Ph.D THESIS

SHAPE AND SIZE VARIABILITY IN LOWER SECOND MOLARS OF EXTANT HOMINOIDS AND EXTINCT HOMININ SPECIES WITH PARTICULAR REFERENCE TO MODERN *HOMO SAPIENS* AND ITS POTENTIAL FOR USE AS AN ANALOGUE SPECIES IN THE CONTEXT OF FOSSIL HOMININ DENTAL VARIABILITY COMPARISONS

A thesis submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of PhD.

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Signed on _____ in Johannesburg.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of PhD in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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ABSTRACT

Teeth make up the bulk of hominin fossil material and are useful in taxonomic assessments. In this thesis, discriminant function, principal components and randomised CV analyses on large samples of lower second molars (n=778) from five extant reference species, both sexually dimorphic and non-dimorphic, provide estimates of ranges of size-shape variability to be expected within a single species. However, there is evidence that diet-driven tooth-size reduction and cusp simplification has expanded the ranges of shape and size variability of *Homo sapiens* in some populations, in areas exposed to soft, undemanding diets since the transition to agriculture and increased use of cooking, food processing and ceramics from about 12500 years ago. Molar size and shape changes are less evident in communities retaining a hunter-gatherer subsistence strategy, requiring strong dentognathic structures with robust teeth to masticate harder, tougher foodstuffs. These factors, driving divergent variability in tooth size and shape, are unique to modern humans.

Using a novel mathematically-based landmarking methodology, developed to allow the inclusion of severely worn teeth, intra-species size-shape variability was assessed from 63 lower M2s representing nine African Plio-Pleistocene species. The first hypotheses tested in this thesis address the question of which extant hominoid species might be suitable for use as analogue species for comparisons with fossil hominin molars, and whether uniquely modern-human anomalous size-shape variability exhibited by lower second molars might disqualify modern *Homo sapiens* for such analyses. Secondly, where lower second molar size-versus-shape variability ratios measured for fossil species do not match those of either a sexually dimorphic or a non-dimorphic extant

species, evaluations are made as to whether samples attributed to single hominin species might actually represent specimens from more than one species present in the relevant assemblages, whether sexual dimorphism may have been greater in fossil species than in extant species, and whether some individual specimens attributed to any fossil species might be misclassified.

Results of the analyses indicate that uniquely human subsistence strategy divergences are identifiable in the size-shape variability of lower second molars. Furthermore, specimens representing *Australopithecus afarensis, Australopithecus africanus* and *Paranthropus robustus* in this study exhibit very high variability and may indicate the presence of more than one species in their respective assemblages.

Table of Contents

LIST OF FIGURES

LIST OF TABLES

DEDICATION

I dedicate this study to my husband, Dennis, for the unerring support he has given me.

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CHAPTER ONE – INTRODUCTION

1.1 EXTANT HOMINOID SYSTEMATICS AND THEIR RELEVANCE TO FOSSIL HOMININS

Studies into the population systematics of extant hominoids are of great significance to primatologists, anthropologists and paleoanthropologists alike. Primatologists utilise such studies of diversity to obtain a better understanding of the natural history of the hominoids and to focus their energies, for instance, on conservation (for example, Wolfheim, 1983; Oates, 1996; Butynski, 2003; Kalpers et al., 2003; Kormos et al., 2003; Taylor and Goldsmith, 2003; Bergl, 2006; Oates et al., 2007; Williamson & Fawcett, 2008; Plumptre et al., 2010; Junker et al., 2012), particularly if specific regions see a decline in population numbers. These studies are of great interest to anthropologists and palaeoanthropologists as well, and one of the applications for species-subspecies diversity studies is to provide analogues upon which to base conclusions regarding alpha taxonomy and the naming of new species in the fossil hominin context (Vitzthum, 1984; Ferguson, 1989; Wood et al., 1991; Uchida, 1992, 1996; Albrecht & Miller, 1993; Shea et al., 1993; Richmond & Jungers, 1995; Braga, 1995; Plavcan & Cope, 2001; Albrecht et al., 2003; Pilbrow, 2003; Braun et al., 2004; Mitteroecker et al., 2004; Scott & Lockwood, 2004; Lee, 2005; Baab, 2008; Lordkipanidze et al., 2013). An understanding of variability within and between species and sub-species in extant species is therefore key to predicting how much variability to expect in fossil hominin species.

Major divisions among species of extant genera are identified using morphological, ecological, behavioural and genetic data. However, the delineation of species themselves

is a matter of some contention. Firstly, there are different species concepts that would result in differing delineations (see, for instance, Simpson, 1961; Mayr, 1963, 1969; Paterson, 1985; Eldredge, 1993; Kimbel & Martin, 1993; Groves, 2002; Groves & Grubb, 2011; Groves, 2014) and secondly, researchers do not always agree on where boundaries between species should be drawn, either because such boundaries appear "fuzzy" or because there is not always agreement as to when to declare a new species (de Queiroz, 2005; Gonder et al., 2006; Groves, 2014; Groves & Grubb, 2011; Zachos, 2016; Thackeray & Schrein, 2017). Further to this, in the context of fossil hominin taxonomy, the palaeontological species concept must be delineated on the grounds of morphological similarity or dissimilarity alone, as it is not possible to observe soft tissue morphology, small-scale ecological niche differences or behaviours of fossil hominin groups, nor is genetic structure always available to the researcher in the case of fossilised material.

Nevertheless, studies into the systematics of extant hominoid groups confirm that delineations made on the basis of morphological variability are well corroborated by genetic and other observable data (such as behavioural data), and this provides a firmer diagnosis upon which to allocate extant groups into species and sub-species, and from which to infer phylogenetic histories. Because certain extant hominoid species are considered to be closely related to extinct hominin species, and in many cases these extant species exploit similar ecological niches to those presumed to have been exploited by palaeontological hominin species, such extant groups are considered to be valuable proxies or analogues that provide important information about expected ranges of morphological variability within and between species (Kimbel & Martin,

1993). Variability in respect of body size, and by extension, skeletal elements such as teeth, is markedly noticeable in some extant species (Harvey et al, 1978; Gingerich and Smith, 1984; Plavcan and van Schaik, 1993; Uchida, 1998a, b; 2004, 2010, Singleton, 2011) due to high levels of sexual dimorphism, and it is usually considered useful to include a known sexually dimorphic species from *Gorilla* or *Pongo* as well as less dimorphic species in comparisons of ranges of variability between skeletal elements of fossil and extant analogue species (Ackermann, 2003; Plavcan, 2005; Plavcan, 2012).

1.2 PREVIOUS RESEARCH AND RATIONALE FOR THIS THESIS

Since teeth are the most commonly preserved skeletal element in the fossil record, likely due to their robust physical and chemical properties, dental palaeoanthropological studies have been common, with numerous studies focused on assessing the taxonomic significance of variability in tooth morphology observed in the fossil record. These studies typically are conducted using extant analogue species as a framework for a comparative database. Previous research (Dykes, 2014) compared patterns of variability of lower first molar size and shape in morphospace (using principal components analyses, PCA) and other statistical shape and size measurements between samples of *G. g. gorilla, P. t. schweinfurthii, P. paniscus,* modern *H. sapiens,* and specimens from various fossil hominin species, such as *A. afarensis, A. africanus, P. robustus, P. boisei, H. habilis, H. erectus/ergaster* and *H. rudolfensis.* The largest samples in the study were those representing *P. robustus* and *A. afarensis.* Both of these have been considered to be sexually dimorphic species, due to size variability observed between specimens (Lockwood et al., 2007; Keyser, 2000; Reno et al., 2003, 2010), so emphasis was placed upon comparing these two species' patterns of size and shape

variability with the pattern observed for modern *G. g. gorilla*, which is considered the most sexually dimorphic extant hominoid (O'Higgins and Dryden, 1993; Richmond and Jungers, 1995; Taylor, 1997; Plavcan, 2001, 2002). Dykes (2014) documented considerable size variability of *G. g. gorilla* lower first molars along PC1 (the x-axis) of a "formspace" PCA and extremely little variance along PC2 (shape) (a Formspace PCA is a "size-shape" PCA, wherein size loads along PC1, usually plotted along the x-axis, and shape loads along PC2, usually plotted along the y-axis). Moreover, there was no overlap between female and male specimens; all lower first molars from females grouped within lower values along PC1 (smaller teeth) and all those from males grouped within higher values along PC1 (larger teeth). The "pattern" observed for this sexually-dimorphic species was, therefore, a "horizontal" clustering – size variability, split between the sexes, and very little vertical (shape) variability existed.

Results of the study (Dykes, 2014) also indicated that the paranthropines were more or less concordant in their spatial patterning (size versus shape variability) with the patterns observed for modern gorillas, although perhaps with a little more variance explained by PC2, i.e. slightly more shape variability than observed in the *Gorilla* sample. Specimens attributed to *A. afarensis,* however, were considerably more variable than extant taxa in shape, as well as in size, and the patterning did not seem to emulate any of the African great ape species in the study. There appeared to be a core group that clustered horizontally (i.e. exhibited size variability rather than shape variability) around the holotype, LH 4, including specimens from the large assemblage, the AL 333 group, but there were some specimens that consistently did not group alongside the remainder of the specimens irrespective of which methodology was used (principal

components analyses, Procrustes distances, discriminant functions analysis, log se_m regression analyses, etc.). It was concluded that either *A. afarensis*, at least as defined by the specimens studied, was an unusually variable species, indicating that the collection of specimens attributed to the species combined extremely different morphotypes (variability in both size *and* shape, which was inconsistent with patterns observed for the other African great ape species), or that some specimens may perhaps have been misallocated to this species, AL 288-1 ("Lucy") in particular. This conclusion would seem to concur with that of other researchers, such as Ferguson (1989) who postulated that specimens attributed to *A. afarensis* may, in fact, belong to more than one species, and Schmid (1989), who found significant anatomical polymorphisms between "Lucy" and other specimens considered to be more typical of the species.

The only extant hominoid group that showed significant variability in both size and shape of lower first molars in the study (Dykes, 2014) was the modern *H. sapiens* group. However, there seemed to be no indication that wide ranges of shape and size variations were due to sexual dimorphism, as there were molars belonging to both males and females clustering in all of the shape-size spectra, from the smallest and narrowest molars to the largest molars and to the broadest molars in the study. Instead, there appeared to be groupings of molars along population-level lines. In the sample representing modern *H. sapiens*, there were teeth of individuals from KhoeSan communities, individuals of European or mixed-European descent and individuals from several Bantu language-speaking groups. Variability seemed to be driven by historically different lineages, or, more interestingly, by differences in subsistence strategy, a finding that was consistent with research on other skeletal elements (Siddiqi, 2012;

Püschel and Benítez, 2014) and on tooth-size reduction in economies that had been exposed for longer periods to a transition to widescale agriculture (e.g. Dahlberg, 1960; Pinhasi et al., 2008; Emes et al., 2011).

There was a major limitation to this research, however. Sample sizes were small. There is good reason to limit sample sizes in comparisons between extant and extinct species: the availability of lower first molars to represent each fossil hominin species is extremely limited, and size-matched extant reference species samples perhaps provide a more realistic comparative basis upon which to make judgements of exactly how much variability should be expected. However, ideally, size-matched samples should be randomly selected from a larger "population" representing the full range of variability for all the species in the study, including specimens representing all of the subspecies within these species, and all of the populations that might contribute size-shape variations at the subspecies level (or at the species level, in the case of modern humans and bonobos). One way to overcome this problem would be to maximise sample sizes, and to make sure that representative individuals, down to the population level, were included in the study. Such a sample would make it possible to resample smaller subsets randomly to match more representatively the size and composition of the samples of fossil hominin species. Another limitation of the study (Dykes, 2014) was that the sample representing *A. africanus* was extremely small. At the time, there was limited access to dentition from Sterkfontein Member 4. The present study avoids this problem by increasing the sample of specimens attributed to *A. africanus* to n=16, which matches the sample size of specimens attributed to *A. afarensis*. This present thesis will therefore expand upon the preliminary work performed in the previous dissertation, and extends

the research to study lower second molars. It should also add some insights into the body of research that has gone before it, particularly when it applies to the use of extant species as analogues for estimating expected size-shape variance in the dentition of fossil hominin species.

Caution needs to be taken in presuming that extant hominoid species can invariably be considered analogous in terms of their range of variability in the shape and size of their skeletal elements to that of the same skeletal elements in fossil hominin species (Ackermann, 2003). First and foremost, variability within any species is known to increase with population size, as accelerated levels of random changes occur over time between individuals in expanding populations (Hawks et al, 2007), particularly if groups break away and exploit new environments. When comparing ranges of variability in the shape and size of any skeletal element in modern *Homo sapiens,* due attention needs to be paid to the fact that human population levels exceeded 7 billion people in 2011 (Bloom, 2011), and that no other extant hominoid or extinct hominin species is comparable to our own species in number, nor in our globalisation – our occupation and utilisation of all available adaptive niches worldwide – which itself has provided additional ecological causes for genetic changes in modern humans, driven by genetic drift and selection (Perez and Monteiro, 2008). Additionally, patterns of variability in skeletal elements may be due to external non-random factors of change, such as diet (Ruff, 1993, 2002; Fumagalli et al., 2015), environmental pressures (e.g. Parsons, 1988; Pearson, 2000; Bogin and Rios, 2003; Stock, 2006; Hancock et al., 2010; Gardner et al., 2011), malnutrition and disease (Macintosh et al., 2016), activity levels/occupations (Sehrawat and Pathak, 2011), and general subsistence strategies

(Stock, 2006; von Cramon-Taubadel; 2011, Püschel and Benítez, 2014). In the context of skeletal elements that are affected by subsistence lifestyles and activity levels, divergences in these subsistence behaviours that extend deep into the past within the same species can cause patterns of morphological variability (Siddiqi, 2012; Püschel and Benítez, 2014) that are unique to that species and this may give cause to exercise caution when utilising these species as analogues for patterns of variability in fossil species.

1.2 GENERAL AIMS OF THE STUDY

This study aims to assess the range of variability observed in the shape and size of the post-canine dentition (i.e., lower second molars) of extant hominoid species (*G. gorilla; G. beringei; P. troglodytes; P. paniscus; H. sapiens*), and compare such variability to that which is found in specimens attributed to various fossil hominin species (*A. afarensis; A. africanus; P. robustus; P. boisei; A. sediba; H. naledi; H. ergaster; H. habilis/rudolfensis*). It also aims to recommend a qualitative *and* quantitative basis for assessing ranges of variability of post-canine dentition of extant hominoid species as proxies for presumed fossil hominin species, by attempting to establish the importance (or not) of sexual dimorphism, dietary variability and other possible parameters that might affect the extant species' analogue status (e.g. historical consistency: Ackermann, 2003).

