: Habitat will have no statistically significant effect on interspecific primate cranial morphology and show no patterning of morphological variance

- Intraspecies Primate Crania: Habitat will have no statistically significant effect on intraspecific primate cranial morphology and show no patterning of morphological variance
- Interspecies Primate Mandible: Habitat will have no statistically significant effect on interspecific primate mandible morphology and show no patterning of morphological variance
- Intraspecies Primate Mandible: Habitat will have no statistically significant effect on interspecific primate mandible morphology and show no patterning of morphological variance

4.2 Pilot Procedures and Objectives

Three pilot studies were conducted to test the efficacy of the geometric morphometric model. The objectives of the pilot phase were as follows:

- To define the biologically homologous points on primate mandible and crania for collecting landmarking data
- To research and pilot test suitable data collection instruments, i.e. digital imaging technology and landmark placement software
- To research and pilot test different data analysis tools to complement the data collection output with a view to answer ultimate research questions
- To gain an in-depth understanding of the landmark-based geometric morphometric framework and how this would fit into the comparative nature of the study

- To gain an understanding of the variables for consideration when geometric morphometric analysis is performed
- To test and refine the finalised methodology using chosen data collection and analysis tools

4.2.1 Material Research and Development

Directed by the research proposal, this study would use modern 3D scanning technology and analytical software capable of harnessing raw shape data and facilitating a geometric morphometric analysis. Preliminary research identified various relevant modes of scanning and analytical tools. It was, therefore, necessary to perform initial tests to narrow down the most effective equipment for the study.

4.2.1.1 3D Scanners and Specimen Digitisation

Computer-assisted palaeoanthropology is a popular form of methodology and is championed by numerous scholars (e.g. Marfart *et al*., 2004; Katz and Friess, 2014; Neubauer *et al*., 2010; Smith *et al*., 2014; Zollikofer *et al*., 2005) who suggest that, as well as providing a very accurate level of data collection, such techniques also have great potential for disseminating knowledge to the public. Groups, such as the EVANS society, work towards making available all studies and resulting data regarding virtual anthropology in the hopes of furthering our knowledge of morphometrics and physical anthropology on a global scale.

With growth in popularity comes advances in relevant technology, and as such, scholars are now able to expand their research using innovative methods. Marfet *et al.* (2004) discuss how statistical geometric morphometrics has been chiefly applied to two-dimensional CT image analyses or a limited number of specific landmark points. Technology such as 3D laser scanning allows for a globalized view of specimens that do not limit the number or location of landmarks that can be used and therefore bridges a gap in the knowledge of geometric morphometrics by markedly widening the data readily available for collection.

3D laser scanning is a non-destructive tool that provides an accurate representative model for quantitative analysis. Freiss (2012:1) advocates the use of laser scanners, arguing that such technology offers sufficient precision following allowable errors within standard anthropometry. A scanner will often have a known, quantifiable measurement of error that can be accounted for within the study.

Portable 3D laser scanners are used in medical fields such as dental, orthopaedics, plastic surgery, and craniometry and have been argued as data collection tools. For example, Kau *et al*. (2005), in their assessment of reliability concerning 3D laser scanning, argued that 3D imaging is a dependable tool in assessing changes in craniofacial morphology due to treatment and growth. Aung *et al*. (1995) analysed the accuracy of 3D laser scanning compared to traditional anthropometric measurements and concluded laser scanning to be a 'useful tool' in addressing facial measurements. However, they suggest that accurate locations of specific landmarks and reliable operator skills are important factors that must be enforced when using 3D imaging technology.

Within palaeoanthropology, 3D laser scanning is beginning to be applied more frequently due to the innovation of technology that is more widely accessible. Freiss *et al.* (2001) employed a 3D laser scanner with human and fossil specimens to assess craniofacial morphological variation and responses to cold adaptations. The team concluded that the human braincase is adapted to minimise heat loss under cold environmental conditions. However, they also argued that facial morphology does not react in this way, and neither does the data conform to the existing models of climate-induced adaptation. Therefore, Freiss *et al.* (2001:35) suggests that paleoanthropologists seek alternative theories for cold adaptations.

The research conducted by Freiss *et al.* (2001) exemplifies the strengths of 3D laser scanning technology as a tool within palaeoanthropology and human evolution. By adopting a 3D approach and analysing the subsequent data, Freiss *et al.* (2001) were able to test theories of environmental adaptation and present further informed conclusions that questioned previous theoretical frameworks.

4.2.1.1.1 Sourcing the appropriate 3D scanner to specification

Functionality and precision dictated the source of a 3D scanner for this study. Desktop laser scanners were the preferred choice as these were relatively inexpensive, large enough to facilitate the scanning of crania and mandible specimens and would be lightweight for transport to museum archives and for demonstration in a seminar or class setting.

A checklist of necessary qualities (see **Table 4.1**) dictated that the ideal desktop scanner would be easily portable, able to scan up to an accuracy of 0.1mm, have a wide scanning range capable of scanning the largest skull specimen and house suitable software able to clean, combine and mesh multiple scans.

Out of the handheld and desktop 3D scanners researched for this study, the SOL, Shining 3D EinScan and Matter and Form scanners had more accurate scanning capabilities compared to the BQ Ciclop and HP Z 3D scanners. The HP Z 3D technology was the only scanner to not offer suitable meshing and cleaning abilities.

Ultimately, the Matter and Form 3D desktop laser scanner was deemed most suitable to carry out digital imaging of the specimen used in this research. The Matter and Form (2014) scanner provides 3D virtual models of up to 18cm x 25cm-sized objects. The lightweight and easily transportable characteristics of this particular foldable scanner were ideal for collecting images of mandible specimens and the accompanying crania. The scanning accuracy captures details' as small as 0.43mm and size within 0.1mm (Matter and Form, 2018).

	Matter and Form 3D Scanner	**BQ Ciclop**	**SOL 3D Scanner**	**HP Z 3D Scanner**	**Shining 3D EinScan**
Easily Portable	✓	✓	✓	✓	✓
Suitable Scanner size (to accomodate largest skull specimen)	✓	-	-	-	-
Software for cleaning and meshing multiple scans	✓	✓	✓	-	✓
Accuracy up to 0.1mm	✓	-	✓	-	✓

Table 4.1: 3D scanning tools and software were chosen for use in this study based on a list of necessary criteria, e.g. portability, accuracy, size of laser scanning dimensions and software capabilities. Easy portability was a desired trait as scanning would take place in a museum setting. A large enough scanning size dimension was needed to be able to capture the detail of the largest skull specimen (*Gorilla gorilla*) and needed to possess accuracy of up to 0.1mm to ensure a precision scan. Accompanying software needed to possess the ability to clean, combine and mesh multiple scans. Ultimately, the Matter and Form 3D scanner was solely shown to possess these necessary qualities.

Figure 4.2, 4.3 and 4.4: Matter and Form 3D Laser scanning human cranium with view of laser and live feed mount, as well as white calibration box on turntable. The images above show the generous size of the desktop scanner in relation to an adult human skull. Due to the lightweight hardware and ease of set-up, the scanning capabilities were exemplified in a live demonstration where the scanner calibrated light levels and background feed and subsequently generated a raw 3D digital image of a hominin mandible replica with one pass of the scan.

4.2.1.2 Landmarks

Landmarks are used in geometric morphometric analyses to define homologous anatomical points on a specimen. The constellation that arises from landmark measurements contains information regarding the shape of the specimen that can then be correlated with all other individuals within the study (Zelditch *et al.*, 2012:23). Zelditch *et al.* (2012:25) define criteria for selecting and placing landmarks of a specimen that include consistency, adequate coverage and repeatability. The section below synthesises the appropriate landmark placement for the primate skull specimens used in this study.

4.2.1.2.1 Defining Landmark Placement

As Zelditch *et al*. (2012) states, homology is an important factor in choosing landmark placement, as this biological point will need to be reproducible among all specimens within the study. For example, a landmark that has been placed on the nasal bone of a skull will correspond to the location of a landmark found on the nasal bone of another skull specimen. Zelditch *et al*. (2012:28) also stress the importance of landmarks having 'adequate coverage of the form'. This is due to unobtainable data where landmarks have not been placed or are considered missing. Covering the entire form of the specimen with sufficient numbers of landmarks allows for a more accurate representation of the overall shape of the specimen.

Repeatability is another criterion that Zelditch *et al*. (2012:29) defines as vital for choosing landmark placements. Measurement error can occur when a landmark cannot be found easily on a specimen. Accuracy and precision are significantly reduced when multiple measurements are taken for a landmark whose position is difficult to locate. In addition to this, landmarks can invariably switch positions to one another. Landmarks that seem to correspond may not match exactly due to the anterior or posterior locations of the landmark. The authors emphasise areas of particular caution that prove to be an issue regarding landmarks switching position, i.e. foramina and sutures (Zelditch *et al.,* 2012:31).

In analysing hominin and primate morphological variation, it is advantageous to implement techniques from craniometric and cephalometric studies that employ traditional landmark placements. Many disciplines employ modern craniometric methods to measure cranial facial form, including orthodontics and forensic science (e.g. Durão *et al.,* 2014; Krogman, 1951; Richard *et al.*, 2014; Kranioti *et al.*, 2008). Such techniques can also be seen widely within paleoanthropological and physical anthropological research. Hermann Schaaffhausen, for example, used primitive forms of craniometric techniques to correctly identify Neanderthal fossils as descendants of man who roamed Europe during the Glacial Period (Zängl-Kumpf, 1992:335).

Implementing a defined set of traditional craniometric landmarks (described in **Table 4.2)** will provide a homologous basis of landmark placement on all primate mandible and cranial specimens involved within this research, which can be easily reproduced. This ensures adherence to the criteria defined by Zelditch *et al.* (2012). Eight further landmark points were added to the mandible set as this inclusion will provide maximum shape data output.

Craniometric Landmarks	**Description of position**
Euryon	The most superior point along the upper margin of the external acoustic meatus (Moore-Jansen *et al*. 1994: 62; Martin and Knussmann 1988: 164).
Bregma	The posterior border of the frontal bone in the mid-sagittal plane (Moore-Jansen *et al*. 1994: 62; Howells 1973: 167).
Frontotemporale	A point located generally forward and inward on the superior temporal line directly above the zygomatic process of the frontal bone (Moore-Jansen *et al*. 1994: 63; Martin and Knussmann 1988: 167).
Frontomalare temporale	The most laterally positioned point on the fronto-malar suture (Moore-Jansen *et al*. 1994: 63; Martin and Knussmann 1988:164).
Ectochonion	The intersection of the most anterior edge of the lateral orbital border and a line parallel to the superior orbital border that bisects the orbit into two equal halves (Moore-Jansen *et al*. 1994: 62; Howells 1973: 168).
Zygoorbitale	The intersection of the orbital margin and the zygomaxillary suture (Moore-Jansen *et al*. 1994: 64; Howells 1973: 170).
Dacryon	The dacryon is the point on the frontal bone where the frontal, lacrimal and maxillary sutures meet (Moore-Jansen *et al*. 1994: 62; Howells 1973: 167; Martin and Knussmann 1988: 166).

Nasion	The point of intersection of the naso-frontal suture and the mid-sagittal plane (Moore-Jansen *et al*. 1994: 63; Howells 1973: 169, Martin and Knussmann 1988: 165).
Zygion	The most laterally positioned point on the zygomatic arches (Moore-Jansen *et al*. 1994: 64; Martin and Knussmann 1988: 167).
Zygomaxillare anterior	The intersection of the zygomaxillary suture and the limit of the attachment of the masseter muscle, on the facial surface (Moore-Jansen *et al*. 1994: 64; Howells 1973: 170).
Prosthion	The most anterior point on the alveolar border of the maxilla between the central incisors in the mid-sagittal plane (Moore-Jansen *et al*. 1994: 63; Howells 1973: 169).
Ectomolare	The most lateral point on the buccal surface of the alveolar margin (Moore-Jansen *et al*. 1994: 62; Martin and Knussmann 1988: 167).
Alveolon	The point where the mid-sagittal plane of the palate is intersected by a line connecting the posterior borders of the alveolar crests (Moore-Jansen *et al*. 1994: 61; Martin and Knussmann 1988:167).
Radiculare	The point on the lateral aspect of the root of the zygomatic process at the deepest incurvature (Moore-Jansen *et al*. 1994: 63; Martin and Knussmann 1988: 164).

Basion	The point at which the anterior border of the foramen magnum is intersected by the mid-sagittal plane opposite nasion (na) (Moore-Jansen *et al*. 1994: 61; Howells 1973: 166).
Opisthion	The point on the inner border of the posterior margin of the foramen magnum in the mid-sagittal plane (Moore-Jansen *et al*. 1994: 63; Martin and Knussmann 1988: 163).
Opisthocranion	The most distant point posteriorly from glabella on the occipital bone, located in the mid-sagittal plane (Moore-Jansen *et al*. 1994: 63; Martin and Knussmann 1988:162).
Lambda	The apex of the occipital bone at its junction with the parietals, in the midline (Moore-Jansen *et al.* 1994: 63; Howells 1973: 168; Martin and Knussmann 1988: 162).
Gonion (go)	The point at which the mandibular corpus and ascending ramus meet; the midpoint of the mandibular angle (Moore-Jansen *et al.* 1994: 63)
Gnathion (gn)	The midpoint on the lower border of the mandible (Wai *et al.* 2015:2); Moore-Jansen *et al.* 1994:63)
Infradentale (id)	Point of alveolar contact with the lower central incisor (Velemínská *et al.* 2008:5; Moore-Jansen *et al.* 1994:63)

Condylion (cdl)	Mental protuberance at the front of the jaw forming the chin
Mental foramen	Two foramina located on the anterior of the mandible surface generally below the 2nd premolar tooth just above the inferior border of the mandible (Soikkonen, 1995:863)
Submandibular fossa	Incurvation seen in the lingual part of the mandible in the lower molar range (Harazono, 2019:137)
Lingual foramen	Singular foramen found on the lingual side of the symphysis of the mandible (McDonnell, 1994:364)
Retromolar trigone	'Roughly triangular' vacant space behind the last molars (Bruch and Treister, 2009:1)
Mandibular foramen	Foramina located on the internal surface of ramus leading to the mandibular canal (Sandhya *et al.* 2015:1)
Coronoid Process	Most superior point of the triangular coronoid process (Inoue *et al.* 2015)

Condylar Process	Most superior point of the condylar process (Marcus *et al.* 1993:336)
Alveolar Process	Thickened bone underneath canine tooth socket on anterior mandibular margin (Srebryznska-Witek *et al.* 2007: 1567)

Table 4.2: Craniometric landmarks with corresponding description of location. Note that semi-landmarks are used along curves between ‘true’ landmarks to describe curvature in more complex structures. After Moore-Janson *et al.* (1994).

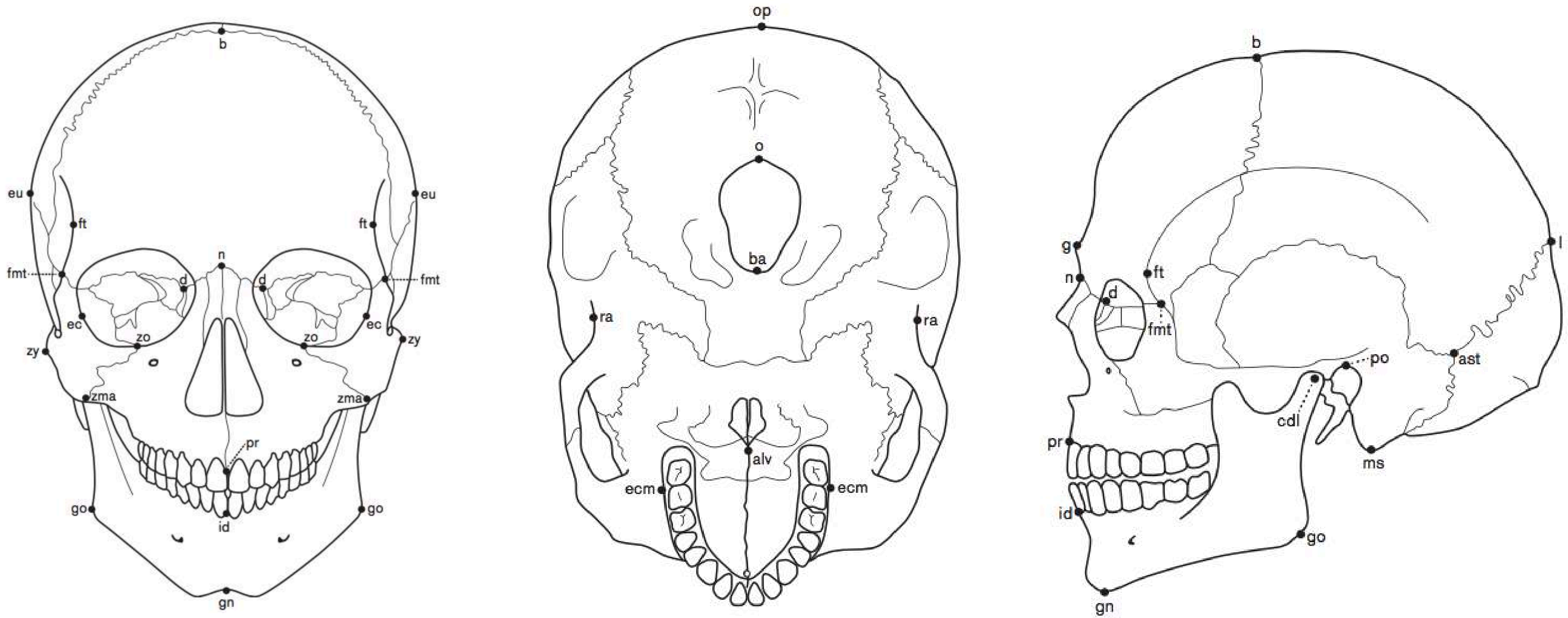


Figure 4.5: Anterior, basal and lateral view of traditional craniometric landmarks (Moore-Jensen *et al.,* 1994:61-62).

4.2.1.3 Landmark Digitisation Software

Before 3D image capture, it was necessary to source suitable software capable of digitising homologous landmarks points onto the virtual images. The software must also be capable of exporting these edited files in a suitable and common file format that could be used in the next phase of data analysis. **Table 4.3** identifies the main landmarking tools available and highlighting their usefulness to this study against a checklist of advantageous features.

Each landmarking tool interface was tested to assess ease of use, the precision of landmark positioning, manoeuvrability, and output of the landmarked image. A 3D digital image of a human skull was landmarked according to traditional and homologous craniometric positions defined by Moore-Janson *et al.* (1994). An essential quality of the landmarking software was the ease of manoeuvrability around the global 3D space of the image. Suitable manoeuvrability ensured clear visibility and enabled precision landmarking, i.e. zooming capabilities that kept resolution strength and easily manipulated the 3D image to reveal smaller bone structures from any angle. **Figure 4.6** and **4.7** shows MeshLabs and R software respectively being tested for suitability as landmarking software using human and primate 3D cranial scans.

The TINA Landmarking Tool was specifically developed to digitise 3D data sets and facilitate the placing of landmarks onto scanned objects and volume rendering capabilities from DICOM files. This would be helpful for the import of 3D scans that were taken as a result of X-ray, CT or more advanced medical imaging tools (Schunke *et al.,* 2012). An advantage of TINA was its ability to handle large datasets as well as the export of landmarked files suitable for further testing and analysis. Testing found the software easy to use and had adequate manoeuvrability in a global environment but lacked the suitable function for automatically generating semi-landmark points along the digitised shape curves, which was vital for this study. **Figure 4.6** shows the testing of MeshLabs software, whereby a 3D digitised human skull was landmarked and exported as multiple file types (OBJ, STL, PLY). The image resolution and global environment were suitable for landmark positioning due to an intuitive user interface; however, MeshLabs, like the TINA landmarking software, lacked a suitable semi-landmark automation function.

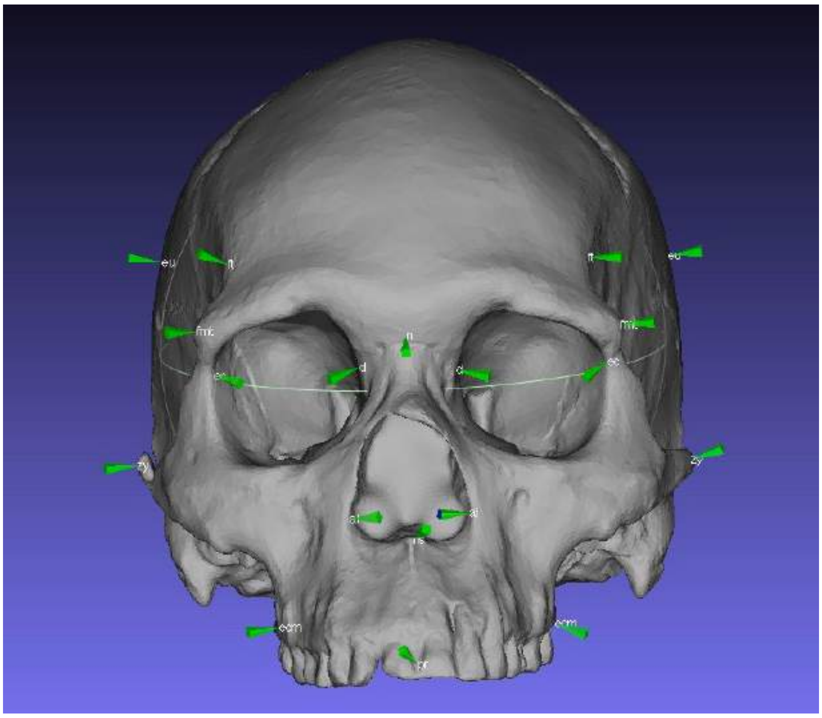


Figure 4.6: MeshLabs landmarking tool tested for accuracy, manoeuvrability and output during pilot testing of data collection tools. The interface and global environment were suitable for landmark positioning but lacked the automated generation of sliding semi-landmarks needed for geometric morphometric analysis.

Similar testing procedures, using Checkpoint by Stratovan, showed this visual analysis software met all necessary requirements. Landmarks could be easily placed, and the software had a suitable interface and manoeuvrable 3D environment. Checkpoint also allowed for importing and exporting of common surface files, as well as the generation of automated sliding semi-landmarks. A limitation of this software is a lack of Integrated Developer Environment (IDE). An IDE feature was preferable to the geometric morphometric study as it affords the freedom to manipulate code where necessary and, therefore, allows for a tailored approach to statistical testing.

The R Project software can apply 3D landmarking to each digital scan and can subsequently automate the placement of sliding semi-landmarks onto curves, the importance of which has been previously discussed in **Chapter 3**. The testing phase of the landmarking software concluded that the R Project platform would be able to suitably facilitate the needs of the study.

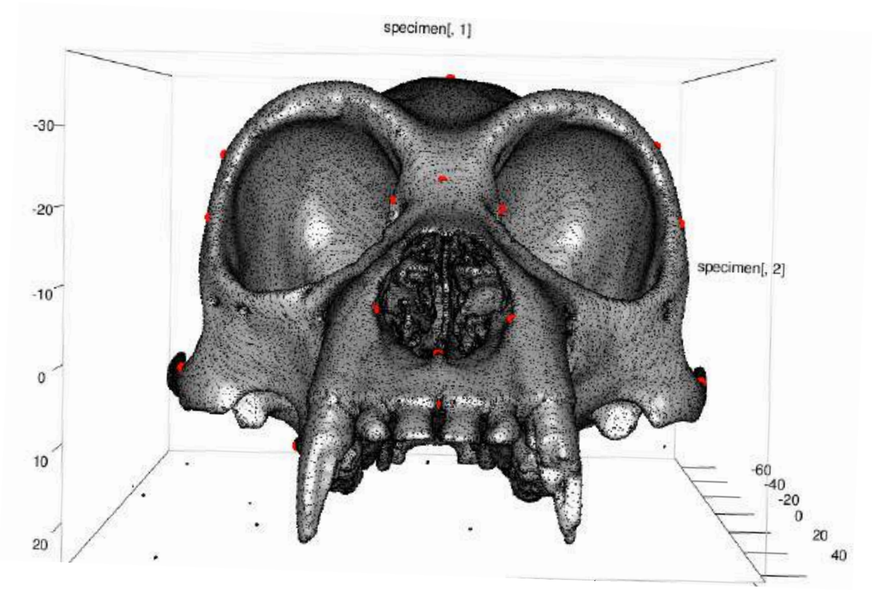


Figure 4.7: R *geomorph* package landmarking hylobate crania during testing phase of data collection technology. This package allows for easy manoeuvrability of the 3D global specimen making landmarking an accurate procedure. Sliding semi-landmarks can be automatically generated with R code which is also a benefit of this software in the form of the IDE, R Studio.

Criteria for landmarking software	TINA	MeshLabs	Checkpoint by Stratovan	R Studio
Able to place landmark points	✓	✓	✓	✓
Automatic generation of sliding semi-landmarks to curves	-	-	✓	✓
Able to load surface data from common file formats PLY, STL, OBJ	✓	✓	✓	✓
3D volume rendering and access to multi-planar view for global specimen landmarking	✓	✓	✓	✓
Online community discussion group	-	✓	-	✓
Integrated Developer Environment (IDE) allowing freedom to manipulate code where necessary	✓	-	-	✓

Table 4.3: During pilot activities, numerous landmarking software were trialled for use within the study. The table shows the suitability of each platform against a checklist of necessary qualities. Possessing an IDE was a favourable aspect in choosing the software as this allows for manipulation of code and offers manoeuvrability in tailoring the GM model and statistical testing to suit the ecomorphological objective. TINA and R Studio software have this capability; however, TINA, as well as

MeshLabs, do not allow for automatic semi-landmarking. TINA and Checkpoint do not currently offer an online community or open source discussion group which is a benefit of R Studio, as coding can be shared and peer reviewed. R Studio was subsequently chosen to apply the 3D landmarks as its suitability facilitated the needs of this study, i.e. multi-planar and 3D rendering for global specimen landmarking, an IDE, open-source community, the ability to work from numerous common working files, and automation of semi-landmarks.

4.2.1.4 Data Analysis Software

Numerous data analysis software were tested for their ability and efficiency to import and prepare the raw landmark data and conduct a full geometric morphometric analysis. Multiple platforms exist for this purpose, all with varying degrees of user interface design and adaptability that would require user training. MorphoJ, for example, is a practical, user-friendly programme that integrates multivariate analysis tools for the collection, manipulation and graphical display of landmarks (Klingenberg, 2011:353). Other systems that were assessed for suitability included Checkpoint Stratovan, Morphologika, EVAN Toolbox and PAST.

Ultimately, the R Project software, accompanied by the IDE R Studio, was chosen to carry out the GM analysis. The R Project platform was previously chosen as the most suitable tool to apply the biologically homologous landmark placements to the digitised specimen images and, owing to the *geomorph* package (Sherratt, 2015a), would be able to facilitate the statistical analyses tested in the pilot study (**Section 4.2.3**) and implemented as part of the final GM analysis.

4.2.1.4.1 Introducing R and geomorph

The R Project is freely available software that comprises numerous integrated packages used for the collection, manipulation, graphical display and distribution of data. A particular coding language, a form of the original S language, is used to create and operate various datasets. Due to its flexibility and constant evolution through open-source development, Venables *et al*. (2015:2) deem R as an ‘environment’ rather than static software that offers inflexible specificity, and so allows researchers and statisticians to become fully interactive with their data analyses. Packages available to R software were created with specific functions in mind. The *geomorph* package, for example, was created to encompass statistical and graphical tools needed for researchers conducting GM analyses (Sherratt, 2015a).

The R environment is a serial interface that allows for the interaction of data analysis to be conducted quickly and with ease. Computational programming language, or command-line scripting, is used within this software, requiring some beforehand training. With the added installation of the *geomorph* package, R is particularly useful for analysing morphometric data (Claude, 2008:6) as it allows for the semi-automation of shape visualisation from landmark point clouds, comparative analysis of shape data in conjunction with phylogenetic frameworks and the graphical exploration and display of this data.

The R environment boasts versatility and flexibility in its variety of tool packages; however, displays a less user-friendly interface than other point-and-click systems, such as MorphoJ and Checkpoint. This meant that learning to understand the R software's input programming language required beforehand user training and the recommended installation of RStudio, which is used as a powerful IDE (Integrated Development Environment), giving the R user a more-friendly interface to work with.

The R environment allows numerous authors to create packages designed specifically for their study's needs, so the platform is constantly evolving and being improved. Also, as there are vast quantities of ‘ready-to-use’ packages for R, such as the *geomorph* package used in this study, there is a plentiful choice to incorporate fully developed statistical and analytical sets into the methodology.

R allows users to check the repeatability of data analysis and also the errors that might exist within the data set; this is due, in part, to the easily accessible and storable list of command lines. Unlike the point-and-click interface of many other geometric morphometric software, i.e., MorphoJ, EVAN Toolbox, etc., varying steps throughout the study are quickly found and reproduced due to the list of the syntax that forms the data analysis – a form of digital code peer-review.

Due to its 3D landmarking, semi-landmarking automation and geometric morphometric and multivariate statistic capabilities, the R Project and accompanying R Studio environment will be used to conduct the analysis using primate specimens. This is due, in part, to the highly successful and useful *geomorph* package created and maintained by Adams, Collyer and Kaliontzopoulou (2020). Owing to the efficiency of this package, data collection is the only aspect of the study that will be completed outside of the *geomorph* package and the R environment (Sherratt, 2015a:4).

4.2.2 Pilot Study 1 – Initial 3D Scanning

The Matter and Form 3D laser scanner requires an optimal environment set up to achieve suitable virtual renderings. This became apparent in the first scanning tests featuring a deer skull, which was chosen due to its relatively small and simple form. **Figures 4.8**, **4.9** and **4.10** show the scans taking place through the software live feed, as well as the digitising on-screen. Noise distortion is present in the background of the renderings due to a busy room environment. As can be seen in **Figure 4.10,** the lighting was too irregular for the scanner to evenly feedback shape and form, causing shadows on the subject and missing areas of surface rendering.

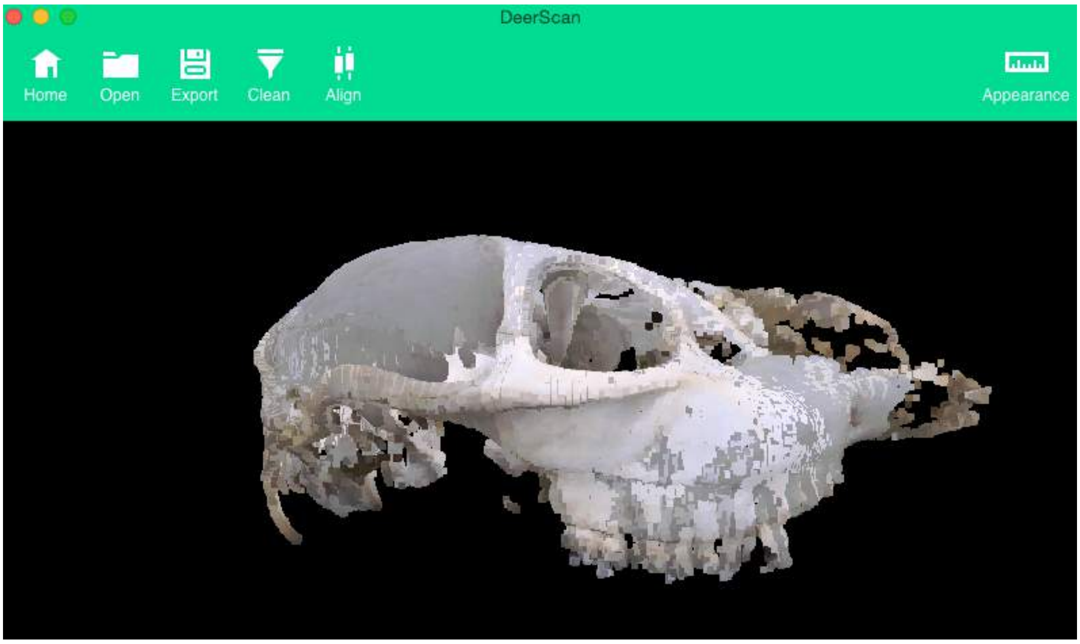


Figure 4.8: Lateral view of the Matter and Form scanner digitising a small deer skull during pilot testing. Shadows are present on the surface of the specimen due to poor lighting and areas of the bone surface are being missed by the laser scanner due to shadowing.

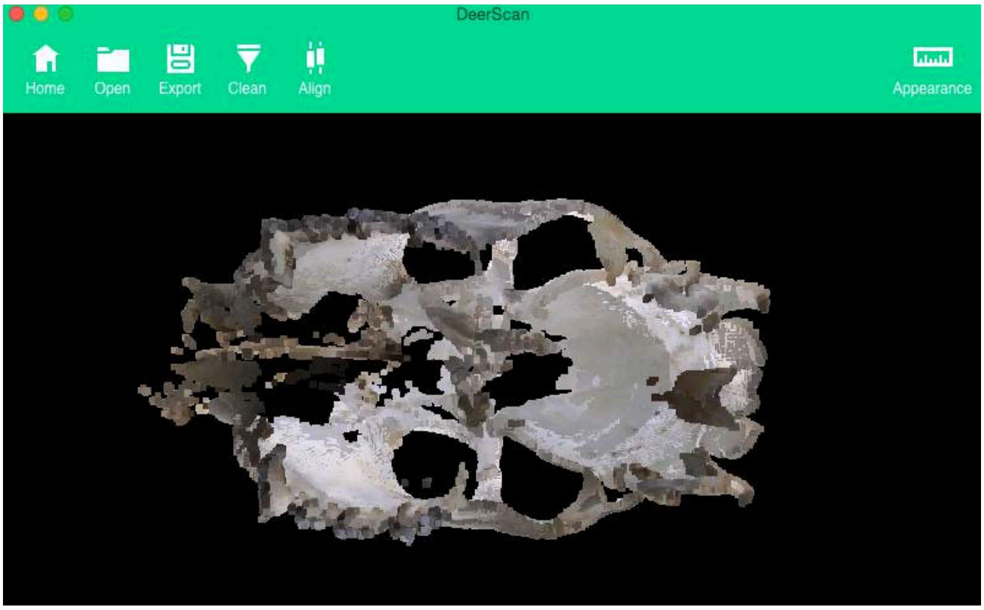


Figure 4.9: Superior view of small deer cranium digitised by the Matter and Form 3D Scanner showing areas of poor scan quality due to shadowing and low lighting.

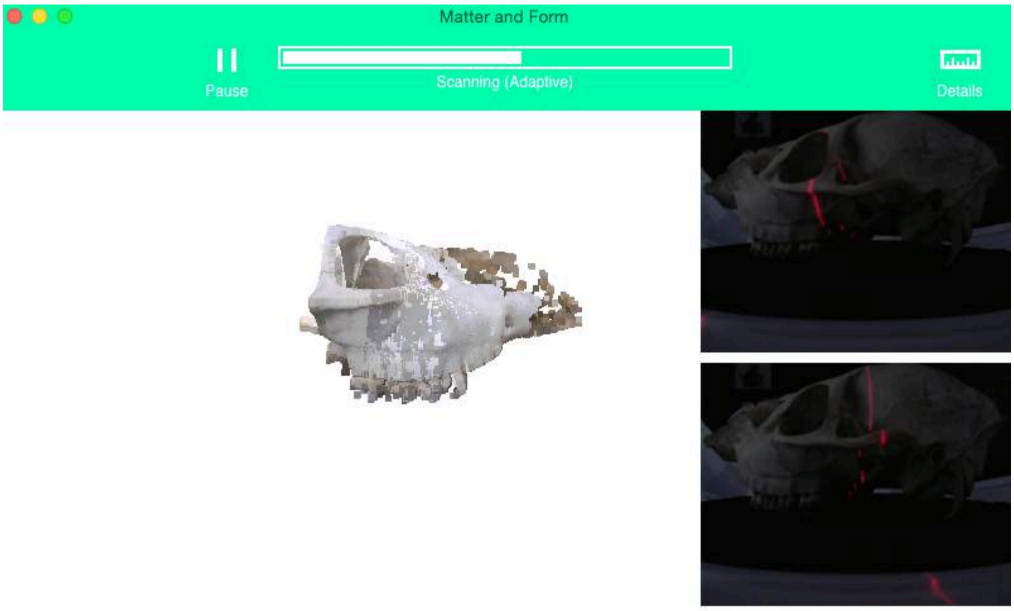


Figure 4.10: Matter and Form software view during scanning session of small deer skull. The right-hand side of the image shows the live feed from the scanner whilst the left-hand side depicts the digitisation of the laser scan. Poor lighting can be seen on the live feed which would ultimately distort the final scan through shadowing.

4.2.2.1 3D scanning sensitivities and required adjustments

Pilot tests of the Matter and Form scanner showed the sensitivity of the equipment to light and room environment. Any background activity affected the scan accuracy and added digital noise to the rendering; shadows affected the surface scanning of the specimen; and fragile, irregular shaped specimens, such as the deer skull, that could easily move about the scanning turntable proved difficult to scan, i.e. when scanning the superior portion of the cranium the specimen wouldn't remain balanced or stationary due to the movement of the plate beneath it.

4.2.2.1.1 Lighting and background

Scanning in a bright and evenly lit environment, as well as calibrating the scanner before each run, would ensure optimum results as confirmed through direct communication with the Matter and Form development team. Keeping the scanning camera facing away from excessively bright or harshly reflective backgrounds, i.e. windows, mirrors, screens etc., would ensure no shadows where cast onto the object's surface. Consequently, a photography tent was sourced (see **Figure 4.11**) so that lighting surrounding the scanner could be controlled and replicated for subsequent scans.

With the scanner placed inside the photography tent and the specimen placed securely on the turntable, evenly diffused light could be controlled using overhead and side lamps, reducing shadowing around the scanner. The opaque backdrop of the photography tent ensured no background noise, i.e. foot traffic, window reflections and uneven room lighting could interfere with the scanning laser, adding points in the shape space that don't exist, and obscuring the final digital image.

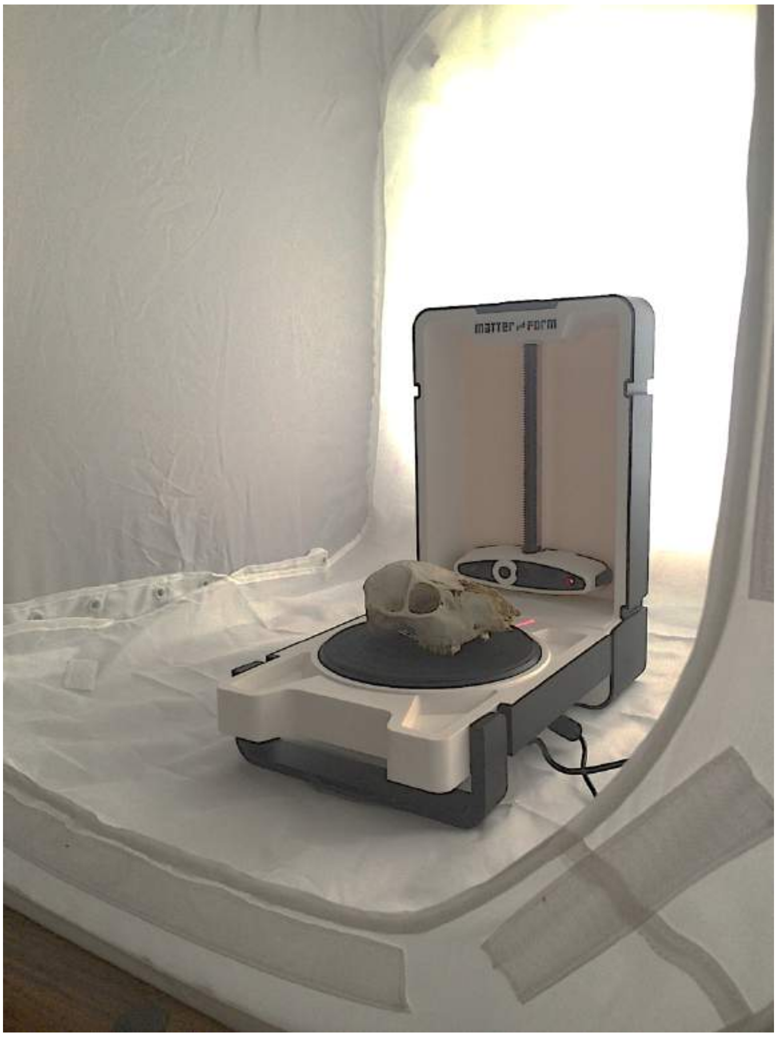


Figure 4.11: Matter and Form 3D laser scanner placed in lighting tent to produce digital rendering of deer skull.

4.2.2.1.1 Securing fragile specimen

Securing fragile and easily disturbed specimens would be achieved via custom packing foam mounts, ensuring the security of the specimen on the scanner turntable without damaging the surface of the object. Multiple scans of each specimen were taken and combined using the Matter and Form merge function, which allowed for a more accurate final result of the digital image. **Figures 4.12** and **4.13** show the adapted scanning process of an *H. ergaster* mandible replica fossil. The updated scanning procedure made use of the light tent, multiple scan passes and stability assurance of the specimen.

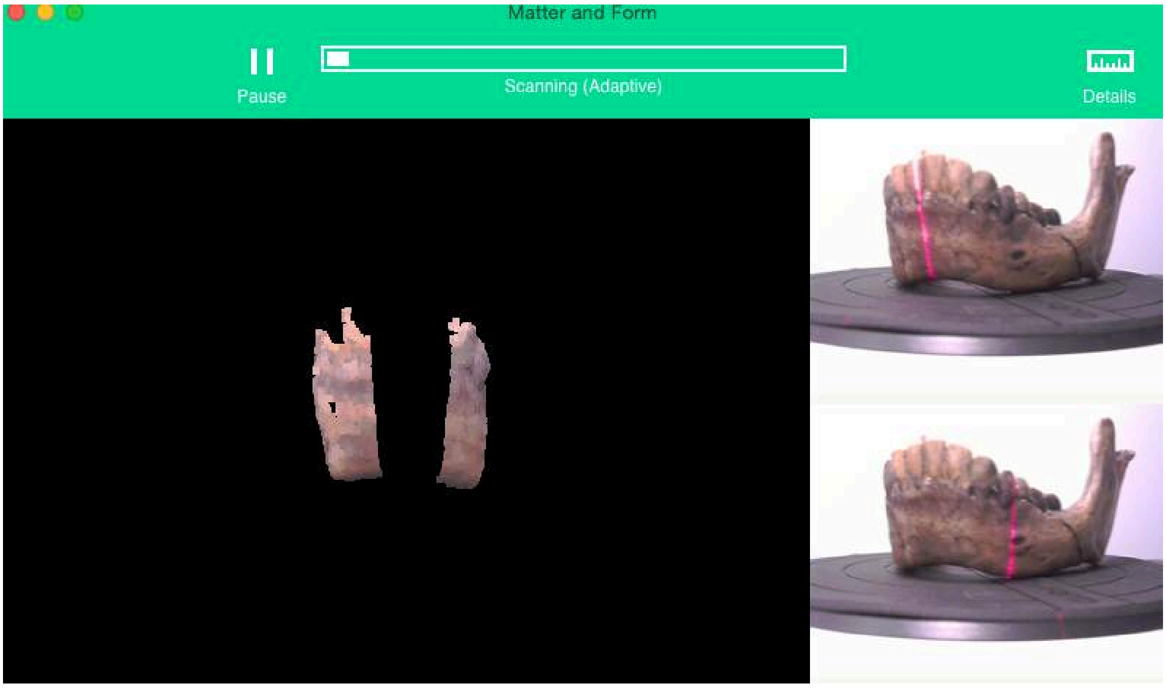


Figure 4.12: Scanning replica mandible fossil BH 102 belonging to H. *ergaster* skull KNM-WT 15000. The live feed on the right of the image shows improved lighting whilst using a photography tent to produce an even and bright environment. This method also reduced background activity ultimately reducing digital noise pollution.

Figure 4.13: Final 3D scan of mandible fossil replica BH 102 of *H. ergaster* skull KNM-WT 15000. Achieving this accurate scan completed the pilot testing phase of the Matter and Form scanner.

4.2.2.1.1 Expanding the dataset to reduce sample size error

Whilst the Matter and Form scanner contained all necessary software needed to process and export 3D scans suitable for GM analysis, one challenge encountered during the pilot test phase was the lengthy scanning time required to produce accurate image results of an entire skull. A single pass of a primate cranium took approximately 6-8 hours to complete, depending on the size of the specimen and the species. Scanning a gorilla skull, for example, was a lengthier process in comparison to a gibbon skull. Longer scanning time meant increased dependability on dedicated lighting and photography tents to ensure a stable background environment. Multiple scans of each specimen would be taken, and the renderings cleaned and combined into meshes in order to strengthen precision and intra/inter-observer reliability.

To reduce the error impact on the raw shape data and ensure validity of results, the dataset collected at the Oxford University Natural History Museum would be expanded by including data from published material. This would mitigate the risk of decreased statistical power, as well as diminished quality of data due to a small sample size. Completed 3D primate skull scans sourced from the Smithsonian Institution's Human Origins Program 3D Collection (Smithsonian Museum of Natural History, 2020) would be used to ensure a large enough sample size. See **Section 4.2** and **Appendix A** for the complete list of selected specimens.

4.2.3 Pilot Study 2 – Compiling Code with R Plethodon Datasets

It was necessary to learn R command line script in order to correctly use the R Project and Studio IDE software. Initial training on R Programming was completed through John Hopkins University's Open Courseware offered by the Department of Biostatistics. Key skills such as configuring necessary software for statistical programming within the environment, readying data into R, accessing packages, writing functions and debugging, were obtained through this course.

The next phase of learning to use R programming was to understand the process of running geometric morphometric analyses in R code. An appealing factor of conducting morphometric analysis in R is the accompanying *geomorph* package (Adams *et al.* 2020; Adams, Otarola-Castillo & Sherratt, 2014; Adams & Otarola-Castillo, 2013). This tool facilitates all stages of a landmark-based geometric morphometric analysis, including digitising landmarks onto 3D objects, generating Procrustes-analysed shape variables, performing the statistical analysis of shape variation within the given dataset, and visualising results of patterning and variation.

Adams (2004; 2010) provides new users to the *geomorph* package an opportunity to better understand the tools provided by allowing them to trial GM analysis on 2D landmark data sets from Plethodon salamander heads. This dataset was run as part of pilot phase 2 to appreciate how each function, and accompanying options, works within the *geomorph* package, and to understand how the primate mandible and cranium dataset should be formatted for use within R.

The 'Quick Guide to *Geomorph* v2.0' (Sherratt, 2014) showed how a GM analysis is conducted through the *geormorph* package using the Plethodon dataset. Sherratt (2014; 2015) notes that complementary packages would need to be installed that support the *geomorph* package and statistical functions that would be required, i.e. *ape, phytools, rgl* and *geiger*. A description of the uses of these packages can be found in section **4.3.2** where the uses of R and *geomorph* in the finalised methodology are discussed in more detail.

Following Sherratt's guide (2014), landmark data was successfully imported into the R workspace and prepared for analysis using array conversion. Locations of missing landmarks were estimated, and group variables were created; subsequently a Generalised Procrustes Analysis (GPA) was performed creating a superimposition of the raw data. The guide exemplifies how to use the varying covariation, phylogenetic comparative and morphological integration methods that the package facilitates i.e. Procrustes ANOVA, Pairwise Group Comparisons and Two-Block partial least squares analysis. This gave a better understanding as to which statistical methods would be most suitable for the study as well as the most powerful methods of shape visualisation, i.e. Principal Components Analysis and Thin-plate Spline deformation grids.

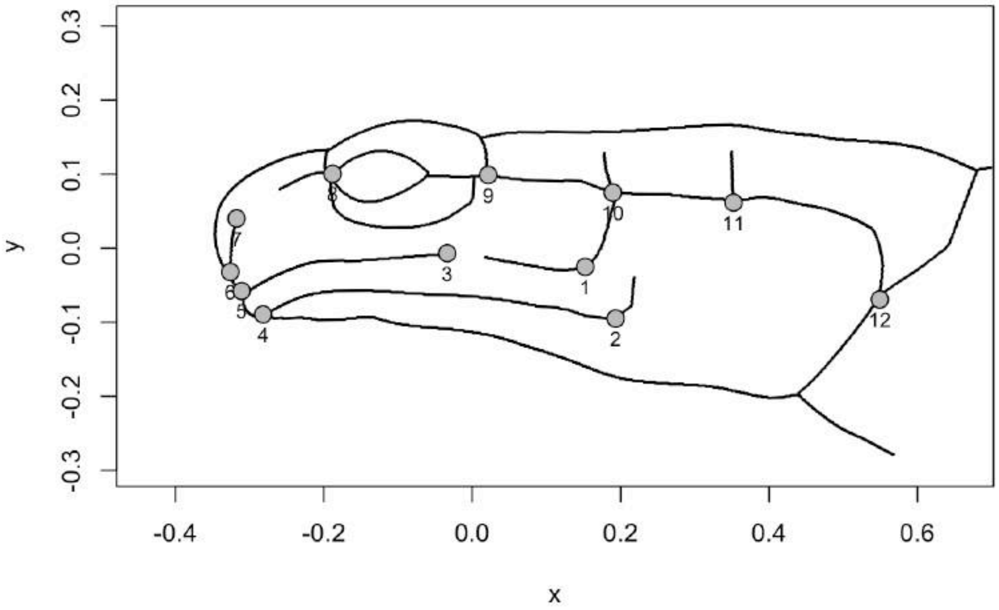


Figure 4.14: 2D landmarks of salamander head dataset available within the *geomorph* package in R.

4.2.3.1 Learning outcomes of trial Plethodon study

One learning outcome of Pilot Study 2 saw the creation of variables and classifiers produced with R code. This was exemplified through the use of the Plethodon data set where the author (Sherratt, 2014) shows how the grouping variables or classifiers within the analysis should be created and imported into R. For this study using various primate specimens, the classifiers will differ in each group testing. For example, a GM analysis will be conducted factoring environmental habitat among different primate species; GM analysis will be conducted on a particular species using the subspecies as a classifier. These classifiers would be defined in Pilot Study 3 and subsequently formatted in excel for use in the final analyses.

Pilot Study 2 also informed a structured design for the statistical analysis used in the next phase of pilot activities. **Table 4.4** shows each statistical test to be used in Pilot Study 3 alongside definitions and advantages.

Statistical Test	**Use**	**Advantages**
Procrustes ANOVA (using permutation procedures)	A covariation method (Zelditch, 2012:455) to quantify the relative shape differences between specimen that is attributable to one or more factors. Estimates the probability or significance of this variation towards a null hypothesis through resampling permutations (Adams and Collyer, 2020; Sherratt, 2014;27).	Allows for testing and quantification of shape variation between multiple factors such as intraspecies, interspecies, and habitat type. Will provide an output that determines if the SES is significant in the 2 degrees of freedom test (Anon, 2016)
Two-block Partial Least Squares (2B-PLS)	A statistical analysis to assess the 'degree of association between two blocks of Procrustes-aligned coordinates' (Sherratt, 2016:53; Rohlf & Corti, 2000).	Two-block PLS will be conducted using shape data as one variable alongside ecological and species type in order to assess covariation.
Principal Components Analysis (PCA)	A dimensionality-reduction method and statistical procedure used to summarize large data sets and emphasise variation and strong patterns. Extracts important information from data set and expresses	Pattern recognition will be used to signify relationships between observations and variables in data sets, i.e. intra- and inter-species shape variance as well as habitat type.

	these as a set of summary indices or ‘Principal Components’ (Eriksson, 2018).	
Thin-plate Spline Deformation Grids (TPS)	Two configurations are deformed and smoothed using Thin-plate Splines and visualised on a curved grid (Sherratt, 2014:50). Used to show deformations that are required to transform from one mean shape to a target coordinate map and are subsequently displayed on the PCA as complimenting visualisations (Bonhomme *et al.,* 2014).	This is an effective tool to model coordinate transformation and are used to visualise the shape deformation between coordinates.

Table 4.4: Definitions and advantages of statistical tests used in this geometric morphometric analytical study. ANOVA and 2B-PLS work to quantify the shape differences between variables and multiple data sets of aligned coordinates. PCA and TPS grids will be used as visualisation tools showing pattern variation and shape deformation between target and reference coordinates.

4.2.4 Pilot Study 3 – GM Analysis of Primate Mandible

Pilot Study 3 followed the proposed methodology from data collection to visualisation of shape variation using the Matter and Form 3D scanner and R Project software. Landmarks were digitised onto primate mandible specimen from 6 species and the GM and statistical functions, i.e. Generalised Procrustes Analysis, Principal Components Analysis, Procrustes ANOVA, Two-block PLS and, Thin-plates Spline warps, were conducted using the *geomorph* R package. A smaller specimen sample was used for this pilot test in order to simplify the approach, as the focus of the test centred on implementation of data preparation and correct use and execution of the chosen statistical methods. Testing of non-shape variables was used to determine the most useful metrics for study.

Pilot Study 1 revealed multiple necessary factors needed to create accurate 3D scans of the primate specimens. Firstly, lighting issues were addressed using a light tent and overhead lamps; the digital scanning took place in a quiet room so that background activity would not be picked up by the laser; and multiple scans were taken from numerous angles of each specimen that could be merged at a later stage to create one accurate 3D rendering. Following collection of the digital renderings, traditional craniometric landmark points (see **Table 4.2**) were digitally superimposed onto all mandible specimen using the *geomorph* command function `digitsurface()`.

Estimating missing landmarks is a necessary function within the GM analysis. Sherratt (2014:16) explains that the '*geomorph* package requires a full complement of landmark coordinates' to ensure accuracy within the study. This can be done with two approaches: the missing values are estimated using Thin-plate Splines that interpolate landmarks on a reference specimen to estimate missing landmark locations onto a target specimen; or a multivariate regression method is used to regress all specimens with missing landmarks on all other landmarks featured on a complete specimen set. The missing landmarks are subsequently predicted by the linear regression model (Sherrat, 2014:17; Gunz *et al.* 2009).

For this Pilot study, estimation of missing landmarks was completed using the Thin-plate Spline approach, which was favoured over a multivariate regression method, as the results from the latter approach carry a greater risk of inaccuracy. Using Multivariate Regression, the results can be influenced by the number (Sherratt, 2014; Adams *et al*, 2020) of specimens in the study, as well as the number and location of missing landmarks. Risk mitigation meant implementing the preferential Thin-plate Spline approach for estimating missing landmarks in this analysis.

Following **Table 4.4** in **section 4.1.3,** the next phase of statistical testing was to perform the Generalised Procrustes Analyses using the fixed landmark datasets. The GPA translated all specimens to an origin location, optimally rotated them using least-squares criterion and scaled the specimens to unit-centroid size (Sherratt, 2016:29). **Figure 4.15** shows a plot of specimen coordinates before and after the Procrustes superimposition of the raw data.

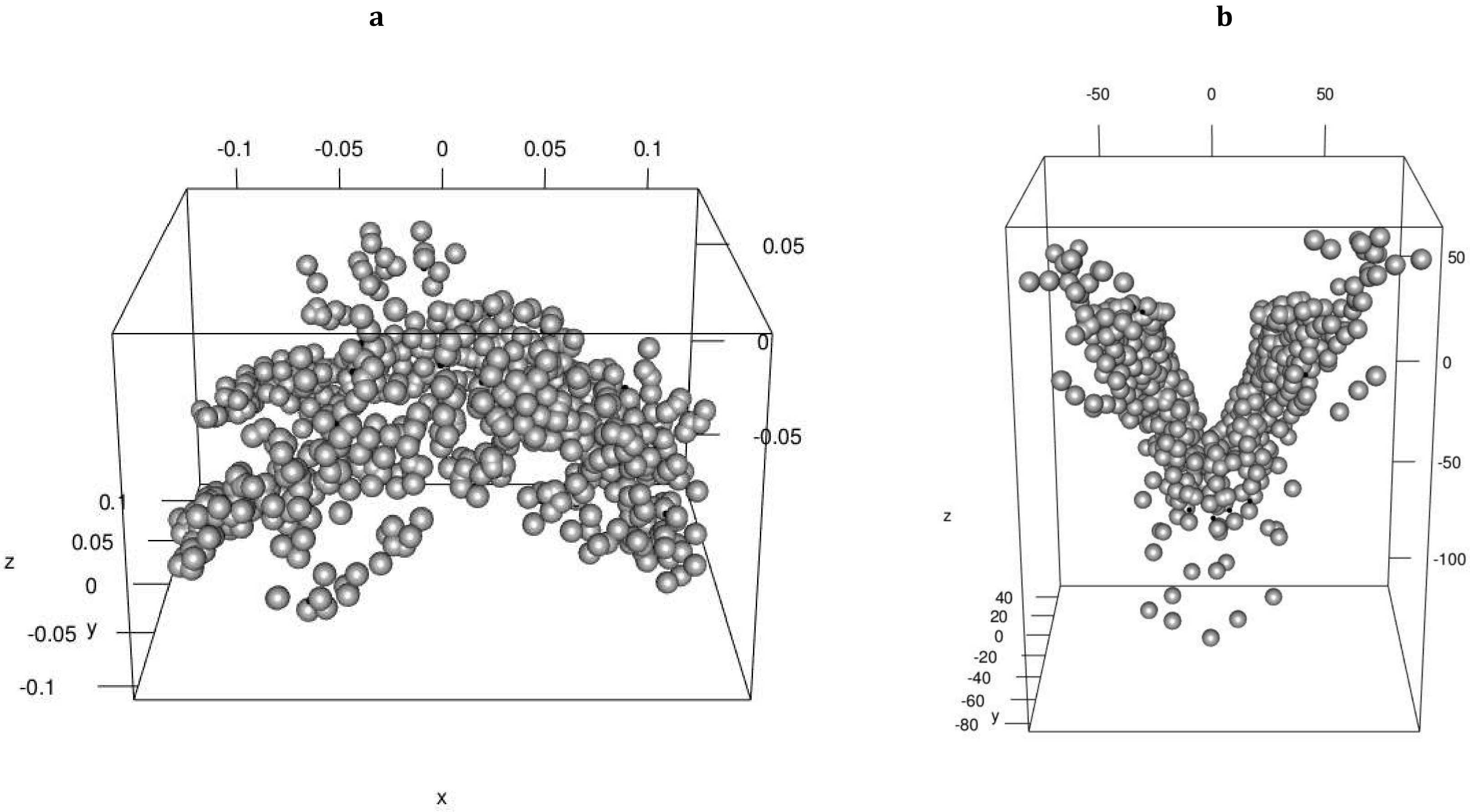


Figure 4.15: Raw landmark coordinates of pilot mandible specimens (a) in comparison to specimen plot after General Procrustes Analysis and superimposition of data (b).

4.2.4.1 Pilot Study Multivariate Statistics

Procrustes ANOVA testing was applied to the pilot data using the `procD.lm` function. This produced an analysis of variance table (**Table 4.5**) using permutation procedures and residual randomisation. This test was used to assess the statistical hypothesis which, in this case, returned a value indicating significant evidence against the null hypothesis that habitat does not influence shape morphology.

	Df	**ss**	**Ms**	**Rsq**	**F**	**Z**	**Sig.**
cs	1	0.027686	0.027686	0.40694	2.7447	1.8693	0.02
residuals	4	0.040348	0.010087	0.59306			
Total	5	0.068033					

Table 4.5: Analysis of variance table for pilot mandible specimen study showing a significance of 0.02 indicating strong differentiation between species quantified shape data and evidence against the null hypothesis.

A Two-block Partial Least Squares analysis determined the degree of variability between the Procrustes-aligned mandible coordinates using the function `two.bl.pls.` **Table 4.6** shows the variability between shape and size (allometry) though this function would ultimately be used to assess the degree of variability between multivariate, non-shape data, i.e. species and ecological variables.

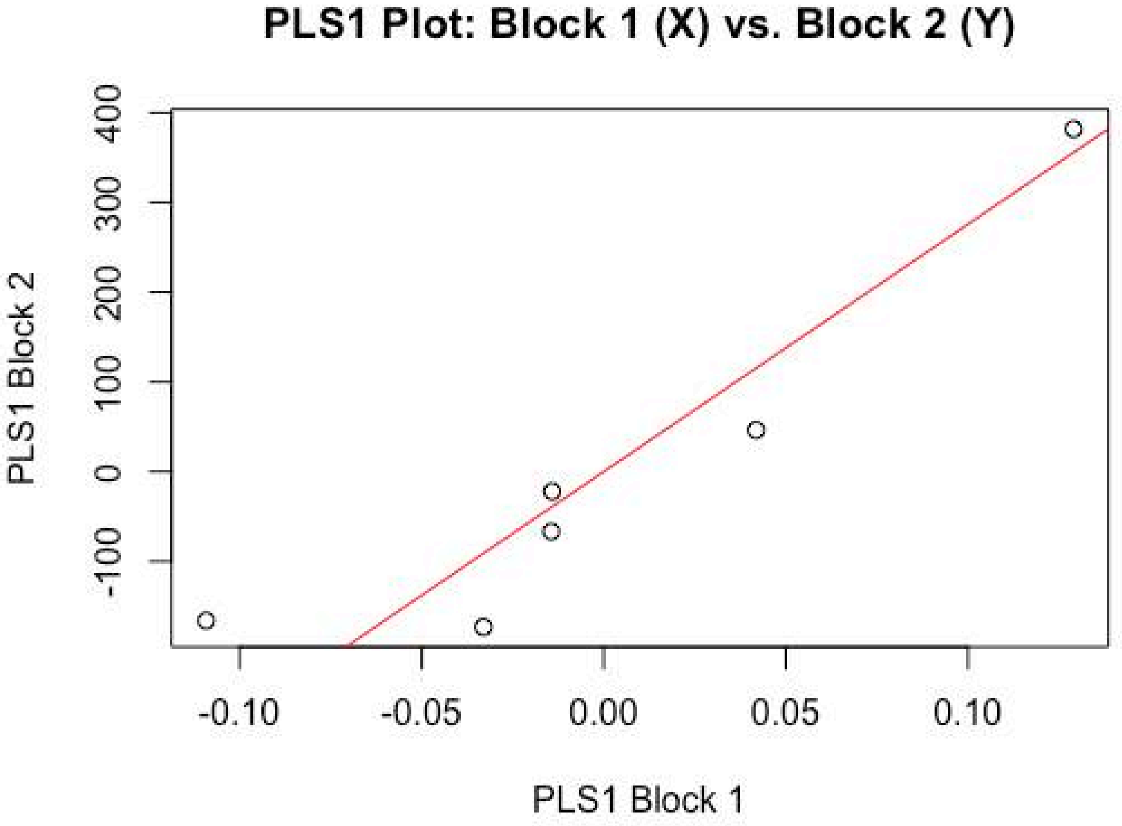
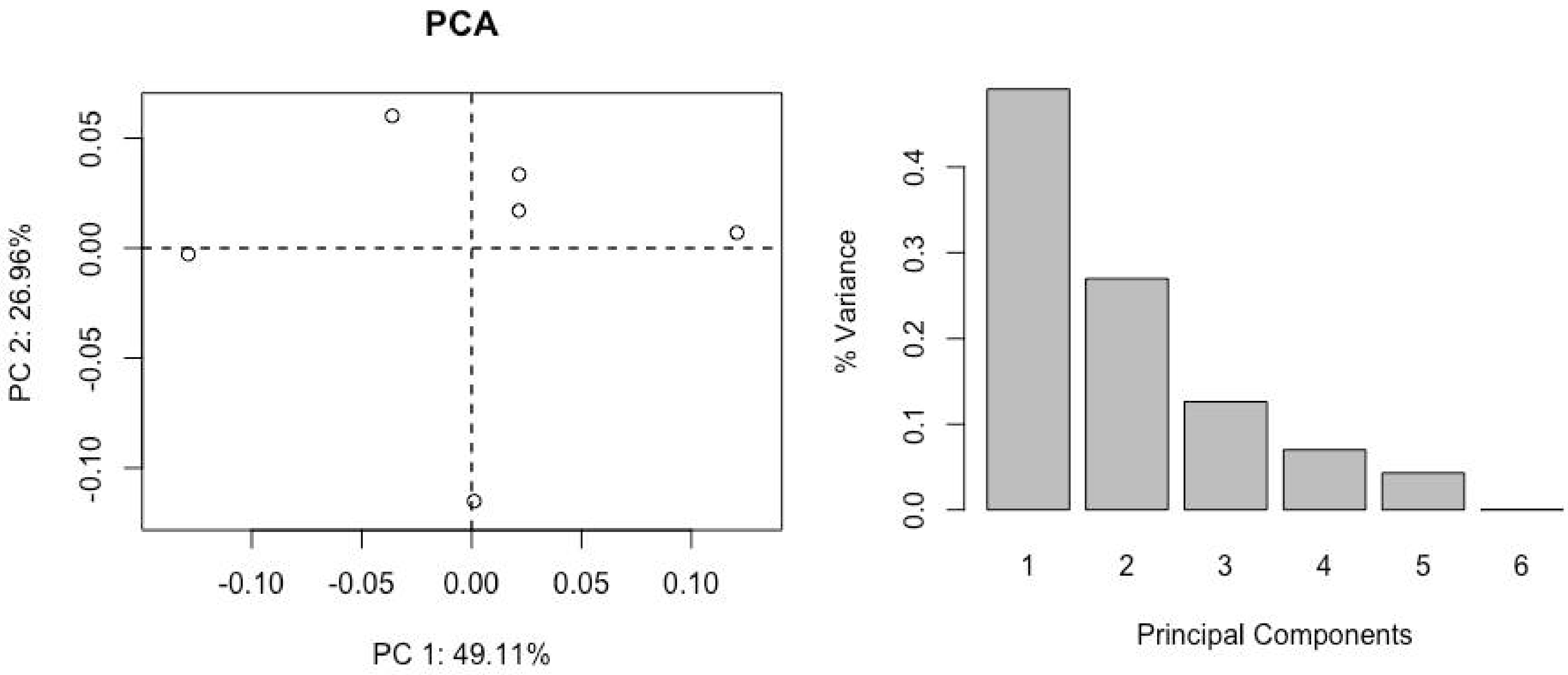


Table 4.6: Two-block Partial Least Squares graph showing degree of variability between shape and size of the pilot mandible data set.

4.2.4.2 Pilot Study Results Visualisation

Basic Principal Components Analysis graphs (**Tables 4.7 & 4.8**) were produced for the pilot mandible specimen group in order to visualise quantified shape variation. This ordination method is useful as visualisation tool due to the simplicity of the plot when formatted correctly. For the final study, amends to the PCA graphs include coloured legends to depict specimen variables and highlight contrasting results, as well as meshed warp grids by way of Thin-plate Spline deformation.



Tables 4.7 & 4.8: Plotted Principal Components Analysis scatter graph and bar chart showing 49.11% variance in the first PC and 26.96% variance in PC2 as well as clustering of specimen in the upper-right quadrant of the scatter plot.

The PCA plots show that the majority of variance lies within the first Principal Component, or PC1, and the scatter graph illustrates considerable clustering between specimen in the upper right quadrant. In-depth analysis of these results was not conducted as the specimen sample size used was deliberately small in order to test the software involved, as well as the quality of the data collection portion of the study.

geomorph allows for four different types of visualisation methods including a 'points' and 'vector' method. Within the R package, the function `mag` allows the user to identify the degree of magnification used to display the shape variance, which for this pilot study was set to `mag = 3`. All visualisation methods functions were tested with the pilot data set to determine the best plots for imaging the final results of the study (see **Figure 4.16** and **4.17**). Thin-plate Spline grids were ultimately chosen as the preferred method of visualisation, alongside Principal Components plots, as they show deformation clearly within x-y and x-z planes. Thin-plate Spline Warp grids were created using the `plotReftoTarget` function (**Figure 4.18**).

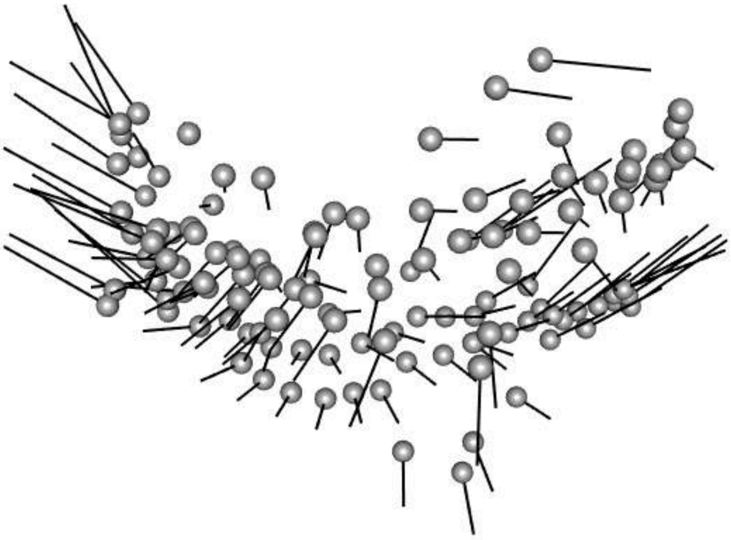
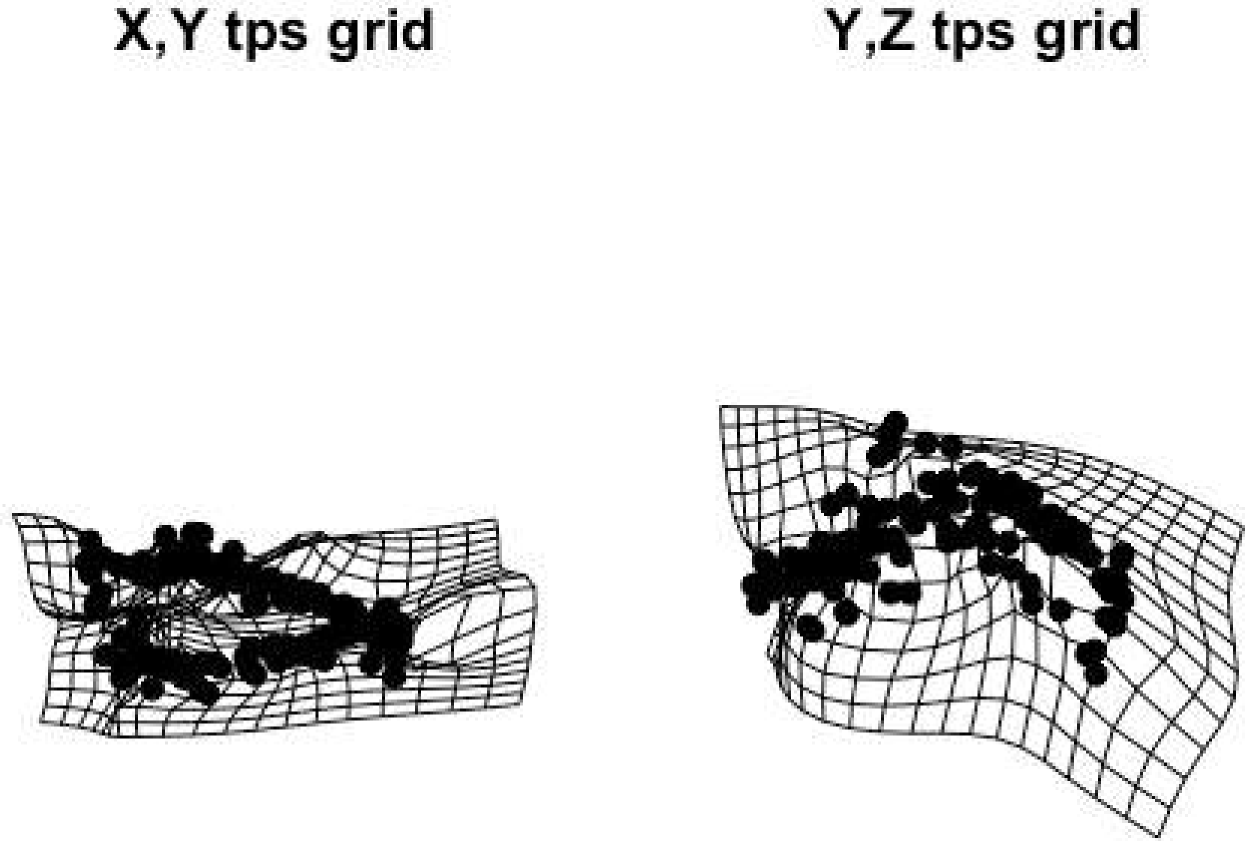


Figure 4.16: Vector visualisation plot testing for pilot mandible analysis. Plot shows the vector displacement between landmarks in the reference and target specimens (Sherratt, 2016:87).

Figure 4.17: Pilot mandible GM analysis visualisation grid using points. The black points represent the target specimen overlaying the grey reference specimen.



X,Y tps grid

Y,Z tps grid

Figure 4.18: Warp grids produced through the Thin-plate Spline method visualising shape deformation between target and reference mandible specimen

4.2.5 Pilot Study Results

The pilot studies informed the methodology structure and research design as well as the suitability of data collection and analysis technology. The Matter and Form 3D Desktop scanner would be used for digitising craniomandibular specimens and the R Studio platform would facilitate the landmarking and GM analysis of collected raw data. R would also complete the analytical process through an output of visual graphical representations of the quantified data. Refer to **Figure 4.19** for structure of research design.

The pilot studies showed that specimen scanning should be conducted under specific lighting conditions, and multiple scans should be integrated for a more detailed rendering of the image. Active background environments would blur the background of the scan leaving digital noise that needed to be cleaned from the final image. To limit digital noise, a light tent was used to house the scanner with correct lighting placements overhead so as to also avoid shadowing on the specimen. Placement of the specimen on the scanning surface was also a considered factor as the specimen would need to be scanned upside down in some cases, to access the underlying surface. As the specimen were made of fragile bone material, their placement on the scanner needed to be firmly secured in all positions needed for scanning.

Pilot testing the *geomorph* package in R assisted the development of the methodology and statistical testing (see **Table 4.4**). Pilot study 3 showed how graph formatting would need to be manually coded so that resulting data could be visualised and understood clearly. Pilot study 3 also informed the variables that would be used in the final methodology i.e. categorising of specimen in relation to specific habitat type.

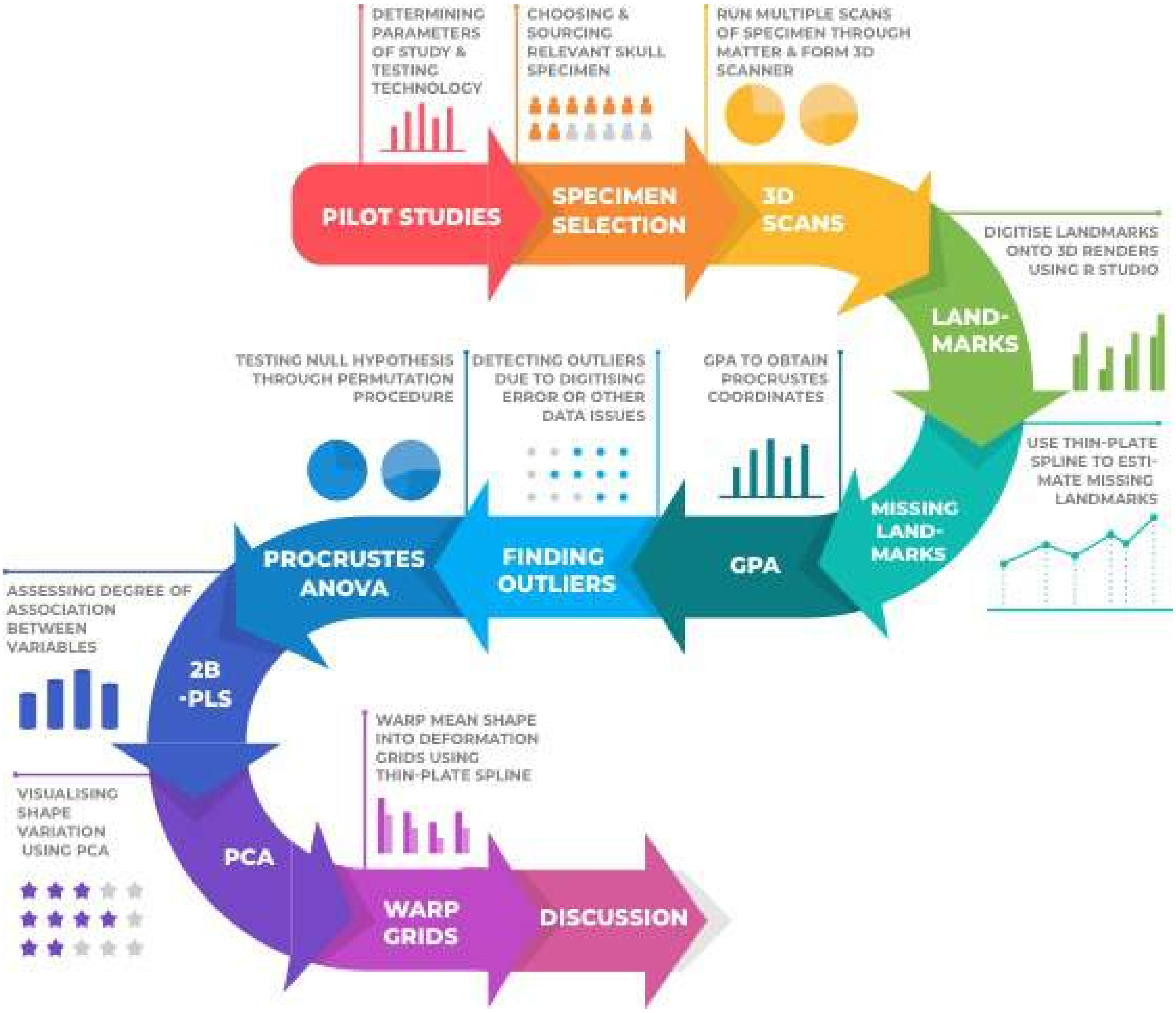


Figure 4.19: Finalised methodology informed through pilot studies and literature review including data collection through 3D scanning and landmarking exercises and data analysis using Generalised Procrustes analyses and multivariate statistics.

4.3 Specimen Selection

The following section introduces the primate species used within the study, describing the habitat types in which they populate, their main morphological characteristics and associated craniometric studies.

This study uses a sample of 107 crania and 108 mandible specimens of extant hominid species (*Pan, Pongo, Gorilla* and *Hylobate* genera) with known environmental niches, to draw similar conclusions regarding extinct hominin clade craniomandibular morphological evolution. For this study, 10 primate skull specimens were 3D imaged at the Oxford University Natural History Museum using the primate collection. However, to gain a substantial sample size, the author of this study gained access to the Smithsonian 3D collection of primate and human skulls. **Table 4.9** shows the number of species and subspecies skull specimen used in this study.

4.3.1 Mitigating Specimen Sample Bias

In selecting specimen for the study, care was taken to avoid sample-bias however, availability of primate skulls and open source 3D scans did not allow for age-matched samples. However, only specimen with fully fused spheno-occipital synchondrosis and fully erupted dentition where included in this study as they could be considered as adults (Singh *et al.* 2011; Flores and Barone, 2012; Cray *et al.,* 2012). **Table 4.18** outlines the sources of potential error in the study including the quality in specimen selection, as well as steps taken to reduce error and increase validity which in this case, used TPS and multivariate regression methods to estimate missing landmarks on incomplete specimen.

Skull Specimen		
Study ID	Genus	Species
HBM01 – HBM05	*Hylobates*	*H. lar*
HM01 – HM12	*Hoolock*	*H. hoolock*
HNM01-HNM11	*Nomascus*	*H. nomascus*
HSM02-HSM13	*Symphalangus*	S. *syndactylus*
PAM01-PAM10	*Pongo*	*P. abelii*
PPYM01-PPYM10		*P. pygmaeus*
PTM01- PTM14	*Pan*	*P. troglodytes*
GBM01-GBM21	*Gorilla*	*G. beringei*
GGC01-GGC20		*G. gorilla*

Table 4.9: List of 115 skull specimen with given study ID relating to genus and subspecies. Ultimately 107 crania and 108 mandible specimens were included in the study.

4.3.2 *Gorilla*

Native to sub-Saharan Africa, gorillas are our next closest relatives after chimpanzees and bonobos (Groves 2002; Hermann 2017; Fleagle 2013), and are known as polygynous, diurnal and predominantly herbivorous primates that live in small family factions (Bradford, 2014; Hermann, 2017).

There are two species of gorilla: *G. gorilla* and *G. beringei,* thought to have diverged from one another approximately 2 million years ago (Barks *et al.*, 2015; Groves, 2001; Grubb *et al.*, 2003). It is generally acknowledged that there are four subspecies of gorillas, i.e. the eastern lowland (*G. g. graueri*), the western lowland (*G. g. gorilla*), the mountain gorilla (*G. g. beringei*) and the cross river gorilla (*G. g. diehli*) (Tuttle, 2003; Doran, & McNeilage, 1998; LiveScience, 2012). However, there is no one consensus as to the taxonomy of these subspecies. This thesis recognises the two species and four subspecies of gorilla as proposed by Groves (2003:300-303) and championed by Tuttle (2003:13), based on their Canonical Discriminant Function analyses of gorilla skulls. The scheme of common names used in **Table 4.10** are also based on Groves (2001) study.

Gorilla Subspecies	**Habitat**
Eastern/ Eastern Lowland Gorilla (*Gorilla beringei graueri*)	Sub-montane and mountainous forests from 650 – 4000m elevation (Butynski, 2001; Cawthorn-Lang, 2005; Sarmiento, 2003)
Mountain Gorilla (*Gorilla beringei beringei*)	Montane forests at the highest elevation than conspecifics from 2200 – 4000m in Virunga Volcanoes (Butynski, 2001; Cawthorn-Lang, 2005)

Western/Western Lowland Gorilla (*Gorilla gorilla gorilla*)	Lowland, tropical, rain and swamp forests at sea level – 1600m (Cawthorn-Lang, 2005; Poulsen & Clark, 2004; Butynski, 2001; Sarmiento, 2003)
Cross-River Gorilla (*Gorilla gorilla diehli*)	Low-lying and sub-montane tropical and sub-tropical forests from 150-1600m elevations (Sarmiento, 2003; Cawthorn-Lang, 2005; Groves, 2003; Albrecht *et al.*, 2003)

Table 4.10: The four subspecies of gorilla with corresponding habitat types ranging from sub-montane and mountainous forests to swamp and lowland tropical forests. Gorilla habitats are distinctly marked by a range in elevation with the lowest-lying habitat at 150m to the highest elevation of 4000m.

4.3.2.1 Gorilla habitat

Ecology and habitat vary greatly between *G. gorilla* and *G. beringei*, with a geographical separation of 750km, and is most dramatic between sub-species (see **Table 4.10**) (Cawthorn-Lang 2005; Tutin & Vedder 2001). Eastern lowland gorillas, *Gorilla beringei graueri*, inhabit sub-montane and mountainous forests from 650 – 4000m elevation (Butynski, 2001; Cawthorn-Lang, 2005; Sarmiento, 2003). *Gorilla beringei beringei*, commonly referred to as the mountain gorilla of the Virunga, are found to live within montane forests at the highest elevation than its conspecifics, from 2200 – 4000m surrounding the Virunga Volcanoes (Butynski, 2001; Cawthorn-Lang, 2005). The Western Lowland Gorilla, *G. g. gorilla*, inhabit lowland, tropical, rain and swamp forests at sea level – 1600m (Cawthorn-Lang, 2005; Poulsen & Clark, 2004; Butynski, 2001; Sarmiento, 2003). Similarly, the most endangered gorilla subspecies, the Cross-River gorilla, or *G. g. diehli,* are located in low-lying and sub-montane tropical and sub-tropical forests from 150-1600m elevations (Sarmiento, 2003; Cawthorn-Lang, 2005; Groves, 2003; Albrecht *et al.*, 2003).

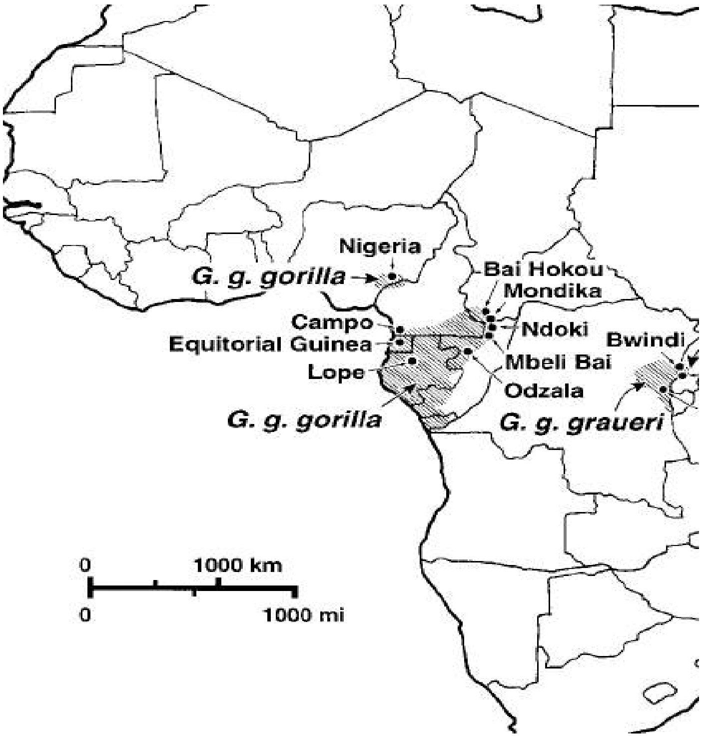


Figure 4.20: Gorilla subspecies geographical distribution and study sites (Doran, & McNeilage, 1998; 121).

4.3.2.2 Gorilla morphology

Aside from existing interspecies morphological variance (Leigh *et al.* 2003), in general the gorilla trunk is bulky and relatively short with a wide chest and arms that are longer than their legs (Bradford, 2014; Fleagle, 2013). The adult gorilla male, commonly referred to as 'silverbacks', receive their namesake from the distinct saddle-shaped patch of silver hair featured on their backs. With a large head and bulging forehead, the sagittal crest on top of the skull is largest in the male gorilla population, and their hands and feet feature opposable thumbs and a big toe (Hermann, 2017;90). Gorillas are mostly terrestrial, rarely standing on their legs but preferring quadrupedal knuckle-walking in ranges from 1000-2000 acres (Hermann, 2017;91).

Gorillas have long, low and narrower neurocrania than their Eurasian great ape counterparts, which is set at a lower level relative to their facial skeleton, resulting in a characteristic klinorhynch appearance (Neux *et al.,* 2013; Singleton *et al.,* 2013). Because of this, large-bodied apes have a prominent supraorbital torus that continues across the glabellar region and above the orbits, which are subrectangular and broad (Bilsborough and Rae, 2007; Russel, 1985). The gorillas zygomatic arch is cross-sectionally thin but vertically deep and displays anteriorly marked and posteriorly scalloped inferior borders from the attached masseter fibres (Bilsborough and Rae, 2007).

4.3.2.3 *Gorilla beringei*

Commonly referred to as 'the mountain gorilla', *Gorilla beringei* is the largest of the subspecies endemic to the mountainous rainforests and subalpine forests of eastern Democratic Republic of the Congo, Rwanda and Uganda. This mammal is herbivorous and particularly folivorous (inclined to a heavily foliage-based diet), as fruit is a rarity in their high-altitude habitat marked by dense terrestrial vegetation. *G. beringei* is known to cover small, overlapping zones and travel in organised groups through ranges of 50-1000km daily (Watts, 1984; Harcourt & Stewart, 2007; Fossey & Harcourt, 1977).