The principal questions being asked are:

1) Are lower second molars successful in delineating diagnostic differences between genera, species, subspecies and even populations of living hominoids?

2) What patterns of both size *and* shape variability of lower second molars are identifiable in the context of extant hominoid species, and can these be attributed to specific causes (e.g. sexual dimorphism)?
3) Do specimens attributed to certain African Plio-Pleistocene fossil hominin species exhibit the same patterns and ranges of shape and size variability?
4) Does the pattern of variability in lower second molars of modern humans confirm studies of patterns of variability in other skeletal elements, concluding that variability might be due to historically divergent subsistence lifestyle strategies between groups?
5) Is there shape variability over and above tooth-size reduction in certain modern human populations?
6) Can a historical time-series analysis of modern *Homo sapiens'* lower second molars confirm tooth-size reduction over time?
7) Should any of the extant species, particularly modern *Homo sapiens,* often used as comparative analogues to provide expected limits for species variability in fossil hominins ideally be excluded as analogues in these comparative studies?

1.3 THE HYPOTHESES TO BE TESTED IN THIS THESIS:

$H1_0$: *Gorilla* species are appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H1_1$: *Gorilla* species are not appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H2_0$: *Pan* species are appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H2_1$: *Pan* species are not appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H3_0$: *Homo sapiens* is appropriate for use as an analogue species (proxy) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H3_1$: *Homo sapiens* is not appropriate for use as an analogue species (proxy) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H4_0$: Specimens attributed to single African Plio-Pleistocene hominin species will exhibit similar ranges of variability in size and shape of lower second molars to those exhibited by analogous extant hominoid species.

$H4_1$: Specimens attributed to single African Plio-Pleistocene hominin species may exceed ranges of variability in size and shape of lower second molars to those exhibited by analogous extant hominoid species.

1.4 OUTLINE OF THE THESIS

Chapter Two of this thesis provides some background information on the types of research that have informed the methodologies used in this study, together with a discussion into the factors, such as diet and subsistence strategy, that are presumed to influence dental variability between and, more particularly, within, species. Chapter Three presents the materials and methods, and the inter- and intra-observer tests used in support of the methods used, particularly the landmarking method designed for this study. Chapter Four presents the results of the analyses. The first question to be addressed is that of whether lower second molars adequately represent the extant species included in this study by classifying reasonably correctly according to genus, species and subspecies, using discriminant function analyses to accomplish this. Classification at the population level is additionally analysed for modern *H. sapiens,* with particular reference to subsistence strategies of different groups. Principal components analyses are then used to visualise size-versus-shape variability in morphospace of sexually dimorphic species, non-sexually dimorphic species and fossil hominin species. Due to imbalances in sample size between extant hominoid and extinct hominin species,

a randomisation exercise is carried out to quantify expected ranges of variability (coefficients of variation) for diagnostic linear measurements of molars for each of the extant species, and the CVs of the fossil hominin samples are then compared with the expected ranges. These results are then discussed in Chapter Five, which starts with a discussion of the findings relating to extant species and continues with an analysis of comparative results for extinct hominin species, one by one. Chapter Six summarises the conclusions drawn from the study.

CHAPTER TWO – BACKGROUND

2.1 LITERATURE REVIEW: DENTAL VARIABILITY STUDIES

Pilbrow, 2003, 2006, 2007, 2010. This series of studies provides a genuine basis for comparisons of the full range of morphological variability of the dentition of hominoids including *Pan, Pongo* and *Gorilla.* For the initial study, Pilbrow (PhD thesis, 2003), collected data and images of the dentitions of these hominoids from every available collection around the world at that time. This created a comprehensive comparative database for these species, which included information down to the population level. These data were used to evaluate the dentition of Miocene apes. Later studies focused on population systematics of chimpanzees (2006), the great apes in general (2007), and gorillas (2010). These extensive studies, together with that of Uchida (2004), inspired subsequent work, such as that of Wood (2016), because of the extent they reflected comprehensively-sampled variability in the taxa. Although the present study has been limited to lower second molars of *Pan* and *Gorilla*, discriminant functions analyses (DFA) have shown (see paragraph 3.2.6 and Chapter 4 below) that lower second molars are capable of distinguishing between groups at the species and subspecies level, for comparative purposes with fossil hominin species. The present study expands on the earlier efforts by Pilbrow (2003, 2006, 2007, 2010) and Uchida (2004) by incorporating different groups of modern *H. sapiens* (i.e. biogeographical groups that are sorted where applicable by subsistence strategies), as well as species of Plio-Pleistocene fossil hominins. Thus, the focus of the present study emphasises patterns of variability, and addresses the suitability of these extant species as analogues for modelling variability in fossil hominin species.

Another difference between this study and the studies by Pilbrow (2003, 2006, 2007, 2010) and Uchida (2004, 1998a, 1998b) is that the present study, as well as its predecessor, concentrates on single tooth types. The latter emphasised lower first molars (Dykes, 2014), while the present study focuses on lower second molars. This focus follows the research of Singleton (2011), who used samples of *P. paniscus* and *P. troglodytes* to investigate shape variation in *Pan* lower molars. Her sample was quite limited (44 molars in total for the two species and two tooth types), but her study investigated molar shape allometry to establish whether differences between common chimpanzee and bonobo lower molar shapes were attributable to allometric scaling or not. She concluded that if allometry were removed from the analysis, chimpanzee and bonobo molars were indistinguishable morphometrically. While the present study is unable to control for allometric scaling because body size information was not available for all of the specimens in the study, molar size is still used as a variable to distinguish between bonobo and chimpanzee molars, as well as male and female gorilla molars. For this reason, all principal components analyses have been based on generalised Procrustes superimpositions (scaled, as well as rotated and translated), but the natural log of the centroid size has been added back as a variable to produce PCAs in "formspace" (shape *and* size) rather than in "shapespace" (shape only) (Mitteroecker et al., 2004), and this variable is also added to the measurements included in the DFA analyses.

Other researchers, such as A. Gómez-Robles, also have concentrated on using single teeth to conduct geometric morphometric shape variability analyses. She and her

colleagues have produced a series of geometric morphometric analyses of different tooth types of hominins, by investigating lower second premolars (Martinón-Torres et al., 2006), upper first molars (Gómez-Robles et al., 2007), lower first premolars (Gómez-Robles et al., 2008), upper second and third molars (Gómez-Robles et al., 2012), and hominin lower first molars (2015). The main focus of these studies has been to include larger samples of teeth from the Middle and Upper Pleistocene of Europe (*Homo heidelbergensis, Homo neanderthalensis*) so there is only a small comparative sample from the Lower Pleistocene. These studies differ from the present study in that no comparative analyses with analogue species, such as *Gorilla* and *Pan* species, are included. Nevertheless, the presentation of a series analysis by tooth type forms a model of study that could be followed for the present research (i.e. from lower first and second molars, upper first and second molars could follow, and conclusions reached in a study synthesising and summarising the results thereafter).

Other prior dental studies investigating metric variability of shape and size of teeth range from studies into odontometrics and classical morphological studies (e.g. Brace, 1980, Brace and Mahler, 1971 and Brace et al., 1987; Wood et al., 1983; Wood and Abbott, 1983; Bermúdez de Castro and Nicolás, 1995; Hanihara and Ishida, 2005), to studies based on 3D imaging (for example, Skinner et al., 2008, 2009; Braga et al., 2010; Benazzi et al., 2011; Crevecoeur et al., 2014). For this present study, 2D images of molar crown morphology are preferred because of the comprehensive databases that are available, or that are able to be built in a relatively short time. Geometric morphometric and other statistical analyses are used because they provide both shape and size sorting, and visualisation within single methodologies. Having been likened to "pre-formed

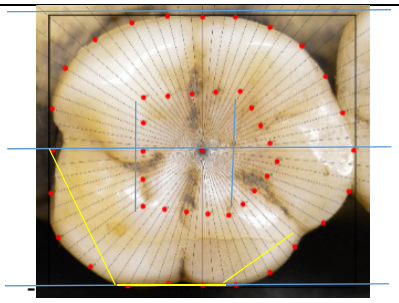
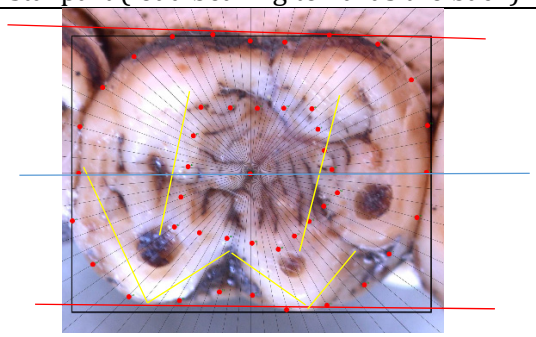
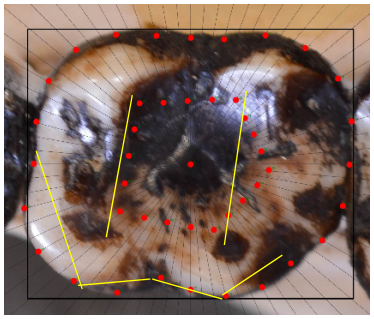
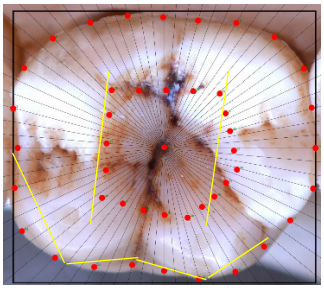
fossils" (Boyde, 1996), no adjustments need be made for ontogenetic changes in teeth as the individual matures to adulthood, as would be the case for other skeletal elements such as crania and long bones. This study makes use predominantly of principal components analyses that retain size as a variable for each specimen, in addition to analysing shape differences.

One major difference between this present study and other landmark-based studies is in the landmarking methodology designed for this study. When carrying out geometric morphometric studies on large samples of teeth, equal numbers of landmarks need to be placed uniformly on all the teeth, whether worn or unworn. Because this study includes a number of very worn (but important) fossil hominin molars (such as Peninj 1, which has much of its crown and the underlying dentine damaged), the methodology for placing of landmarks needed to be based on the most worn of all the molars in the study. This study is therefore novel in that a mathematically-based methodology for landmarking teeth and taking measurements was designed to include worn specimens (e.g. fossil teeth, modern human hunter-gatherer teeth) that would be less reliant on identifying specific anatomical features on the surface enamel of the teeth than is traditionally the case. This methodology would need to be suitable for all groups of extant hominoid and extinct hominin teeth and should be adaptable for all types of shape and size analyses (geometric morphometrics, discriminant analyses, general statistical analyses).

2.2 DIET, SUBSISTENCE STRATEGY AND TOOTH SIZE AND SHAPE

A link between subsistence lifestyles, diet and functional activity levels in skeletal elements is well-noted in the context of teeth (as summarised in Ungar, 2017). In extant hominoids, a general link between diet type and molar morphology is manifested in the direction of cusps in relation to the mesiodistal axis of the dental arcade, with insectivores' reciprocally concave cusps being at sharp angles to the axis (for better shearing ability), folivores' cusps being at a slight angle to the MD axis, and with frugivores' cusps being almost parallel to the MD axis and more rounded rather than sharp, indicating less of a need for hard mastication (Kay & Hiiemae, 1974). A further correlation exists between the slope of individual cusps relative to the horizontal, with the highest, sharpest and most pronounced cusps relative to the cervical plane of the crown being found in folivores, and the flattest cusps being found in eaters of soft fruits and other soft or processed foods (Ungar, 2007a, 2017). Most of these features can also be seen (or inferred) from the horizontal occlusal view, as Table 1 below illustrates.

Table 1. Typical shapes of modern human, gorilla, chimpanzee and bonobo mandibular first molars. Some indications of biomechanical properties can be seen from the occlusal aspect.

OMNIVORE: Modern *Homo sapiens*: rounded and regular cusps; usually relatively wider than the great ape species, although width (and shape) are variable. Shearing plane generally more perpendicular to MD axis	FOLIVORE/FRUGIVORE: Gorillas: very large, but proportionally, consistently very narrow with uneven, pronounced (sharp) cusps. Shearing plane seems to be at an angle to the MD axis, mesial side of tooth narrower than distal part (load bearing towards the back)
	
FRUGIVORE: Chimpanzees: generally narrow molars, but typically less narrow than gorillas; uneven/slanted cusps, but at a lower angle to the MD axis and more rounded/less sharp and flatter than gorilla cusps	FRUGIVORE: Bonobos: consistently narrow in same proportion to chimpanzees; uneven/slanted cusps, but at a lower angle to the MD axis more rounded/less sharp and flatter than gorilla cusps. Different to chimps in size
	

The link between diet and tooth shape and size is observable generally at the level of genus, although it is more complicated than suggested above. For instance, species and genera with similar diets may have differences in their tooth shape, while different populations of the same genus or species may have similarly-shaped teeth, but still exhibit differences in their diet. Ungar (2017) observes that while guenons and mangabeys exploit the same type of diet in the Kibale forest, their teeth and jaws are

different; and mangabeys at Kibale have a different diet to those in the Taï forest, yet their teeth have remained essentially the same shape. Similarly, gorillas and chimpanzees are often sympatric and might seasonally exploit the same fruits by preference to harder foods, when these are in abundance. However, when these foods are scarce, gorillas have been found to resort to a more leafy diet, even including very hard "fallback foods" such as tree bark, enabling them to remain close to their nucleus home ranges despite scarcity of their preferred foods (Tutin et al., 1991; Remis, 1997), while chimpanzees might range further in search of protein-rich animal foods such as honey bees and ants (see, for instance, Marshall and Wrangham, 2007; Yamagiwa and Basabose, 2009). The key point here is not that species with the same diet should automatically have similarly-sized and shaped teeth: what appears to influence form more is preserving the ability to be able to exploit and masticate certain foodstuffs in times of scarcity, and if the fallback food is leafy or hard, teeth need to retain the correct properties to exploit these foods in times of need. To quote Ungar (2017), "It doesn't matter what kind of teeth you have if you eat pudding 11 months a year. But if you need to eat rocks the other month or you'll starve, your teeth had *better* be adapted for rock eating." This is an important consideration when examining fossil hominin teeth.

Paranthropus boisei, as a species, has very robust jaws and teeth, so much so that when OH 5 ("Zinj") was discovered in 1959 by Mary Leakey, this individual was quickly nicknamed "Nutcracker Man". However, when carbon isotope ratio studies were conducted (Cerling et al., 2011), it was found that the diet of this species consisted of an average of 77% of "C4" and "CAM" foods (carbon 4 pathway photosynthesis and "crassulacean acid metabolism" foods) as opposed to C3 foods [nuts, fruits – the

products of trees and shrubs – and the animals (browsers) and insects that feed from them]. C4 foods are mainly tropical grasses and sedges, plant rhizomes, tubers ("corms") and the animals (grazers) and insects, like termites, that feed off these plants (Backwell and d'Errico, 2001; Sponheimer et al., 2005a; Lee-Thorp et al., 2012; Lesnik, 2014). In 22 specimens analysed, there was a range of C4/CAM:C3 ratios from 61 to 91 per cent, meaning that these individuals clearly showed adaptation for C4/CAM foods, and probably a preference for these (maybe a preference for insects and animal meat); if C3 foods were available, they might also exploit these. To summarise, the overall, "macro" structure of teeth appears to hinge around the ability to cope with the masticatory load of the most challenging elements of the diet of the species involved. Local ("micro") variability within the species or genus may be driven by other factors.

Extant species-level dietary variability

Clearly, diet and feeding behaviours may influence intrageneric and intraspecific variability on a smaller scale, particularly when groups become isolated geographically and genetically and are exposed to gradually divergent dietary elements over time. In the case of gorillas, for instance, mountain gorillas (*Gorilla beringei beringei*) in the Virunga area tend to exploit wild celery, which is one of the few slightly less tough plants available throughout the year in the area, and, when available, bamboo, particularly the soft shoots (Vedder, 1984), with little or no fruit incorporated into the diet (Mc Neilage, 2001). In fact, *G. b. beringei* is probably the only true pure folivore in the genus (Watts, 1984). The diet of the Eastern lowland gorilla (*G. b. graueri*) is much more diverse than that of *G. b. beringei.* These gorillas are also predominantly folivorous, but with a moderate dependence on fruit (Casimir, 1975, Goodall and

Groves, 1977; Yamagiwa, 1992), depending on altitude. In higher elevations, the diet consists of about 90% leaves, pith and bark and vines (Casimir, 1975; Yamagiwa, 1992). If they need to use insects as fallback foods, they show a preference for ants (Yamagiwa et al., 1996). Their body size is the largest of the genus (Jungers and Susman, 1984). Eastern lowland and mountain gorillas are therefore classified as the same species, but their body size and their range of dietary variability is very different, mainly due to altitude. We would expect to see these differences mirrored in the teeth (Uchida, 1998a; Pilbrow, 2010). The Western Lowland gorilla species (*Gorilla gorilla gorilla* and *G. g. diehli*) have larger ranges, more variability in behaviour and habitat, significantly more variability in their availability of different foodstuffs and a much higher reliance on fruit, seasonally, than *G. beringei* (Williamson et al., 1990; Nishihara, 1992; Rogers et al., 1992; Remis, 1997).

It is not only in range and diet where differences between the Western Lowland Gorillas and the Eastern Lowland and Mountain Gorillas are apparent. Population numbers for *G. b. graueri* and *G. b. beringei* are perilously low. The higher population levels for *G. g. gorilla* appear to apply to past effective population numbers as well (Tocheri et al., 2016). A number of studies have informed the genetic substructure of the genus (for example, Thalmann et al., 2011; Scally et al., 2013; Prado-Martínez et al., 2013; Xue et al., 2015; Fünfstück and Vigilant, 2015). Thalmann et al. (2011) postulate that *G. g. diehli* ("Cross River" gorillas) only diverged from *G. g. gorilla* about 18 000 years ago and then went through a genetic bottleneck very recently. One or more bottlenecks have affected the genetic substructure of the Eastern species (Thalmann et al., 2007; Scally et al., 2012; Prado-Martínez et al., 2013; Roy et al., 2014; Xue et al., 2015), after the split

between *G. g. graueri* and *G. b. beringei,* some 10 000 years ago. These bottlenecks, in populations with already low numbers, have caused significant inbreeding (Xue et al., 2015), further reducing within-group variability. The main split between the two species, *G. gorilla* and *G. beringei* goes back to some time between 1.2 and 3 million years ago, although there is believed to have been some low levels of gene flow between the two species until about 200 000 - 800 000 years ago (Thalmann et al., 2007). It is expected that *G. g. gorilla* would reflect higher variability in tooth shape differences than would be predicted for *G. beringei* subspecies, due to higher variability in genetic structure, in geographical range and in variability of diet (type and number of foodstuffs exploited), over and above the size differences observed between males and females due to sexual dimorphism.

In the context of chimpanzees, *Pan troglodytes* consists of (currently) four subspecies – the Western chimpanzee (*P. t. verus*), the Cameroon-Nigerian chimpanzees (*P. t. ellioti*), the Central chimpanzees (*P. t. troglodytes*) and the Eastern chimpanzees (*P. t. schweinfurthii*). The Western chimpanzee is behaviourally, genetically and morphologically very distinct from the other subspecies of chimpanzee that have been studied to the East of the Sanaga River. Genetically, there is a deep divergence between Western Chimpanzees and the other three subspecies, with molecular studies indicating a split at around 500 000 years ago (Gonder et al., 2011). To put this in perspective, *Pan paniscus* is believed to have diverged from *Pan troglodytes* around a million years ago (Hey, 2010; Prüfer, 2012), and after the Western Chimpanzees diverged, Central and Eastern Chimpanzees are believed to have continued as a single population until about 100 000 years ago (Hey, 2010, Gonder et al., 2011). Other molecular analyses confirm

the distinctiveness of *P. t. verus* and the homogeneity – even hierarchical nesting (Bjork et al., 2011) - between the other subspecies (Gagneux et al.,1999; Guy et al. 2003; Pilbrow, 2006; Gonder et al., 2006; Fischer et al., 2011). There are also some distinctive behaviours observed in some groups of Western Chimpanzees that are not observed in their cousins to the east, examples being a greater use of tools such as stones and clubs to pound nuts (Boesch and Boesch, 1990), the use of caves for sleeping (Pruetz, 2007), the construction of spears for hunting and playing in water (Pruetz and Bertolani, 2007), the ability to predict the behaviour of fire (Pruetz and LaDuke, 2010), and foraging at night-time (Pruetz and Bertolani, 2009). In respect of their diet, they also show a marked preference for eating termites, much more so than other chimpanzee subspecies (Bogart and Pruetz, 2011). Such are the stark differences between *Pan troglodytes verus* and the other common chimpanzee subspecies that there have been suggestions to elevate this subspecies to the level of species (Morin et al., 1994).

In respect of diets, the diversity of foodstuffs consumed variously among populations of *Pan* is very high. Nishida and Uehara (1983) reported up to 328 different plant foods alone consumed by a population of *P. t. schweinfurthii* in Tanzania, while in populations of *P. t. troglodytes,* estimates range from 174 to 285 plant foods (Hladik, 1977; Tutin and Fernandez, 1993). Variability in plant foods consumed by *P. t. verus* and *P. paniscus* appears to be more constrained, with estimates ranging from 60 to 110 plant species for *P. t. verus* (McGrew et al., 1988; Yamakoshi, 1988) and from 113 to 114 plant types consumed by two different populations of *P. paniscus* (Badrian and Malenky, 1984; Kano and Mulavwa, 1984). Although *P. t. verus* appears to have more restricted access to different plant foods than do the other *P. troglodytes* subspecies, these figures should be

considered in comparison to the highly restricted diets of mountain gorillas *(G. b. beringei*), who were found to consume only 38 plant species in one group and 53 plant types in another group (Watts, 1984). In fact, over 90% of the mountain gorilla diet is made up of only nine staple foods (Virunga gorillas) or 15 staple foods (Bwindi gorillas), with the remaining foodstuffs comprising less than 1% each of dietary intake (Rothman et al., 2007).

Deep genetic divergence and restricted dietary range, together with different habitat, should be expected to manifest themselves in tooth shape differences between *P. t. verus* and the remaining *P. troglodytes* subspecies (Pilbrow 2003, 2006), as well as in differing ranges of variability in shape, between species and subspecies. Regional differences in lower second molar shape between species and sub-species of *Gorilla* and *Pan* might therefore be attributed to differences in diet, habitat and genetic distance (Pilbrow, 2007, Uchida 1998a), but these differences are not as marked as in modern humans, despite lower genetic diversity between modern humans as compared to great ape species (Gonder et al., 1997; Prado-Martínez *et al.,* 2013). In the case of modern humans, molars are found to exhibit more marked intraspecific variability in occlusal crown surfaces (Kieser, 1990; Dykes, 2014), with some populations having extremely large teeth (megadonts) and others having very tiny teeth by comparison (microdonts), and within these general size ranges, there is often considerable shape variability as well (Hanihara and Ishida, 2005).

Molar reduction and diet

Of paramount interest, clearly, is the idea that tooth size and/or morphology is believed to be influenced largely by diet, and that changes in molar size and shape can be driven by adaptive changes (Daubert et al., 2016). Indeed, in the context of the hominin lineage, Brace (1979) has noted that a gradual reduction in molar size was observed in the Middle Pleistocene with later "classical" Neanderthals beginning to show moderate (15%) reduction in tooth size, which he attributed to meat consumption and cooking. Wrangham et al. (2003) also note tooth-size reduction as one of the biological adaptations to meat consumption and cooking. This rate of tooth-size reduction has increased dramatically, although differentially, in the case of modern humans over the past 12 000 years.

It is widely recognised that these significant levels of craniofacial size reduction, accompanied by tooth-size reduction have been linked to the transition to widescale agriculture in certain groups (Bailit and Friedlaender, 1966; Brace & Mahler, 1971; Sofaer, 1973; Brace et al., 1987; Corruccini et al., 1983; Corruccini, 1984; Larsen 1995; Dempsey and Townsend, 2001; Grine, 2002, 2005; Brown and Maeda, 2004; Pinhasi et al, 2007; Emes et al., 2011; Hodder, 2017; Ungar, 2017). Cultivation practices have been documented at a site called Ohalo II in Israel dating to 23 000 years before present (Snir et al., 2015). However, a transition to widescale farming began to take hold in earnest from about 12 Ka in the Southern Levant area (Banning, 1998; Weisdorf, 2005; Twiss, 2007). By this time, wild grains had been specifically selected for higher starch content and modern cereals and domesticated cattle breeds became the norm in these areas. Economies changed from hunter-gatherer communities to agriculture and progressively

to sedentism at different stages in the Near East, Anatolia, North Africa, Europe and ultimately the Far East, during the first millennia of the Holocene, a period known as the Neolithic.

With the transition to widescale agriculture, a number of physiological and genetic changes have taken place in the populations affected by this. At the molecular level, genes that code for starch consumption occur in numerous copies, strongly correlated to the amount of starch consumed. Hunter-gatherers have fewer copies of the AMY1 gene, whereas individuals from areas where a high-starch diet has been consumed over numerous millennia have high numbers of copies of this gene (Perry et al., 2007). With the adoption of dairy farming, the LCT gene that codes for the enzyme lactase, normally present in mammals only from birth until they are weaned, has persisted into adulthood in those communities where dairying was prevalent (Gerbault et al., 2015). This same pattern is observed in tooth enamel-coding genes. For instance, the gene ENAM is one of at least four genes that code for tooth enamel production, in this case producing enamelin, an enamel matrix. In a recent study (Daubert et al, 2016) comparing African-American teeth to those of Americans with European ancestry, approximately 50% of the African-American subjects retained the ancestral allele of the ENAM gene, while the group with European ancestry had a derived allele at a frequency of 96%. Those individuals with the derived allele also had teeth with thinner enamel. This interpreted as a case of adaptive evolution, on the basis that thick enamel in humans is associated with consumption of harder objects, requiring masticatory crushing and grinding; thinner enamel is an adaptation to soft diets (high-starch cereals, cooked and processed foods). The group with the ancestral allele had molars with larger crown length

diameters than those with the derived allele. While it is unsurprising to hear that Americans with relatively recent European ancestry might nearly all have a derived allele (presumably because this allele had already been fixed in these populations following the transition to agriculture in Europe, well before the migration to North America of the ancestors of the subjects in the study), it is interesting to note that approximately 50% of the African-American subjects had already lost the ancestral allele in the short period (comparatively speaking) since their ancestors had arrived in America and had modified their dietary intake. Another study (Horvath et al., 2014) found strong evidence for positive selection in four enamel formation-related genes, suggesting that transcription factors related to the genes would have the potential to regulate genes differentially according to adaptive needs, which would allow for rapid evolutionary changes in enamel thickness.

Further studies indicate that mandibles in mice demonstrate size variability due to differential bone remodelling, depending on diet (Anderson et al., 2014). These authors conclude that this remodelling is expected to enable the evolution of adaptive traits that would be heritable. In cases where a very soft diet was given, the mice experienced size reduction in their mandibles. Another study (Workman et al, 2002) found a link between genes affecting mandibles in mice and those regulating molar shape (based on centroid size), which might imply that as teeth develop, the size and width of the mandible itself might affect the size and shape of mandibular molars. Von Cramon-Taubadel (2011) observed that in modern humans, mandibles of hunter-gatherer communities have largely retained longer mandibles than their soft-cereal and highly-processed food-eating counterparts in populations that underwent an early transition

to agriculture. Corruccini et al., (1983) noted that young individuals, particularly those exposed to modern urbanised diets of foods that are heavily refined, had developed smaller, narrower palates than older individuals within the same community who had been raised on a traditional diet. The younger subjects also suffered from undesirable variability in their dental occlusion that was not typical of the older generation, due to dental overcrowding. Brace (1963, 1964) (Brace et al., 1987) proposed that a "probable mutation effect" was responsible for structural reduction in dentognathic features (teeth, mandibles, maxillae, facial muscles, etc.) as a result of cultural changes in human groups associated with the transition to agriculture, cooking and pottery use.

The indication seems to be that adaptation, both phenetic and genetic, can occur very rapidly under changing environmental factors (such as a reduction in masticatory load), resulting ultimately in a divergence in dentognathic sizes between those groups that have remained with a hunter-gatherer subsistence strategy as opposed to those populations who have been exposed to agriculture, industrialisation, and increasingly sedentary lifestyles in other areas of the world. On the other side of the scale, a number of Australian Aboriginal communities, who have continued with a hunter-gatherer or terrestrial forager subsistence strategy, have the largest molars of all modern *H. sapiens* (Campbell, 1925; Brace, 1980, Hanihara and Ishida, 2005).