Figure 4.21: *G. beringei* skull and mandible (Canington, 2018) exemplifying their wide mandibular corpus and symphysis, as well as higher mandibular condyle relative to the occlusal plane of the mandible as noted by Taylor (2002) in comparison to *G. gorilla* morphology.

4.3.2.4 *Gorilla gorilla*

The western gorilla species, *G. gorilla*, and its eastern counterpart, *G. beringei,* inhabit equatorial Africa and are separated by approximately 1000km. Colloquially known as the 'western gorilla', there is much more seasonality in the *G. gorilla* diet compared to its conspecifics, emphasising fruit, insect and herb consumption where resource abundance allows (Doran, & McNeilage, 1998; 123). Tutin *et al.* (1991) comment that the foraging profile and degree of arborealism in western lowland gorillas are comparable to that of chimpanzees with the addition of aquatic herbs and seasonal bark which these gorillas regularly consume (Goldsmith, 1996; Tutin & Fernandez, 1993).

Figure 4.22: Comparison of male (left) and female (right) Western *G. gorilla* skulls (Descouens, 2011) showing morphological variance through sexual dimorphism i.e. prominent male brow protuberance, sagittal crest and canines.

4.3.2.5 Gorilla craniometric studies

There are relatively few studies comparing species *Gorilla gorilla* and *Gorilla beringei* skull variation. Bruner and Manzi (2001) used classical metric analyses and Generalised Least Squares, or GLS, landmark superimposition to show that much of the morphological variation that exists between gorilla species and *Pan* in particular, is due to size-related differences. Ackermann and Bishop (2009) identified rare craniodental variants including varying levels of frequency regarding supernumerary teeth, as well as sutural anomalies, through non-metric data.

Stumpf *et al.* (2003) used geometric morphometrics applications to study the variation in gorilla species skull specimens to better understand the morphological variation between the subspecies and determining the influence of body size on cranial morphology. Based on the multivariate analysis, the results showed several patterns of morphological distinctiveness between species based on region and identified the mountain gorillas of the Virunga (*G. beringei beringei*) as being the most distinct. Stumpf *et al.* (2003:59) also conclude that this area of study requires more in-depth research suggesting that a phylogenetic approach would be of considerable value, in combination to phenetic study, to clarify the significance of the skull morphological disparity between gorilla species.

Albrecht *et al.* (2003) used Principal Components Analysis and a population-thinking approach to demonstrate intraspecific patterns of variation between male and female gorilla skulls. This research was used as a conceptual framework to correspond to population taxonomy of a polytypic species, such as gorilla, which the team concluded can be applied to studies of fossil species recognition. Ultimately, Albrecht *et al.* (2003) used this procedure to propose their taxonomic scheme of gorillas which included three species *G. gorilla*, *G. beringei* and *G. diehli*.

A review of the current literature surrounding gorilla skull morphology shows a distinct lack of metric-based research involving patterns of variation in relation to habitat type. The majority of these studies are ontogenetic, allometric and taxonomically related research e.g. Shea, (1983), Mitteroecker *et al.* (2004), Bruner and Manzi (2001), Ackermann *et al.* (2006) and (2007), Scott *et al.* (2018). This thesis provides an ecomorphological approach to gorilla skull GM analyses allowing for a quantification of shape variation between the gorilla conspecifics and adding to craniomandibular morphological data of these endangered species. **Table 4.11** details the number of *Gorilla gorilla* and *Gorilla beringei* specimen used in this study.

Gorilla species	**Institution**	**Specimen ID**
Gorilla beringei	SMH	USNM259884 USNM260582 USNM395636 USNM396934 USNM395636 USNM396938 USNM397351 USNM545034 USNM545037 USNM545036 USNM545034 USNM397353 USNM545032 USNM545031
Gorilla gorilla	SMH	USNM599170 USNM599169 USNM599168 USNM599167

		USNM599166
		USNM599165
		USNM588746
		USNM585726
		USNM574138
		USNM297857
		USNM252580
		USNM252579
		USNM252578
		USNM252577
		USNM252576
		USNM252575
		USNM220380
		USNM220325
		USNM220324

Table 4.11: *Gorilla* genus skull specimens used in the present study including 19 *Gorilla gorilla* and 14 *Gorilla beringei* skulls virtually imaged by the Smithsonian Natural History Museum.

4.3.3 Gibbons

Gibbons are known as the 'smaller' or 'lesser apes' but with a total of 4 genera and 18 species, they comprise the largest of the ape groupings. The Hylobatidae family differ from the 'great apes' in that they are much smaller, show a low level of sexual dimorphism, i.e. are sexually monomorphic (Plavcan, 2001), and do not partake in nest-making or sleep platform behaviour (Walker, 2005).

Gibbons are the most specifically diverse and the most anatomically primitive of the living apes. However, in certain aspects, they are the most specialised, i.e. having the longest forelimb size relative to their body (Fleagle, 2013). They travel by brachiation (arm swinging) and live in small and monogamous groups (Lappan & Whitaker, 2009).

Gibbon Genus	**Species**	**Habitat**
Western Hoolock Gibbon (*Hylobatidae hoolock)*	*H. hoolock* *H. leuconedys* *H. tianxing*	Found in India, Bangladesh and Myanmar inhabiting evergreen/ semi evergreen, rain, scrub and often mountainous forests (Groves, 1967; Kakati *et al.,* 2013; Brockelman *et al.* 2019).
Hylobatidae hylobates	*H. lar* *H. albibarbis* *H. agilis* *H. muelleri* *H. molock* *H. pileatus* *H. klossii*	Inhabit Southeast Asian tropical rainforests. Known to have large home range sizes from 17-40 hectares. Lives in high canopies with an altitude range limited to 1,200m (Gron, 2010; Brockelman & Geissman, 2008; Beaman, 2014).
Hylobatidae nomascus	*N. annamensis* *N. concolor* *N. nasutus*	Inhabit north-western Vietnam, northern Laos and a stretch of forest in the southern Yunnan province of China. Living at

	N. hainanus *N. leucogenys* *N. siki* *N. gabriellae*	elevations of between 300 and 600m and perferring subtropical climates (Cawthorn-Lang, 2010; Dao Van Tien, 1983; Geissmann *et al.* 2000).
Hylobatidae symphalangus	*S. syndactylus*	Found in the Sumatran Mountains of Indonesia and the mountainous regions of the Malay Peninsula in tropical and terrestrial mid-upper canopies of lowland and hill forests (Eastridge, 1999: Chivers, 1979).

Table 4.12: The four genera and 18 subspecies of gibbon (Hylobatidae) with corresponding habitat types consisting of lowland evergreen, semi-evergreen scrub, tropical and rainforests.

4.3.3.1 Gibbon Habitat

Gibbons reside in a mosaic of Southeast Asian forests including semi-deciduous, tropical, evergreen, scrub, mountainous and rainforests (Groves, 1967; Kakati *et al.,* 2013; Brockelman *et al.* 2019; Cawthorn-Lang, 2010; Geissmann *et al.* 2000; Eastridge, 1999: Gron, 2010; Brockelman & Geissman, 2008; Beaman, 2014). Owing to the dense and moist forest ecosystems in which they live, gibbons are among the most frugivorous primate families consuming a fruit-heavy diet with the occasional addition of leaves, insects and flowers (McConkey and Ario, 2002).

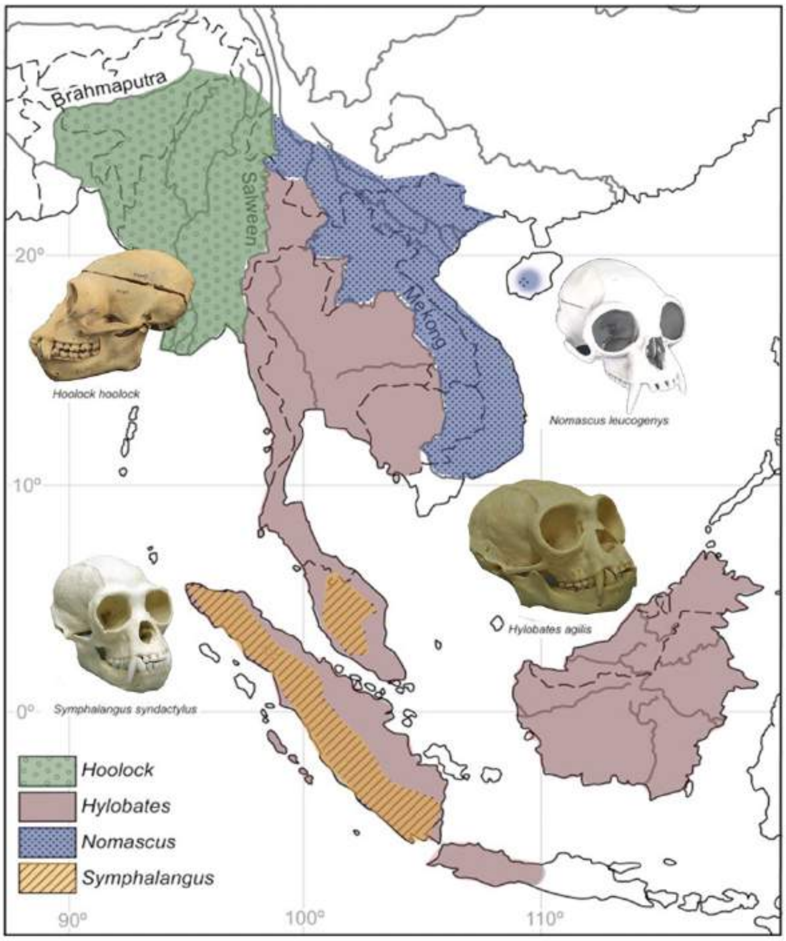


Figure 4.23: An approximation of gibbon geographic distribution by genus (adapted from Fleagle, 2013). The western most genus, the *Hoolock* gibbon, is found ranging from eastern India, through Bangladesh and Myanmar to part of the Yunnan Province in China. The Hylobates genus inhabits china, southern Myanmar, Thailand, eastern Cambodia and the Malay peninsula with surrounding Sumatran islands. The siamangs (*Symphalangus syndactylus*) are found on Sumatra and in peninsular Malaysia. The genus *Nomascus* inhabits southern China as well as Vietnam, eastern Cambodia and the Hainan Island (Fleagle, 2013; Chan *et al.*, 2010).

4.3.3.2 Gibbon Morphology

All gibbon species are relatively small weighing between 5-11kg (Clarke *et al.* 2006). Compared to the ‘great apes’, gibbons have shallower faces and mandibles, shorter snouts

(Liedigk *et al.* 2012) and large orbits with a wide interorbital distance (Denion *et al.* 2015). The gibbon braincase exhibits no nuchal cresting, is globular in shape and occasionally features a sagittal crest (Fleagle, 2013; Balolia *et al.* 2017).

Compared to the great apes, the gibbon skull is lightly constructed with a thin walled neurocranium of about 80-125 cm^3 capacity, a low vault and an ovoid profile. The frontal bone extends backward between the parietals and the sphenoid sutures to the parietals on the vault wall (Bilsborough and Rae, 2007). Gibbons have a short and fairly projecting face. The premaxilla and maxillary palatine process are separated by broad palatine fenestra within the nasal cavity which links to the oral cavity (McCollum and Ward, 1997).

Hylobatid orbits are rectangular and relatively large with powerfully developed lateral margins (Bilsborough and Rae, 2007). The orbits are positioned anteriorly in an almost jutting fashion and the lacrimal fossa extends beyond the rim to sit on the maxilla (Shea, 2013; Schultz, 1969; Schwartz, 1997). Their 'peculiar thickened rims' are suggested as synapomorphies of the group as stated by Groves (1989:155). The hylobatid circumorbital region, as in many of the lesser apes, is defined by highly elaborate external marketing and colouration (Geissman, 2004) and Shea (2013:130) suggests this underlying bony foundation could be modified to function specifically for facial communication using these soft tissue features.

The gibbon mandible and palate are long and both symphysis and corpus and lightly built in comparison. The ramus is broad, short and vertical with slight expansion near the gonial angle (Bilsborough and Rae, 2007). Gibbon dental morphology is identified by characteristic molars featuring rounded cusps and broad basins (Myers, 2000). Unlike gorilla’s sexually dimorphic dentition, both sexes in gibbons develop long canines and ‘blade-like’ anterior premolars on the lower jaw designed to sharpen the upper canine (Fleagle, 2013; Fanin, 2019).

4.3.3.3 *Hylobatidae hoolock*

The highly arboreal *H. hoolock* is endemic to evergreen, rain and scrub forests in tropical and terrestrial habitat regions within India, Northern Burma and China (Groves, 2001; Brandon-Jones *et al.* 2004; Chatterjee, 2009). Wolfheim (1983) describes this species as preferring undisturbed forests at an elevation from 152 to 1379 km and of all the gibbon species, have the farthest extending range from north to east.

As the second largest of the gibbons, following the lesser ape siamangs, *H. hoolock* weighs between 6-8kg and is characterised by longer hair, slightly triangular-shaped heads and curved brow streaks. This species is dichromatic with entirely black-haired adult males and lighter brown-haired females (Chivers, 1977; Chivers & Gitins, 1978; Krebs, 2001).

Figure 4.24: Lateral view of female *H. hoolock* gibbon skull showing large canines characteristic of this sexually monomorphic species, globular neurocranium, protruding orbital rim and large orbits (Dokkyo Med, 2005).

4.3.3.4 *Hylobates lar*

Often known as ‘the white handed gibbon, *Hylobates lar* can be found in the tropical rainforests of Southeast Asia and are known to have the largest latitudinal range of all gibbon subspecies, with homes range sizes from 17-40 hectares. This species lives in high canopies with an altitude range limited to 1,200m and is rarely found in the forest understory (Gron, 2010; Brockelman & Geissman, 2008; Beaman, 2014).

H. lar adults averagely weigh between 5-8kg (males) and 4.5-7kg (females). They are arboreal moving through their rainforest canopy habitat using brachiation but are capable of walking and running when terrestrial movement is necessary (Vereecke *et al.* 2006; Gron, 2010). Their diet is varied between fruits, leaves and insects though the fig fruit is known to take up a larger proportion of their daily intake (Palombit, 1997; Gron, 2010; Bartlett, 1999).

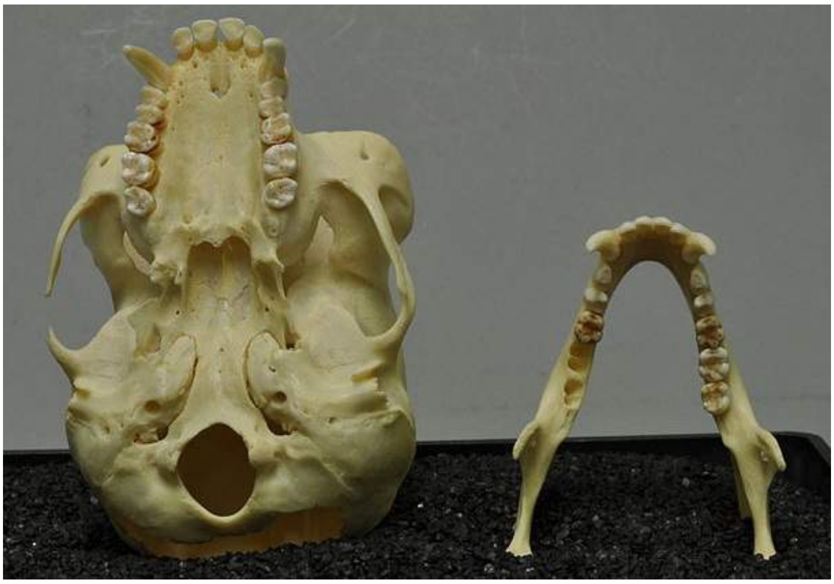


Figure 4.25: *Hylobates lar* cranium (posterior view) and mandible (anterior view) (Rassinger & Cammerer, 2011a).

4.3.3.5 *Nomascus leucogenys*

The 'white-cheeked gibbon', *N. leucogenys,* are found in north-western Vietnam, northern Laos and a stretch of forest in the southern Yunnan province of China. Living at elevations of between 300 and 600m, this species prefers subtropical climates within both native primary forests and regenerated but mature secondary forests (Cawthorn-Lang, 2010; Dao Van Tien, 1983; Geissmann *et al.* 2000).

N. leucogenys is a mainly frugivorous species but will incorporate leaves and insects into their diets when seasonal fruits are not available (Cawthorn-Lang, 2010). They are highly arboreal, moving quickly through the canopy with great ease and covering up to 3 meters in one swing (Nowak, 1999; Leighton, 1987). Though arboreal grace and dexterity are a trait of their proportionally long arms and fingers, accidents still happen with such speed in the canopy (Geissman *et al.* 2000; Cawthorn-Lang, 2010). Rumbaugh & Washburn (2003) note that it is commonplace to find healed bones in the corpses of white-cheeked gibbons.

Figure 4.26: Lateral and frontal view of adult male *Nomascus leucogenys* housed at the Natural History Museum (Harding, 2012).

4.3.3.6 *Symphalangus syndactylus*

S. syndactylus, commonly referred to as 'siamangs', are found in the Sumatran Mountains of Indonesia and the mountainous regions of the Malay Peninsula. Weighing an average of 10-12kg, siamangs are the largest of the gibbon species and spend much of their time in the tropical and terrestrial mid-upper canopies of lowland and hill forests (Eastridge, 1999: Chivers, 1979).

With a characteristically large brain case and short-muzzled face, this species is highly territorial, marking their space vocally. They can move bipedally over the forest floor as well as using brachiating hand-over-hand swinging movements to acrobatically manoeuvre through the forest canopy. Siamangs eat the highest proportion of leaves than any other gibbon (approx. 43-48%), complimenting the rest of their diet with fruits, insects and sometimes small vertebrates (Preuschoft, 1990; Nowak, 1999; Eastridge, 1999).

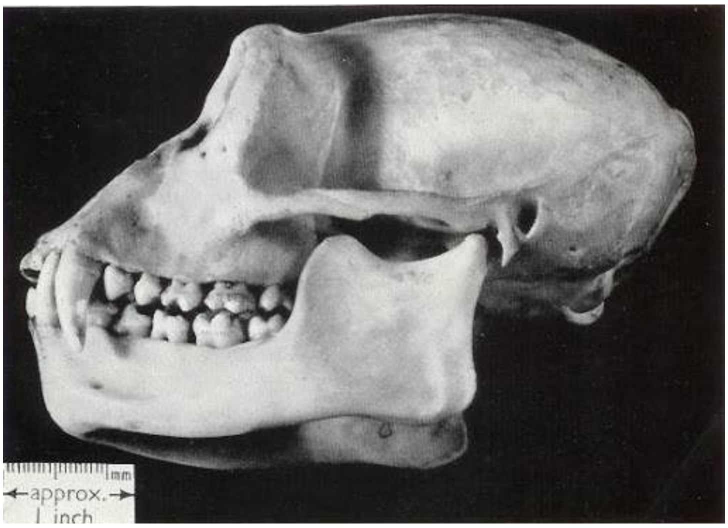


Figure 4.27: *Symphalangus syndactylus* skull (2012) showing broad ramus, shallow mandible and catarrhine dental formula. Compared to their gibbon conspecifics, the siamang features larger characteristics, e.g. brow protuberance, canine length.

4.3.3.7 Gibbon craniometric studies

As stated by Shea (2013:119), there is currently little research focusing on ‘lesser apes’ (Hylobatidae) thus resulting in an obscuring of character novelties corresponding to the advent of greater apes (Hominidae). To date, there are no craniomandibular GM studies encompassing gibbon and siamang species in relation to habitat. It should be noted that, according to Tyler (1993), hylobatid apes have experienced a decrease in size throughout their evolutionary timeline. Shea (1993:119) comments that this evidence of size decrease in hylobatids exemplifies the importance of allometric influences and size associations in studies regarding the evolutionary history of primate skulls. For this reason, four hylobatid genera and species specimens have been included within the present study (see **Table 4.13**).

***Hylobatidae* species**	**Institution**	**Specimen ID**
Hylobatidae lar	SMH	USNM083262 USNM083263 USNM083264 USNM083265 USNM083515 USNM083947 USNM083948 USNM104438 USNM111970

		USNM111988 USNM111989 USNM111990 USNM112574 USNM112710 USNM113176 USNM113177 USNM113179 USNM113180 USNM114499
Hylobatidae nomascus	SMH	USNM240490 USNM240491 USNM240492 USNM240493 USNM257995 USNM257996 USNM296921 USNM320787 USNM320789 USNM464992 USNM542282 USNM320786
Hylobatidae hoolock	SMH	USNM279146 USNM545009

Hylobatidae symphalangus	SMH	USNM114497 USNM141160 USNM143577 USNM143580 USNM143581 USNM171981 USNM271048 USNM283563 USNM364967 USNM395514 USNM395691 USNM396648 USNM519573

Table 4.13: *Hylobatidae* skull specimens used in the present study including 19 *Hylobatidae lar*, 12 *Hylobatidae nomascus*, 2 *Hylobatidae hoolock* and 13 *Hylobatidae symphalangus/S. syndactylus* virtually imaged by the Smithsonian Natural History Museum.

4.3.4 Panins

The colloquially termed 'Panins', or *Pan* genus, consists of two extant primate species: *Pan troglodyte* or 'Chimpanzee' and *Pan paniscus*, commonly referred to as 'bonobo'. Both species are native to sub-Saharan Africa and can be found inhabiting the Congo Jungle. Compared to *P. paniscus*, *P. troglodyte* has a larger range with Eastern, Western and

Nigerian colonies. Chimps and bonobos are humans closest living relative with Prufer *et* al. (2012) finding more than three per cent of the human genome being more closely related to either the chimp or bonobo genome than they are to one another.

The *Pan* species diverged from one another around 2 million years ago and differ noticeably in morphology and key social and sexual behaviours (Frans de Waal, 2006; Hare *et al.* 2007; Furuichi, 2009; Hammock & Young, 2005; Prufer *et al.* 2012).

Pan Species	**Habitat**
Chimpanzee (*Pan troglodyte*)	Found living in 22 African countries (Butynski, 2001; Bermejo, 1999; Nishidia *et al.* 2001) in low altitude rainforests, open woodland, semideciduous and evergreen forests (Hunt *et al.* 2002; Goodall, 1986; Cawthorn-Lang, 2006).
Bonobo (*Pan paniscus*)	Inhabit several vegetated type habitats within the Congo Basin, including tropical rainforests, swamp forests and open, wet marshlands (Fruh & Hohmann, 1993; Williams, 2004).

Table 4.14: The two species of *Pan*, *Pan paniscus* and *Pan troglodyte,* with corresponding habitat types consisting of woodland, marshlands, evergreen, swamp and rainforests.

4.3.4.1 *Pan* Habitat

The *Pan* genera inhabit the widest range compared to any of the 'great apes' (Humle *et al.* 2016). Chimpanzees reside in tropical rainforests, grasslands and woodlands throughout central and western Africa with some populations known to inhabit savannah landscapes (Nowak, 1999; Jones *et al.* 1996). Bonobos are found in the Democratic Republic of Congo in forests south of the Congo River. The varied mosaic of habitat types that *Pan* species inhabit enables predominately arboreal locomotion, with bipedalism being observed as a primarily postural behaviour on arboreal substrates (Stanford, 2006).

Chimpanzees and bonobos sleep in the forest canopy, where they also consume most of their diet, heading to the forest floor only for foraging opportunities (Karline *et al.*, 2014). They are omnivorous, eating young leaves, seeds, bark and resin but relying heavily on ripe fruits (Nowak, 1999). Their diets vary seasonally and will supplement their food intake with insects, eggs and small vertebrates during times of low fruit density (Karline *et al.,* 2014; Tomasello, 1994).

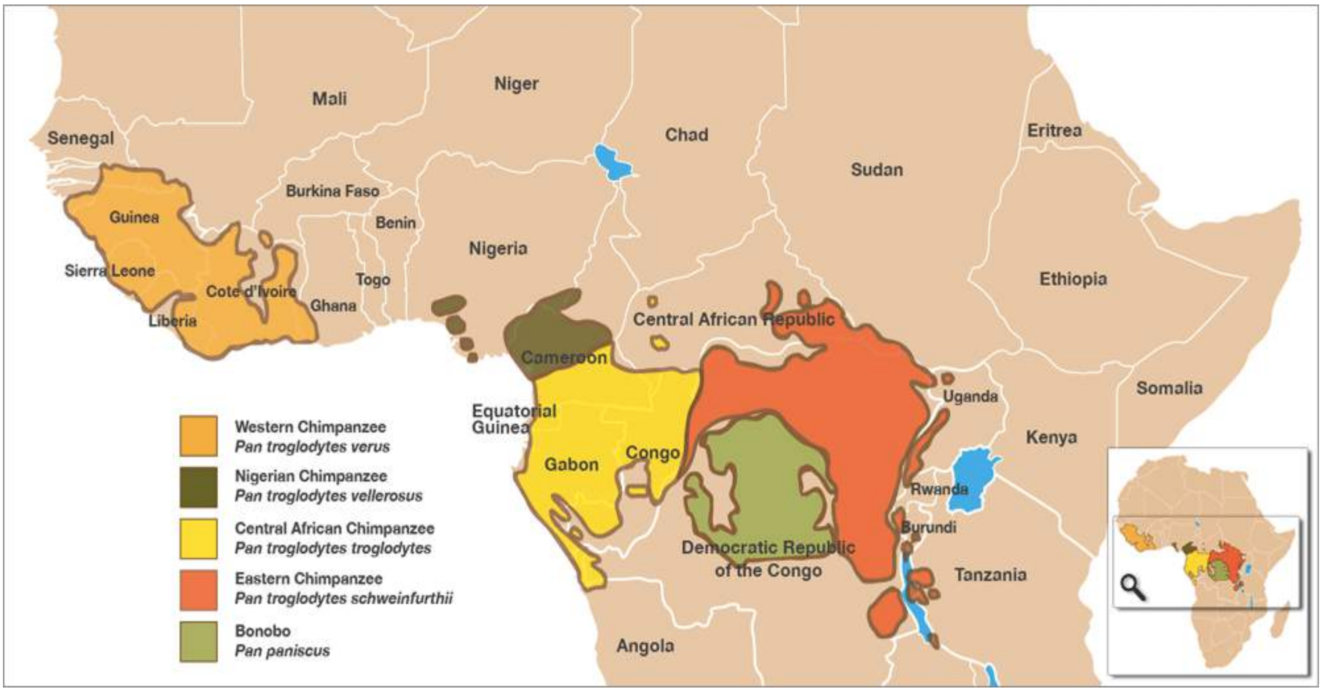


Figure 4.28: Geographic range of Pan genus (JGIC, 2016) showing wide ranging distribution of *P. troglodyte* (chimpanzee) populations from central to western African with neighbouring conspecific *P. paniscus* (bonobo) inhabiting the Democratic Republic of the Congo.

4.3.4.2 *Pan* Morphology

Chimpanzees and bonobos differ physiologically, with the latter species exhibiting a slenderer build and fewer sexually dimorphic variances than its conspecific. *P. pansicus* is smaller than *P. troglodyte* species but has a narrower chest, longer limbs and a less prognathic face with a more globular neurocranium. Bonobos also have a darker face compared to chimpanzees (Fleagle, 2013; Boesch *et al.* 2002; Stumpf, 2011).

The skull morphology of chimp and bonobo species are distinct. They have pronounced and sharp canines and large lower premolars used for an omnivorous diet and for threat displays or as weapons (Williams, 2018). The foramen magnum is positioned towards the back of the skull where the spinal cord exists at a slight angle, allowing for levels of terrestrial and arboreal locomotive behaviour. Interestingly, Luboga and Wood (1990) examined variation within the *Pan* species foramen magnum placement and found *P. paniscus* to exhibit more anteriorly positioned foramina magna than *P. troglodyte*. This reflects the functional-adaptive foundations of the basicranial form in *Pan* species (Kimbel *et al.,* 2014; Russo and Kirk, 2013).

Figure 4.29: Chimpanzees (left) and bonobos (right) side comparison (The Human Journey, 2017) showing the morphological differences between these conspecifics. Bonobos exhibit narrower shoulders, smaller heads and more slender build. Bonobos are born with darker faces which is a characteristic that chimpanzees produce through maturity (Vise, 2018).

4.3.4.3 *Pan troglodyte*

The common chimpanzee is more robust than the bonobo species (*P. paniscus*) with males weighing up to 60kg and both males and females standing at an average height of 2.68ft (Rowe, 1996; Cawthorn-Lang 2006). Chimpanzees are both terrestrial and arboreal preferring to sleep in the tree canopy within specially built nests (Doran, 1996; Rowe, 1996). Spanning a total of 22 countries, the highest *P. troglodyte* population density is found in Central Africa (Butynski, 2001; Bermejo, 1999; Nishidia *et al.* 2001).

Chimpanzees are highly adaptable living in various ecological settings, i.e. low altitude rainforests, open woodland, semideciduous and evergreen forests (Hunt *et al.* 2002; Goodall, 1986; Cawthorn-Lang, 2006). Their diet consists mainly of fruits with the addition of leaves, bark, bird's eggs and insects. They are also known to eat small to medium-sized mammals, most commonly *Procolobus* and *Cercopithecus* monkeys, and have adapted to use natural tools, such as sticks and stones, to obtain foods (Boesch & Boesch-Achermann, 1989; Goodall, 1989; Cawthorn-Lang, 2006).

Figure 4.30: *Pan troglodyte* skull (Rassinger & Cammerer, 2011b) showing prognathic and concave facial structure, protruding brow ridge, globular braincase and large canines.

4.3.4.4 *Pan* Craniometric Studies

Pan craniometric studies have primarily been used in comparative research to understand the systematic relationship between hominid species (e.g. Cramer, 1977; Jungers and Susman, 1984; Shea and Coolidge, 1988; Shea *et al.,* 1993; Lockwood *et al.,* 2004; Ahern, 2005). Research that involves multivariate statistics and morphometrics are typically phylogenetic and ontological in nature (e.g. Millet, 2001; Taylor and Groves, 2003; Weaver and Stringer, 2015).

Shea and Coolidge (1988) used a combination of univariate and multivariate analyses to conduct a craniometric study of three geographical subspecies of *Pan* (*P. t. verus*, *P. t.*

troglodytes and *P.t schweinfurthii*). This study revealed significant discrimination between the subspecies based on known provenance but reported markedly less morphometric differentiation in *Pan troglodyte* than seen in other great ape subspecies. The authors suggest this as a reflection of a more recent differentiation in the *Pan* species as well remaining adaptation to a wider and more generalised ecological niche. At the time of publishing, bonobos were classified as pygmy chimpanzees belonging to the *P. troglodyte* species. However, Shea and Coolidge's (1988) results supported the separation of bonobo from the *P. troglodyte* species.

Ahern (2005:287) states that understanding the positioning of the foramen magnum, as it pertains to bipedality, in fossil skulls can be used as evidence towards hominid systematics, particularly for the earliest hominins, i.e. *Sahelanthropus* and *Ardipithecus* (Brunet *et al.,* 2002; White *et al.,* 1994). Ahern used linear regression and discriminant function statistics combined with 2D landmark-based metrics to understand whether the distance between basion and bipiorion (BSBIP) and/or bicarotid (BSBIC) is useful in distinguishing *P. troglodyte* from other hominid species including *H. sapiens*, *Australopiths* and *H. ergaster*. Based on the results, Ahern (2005:276) recommend that BSBIP is not used to assess hominin status unless used bivariately with BSBIC data.

Taylor and Groves (2003) used multivariate craniometric and ondontometric data to evaluate the mandibular variation in *P. troglodyte* and *G. gorilla* and to better understand the intraspecific taxonomy of these species which the authors describe as being in a 'state of flux'. Ontogenetic and morphometric same-sex pair wise comparisons were reported using ANOVA, ordinary least squares and ANCOVA or analysis of covariance. The results of this research supported the species-level distinction between bonobos and chimpanzees, as well as substantiating a greater degree of variance compared to the chimpanzee within-species group.

A trend in this review of *Pan* craniometric research shows a heavy focus on phylogenetic and ontogenetic aims with a clear lack of habitat variable in relation to the morphometric data. This thesis extends the work of previous investigators by using a comparative GM approach with an emphasis on ecology. **Table 4.15** details the number of *P. troglodyte* specimen used in this study including where the skulls were sourced.

Species	Institution	Specimen ID
Pan troglodyte	NHM	O.C 2050a
		O.C 2050b
		O.C. 2049
		O.C 2049b
		O.C 2048e
	SMH	USNM084655
		USNM174699
		USNM174700
		USNM174701
		USNM174702
		USNM174703
		USNM174704
		USNM174706
		USNM174708

Table 4.15: 14 *Pan* species specimen 3D digital skull scans from Oxford University Natural History Museum and Smithsonian Natural History Museum database for use in the present study.

4.3.5 Orangutan

There are three species of orangutan: *Pongo abelii*, *Pongo pygmaeus* and recently identified *Pongo tapanuliensis,* which are native to Malaysia and Indonesia (Xu and Arnason, 1996; Locke *et al.,* 2011; Cribb *et al.,* 2014; Goldman *et al.,* 2017, Nater *et al.,* 2017). Orangutans inhabit tropical rainforests and are mainly arboreal. They are primarily frugivorous with leaves taking up 11-20% of their diet. Orangutans will further supplement their diet with an increased intake of leaves and flowers in times of fruit scarcity (Payne and Prundente, 2008).

Pongo Species	**Habitat**
Sumatran Orangutan (*Pongo abelii)*	Inhabits fragmented tropical, lowland forests found on the northern tip of Sumatra, Indonesia (Rijksen, 1978, Urban, 2008)
Bornean Orangutan (*Pongo pygmaeus)*	Inhabits the hilly and swampy tropical rainforests of the Southeast Asian island of Borneo (Udvardy, 1975; Schulz *et al.* 2011; Lang, 2010).
Tapanuli Orangutan (*Pongo tapanuliensis)*	Surviving in less than 1,200 km^2 in the rainforests of Batang Toru, northern Sumatra, Indonesia (Lake Toba region) (Laurance *et al.,* 2020)

Table 4.16: The three species of *Pongo* (*Pongo abelii, Pongo pygmaeus and Pongo tapanuliensis)* with corresponding habitat types consisting of hilly, swampy and tropical rainforests (Urban, 2008; Shulz *et al.,* 2011; Laurance *et al.,* 2020).

4.3.5.1 *Pongo* Habitat

Found on the islands of Sumatra and Borneo respectively, *P. tapanuli*, *P. abelii* and *P. pygmaeus* are geographically separated from one another (Kaplan & Rogers, 1994; Cawthorn-Lang, 2005). Orangutans inhabit low elevation primary tropical rainforests as well as mature secondary forests. These old forests habitats consist of lowland swamp as well as hilly and mountainous areas (Rijksen, 2001; Rijksen & Meijaard, 1999). Inhabiting a mosaic of habitat types and following a largely frugivorous diet, orangutans benefit from high quantities of food throughout the year (Russon *et al.* 2001; Cawthorn-Lang 2005).

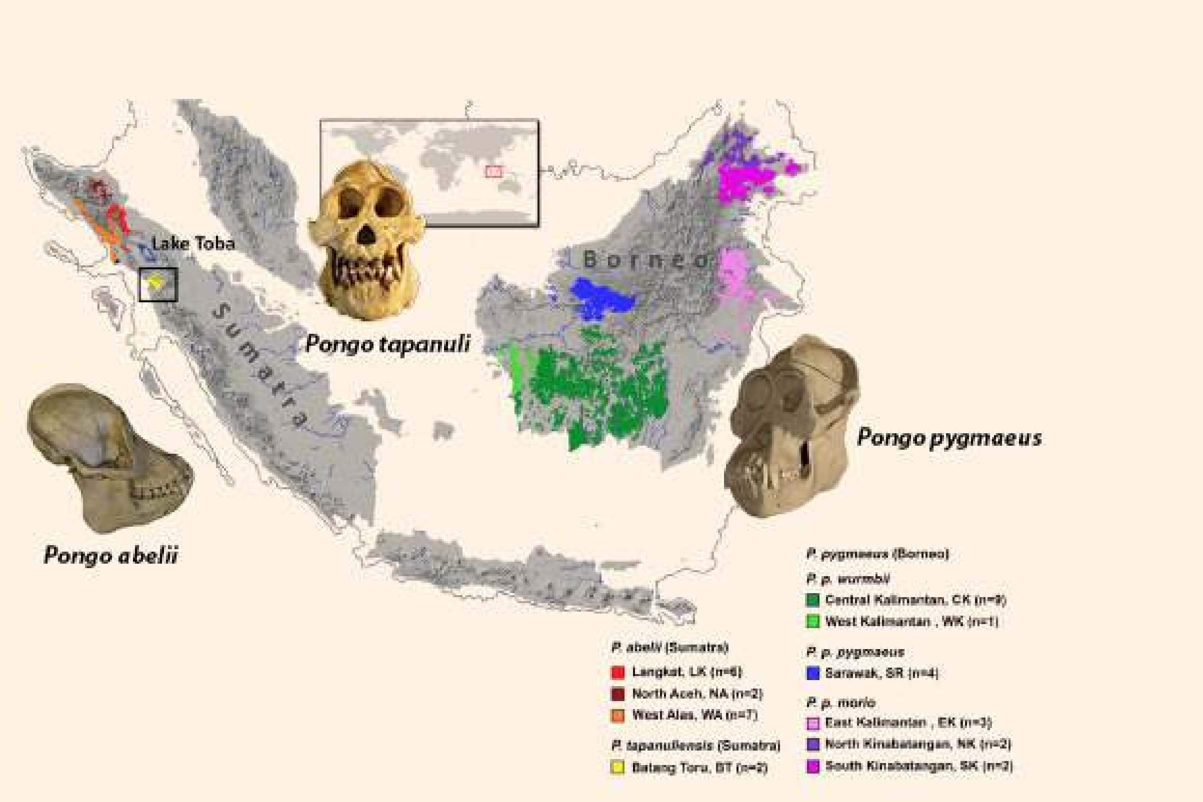


Figure 4.31: Orangutan Distribution Map adapted from Anderson (2017). Distribution shows *Pongo pygmaeus* subspecies (*P. p. morio, P. p. pygmaeus* and *P. p. wurmbi*) inhabiting various Bornean regions of Kalimanton, Kinabatangan and Sarawak. *P. abelii* populations are found distributed in the north of Sumatra e.g. Langkat, Norch Aceh and Wes Alas, and *P. tapanuliensis* populations inhabit the Sumatran region of Batang Toru (Singleton *et al.* 2004).

4.3.5.2 *Pongo* Morphology

Orangutans display a significant level of sexual dimorphism particularly in height and weight (Payne and Prudente, 2008). Males also have longer limbs, can develop facial flanges or cheek pads in maturity (Winkler, 1989), develop a large sagittal crest, larger throat pouches and longer canines compared to their female counterparts (van Schaik and MacKinnon, 2001). In general, orangutans are covered in coarse hair ranging along a spectrum of reddish orange to brown in colour, have small noses and ears which are unlobed and have a prognathous and concave facial shape (Grove, 1971).

Despite having four long fingers, orangutans have a markedly shorter opposable thumb which provides a stronger grip when travelling arboreally (Rose, 1988). When moving through the treetop canopy, orangutans use both hands and feet to hold onto branches (Rodman, 1993). Occasionally orangutans are seen to move bipedally on the terrestrial forest floor but will favour moving quadrupedally walking on their fists, unlike the majority of their great ape counterparts who prefer knuckle-walking (Rowe, 1996; Cawthorn-Lang, 2005).

The orangutan facial skeleton is sub-nasally prognathic with a convex alveolar clivus. As a more airorhynch ape species, the orangutan neurocranium is comparatively small and set above the facial skeleton ensuring that both frontal and occipital contours are relatively vertical (Bilsbourough and Rae, 2007). *Pongo* has characteristic ellipsoid orbitals, a narrow interorbital span, flaring zygomas and strong lateral orbital bars to provide the bony structure for their dimorphic flanges. Researchers, such as Shea (1988), Brown and Ward (1998) and Winkler (1989), have suggested that there may be an interrelating function between the zygomatic and lateral orbital morphology and the sexually dimorphic flanges (Hens, 2005; Shea, 2013). Moya-Sola and Kohler (1993) have suggested that it may be possible to recognise the presence of this soft tissue signalling features in fragmentary fossils (Shea, 2013:130).

The orangutan mandible is large with a deep mandibular corpus, and the symphysis is reinforced by a pronounced superior and inferior transverse tori (Bilsborough and Rae, 2007; Brown and Ward, 1988). *Pongo* dentition reflects their predominately frugivorous diet. Their canines are conical and dimorphic, and their cheek teeth are relatively large compared to their trunk size. The lower incisors are narrow and high-crowned in comparison to the upper set which are more pointed, convex in curvature and the most heteromorphic in comparison to all extant hominoids (Bilsbourough and Rae, 2007; Pilbrow, 2003).

4.3.5.3 *Pongo abelii*

Pongo abelii, commonly known as the Sumatran orangutan, inhabit the fragmented tropical, lowland forests found on the northern tip of Sumatra, Indonesia (Rijksen, 1978, Urban, 2008). Sumatran orangutans spend the vast majority of their time in the canopy even building treetop nests to sleep or nap (Rijksen *et al.,* 1978).

Sumatran orangutans are distinguishable from Bornean orangutans by their slenderer build, longer red hair, white hairs on the face and groin, as well as long beards present on both males and females (Urban, 2008; Cocks, 2003). Female *P. abelii* can reach up to 1.3m tall and their weights range from 30-50kg. Males can reach up to 90kg and at a maximum height of 1.8m showing significant sexual dimorphism within this species (Maple, 1980; Rijksen *et al.*, 2003).

Figure 4.32: Sumatran orangutan complete skull (*Pongo abelii*) showing large canines and pronounced prognathism as well as protruding sagittal crest and concave facial shape (CalAcademy, 2020).

4.3.5.4 *Pongo pygmaeus*

Pongo pygmaeus is found in the Indo-Malayan realm inhabiting the hilly and swampy tropical rainforests of the Southeast Asian island of Borneo (Udvardy, 1975; Schulz *et al.* 2011; Lang, 2010). Bornean orangutans are mainly frugivorous and will migrate depending of fruit availability spending the majority of their time in the treetop canopies and rarely descending to the ground (Strobel, 2013: Lang, 2010).

Bornean orangutans are morphologically distinct from their Sumatran cousins with an overall heavier and thicker skeletal build, as well as larger flanges and throat pouches seen in males (Ancrenaz *et al.,* 2008; Strobel, 2013). This species also exhibits bimaturism meaning two different forms of males which are categorised as being flanged or unflanged. The latter form resembles the females of the *P. pygmaeus* population as they grow to the same size, though they may become flanged at any time which is a reflection of age as well social hierarchies within the group (Ancrenaz *et al.,* 2008; Lang, 2010; Strobel, 2013).

Figure 4.33: *Pongo pygmaeus* skull showing significantly pronounced sagittal crest as seen in male maturity, a more pronounced and protruding brow bone and more robust build in comparison to *P. abelii* (De Stefano & MUSE, 2016).

4.3.5.5 Pongo craniometric studies

Pongo morphometric research is most commonly used in comparison with hominin data in studies of phylogeny and taxonomy (e.g. Bastir *et al.* 2010). There are few studies that utilise 3D geometric morphometric procedures to understand the interspecific morphological variance between the three *Pongo* species (Nater, 2017).

Senck and Coquerelle (2015) utilised a geometric morphometric approach, via Partial Least Squares, to detail the morphological integration and variation that exists in *P. pygmaeus* skull specimens' facial orientation. This study used a landmark and semi landmark-based approach in 3D space which was used to investigate the covariation patterns existing between the 43 adult specimens. The team found strong integration between the shape of the orbits and the cranial base as well as the shape and orientation of the palate and premaxilla. The results showed mature males to have a more ventrally oriented lower face which Senck and Coquerelle (2015) suggest could be due to reconfiguration of the cranial complex during the extended male growth phase of *Pongo*. To further Senck and Coquerelles' intraspecific tests, this thesis includes an interspecific Two-Block Partial Least Squares procedure to better understand *Pongo* cranial morphology alongside environmental variables allowing for a more detailed covariation investigation.