In sum, non-neutral genetic adaptations seem to have occurred uniquely in modern *H. sapiens* as groups migrated into new environments and particularly as a transition to widescale agriculture took hold in the Near East, North Africa and Europe. During this Neolithic agricultural transition period, there was a rapid increase in new nucleotide

polymorphisms (DNA point mutations) in tandem with population size increases (Hawks et al., 2007). It is clear that unique factors have been driving physiological and molecular changes in our species. These should be taken into consideration when choosing extant species to stand proxy as extant analogues for palaeontological hominin species.

Diet type, diet variability, geographical range and the selection of analogues

It is possible to begin to reconstruct palaeoecologies and diets of fossil species (e.g. Peters, 2007; Reed & Rector, 2007), albeit in very broad brush strokes (Ungar, 2007b, 2017). Given that certain extant species are believed to have very similar diets and similar geographical ranges as those fossil species (e.g. for *A. afarensis,* Ryan & Johanson, 1989; Teaford & Ungar, 2000a; Ungar, 2004; Grine *et al.,* 2006, Estebaranz *et al.,* 2009), there would seem to be a case to be made for more robust assumptions as to which extant species might be better candidates as "analogue species" (proxies to represent within-species variability) for presumed fossil species than others. These assumptions can be further qualified by considering which extant species best represent analogous species for specific skeletal elements (Lee, 2005).

Palaeoanthropological modelling should take into account not just overall numeric or statistical ranges in size and shape variability, but all sorts of additional factors such as diet, population size, geographical range/habitat (Sept, 2007) and, as discussed above, changes in the degree of dependence on food technology (such as cooking and other processing technologies) (Wrangham, 2007). Table 2 illustrates diets among extant

species that are relevant to this study, which are normally used as proxies for fossil hominin species dental variability.

Table 2. Diet types of extant hominoid species typically used as analogue species.

Genus/species	Degree of sexual dimorphism in molars; description of morphology	Diet type % soft:hard foods
Gorilla spp.	HIGH. Preliminary research shows marked size difference in molar size but not molar shape between the sexes. Very steep cusps. Cusps more angled in relation to MD axis	Primarily C3 **Primarily folivores/frugivores** 46-54% fruit flesh *(G. g. gorilla*); 0.2-8% (*G. b. beringei);* 7-38% (*G. b. graueri*)
Pan troglodytes	LOW. Male lower M1s were generally smaller than females. No marked shape difference Less steep cusps. Medium angularity from MD axis.	Primarily C3 (up to 300 food types reported, including animal proteins, depending on species) **Primarily soft-object frugivores** 70-80% fruit flesh *(P. t. troglodytes;* 48% (*P. t. schweinfurthii);* 50-57% (*P. t. verus);*
Pan paniscus	LOW. Preliminary research shows little size or shape difference between the sexes. Less steep cusps. Medium angularity from MD axis.	Primarily C3 **Primarily soft-object frugivores** Approx. 57% soft fruits (relatively rich food sources available). In some groups (e.g. at Wamba), the % of soft fruits goes up to 83%
Modern *Homo sapiens*	GLOBALLY LOW. However, marked variability in both size and shape of molars between groups at the population level, dictated by geography (subsistence/diet type). Very flat cusps. Very balanced cusps, generally parallel to MD axis.	**Omnivores** Too varied to generalise. Hunter-gatherer groups have varied proportions of meat and plant foods consumed; Western diets have varied proportions of soft:hard foods, with a tendency towards consuming far more soft and ultra-refined high GI foods than hunter-gatherer societies.

(Following Smith, 1999, and using studies already cited above).

Palaeodiets – how diet is reconstructed in extinct hominin species

Different diets (type and variation in number of elements) within single genera and even species observable today are thus likely to affect tooth size and shape (compare *G. b. beringei,* which is almost completely folivorous, to *G. g. gorilla,* which has a high proportion of fruit in the diet and much more variability in the number of elements consumed). Diets are not necessarily dictated directly by the available foodstuffs within the range of the species living in a certain area, as witnessed by the differing behaviours of sympatric hominoids in Africa today (Stanford, 2006). When considering fossil hominin species, inferences about diet are even harder to make.

Palaeodiets are increasingly being reconstructed using a number of methodologies, some more informative or reliable than others. Firstly, inferences are made from morphology and biomechanics. As indicated previously, cusp patterns and slopes may indicate in broad brush strokes the principal diet type (insectivore, folivore, frugivore, etc.), or at least give an indication of fallback foods (e.g. Evans and Sanson, 1998; Berthaume, 2013, 2014; Berthaume et al., 2014). Biomechanics - strain gauges and bite forces – (e. g. Demes and Creel, 1988; Ravosa, 2000; Hylander, 2013; Taylor and Vinyard, 2013) have also been applied to the masticatory complex to infer diet type and hardness, but these biologically-based methodologies tend to provide information at the "macro" level, rather than tease out nuances on a day-to-day level.

Tooth microwear (e. g. Walker, 1981; Puech et al, 1984; Ryan and Johanson, 1989; Ungar et al., 2006a, b; Ungar et al., 2008; Ungar, 2011; Martínez et al., 2016) can

distinguish between extremes of diet type – for instance, hard food consumption, which is marked principally by pits that render the surface of the enamel "complex", and leafy food consumption, which leave striations in parallel lines across the tooth and are described by researchers as a pattern indicative of "anisotropy" (Scott et al., 2005). Microwear also has its limitations, however. While it can be useful for gaining information about the last meal (or penultimate meals), anything further back into the past is likely to have been obliterated by more recent scratches (Grine, 1986). A further complicating factor is that some plants (e.g. underground storage units, tubers and roots of plants) would probably be consumed alongside the dirt and grit from the soil from which they were taken, and the pitting and tooth damage left by the quartz crystals and other hard items might mask the information provided by the foodstuff itself (Lucas et al., 2013), which would result in false inferences about the diet.

Other indirect lines of evidence (cut-marks on bones and other fossil site refuse, prevalence of browsers versus grazers at fossil hominin assemblages, coprolites and other means of reconstructing past palaeoecologies) provide good insights into foodstuffs that were available to hominins at different stages of history and in different locations, but an association is not always easy to prove. The availability of foodstuffs does not always guarantee that the species inhabiting the areas in question made full use of the range of plants and animals found there, as noted already in the case of sympatric gorillas and chimpanzees (Tutin et al., 1991, 1993; Yamagiwa et al., 1992; Stanford, 2006; Yamagiwa & Basabose, 2009).

More informative still would be methodologies that include chemical, and particularly isotopic, analyses to infer the inclusion of certain foodstuffs in the diet. Some recent studies have provided information about diet from analyses of dental calculus (Henry et al., 2010, 2012; Henry, 2010; Odes, 2013), but again, the phytoliths and traces of starches that might be recovered from calculus must be treated as a "Last Supper" clue to what the specimen must have ingested recently. Of great importance to researchers is the use of stable carbon isotopes and ratios of strontium and barium in relation to calcium in teeth. The more herbivorous an animal, the higher the levels of barium and strontium in their tissues. Animals feeding on the meat of these herbivores would preserve a lower ratio, and so on up the food chain. Recently, stable carbon isotope studies have provided great insights into fossil hominin diets, as mentioned above in the context of the diet of *Paranthropus boisei.* Modern chimpanzees and gorillas ingest almost purely C3 foods (tree- and bush-related plants, such as leaves, bark, fruit, nuts, etc.). Modern humans make use of C4 grasses and foodstuffs to a much larger extent (e.g. corn and sugar cane, and the animals that feed from C4 grasses). Hominins over time have progressed from relying upon a purely C3-based diet (e.g. *Ardipithecus ramidus*) to a diet that incorporates more or less of a C4-based component (White et al., 2009).

The diets of fossil hominin species included in this study

Recent stable isotope studies into the diet of *Australopithecus afarensis* produced some interesting, and variable, results (Wynn et al., 2013, 2016). Of the 20 specimens studied in 2013, the ratios between C3 and C4 foodstuffs was significantly more variable than

would be expected, and there seemed to be no statistically significant trend through time in the Hadar Formation. Even within a very narrow stratigraphic layer, the variability of dietary intake between these types of food was extremely high. This level of "dietary flexibility" was described as unusual (Wynn et al., 2016), particularly compared to other mammals in the area during the timeframe in consideration. This lack of a direct temporal trend or regional preference for C3 or C4 foods between specimens attributed to *A. afarensis* invites further consideration when examining patterns of variability in tooth size and shape.

Diets of *A. africanus* and *P. robustus* at first glance might be considered to have been very similar with respect to their stable carbon isotope ratios, at least on average (about 40% C3:non-C3 foods consumed by *A. africanus* and 35% by *P. robustus*) (Sponheimer et al., 2005a), although microwear on the teeth would indicate that their diets did differ, with *P. robustus* consuming more hard foods (Ungar et al., 2010). Some of this non-C3 diet may have been made up by termites, having a mixed C3:C4 signal, and rhizomes and tubers of plants. However, as more specimens are added to the analysis, there appears to be a wider range of readings of ratios of C3:non-C3 foods consumed by specimens attributed to *A. africanus*, from almost purely C3 plants to a mixture of predominantly non-C3 plants. In fact, the range for *A. africanus* (spanning the period from about 2.7 Ma to 2.1 Ma and from two different sites, Makapansgat and Sterkfontein) rivals the wide range of readings found for *A. afarensis* (Sponheimer and Lee-Thorp, 1999; Sponheimer et al, 2005a; van der Merwe et al., 2008; Lee-Thorp et al., 2010; Sponheimer et al., 2013).

The C3:non-C3 values of *P. robustus* are slightly less variable, although 22 of the 23 specimens analysed were all from one site, Swartkrans, while the lone other was from nearby Kromdraai (Lee-Thorp et al., 1994; Lee-Thorp et al., 2000; Sponheimer, et al., 2005). The massive Gondolin molar, currently attributed to *P. robustus,* has not been included into these studies as yet, but it will be interesting to see whether its diet differed significantly from the other *P. robustus* specimens from Swartkrans. Interestingly, the range of C3:non-C3 values for *P. robustus* do not overlap at all with those from *P. boisei,* which, as noted earlier, averaged 77% non-C3 foods, with a range from 61% to 91%.

Disregarding differences in range of C3:non-C3 values between *A. africanus* and *P. robustus,* and returning to the fact that the average ratio was similar for both (35-40%), another possible point of similarity is the strontium-calcium ratios. In one study (Sponheimer et al, 2005b), both species showed higher ratios than other mammals, including baboons, which would imply that their intake of meat would be similarly lower, or certainly no more, than that of baboons. However, a later analysis of both strontium and barium ratios to calcium (Balter et al., 2012) noted that there was more variability in the ratios for *A. africanus* than there was for *P. robustus,* which again implies greater variability in the diet (as already noted). This study suggests that *A. africanus* may indeed have consumed meat as well as leaves and fruits, perhaps seasonally, while *P. robustus* had a more restricted diet, probably emphasising woody plant products, and thus was indistinguishable from the diet of browsers. Balter et al. (2012) also analysed the teeth of some early *Homo* specimens, found in South Africa,

and unlike *P. robustus,* these individuals appear to have preferred a diet that included more meat.

Certainly, this confusing picture of dietary variability (*A. africanus*), and dietary restriction *(P. boisei* towards plant foods, mainly C4 plants; Early South African *Homo* towards meat) has been noted in palaeoenvironmental studies. There was an important transition from the Pliocene to the start of the Pleistocene (about 2 Ma) that saw closed woodland areas transform to more open savanna land, both in East and South Africa, due to increasing aridity (Reed, 1997). The earliest *A. africanus* specimens came from Makapansgat, (3.2-2.7 Ma), where most of the mammals in the assemblage were C3-eaters with some grazers (Reed, 1997), and the list of species would indicate some grassland as well as riparian wooded areas and bushland. Likewise, in the (early) Sterkfontein environment from about 2.8 to 2.6 Ma, a mosaic ecology is indicated from the preserved plant fossils, including dense forest areas that would be more typical today of Central Africa (Bamford, 1999), which also indicates that there must have been reasonable amounts of rainfall during this period. Member 4, from where most of the specimens in this study are taken, is dated at 2.6 to 2.4 Ma. The mammals collected from this assemblage indicate that the area would have been covered by open woodland with bushland and thickets (Reed, 1997). Some open savanna may also have been present. By the time that later fossils were found at Swartkrans (1.8 – 1.2 Ma) and Kromdraai (1.5 to 1.0 Ma) in deposits dominated by *P. robustus*, but with some early *Homo* also present, there must have been an expansion of grassy areas, with scrub woodland, or wooded grasslands, accompanied by denser woodland or forest along the river and associated reed beds that runs through the Swartkrans site (Reed, 1997). This added to the mosaic-

type environment in the Pleistocene, which was also occurring in East Africa (Lee-Thorp et al, 2007).

The diet of *A. sediba* at approximately 2 Ma seems to have been almost totally biased towards C3 foods, which is quite surprising, given the apparent availability of C4 foods during the time period in question (Henry et al., 2012). While *H. naledi* has not yet been subjected to stable carbon isotope analyses or strontium/barium:calcium analyses, a recent analysis by Towle and colleagues (2017) has identified an unusual amount of pitting, visible macroscopically on around 44% of the teeth, which is higher than other species exhibited (specifically, *A. africanus, P. robustus* and extant chimpanzees, gorillas and baboons). The excessive amount of damage to the teeth suggests a diet containing grit – perhaps grit from accompanying soft foods such as tubers or root products – and that this diet was significantly different to those of other hominins from South Africa. There were some modern human samples that seemed to have damage levels as high as or higher than those of *H. naledi* (Inuit and a sample from Italy from the 2nd to 3rd century BP), but the damage, while extensive, was not comparable in nature. Further studies are pending.

The main dietary novelty that is evident with later and later species of *Homo* is the increased consumption of meat over time, which is accompanied by a steady reduction in tooth size (Guatelli-Steinberg, 2016). According to studies of cut-marks (Potts et al., 1981; Shipman, 1986), there is evidence of scavenging of carcasses from carnivores, as cut-marks made by tools are superimposed over carnivore tooth marks. Hunting was also probably prevalent at the same time (Ferraro et al., 2013), and was certainly

prevalent by the time *H. erectus (ergaster)* appeared on the scene. The use of fire and cooking is contested, but certainly, even if *H. ergaster* was not capable of starting fire, there is evidence that fire might have been harnessed and controlled at least, e.g. at Wonderwerk cave, dating to about a 1 Ma (Berna et al., 2012). In this study, we would therefore expect to see tooth size reduction evident in hominin lower second molars as time progresses, and probably some between-species variability in shape.

CHAPTER THREE – MATERIALS AND METHODS

3.1 MATERIALS

In order to quantify variability in the post-canine dentition of any one extant species, it is useful to obtain as large a sample as possible for each species. To this end, permission was obtained to access the extensive Pilbrow Database of images of the dentitions of gorilla and chimpanzee species (Pilbrow, 2003), to which was added a collection of images of modern human and extinct hominin lower molars, collected over four years from various collections around the world. Lower second molars were selected to describe variability in each species' post-canine dentition, as these are usually well-represented in museum collections, are less worn than first molars and are less variable than third molars.

3.1.1. Summary of specimens included in the study, source, etc.

A full list of specimens included in this study is given in Appendix 1, together with a list of the museum collections where the specimens were photographed. These are summarised in Table 3 and Table 4, relating to a total of 841 occlusal-view images of lower second molars. This total comprises images of lower second molars of *Gorilla,* (254), *Pan* (255), *Homo sapiens* (269) and fossil hominin specimens (63). Specimens of lower second molars of *Gorilla* and *Pan* are listed by species and subspecies (the level at which fossil hominin species are typically analysed) and not by population, but it should be noted that at the population level, *Gorilla* is well represented, with images from all 14 of the population groups recognised by Pilbrow (2010), and that 15 of the 16

population groups of *Pan* recognised by Pilbrow (2006) are represented by images of lower second molars in this study: while there were no usable lower second molar images for population 3 of *Pan,* a small population in Nigeria attributed to *P. t. ellioti,* this subspecies is still represented by population 4*.* In the case of modern *H. sapiens,* a list of 241 specimens (included in the comparative analyses of extant hominoids) is, however, provided at the population level, together with a breakdown by subsistence strategy, as these factors are used to inform additional analyses of molar size and shape variability, unique to modern humans. A further 28 specimens, all from Great Britain (not included in the main analyses of extant species' lower second molar variability) are listed by historical time period, and these form the basis of a separate analysis of tooth size and shape changes over time.

Three fossil species (*A. afarensis, A. africanus* and *P. robustus*) represent the main focus of this present study. Limited numbers of specimens from *P. boisei, A. sediba, H. naledi, "*Early *Homo"* and *H. ergaster* are also included. In all cases, even in instances where access to other specimens was limited for various reasons, the species holotype, or a mandibular proxy for the holotype, has been able to be included, to represent a "typical" lower second molar for these species. These specimens are instructive for comparative purposes even though sample sizes were limited: in cases where a specimen representing one of the three principal fossil hominin species fails to group with its allocated species, it is informative to see whether it "trends" towards the holotype (or proxy thereof) of another hominin species.

Table 3. Summary list of specimens of extant species included in this study, with the ratio of males to females per species/subspecies.

Species / Sub-species	Number of specimens	Sex ratio M:F	Source collections[1]
G. b. beringei	25	48:52	BMNH, MNHN, MCZ, RG
G. b. graueri	50	60:40	BMNH, FMNH, ZMB
***G. beringei* total**	**75**	56:44	
G. g. diehli	10	90:10	BMNH, ZMB
G. g. gorilla	169	63:37	AMNH, AS/Z, BMNH, FMNH, MNHN, MCZ, PCM, RG, USNM, ZMB, ZSM
***G. gorilla* total**	179	64:36	
***Gorilla* total**	**254**		(14 of 14 total populations of *Gorilla* represented)
P. t. verus	43	42:58	AS/Z, AMNH, BMNH, MNHN, MCZ, PM, RG, USNM
P. t. ellioti	5	60:40	ZMB, PCM
P. t. troglodytes	108	39:61	AS/Z, FMNH, MNHN, PCM, RG, USNM, ZSM
P. t. schweinfurthii	58	53:47	RG, USNM, ZMB
***P. troglodytes* total**	214	44:56	
P. paniscus	41	39:61	RG, MCZ
***Pan* total**	**255**		(15 of 16 total populations of *Pan* represented)
Modern *H. sapiens*	**269**	60:40	UW-DART*, IZK, MNHN-MDH, DW-CAM

***H. sapiens* (recent) by population:**	Number	Subsistence strategy
KhoeSan	16	Hunter-gatherer
Babinga	7	Hunter-gatherer
SA Bantu-language groups	23	Small-scale agriculturalists
Teita	8	Small-scale agriculturalists
Australian Aboriginal	27	Hunter-gatherer
Polynesian	11	Mixed/horticulturalists
New Guinean	16	Mixed/horticulturalists
East Asian	16	Mixed/pastoralists
South Indian	10	Mixed/unknown
South Asian	5	Mixed/unknown
Balkan	18	Agriculturalists
Semitic	11	Early (Intensive) Agriculturalists
Mesopotamian/Iranian/Turkish	9	Early (Intensive) Agriculturalists
Western European	35	Intensive agriculturalists
Amerindian	18	Later agriculturalists
Inuit	11	Fisher-gatherer
Subtotal	241	
***H. sapiens* - historical (not included in "extant hominoid" analyses)**		
Neolithic British	11	(time series specimens)
Anglo-Saxon British	11	
Medieval British	6	
Subtotal	28	
Grand total (*H. sapiens*)	**269**	

[1] All collections/museums listed for species of *Gorilla* and *Pan* were visited by Dr V Pilbrow (Pilbrow, 2003). Collections listed for Modern *H. sapiens* and for extinct hominin species were visited by S J Dykes. All specimens in this study are represented by occlusal-view images of lower second molars.

* Blanket Ethics Waiver Number W-CJ-14064-1

Table 4. List of extinct hominin specimens included in this study.

Specimen #	Species (Current conventional taxonomic allocation[2])	Original /Cast[3]	Source Collection/Museum[1]
LH 4	*A. afarensis*	Original	KNM
LH 23	*A. afarensis*	Cast	WITS
AL 207-13	*A. afarensis*	Cast	WITS
AL 333-59	*A. afarensis*	Cast	WITS
AL 333-W27	*A. afarensis*	Cast	WITS
AL 241-14	*A. afarensis*	Cast	WITS
AL 333-W57	*A. afarensis*	Cast	WITS
AL 333-W60	*A. afarensis*	Cast	WITS
AL 145-35	*A. afarensis*	Cast	WITS
AL 277-1	*A. afarensis*	Cast	WITS
AL 288-1	*A. afarensis*	Cast	WITS
AL 400-1A	*A. afarensis*	Cast	WITS
Al 128-23	*A. afarensis*	Cast	WITS
AL 188-1	*A. afarensis*	Cast	WITS
AL 266-1	*A. afarensis*	Cast	WITS
AL 333-W1	*A. afarensis*	Cast	WITS
Stw 404	*A. africanus*	Original	WITS
Stw 560e	*A. africanus*	Original	WITS
Stw 519	*A. africanus*	Original	WITS
Stw 412	*A. africanus*	Original	WITS
Stw 109	*A. africanus*	Original	WITS
Stw 327	*A. africanus*	Original	WITS
Stw 384	*A. africanus*	Original	WITS
Stw 540	*A. africanus*	Original	WITS
Stw 308	*A. africanus*	Original	WITS
Stw 555	*A. africanus*	Original	WITS
Stw 234	*A. africanus*	Original	WITS
Stw 498	*A. africanus*	Original	WITS
MLD 18	*A. africanus*	Original	WITS
MLD 2	*A. africanus*	Original	WITS
Sts 52b	*A. africanus*	Original	WITS
MLD 24	*A. africanus*	Original	DITS
TM 1517	*P. robustus*	Original	DITS
SK 37	*P. robustus*	Original	DITS
SK 6	*P. robustus*	Original	DITS
SK 23	*P. robustus*	Original	DITS
SK 25	*P. robustus*	Original	DITS
SK 55	*P. robustus*	Original	DITS
SK 1587a	*P. robustus*	Original	DITS
SK 1	*P. robustus*	Original	DITS
SK 5	*P. robustus*	Original	DITS
SK 843	*P. robustus*	Original	DITS
SKW 5	*P. robustus*	Original	DITS
GDA 2	*P. robustus*	Original	WITS

Peninj 1	*P. boisei*	Original	TNM
KNM-ER 15930	*P. boisei*	Original	KNM
MH 1	*A. sediba*	Original	WITS
MH 2	*A. sediba*	Original	WITS
UW 101-1261	*H. naledi*	Original	WITS
UW 101-001	*H. naledi*	Original	WITS
UW 101-377	*H. naledi*	Original	WITS
UW 101-1142	*H. naledi*	Original	WITS
UW 101-507	*H. naledi*	Original	WITS
UW 101-145	*H. naledi*	Original	WITS
UW 101-789	*H. naledi*	Original	WITS
OH 7	*H. habilis*	Original	TNM
OH 16	*H. habilis*	Original	TNM
KNM-ER 1802	*H. rudolfensis*	Original	KNM
KNM-ER 60000	"Early *Homo" (H. rudolfensis?)*	Cast	WITS
SK 15	"Early *Homo"*	Original	DITS
KNM-ER 992	*H. ergaster (erectus)*	Original	KNM
KNM-ER 806b	*H. ergaster (erectus)*	Original	KNM
OH 22	*H. ergaster/heidelbergensis*	Original	TNM
TOTAL	**63 specimens**		

[2] Species allocations according to current literature and summarised in many instances in Wood (2011).

[3] In cases where access to original specimens was limited by the collections managers involved (permits did not cover full access to all original specimens or prior required permissions from numerous individual team leaders were difficult to obtain), high-quality casts have been used, where available. In all instances, occlusal crown perimeters were well established in the images. *Australopithecus afarensis* was consequently mainly represented by high quality casts, and other species were limited in sample size, but were still included as they were represented by species holotypes or proxies thereof.

Table 5. List of abbreviations for museums/collections.

Abbreviation	Collection / Museum
AMNH	American Museum of Natural History, New York
AS/Z	Anthropologisches Institüt und Museum der Universität Zürich-Irchel, Zürich
BMNH	British Museum of Natural History, London
DITS	Ditsong Museum, Pretoria
DW-CAM	Duckworth Collection, Cambridge University
FMNH	Field Museum of Natural History, Chicago
IZK	Iziko Museum, Cape Town
KNM	Kenya National Museum, Nairobi
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHN-MDH	Musée de L'Homme, (part of MNHN), Paris
PCM	Powell-Cotton Museum, Kent
PM	Peabody Museum, Cambridge
RG	Musée Royal de L'Afrique Centrale, Tervuren, Belgium
TNM	Tanzania National Museum, Dar est Salaam
USNM	United States National Museum, Washington, D.C.
UW-Dart	Raymond Dart Collection, Anatomical Sciences, University of the Witwatersrand, Johannesburg
WITS	University of the Witwatersrand fossil collection
ZMB	Zoologisches Museum, Berlin
ZSM	Anthropologische und Zoologische Staassammlung, Münich

3.2 METHODS

3.2.1 Background to a mathematically-derived landmarking methodology for shape-and-size analyses

Shape-and-size analyses based on 2D images of the occlusal crown surface of teeth typically rely on the identification of anatomical features such as grooves and cusp tips to provide sites for enamel surface landmarks and/or points from which to calculate relative lengths and angles. In some instances, these surface features are all but obliterated, and the researcher faces the possibility of yet further reductions in sample sizes, which is exacerbated when the specimens in question are highly significant—for example, the holotype (type specimen), or proxy thereof, of a palaeontological species.

The method of landmarking designed specifically for this study capitalises on the few anatomical landmark sites that remain discernible, despite potentially considerable wear. Sites along the perimeter of the lower molar crown in the occlusal view are featured, namely the points where grooves separating the five main cusps intersect with the perimeter edge of the tooth in the image. These intersections are consistently visible despite high levels of surface wear, and convey relevant diagnostic information for the purposes of analysing tooth shapes and sizes. This study uses a mathematical approach to landmarking lower second molars, wherein landmarks are initially placed anatomically, using the main inter-cusp groove intersections at the perimeter (Type I landmarks) (Dryden & Mardia, 1998, pp. 3-4), and thereafter using mathematically-derived landmarks (Type III landmarks) (Dryden & Mardia, 1998, pp. 3-4) at points on and around the crown surface in the image. Collectively, these landmarks relay balanced

information regarding general cusp orientations, centre points, outline shapes and diagnostic diameter measurements.

The chosen mathematical approach was primarily developed to enable worn teeth to be included in a comparative analysis of tooth shape and size, which has the important result of enlarging the fossil and modern human sample to include specimens that would be otherwise excluded, and of allowing for better balance between males and females in a sample, where one sex is represented predominantly by worn teeth. Because it relies on easily identifiable points (visually or mathematically) on and around the surface enamel in the tooth image, and requires no need to identify cusp peaks and cristids, etc. from 2D images, it has the additional advantage of being more automatic in nature, and, therefore, of being reasonably rapid and fully repeatable. Being less subjective in identifying anatomically-based landmark sites and with only five of these to identify, there is also less chance of inter/intra-observer error in the placement of landmarks. The use of landmarks additionally creates flexibility in the selection of analyses to be used: from geometric morphometric methods based on landmarks to statistical analyses based on raw measurements or Euclidean distances. It is also adaptable to all mandibular molar teeth (and ultimately, maxillary molars) belonging to extant hominoid and extinct hominin species, worn or unworn. Sample sizes may also be enlarged by using low-resolution photographs from published data (e.g. while photos from non-recent seminal papers and books pixelate on enlargement, this methodology accommodates the lack of definition on the enamel surface in the image).