Comparative research that encompasses *Pongo* craniometric data has been used to further understand hominid taxonomy and assist fossil recognition studies. Bastir *et al.,* (2010) for example, used a geometric morphometric approach with multivariate regression and Thin-plate Spline analyses to examine a large dataset of great ape, including *Pongo pygmaeus,* and hominin basicranial specimen. The aim of their research focused on investigating the structural role of the basicranium in primate skull development. Their results suggest basicranial evolution to have significant influence on brain and facial size and supports Biegerts' (1957) hypothesis, explaining why larger faced Neanderthals feature less basicranial flexion than similarly encephalised humans with smaller faces (Trinkaus, 2003). The data that Bastir *et al.* (2010) used for *P. pygmaeus* craniometrics were sourced from other literature and the study fails to include further *Pongo* species in the data groups.

There is a lack of craniometric research which includes all *Pongo* species, from both an interspecific and intraspecific stance. **Table 4.17** details the number of *Pongo pygmaeus and Pongo abelii* specimen used in this study including where the skulls were sourced. The Tapanuli orangutan skull, however, has not been included in this study due to lack of available specimen for digital imaging.

Species	**Institution**	**Specimen ID**
Pongo pygmaeus	NHM	O.C. 2043 O.C. 2043a O.C. 2043b O.C. 2043c O.C. 2043d
	SMH	USNM013965 USNM142170 USNM142169 USNM142171 USNM142180
Pongo abelii	SMH	USNM143586 USNM143587

		USNM143588 USNM143590 USNM143591 USNM143593 USNM143594 USNM143595 USNM143596 USNM143597

Table 4.17: 20 *Pongo* specimens, including 10 *Pongo pygmaeus* and 10 *Pongo abelii*. 3D digital skull scans from Oxford University Natural History Museum and Smithsonian Natural History Museum database**.**

4.3.6 Specimen sex identification

The level of sexual dimorphism within the specimen data set will be assessed one size has been removed from the shape data via Procrustes analysis. This will determine whether sex needs to be considered as a variable in the subsequent statistical testing relating to habitat. The majority of specimen have been assigned male or female by archivists at the Oxford Museum of Natural History and the Smithsonian Institution; however, there were a few specimens which required sex identification before the geometric morphometric analysis could take place. Sex was assigned based on the criteria in **Table 4.18.**

Species	**Sexual Dimorphic Differences in the skull**
Gorilla	In comparison to their male counterparts, female gorilla skulls are smaller in size, display a reduced nuchal crest, a lack of sagittal crest (Baliola *et al.*, 2018), a less pronounced brow ridge and proportionally smaller canine teeth (Taylor, 2006).
Hylobates	Gibbons tend to display slight sexual dimorphism in terms of skull size; however, this is more substantial in siamangs with males exhibiting a larger cranial size. As mentioned by Mootnick (2006) it is extremely difficult to identify sex between male and female gibbons due to the lack of size related sexual dimorphism. For this reason, identification is usually based on sexual dichromatism. In this study, the sexual variance of the gibbon skull specimen was identified through museum record to avoid inaccuracy.

Pan	Adult male chimpanzee skulls are slightly larger than females due to a higher duration of growth rate (Reynoso, 2021). They also exhibit a moderate difference canine size and some males may display a small sagittal ridge that is non-existent in the female population (Bilsborough and Rae, 2007).
Pongo	Male orangutans generally have a broader facial structure with a dramatic flaring of the zygomatic bone (Hens, 2005) and sexually dimorphic canines (Fleagle, 2013).

Table 4.18: Sexually dimorphic skull characteristics to aid in identification of sex of primate specimen.

4.3.7 Specimen habitat grouping

Ecological variables were assigned to each specimen's 3D data clouds and inserted as classifiers within the geometric morphometric analysis in the form of an .csv file. Habitat type for each species was assigned based on regional location and known geological distribution of the species. Habitat variables are classified as follows: rainforests (1), swamp forests (2), tropical forests (3), lowland forests (4), montane forests (5), riverine forests (6), brush (7), dry savannah (8), subtropical forests (9), evergreen forests (10), hill forests (11) and peat swamps (12).

4.3.7.1 *Gorilla*

Gorilla beringei specimens have been assigned lowland tropical rainforest, transitional rainforest and Afromontane habitat types based on the source of the specimens and known ecological inhabitants, as reported by Sarmiento (2003) and McNeilage (2001). *Gorilla gorilla* specimens have been assigned rain (1), swamp (2) and riverine forests (6), or lowland tropical forests (3, 4) and brush, (7) as indicated by the origin region of the skull's and as identified by Ilambu (2001).

4.3.7.2 *Pongo*

The *Pongo abelli* specimen were classed with lowland forests (4), mountain forests (5), and peat swamps (12) based on the regional source of the skulls, i.e. forested patches of northern Sumatra, Indonesia. The *Pongo pygmaeus* specimen were classified within lowland forest (4) habitat types based on documented Indonesian and Malaysian origins (Meijaard and Dennis, 2004).

4.3.7.3 *Pan*

Pan troglodyte skulls were classified within dry savannah (8), montane (5) and swamp forests (2) depending on origin of the specimen and based on Meijaard's (2016) classification of primate landscapes and preferred habitats, with additional consideration to the proposed 'forest-savanna' gradient put forth by van Leeuwen, Hill and Korstjens (2020). Including more detailed descriptions of the *P. troglodyte* habitat, in the form of 'montane, dry or swamp' classifications, recognises a forest mosaic category more suitable for this species, rather than the traditional and less descriptive 'forest-savannah' classification.

4.3.7.4 *Hylobatidae*

Based on known specimen origin, *H. hylobates* were classified within tropical evergreen (3, 10) and subtropical evergreen mountain forests (5, 9, 10); *H. lar* were classified within dry evergreen forests (10); *H. nomascus* specimen were classified within subtropical evergreen forests (9, 10); and *S. syndactylus* were classified within tropical hill (3, 11) and lowland forests (4).

4.3.8 Summary

Section 4.3 has introduced the species used in this study including details regarding their ecological niches, morphological and cranial diversity. Previous craniometric studies of each species has been reviewed and habitat type variables have been identified to be used within the geometric morphometric analysis. The next section details the methods of data collection starting with the 3D digitising of the specimen through to landmark digitisation and data preparation.

4.4 Methods of Data Collection

Data was collected in the form of 115 sets of three-dimensional raw landmark coordinates superimposed onto digital images of primate crania and mandible specimens. Further readily available 3D skull scans were acquisitioned from the Smithsonian Museum in order to reach an optimum specimen sample size for this study (see **Appedix A** for a full list of specimen ID). Landmark digitisation and the following data acquisition and statistical analysis were completed using RStudio software.

For both Principal Components and Two-block Partial Least Squares analyses, geographic and habitat type variables were considered a proxy for climate variables as specific regional data were not paired with specimen collection information. This method has been successfully used in such geometric morphometric studies as McGuire (2010) and Shelleman (2015) where climate data paralleled the geographic axes of PLS analyses. Habitat type was paired at the sub-species level, i.e. recorded as two sets of grouping variables or factors and exported as an .csv into the R workspace alongside the coordinate data.

4.4.1 3D Image Capture

3D scanning variables such as calibration, lighting, auto-tuning and background noise were considered before image capture took place. When these variables are set to the optimised levels for the specimen involved, this serves to reduce intra-observer error, and the scan will be completed with further accuracy.

The 3D laser scanner works by projecting a beam of light onto a surface whose distance measurements are subsequently picked up by a sensor within the device. The 360° rotational table allows the scanner to automatically find areas on the object that is to be scanned. Through triangulation, the scanner can reconstruct and plot the points of the scanned surface visualised as a 3D model.

Calibration of the laser scanner provides enhanced quality 3D images and ensures geometric accuracy. The Matter and Form scanner houses a black and white checked measurement block that, when placed in various positions, allows the scanner to perform calibration tests. A second calibration session is implemented when the object for scanning is set onto the devices turntable, which ensures maximum precision of scanning.

The suggested lighting for scanning is ambient indoor, diffused white lighting. Brightness can warp the scanned image, and lack of light will provide an image that is darker in colour or can cause areas to be missed when scanning (Mason, 2018). Auto-tuning the scanner will provide better-quality scans. Objects that have multiple contrasting or dark colours will need 'High Contrast Scanning' which can be manually set through the Matter and Form software found in the 'Advanced Settings' menu (Matter and Form, 2018). Background movement can cause points to appear in the space around the specimen being scanned. The complementing software allows for the erasing of these points with a cleaning and cropping tool that can be fixed to various radius sizes depending on needs.

For optimum accuracy and to further reduce intra-observer error, a random number of specimens were scanned twice. As separate saved files, these scans can then be combined through the Matter and Form software to create one 3D model that contains a higher frequency of data information. The raw data was cleaned and manually edited through the Matter and Form software to ensure the final data set is sufficient for analysis. The final 3D image can be saved as various forms, such as .ply and .stl. The image can also be made into mesh files, i.e., .obj, which combines the points found by the scanner into a meshed image.

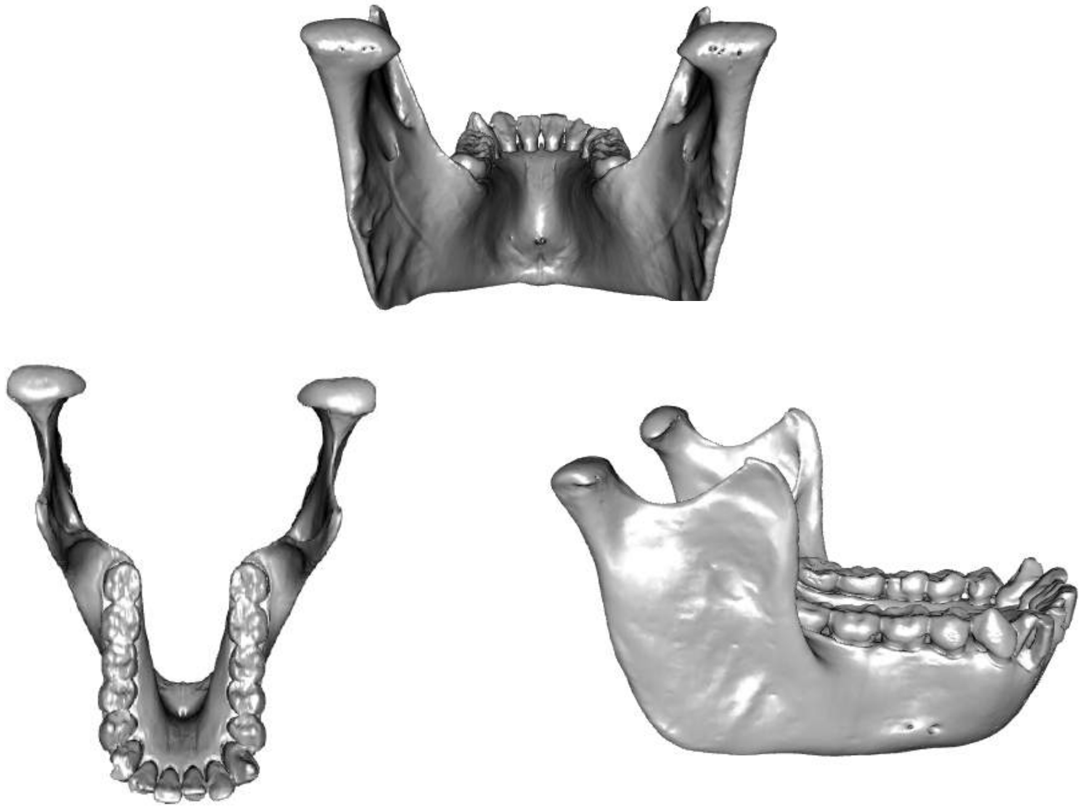
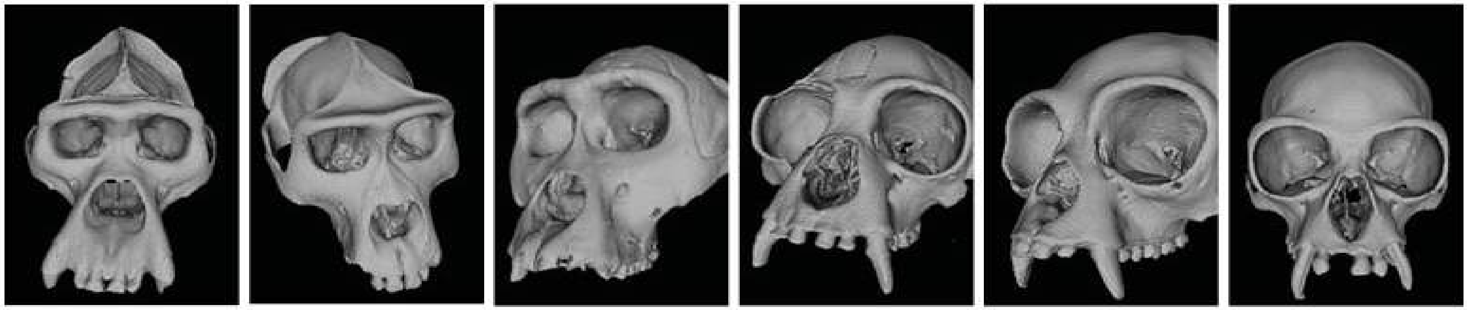
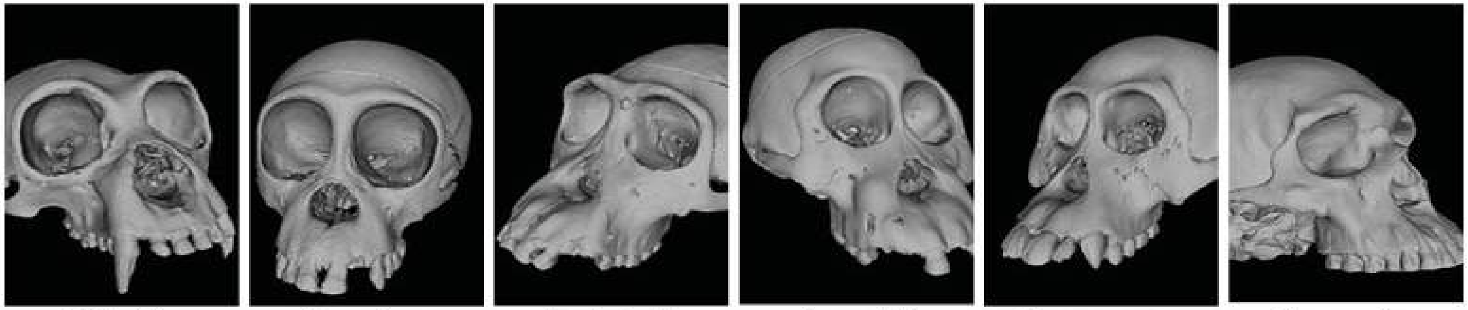


Figure 4.34: Example mandible scans of gorilla specimen completed with Matter and Form 3D desktop scanner. Multiple passes of the scanner are needed to create a more precise meshed digital image which contains as much shape data as possible.



Gorilla berengei ***Gorilla gorilla*** ***Gorilla diehli*** ***Hylobatidae bunopithecus*** ***Hylobatidae hylobates*** ***Hylobatidae nomascus***



Hylobatidae symphalangus ***Pan paniscus*** ***Pan troglydyte*** ***Pongo abelli*** ***Pongo pygmaeus*** ***Homo sapiens***

Figure 4.35: Sample of raw 3D scans showing the primate species sourced for study. Each specimen is scanned multiple times and combined to create a detailed and accurate form of the skull. The global scans depict the full form of the specimen and are manoeuvrable in a 3D environment so that craniometric landmarks can be applied from a basilar, anterior and lateral view in R Studio.

4.4.2 Landmark Digitisation

Using R Studio software, landmarks and sliding semi-landmarks were plotted onto the biologically homologous points and curves of the specimens; 25 fixed and 100 sliding semi-landmarks for mandibles; 28 fixed and 100 sliding semi-landmarks for crania (see **Tables 4.2** and **4.3**). The landmarks are carefully positioned, as they provide the overall shape that will be analysed for variation (see **Figure 4.36**).

4.4.2.1 Sliding semi-landmarks

Where shape differs among the skulls of the specimens, sliding semi-landmarks are placed that are 'sled' during the data preparation portion of the computational analysis. Semi-landmarks are used alongside traditional landmarks to quantify and analyse homologous curves and surfaces and the number of semi-landmarks used generally depends on the complexity of the curves and surfaces of the shape (Gunz & Mitteroecker, 2013:1). The sliding semi-landmarks were averaged so that the GM software recognises the numerous points as one homologous point rather than many along a curving line, ensuring a 'geometric correspondence' (Gunz & Mitteroecker, 2013:103). To computationally incorporate sliding semi-landmarks, the Bending Energy sliding method was used, instead of the Procrustes method, as it beneficial for larger shape variation and minimises the problem of overlapping sled semi landmarks.

Schaefer et al. (2004:472) used sliding semi-landmarks in their study concerning the craniofacial sexual dimorphism and allometric patterns of extant hominids. The team used a cubic spline fitted over already fixed traditional landmark coordinates, to plot semi-landmark points of equidistance. These landmarks could slide along the curves they were fitted to 'minimise net bending energy' (Schaefer et al., 2004:472) of the entirety of the data set from its individual Procrustes average and should be considered as homologous. Schaefer et al. (2004) exemplify successful research conducted with the use of sliding semi-landmarks as, amongst various other observations, the team concluded that sexual dimorphism seemed most prevalent among orangutans and gorillas and less so in the remaining human, chimp and bonobo specimens (Schaefer et al., 2004:476).

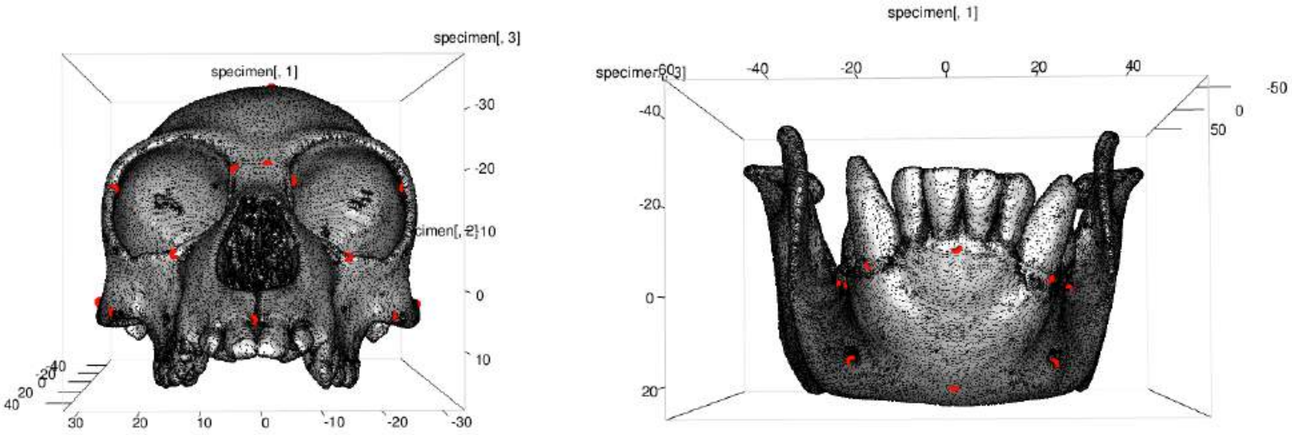


Figure 4.36: Primate cranium and mandible with corresponding fixed landmarks completed in RStudio using the `digitsurface` coding function.

4.4.3 Measurement Error

Possible sources of measurement error were identified and reliability of all equipment and technology used within the study tested for accuracy. Measurement error, or observational error, is defined as the 'difference between a measured value and its true value' (Dodge, 2003).

During data collection, it was necessary to understand the errors in measurement that may influence the final results. These can arise in a multitude of fashions, i.e. gross human error, systematic, random or environmental error (Trochim, 2020). **Table 4.19** describes the sources of potential error in the study as well as steps taken to reduce error and increase validity.

In order to reduce observational/measurement error, all equipment used in the study were pilot tested prior to carrying out the final methodology. 3D scans were taken of a sample set of cranial and mandible specimen to assess the visual precision of the digitised image as well as the quality of the exported raw data uploaded to R. The manufacturer of the equipment was sought for expert advice of best use which involved stabilising the background environment using dedicated lighting, a photography tent and multiple passes of the scanner to combine a final meshed digital image.

The sole user conducting the study through tested equipment was diligently trained to handle the relevant hardware/software so as to reduce human error. Landmarking using R Studio was tested on the pilot scans multiple times so that familiarity with the controls and function of the IDE would significantly reduce user error. All data entry, including digital imaging and landmark configurations, were conducted and reviewed so as to verify the accuracy of collected data before computational analysis.

Statistical procedure was applied to collected landmark data so as to find potential outliers and minimize risk of systematic and random error. The *geomorph* package enabled the identification of any potential outlying specimen using the `plotOutliers` function (see **Table 4.20**). This function orders all specimen by their Procrustes distance from the mean shape and returns a plot visualising specimen who fall above the upper quartile as distinguishable red outliers (Sherratt, 2016). Remotely plotted specimen shapes were visually inspected to identify outlier configurations, as compared to the consensus, in order to identify any errors in digitisation or data collection malfunctions.

Source of potential measurement error	Issues	Steps taken to improve accuracy
Measurement device precision (Matter & Form 3D Scanner)	Precision measurement is vital in a geometric morphometric study to reduce error impact on shape data. Accurate image capture is necessary for data analysis and validity of results (Arnqvist & Martensson, 1998).	The Matter & Form 3D scanner tech spec ensures within 0.1mm accuracy. Multiple scans were taken of every specimen and combined to enhance accuracy.
Quality of Specimen	Many multivariate methods used within geometric morphometric analysis are 'intolerant of missing data' and so relies on complete shape coordinates (Arbour and Brown, 2013).	Thin-plate Spline and multivariate regression methods used to estimate missing landmarks on broken or missing craniometric points (see section 4.4.2)

Environment of measurements taken	Described in section 4.1.2, sensitivity of scanning equipment meant that the optimal environment needed to be staged in order the reduction of background noise and shadowing, allowing for accurate digital imaging.	Optimum environment was achieved through minimising bright or harshly reflective backgrounds i.e. windows, mirrors, screens etc., ensuring shadowing is kept to a minimum, and lighting is controlled by using a photography tent, Ensuring the scanner and specimen were placed on stable desktop surface.
Intra-observer error in landmarking process	The definition of landmarks is unequivocal (see Tables 4.1 and 4.2). The biologically homologous points used in this study are well-documented as traditional craniometric landmarks and defined through one source. However, the	Using *geomorph* function to identify potential outlying specimen are plotted as red with a returned specimen ID. Where outliers exist, the specimens are landmarked once more, and the GPA analysis is performed without potential outliers.

	various sizes of primate mandible and crania can cause incidence of error as there will exist small variances around landmark positions, i.e. the position of the Mental Foramen (Moore-Janson et al., 1994).	

Table 4.19: A list of identified sources of potential measurement error, based on Arnqvist and Martenssons' (1998) sequential partitioning of error, and the solutions to improve accuracy and validity during data collection.

4.5 Methods of Data Analysis

This section details the methods of statistical testing used to conduct the geometric morphometric analysis from the landmark-based data sets obtained through data collection. The raw landmark coordinate data files were grouped into large data sets depending on the classified variables before statistical testing began, i.e. interspecies and intraspecies, mandible and cranium specimens, similar habitat types. For reference, **Figure 4.19** shows the workflow for this methodology.

4.5.1 Generalised Procrustes Analysis

The initial task within the GM analysis was to perform a General Procrustes Analysis (GPA) on the raw data that had been imported into R. GPA is a popular method of shape alignment particularly within computational imaging (Cho *et al.*, 2013:1549). It is essential to manipulate shape data to a common alignment, within geometric morphometric analyses, so that the subsequent functions will focus purely on data regarding shape variation and disregard unimportant factors, such as size. This is achieved through Euclidean Transformations that translate, scale and rotate various shapes according to a specific reference shape, minimizing the sum of the squared distances between the two groups (Cho *et al.*, 2013:1549).

Within R, GPA was achieved through the `gpagen` function for the 3D landmark dimensions. Subsequent functions are included to define the type of landmarks that are present i.e. semi landmarks on a curve, fixed landmark points or a combination of these. An option to conduct a GPA for bilateral symmetry is available as the `bilat.symmetry` function however, in the form of fossils, symmetry is not always a definable feature and therefore cannot be relied upon within this study.

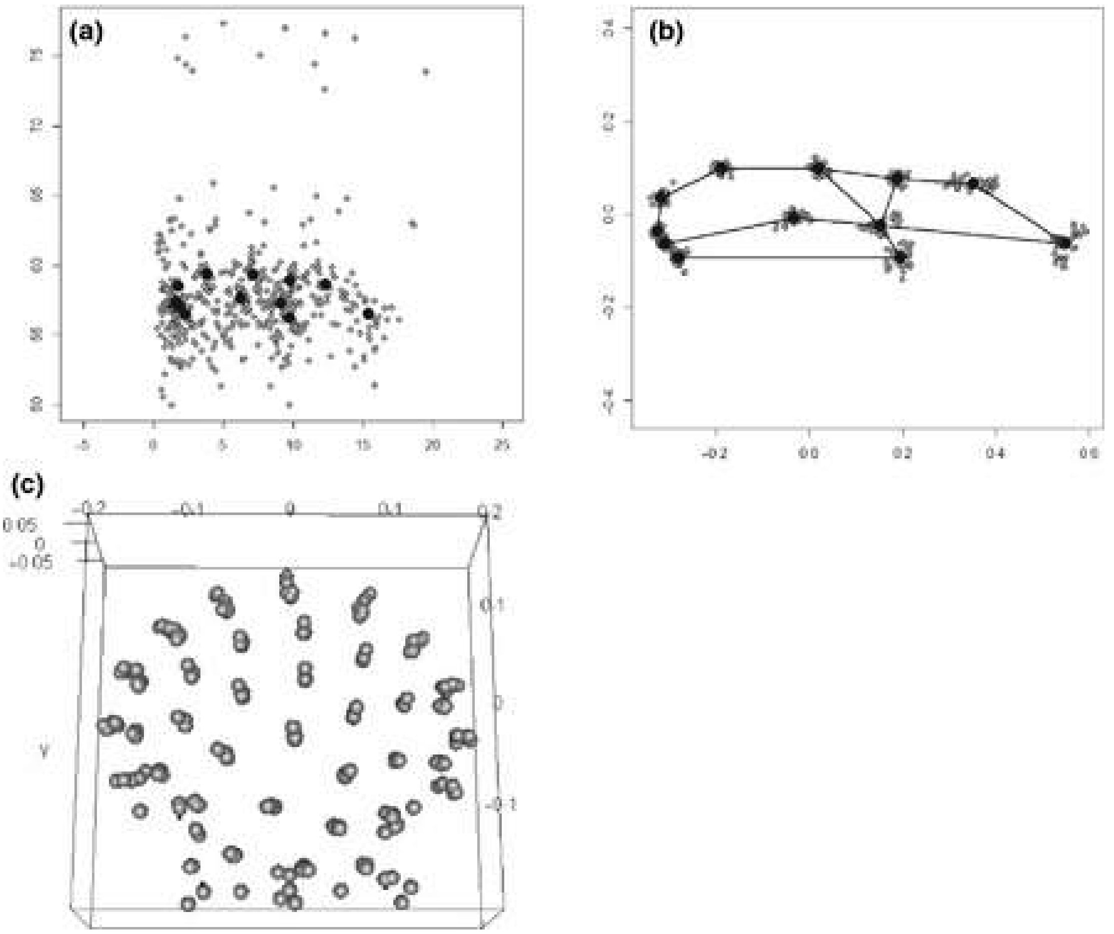


Figure 4.37: Example of raw landmark Plethodon data (a) and plotted Procrustes superimposition (b) as a result of the Generalised Procrustes Analysis providing the transformed data ready to be used in the next

function of a geometric morphometric analysis. Function performed using *geomorph* in R (Adams & Otarola-Castillo, 2013).

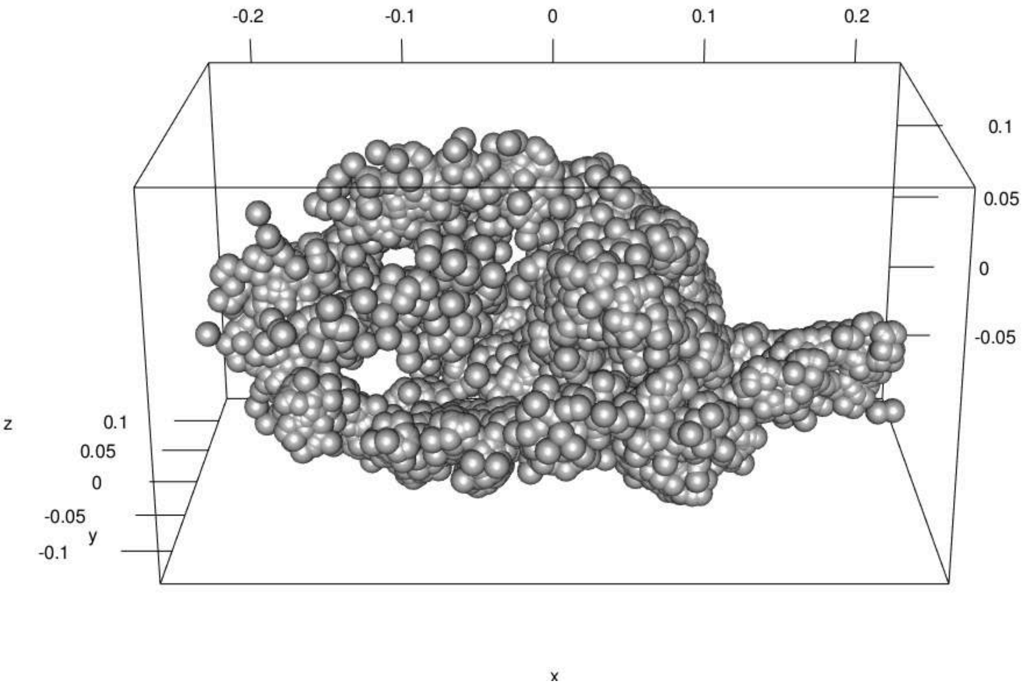


Figure 4.38: Procrustes-aligned cranial landmarks of all primate specimen in the study. These Procrustes coordinates will be the points used for further statistical testing in the study.

4.5.2 Estimating Missing Landmarks

Where distortion and broken bone exists in the mandible and crania specimens, it was necessary to estimate missing landmarks using Thin-plate Spline and statistical reconstruction implemented by multiple Multivariate Regression methods. This has been achieved through the *geomorph* package using the function `estimate.missing(A, method = c(“TPS”, “Reg”))`. This function takes a specimen set as an array containing 3D landmark coordinates and preforms the function automatically. The function estimates missing landmarks locations for incomplete specimens which have been represented as NA in the x,y,z coordinates.

Firstly, the Thin-plate Spline interpolation estimates landmarks on an incomplete target specimen from a reference specimen. The reference specimen is collated from a set of specimens that have an observed completed set of landmarks. The incomplete specimens are aligned to the reference by the landmark coordinates that are present in both. Thin-plate Spline is then used to estimate the location of any missing landmarks within the incomplete specimens (Sherratt, 2016: 26).

Subsequently, a multivariate regression is performed where missing value landmarks are regressed onto the data set containing complete landmarked specimens. A liner regression model predicts the values of the missing coordinates. The regression is then implemented onto scores along the initial set of Partial Least Squares (PLS) axes for both completed and incomplete sections of landmarks (Gunz *et al*. 2009; MacLeod, 2010).

4.5.2.1 Finding Potential Outliers

Checking for repeatability of landmarks is vital, as landmarks that move, become lost in the image capture or measurement procedure, can produce errors in the data. Zelditch *et al*. (2012:54) states that systematic errors and digitizing errors can be identified as either an approximately elliptical or circular scatter of points. To correct this, outlying landmarks were removed or re-digitized onto the specimen. Reliability is then tested for using the same translate, rotate and rescale operations as Procrustes alignment.

The `plotOutliers()` function of the *geomorph* package creates a plot ordering the Procrustes-aligned specimens by their distance from the mean shape, which is averaged using the `mshape()` function. The outlier plot shows the median as an unbroken line and the upper quartile as dashes forming a line along the graph. The lines summaries the quantified distances from the mean shape that exist within the specimen sample. Specimen that fall beyond the upper quartile range are considered potential outliers and are plotted as red with a returned specimen ID. Where outliers exist, the specimens are landmarked once more, and the GPA analysis is performed without potential outliers.

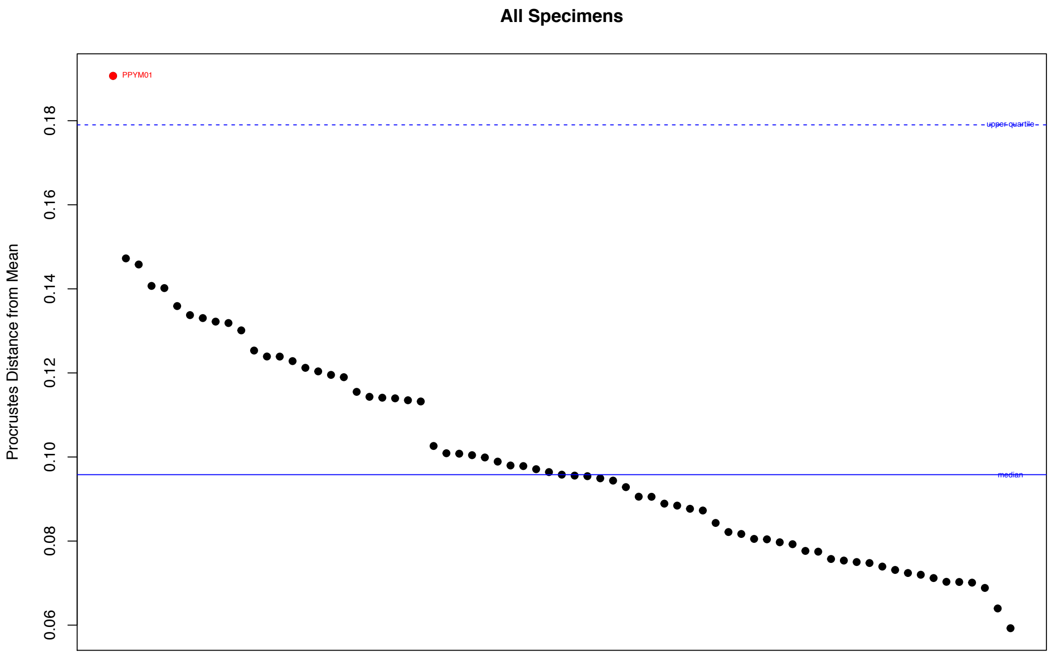
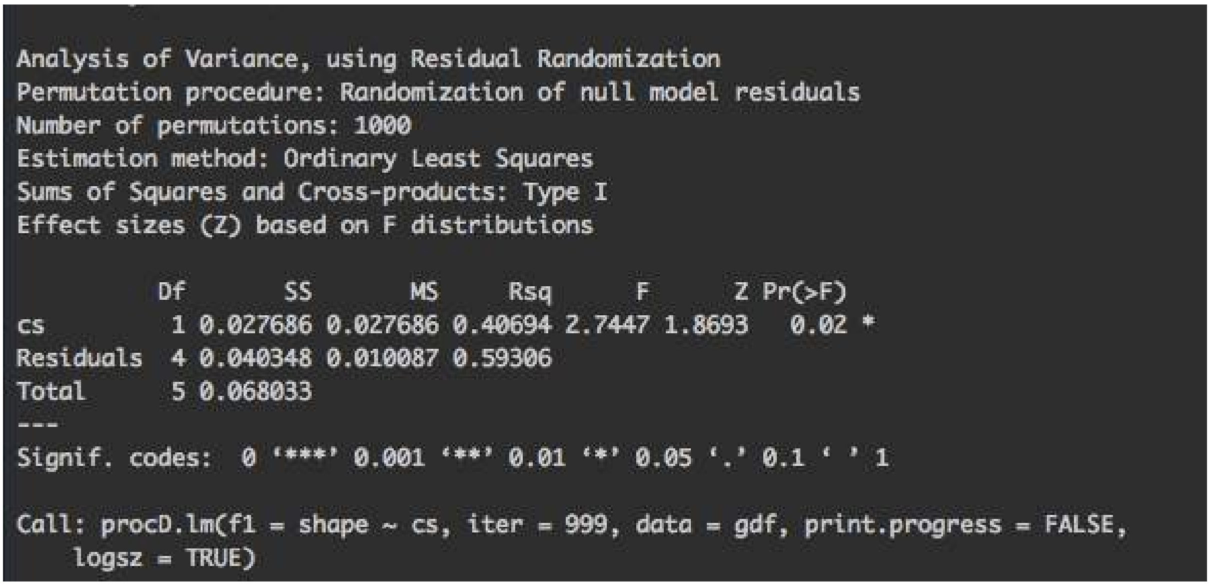


Table 4.20: Results of outliers. PPYM01 (*Pongo pygmaeus*) has been identified as an outlying specimen and subsequently re-landmarked and tested through GPA.

4.5.3 Procrustes ANOVA

Using permutation procedures, Procrustes ANOVA was used to assess the statistical hypotheses describing the patterning of shape variation in the Procrustes-aligned coordinates (Sherratt, 2015: 33) between species. The Procrustes ANOVA tests revealed p-values for all dataset variables, in the form of a table, by using the *geomorph* function `procD.lm(f1, data = NULL, iter = 999)` where `f1` is a linear model formula (y~x1+x2 (y as 2D array of shape data)) and `iter` is the number of iterations in the dataset for significant testing. **Table 4.21** defines each of the statistical calculations reported by the Procrustes ANOVA analysis.



```
Analysis of Variance, using Residual Randomization
Permutation procedure: Randomization of null model residuals
Number of permutations: 1000
Estimation method: Ordinary Least Squares
Sums of Squares and Cross-products: Type I
Effect sizes (Z) based on F distributions

          Df       SS       MS     Rsq      F      Z Pr(>F)
cs         1 0.027686 0.027686 0.40694 2.7447 1.8693   0.02 *
Residuals  4 0.040348 0.010087 0.59306
Total      5 0.068033
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Call: procD.lm(f1 = shape ~ cs, iter = 999, data = gdf, print.progress = FALSE,
    logsz = TRUE)
```

Figure 4.39: Example of Procrustes ANOVA results indicating the p-value for dataset analysed using the *geomorph* package in R.

	Represents	Definition
Df	Degrees of Freedom	Degrees of Freedom equal the size of the independent values in a dataset minus 1 or Df = N -1 (NIST, 2013).
SS	Sum of Squares	A measure of deviation from the mean, or total variation, calculated by considering the sum of squares of the study factors and of error or randomness (Greenwood and Banner, 2015).
MS	Mean Squares	Found by dividing the variance by the Degrees of Freedom. Variance which is found by dividing the SS result by the Df (Jones, 2018)
Rsq	R-squared	In a regression model, the R-squared statistic measures the variance proportion for a dependent variable which is explained by an independent variable, i.e. to what extant one variable is explained by another (Fernando, 2020).
F	F-test	Independent variables divided by their respective Degrees of Freedom (Jones, 2018)
Z	Z-test	A null hypothesis test where the test statistic follows a normal distribution (Sprinthall, 2011).
Pr(>F)	P-value	The estimated probability of rejecting the null hypothesis (Biau *et al.*, 2010)

Table 4.21: Definition and explanation of the elements within the Analysis of Variance table returned by the Procrustes ANOVA procedure.

4.5.4 Two-block Partial Least Squares

Two-block partial least squares analysis is useful in the discussion as to whether habitat affects craniomandibular morphology as, though it is related to multi-regression methods, it does not assume that one variable is the cause of another, rather treating the variables symmetrically in order to find any types of relationships that exist between the two.mThis type of statistical testing was used successfully in a study conducted by Fadda and Corti (1998) who compared 3D landmark skull coordinates with ecological variables of the African rodent, *Arvicanthis*. Using Two-block PLS, the team demonstrated consistent patterning of morphometric variation across varying biomes.

Using the `two.b.pls` function, Two-block Partial Least Squares analysis was performed on the crania and mandible datasets with resulting plots indicating the degree of association between variables, i.e. intra-species, inter-species, and habitat type, in relation to the Procrustes-aligned coordinates of each dataset (Rolf and Corti, 2000). Where low P-values (<0.05) are returned as a result of the 2B-PLS analysis, this will be considered to be evidence in direct contrast to the null hypothesis, which in this study, states that environmental pressures do not affect morphology. The returned p-values will show whether intervention of habitat is statistically significantly in the evolution of craniomandibular morphology and the effect size will quantify how much intervention exists between the two variables. Cohen (1988) states that a ‘small’ effect size can be reported if the value returned is d = 0.2, 0.5 is representative of a ‘medium’ sized effect value, and 0.8 reflects a ‘large’ effect size. McLeod (2019) adds to this explanation stating that if ‘two groups’ means do not differ by 0.2 standard deviations or more, the difference is trivial, even if it is statistically significant’.

4.6 Visualisation of Shape Variation

One of the most important resulting factors of a geometric morphometric study are the visualisations of shape data variation. Klingenberg (2013) stresses the importance of visualisation of shape changes within geometric morphometric research, stating that interpretations of the ‘relative displacements of landmarks in the context of their overall arrangement’ are necessary. For this study, ordination methods are used to visualise the quantified data for the reader to better relate the statistical analyses to a more tangible result. Visualisation plots, such as deformation grids and Principal Component scree and scatter graphs, are an efficient way of disseminating complex research to a wider audience.

4.6.1 Principal Components Analysis

Dunteman (1989:7) describes Principal Components Analyses (PCA) as a statistical technique, which allows researchers to define a dataset with a minimal amount of uncorrelated variables representative of most of the original raw data information. PCA is a descriptive tool allowing the researcher to obtain precise data regarding the patterns existing within shape variation (Zelditch *et al*., 2012:147).

PCA is useful in that further research opportunities can be understood from the covariances that appear among the original variables in a dataset. Research can focus on the cause of these covariances, explaining the behaviour of a set of random variables when subjected to probability and statistical testing (Zelditch *et al*., 2012:136). The parsimonious application of PCA is beneficial, as a small dataset consisting of principal components is far more understandable and desirable when conducting further analyses in a study (Dunteman, 1989:8).

The *geomorph* package allows the user to perform Principal Components Analyses which graphically visualise the shape variation among specimen groups. Plotting the initially Procrustes-aligned specimens along principle axes within a tangent space and subsequently reporting the variation in percentage along each axis achieve a completed PCA (see **Table 4.4**). Additionally, deformation grids can be used to further display the shape variation among selected specimens (Sherratt, 2015a: 25-29).

Using the function `plotTangentSpace`, PCA was performed for the variable data groups allowing for inspection of existing shape patterns. The visualised PCA using the *geomorph* package allowed for clear and understandable graphical representation of the quantified shape data in relation to the chosen variables.

4.6.2 Thin-plate Spline Deformation Grids

Deformation grids were created for each dataset through the Thin-plate Spline method using the function `plotRefToTarget`. This method generates Thin-plate Spline deformations in the x-y and x-z planes for 3D datasets (Sherratt, 2015a; Claude, 2008). The Thin-plate Spline grids are a method of displaying shape change and depicting the relative deformation of landmark coordinates from a target to a reference shape according to the minimum bending energy necessary to complete the transformation (Bookstein, 1989). The deformation grids are an important visualisation tool for morphological shape analysis and will be used as accompaniments to the PCA graphs for further interpretation of the results.