3.2.2 Image Capture

Images used in this present study were captured using 2D photography, and identical methods were used by Pilbrow (whose database provided all the African great ape images used for this study) and by Dykes (all hominin and modern human molar images): a Nikon digital camera was mounted on a tripod with a macro lens placed vertically above the specimen in question, and orthogonal to the occlusal enamel surface. An adjustable scale bar was placed adjacent to the enamel surface, in the same plane, so that both the enamel surface and the scale bar were in the same plane of focus. The specimen was located at the centre of the frame to avoid parallax errors (Busch, 2006). To ensure that each tooth was correctly oriented in the image, the cervical plane of the tooth was carefully oriented horizontally before image capture. Amira® 3D software established that any slight differences (be they intra-observer or inter-observer) in judging this cervical plane (which would be manifested primarily in differences in tilt of the tooth across the buccolingual axis) resulted in no significant difference in outputs up to 4 degrees of tilt either way (see Dykes, 2014, paragraph 3.3.2.3 and Figure 3.2). A further sensitivity analysis was carried out to measure differences in the capturing of images (inter/intra-observer) incurred by moving the position of the lens slightly away from a perfectly orthogonal position above the centre of the tooth. Three similar 2D photographs which had been captured of the same tooth on different occasions from slightly varied positions above the tooth were individually inserted into a 3D image of the same tooth using Amira® software, and the differences between the images were measured along the x, y and z planes. There was very little difference between the tilt of the images (0.014 degrees along the x plane, 0.107 degrees along the y plane and 0.098 degrees along the z plane).

3.2.3 Image Processing

Before landmarking began, and in keeping with the format used for previous research (Dykes, 2014), all teeth were standardised to appear as left-side teeth (right-side teeth were mirror-imaged) using GIMP® software. In each image, using horizontal and vertical guide lines in GIMP®, the buccal edge of the tooth was oriented downward in the image, the lingual edge upward, and the longitudinal or mesiodistal (MD) axis of the tooth [Goose (1963); Wood (1991)] runs horizontally in the image from the mesial edge (left side of the image) to the distal edge (right side of the image) – in many instances, slight rotation of the image was required to achieve this alignment. The perimeter outline was reconstructed digitally in Adobe Illustrator®, as required, to correct for inter-proximal wear (or other small areas of damage), according to the protocols used by Wood and Abbott (1983), using the 100% smoothing tool to extend the curvature of the tooth in the damaged areas, computationally, in order to limit the potential for observer error (see Appendix 2 for further details). Thereafter, a horizontal "bounding box" was superimposed around the perimeter outline of the tooth to provide proxies for the "corrected" MD diameter and the "maximum" buccolingual (BL) axis (Wood and Abbott, 1983, p. 202), which is taken at 90° to the MD axis (Goose, 1963). The bounding box also serves to locate the geometric centre of the tooth and to mark MD and BL measurement points for input into the analysis. An inter-observer test was conducted to quantify the error incurred if there were slight differences in calculating the orientation of the bounding box and the geometric centre of the tooth. The percentage errors for the x and the y coordinates for locating the tooth centre ranged from 0.066% to 0.588% with an average of 0.295% along the x axis and from 0.189% to 0.388% with an average of 0.316 % along the y axis.

3.2.4 Landmarking

For each tooth, the five inter-cusp grooves were located where they intersected the perimeter of the crown in the occlusal view, and from these five anatomical landmarks, the remaining landmarks were calculated and placed as described in Figure 2 and Table 6. The rationale behind the placement of the chosen landmarks was to find a balance in the number of landmarks so as to identify optimally:

a) overall size and shape proportions (mesiodistal and buccolingual diameters as measured from points around the bounding box);
b) perimeter shape, which has been found to be diagnostic, especially in the case of worn teeth (Benazzi et al., 2012);
c) cusp size, shape and orientation relative to the geometric centre of the tooth crown (in occlusal view) (landmarks specifically placed to trace the orientation of the cusps from the centre of the tooth via the centres of the cusps to the centre point of each cusp arc at the perimeter of the tooth);
d) buccal development groove, that is, a separation between the hypoconid and the protoconid along the buccal perimeter edge of the tooth (*cf*. Table 1 and Figure 3). This groove is quantifiable using angles and measurements along either side of the groove when observed in the occlusal view. In gorillas, this groove is highly pronounced and gives an indication of the sharpness of the two principal buccal cusps. In modern humans, on the other hand, the perimeter of the tooth crown is often devoid of any buccal development groove, instead being smoothly straight or even concavely rounded. *Pan* species are intermediate to gorillas and modern humans in this regard;

e) orientation of the mesial cusps (metaconid and protoconid) and, particularly, the distal cusps (hypoconid and entoconid) in relation to the longitudinal axis of the tooth (mesiodistal axis) and in relation to each other. This is also key to differentiating between species, subspecies and population-level groups. As shown in Figure 2, landmarks were placed to mark the orientation of centres of the mesial cusps and of the distal cusps. From these cusp centres, a line was extended to the lingual edge and the buccal edge of the tooth, passing through these cusp centres (yellow dotted line in Figure 2), to provide buccolingual measurements across both parts of the tooth (mesial and distal cusp BL measurements – landmarks 12 and 18 on the mesial side, landmarks 13 and 17 on the distal side. In gorillas and paranthropines, the hypoconid is more buccally-oriented than buccodistally-oriented: this gives the distal cusps a more acute angle through the mesiodistal axis than would be the case for chimpanzees, most australopiths and specimens of the genus *Homo.* The ratio of buccolingual diameter measurements across the mesial cusps and across the distal cusps differs at the genus level and can be diagnostic (gorillas and paranthropines tend to have a higher measurement across the distal cusps than across the mesial cusps; australopiths typically have a higher mesial buccolingual diameter than distal buccolingual diameter);

f) orientation and extent of the hypoconulid, which is linked to the orientation of the hypoconid. *Gorilla*-type patterns and *Pan/Homo*-type patterns are identifiable on fossil hominin molars, as depicted in Figure 1 below, and these features were included in the measurements and angles that formed the basis for the DFA. An australopith tooth typically has a distally-oriented hypoconulid and a bucco-distally oriented hypoconid (*Pan*-type orientation); a paranthropine

tooth, on the other hand, typically has a buccally-oriented hypoconid and a bucco-distally oriented hypoconulid (*Gorilla*-type orientation).

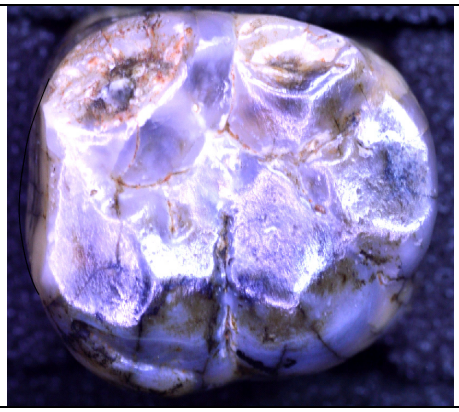
	
Australopithecus tooth: typically follows the chimpanzee pattern in the way that the cusps are oriented; the BL diameter measurement tends to be larger across the mesial cusps than across the distal cusps. Hypoconid is bucco-distally oriented. Hypoconulid is distally oriented.	*Paranthropus* tooth: typically, the hypoconid is more buccally oriented as in the gorilla cusp orientation pattern. The entoconid may be split (C6 tends to appear to form part of the entoconid). BL diameter measurement tends to be greater across the distal cusps than across the mesial cusps.

Figure 1. Typical australopith and paranthropine lower second molars showing some diagnostic differences between the two genera.

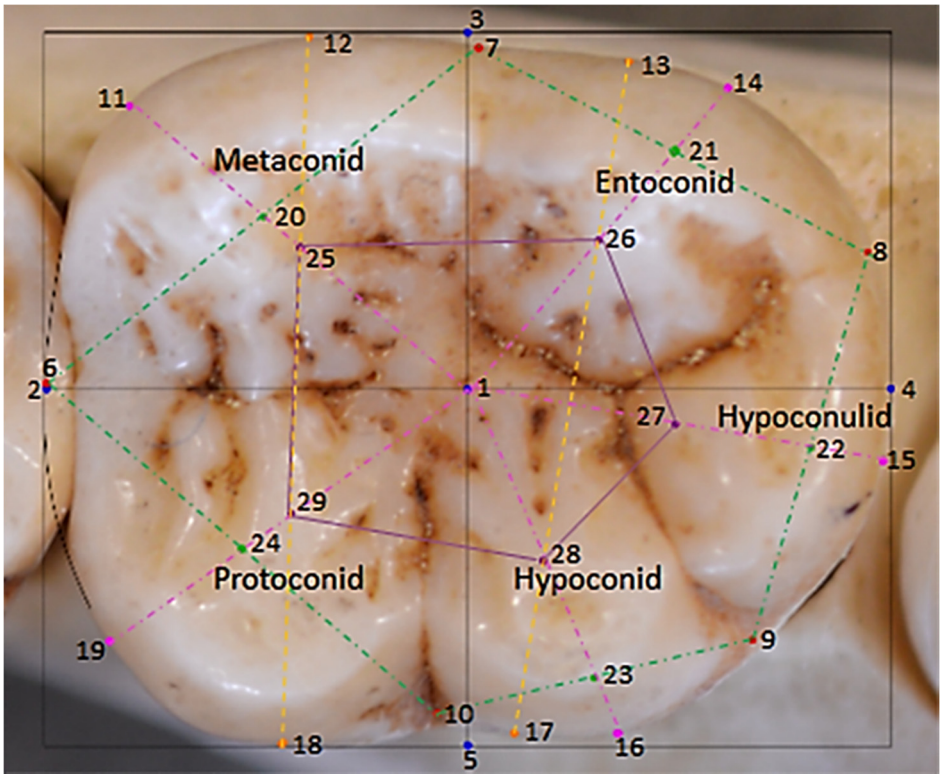


Figure 2. Landmarks placed mathematically on and around the surface enamel in the image (*P. t. troglodytes* lower second molar).

Table 6. Placement of landmarks.

Bounding box enclosing tooth (Type III landmarks):		*Midlines of cusps* (Type III landmarks)*:*	
1	Geometric centre of tooth	20	Midpoint between landmarks 6 and 7
2	Mesial-most edge of the MD axis	21	Midpoint between landmarks 7 and 8
3	Lingual-most edge of the BL axis	22	Midpoint between landmarks 8 and 9
4	Distal-most edge of the MD axis	23	Midpoint between landmarks 9 and 10
5	Buccal-most edge of the BL axis	24	Midpoint between landmarks 10 and 11
Intersections of cusp grooves at perimeter (Type I landmarks):		*Mathematical "cusp centres"* (Type III landmarks)*:*	
6	Between metaconid and protoconid	25	Metaconid between landmarks 1 and 11
7	Between metaconid and entoconid	26	Entoconid between landmarks 1 and 14
8	Between entoconid and hypoconulid	27	Hypoconulid between landmarks 1 and 15
9	Between hypoconulid and hypoconid	28	Hypoconid between landmarks 1 and 16
10	Between hypoconid and protoconid	29	Protoconid between landmarks 1 and 19
Intersections of cusp midlines at perimeter (Type III landmarks):		*Perimeter markers – mesial and distal cusps* (Type III landmarks):	
11	Midpoint of cusp arc of metaconid at the perimeter edge	12	Perimeter marker for measuring mesial cusp breadths and angles (lingual edge)
14	Midpoint of cusp arc of entoconid at the perimeter edge	18	Perimeter marker for measuring mesial cusp breadths and angles (buccal edge)
15	Midpoint of cusp arc of hypoconulid at the perimeter edge	13	Perimeter marker for measuring distal cusp breadths and angles (lingual edge)
16	Midpoint of cusp arc of hypoconid at the perimeter edge	17	Perimeter marker for measuring distal cusp breadths and angles (buccal edge)
19	Midpoint of cusp arc of protoconid at the perimeter edge		

For purposes of reproducibility, additional details, regarding the rotation of images of misaligned teeth, the correction of tooth wear and the interpretation of five cusp intersections in cases where some cusps seem split, or where a fifth cusp is not readily discernible, are provided in Appendix 2.

Once the landmarks were sited, 19 variables of size, inter-landmark distances, angles and ratios were calculated to provide inputs into a discriminant function analysis (DFA), as illustrated in Figure 3 and described in Table 7.

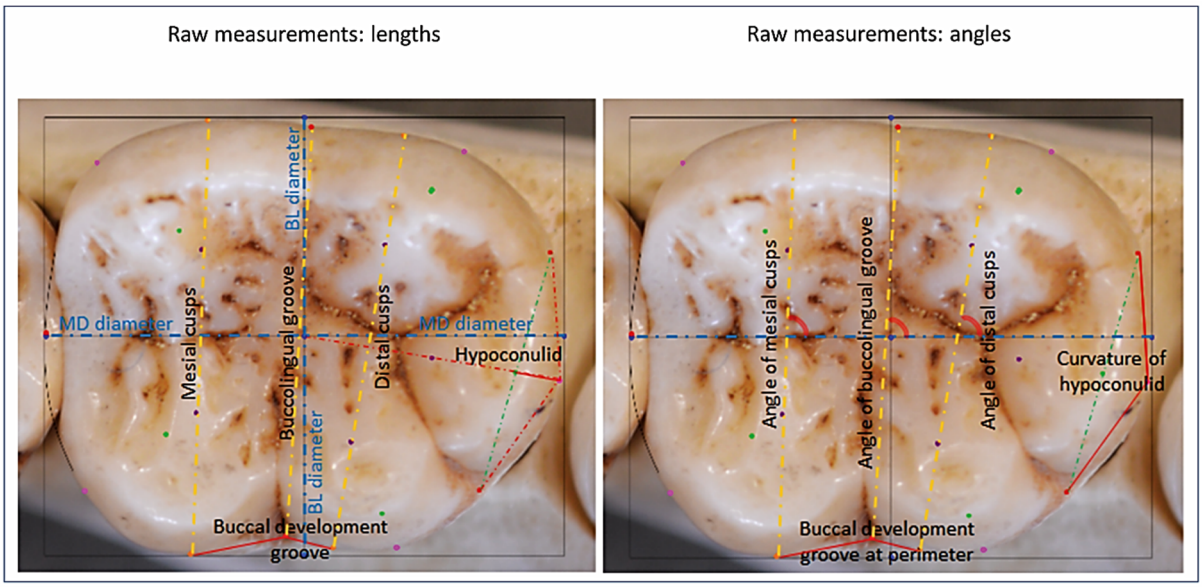


Figure 3. Angles and raw distances measured. (*P. t. troglodytes* lower M2)

Table 7. Measurements taken

Measurements taken for DFA analyses

Type	Description
Size	Natural logarithm (ln) of the centroid size[1].
Angle	Angle (radians) of the buccal development groove at the perimeter edge of the tooth
Angle	Angle (radians) of curvature of the hypoconulid
Angle	Angle (radians) of mesial cusps relative to the mesiodistal axis of the tooth
Angle	Angle (radians) of distal cusps relative to the mesiodistal axis of the tooth
Angle	Angle (radians) of the buccolingual groove relative to the mesiodistal axis of the tooth
Ratio	Ratio between mesial and distal cusp angles
Linear	Length of tooth: mesiodistal (MD) diameter
Linear	Maximum breadth of tooth: buccolingual (BL) diameter
Linear	Breadth of crown at mesial cusps
Linear	Breadth of crown at distal cusps
Linear	Measurement from lingual to buccal sides of the buccolingual groove
Linear	Measurement of linear extent of the curve of the hypoconulid cusp arc
Linear	Buccal development groove: measurement along mesial side
Linear	Buccal development groove: measurement along distal side
Ratio	Mesiodistal-buccolingual (MD:BL) ratio
Ratio	Ratio between mesial cusps and distal cusps
Ratio	Ratio between buccal groove length and mesiodistal length
Ratio	Hypoconulid curvature ratio: measurement of linear extent of the curve of the hypoconulid arc as a proportion of the whole distance from the centre of the tooth to the perimeter edge of the tooth at the hypoconulid

[1] The centroid is the average landmark position in Euclidian space between all the landmarks, and its size is equal to the square root of the sum of the distances between all of the landmarks and this centroid position (see, for example, Mitteroecker et al., 2013). This calculation can be performed manually or via Excel®, or more simply by using Morphologika® or other shape analysis software. The natural logarithm of the centroid size is frequently added back as a variable in a shape-and-size or "Formspace" analysis (Mitteroecker et al., 2004). This additional size measurement is included as it provides a composite measure of overall size differences between teeth that simple mesiodistal and buccolingual measurements cannot provide: in the case of teeth, size is a major discriminator between groups (Uchida, 1998a, 1998b; Pilbrow, 2006, 2010; Dykes, 2014).

3.2.5 Analyses

3.2.5.1 Discriminant Function Analysis (DFA)

The 19 measurements described in Table 7 were input into a series of discriminant function analyses (DFA) to establish how well lower second molars were correctly classified into known extant species and subspecies groups. In each case, a standard DFA was conducted using PAST® software, producing classification accuracy and canonical loadings tables. The percentage accuracy was also reported for a jackknifed DFA in each case (omitting one specimen from each group in the classification). An additional stepwise DFAs in SPSS® was carried out in the case of the extant species, using the squared Mahalanobis' distance method, to calculate Euclidian distances between functions at group centroids (together with the statistical significance thereof), and a near-neighbour joining tree or dendrogram was produced in SPSS® from the distance matrix produced. This methodology had previously been utilised by Pilbrow (2003, 2006, 2010) and it is employed in this study as well, to test for major discrepancies in analysis results due to differences in the landmarking methodology used in the present study. The stepwise DFA method also has the advantage of cross-checking whether significant variables, contributing to important canonical loadings when all the variables were input together, might prove to be redundant variables when the stepwise method was utilised, in which case the significance of the loadings could be reported with qualifications. The fossil species were subjected to a similar but separate DFA analysis using PAST® software, firstly including species for which the sample size was $n \geq 7$ and secondly including species groups with smaller sample sizes (for visualisation purposes). There was no missing data reported for any of the analyses.

3.2.5.2 Principal Components Analysis (PCA)

The 29 landmarks described above in Figure 2 and Table 6 were used as the basis for principal components analyses, conducted using Morphologika®. Since size-versus-shape patterning quantification is the primary objective of this present study, these analyses featured the use of Procrustes formspace to visualise these patterns in morphospace for extant hominoid species (sexually dimorphic and non-sexually dimorphic) and fossil hominin species. In a formspace analysis, shapes are transformed using a Generalised Procrustes Analysis, which translates, rotates and scales all shapes to superimpose them maximally, but size is factored back into the analysis by means of adding the natural log of the centroid value for each shape (Mitteroecker et al., 2004, Mitteroecker et al., 2013). Size then becomes the major loading along the first principal component axis (the x-axis) and the first principal component for shape then plots along the y-axis (PC2). Relative warp changes are also plotted at the extremities of each axis in the form of wireframe images to clarify interpretations of the variance being explained along each axis. The first two PCs only are plotted for each analysis because this study is focussing on relative ranges between size (PC1) and shape (PC2).

This analysis particularly aims to establish whether patterns of relative size-shape variability emerge that distinguish between species known to be highly sexually dimorphic versus those whose level of sexual dimorphism is negligible or less marked. An analysis of extinct hominin specimens was carried out and plotted along the first two principal components in formspace (PC1 again accounting predominantly for size variability and PC2 accounting for the main component of shape variability). Two PCA

analyses were then carried out combining the extant hominoid species and the extinct hominin species: firstly, comparing the hominin species to the full samples of hominoid species (maximised reference sample size per extant species – up to 241 specimens per species in this study) and secondly, for illustrative purposes, comparing the samples representing the hominin species to limited-size, random samples (n = 16) for the extant hominoid species, to provide a more realistic, "matched sample size" comparison for the extinct hominoid species, the maximum sample size of which was 16 specimens.

The rationale for this second analysis is that the specimens representing each fossil hominin species could arguably be viewed as representing a "random sample" of individuals, taken, presumably, from a larger population. A limited sample of 16 individuals, randomly chosen from this larger population, would be unlikely to include each and every one of the outliers at all of the extremes of size and shape of the population at large, so a typical range of values for the main components of shape and size variability would be expected to be lower than the full range for the population itself. Since it is impractical to run iterative PCA analyses to compare fossil samples with hundreds of randomly-selected samples of 16 individuals from the extant species, a single "representative" sample of 16 individuals was chosen for each extant species after examining the results of a randomisation analysis (see paragraph 3.2.5.3). One "average" random sample of 16 individuals was selected to represent each extant species, with CV values as close to the mean values of the 1000 random samples as possible (i.e. the random sample chosen has the "most likely" range of values for a sample of n=16, rather than the "extreme" range of values for the whole reference sample of up to n=241). The second PCA plot with smaller samples of 16 for each

species also provides the opportunity to visualise how sexual dimorphism may be identified in morphospace – with only 8 males and 8 females represented on the plot for each extant species, a visual distinction can be made between the sexes using appropriate colour coding for each representative sample of the extant species. If males and females plot generally separately from each other along the x-axis (PC1, representing size variance), this size-sorting would indicate sexual dimorphism. Should there be homogeneity in the way males and females plot along the x-axis, this lack of size differentiation between the sexes would indicate a lack of sexual dimorphism within that species.

Ranges of variability as measured from both PCA plots – maximised samples and the representative, reduced-size samples for the extant species – are measured along both axes, PC1 representing predominantly size variability and PC2 representing predominantly shape variability. "Patterns" of size-versus-shape variability for extant species are then analysed for comparison with the patterns observed in morphospace for the extinct hominin species (the ranges for the reduced-size samples being presented with a measure of caution).

3.2.5.3 Randomisation analyses with coefficients of variation

As discussed in paragraph 3.2.5.2, fossil samples for each extinct hominin species are extremely sparse in nature, and are considered to be equivalent to "random" samples from a much larger population: neither the largest, the smallest, the broadest nor the narrowest of the molars of a whole population of the hominin species in question is

expected to be represented, with any high degree of probability, within one small sample taken from it. Comparing a limited, similarly-sized sample, randomly and repeatedly sampled from the larger available sample of each species of extant hominoid to the available sample of fossil hominin teeth provides a form of "bootstrapping", which gives a more realistic idea of expected ranges of variability to be expected in such a small sample. Sample sizes of teeth attributed to a given fossil hominin species in this study did not exceed 16 per species. In order to predict the expected range of variability from any sample of 16 molars within the same known species, a randomisation analysis was conducted, using a custom-written macro in Microsoft Excel®. In this analysis, 1000 samples of 16 specimens were randomly drawn (with replacement) from the larger available reference samples from each extant species in the study. Since one of the main questions being asked in this study concerned patterns of size and shape variability in sexually dimorphic species and species that are not sexually dimorphic, each sample of 16 specimens was equally balanced between males and females. It was also decided to limit the randomised samples to 16, and not to lower the number of specimens in each sample (extant or extinct in nature) to match species groups such as *H. naledi* (n=7), in light of research that shows that samples of less than 8 specimens return coefficients of variation that are "depressed" in magnitude due to the sample size (Plavcan and Cope, 2001).

The coefficient of variation (the standard deviation divided by the mean value of each sample, expressed as a percentage) was calculated for the three main raw variables found to have contributed most to the canonical loadings in the DFA analyses – these being the mesiodistal diameter of the molars and the buccolingual diameters across the

mesial cusps and the distal cusps. The coefficients of variation (CVs) of the three measurements for each of the 1000 randomly selected samples per species were plotted in the form of a frequency distribution per measurement and per species to ascertain how many times out of a thousand the CV would equate to "x%" or higher. The question being asked was "what is the probability "p" of finding a CV this high (as the CV calculated for a fossil species) in any sample of 16 individuals from a given extant species?"

3.2.5.4 Sexual dimorphism indices and box-and-whisker plots

Statistical comparisons of sexual dimorphism in the size of second molars are presented graphically using SPSS®, and also as indices, calculated using Microsoft Excel®. In this study, centroid size was used to calculate differences in size between molars belonging to females and to males in each extant species and/or subspecies group, and in this study, the ratio provided is the female to male size ratio of the molars.

3.2.6 Tests of methodology

Because this study makes use of a purpose-designed landmarking method using predominantly mathematically-derived landmarks and measurements rather than the traditional anatomically-based landmarks, tests were conducted to establish a) whether the mathematical landmarks (Type III landmarks) would be as accurate as anatomically-based landmarks (Type I landmarks) in classifying known species and subspecies groups for extant hominoid species, and b) whether a sufficient number of landmarks were used, and specifically used in a balanced manner, in order to

adequately reflect typical shapes of each extant hominoid species represented in the study, as well as to highlight major diagnostic shape differences between them.

A) Testing Type III landmarks against Type I landmarks

The Type III landmarking and measurement methodology was tested for accuracy against a traditional methodology using only anatomically-based landmarks, taking a subset of photographs from a prior study (Pilbrow, 2006). Using identical photographs of 255 chimpanzee lower second molars, all from the Pilbrow photographic database, (thus removing inter-observer error due to different photographers), results of a step-wise within-groups discriminant function analysis were compared between the two methodologies for classifying the known species and subspecies of *Pan*. Average classification accuracy of 67.5% for the mathematical method converged successfully on the 67.8% accuracy of the anatomically-based landmarking methodology, with highest accuracy exhibited in classifying *P. paniscus,* followed by *P. troglodytes verus*. Lower accuracy, including significant overlap, was exhibited for *P. t. troglodytes, P. t. ellioti* and *P. t. schweinfurthii*. Cross-validated results showed slightly higher accuracy overall for the mathematical/Type III landmarking method over the traditional method, with 62.4% and 61.6% accuracy levels, respectively. These results were in keeping with groupings predicted according to molecular and other studies (Gagneux et al. 1999; Guy et al. 2003; Taylor & Groves 2003; Won & Hey 2005; Gonder et al. 2006; Skinner et al. 2009; Bjork et al. 2011; Fischer et al. 2011; Gonder et al. 2011). It is worth noting that the same three length and width measurements contributed to the canonical loadings in both methodologies and, despite differences in the calculation of these inputs, R-squared values between 0.97 and 0.99 showed strong correlation in these raw

measurements. This supports the use of Type III landmarks and mathematical calculations for taking measurements of shape and size analyses of molars including badly worn fossil hominin and modern human (hunter-gatherer) teeth. The results of the classification accuracy table and the convex hull plots of the DFA results are shown in Table 8, Table 9 and Figure 4.

Table 8. Classification results – Traditional method.

		Predicted Group Membership in percentages				
		P. t. verus	*P. t. ellioti*	*P. t. troglodytes*	*P. t. schweinfurthii*	*P. paniscus*
Original	*P. t. verus*	83.7	2.3	7.0	7.0	0.0
	P. t. ellioti	0.0	60.0	20.0	20.0	0.0
	P. t. troglodytes	6.5	14.8	58.3	14.8	5.6
	P. t. schweinfurthii	8.6	10.3	12.1	58.6	10.3
	P. paniscus	0.0	2.4	7.3	0.0	90.2
Cross-validated	*P. t. verus*	81.4	2.3	7.0	7.0	2.3
	P. t. ellioti	0.0	0.0	80.0	20.0	0.0
	P. t. troglodytes	7.4	16.7	51.9	15.7	8.3
	P. t. schweinfurthii	10.3	10.3	13.8	53.4	12.1
	P. paniscus	0.0	4.9	7.3	2.4	85.4
Classification accuracy: 67.8%; 61.6% cross-validated						

Table 9. Classification results – Mathematical method.

		Predicted Group Membership in percentages				
		P. t. verus	*P. t. ellioti*	*P. t. troglodytes*	*P. t. schweinfurthii*	*P. paniscus*
Original	*P. t. verus*	83.7	9.3	2.3	4.7	0.0
	P. t. ellioti	20.0	60.0	0.0	20.0	0.0
	P. t. troglodytes	6.5	11.1	62.0	15.7	4.6
	P. t. schweinfurthii	3.4	20.7	19.0	53.4	3.4
	P. paniscus	0.0	4.9	2.4	7.3	85.4
Cross-validated	*P. t. verus*	81.4	9.3	4.7	4.7	0.0
	P. t. ellioti	20.0	40.0	20.0	20.0	0.0
	P. t. troglodytes	8.3	13.9	55.6	17.6	4.6
	P. t. schweinfurthii	6.9	19.0	19.0	48.3	6.9
	P. paniscus	0.0	4.9	2.4	9.8	82.9
Classification accuracy: 67.5%; 62.4% cross-validated						

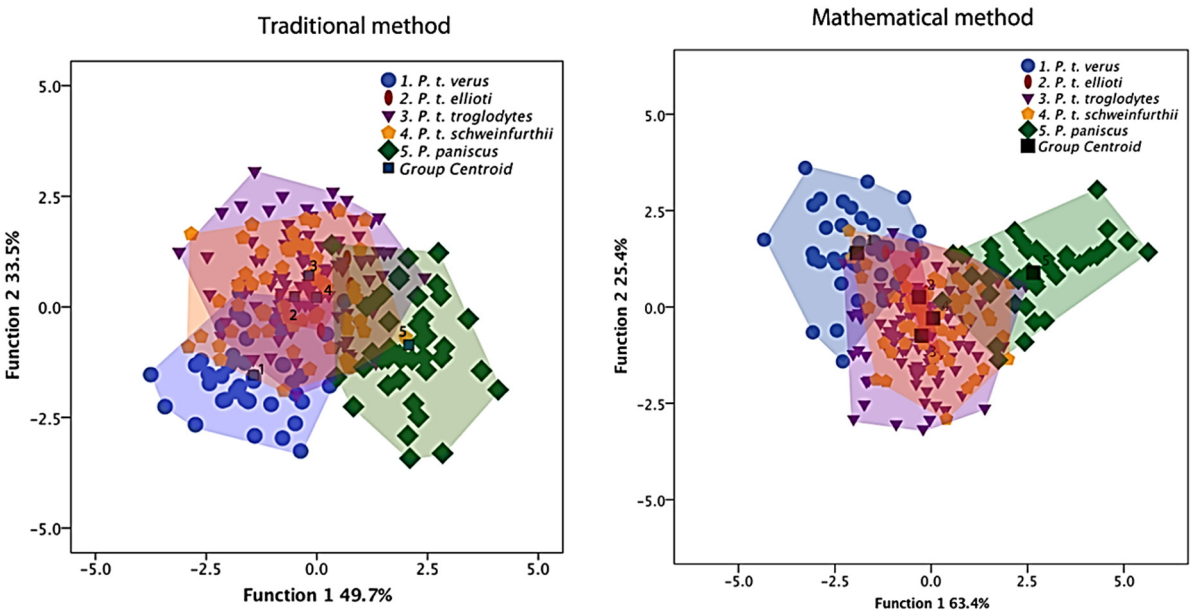


Figure 4. Convex hull plots of DFA results along Functions 1 and 2 for traditional and mathematical landmarking methods.