4.7 Summary

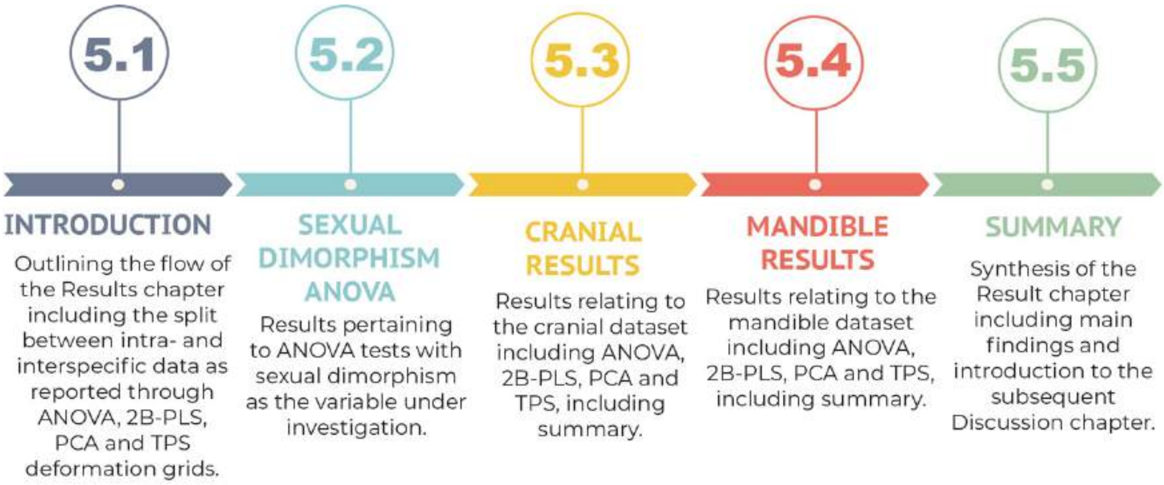
This chapter has shown the species selection and development of the geometric morphometric process used in this study. The final methodology has been outlined that would be used to 3D image capture, collect and process specimen shape data, and the statistical (ANOVA and Two-block partial least squares) and visual analysis (Principal Components Analysis and Thin-plate Spline deformation grids) used to assess and visualise the patterns of variation between primate datasets. Specimen crania and mandible specimens were sourced from the Oxford University and Smithsonian Natural History Museums Zoological collections. Known regional location and habitat of each specimen will be assigned as ecological variables or habitat-classifiers for each species. Species will therefore be used as a proxy for habitat type. Pilot studies informed the most suitable technology for this research. The Matter and Form 3D desktop scanner and R software (with accompanying Studio IDE) were identified as appropriate platforms to conduct data collection, digital landmarking, geometric morphometric and statistical analyses.

Chapter Five reports and visualises the results returned from the geometric morphometric analysis of both inter- and intraspecific groups of craniomandibular datasets.

P-values, effect sizes and correlation coefficients are reported as a result of ANOVA and 2B-PLS testing. A plotted line of best fit accompanies the 2B-PLS results indicating the degree of shape co-variation along the major axis, reflecting the coefficient returned as r-pls, or the Pearson R correlation, which indicates strong, moderate, or weak linear relationships between morphology and environmental variables.

PCA scatterplots are colour indicative showing existing species clusters and morphospace distributions of Principal Components for within-species and between-species groups in relation to habitat type. Thin-plate Spline deformation grids accompany the scatterplots alongside the PC variance axes to show warping for the minimum and maximum shapes of the two most important Principal Components.

5 RESULTS



Outlining the flow of the Results chapter including the split between intra- and interspecific data as reported through ANOVA, 2B-PLS, PCA and TPS deformation grids.

Results pertaining to ANOVA tests with sexual dimorphism as the variable under investigation.

Results relating to the cranial dataset including ANOVA, 2B-PLS, PCA and TPS, including summary.

Results relating to the mandible dataset including ANOVA, 2B-PLS, PCA and TPS, including summary.

Synthesis of the Result chapter including main findings and introduction to the subsequent Discussion chapter.

Figure 5.1: An outline of Chapter Five showing the flow of each results and summary section.

5.1 Introduction

Results from the geometric morphometric analyses are split into two parts; cranial and mandibular data and further split into interspecific and intraspecific results. The results are reported via ANOVA for both sexually dimorphic and habitat-specific variables, Two-block Partial Least Squares (2B-PLS), Principal Components Analysis (PCA) and Thin-plate Spline (TPS) warps.

5.2 Sexual Dimorphism ANOVA Testing

Procrustes ANOVA tests were initially conducted to understand the degree to which sexual dimorphism affects the shape of the cranium and mandible once the Generalised Procrustes Analysis had removed size. The results of this ANOVA testing are reported in this section for both individual species and the corresponding genus.

The primary descriptor of the ANOVA tests is '`Log(CSize):Sex`' which reports the effects of shape against the sex variable and is quantified through the Pr(>F), or the p-value. The statistical significance reported by the p-values indicates whether a sex variable needs to be considered as part of the habitat-specific morphological analyses. A summary is included at the end of the results tables to conclude the findings as significant or negligible to the rest of the morphometric study.

5.2.1.1.1 Cranial Sexual Dimorphism ANOVA Results

***GORILLA* INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

GORILLA	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.15008	0.150080	0.31327	12.6326	5.4486	0.001
SEX	1	0.01017	0.010170	0.02123	0.8560	-0.2715	0.609
LOG(CSIZE):SEX	1	0.00994	0.009936	0.02074	0.8364	-0.3098	0.641
RESIDUALS	26	0.30889	0.011880	0.64476			
TOTAL	29	0.47908					

G. *GORILLA*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.085173	0.085173	0.38359	7.6813	4.0120	0.001
SEX	1	0.009406	0.009406	0.04236	0.8483	-0.2850	0.610
LOG(CSIZE):SEX	1	0.005493	0.005493	0.02474	0.4954	-1.6428	0.942
RESIDUALS	11	0.121972	0.011088	0.54932			
TOTAL	14	0.222043					

G. *BERINGEI*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.035582	0.035582	0.21253	3.6348	3.6137	0.001
SEX	1	0.012762	0.012762	0.07623	1.3037	0.8170	0.208
LOG(CSIZE):SEX	1	0.011392	0.011392	0.06804	1.1637	0.4949	0.308
RESIDUALS	11	0.107682	0.009789	0.64319			
TOTAL	14	0.167419					

Table 5.1: ANOVA testing p-values and statistical significance of sexual dimorphism within gorilla species, *Gorilla gorilla* and *Gorilla beringei*. All returned p-values (0.641, 0.942 and 0.308, respectively) indicate that gorilla male and female morphological characteristics have no significance in relation to centroid size in this dataset.

***PONGO* INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

PONGO	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.050732	0.050732	0.24080	5.9200	4.3625	0.001
SEX	1	0.014480	0.014480	0.06873	1.6896	1.5792	0.055
LOG(CSIZE):SEX	1	0.008353	0.008353	0.03965	0.9747	0.0989	0.457
RESIDUALS	16	0.137115	0.008570	0.65082			
TOTAL	19	0.210680					

P. *ABELII*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.032172	0.032172	0.31355	3.7492	3.0201	0.004
SEX	1	0.014237	0.014237	0.13876	1.6591	1.4280	0.068
LOG(CSIZE):SEX	1	0.004709	0.004709	0.04590	0.5488	-1.0652	0.852
RESIDUALS	6	0.051486	0.008581	0.50179			
TOTAL	9	0.102605					

P. *PYGMAEUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.026603	0.0266031	0.28574	3.1034	2.33645	0.004
SEX	1	0.007088	0.0070884	0.07614	0.8269	-0.24561	0.545
LOG(CSIZE):SEX	1	0.007977	0.0079769	0.08568	0.9305	0.04481	0.456
RESIDUALS	6	0.051434	0.0085723	0.55245			
TOTAL	9	0.093103					

Table 5.2: ANOVA testing p-values and statistical significance of sexual dimorphism within *Pongo* species, *P. abelii* and *P. pygmaeus*, Procrustes-aligned cranial shape. High p-values indicate low statistical significance between male and female specimen across the *Pongo* dataset. ANOVA relating to the male and female specimen in the *P. abelii* dataset returned a high p-value of 0.852 and 0.456 in the *P. pygmaeus* dataset.

***PAN* INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

P. *TROGLODYTE*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.027504	0.0275040	0.20462	4.0882	4.4312	0.001
SEX	1	0.006512	0.0065120	0.04845	0.9679	0.0308	0.518
LOG(CSIZE):SEX	1	0.006210	0.0062103	0.04620	0.9231	-0.1174	0.554
RESIDUALS	14	0.094188	0.0067277	0.70073			
TOTAL	17	0.134414					

Table 5.3: ANOVA tests reporting p-values and statistical significance of sexual dimorphism within the Procrustes aligned cranial shape of *Pan troglodyte*. A p-value of 0.554 indicates low statistical significance between male and female specimen, which is explained by the small size of this specimen sample.

***HYLOBATES* INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

HYLOBATES	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.07137	0.071366	0.17131	8.8249	5.5402	0.001
SEX	1	0.00718	0.007182	0.01724	0.8881	-0.1830	0.540
LOG(CSIZE):SEX	1	0.00648	0.006477	0.01555	0.8010	-0.4500	0.676
RESIDUALS	41	0.33156	0.008087	0.79590			
TOTAL	44	0.41659					
H. *NOMASCUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.029694	0.0296942	0.29008	3.9439	3.2610	0.006
SEX	1	0.007854	0.0078544	0.07673	1.0432	0.2279	0.398

LOG(CSIZE):SEX	1	0.004584	0.0045840	0.04478	0.6088	-1.2376	0.892
RESIDUALS	8	0.060233	0.0075292	0.58841			
TOTAL	11	0.102366					

H. *LAR*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.013475	0.0134750	0.10014	1.8688	1.9625	0.038
SEX	1	0.007023	0.0070233	0.05220	0.9740	0.0965	0.461
LOG(CSIZE):SEX	1	0.005901	0.0059009	0.04385	0.8184	-0.3820	0.646
RESIDUALS	15	0.108159	0.0072106	0.80381			
TOTAL	18	0.134558					

S. *SYNDACTYLUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.042852	0.042852	0.42714	6.9024	3.4685	0.004
SEX	1	0.004483	0.004483	0.04469	0.7221	-0.5069	0.683
LOG(CSIZE):SEX	1	0.003322	0.003322	0.03312	0.5352	-1.2121	0.899
RESIDUALS	8	0.049666	0.006208	0.49506			
TOTAL	11	0.100323					

Table 5.4: ANOVA testing p-values and statistical significance of sexual dimorphism within *Hylobatidae* Procrustes-aligned cranial shape. An overall p-value of 0.676 indicates low statistical significance between male and female specimen. ANOVA results for *H. nomascus*, *H. lar* and *S. syndactylus* returned low p-values of 0.892, 0.646 and 0.899, respectively, indicating the weak statistical power of such a small sample size. *H. hylobates,* specimens were not included in this testing as all cranial specimen in this dataset were assigned female.

5.2.1.1.2 Mandible Sexual Dimorphism Results

GORILLA **INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

GORILLA	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.059333	0.059333	0.27759	10.5224	4.2310	0.001
SEX	1	0.003012	0.003012	0.01409	0.5342	-1.9761	0.975
LOG(CSIZE):SEX	1	0.004793	0.004793	0.02242	0.8500	-0.3180	0.621
RESIDUALS	26	0.146606	0.005639	0.68589			
TOTAL	29	0.213744					

G. *GORILLA*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.029674	0.0296743	0.30027	6.5587	2.85940	0.001
SEX	1	0.004121	0.0041212	0.04170	0.9109	-0.0369	0.504
LOG(CSIZE):SEX	1	0.006212	0.0062122	0.06286	1.3730	0.97965	0.165
RESIDUALS	13	0.058817	0.0045244	0.59517			

TOTAL	16	0.098825					
G. BERINGEI	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.029674	0.0296743	0.30027	6.5328	2.84408	0.001
SEX	1	0.004580	0.0045805	0.04635	1.0084	0.16401	0.429
LOG(CSIZE):SEX	1	0.005519	0.0055192	0.05585	1.2151	0.63517	0.253
RESIDUALS	13	0.059051	0.0045424	0.59753			
TOTAL	16	0.098825					

Table 5.5: ANOVA results reporting p-values and statistical significance of sexual dimorphism within *Gorilla* Procrustes-aligned mandible shape. An overall p-value of 0.621 indicates low statistical significance between male and female specimen. ANOVA results for *G. gorilla* and *G. beringei* returned high p-values of 0.165 and 0.253, also indicating low statistical significance.

***PONGO* INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

PONGO	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.023802	0.0238020	0.16620	3.3012	2.75305	0.001
SEX	1	0.007324	0.0073243	0.05114	1.0158	0.17498	0.432
LOG(CSIZE):SEX	1	0.003934	0.0039340	0.02747	0.5456	-1.23816	0.902
RESIDUALS	15	0.108151	0.0072101	0.75519			
TOTAL	18	0.143212					
P. *ABELII*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.020221	0.0202214	0.23375	3.5014	2.7233	0.001
SEX	1	0.014183	0.0141826	0.16394	2.4558	1.4941	0.090
LOG(CSIZE):SEX	1	0.017454	0.0174542	0.20176	3.0223	2.6056	0.019
RESIDUALS	6	0.034651	0.0057752	0.40055			
TOTAL	9	0.086509					
P. *PYGMAEUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.007871	0.0078714	0.16882	1.4218	1.0195	0.173
SEX		0.038754	-	-	-	-	-
LOG(CSIZE):SEX	1	17086	17086	-	2.9212	-	0.1312
RESIDUALS	7	0.038754	0.0055363	0.83118			
TOTAL	9	0.046626					

Table 5.6: ANOVA results showing mainly high p-values and low statistical significance of sexual dimorphism within *Pongo* in relation to the overall genus p-value of 0.902 and 0.1312 in relation to *P.*

pygmaeus. This sample set is too small to indicate true sexual dimorphic effects on shape as signified by the null values reported in the table.

PAN **INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

P. *TROGLODYTE*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.024045	0.0240453	0.31008	4.1635	2.68717	0.003
SEX	1	0.006832	0.0068318	0.08810	1.1830	0.46940	0.313
LOG(CSIZE):SEX	1	0.006242	0.0062422	0.08050	1.0809	0.23076	0.400
RESIDUALS	7	0.040426	0.0057752	0.52132			
TOTAL	10	0.077546					

Table 5.7: ANOVA results showing p-values and statistical significance of sexual dimorphism within *Pan troglodyte* specimen. P-values indicate that male and female morphological characteristics have no significance in relation to centroid size in this dataset.

HYLOBATES **INTRASPECIES SEXUAL DIMORPHISM PROCRUSTES ANOVA**

HYLOBATES	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.047189	0.047189	0.1878	8.710	3.7333	0.001
SEX	1	0.004794	0.004794	0.0190	0.884	-0.1851	0.570
LOG(CSIZE):SEX	1	0.004189	0.004189	0.0166	0.773	-0.4850	0.685
RESIDUALS	36	0.195030	0.005418	0.7763			
TOTAL	39	0.251202					
H. *NOMASCUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.016484	0.016484	0.3169	4.393	2.6567	0.006
SEX	1	0.006280	0.006280	0.1207	1.673	1.3647	0.095
LOG(CSIZE):SEX	1	0.002975	0.002974	0.0572	0.792	-0.5476	0.703
RESIDUALS	7	0.026263	0.003751	0.5050			
TOTAL	10	0.052002					
H. *HYLOBATES*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.003072	0.003072	0.1993	0.703	-0.8559	0.745
SEX	1	0.005215	0.052157	0.3385	1.193	0.3203	0.451
LOG(CSIZE):SEX	1	0.002750	0.002750	0.1785	0.629	-0.1449	0.757
RESIDUALS	1	0.004369	0.004369	0.2836			
TOTAL	4	0.015408					
S. *SYNDACTYLUS*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.039545	0.039545	0.4395	7.545	2.3175	0.004
SEX	1	0.002719	0.002719	0.0302	0.518	-1.4782	0.928

LOG(CSIZE):SEX	1	0.005779	0.005779	0.0642	1.102	0.3301	0.374
RESIDUALS	8	0.041929	0.005241	0.4660			
TOTAL	11	0.089972					

H. *LAR*	Df	SS	MS	Rsq	F	Z	Pr(>F)
LOG(CSIZE)	1	0.004575	0.004575	0.0766	0.841	-0.2348	0.584
SEX	1	0.007921	0.007920	0.1327	1.456	0.9778	0.163
LOG(CSIZE):SEX	1	0.003678	0.003677	0.0616	0.676	-0.5846	0.700
RESIDUALS	8	0.043493	0.005436	0.7289			
TOTAL	11						

Table 5.8: ANOVA results indicating high p-values and low statistical significance of sexual dimorphism within hylobates genus and individual species *H. hylobates*, *H. nomascus*, *H. lar* and *S. syndactylus*. All returned p-values of <0.3 indicate that male and female morphological characteristics have no significance in relation to centroid size in this dataset.

5.2.1.1.3 Sexual Dimorphism Summary

For both cranial and mandibular datasets, ANOVA tests revealed high p-values in all genera and corresponding species, indicating that sexual dimorphism has low statistical significance in relation to the Procrustes-aligned shape variables. This result indicates that the sexual dimorphism evident in all data groups is mostly explained through size. This also indicates that this dataset sample is small enough to consider the sex variable as negligible and will not be considered in the habitat-specific testing in the following sections.

5.3 Cranial Results

107 cranial specimens were 3D scanned and digitally landmarked with 19 corresponding fixed points which were subsequently aligned using General Procrustes Analysis. The following Principal Components Analysis, 2B-PLS and Thin-plate Spline warps are used to identify patterning of variance among species living in differing habitats. Ecological variables were assigned based on known origin region of the specimen and classified by specific habitat types corresponding to those locations (see **Table 5.9**). These variables were incorporated into the geometric morphometric analysis using an Excel spreadsheet assigning habitat classifiers to the relevant species.

ID	SPECIES	HABITAT
HBM01 – HBM05	*Hylobatidae hylobates*	Tropical evergreen forests; subtropical evergreen mountain forests
HM01 – HM12	*Hylobatidae lar*	Dry evergreen forests
HNM01-HNM11	*Hylobatidae nomascus*	Subtropical evergreen forests
HSM02-HSM13	*Symphalangus syndactylus*	Tropical hill forests; lowland forests
PAM01-PAM10	*Pongo abelii*	Lowland forests; mountain forests; peat swamps
PPYM01-PPYM10	*Pongo pygmaeus*	Lowland forests
PTM01- PTM14	*Pan troglodytes*	Dry savannah forests; montane forests; swamp forests

GBC01-GBC21	*Gorilla beringei*	Lowland tropical rainforest, transitional forests and Afromontane habitat
GGC01-GGC20	*Gorilla gorilla*	Rain, swamp and riverine forests, lowland tropical forests and brush

Table 5.9: Ecological variables were assigned to specific specimen 3D data clouds and inserted as classifiers within the geometric morphometric analysis in the form of an .csv file. Habitat type for each species was assigned based on regional location and distribution of the specimens. For example, *Gorilla beringei* specimens have been assigned lowland tropical rainforest, transitional rainforest and Afromontane habitat types based on the source of the specimen and known ecological inhabitants as reported by Sarmiento (2003) and McNeilage (2001). *Gorilla gorilla* specimens have been assigned rain, swamp and riverine forests, or lowland tropical forests and brush, as indicated by the origin region of the skull and as identified by Ilambu (2001).

5.3.1 Intraspecies Cranial Results

The following sections show the multivariate statistical tests conducted on Procrustes-aligned landmark datasets, which correspond to intraspecific groups. Habitat-specific ANOVA and Two-block Partial Least Squares (2B-PLS) results are reported showing the statistical significance and quantifiable relationship between ecological variables and morphological variance. Principal Components Analysis graphs and Thin-plate Spline Warps are presented, further showing any patterns of variance that exist in the intraspecific datasets.

5.3.1.1 ANOVA and 2-BLS analysis

Procrustes ANOVA and 2B-PLS tests were used to understand the effects of habitat on intraspecific cranial morphology. Results are shown within a table encompassing effect size, p-value and r-pls. These results indicate the strength of the relationship which exists between the environment and morphological variance by genus. 2B-PLS plots show the covariance between shape and habitat along the major axis of the graph, which is visualised as a line of best fit.

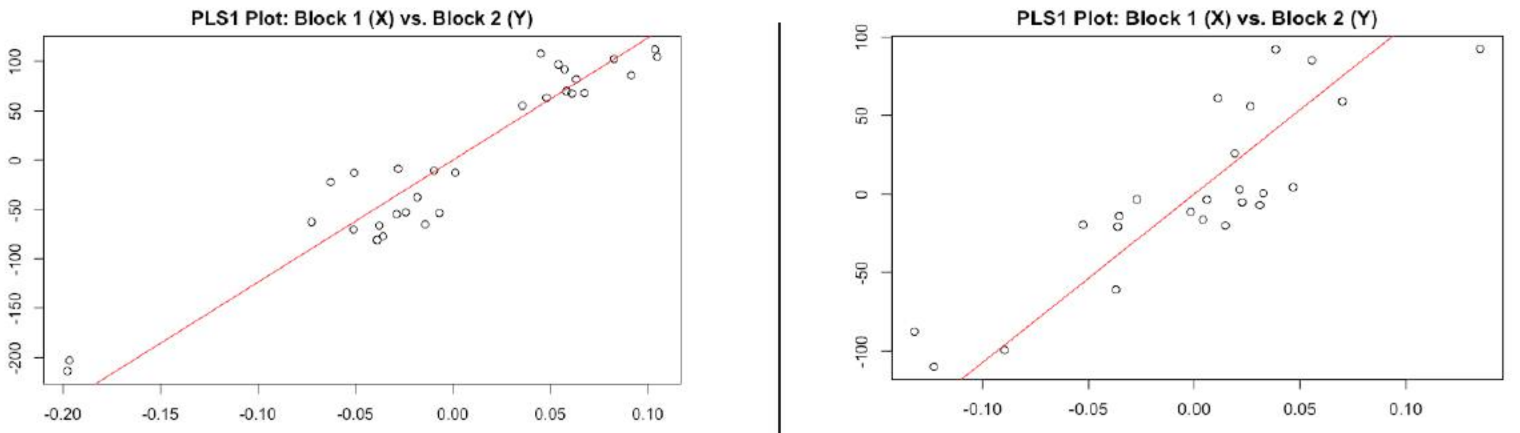
5.3.1.1.1 Habitat-specific Intraspecies Cranial ANOVA and 2B-PLS

ANOVA and 2B-PLS analysis performed on the intraspecific, Procrustes-aligned cranial coordinates returned a p-value of 0.001 with the exception of *Pan*, which showed a more statistically significant 0.008 p-value. This anomaly is explained by the group consisting of one species, *P. troglodyte,* instead of two or more conspecifics as in the accompanying within-species groups. All intraspecific groups returned a p-value in direct contrast to the null hypothesis, with differing effect sizes (see **Table 5.2**).

The effect sizes for each species groups differ with an extreme difference of 2.061 between *Pan* and gorilla. The *P. troglodyte* species effect size is the smallest as expected due to the single species analysed in this specific group. The gorilla group experienced the largest effect size, reporting 5.892 and showing the most variance by the intervention of habitat.

Species	**Effect Size**	**P-value**	**r-pls**
Gorilla	5.0892	0.001	0.951
Hylobates	4.7913	0.001	0.857
Pongo	3.0193	0.001	0.9
Pan	2.2282	0.008	0.862

Table 5.10: Effect size and p-value summary of within-species cranium dataset showing statistical significance towards rejecting the null hypothesis for all species datasets except *Pan*. All effect sizes returned can be described, using Cohen's (1988) terminology, as 'small' or as 'medium' but are not trivial. The Pearson R correlations all report strong positive linear relationships meaning all intraspecific specimen show high levels of covariation between habitat and morphology.



A) Gorilla Interspecies Group

B) Hylobatidae Interspecies Group

C) Pan Interspecies Group

D) Pongo Interspecies Group

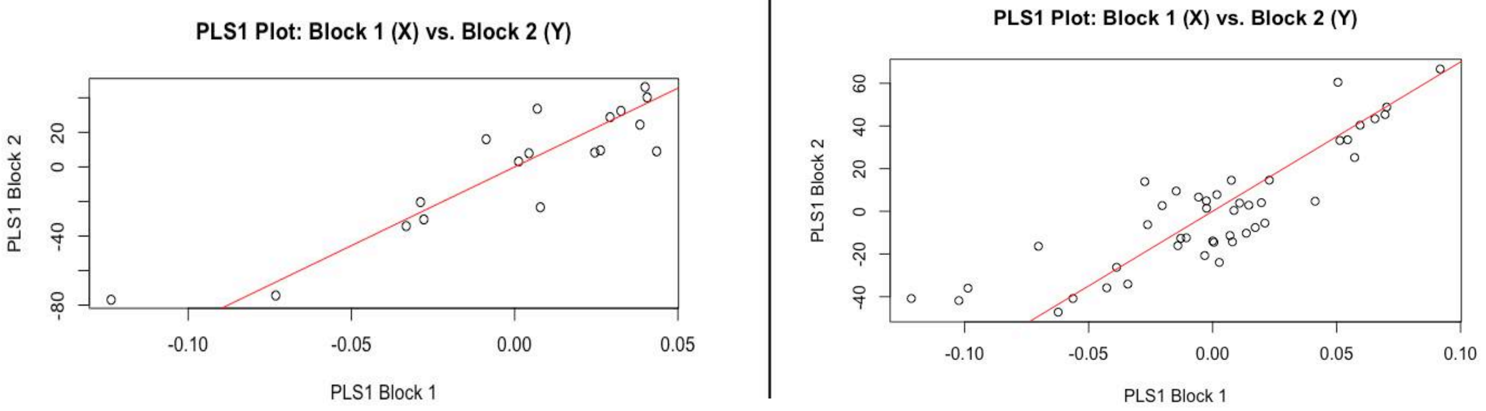


Figure 5.2: 2B-PLS plots showing covariance between shape and habitat along the major axis showing the line of best fit a) *Gorilla* b) *Hylobates* c) *Pan* and d) *Pongo* intraspecific groups.

5.3.1.1.2 Habitat-specific Intraspecies Cranial Principal Components Analysis and TPS

Principal Component Analysis plots were requested in R to understand the shape-space occupied for the within-species group (**Figures 5.3**, **5.4**, **5.5**, and **5.6**) in relation to habitat type. Thin-plate Spline warp grids accompany the PCA plots to visualise deformation along each axis.

Figure 5.3 shows the distribution of morphospace occupation for the *Gorilla* cranial specimen, where the first two Principle Components describe 49.03% of the observed overall shape variation. *G. gorilla* follows a wider distribution pattern in comparison to *G. beringei,* whose ordination predominately sits in the lower-left quadrant of negative PCA1, with four specimen exceptions sitting at 0 and moving into positive values. *G. gorilla* specimen, in contrast, are mostly found with positive PC values showing visually wider dissemination of plots than their counterpart, with the exception of two specimens sitting in the negative (top-left quadrant). The Thin-plate Spline warps returned for the gorilla dataset shows deformation particularly along the sagittal and nuchal crest and supraorbital torus.

The habitat differences between these conspecifics are marked by elevation, which is suggested as the variance in quantified shape-space returned by the PCA. *G. beringei*, commonly referred to as the ‘mountain gorilla’, lives at the highest elevation of 2200 – 4000m, whereas *G. gorilla*, or the ‘western lowland’ gorilla, inhabits lowland areas about sea level (1600m) (Cawthorn-Lang, 2005).

With the largest effect size amongst the intraspecies datasets, as indicated by the 2B-PLS analysis (5.0892), habitat variation between gorilla species has had the most quantifiable statistical significance on cranial morphology than any other species analysed in this study. The gorilla dataset also returned the highest r-pls score at 0.951, indicating the strongest positive linear relationship between intraspecies datasets.

The Two-block Partial Least Squares analysis performed for the within-species *Hylobates* dataset returned a p-value of 0.001 and an effect size of 4.7913, which is the second largest out of all intraspecies datasets in this study. These results indicate statistical significance against the null hypothesis and the third strongest, positive linear relationship between habitat and cranial morphology at a value of r-pls: 0.857.

The gibbon within-species PCA graph (**Figure 5.4**) shows a 42.07% variance in the first 2 PCs*.* The PCA shows all species as cranially distinct; however, there are considerable overlapping clusters between *H. hoolock, H. nomascus and H. hylobates.* The *S. syndactylus* specimens are the exception to this rule, predominantly staying within negative PCA values with four outlying specimens reaching positive values. This deviation of *S. syndactylus* from its conspecifics' clustering is also reported in the following interspecific cranial PCA, with specimen grouped in the upper right quadrant alongside *Pongo* specimen. This trend supports a clear distinction between evergreen/semi-evergreen forest inhabitants (*H. hoolock*, *S. syndactylus* and *H. nomascus*) and lowland forest inhabitants.

The intraspecific gibbon Thin-plate Spline grids, located at the PC1 and PC2 axes of the scatterplot, show marked parietal and frontal bone deformation most obvious on the lateral view of the warp grids. High-energy deformation exists in the facial skeleton, which is associated with the variable degree of airorhynchy in this genus, i.e. *S. syndactylus* displays a more dorsally flexed facial structure than other gibbon species (Shea, 1988). Deformation can also be seen in the region of the warp grid associated with canine length and structure, i.e. *S. syndactylus* have less lingually curved canines than other Gibbons in the study (Kay and Ungar, 1997, 2000; Bilsborough and Rae, 2007).

The Two-block Partial Least Squares analysis performed on the *Pongo* dataset returned a p-value of 0.001, an effect size of 3.0193, and a Pearson R coefficient of r-pls: 0.9. This analysis shows statistical significance against the null hypothesis described by a small effect size which is further represented by a strong, positive linear relationship as reported as the line of best fit in **Figure 5.2**.

The PCA graph (**Figure 5.5**) returned for the *Pongo* cranium dataset shows 46.3% variance in the first 2 PCs, with distinct clustering between *P. abelii* and *P. pygmaeus* and an emphasis of specimen sitting within positive PCA values. Visual inspection of PCA clusters shows equally dispersed patterning within *P. abelii* specimen and *P. pygmaeus*. This is significant as the latter species inhabits a wider range of biomes (Chan *et al.*, 2010) than *P. abelii*, suggesting minor craniomandibular morphological disparity when environment is used as the contrasting variable in the *Pongo* genus. Considerable warping can be seen in the PC1 Thin-plate Spline grids, particularly from a lateral view and on the sagittal crest from the PC1 anterior view.

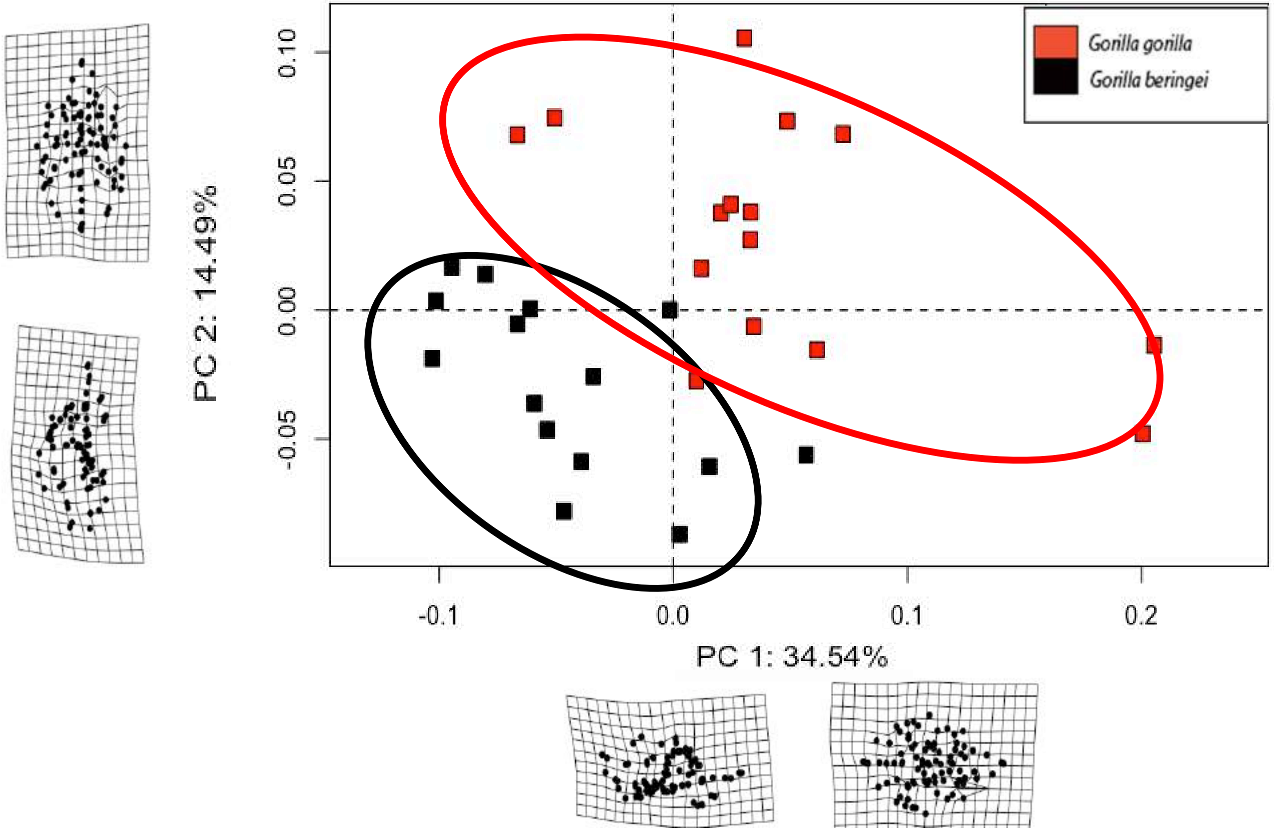


Figure 5.3: *Gorilla* within-species PCA graph showing 49.03% variance in the first two Principal Components and clusters separating *G. gorilla* and *G. beringei* species, indicating significance in morphospace distribution and supporting large effect size (5.0892) reported by 2B-PLS analysis.

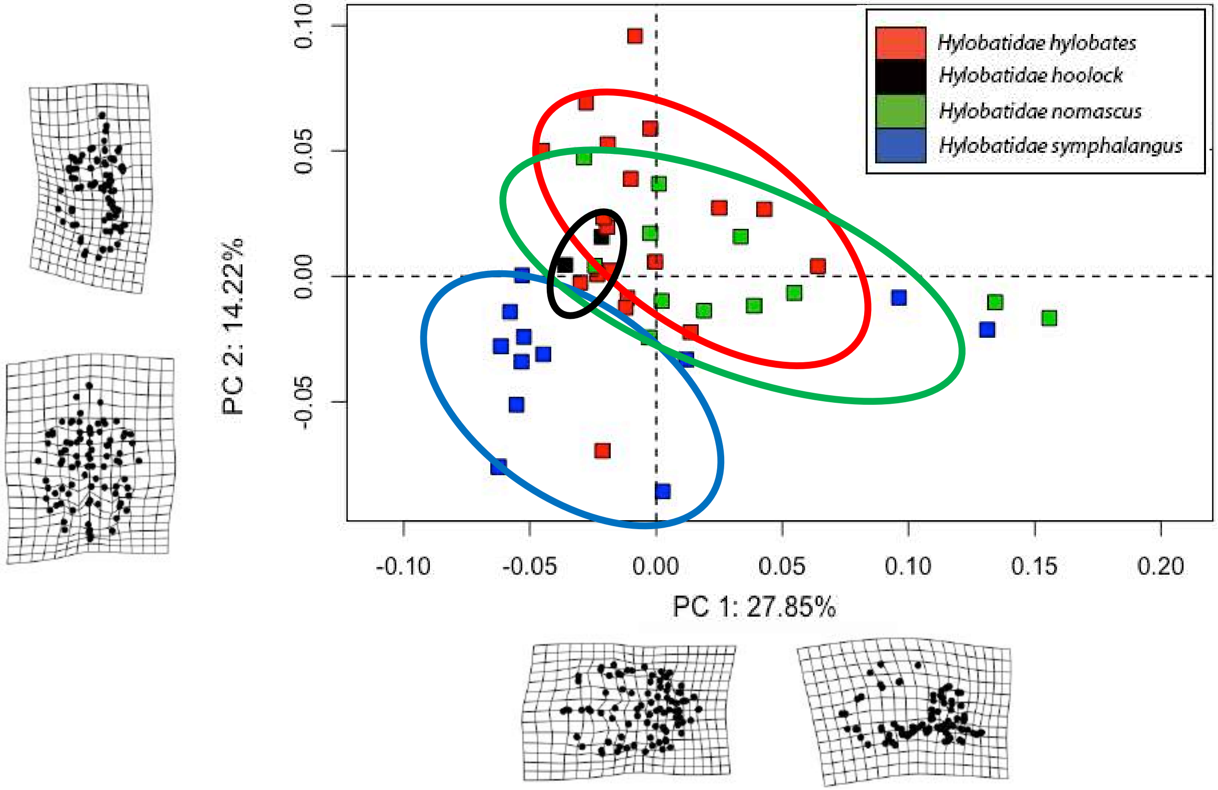


Figure 5.4: *Hylobates* within-species PCA graph showing 42.07% variance in the first two Principal Components and clusters separating *H. hoolock, S. syndactylus, H. nomascus and H. hylobates.* TPS grids show marked parietal and frontal bone deformation most obvious on the lateral view of warp grids.

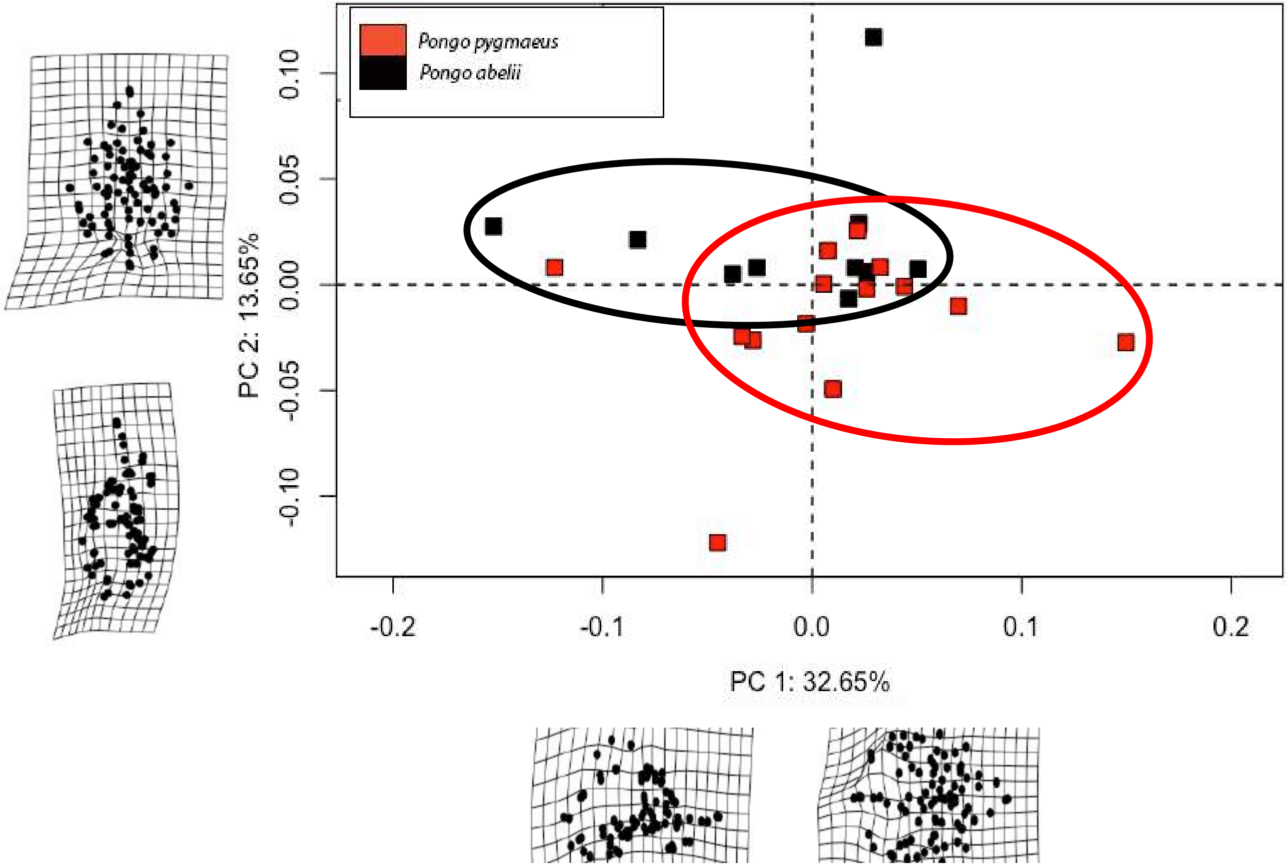


Figure 5.5: PCA graph showing 46.3% variance in the first two Principal Components of *Pongo* cranial dataset with distinct clustering between *P. abelii* and *P. pygmaeus* and an emphasis of specimen sitting within positive PCA values. Considerable warping can be seen in the PC1 TPS grids, particularly from a lateral view as well as on the sagittal crest from the PC1 anterior view.

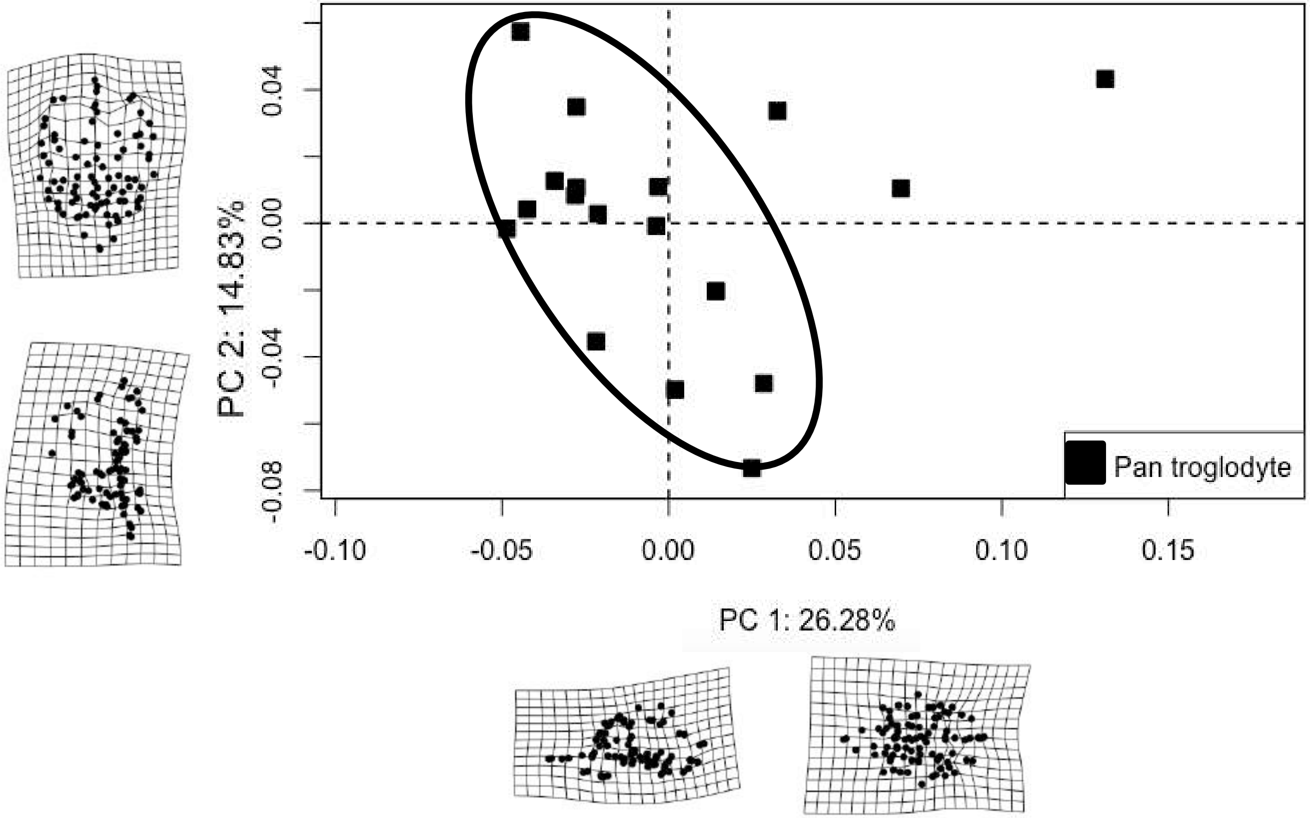


Figure 5.6: PCA graph showing 41.11% variance in the first two Principal Components of the *Pan troglodyte* dataset with a median cluster between -0.05 and 0.05 PCA1 values with the exception of 3 outlying specimens further along the positive axis.

Figure 5.6 represents the PCA graph for *P. troglodyte,* which shows 41.11% total variance in the first 2 PCs of the dataset. Visual inspection reports a median cluster between -0.05 and 0.05 PCA1 values, with the exception of three outlying specimens further along the positive axis. Thin-plate Spline Warps created for PC1 and PC2 of the *Pan* dataset show deformation focused towards the occipital bone and either side of the coronal suture to the rear of the parietal bone.

Two-block Partial Least Squares analysis reported a substantive but small effect size significance of 2.228, which is the lowest amongst the intraspecies datasets. However, the correlation coefficient shows a strong positive linear relationship (r-pls: 0.862), indicating environment as an important factor of cranial morphology (see **Figure 5.2**). The p-value is returned as 0.008, which is statistically significant enough to reject the null hypothesis but is closer to the 0.05 control than the rest of the interspecific datasets.

As this group includes specimen from one species (*P. troglodyte*), unlike its conspecifics with more than one species datasets, it appears there is less statistical significance between morphological variation and habitat. This, however, may be indicative of the small sample size.

5.3.2 Interspecies Cranial Results

This section reports the multivariate statistical results conducted on Procrustes-aligned landmark datasets corresponding to interspecific cranial groups. Results are reported using ANOVA, 2B-PLS, Principal Components Analysis and Thin-plate Spline Warps.

5.3.2.1 ANOVA and 2B-PLS analysis

One dataset encompassing all cranial specimen from *Gorilla*, *Hylobatidae*, *Pongo* and *Pan* species was subjected to ANOVA and 2B-PLS testing to understand the effects of habitat on interspecific cranial morphology. The results are shown as effect size, p-value and r-pls, indicating the strength of the relationship existing between environment and cranial morphological variance. A 2B-PLS plot shows the covariance between shape and habitat along the major axis of the graph and visualised through a line of best fit.

5.3.2.1.1 Habitat-specific Interspecies Cranial ANOVA and 2B-PLS

ANOVA and 2B-PLS analysis preformed on the interspecific, Procrustes-aligned cranial coordinates returned a p-value of 0.001 and an effect size of 11.09. These scores reflect a strong correlation between environment and morphological variance and shows significance in rejection of the null hypothesis, which states that there is no statistically noteworthy indication that environment type influences the morphology of the cranium in primates. The correlation coefficient, a measurement reporting the strength of linear relationships between variables and exemplified as the line of best fit in **Figure 5.7**, shows a strong positive relationship in the interspecific cranial dataset (r-pls: 0.945).

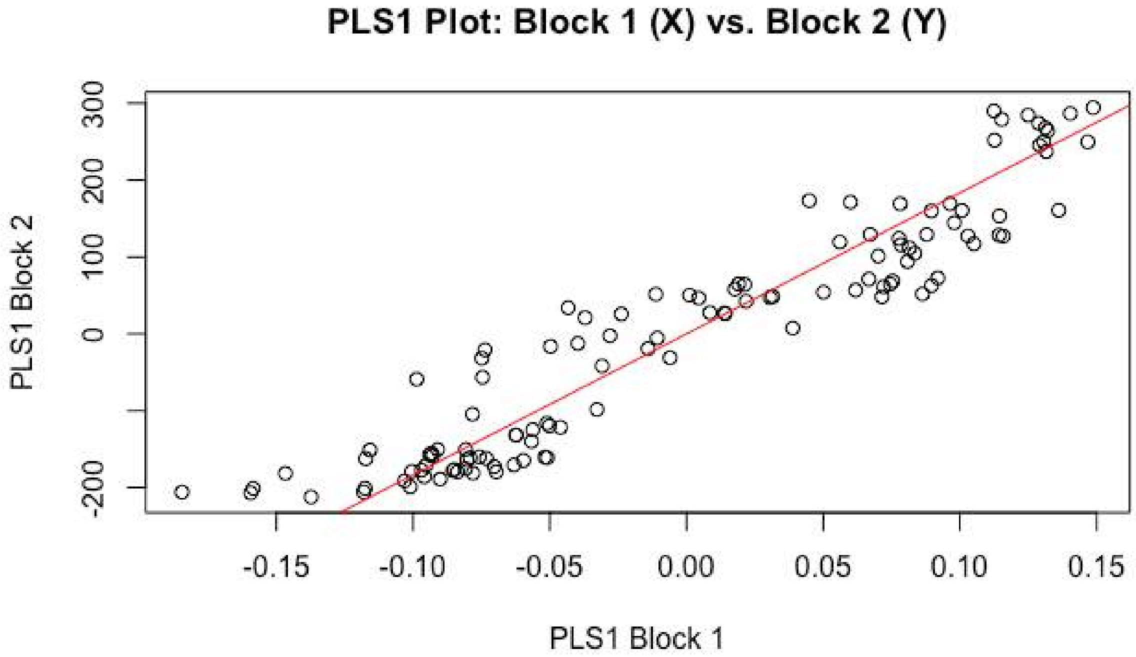


Figure 5.7: Plot of first 2B-PLS dimensions for interspecies cranium data showing the major axis of shape covariation as a line of best fit. PLS block 1 represents the classifying habitat variable and species proxy, and block 2 represents the form of the specimens' shape.

5.3.2.1.2 Habitat-specific Interspecies Cranial Principal Components Analysis and TPS

Principal Components Analysis was used to investigate the shape-space occupied by 107 cranial specimens across nine species living in differing habitats (see **Table 5.9**) in order to assess the degree to which species living in similar biomes experience similar phenotypic affinities (assessed in this section by cranial shape) (**Fig. 5.8**).

The first two Principal Components (PC1 and PC2) described 53.27% of the overall observed shape variation for the interspecific cranial data. Visual inspection of PC1 and PC2 values show two obvious clusters. On the lower half of the PC1 values, to the left of the scatterplot, we see a larger distribution of specimen showing a dominant, more diverse spread of intraspecific, as well as overlapping, genera trends. A cluster of *G. gorilla* and *P. abelii* species is seen in the top right quadrant of the positive PC1 values, with the addition of *S. syndactylus*, indicating a commonality in morphospace occupation for species living in lowland and low-lying tropical forest habitats.

Specimen dominating the lower portion of PC1 values exist in swamp, montane, and evergreen forests. The hylobate genera (excluding *S. syndactylus*) populate the scatterplot with a widely distributed, but also diagonally defined, clustering of evergreen and sub-evergreen forest inhabitants (*H. hylobates*, *H. nomascus* and *H. hoolock*). The species *P. pygmaeus*, *H. hylobates* and *P. troglodyte* exist in both negative and positive quadrants of PC1, with the latter species most prominently dominating the lower right quadrant.

Upon visual inspection, *Hylobatidae nomascus*, *Hylobatidae hylobates* and *Pongo pygmaeus* cover a larger proportion of the PCA graph compared to the other specimens in the study. *H. hylobates,* indicated by dark blue plot points, spans both positive and negative PC values, the majority of which sit in the upper left quadrant, with two potentially outlying specimen in the lower right quadrant. *P. pygmaeus,* represented by dark brown plots, sits within the majority cluster of specimens, towards the left side of the graph with two outlying plots located towards negative PC2 loadings. *H. nomascus* plots, represented by light blue, also sit within the larger distinctive cluster towards the left quadrants of the plot, with three outlying specimens located with the separate clustering of lowland and tropical forest specimens in the upper right quadrant.

Thin-plate Spline grids have been created as principal-partial warps meaning they represent eigenvectors that specify high to low energies (localised and generalised) patterns of deformation encompassing all landmarks. TPS grids created for the interspecies cranial datasets PC1 and PC2 loadings shows the most extreme deformation to the proportions of the viscerocranium through variance in facial prognathism, as well as marked warping to the neurocranium, particularly to the parietal and occipital bones.

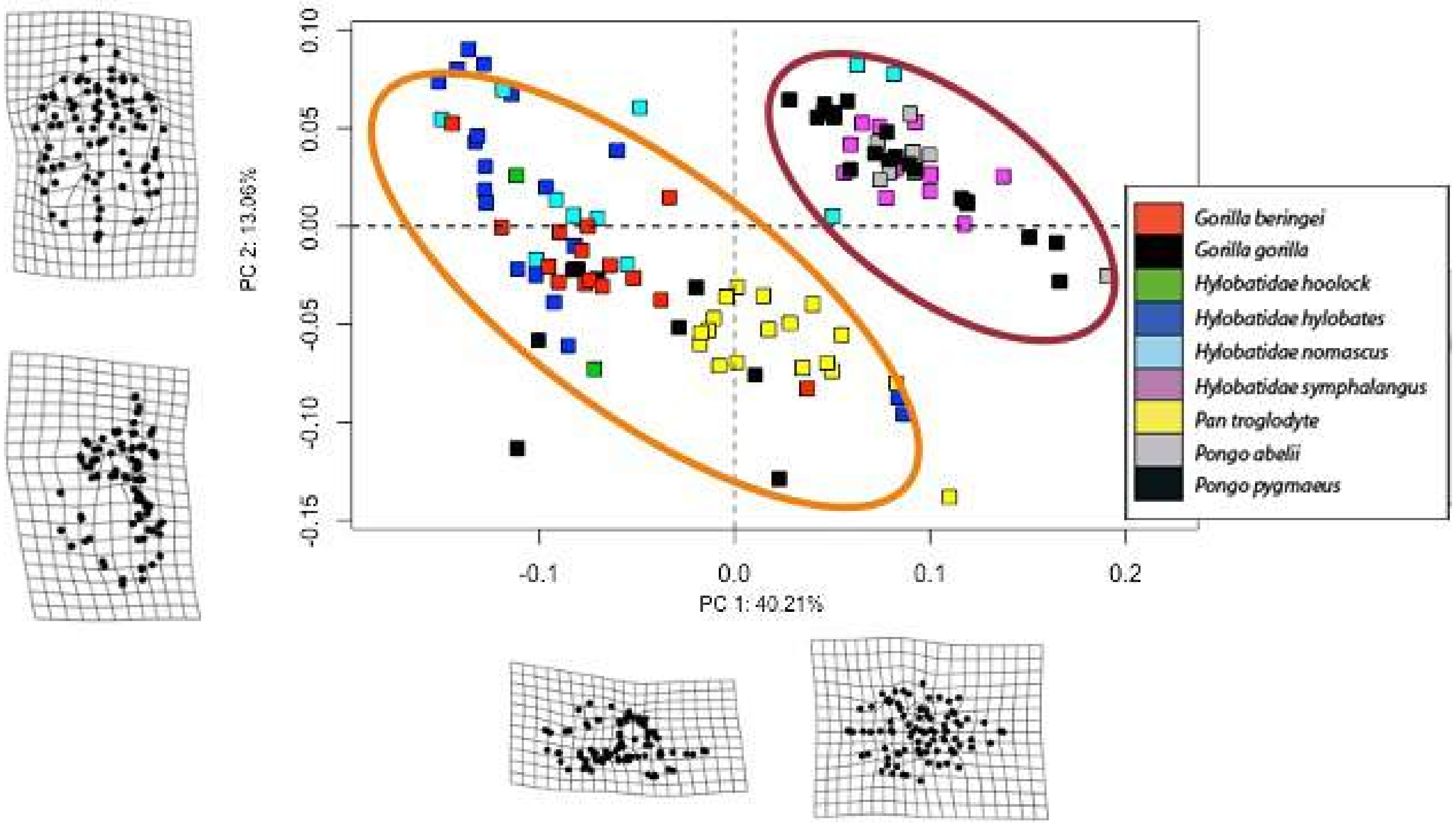


Figure 5.8: Principal Components Analysis scatterplot reporting 53.27% overall observed shape variance in PC1 and PC2 of the interspecies crania dataset. Ovals on the plot indicate obvious clustering between species living in lowland/tropical forest habitats and those living in swamp, montane and evergreen forests.

5.3.3 Cranial GMA Results Summary

In summary, habitat has a significant influence on the cranial morphology of *Pan*, *Gorilla*, *Hylobatidae* and *Pongo* species. All p-values returned are statistically significant, i.e. <0.05, and therefore the null hypothesis is rejected. The interspecific cranial Principal Components Analysis reported 53.27% overall observed shape variance in PC1 and PC2 with significant clustering of tropical and lowland forest-dwelling groups versus swamp, montane and evergreen forest inhabitants. The 2B-PLS analysis returned a significantly large effect size of 11.09 and a very strong positive relationship between variables (r-pls: 0.945).

The *Gorilla* species (*G. gorilla* and *G. beringei*) report the largest effect size (5.0892) of intraspecific morphological variance in comparison to all other species in this study, with the single *Pan* species reporting the smallest variance size (2.2282) in relation to habitat. The gibbon specimen shows the second largest effect size (4.7913) intraspecifically and a strong positive ecomorphological relationship as returned via r-pls, which is reported as comparatively smaller than the *Gorilla*, *Pongo* and *Pan* 2B-PLS datasets. The intraspecific *Pongo* dataset returned an effect size of 3.0193 and the second largest pls score indicating a strong positive relationship between variables. An overall summary of the ANOVA, PCA and 2B-PLS (**Table 5.3**) shows the contrasting PCA variance relating to the intraspecific cranial analyses, with *Gorilla* species showing the largest variance and Pan reporting the least.

Thin-plate Spline warps showed high-energy deformation to the occipital bone, either side of the coronal suture to the rear of the parietal bone, and to the sagittal crest, which is seen in all intraspecific groups to differing degrees. Interpreting the allocated morphospace of the Principal Components analyses showed a trend that supports a clear distinction between evergreen/semi-evergreen, montane and swamp forests compared to lowland and tropical forest inhabitants. This distinction is seen in both within-group and between-group datasets.

PCA Variance, Null hypotheses and statistical significance (p-value, effect size, Pearson R Correlation)					
	PCA %	p-value	Effect size	r-pls	Accept/Reject
	Group 1 Interspecies Primate Crania: Habitat will have no statistically significant effect on interspecific primate cranial morphology and show no patterning of morphological variance				
All species	53.27%	0.001	11.09	0.945	Reject
	Group 2 Intraspecies Primate Crania: Habitat will have no statistically significant effect on intraspecific primate cranial morphology and show no patterning of morphological variance for within-groups				
Gorilla	49.03%	0.001	5.0892	0.951	Reject
Hylobates	42.07%	0.001	4.7913	0.857	Reject
Pongo	46.3%	0.001	3.0193	0.9	Reject
Pan	41.11%	0.008	2.2282	0.862	Reject

Table 5.11: A summary of the Principal Components Analysis variances in the first two PC's, the p-values, effect sizes and partial least squares coefficient scores for between-species and within-species cranial datasets.

5.4 Mandible Results

108 mandible specimens from four genera and nine species of primate were 3D imaged, digitally landmarked, Procrustes-aligned, and put through geometric morphometric statistical testing. Below are the results for inter-and intraspecific data sets with habitat type as the primary variable. Ecological variables were assigned based on known species location and habitat (see **Table 5.12**). These variables were incorporated into the geometric morphometric analysis through an Excel spreadsheet which assigned habitat classifiers to the relevant species.

ID	SPECIES	HABITAT
HBM01 – HBM05	*Hylobatidae hylobates*	Tropical evergreen forests; subtropical evergreen mountain forests
HM01 – HM12	*Hylobatidae lar*	Dry evergreen forests
HNM01-HNM11	*Hylobatidae nomascus*	Subtropical evergreen forests
HSM02-HSM13	*Symphalangus syndactylus*	Tropical hill forests; lowland forests
PAM01-PAM10	*Pongo abelii*	Lowland forests; mountain forests; peat swamps
PPYM01-PPYM10	*Pongo pygmaeus*	Lowland forests

PTM01- PTM14	*Pan troglodytes*	Dry savannah forests; montane forests; swamp forests
GBM01-GBM21	*Gorilla beringei*	Lowland tropical rainforest, transitional forests and Afromontane habitat
GGC01-GGC20	*Gorilla gorilla*	Rain, swamp and riverine forests, lowland tropical forests and brush

Table 5.12: Ecological variables were assigned to specific specimen 3D data clouds and inserted as classifiers within the geometric morphometric analysis in the form of a .csv file.

5.4.1 Intraspecies Mandible Results

This section reports the multivariate statistical results conducted on Procrustes-aligned landmark datasets corresponding to intraspecific mandible groups. Results are reported using ANOVA, 2B-PLS, Principal Components Analysis and Thin-plate Spline Warps.

5.4.1.1 ANOVA and 2-BLS analysis

Individual genera were subjected to ANOVA and 2B-PLS testing to understand the effects of habitat on intraspecific mandibular morphology. The results are shown as effect size, p-value and r-pls which indicate the strength of the relationship existing between environment and mandibular morphological variance. A 2B-PLS plot shows the covariance between shape and habitat along the major axis of the graph and visualised through a line of best fit.

5.4.1.1.1 Habitat-specific Intraspecies Mandibular ANOVA and 2B-PLS

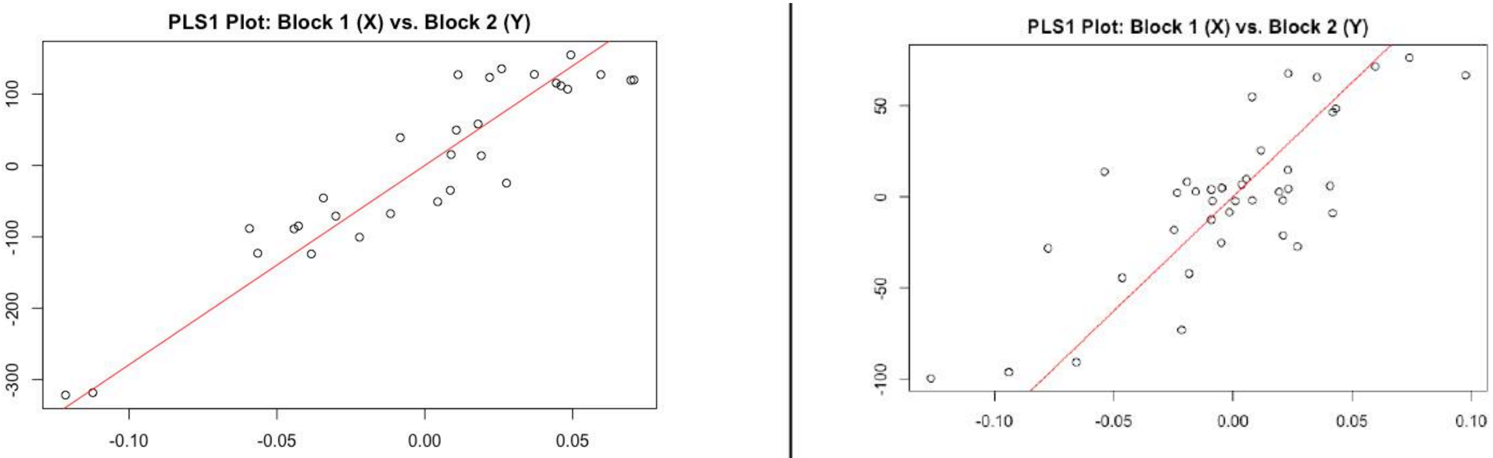
All intraspecific groups returned a p-value in direct contrast to the null hypothesis with the exception of *Pan*. The single *P. troglodyte* species variance patterning is not statistically significant enough to reject the null hypothesis which could be due to a smaller sample size inclusive on one species. Pongo returned a p-value of 0.03 indicating comparably less statistical significance than *Gorilla* or *Hylobates*. Pan exhibited the smallest effect size (1.5809) with *Gorilla* exhibiting the most out of all species included in the study (4.1207) (see **Table 5.13**).

The 2B-PLS graphs depicting a line of best fit (**Figure 5.9**) mirror the returned PCA variance especially in *Pongo* which shows a visually wider distribution across the graph indicating great diversity and least trend patterning than all other species. However, the *Hylobates* intraspecies 2B-PLS plot show a larger range of plots sitting between -0.10 – 0.10 in comparison to other species plots with a more definitive cluster of specimen points sitting in the middle of the line of best fit.

Species	Effect Size	P-value	r-pls
Gorilla	4.1207	0.001	0.931

Hylobatidae	3.6393	0.001	0.792
Pongo	2.7946	0.03	0.862
Pan	1.5809	0.07	0.893

Table 5.13: Effect size and p-value summary of within-species mandible dataset showing statistical significance towards rejecting the null hypothesis for all species datasets with the exception of *Pan*. *Pongo* exhibits a considerably larger p-value in comparison to other species groupings and also in comparison to the p-value demonstrated for the cranial dataset.



PLS1 Plot: Block 1 (X) vs. Block 2 (Y)

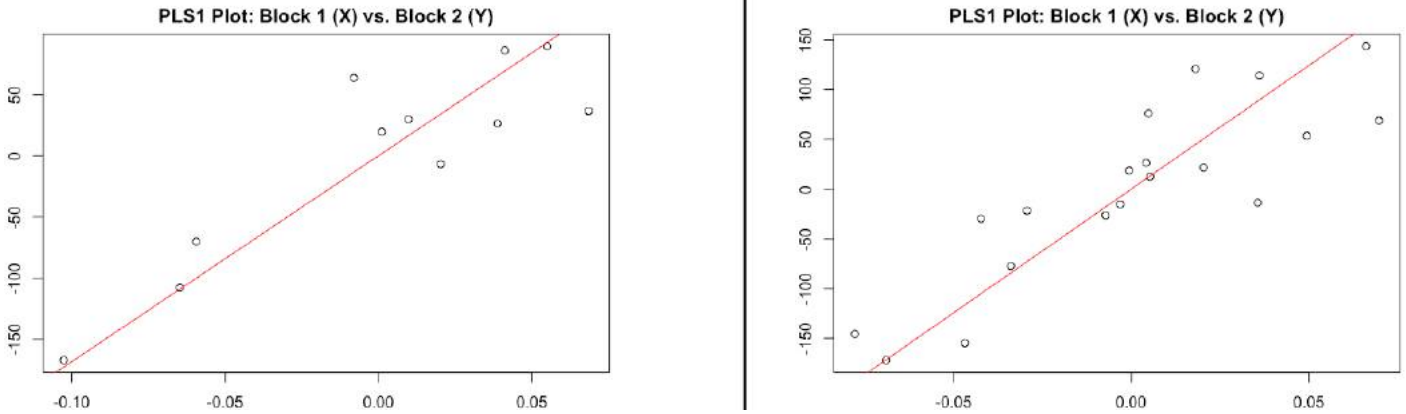
PLS1 Plot: Block 1 (X) vs. Block 2 (Y)

A) Gorilla Intraspecies Group

B) Hylobatidae Intraspecies Group

C) Pan Intraspecies Group

D) Pongo Intraspecies Group



PLS1 Plot: Block 1 (X) vs. Block 2 (Y)

PLS1 Plot: Block 1 (X) vs. Block 2 (Y)

Figure 5.9: 2B-PLS plots showing strong relationships and positive covariance between shape and habitat along the major axis showing line of best fit a) *Gorilla* b) *Hylobates* c) *Pan* and d) *Pongo* intraspecific mandible groups.

5.4.1.1.2 Habitat-specific Intraspecies Mandibular Principal Components Analysis and TPS

To understand the occupation of morphospace and variance between within-species groups, Principal Component Analysis plots were created to show the variance recorded in the first 2 PC's for all species groups. Thin-plate Spline warp grids accompany both PC1 and PC2 axis showing the degree of localized or generalised deformation.

Figure 5.10 shows the distribution of morphospace occupation of the *Gorilla* mandible data set. The first two Principal Components describe 45.35% of the overall observed shape variation between *G. gorilla* and *G. beringei* specimen, which is less than the total variance exhibited in the *Gorilla* crania specimen PCA. *G. beringei* shows a wider distribution pattern than its counterpart, spanning both negative and positive PC loadings, whereas *G. gorilla* sits predominately in the positive axis. This is supported by the strong coefficient (r-pls 0.931) and largest effect size of the species datasets (4.1207) reported by the 2B-PLS analysis.

Marked by a difference in high-altitude and broader diet of more diverse plant and leaf foods, the mountainous *G. beringei* species is known to present less dental deterioration and wear than its lowland, more frugivorous counterpart. Researchers suggest this is due to the relatively soft diet based around ground vegetation and leaves rather than hard seeds and shelled nuts (Galbany *et al.* 2016; Plataforma SINC, 2016). The Thin-plate Spline warp grids show high energy deformation in both ramus, gonial angle (PC2), and anterior dentition (PC1), which could be a reflection of morphological variance dictated by jaw stress adaptation and consumption of softer foods.

The PCA graph (**Figure 5.11**) returned for the *Hylobates* mandible data set shows 43.91% of total variance in the first 2 PCs; 1.84% more than the total variance reported for the first two hylobatid cranial PCs. All species groupings span both negative and positive PC loadings with a *S. syndactylus* cluster located in the furthest negative loadings. Previously clustered closely with *G. beringei* in the interspecific PCA graph, the negative loadings reflect a species whose diet consists of young leaves, shoots, flowers and root material. The more frugivorous gibbons' cluster locations sit averagely in the middle of the PCA graph, similarly to *G. gorilla* in the Gorilla PCA dataset. This similar patterning of variation is reflected in the 2B-PLS analysis as the *Hylobatidae* group show the second largest effect size (3.6393) next to Gorilla. The *Hylobates* Thin-plate Spline warps show high energy deformation particularly to the gonial angle.

The *P. troglodyte* PCA (**Figure 5.12**) reports a variance of 55.54% in the first 2 PCs. This species shows a very wide distribution of specimen spanning both negative and positive PC's with no obvious clustering or patterning of variance. The Thin-plate Spline deformation grids show the most transformative bending to the width (PC1) and height (PC2) of the mandible body. This dataset returned the smallest effect size and the least statistical significance between environment and morphological variance most likely due to the small sample size and non-comparison to conspecifics.

With a total variance of 46.89% in the first 2 PCs, the PCA graph (**Figure 5.13**) depicting morphospace occupation in the *Pongo* group shows a higher degree of diversity patterning in *P. abelii* comparable to *P. pygmaeus,* though both species span negative and positive PC loadings. The Thin-plate Spline grids show deformation particularly at the site of the gonial angle, ramus height and the width of the mandible body. There are two obvious clusters between the species which reflects the propensity for *P. pygmaeus* to adopt a more vegetative diet with less fruit consumption than its Sumatran counterpart.

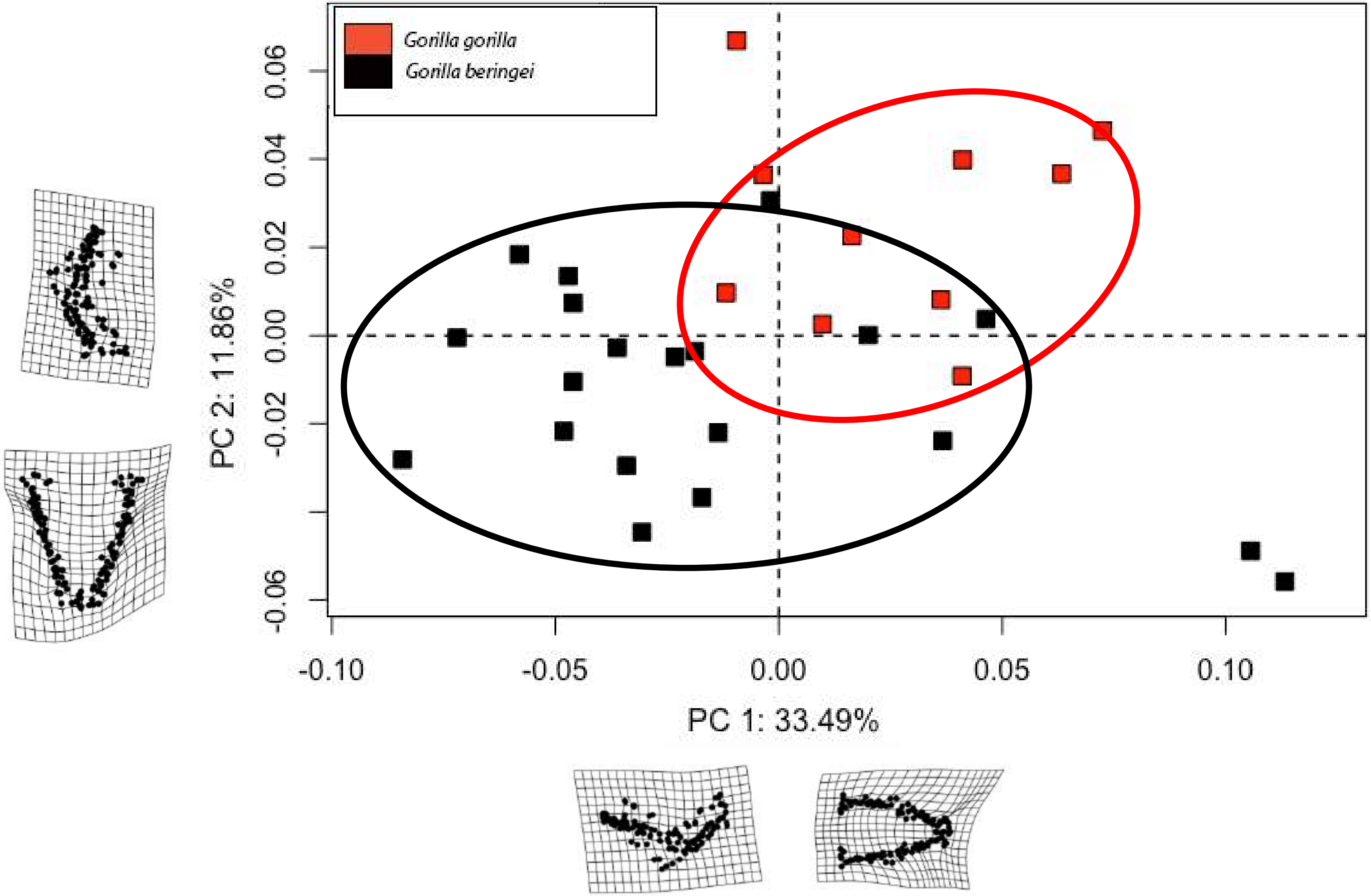


Figure 5.10: PCA graph showing 45.35% of total variance in the first two PCs of the *Gorilla* mandible dataset. TPS grids showing high energy deformation in in both ramus and mandibular angle (PC2) as well as anterior dentition (PC1).

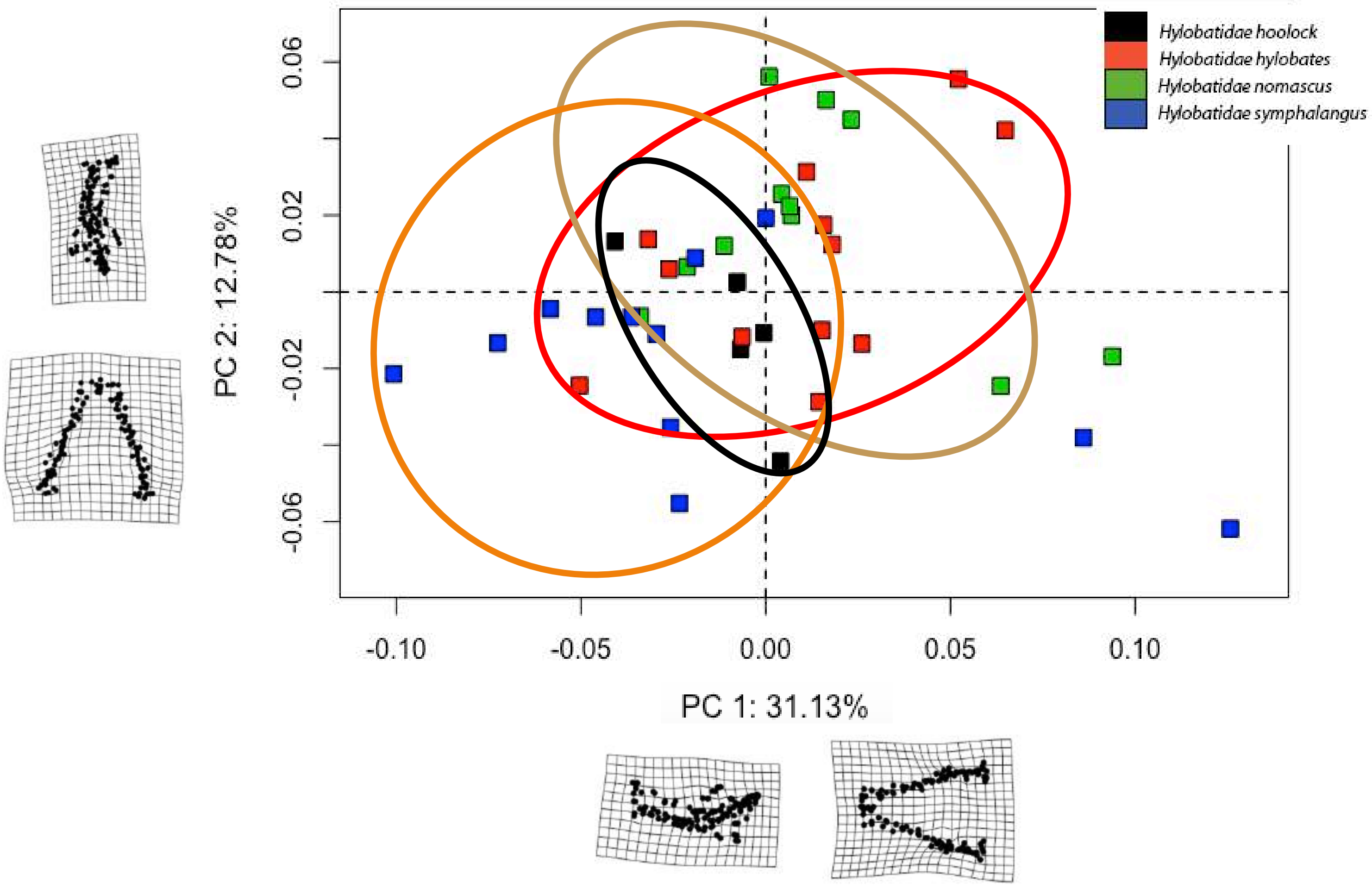


Figure 5.11: PCA graph showing 43.91% of total variance in the first two PCs of the *Hylobates* dataset. TPS grids showing high energy deformation in gonial angle (PC2) and anterior dentition (PC1).

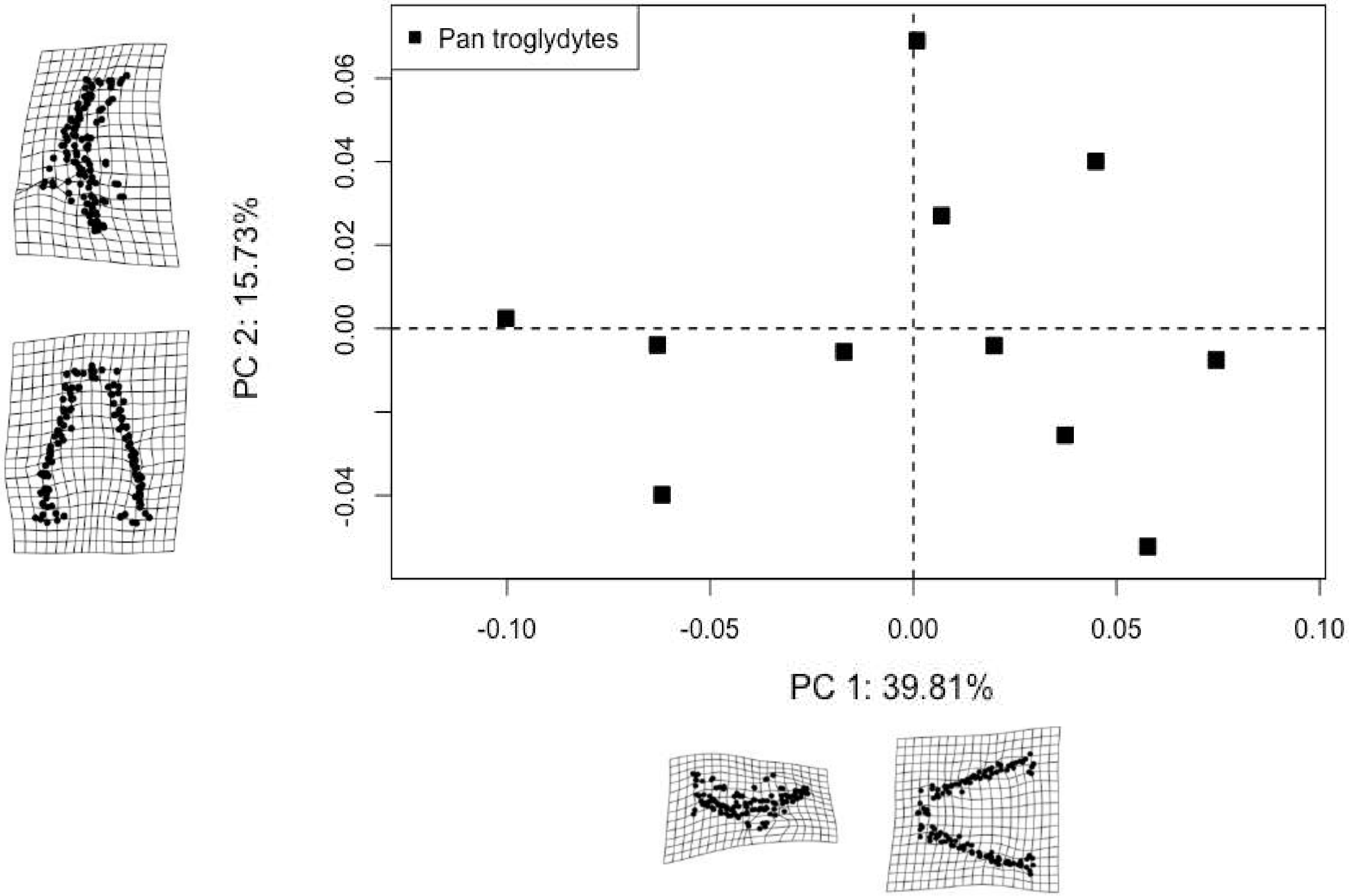


Figure 5.12: PCA graph showing 55.54% of total variance in the first two PCs of the *Pan troglodyte* dataset. show the most transformative bending to the width (PC1) and height (PC2) of the mandible body.

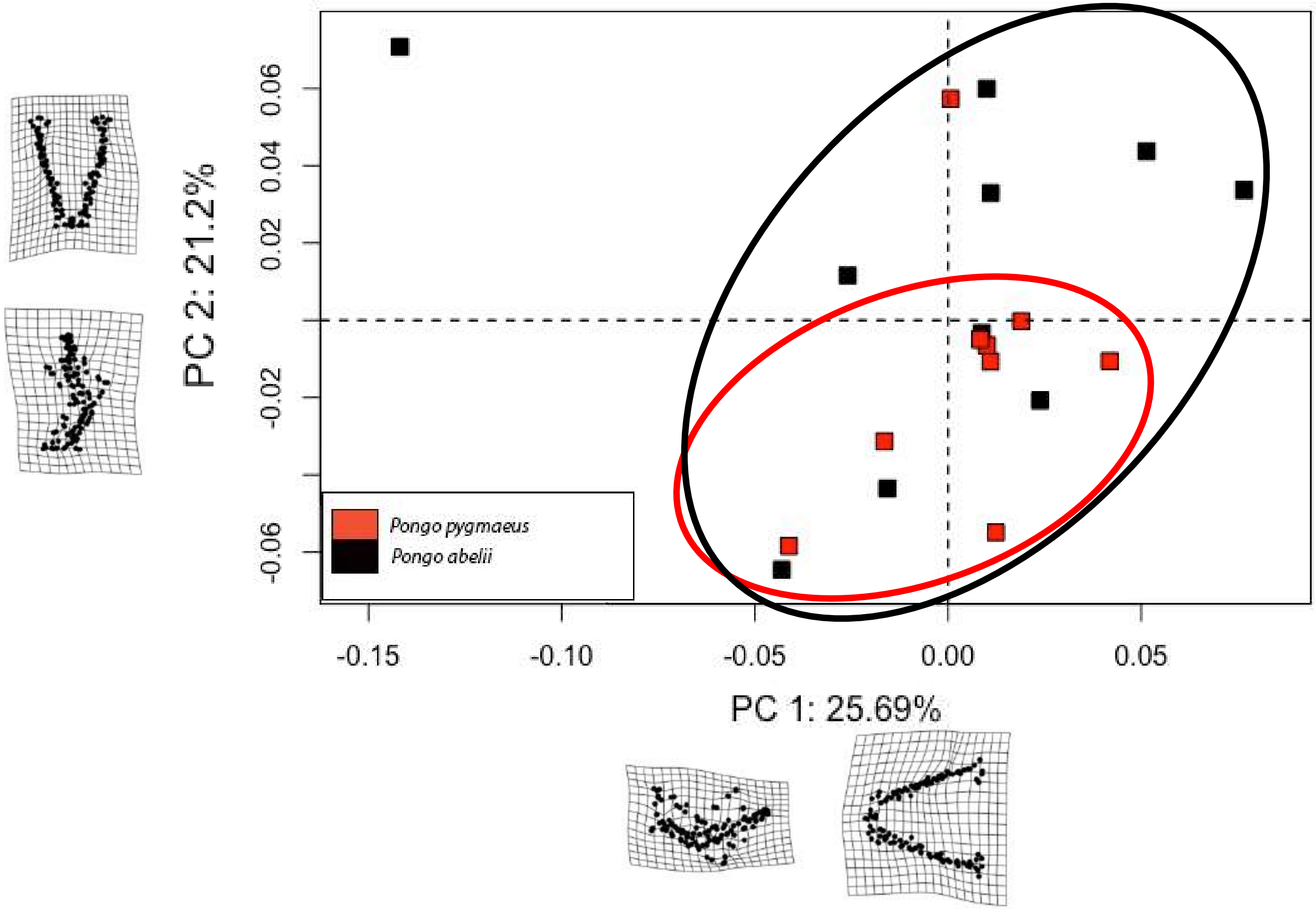


Figure 5.13: PCA graph showing 46.89% of total variance in the first 3 PC's of the *Pongo* mandible dataset. Thin-plate Spline grids show deformation at the site of the gonial angle and the width of the mandible body.

5.4.2 Interspecies Mandible Results

5.4.2.1 ANOVA and 2-BLS analysis

The following sections show the multivariate statistical tests conducted on Procrustes-aligned landmark datasets which correspond to interspecific mandibular groups. Habitat-specific ANOVA and Two-block Partial Least Squares (2B-PLS) results are reported showing the statistical significance and quantifiable relationship between ecological variables and morphological variance. Thin-plate Spline warps accompany Principal Components Analysis to further show patterns of variance that exist in the interspecific dataset.

5.4.2.2 ANOVA and 2-BLS analysis

Procrustes ANOVA and 2B-PLS tests were used to understand the effects of habitat on interspecific mandible morphology and reported as Effect Size, P-value and r-pls. These results indicate the strength of the relationship which exists between environment and morphological variance by genus. 2B-PLS plots show the strength of the relationship between shape and habitat variables along the major axis of the graph which is visualised as a line of best fit.

5.4.2.2.1 Habitat-specific Interspecies Mandibular ANOVA and 2B-PLS

Low P-values of <0.05, are considered to be evidence in direct contrast to the null hypothesis, which in this study, states that there will be no statistical significance to indicate that habitat type affects primate mandible morphology. ANOVA and 2B-PLS performed on the GPA-aligned Procrustes mandible coordinates returned a P-value of 0.01, which indicates statistically significant evidence against the null hypothesis. Two-block Partial Least Squares analysis returned an effect size of 11.07 indicating a strong correlation between habitat type and primate mandible morphological variance.

The returned Pearson's Correlation Coefficient, used to report the strength of linear relationships between variables (exemplified as the line of best fit in **Figure 5.14)**, visualises the strong positive relationship in the interspecific mandible dataset (r-pls: 0.955).

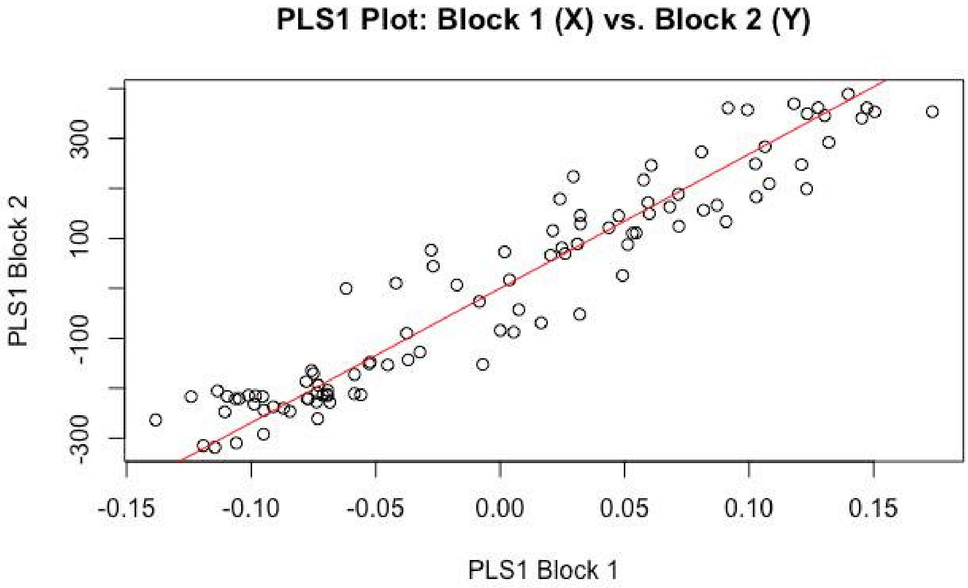


Figure 5.14: Plot of first 2B-PLS dimensions for interspecies mandible data showing major axis of shape covariation as the line of best fit for the returning correlation coefficient (r-pls: 0.955).

5.4.2.2.2 Habitat-specific Interspecies Mandibular Principal Components Analysis and TPS

The Principal Components Analysis conducted on the General Procrustes data frame shows that much of the variance exhibited between the interspecific mandible specimens are captured by the first two axes (PC1 49.32% and PC2 14.39%), with a statistically significant result of 63.71% combined. In comparison to the interspecific cranial Principal Components Analysis, within-species mandible shape space encompasses 10.44% more variance in the first two PCs.

Visual inspection shows obvious clustering; a smaller group consisting of positive PC values only and a larger group spanning a positive and negative distribution. The larger cluster contains all genera in the study with the exception of *Pan* which sits in the smaller grouping alongside *P. pygmaeus, S. syndactylus* and *G. beringei*. This positive PC loading cluster reflects specimen whose diet is more varied than their conspecifics, consuming more leaf, shoot, flower and insect material, alongside fruits which is both reflected behaviourally, ecologically and in the seasonal availability of food types. Both clusters include an obvious widespread scattering trend of outlying specimen showing a high degree of diversity within the entire dataset.

Gorilla gorilla and *Pongo abelli* display the largest distribution of specimen plots in the morphospace with *G. gorilla* plots (represented as black squares) spread across negative and positive PC loadings in the lower left and right quadrants. *P. abelli* (red squares) shows majority plots in the lower right quadrant of positive PC loadings with the exception of three specimens within the negative. The Hoolock specimen, represented in green, are also notably widespread with an outlying plot sitting in the centre of the graph. *Hylobatidae hylobates* shows a distinctive and tight clustering in the upper left quadrant of negative PC1 and positive PC2 loadings. An outlying *Pan troglodyte* specimen (yellow plot) can be seen separate to the clustering in the upper right quadrant, rather sitting alongside *G. beringei* plots in the negative PC1 morphospace.

Thin-plate Spline warps returned for both PC1 and PC2 eigenvectors show high-energy, localized expressions of deformation. PC2 shows strong sagittal bending and deformation to the width and length of the mandibular body. PC1 warps show significant structural variance in the mandibular ramus and gonial angle, as well as in the forward projection of the mandible body.

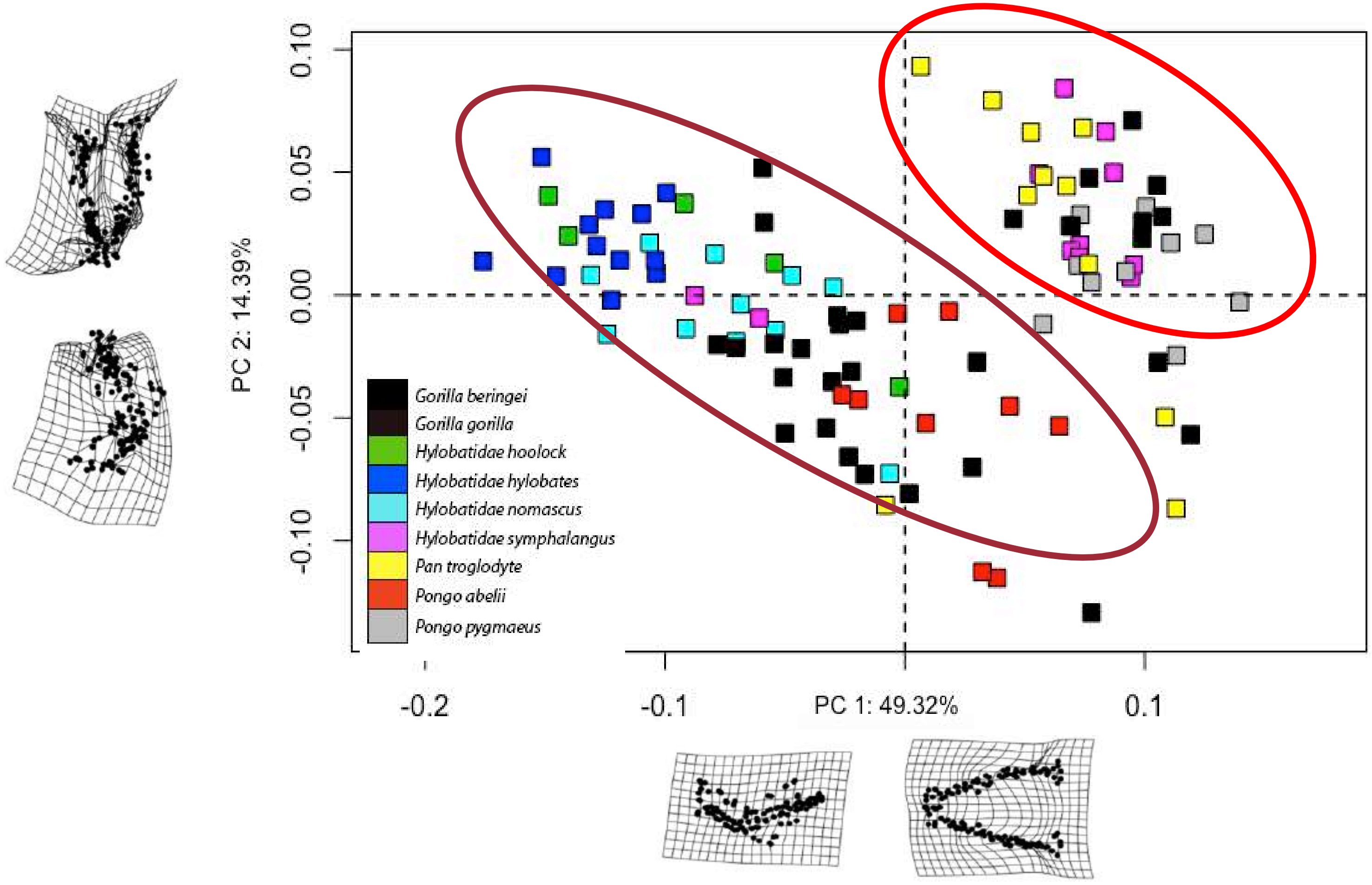


Figure 5.15: Principal Components Analysis scatterplot reporting 63.71% overall observed shape variance in PC1 and PC2 of the interspecies mandible dataset. Ovals on the plot indicate obvious clustering between highly frugivorous species and species who consume a wider variety of folivorous plant foods.

5.4.3 Mandible GMA Results Summary

To summarise, habitat has a more significant influence on the mandible morphology of *Pan*, *Gorilla*, *Hylobates* and *Pongo* species than does the cranium, with an overall reported 63.71% of overall variance observed in the first two PCs. This is an increase of 10.44% comparable to the interspecific cranial dataset. All p-values returned for the between-group mandible dataset are statistically significant, i.e. <0.05; therefore, the null hypothesis is rejected. Obvious clustering within the PCA plot indicated similar patterns of variance between highly frugivorous species and species who consume a wider variety of food types. The 2B-PLS analysis returned a significantly large effect size of 11.07 and a positive, strong relationship between species and habitat variables (r-pls 0.955).

The singular *Pan* species (*P. troglodyte*) showed the largest variance in the within-group Principal Components Analyses with an observed total variance of 55.54% in the first two PCs. The intraspecific *Pongo* dataset reported the second largest overall variance in PC1 and PC2 at 46.89% followed by the *Gorilla* (45.35%) and *Hylobates* (43.91%) datasets respectively.

Effect sizes and Pearson R correlations report *Gorilla* has having the largest and strongest, positive relationship between variables (4.1207 and r-pls 0.931 respectively). The *Hylobates* dataset reported the second largest effect size at 3.6393 (r-pls 0.792) and the *Pongo* dataset returned an effect size of 2.7946 but also showing the orangutan group to have the third strongest positive relationship trend as returned by the 2B-PLS analysis (r-pls 0.863).

Even though the *Pan* dataset returned the largest PCA variance in the first two components, as well as the second largest positive relationship trend as reported by 2B-PLS analysis, this intraspecific group returned a p-value of 0.07. This means the null hypothesis is accepted in this case which indicates habitat has less significance on the craniomandibular morphology of *P. troglodyte* species. However, this is most likely due to each specimen being allocated with the same habitat type. Access to a larger sample size, which includes *Pan paniscus,* would further understanding of intraspecific morphological variation in relation to habitat specific to chimpanzees.

Interpretation of the allocation of morphospace for the intraspecific groups Principal Components Analysis, alongside visual inspection of the Thin-plate Spline deformation grids, showed a trend in dietary specialisations. The warp grids showed high-energy bending to the mandible body, angle and ramus between conspecifics whose diets differ by level of folivory and frugivory. Species whose diets are more varied and focus heavily on fruits, i.e. *P. pygmaeus, S. syndactylus* and *G. gorilla*, are plotted in the upper right positive quadrant of the interspecific Principal Components graphs. **Table 5.14** summarises the Principal Component variance for within-group and between-group datasets as well as the effect sizes, p-values and r-pls scores returned by the 2B-PLS analysis.

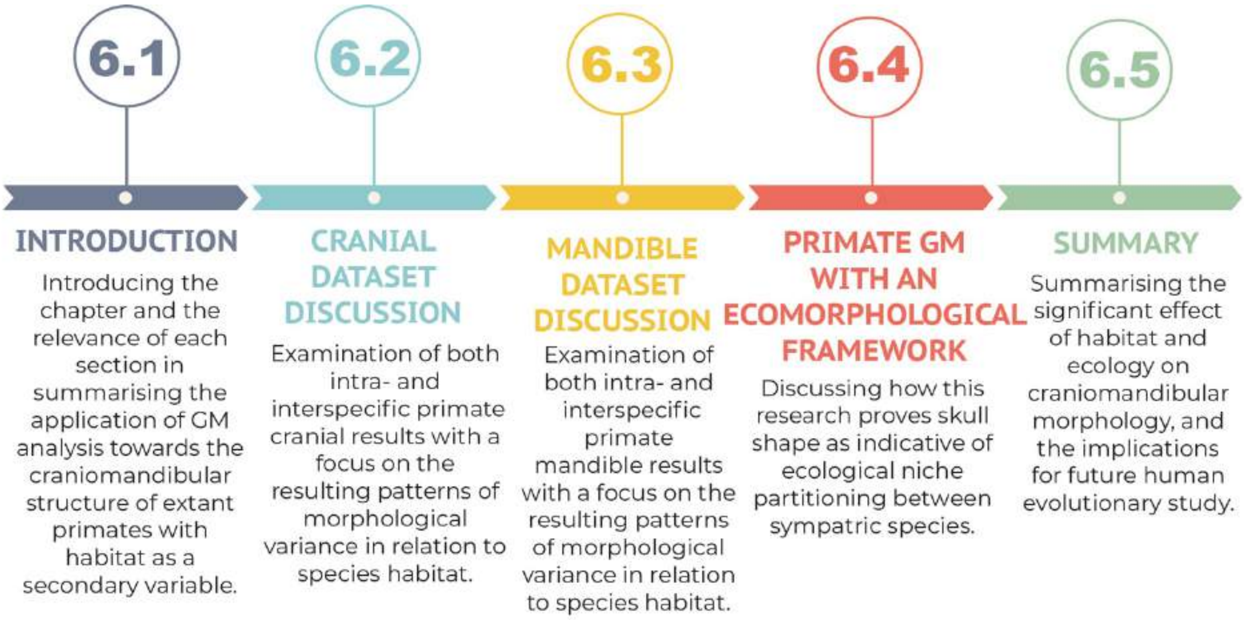
PCA Variance, Null hypotheses and statistical significance (p-value, effect size, Pearson R Correlation)					
	PCA %	p-value	Effect Size	r-pls	Accept/Reject
Group 3 Interspecies Primate Mandible: Habitat will have no statistically significant effect on interspecific primate mandible morphology and show no patterning of morphological variance					
All species	63.71%	0.01	11.07	0.955	Reject
Group 4 Intraspecies Primate Mandible: Habitat will have no statistically significant effect on intraspecific primate mandible morphology and show no patterning of morphological variance					
Gorilla	45.35%	0.001	4.1207	0.931	Reject
Hylobates	43.91%	0.001	3.6393	0.792	Reject
Pongo	46.89%	0.03	2.7946	0.862	Reject
Pan	55.54%	0.07	1.5809	0.893	Accept

Table 5.14: A summary of the Principal Components Analysis variances in the first two PC's, the p-values, effect sizes and Two-block Partial Least Squares coefficient scores for between-species and within-species mandible datasets.

5.5 Summary

Chapter Five has reported the quantitative geometric morphometric results showing the effects of sexual dimorphism and habitat variables on the shape of extant primate skulls. Results show sexual dimorphism to have little effect on the dataset used in the study after the removal of size from the shape data. Habitat has been reported as having a greater degree of influence on the primate mandible than the cranium. Principal Components Analysis report clusters between groups of similar habitats in both cranial and mandibular specimen. **Chapter Six** will discuss these results in relation to the research questions and the broader implications they have for further human evolutionary and morphometric study.

6 DISCUSSION



6.1
INTRODUCTION
Introducing the chapter and the relevance of each section in summarising the application of GM analysis towards the craniomandibular structure of extant primates with habitat as a secondary variable.

6.2
CRANIAL DATASET DISCUSSION
Examination of both intra- and interspecific primate cranial results with a focus on the resulting patterns of morphological variance in relation to species habitat.

6.3
MANDIBLE DATASET DISCUSSION
Examination of both intra- and interspecific primate mandible results with a focus on the resulting patterns of morphological variance in relation to species habitat.

6.4
PRIMATE GM WITH AN ECOMORPHOLOGICAL FRAMEWORK
Discussing how this research proves skull shape as indicative of ecological niche partitioning between sympatric species.

6.5
SUMMARY
Summarising the significant effect of habitat and ecology on craniomandibular morphology, and the implications for future human evolutionary study.

Figure 6.1: Chapter Six roadmap summarising the discussion sections pertaining to the results and the implications towards human evolutionary study.

6.1 Introduction

This discussion section summarizes the application of geometric morphometric analysis to the craniomandibular structure of extant primates with habitat as a secondary variable, the results of which are presented in **Chapter Five**. Firstly, examination of both intra- and interspecific primate cranial and mandible results is presented with a focus on the resulting patterns of morphological variance in relation to species habitat. Secondly, a look into the comparative nature of this study is examined to ascertain the impact of extant primate GM methodology on early paleoanthropological study with a view to understand the implications of the following hypotheses as detailed in **Chapter Four**:

- Quantitative geometric morphometric analysis can be used to better understand the relationships between evolutionary adaptive response and environmental patterns
- Hominin and primate species that live in comparable climates adapt similar craniomandibular morphological traits
- Facial morphology can be used as a predictor of environmental type and can therefore be used for comparative studies
- Specific environmental niche conditions will lead to a retention of primitive traits

6.2 Cranial Dataset Discussion

6.2.1 Interspecific Primate Cranial Ecomorphology

A total of 107 primate crania were 3D scanned and digitally landmarked with 19 corresponding fixed and traditional craniometric points that were subsequently Procrustes-aligned using General Procrustes analysis. ANOVA, Principal Components Analysis, Two-block Partial Least Squares and Thin-plate Spline deformation grids were used to identify patterns of variance among each species group in relation to their habitat types.

Section 5.2 reports distinct trends in variation and habitat type in both inter- and intraspecific cranial groups of primates. All groups in the study reported evidence significant enough to reject the null hypotheses (see **Table 5.2**), including a smaller intraspecific sample size of *P. troglodyte* specimen, providing quantified evidence that habitat type has considerable effect on cranial morphology. Major finds of this study describe: a) similar patterns of variation between species living in similar biomes; b) variation patterning amongst species of differing locomotive habits; and c) masticatory adaptations towards dietary specializations.

6.2.1.1 Morphological variation caused by habitat type

The interspecific Principal Components Analysis scatter plot showed 53.27% overall observed shape variation in the first two PCs. A large distribution of specimen located on the lower half of the PC1 values showed a dominant and diverse spread of genera. This cluster excludes *G. gorilla*, *P. abelii* and *S. syndactylus,* which are seen in the top right quadrant of positive PC1 indicating a commonality in morphospace occupation for species living lowland tropical rainforest habitats.

The species found in the lower portion of PC1 values are known to exist in swampy, mountainous and evergreen forests, or habitats that are more varied in leafy plant material and exhibit more fruit scarcity than lowland tropical rainforest environments (Basabose, 2002; Goldsmith, 2003; Yamagiwa *et al.* 2005). The hylobate genera, excluding *S. syndactylus*, are widely and diagonally distributed across the Principal Component scatterplot with a defined clustering of evergreen and sub-evergreen forest inhabitants (*H. hylobates*, *H. nomascus* and *H. hoolock*). *Pongo pygmaeus, H. hylobates* and *P. troglodyte* exist in both negative and positive quadrants of PC1 with the latter species most prominently dominating the lower right quadrant.

From the interspecific Principal Components Analysis, there was an expectation to see separation patterning between the crown hominoids (Hominidae and Hylobatidae), or Eurasian and African primates, due to the secondarily primitive craniofacial morphotype as described by Rae (2004). However, there is a clear distinction instead of species living in lowland and tropical forest habitats compared to those living in swamp, montane and evergreen forest settings - this can be seen in both between- and within-group datasets. gibbons, or Hylobatidae, are considered the ‘lesser apes’; smaller in size and stature in comparison to the Hominidae ‘great apes.’ Investigating cranial evolution and morphology has been particularly challenging between the hylobatids and hominids due to this body size disparity (Leslie and Shea, 2016). Allometric study, or the study of body size (or scale) differences in organisms (Griffen *et al.* 2018), is often investigated using Geometric Morphometric analysis (e.g. Gould, 1975; Gingerrich, 1982; Jungers, 1984; Potter, 1986; Leslie and Shea, 2016; Henderson *et al.* 2017). However, in the present study, size was eliminated from the raw landmark data using General Procrustes analysis, providing a uniform shape-space basis to investigate morphological variance.

In Rae's (2004) study regarding Miocene hominoid craniofacial morphology and the emergence of the great apes, parsimony analysis was used to demonstrate a mosaic pattern of derived facial characteristics between species specimen, which suggested a reversal of facial traits in gibbons and suggested their derivation from a 'great ape' face. Without size related data, the present studies multivariate statistics supports facial similarities between the crown hominoids when size is removed.

As discussed below, the features associated with habitat type pattern variances can be explained by both dietary specialisation and locomotive behaviour e.g. differences in robustness, positioning of functional locomotive features, dentition and face shape.

6.2.1.2 Morphological variation caused by dietary specialisation

The mandible dataset reported distinct morphological variation patterning between more folivorous and frugivorous species (discussed in **Section 6.1.2**), which is directly related to the environment in which those species inhabit. The morphological distinction between cranial specimen and habitat type is suggested as a further indicator of levels of frugivory and folivory, as the forest biomes that crown hominoids inhabit offer differing levels of fruit seasonality, as well diversity and distribution of plant material (Yamagiwa *et al.* 2005:1346).

The density of terrestrial herbaceous vegetation (THV) is far lower in lowland forests in comparison to montane, swamp and evergreen forests, which in turn experience a far lower yield of fruit seasonality (Basabose, 2002). Whilst terrestrial herbs are a feature of tropical forests, this source of dietary subsistence is consumed by their primate constituents as a supplement during periods of fruit scarcity (Goldsmith, 2003; Yamagiwa *et al.* 2005; Tutin *et al*., 1993). The patterning of variation in the PCA scatterplot (**Figure 5.7**) reflects morphological similarity between species living in habitats that exhibit high seasonality of fruit, i.e. lowland and tropical forests, which ensures a greater diversity of fruiting trees and therefore is highly suited to mammals with an adapted folivore diet.

Gorilla beringei, for example, was shown to inhabit negative PC values in contrast to its *G. gorilla* conspecific and displayed are larger diversification in specimen range on the scatterplot (**Figure 5.8**). *G. beringei* inhabit 'cloud' montane forests at high altitudes and are regarded as terrestrial folivores, where herbaceous vegetation is consumed as a staple food (Fossey & Harcourt, 1997; Yamagiwa *et al.* 2005; Watts, 1984). The western lowland *G. gorilla* consumes mainly a diverse and seasonal fruit-based diet with folivorous tendencies when fruit yield is low (Kuroda *et al.,* 1996; Tutin & Fernandez, 1992, 1993). Galbany *et* al. (2016) also reports a morphological variance between *G. gorilla* and *G. beringei* species through tooth wear associated with dietary specialisation. Lowland gorillas exhibit higher levels of enamel wear compared to montane gorillas whose dentition is adapted to a softer diet based on ground vegetation and leaves. This distinction is clearly supported by the PCA results which are marked by variance in subsistence and habitat type, and further exemplified by the morphospace occupation variation between *Pongo* specimens.

The inclusion of *Pongo abelii* in the positive PC cluster of lowland dwelling species (see **Figure 5.8**) i.e. *S. syndactylus* and *G. gorilla,* is further support for patterns of variation that are influenced by habitat and most specifically by dietary habits. Similar to *G. gorilla*, *Pongo abelii* is known to consume more fruit than its counterpart *P. pygmaeus* (Harrison, 2019; Harrison *et al.* 2020), which sit within negative PC loadings distinctly separated through morphospace diversification.

Although gibbons are shown to be the most diverse of the taxa, spanning across all PC quadrants in **Figure 5.8** with an expected distinction of the large siamang, *S. syndactylus*, the trend of habitat distinction is less clear than reported in other species in the study. *S. syndactylus* specimens, in particular, sit within a highly frugivorous cluster of primate species, alongside *Gorilla gorilla* and *Pongo abelii*; however, in comparison to its conspecifics, siamangs consume a higher proportion of leaves (approx. 43-48%) (Preuschoft, 1990; Nowak, 1999; Eastridge, 1999) and inhabits a diverse range of lowland, rain and montane forests. (Eastridge, 1999: Chivers, 1979).

In keeping with the trends seen in **Figure 5.8**, it would be expected to see a clustering of siamang spanning the negative PC clusters alongside the more folivorous species, with the remaining gibbon specimens moving through to positive PC loadings. So why is the 'lesser ape' hylobates species showing a pattern of variance less influenced by dietary preference in comparison to other species in the study? Levels of locomotive behaviour are suggested as the cause which is evidenced through the Thin-plate Spline deformation grids and further examined in **Section 6.1.1.3.**

6.2.1.3 Morphological variation caused by locomotive behaviour

As discussed, **Figure 5.8** showed distinct clustering of *G. gorilla*, *S. syndactylus* and *P. abelii* specimens in positive PC loadings. Further to similarities in levels of frugivory, another obvious distinction between *G. gorilla* and *P. abelii* in comparison to the negative PC clusters, is that these species are the smaller and more gracile of their conspecifics (Urban, 2008; Cocks, 2003; Watts, 1984; Harcourt & Stewart, 2007; Fossey & Harcourt, 1977; Doran, & McNeilage, 1998; Tutin *et al.* 1991). Quantification of allometric growth and cranial shape, as well as the ratio of body to brain size, are well documented (Shea, 2013). However, this also does not explain the appearance of siamangs in the positive cluster as, comparable to the other gibbon species in this study, *S. syndactylus* is larger and more robust (Eastridge, 1999: Chivers, 1979).

Turning to the Thin-plate Spline grids for further clarification, interspecific reports for PC2 show high-energy deformation to the supraorbital margin, area of sagittal crest positioning, and widening of the zygomatic arch (see **Figure 5.8**), which can be explained through dietary specializations (Edmonds, 2016; Makedonska, 2012). PC1 grids show a narrowing of the basicranium and projection of facial prognathism, which is less explained through masticatory function but instead turns the attention to locomotive adaptations.

Siamangs are known as more quadrumanous climbers in comparison to gibbons (Fleagle, 1976), which is a mode considered to have replaced brachiating in the larger bodied apes through adaptive response (Hunt, 2003). In the same positive cluster, *G. gorilla* is the more arboreal of its species (Remus, 1999) and *P. abelii* is known to rarely descend from its treetop home in comparison to *P. pygmaeus* (Loken *et al.,* 2013; Rijksen, 2001; Rijksen & Meijaard, 1999). Thin-plate Spline deformation grids returned for the intraspecific *Gorilla* principal component analysis showed a narrowing of the nuchal crest related to PC1 (see **Figure 5.3**). Further support of cranial morphology as influenced by greater arboreal behaviour, is evidenced in the domination of positive PC loadings of interspecific *G. gorilla* PCA.

The implication of deformation towards areas of known locomotive adaptation, i.e. the nuchal crest and foramen magnum, in relation to clustering of more arboreal primates in comparison to their conspecifics is significant, particularly to the study of evolutionary locomotion in late Miocene and early Pliocene hominoids. Fleagle (1976), for example, used a comparative study of siamang locomotion and posture to suggest that quadrumanous climbing during feeding is a 'basic hominoid locomotor adaptation'. As Ward (2002) argues, reconstructing early hominin transition to bipedalism and the specialization of locomotive function is key to understanding human evolution, as this can provide inferences towards postcranial adaptation, brain-function, tool-use and migration.

Understanding the degree and importance of arborealism in early hominins is a currently contentious subject, particularly for *Australopithecus afarensis* and *Sahelanthropus tchadensis.* Ward (2002) argues that it is prudent to 'elucidate the factors influencing morphology' which through the current study suggest environment has a quantifiably strong effect on locomotive habits. The variation of cranial morphology in relation to locomotion and home range size seen in extant primates has considerable advantages towards the study of late Miocene and early Pliocene hominins, whose behaviour can only be inferred through fossil features (Pawlowski, 2007).

Fossil assemblages recovered of the late Miocene hominin, *Sahelanthropus tchadensis*, include a complete through highly damaged cranium (TM 266-01-60-1), as well as mandibular and dental fragmentation (Brunet *et al.* 2002, 2005; Su, 2013). A short cranial base with anteriorly positioned foramen magnum, orthogonal to the orbital plane, infers a shared derived feature with later hominins and is suggestive of habitual bipedalism and an upright posture (Su, 2013; Zollikofer *et al.* 2005; Guy *et al.* 2005; Brunet *et al.* 2002). Further understanding of the degree at which *S. tchadensis* moved terrestrially would add significant contribution to the theoretical discussion of evolutionary bipedalism in modern humans. Inclusion of *S. tchadensis* in a comparative geometric morphometric analysis which includes habitat variables could help to improve our understanding of this early hominins favoured locomotive behaviour.

Soligo and Smaers (2016) ecomorphological framework (**Figure 2.14**) utilises functional capacity of morphology in relation to fitness consequences and organism performance as modalities of environmentally influenced morphological adaptation. This method highlights the importance of the behavioural significance of anatomical traits and the feedback effect on organism morphology. Therefore, in considering the behavioural implications of favoured locomotive function, landscape management should be acknowledged to better understand the relationship between habitat type, primate space uses and cranial morphology (Reynolds, Bailey & King, 2011; McHenry, 1994; Ofstad *et al.,* 2016).

Biomechanical forces and energetic requirements related to respiration and mastication are selective pressures which influence the size and shape of the cranium (Galan-Acedo *et al.,* 2019; Lesciotto and Richtsmeier, 2019). As habitat type influences food source and foraging strategy, it is essential to consider the effects of locomotion as a biomechanical force in relation to home range size variation and metabolic constraints which act as pressures on cranial morphology (Crompton and Thorpe, 2008; Ofstad *et al.,* 2016).

Home range size and metabolic influences on encephalisation act as selective pressures, which play a key role in craniofacial integration and function particularly in components such as the eyes, nasal and oral cavity and pharynx (Leiberman, Ross & Ravosa, 2000; Gittleman & Harvey, 1982; Harvey & Clutton-Brock, 1981; Damuth, 1981). Encephalisation has been a major component in primate skull development and brain size relative to the cranial base length appears to have had the most dominant influence on basicranium variation e.g. facial orientation, posture, facial size (Leibermann, Ross and Ravosa, 2000). Whilst skull size and allometry have been excluded from this study so as to focus solely on shape variation (Klingenberg, 2016), it stands to reason that the clustering in interspecific cranial variation patterning could be a reflection of brain size influences forcing morphological similarities within between-group datasets. However, the Principal Components Analysis cluster of *G. gorilla*, *P. abelli* and siamang in the positive PC range does not correlate with a trend towards increased home range size and relative brain size in comparison to their conspecifics.

Gorilla gorilla is known to travel longer daily distances than the mountainous *Gorilla berengei* (Doran *et al.*, 2004; Bermejo, 2004; McFarland, 2007), which Seiler *et al.,* (2020) suggests may reflect the lower density of herbaceous vegetation in lowland forests. *Pongo abelli*, on the other hand, has a smaller home range (Elder, 2016), and lives in an environment which is generally more productive in food sources compared to *Pongo pygmaeus* who experiences far greater fluctuation in mast fruiting and food shortages and therefore travels further distances for subsistence*.* This is also true of S. *syndactylus* whose home range is far more limited than *Hylobates lar* who is less dependent on fruit than its siamang conspecific (Gittins and Raemaekers, 1980; Harrison *et al.,* 2020).

Although encephaly and relative brain size is greater in species who travel through larger home ranges, and is also greater in fruit-eating species (Seyfarth and Cheney, 2002), home range comparisons show foraging travel distances to have less significant influence on cranial variation patterning compared to the mode of locomotion itself, i.e. the level of arboreal or terrestrial behaviour. This finding strengthens Harvey and Clutton-Brock's 1981 study on primate home-range sizes and metabolic needs, the data of which shows an empirical relationship between home-range size and diet distinguishable between arboreal and terrestrial species. Further studies which include brain size allometry and cranial morphology in relation to ecology would provide further evidence to habitat specific metabolic needs and subsistence behaviours, including whether diet has a stronger influence on pattern variation than preferred locomotive function.

6.2.1.4 Phenotypic plasticity and synapomorphic features

The interspecific Principal Components Analysis scatterplot shows environmentally induced phenotypic plasticity reported by distinct cranial morphological patterns of variance. The findings report cranial features, which have hitherto been understood as synapomorphic, may not strictly be assigned as hominoid (Moya Sola *et al.* 2004; Shea, 2013:126). This is supported by the unexpected mixed grouping of lesser and great apes of similar habitat type.

The interspecific Thin-plate Spline deformation warps, for example, show an elongation of the midface in PC2 and widening of the neurocranium and zygomatic arch in PC1, previously known as great ape character novelties (Shea, 2013). However, all Hylobates specimen, excluding siamang, are dispersed widely across PCs and integrated throughout the African great ape specimen plots, with *S. syndactylus* featured alongside positive PC clusters. This indicates patterns of variance and diversification of these synapomorphic features are found more specifically within-species rather than between crown hominid species.

Whilst facial prognathism is a point of deformation within the interspecific Thin-plate Spline grids, there is no distinction between the Principal Components Analysis species groupings relating to airorhynchy (retro flexion of the facial skeleton on the cranial base) or klinorhynchy (a suggested derived trait in African apes) (Bilsborough and Rae, 2007). A distinction between *Pongo* species and *S. syndactylus* would be expected due to their more pronounced airorhynchy compared to the rest of the species in the study. The absence of this group distinction in relation to habitat type suggests that related facial characteristics, such as kyphosis or brow ridge protrusion, may have occurred through a combination of social adaptation or global influences, such as phylogeny and size, rather than specifically formed in relation to the masticatory apparatus and stress-loading.

A visual inspection of the interspecific cranial Thin-plate Spline grids shows that deformation to the brow ridge area in both PC1 and PC2, which shows kyphosis to be an in-directly strong influence on the upper face. However, the absence of airorhynch/klinorhynch groupings on the PCA grid shows that diet and habitat type is not the only influencing factor of this facial characteristic. This find is supported by Godinho *et al's* (2018) study on the main competing hypotheses of hominid brow ridge development and adds further weight to the argument that neither spatial nor mechanical forces are sole influencers of supraorbital ridge development.

Thin-plate Spline warps showed high-energy deformation to the occipital bone, either side of the coronal suture to the rear of the parietal bone, and to the sagittal crest seen in all intraspecific groups to differing degrees. This shows these specific areas as being highly integrative primary influences of covariation in primates. The fact that orangutans and gibbons are seen to also report this trend in oral/zygomatic patterning indicate these features to be synapomorphic in the hominid family (Weber and Krenn, 2016). This finding should be further developed through ecomorphological study that includes fossil skull specimens to understand if this trend is evident in earlier hominin lineages.

Environmental plasticity has had significant effect on integrative cranial features such as the occipital bone, oral and zygomatic patterning and sagittal crest, as seen in the PCA and Thin-plate Spline warp deformations. However, not all plots on the interspecific principal components graph indicate variation patterning by dietary or locomotive preferences. *Pan troglodyte* specimen plots positioned closer to the more herbivorous gorilla, *G. beringei*, in the Principal Components Analysis, supports Bilsborough and Rae's (2007:1035) assertion that the two species resemble one another cranially despite differences in dietary niches. This shows the importance of phylogenetic inertia and development constraints in determining cranial morphology. The effects of environmental stimuli on ontogenetic levels in great apes and hylobates crania could shed further light as to the weighting between developmental and environmental plasticity in primates (Vrba, 2007).

6.2.2 Intraspecific Primate Cranial Ecomorphology

Interspecific GM analysis of *Pan*, *Gorilla*, *Pongo* and *Hylobatidae* skulls have shown statistical significance in favour of habitat affecting cranial morphology particularly due to locomotive behaviour and dietary specialisation. This is further reflected within intraspecific GM datasets showing similar patterns of variance in masticatory adaptation, as well as anatomical cranial variation related to levels of arborealism.

6.2.2.1 Intraspecific morphological variation through posture and locomotive behaviour

The effect size (5.0892) between *G. beringei* and *G. gorilla* is reported as the largest in the intraspecific study, showing ecological variation to have great significance on the morphology of the cranium. Defined by differences in degree of folivory/frugivory, lower altitudes and overall body size, the PCA graphs show the highest degree of diversity in *G. gorilla*. This is further supported by Bark *et al's* (2015) study of brain organization of gorillas which they concluded to be significantly variable between *G. gorilla* and *G. beringei*, due to a divergence in ecological adaptation. The team also commented on the engagement of more arboreal locomotion in *G. gorilla*, whom they noted must rely more on cerebellar circuits. They noted that, due to *G. gorilla* consuming more fruit and moving through greater home ranges in comparison to their mountainous counterpart, they may depend more on hippocampus spatial mapping functions.

This is interesting to the current study as neuroanatomical variation will undoubtedly appear in the osteological morphology of the cranial vault, where convolutional markings are impressed. Environmental factors of diet and locomotion are shown as influential factors towards the PCA clustering of unlikely Eurasian and African groupings (see **Figure 5.8**) and provides further evidence of habitat as a strong influencer of craniomandibular morphological evolution in the hominid clade.

Although gibbon genetic diversity is yet to be explored in direct comparison to extant 'great apes', Hylobates are considered to be the most diverse of the primate species (Chan *et al.,* 2013) and through genomic DNA sequencing, Kim *et al.* (2011) concluded

Hylobatidae within- and between-group species to have a high level of genetic diversity, which is known to mirror high-levels of intraspecific cranial variation (Zichello *et al.* 2018). It would then stand to reason that the largest morphological variance and effect sizes would be attributed to gibbons. However, the intraspecific GMA reported in this study shows hylobates crania as having the second most morphological variation in the first PC's, in relation to habitat, after *Gorilla*.

As Foley (1997) states, the size of the *Gorilla* skull often overlaps with that of *Homo habilis* in brain size due to the African ape cranium being far larger than any fossil hominin (Tobias, 1964; Hopkins, Lyn & Cantalupo, 2009). When corrected for their huge body size, gorillas relative brain size is the same as, if not slightly smaller, than chimpanzees (Foley, 1997). However, as size and allometry are not included within the present study, the large variance proportions in *Gorilla* species is purely explained through shape data.

Analyses of DNA sequence variation conducted by Ackermann and Bishop (2009) indicate gene flow as having a major role in gorilla diversity, continuing until 80,000 years ago (Meder and Groves, 2012). Perhaps this large degree of cranial variance seen between *Gorilla* species, in the present study, is a result of spatial isolation through habitat promoting adaptation. *Gorilla beringei*, in particular, show very low population numbers, occupy an extremely limited habitat (Canington, 2018), and have shown the best evidence for inbreeding in the craniofacial form, e.g. strabismus (Xue *et al.,* 2015). Hylobates, on the other hand, although molecularly the most diverse primate genus in this study (Zilman, Mootnik & Underwood, 2011), are not shown to be the most cranially morphologically diverse, which may reflect their widespread habitat, home range and population size (Reichard, Hirai & Barelli, 2016).

The large variance seen in the *Gorilla* sp. Principal Component Analysis is further explained through Thin-plate Spline deformation grids and relates to cranial modalities that reflect locomotive preference. The TPS grids show high energy deformation to the basicranium in both PC1 and PC2 loadings with *G. beringei* clustered towards negative PCs with *G. gorilla* inhabiting more diverse morphospace. This trend deformation between more arboreal and terrestrial species is seen across all intraspecific TPS grids, with lesser energy deformation in Pongo and Pan. Basicranial variance in relation to preferential locomotion is a finding that is supported by Villamil's (2017) study on locomotion and basicranium anatomy in primates and marsupials.

Further evidence towards locomotive function influencing morphology can be seen in the Thin-plate Spline grids. High-energy deformation is evident at the site of the nuchal crest seen in both PC's of *Pongo*, *Pan*, *Hylobatidae* and *Gorilla* intraspecific datasets. The nuchal crest is important for maintaining head posture in a quadrupedal position. Humans in contrast to the great apes have a smaller nuchal crest and related muscle attachments, as our upright, bipedal posture reduces the need for large neck muscles to balance the weight of the skull (Zuckermann, 1954; Dunbar *et al.,* 2008).

The Thin-plate Spline grids deformation to the nuchal crest site supports the cluster patterns seen in the Principal Components Analysis grids that separate arboreally-inclined species from their conspecifics. This trend is evident in Hylobates (see **Figure 5.4**), where the more arboreal siamang (Fleagle, 1976; Hunt, 2003) sits in negative PC's distinct from the other Hylobates species who inhabit a diverse range of PC's. The *Pongo* dataset also exhibits this trend with *Pongo abelli* inhabiting more negative PC's than *Pongo pygmaeus* who are larger and less arboreal (Rilksen & Meijard, 1999; Rilksen, 2001; Loken *et al.,* 2013). The exception to this rule can be seen in **Figure 5.3** which shows the more terrestrial *G. beringei* specimens plotted towards negative PC1 and PC2 scores separate from the smaller *G. gorilla* (Remus, 1999), who occupies a wider ranging morphospace, dominating positive PC's. This may be due to more powerfully developed crest formations in relation to body mass that can grow into a uniform shelf on bone in adult *G. beringei* populations that is as much as 4cm wide (Ashton and Zuckermann, 1956).

To summarise, although the Principal Components Analysis shows definitive trend patterning between more arboreal and terrestrial groups, the nuchal crest deformation reported by Thin-plate Spline grids cannot provide definitive answers as to the postural and locomotive habits of primates. As Villamil (2017) notes, the relationship between cranial morphology, posture and locomotion is complicated by the multiple interactions between the brain, face and body. The present study finds distinct deformation in the craniofacial features of all intraspecific datasets that have biomechanical implications towards dietary specialisation (Coiner-Collier *et al.,* 2016; Burini & Leonard, 2018), which is further explained by trophic guild, i.e. levels of frugivory and folivory (Galen-Acedo *et al.,* 2019).

6.2.2.2 Intraspecific morphological variation reflecting levels of frugivory and folivory

Although Coiner-Collier *et al.* (2016) did not find a correlation between food-type preference and biomechanical function of cranial form in primates, the present study does indicate cranial morphology as influenced by levels of frugivory and folivory. This can be seen in both Principal Components Analysis clusters and related Thin-plate Spline grids. High-energy deformation is consistently found throughout the intraspecific datasets pertaining to zygomatic arch width, facial prognathism, sagittal and temporal crests.

The sagittal crest is a median, vertical bony ridge which runs along the dorsal midline of the braincase of many mammals (Holbrook, 2002). The presence of a sagittal crest serves as a primary attachment for the temporalis muscle associated with chewing function (Baliola, Soligo & Wood, 2017). The Thin-plate Spline grids reported for *Gorilla* and *Pongo* show a trend towards smaller sagittal crest deformation in the more frugivorous species *P. abelli* and *G. gorilla*. This suggests larger mastication loading through the muscle attachment of the sagittal crest in species that are chewing tougher foods for longer periods of time, i.e. the favour in herbaceous supplementation in *Gorilla beringei* and *Pongo pygmaeus* species. This finding is supported by Baliola *et al* (2017) who reported a significant relationship between tooth wear rank and sagittal crest size in gorillas and orangutans. The present study also finds a link between larger bodied *Pongo* and *Gorilla* specimen and larger sagittal crest formations that is also supported through previous morphometric analyses conducted by Baliola, Soligo & Wood (2017) and Bilsborough and Rae (2007).

Implications of a trophic guild and sagittal crest formation trend could shed light on the distinct cranial morphology of hominins, such as the robust *Paranthropus boisei*. As specialist hard object feeders (Sponheimer & Thorp, 2007), *P. boisei* fossils show a uniquely compounded sagittal-nuchal crest and very wide zygomatic arch also associated with mastication force loading (Welker, 2020). The diet of *Paranthropus boisei* has been analysed through stable isotopes showing molecular evidence of a C_4 biomass diet which represents grasses and sedges, providing evidentiary support that *P. boisei's* morphological adaptation of the sagittal crest and zygomatic arches represents an adaption towards masticating large quantities of low-quality vegetation rather than hard objects (Cerling *et al.,* 2011). The present studies' geometric morphometric analysis supports this trend of chewing herbaceous plant material, and not necessarily hard material, relative to larger sagittal crest size through quantified morphometrics. This shows geometric morphometric analysis as an important tool in providing substantial ecomorphological evidence in support of hominin trophic guilds in future palaeoanthropological research.

This trend is less clear in the gibbon dataset suggesting sagittal crest morphology and diet to have a less significant relationship. The sagittal crest, however, is warped to a lesser degree indicating a less pronounced ridge as specimen plots enter positive PC2 morphospace, which includes *H. nomascus* and *H. hylobates* specimen. The Thin-plate Spline grids also show marked deformation in the zygomatic arch region which can be seen in the *Pongo* and *Gorilla* datasets.

Zygomatic width is clearly associated with habitat and patterns of morphological variance in the skull, indicated through high-energy deformation in the intraspecific datasets Thin-plate Spline grids. There is a multitude of evidence towards the morphology of the primate zygomatic arch and functionality in mastication strain levels (Edmunds, 2017). This strengthens Vilamill's (2017) argument that diet is an influential factor towards the craniofacial morphology of primates.

Thin-plate Spline grids associated with *Gorilla* (**Figure 5.3**) and *Hylobatidae* (**Figure 5.4**) show high-energy deformation to the zygomatic region in relation to species who consume a more herbivorous/folivorous diet than their conspecifics. Siamang and *Gorilla beringei* specimen are located towards negative PCs that are correlated with a widening of the zygomatic arch indicating a patterning of cranial morphology influenced by trophic guild. This is less evident in the intraspecific orangutan dataset where the Thin-plate Spline deformation is slight; however, there is a trend for the more folivorous *Pongo pygmaeus* specimen to spread into negative Principal Components where the highly frugivorous *Pongo abelli* does not.

6.2.3 Primate Crania GMA Summary

The mandible has long been used as the main holotype of phenotypic study due to the inferences that can be made regarding diet and habitat and as such, there are few studies detailing a 3D quantitative, multivariate approach concerning primate cranial ecomorphology (e.g. McNulty, 2004; O'Higgins, 2000; Rae, 2004). Complete fossil hominin skulls are rare, so comparative methodology is often the first port of call for studying hominin facial adaptation.

Interspecific cranial geometric morphometric study has shown a distinct clustering between primates of similar habitat, similar levels of frugivory and similar locomotive preference. More arboreal and frugivorous species are reported as having similar morphological variance patterning in contrast to their more folivorous and terrestrial counterparts. Behavioural aspects forced by habitat, i.e. home range size, does not appear to have specific and significant effect on cranial variance patterning compared to dietary and locomotive preference, and there is no reported distinction between African great ape hominids and Eurasian Hylobate specimen. This, however, could be explained through ontogeny as suggested by Bilsborough and Rae (2007).

Intraspecific cranial study has shown *Hylobatidae* and *Pongo* as being cranially highly variable with the largest reported variance between the *Gorilla* species, *G. gorilla* and *G. beringei.* Trophic guilds, levels of frugivory and folivory, are represented in the individual Thin-plate Spline deformation grids through morphology related to masticatory function, e.g. sagittal crest, zygomatic arch width, facial kyphosis/prognathism and temporal region. Though there are definite pattern trends towards clusters of arboreal and terrestrially inclined species, the intraspecific deformation grids high-energy bending of the nuchal crest cannot be correlated definitely through a posture and habitat type relationship.

DeSantis *et al.* (2020) argues that there is a broad association between primate diet and cranial form; however, the methodology presented in the current study has been shown as a progressive approach to better understanding the patterns of variation in cranial form in relation to habitat, and so benefits current discussion surrounding the use of comparative and multivariate methodologies in paleoanthropological study (Venditti & Pagel, 2015; Zelditch *et al.* 2012). Evidence in this study also suggests that cranial diversity is less determined by diet or habitat type than mandibular and dental characteristics of primates, which is supported by Bilsborough and Rae's investigation, 'Hominoid Cranial Diversity and Adaptation.' (2007:1095).

6.3 Mandible Dataset Discussion

6.3.1 Interspecific Primate Mandible Ecomorphology

108 mandible specimens from four genera and nine species of primate were 3D imaged and digitally landmarked. The virtual renderings were Procrustes-aligned and subject to geometric morphometric statistical testing, i.e. ANOVA, PCA, 2B-PLS and TPS.

Section 5.2 demonstrated unique and distinct patterns of variation both inter- and intraspecifically in the mandible specimen. Four significant findings are reported: 1) GM analysis reported obvious morphospace separation between highly frugivorous and more folivorous primates; 2) as reported by PCA variance, habitat has greater influence on mandible morphology than on cranial structure of primates, which here is suggested to be influenced by dietary habits; 3) Thin-plate Spline grids reported high-energy deformation, most notably to the gonial angle, ramus and width and height of the mandibular corpus, which is variable in intraspecific groups; and 4) the single species within-group GMA reported little statistical significance in relation to mandibular morphology as seen in the *P. troglodyte* dataset.

6.3.1.1 Mandible morphological variation caused by dietary specialisation

The first major finding of the mandible group GMA contributes to the discussion regarding diet and mandibular form. The GM analysis performed on primate between-group mandible specimens showed similar patterning of variance among more folivorous species. Highly frugivorous species span mostly negative and smaller positive PCS whilst species who consume greater leafy plant material cluster in high positive PC morphospace. This patterning is reflected between species (interspecific groups) whose diets differ in percentage of plant material and fruit intake.

As dietary specializations are a known cause of mandibular and dental evolution (Taylor, 2006b), commonality in positive loading morphospace occupation seen in **Figure 5.15** can be explained through an inclination to consume a more ecologically diverse diet i.e. more folivorous species. This significant finding provides evidence towards the hypothesis that similar ecomorphological traits are identifiable amongst primate species that can be quantified through geometric morphometric analyses. This finding is also mirrored in studies of the primate craniodental form suggesting morphology reflects dietary differences directly related to the degree of folivory and frugivory within species (Taylor, 2002; Spears & Compton, 1996; Uchida, 1996, 1998; Shea, 1983).

Evidence of this is seen in **Figure 5.10**, where *G. beringei* specimen sit within positive PC's in contrast to the majority of *G. gorilla* specimen plots. The high-altitude, mountainous *G.*

beringei species consumes an approximate 86% of plant matter encompassing mostly leaves, shoots and stems. 2% of *G. beringei's* diet is made of fruit in contrast to the Western Lowland *G. gorilla* species whose diet consist of 86% fruit (Harcourt & Fossey, 1977; Watts, 1984; Calvert, 1985; Popovich & Direnfeld, 1997; Nishihara, 2002).

Although *P. abelii* specimens traverse both positive and negative loads, *P. pygmaeus* clusters specifically in the positive alongside *G. beringei*, *P. troglodyte* and *S. syndactylus.* As *P. pygmaeus* is known to consume tougher vegetation during periods of low fruit yield, the positive PCs, as seen in the *Gorilla* clusters, reflect species whose diet consists of more rough plant material and less fruit than their counterparts (Taylor, 2006; Smith *et al.* 2012).

The *S. syndactylus* (Siamang) specimen mirrors this trend sitting within positive PC loadings in contrast to *H. hylobates*, *H. hoolock* and *H. nomascus* who cluster diagonally within negative PCs. Siamangs are less frugivorous (30% fruit) in comparison to agile (60%) or Lar gibbons (50%), opting for young leaves and shoots, as well as flowers and insects, to complete their nutritional intake (Harrison, 2019; Harrison *et al.* 2020). *Pan troglodyte* specimens also sit within positive PC loadings which is expected compared to all the species analysed in this study, as chimpanzees have a known natural propensity to 'experiment with exotic foods introduced into their habitats' (McLennan, 2013; Takahata *et al*. 1986).

As Taylor (2006b) suggests, primates vary along a gradient of folivory and frugivory, and as can be seen in **Section 5.2.**, there is clear indication that highly folivorous primates show similar patterns of variation in comparison to their more frugivorous counterparts. This proposed method of GM analysis could be used comparatively to assess the pattern of variation between extinct and extant hominids and further our understanding of the dietary habits and ecological constraints of early hominins. The implications of this are ten-fold as levels of frugivory and folivory could suggest low fruit yield seasonality, behavioural foraging adaptions in high-predatory habitats, and inferences referring to mandibular biomechanical functions.

The stark contrast between intraspecific variation that correlates between dietary habits also reflects the habitats within which those species live and is an indicator of their territorial ecology, i.e. swamp, montane and evergreen forest species are distinct from tropical, lowland dwelling forest species; a result which is replicated in the cranial dataset.

A second finding of this study shows that between-species mandible shape space encompasses 10.44% more variance in the first two PCs comparable to the interspecific crania dataset. This suggests less morphological plasticity in the cranium in regard to environmental adaptation than seen in the mandibular form. Interestingly, Figueirido *et al.* (2011) concluded the same patterning in carnivoran skull shapes analysed through eigenshape analysis where they saw less morphological signatures in the cranial data sets in comparison to mandible specimen. The team suggested this as a result of a compromise between various functional demands in the cranium, i.e. olfactory sense, vision, brain processing etc., whereas the mandible's sole function is dedicated to food acquisition and processing.

Marcé Nogué *et al.* (2020) have recently studied shape variation in early hominin and extant primate mandibles by way of PCA and focused on biomechanical functionality as a way to distinguish trends in hard and soft food eaters. Although the shape data showed moderate covariation, the team failed to conclude a distinguishing pattern of ingesta related signals. To expand upon this study, we have shown how 2B-PLS in conjunction with PCA and using known environmental variables can indicate correlative patterning between shape and dietary inclinations indicating the progressive future implications of this comparative methodology.

As Lague *et al.* (2009) states, more than 50% of identified early hominin species have mandible specimen as their holotype. In conjunction with the proposed comparative GM methodology, mandible ecomorphology could further our understanding of questionable dietary adaptations through visual inspection of quantified morphospace occupation patterning related to form. The implications of this finding shows that studies focused on hominin dietary and environmental investigation will yield greater quantified and statistical significance when analysing the entirety of the mandibular form in conjunction with known habitat data where possible, and will be most effective when utilizing 3D GMA and multivariate statistics, i.e. 2B-PLS, PCA and TPS.

Stedman *et al.* (2004), who led the study ‘Muscle sculpts bones’, argues that a 2.4 Mya mutation in hominins led to a reduction in a main protein (MYH16) used to build the bulky masticatory apparatus seen in primates. A weaker jaw, Stedman *et al.* states, could have led to *Homo sapiens* encephalisation and superior intelligence over time. After identifying the missing gene, the team compared human skulls to other extant primates and noted that even the most distantly related primates shared the same specialised jaw muscles, i.e. sagittal crests, that are non-existent in humans despite our close familial relationship to gorillas (Stedman, 2004:415).

As the early *Homo* diet became less focused on tough and fibrous plant material and more inclusive of meat (Ungar, Grine & Teaford, 2006), there is a reduction in the jaw muscles and the removal of the large chewing apparatus such as the sagittal crest (Tuttle, 2021). A softer diet requires less exertion and puts less strain on the masticatory apparatus – a process also modifies the cranial structure due to the forces acting upon it (Stedmann, 2004).

The results of this study report apparent trends for species with softer diets showing similar patterns of variation in comparison to those with tougher, more folivorous diets, in both cranial and mandibular specimens. Interestingly, the more practiced folivores are also the species known to exhibit larger and more robust crania and jaw bones than their conspecifics, i.e. *G. beringei, S. syndactylus*, *P. pygmaeus* and *P. troglodyte* are identified as consuming a higher proportion of chewy plant material than their highly frugivorous counterparts (Yamagiwa *et al.* 2005; McLennan, 2013; Taylor 2006b).

These resulting trends support Stedmann's (2004) view that diet can affect the size and function of the masticatory apparatus which in turn has a significant effect on the size of the cranium. To further this, it would be beneficial to use the proposed 3D GMA methodology to analyse the neurocranium of an interspecific primate data set in order to highlight any existing patterning between softer, frugivorous diets and an increase in brain case size. This would add further clarification to the argument of whether encephalisation in early hominins is influenced through unpredictable climatic forces, as a result of allometry or strongly influenced through diet.

Another major finding to this study is that both the intra- and interspecific Thin-plate Spline warps showed a trend of high-energy deformation in the gonial angle and ramus, as well as positive anterior projection of mandible prognathism, specifically when habitat is used as the secondary variable. This finding is supported by an allometric study of primate mandibles conducted by Taylor (2002) which showed an increase in mandibular corpus thickness contemporary with the inclusion of more resistant food consumption, and has elsewhere been defined in macaques (Anton, 1996) and colobines (Ravosa, 1996). Variance in hominid mandibular corpus morphology is also mirrored in such studies as Pitirri & Begun (2018), Smith (1983) and Lague *et al.* (2009).

Mandible specimen are well represented in the hominin fossil record and as such mandibular corpus shape variation is commonly used for hominid species recognition (Robinson, 2012; Raia *et al.* 2018) however, few studies have utilized 3D visualisations, GMA and multivariate statistics to provide a correlation between habitat type, diet and morphological shape variation.

Whilst diet cannot account for all patterns of morphological variation in primate mandible form (allometry and ontogenetic development must also be taken into account) (Young and Shapiro, 2018), the results of this particular GMA study show habitat as a significant factor and correlates with earlier investigative ecomorphological results (Taylor, 2002; Raia *et al.* 2018). For example, TPS grids reported for intraspecific *Gorilla* dataset shows the most deformation at the gonial angle than any other within-group set. This compliments Taylor's (2002) findings which report *G. beringei* to have a significantly larger masticatory morphology than any other primate taxa, including that of its lowland conspecific.

In the current study, *Pan troglodyte* mandible where subject to GMA and multivariate testing as an intraspecific (single species) group. Adding an interesting caveat to the results, this particular group showed little statistical significance as a result of ANOVA testing, and therefore supports the null hypothesis. It would be beneficial to recreate the study with single species mandibular specimen of known regions to understand if a larger sample size would affect this result. For early hominin studies of the future, it would be valuable to understand the limitations of single species datasets in a large scale ecomorphological study and whether closer regional variation exists in hominid mandible morphology.

Rae and Bilsborough (2007) claim that hylobatids can be distinguished from great apes because of their more mandible. Examining the multi-taxa Principal Components plots in this study, hylobatids are not singled out exclusively as being so morphometrically defined once size associations are removed. This find is supported by detailed plots of extant and fossil hominids created by Kunimatsu *et al.* (2004), which also fail to provide a fundamental distinction between extant great and lesser apes once the issue of size is addressed.

Palatal depth at M2 and the height of the root of the zygomatic arch are also considered great ape synapomorphies. This study shows that these features are potentially influenced by size as, once this factor is removed, the morphological distinction between lesser and great apes becomes less defined. Not discounting probable overlap, Shea (2007:126) supports this find stating that greater zygomatic arch heights and palate depth may in fact be characteristic of living hominoids in contrast to late Miocene fossil species.

6.3.2 Intraspecific Primate Mandible Ecomorphology

All intraspecific mandible groups returned a p-value in direct contrast to the null hypothesis, with the exception of Pan. This shows environment to have a statistically significant effect on the morphology of the primate mandible. Similar to the cranial analysis, the *Gorilla* dataset returned the largest effective size with *Pongo* exhibiting comparatively less statistical significance than gorilla or hylobatid species.

The Thin-plate Spline warps associated with the intraspecific *Gorilla* Principal Components Analysis shows high-energy deformation to the ramus and mandible angle (PC2), as well as the anterior dentition (PC1). As the *G. beringei* species is reported as presenting less dental deterioration than the more frugivorous *G. gorilla* (Galbany *et al.,* 2016; Plataforma SINC, 2016), this morphological variance could be a reflection of jaw stress adaptation and a consumption of softer foods.

The hylobatid mandible PCA reported 1.84% higher total variance in the first 2 PCs (43.91%) in comparison to the cranial dataset, suggesting environment to have more influence on the morphology of the mandible than the cranium. All species in the scatterplot span both negative and positive PC morphospace except for siamang who cluster within negative PC loadings, which reflects dietary specialisation. Siamangs diet is heavily focused on young leaves, flowers, shoots and root material which takes longer to chew than a diet heavy in soft fruits (O'Brien *et al.,* 2003; Nurcayho, 2001). The gibbon Thin-plate Spline warps show deformation to the gonial angle in particular. This variance is related to muscle variance and chewing force; less muscle mass reduces the gonial angle (Jensen and Palling, 1954; Ogawa *et al.,* 2012).

The intraspecific *Pongo* PCA returned a total variance of 46.89%, the third largest of the group, and a significantly higher degree of diversity patterning in *P. abelli* comparable to *P. pygmaeus*. Similar to the *Hylobates* findings, Thin-plate Spline warps returned for orangutan species showed deformation towards the gonial angle, as well as the width of the mandible. This may be associated with the orientation of the palate which is known to be particularly high in orangutans. The variance in the width of the mandible of *Pongo* is interesting as Neux *et al.* (2015) have found significant relationships between the mandibular ramus and cranial face that the authors note is linked to important functions such as airorhynchy, diet and mandible muscular insertions. The unique cranial features of *Pongo* are suggested as influenced through mandibular form and function which is determined through dietary specialisation (Ackermann, 2002; Neux *et al*., 2015:10). As *P.*

abelli and *P. pygmaeus* differ in levels of frugivory and folivory, it is suggested here that force loading differences between food textures has influenced the variance in these conspecifics' mandible morphology.

6.3.3 Primate Mandible GMA Summary

Interspecific mandible geometric morphometric study has shown a distinct clustering between primates of similar trophic guild and level of frugivory and folivory. Principal Components Analysis also reports a distinction in habitat type with clusters of swamp, montane and evergreen forest species separate from tropical, lowland forest species. This is also a theme seen in the cranial PCA results however, mandible variance, both intra- and interspecifically, shows a larger degree of variance than is reported for the crania datasets. This suggests habitat to have significantly more influence on the morphology of the mandible compared to the cranium.

Diet specialisations are seen to impact specific features of the mandible depending on the genus. Intraspecific Thin-plate Spline warps show deformation to the gonial angle and ramus width which reflects differing strains of masticatory function between species with softer fruit dominated diets versus folivorous species. These modalities are known as influential and integrative modalities which effect the craniofacial structure in primates.

This quantitative methodology has proven habitat to have a great effect on mandible morphology particularly in relation to diet and subsistence. Further comparative study would shed light on the effects of mandibular morphological evolution and its direct influence on the facial structure as a result of diet and habitat. Including extinct hominid fossils would indicate similarities in pattern variation and morphospace occupation that would help to elucidate whether locomotive biomechanics or dietary specialised mandible morphology have greater effect on the facial structure of early hominins.

6.4 Primate GM application with an ecomorphological framework

Ecomorphology is ‘the characterisation of the adaptive relationship between an organism’s morphology and its ecological role’ (Soligo and Smaers, 2016:608). The study of primate origins is limited due to the absence of ecomorphological data and so relies on a fragmentary fossil record and comparative phylogenetic analysis of extant species (Betz, 2006). Prominent ecomorphological studies can be characterised as either emphasising the importance of locomotive behaviour as an adaptive response, or as emphasising the importance of diet in influencing organism morphology (Soligo and Smaers, 2016).

Comparative geometric morphometric studies in palaeoanthropology have primarily focused on ontogeny and biomechanical function with sparse ecomorphological research using a quantitative method. Understanding ecomorphological relationships of extant primates is important in reconstructing the ecomorphology of extinct hominin species.

6.4.1 The primate skull as an ecomorphological indicator

This thesis has shown that skull shapes can be used as indicators of ecological niche partitioning between sympatric species. This is evident in the *Pan* and *G. gorilla* species who exhibit distinct dietary specialisations. These two species live within similar habitats, in some cases in the same region (Macho and Lee-Thorp, 2014), but adopt different dietary habits and morphometrically dissimilar skull shapes, i.e. the ‘risk aversion’ hypothesis for highly folivorous species (*P. troglodyte*) as a means to avoid starvation (Janson and van Schaik, 2009; Chaney, 2015; Stone, 2007; Macho and Lee-Thorpe, 2014).

Skull shape is clearly an indicator of feeding behaviours, i.e. levels of frugivory and folivory within species groups. This is particularly important for the study of early hominins as evidence for early dietary specialisations are historically investigated through dental allometry, structure and occlusal morphology, as well as nonadaptive studies such as dental microwear and chemistry (Ungar and Sponheimer, 2013).

The methodology used in this study has shown dietary specialisation as a main driver of morphology but that this is not the only influencing factor. The cranium has been shown to have been defined by locomotive behaviour in particular with levels of arboreality and terrestrialism creating significant morphological differences in interspecific and intraspecific groups. These results support Soligo and Smaers (2016) view that ecomorphological frameworks should be multi-disciplinary and can’t rely on one aspect of organismal behaviour alone.

This geometric and ecomorphological approach has proved beneficial to the study of paleoanthropological study as it shows locomotion and dietary specialisation as interrelated factors, which have historically been studied independently. This comparative methodology also shows altitude and habitat type to influence skull morphology and the subsistence behaviours in extant apes. Therefore, early hominin ecomorphological studies should include postcranial data and contemporary palaeoecological data where possible. Biomechanical function, behaviour, ontogeny and phylogeny should also be factors included in geometric morphometric studies in order to provide a complete review of ecological adaptation.

As Thorpe (2016) states, we cannot expect all fossil forms to reflect that of extant species, but the referential modelling process does not necessarily require such rigidity. The referential model does not need to be the whole organism, rather a single feature or system from one or multiple species, i.e. endocasts patterning or femur morphology. By understanding how living species are able to interact with their environment despite existing skeletal constraints, we can better understand the possible behaviours that a particular fossil species might exhibit without expression or how selective pressures may be resolved in the skeleton.

6.5 Summary

The aim of this research was to investigate:

- to what extent does ecology influence the morphology of primate skull shape and,

- the main environmental pressures that encourage morphological variance in hominins

These research questions have been answered through 3D geometric morphometric and multivariate statistics, which provided quantifiable evidence that habitat and ecology have a significant effect on craniomandibular morphology.

6.5.1 Main Findings

Heterochrony and allometry are factors that take the spotlight in studies concerning the skeletal form (Klingenberg, 1998; Berge and Penin, 2004); however, this study has shown ecomorphological patterning to be an important factor in the evolution of hominid craniomandibular morphology. Morphological variation influenced by habitat is most notably seen in the masticatory apparatus of great ape and hylobatid species, i.e. zygomatic arches, thickness and width of mandibular corpus, sagittal crest positioning, as well as gonial angle and ramus morphology; and cranial locomotive adaptation, i.e. basicranium width, nuchal crest formation and foramen magnum position. Interestingly, species living in similar biomes (as opposed to species living in the same region), species who eat similar ratios of folivorous and frugivorous material, as well as species who are more arboreal than their conspecifics, display similar patterns of variation.

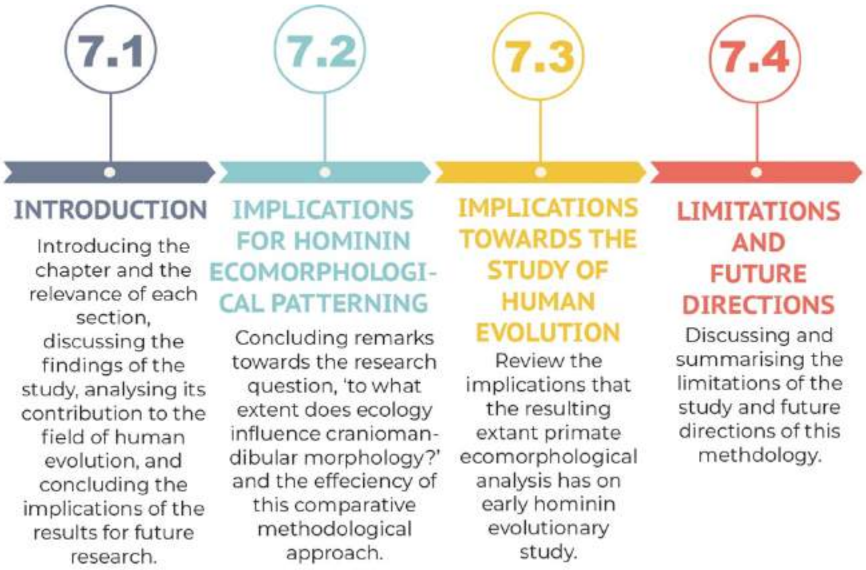
It has also been shown that primate species living in comparable habitats will adapt similar craniomandibular morphological traits, which is reported as similar patterns of variation between-species, e.g. overall larger, wider skulls and masticatory apparatus as a response to tougher plant diets. Therefore, general assumptions regarding unknown habitat can also be made from various facial morphological indicators. The distinct clustering between interspecific Eurasian and African cranial specimen shows habitat to have a great influence on the cranial structure regardless of region. *G. gorilla*, *P. abelii* and siamang specimen clusters show a similar pattern of variation which reflects arboreal preferences in environments akin to lowland and tropical forests. This is supported by basicranial deformation seen in corresponding Thin-plate Spline warps particularly in high-energy warping of the nuchal crest.

Interspecific Principal Components Analysis and intraspecific cranial Thin-plate Spline warps show similar patterns of variation which reflect dietary specialisations, e.g. deformation to the zygomatic arch and temporal narrowing. Interspecies mandible Principal Components Analysis supports this distinction in habitat type and the assembly of crown hominids, showing patterns of variation that suggest levels of frugivory and folivory. Thin-plate Spline warps indicate keys areas of specific variation including mandibular ramus gonial angle deformation, signifying variance in biomechanical function and force loading attributed to food texture.

The results show environmental plasticity to have a significant effect on both cranial and mandibular morphology. The cranial interspecific Principal Components Analysis, in particular, shows environmentally induced phenotypic plasticity across all genus including Hylobates relating to features that are currently understood as synapomorphic, i.e. widening of the neurocranium and zygomatic arch. The inclusion of Hylobates in this variance shows as unexpected grouping of lesser and great apes indicating character novelties that may not be so clearly defined as synapomorphic.

In summary of the testable hypotheses, quantitative GM analysis and multivariate statistics has been used to better understand the relationships between evolutionary adaptive response and environmental pressures. This has been successfully shown through the main findings of this study, including ANOVA tests supporting statistical significance against the null hypotheses; distinct patterns of variation separating intra- and interspecific datasets indicating morphological disparity through dietary specialities primary methods of locomotion, that are further emphasised through high-energy deformation Thin-plate Spline grids.

7 CONCLUSION



INTRODUCTION

Introducing the chapter and the relevance of each section, discussing the findings of the study, analysing its contribution to the field of human evolution, and concluding the implications of the results for future research.

IMPLICATIONS FOR HOMININ ECOMORPHOLOGICAL PATTERNING

Concluding remarks towards the research question, 'to what extent does ecology influence craniomandibular morphology?' and the effeciency of this comparative methodological approach.

IMPLICATIONS TOWARDS THE STUDY OF HUMAN EVOLUTION

Review the implications that the resulting extant primate ecomorphological analysis has on early hominin evolutionary study.

LIMITATIONS AND FUTURE DIRECTIONS

Discussing and summarising the limitations of the study and future directions of this methdology.

Figure 7.1: Chapter Seven roadmap showing the utilisation of each section in providing conclusive remarks on the geometric morphometric methodology, the implications of the results in studying human evolution and ecomorphological patterning, and the limitations and possible future directions of the study.

7.1 Introduction

This conclusive chapter will discuss the findings of the study, analyse its contribution to the field of palaeoanthropological study, and assess the implications of the results for future research.

7.2 Implications for Hominin Ecomorphological Patterning

A primary aim of this research was to produce a replicable comparative methodology utilizing modern 3D digital imaging and geometric morphometric analytical tools to examine pattern variation in extant primate cranial and mandibular specimen. Through ANOVA and Two-block Partial Least Squares conducted on Procrustes-aligned landmarked specimen shapes, Principal Components graphs and Thin-plate Spline warps showed 1) patterns of variation that grouped species of similar dietary behaviour as informed by habitat; 2) morphological patterning by habitat type; 3) patterns of variation grouping species of similar locomotive behaviours; 4) specific physical modules of the mandible and cranium that are highly influenced by ecology.

In answer to the initial research aim '*to what extent does ecology influence primate craniomandibular morphology?*' this thesis has shown that habitat type is a strong influence on primate skull morphology, and that the mandible in particular shows greater patterns of variation in relation to environment than does the cranium. Mandible variance reported 63.71% of overall variance observed in the first two PCs, which was an increase of 10.44% comparable to the interspecific cranial dataset.

Secondly, locomotive behaviours and dietary specializations are quantified in this research as the primary factors most strongly influenced by environment and habitat type. However, developmental plasticity is also a factor that can't be ignored and studies including ontogeny should include an ecomorphological framework to better understand the levels at which environmental and developmental plasticity influence hominid skull variation patterning.

7.2.1 Morphological patterning by habitat type

The geometric morphometric analysis conducted on both cranial and mandible datasets revealed similar morphological patterns of variation between species living in similar biomes, rather than species living in the same region. It was expected to see clusters of variances that described both an African and Eurasian split due to the localities of the crown hominoid specimen used in the study (Rae, 2004). However, the analysis returned a significant distinction in morphological variance patterning between lowland and topical forest habitats in comparison to swamp, montane and evergreen forest territories. This patterning can be seen in both inter- and intra-species datasets implying a powerful and significant influence of biome-type on skull morphology.

7.2.2 Morphological patterning by locomotive behaviour

The cranial GM analysis revealed variation patterning distinguishing between species primary locomotive behaviours. Thin-plate Spline grids reported high-energy deformation within areas of known locomotive adaptation in relation to habitat type, i.e. narrowing of the basicranium, positioning of the foramen magnum, and projection of facial prognathism. The implication of this, in combination with clusters of primates of similar locomotive behaviours, shows comparable morphological variance influenced by habitat, particularly for species that exhibit greater arboreal behaviour than their conspecifics. This is supported by qualitative reports of arborealism in various primate species by Fleagle (1976), Remus (1999), Ward (2002), Hunt (2003) and Loken *et al.,* (2013).

7.2.3 Morphological patterning by dietary specialisation

The results from this research supports Taylor's (2006b) suggestion that primates vary along a gradient of folivory and frugivory. This thesis has quantified the morphological disparity that exists between extant primates living in various habitats and identified specific similarities between species that are highly folivorous in comparison to their more frugivorous counterparts. Taylor's (2006b) dietary specialisation hypothesis is also supported through the distinct high-energy bending in both inter- and intraspecific cranial and mandibular datasets by way of Thin-plate Spline grids. These findings reflect the biomechanical functionality necessary for diets consisting of tougher food material, as seen in high-energy deformation of the zygomatic arches, thickness and width of the mandibular corpus, sagittal crest positioning, as well as gonial angle and ramus morphology.

7.3 Implications towards the study of human evolution

A major aim of this research was to review the implications that the resulting extant primate ecomorphological analysis has on early hominin evolutionary study. As the findings suggest that ecology and habitat type is highly influential towards craniomandibular morphological evolution, it would be advantageous for more evolutionary studies to incorporate ecomorphological and comparative methodologies.

Whilst the phylogeny of extant primates is generally widely accepted, the relationship of late Miocene and early Pliocene hominins in the Hominidea family is far from conclusive (Shea, 2013:124). As well as quantifiably visualising the more commonly cited synapomorphic cranial features seen in great apes, i.e. zygomatic arch and palatal depth (Moya Sola *et al.* 2004; Shea, 2013:126), this thesis has shown that environmentally induced phenotypic plasticity is highly evident in primate features.

This thesis has also shown that features, which have hitherto been identified as synapomorphic, e.g. midface (palatal) kyphosis (Ross and Henneberg, 1995), may not accurately be assigned as strictly hominoid, as exemplified by the clusters of prognathic features exhibited by hylobatids, as well as the more terrestrial species in this study. This is also exemplified by the lack of klinorhynchy/airorhynchy distinction in *Pongo* specimen specifically. Further data is needed to support this finding that habitat type is less influential towards levels of airorhynchy and klinorhynchy in hominoid species, however, this finding does support current arguments that mechanical and spatial hypotheses cannot solely explain the development of this particular facial characteristic.

Another finding that directly influences early hominin classification is the understanding of dietary and locomotive adaptation and plastic input on the skull. Though many studies have demonstrated masticatory adaptation in relation to primate evolution (e.g. Taylor, 2002; Vineyard *et al.* 2008), little inference has been made regarding midfacial, palatal and orbital features in relation to dietary specialization. The findings from this study do not indicate a high degree of habitat influenced adaptation in these areas and so features, such as the prominent supraorbital torus of the great apes, should be analysed further to provide alternative explanations for their evident adaptation in the hominoid phylogeny (Ross and Metzger, 2004;387; Shea, 2013:129).

A further implication of this study is the developed methodology. This research utilized a digital and statistical technique shown to quantify pattern variation pertaining to preferred and primary forms of locomotion, i.e. the degree of arborealism vs terrestrially inclined species. This has major implications towards paleoanthropological study as the locomotive patterning of early hominins is contentious (Crompton *et al,* 2008; Su, 2013). For example, the locomotive behaviours of the late Miocene hominin, *Sahelanthropus tchadensis* has been greatly debated (e.g. Wolpoff *et al.* 2002; Wood and Harrison, 2011). The foramen magnum of the TM 266-01-60-1 cranial specimen indicates habitual bipedalism and an upright posture (Brunet *et al.* 2002). Including the restored digital images of a specimen such as this, as well as what we know from paleoclimatology evidence of a diverse forest and grassland habitat, may show whether this species falls into a distinct grouping of avidly arboreal or terrestrial species, or perhaps somewhere in the middle, thus identifying a primary form of locomotion.

Landmark digitising and 3D geometric morphometrics are popular tools in palaeoanthropology. However, the open-source capabilities of computerised morphometric studies are not fully utilised. Precise 3D renderings of fossil specimens can be easily shared, meaning researchers can access fossil material that they may not have previously. Software, such as the R Project, can be used for researchers to quickly replicate a study as long strings of coding and results, which would typically be difficult to disseminate. Data can be made available for download, reuse and peer-reviewed testing. The open-source nature of this platform means that it is constantly evolving based on the researcher's needs who, if proficient in the particular coding style of R, can work within the platform to suit their methodological needs, rather than being constrained by the software’s interface capabilities.

7.4 Limitations and Future Directions

The limitations noted in this study are in fact excellent opportunities of expansion in future related studies. Areas of enhancement to the methodology include larger sample sizes, the addition of allometric study and utilizing reconstructive landmark approximation to allow for early hominin specimen inclusion in the datasets.

Unfortunately, a limitation of this research is the small sample size, specifically seen in the *Pan* dataset. As a large database of chimpanzee and bonobo 3D scans does not currently exist, creating further digital *Pan* skull renders would be advantageous to increase the sample size. Allometric variation patterning in comparison to habitat would also expand this study greatly, as size and shape is reported as a major factor in cranial evolution. These results, alongside the variation pattern seen in this thesis, would provide deeper insight into the physiological bearing of nutritional values in dietary specialization as influenced by habitat preference and behaviour.

The 3D rendering technology used in this study is also capable of quantification of variance through approximate reconstructive landmarking. Utilizing early hominin crania, whether complete or incomplete, could be included in this study alongside known habitat type from palaeoecological record. This would facilitate the initial positioning of early hominin skulls within the interspecific Principal Components Analysis graphs alongside ecological variables; an investigation which has not yet been explored using this methodology.

Notwithstanding the aforementioned limitations, this thesis has successfully demonstrated habitat as an influential force on craniomandibular morphology both inter- and intraspecifically. The methodology has provided quantifiable evidence showing environmental plasticity to have a significant effect on both cranial and mandibular morphology and demonstrated that the current understanding of great ape and hylobatid synapomorphies are not so clearly defined, which exemplifies the importance of including lesser ape specimen in future comparative studies of human evolution. Utilising 3D digital imaging and open source analytical software, this study has provided a unique view into an ecomorphological and geometric morphometric framework that can further be used comparatively within early hominin evolutionary study.

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9 APPENDICES

APPENDIX 1: PRIMATE SKULL SPECIMEN LIST

SPECIES	INSTITUTION	SPECIMEN ID
Pan troglodyte	NHM	O.C 2050a
		O.C 2050b
		O.C. 2049
		O.C 2049b
		O.C 2048e
	SMH	USNM084655
		USNM174699
		USNM174700
		USNM174701
		USNM174702
		USNM174703
		USNM174704
		USNM174706
		USNM174708
Hylobatidae lar	SMH	USNM083262
		USNM083263
		USNM083264
		USNM083265
		USNM083515

		USNM083947 USNM083948 USNM104438 USNM111970 USNM111988 USNM111989 USNM111990 USNM112574 USNM112710 USNM113176 USNM113177 USNM113179 USNM113180 USNM114499
Hylobatidae nomascus	SMH	USNM240490 USNM240491 USNM240492 USNM240493 USNM257995 USNM257996 USNM296921 USNM320787 USNM320789 USNM464992

		USNM542282 USNM320786
Hylobatidae hylobates	SMH	USNM279146 USNM545009
Hylobatidae symphalangus	SMH	USNM114497 USNM141160 USNM143577 USNM143580 USNM143581 USNM171981 USNM271048 USNM283563 USNM364967 USNM395514 USNM395691 USNM396648 USNM519573
Pongo pygmaeus	NHM	O.C. 2043 O.C. 2043a O.C. 2043b O.C. 2043c O.C. 2043d
	SMH	USNM013965

		USNM142170 USNM142169 USNM142171 USNM142180
Pongo abelii	SMH	USNM143586 USNM143587 USNM143588 USNM143590 USNM143591 USNM143593 USNM143594 USNM143595 USNM143596 USNM143597
Gorilla beringei	SMH	USNM259884 USNM260582 USNM395636 USNM396934 USNM395636 USNM396938 USNM397351 USNM545034 USNM545037 USNM545036

		USNM545034 USNM397353 USNM545032 USNM545031
Gorilla gorilla	SMH	USNM599170 USNM599169 USNM599168 USNM599167 USNM599166 USNM599165 USNM588746 USNM585726 USNM574138 USNM297857 USNM252580 USNM252579 USNM252578 USNM252577 USNM252576 USNM252575 USNM220380 USNM220325 USNM220324

APPENDIX 2 MANDIBLE CLASSIFIERS

ID	**SPECIES**	**HABITAT**
HBM01 – HBM05	*Hylobatidae hylobates*	Tropical evergreen forests; subtropical evergreen mountain forests
HM01 – HM12	*Hylobatidae lar*	Dry evergreen forests
HNM01-HNM11	*Hylobatidae nomascus*	Subtropical evergreen forests
HSM02-HSM13	*Hylobatidae symphalangus*	Tropical hill forests; lowland forests
PAM01-PAM10	*Pongo abelii*	Lowland forests; mountain forests; peat swamps
PPYM01-PPYM10	*Pongo pygmaeus*	Lowland forests
PTM01- PTM14	*Pan troglodytes*	Dry savannah forests; montane forests; swamp forests
GBM01-GBM21	*Gorilla beringei*	Lowland tropical rainforest, transitional forests and Afromontane habitat
GGC01-GGC20	*Gorilla gorilla*	Rain, swamp and riverine forests, lowland tropical forests and brush

APPENDIX 3 CRANIAL CLASSIFIERS

ID	**SPECIES**	**HABITAT**
HBM01 – HBM05	*Hylobatidae hylobates*	Tropical evergreen forests; subtropical evergreen mountain forests
HM01 – HM12	*Hylobatidae lar*	Dry evergreen forests
HNM01-HNM11	*Hylobatidae nomascus*	Subtropical evergreen forests
HSM02-HSM13	*Hylobatidae symphalangus*	Tropical hill forests; lowland forests
PAM01-PAM10	*Pongo abelii*	Lowland forests; mountain forests; peat swamps
PPYM01-PPYM10	*Pongo pygmaeus*	Lowland forests
PTM01- PTM14	*Pan troglodytes*	Dry savannah forests; montane forests; swamp forests
GBC01-GBC21	*Gorilla beringei*	Lowland tropical rainforest, transitional forests and Afromontane habitat
GGC01-GGC20	*Gorilla gorilla*	Rain, swamp and riverine forests, lowland tropical forests and brush

APPENDIX 4 R SCRIPT EXAMPLE GMA CODE

```
> setwd("/Volumes/harddrive/R Directory/RESULTS/Crania/Interspecies") #calling directory of landmarked interspecific cranial specimen
> install.packages("geomorph", “rgl”, “geiger”, “ape”)
> library(geomorph) #load installed packages
> sliders <- as.matrix(read.csv("surfslide.csv", header = T)) #calling sliding landmark data
> craniumlist <- list.files(pattern = ".nts")
> craniumdata <- readmulti.nts(craniumlist) #created list of .nts files as data file
> a <- two.d.array(craniumdata) #turning data into 2D array
> skullclassifiers <- read.csv("Cranial Classifiers Interspecies.csv", header = T, row.names = 1) #calling species and habitat classifiers as .csv file
> skullclassifiers$Species #checking species classifiers
> skullclassifiers$Habitat #checking habitat classifiers
> newcraniumdata <- na.omit(craniumdata) #removes rows with missing values
> estimate.missing(newcraniumdata, method = c("TPS", "Reg")) #estimate missing landmark data - no missing data returned
> Y <- gpagen(newcraniumdata) #conducting GPA alignment
> plot(Y) #plotting GPA
> gdf <- geomorph.data.frame(Y, species = skullclassifiers$Species, habitat = skullclassifiers$Habitat) #creating dataframe
> fit.classifiers<- procD.lm(coords ~ log(Csize) * species/habitat, data = gdf, print.progress = FALSE) #Procrustes ANOVA with variables
```

```
> anova(fit.classifiers)
> PCA1 <- gm.prcomp(Y$coords)
> plot(PCA1) #Plotting PCA
> summary(PCA1)
> gp <- as.factor(paste(skullclassifiers$Species)) #creating species group for legend table addition
> par(mar=c(2, 2, 2, 2))
> plot(PCA1, pch=22, cex = 1.5, bg = gp, phylo = TRUE) #assigning group colours and legend for PCA plot
> legend("topleft", pch=22, pt.bg = unique(gp), legend = levels(gp))
> text(par()$usr[1], 0.1*par()$usr[3], labels = "PC1 - 40.21%", pos = 4, font = 2)
> PLA <- two.b.pls(Y$coords, Y$Csize) # 2B-PLS analysis
> PLA
> plot(PLA) #finalised plot 2B-PLS analysis
> pcagp <- as.factor(paste(skullclassifiers$Species, skullclassifiers$Habitat))
> col.gp <- rainbow(length(levels(pcagp)))
> names(col.gp) <- levels(pcagp)
> col.gp <- col.gp[match(pcagp, names(col.gp))]
> plotRefToTarget(ref, Y$coords[,,1], method = "TPS", mag = 3) #creation of Thin-plate Spline warps for PCA plot
> plotRefToTarget(ref, Y$coords[,,1], method = "vector", mag = 3)
> preds <- shape.predictor(Y$coords, x= NULL, Intercept = FALSE, pred1 = -0.1, pred2 = 0.1)
> M <- mshape(Y$coords)
> plotRefToTarget(M, preds$pred1)
```

```
> plotRefToTarget(M, preds$pred2) #mean shape ref to target plot
```