Results based on the traditional method (left) and on the mathematical method (right). *Pan paniscus* (green) separates well from *Pan troglodytes*, and *Pan troglodytes verus* (blue) separates clearly from the remaining three subspecies, as expected from molecular studies. *Pan troglodytes schweinfurthii* is nested within *Pan troglodytes troglodytes*, also as expected from molecular studies (e.g. Bjork et al., 2011).

B) Degree of fidelity in capturing diagnostic shapes of representative molars for different species

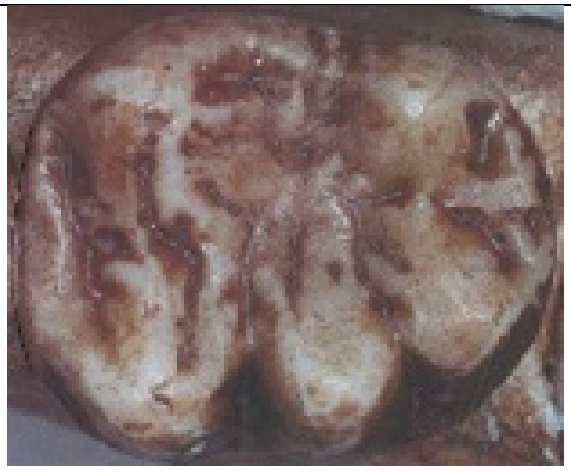
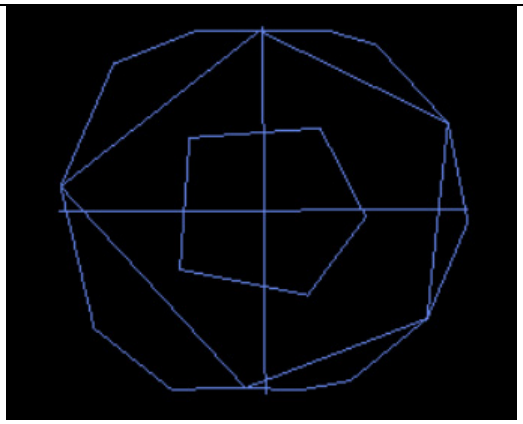
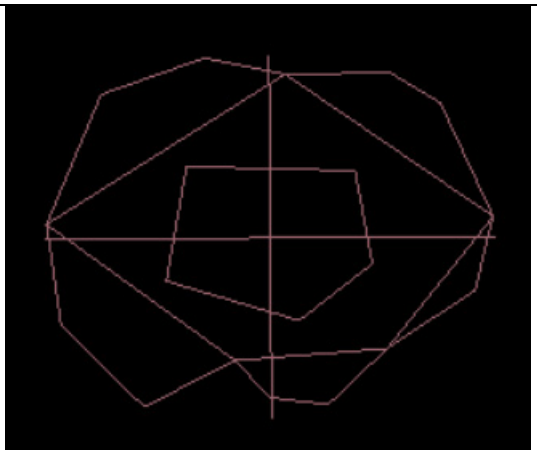
Adequacy of the 29 landmarks selected to represent the significant diagnostic differences identified between different species' molars was also tested by comparing "consensus" molar wireframes from PCA plots for the extant species to images of molars that had been identified as being "typical" of these species in shape and dimension (*c.f.* Table 1), and whose shape had, at the design phase of the methodology, informed the choice of landmark placements to maximise these differences (see subsection 3.2.4). In particular, are the cusp directions and relative proportions, the outer perimeter and the buccal development groove adequately represented in the wireframes? The

"consensus" molar is the shape of the tooth at the intersection of the first two principal component axes (x=0, y=0), and can be visualised by the shape of the relative warp wireframe at this point on the plot. It effectively describes the form of the "averaged" molar shape for all the specimens in the PCA representing that species. This wireframe is extremely helpful in analysing the main factors of variance in molar tooth shape along the axes of all principal components analyses conducted for this study, with the relative warps along each axis being easily followed in Morphologika®, using a slider available in the software. It is also useful for visualising how individual molars differ from the consensus tooth on each plot. Results of the comparison between the actual (representative) molars and the wireframe consensus molars are presented in Table 10 for modern humans and gorillas.

This comparative exercise (photographic image of a "representative" specimen tooth for each species versus the consensus wireframe image produced by PCA plots including all the modern human molars and all the gorilla molars) provides confirmation that 29 landmarks are sufficient to represent the salient information. Experiments had been conducted at the landmark planning stage, with 14, 19, 24, 34 and 39 landmarks each, but in each case, there was either a loss of information (e.g. perimeter shape), making the wireframe difficult to interpret, or the balance between landmark types was lost (too much tooth perimeter shape, not enough cusp-arrangement detail or vice versa). PCA plots using 29 landmarks showed good separation between species clusters in morphospace that was not improved by adding additional landmarks.

Table 10. Test of accuracy for shape capture: wireframe relative warps

(Test to establish whether wireframe relative warps of "consensus" teeth plotted in PCAs for modern humans and *Gorilla* matched the "representative" teeth from these groups that formed the basis for the choice of landmark placements)

	
Modern human tooth "consensus" wireframe (below): Note the low MD:BL ratio (very broad tooth), the distally-oriented hypoconulid and the direction of the other four cusps, almost perpendicular to each other. The buccolingual diameter line does not exceed the outline of the tooth by very much margin because the tooth is somewhat rounded at the buccal and lingual edges rather than indented. An inferred line drawn between the approximated centre points of the entoconid and hypoconid (main distal cusps) would be almost parallel with the line depicted between the approximated centre points of the metaconid and protoconid (mesial cusps). Both lines are only slightly less than 90 degrees from the MD axis (near horizontal in the image)	Gorilla "consensus" wireframe (below): Note the high MD:BL ratio (very narrow tooth) and the marked buccal development groove (V-shaped indent along the buccal edge), the buccally-oriented hypoconid, the buccally-oriented hypoconulid and the metaconid which extends almost to the mid-line distally of the tooth. Note also that the line drawn between the approximated centre points of the metaconid and the protoconid (the two mesial cusps, buccolingually) is more slanted against the midline than that of the modern human. Whereas in the modern human the line drawn between the approximated centre points of the distal cusps (entoconid and hypoconid) is almost parallel to that between the mesial cusps (both almost vertical in the image), the gorilla's distal cusps are at an even greater slant to the midline of the tooth than are the mesial cusps.
	

CHAPTER FOUR – RESULTS

4.1 CLASSIFICATION ACCURACY BASED ON LOWER SECOND MOLARS

4.1.1 Classification accuracy at the species level: five extant species

Lower second molars classify to a high level of accuracy at the species level for the extant species in the study (92.3% accuracy). The majority of individuals that were misclassified were incorrectly classified within the same genus. There were no misclassifications between molars belonging to specimens from *Gorilla* and those from other genera. Minor overlap between *H. sapiens* and species of *Pan* was observed in DF space (Figure 5), specifically in a few cases where modern human molars were uncharacteristically narrow in the buccolingual dimension and *Pan* molars were broadest buccolingually (see Appendix 3 for additional data).

Table 11. DFA classification accuracy at the species level for five extant species in the study

		Predicted Group Membership					
		G. beringei	*G. gorilla*	*P. troglodytes*	*P. paniscus*	*H. sapiens*	TOTAL
Count	*G. beringei*	54	21	0	0	0	75
	G. gorilla	11	168	0	0	0	179
	P. troglodytes	0	0	203	7	4	214
	P. paniscus	0	0	7	34	0	41
	H. sapiens	0	0	7	1	233	241
%	*G. beringei*	72.0	28.0	0.0	0.0	0.0	100.0
	G. gorilla	6.1	93.9	0.0	0.0	0.0	100.0
	P. troglodytes	0.0	0.0	94.9	3.3	1.9	100.0
	P. paniscus	0.0	0.0	17.1	82.9	0.0	100.0
	H. sapiens	0.0	0.0	2.9	0.4	96.7	100.0

a. 92.3% of original grouped cases correctly classified.

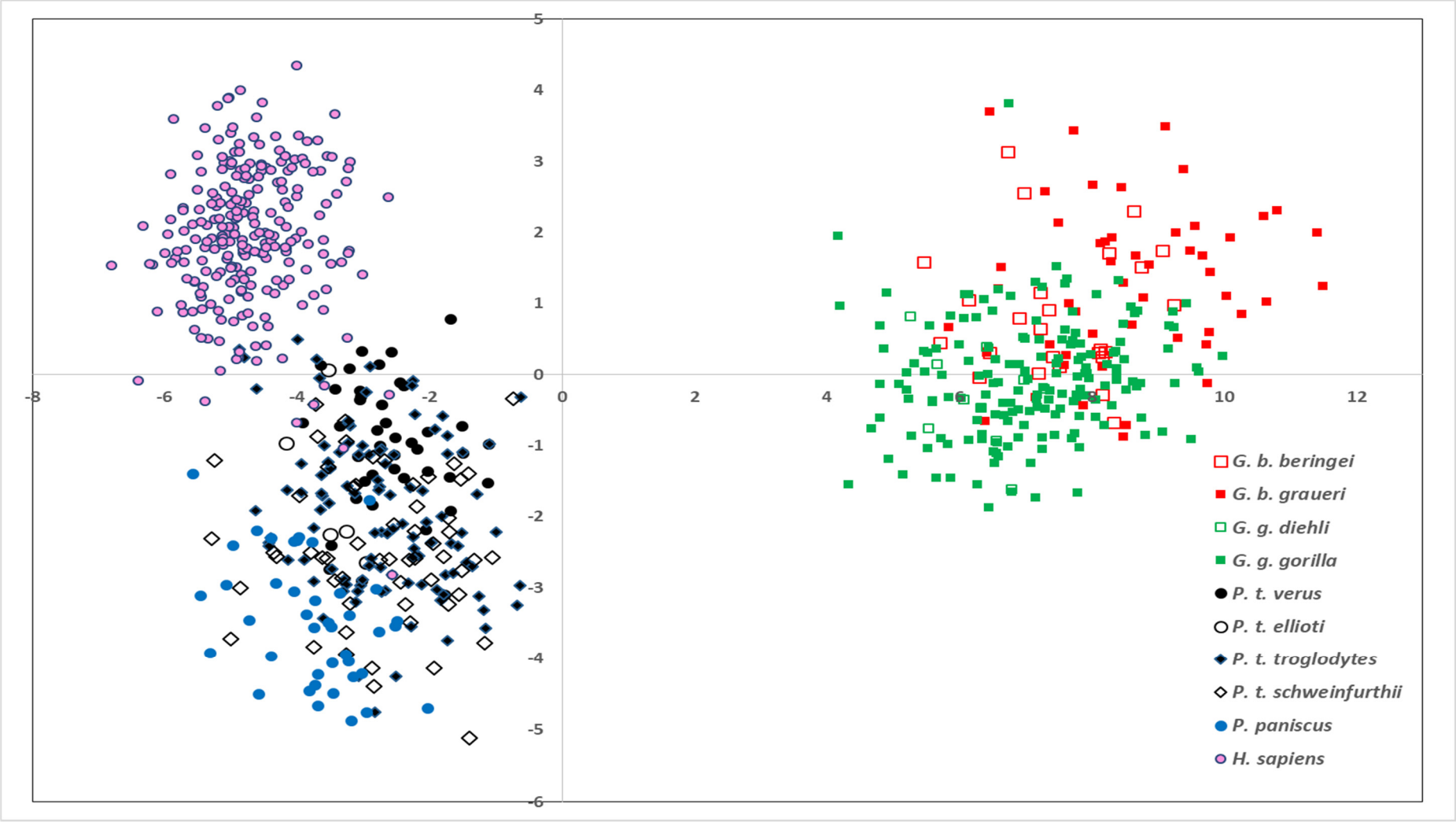


Figure 5. DFA results at the species-subspecies level for five extant species in the study

Axis 1 represents 87.5% of variance (Eigenvalue for Function 1 = 28.8); Axis 2 represents 9.3% of the variance (Eigenvalue for Function 2 = 3.1)

Table 12. Discriminant Function Coefficients - DFA at the species level

Standardized Canonical Discriminant Function Coefficients				
	Function			
	1	2	3	4
LnCentroid	0.686	0.042	-4.101	-3.189
Angle-Bucc grv	-0.331	0.519	0.216	0.099
Angle-Hypcnld	-0.263	-0.265	-0.022	-0.695
Angle-Mesial	1.009	1.789	-0.002	2.885
Angle-Distal	1.907	3.553	0.051	3.068
Angle-BL groove	-0.074	-0.755	0.078	0.403
angle ratio-Mes:dist	1.544	2.699	0.137	2.255
length-MD	0.958	1.691	1.468	-4.056
length-BL	0.349	-1.919	0.387	-1.236
breadth-Mesial	-1.266	2.158	-2.375	-1.657
breadth-Distal	1.115	-2.716	2.338	1.952
breadth-BL groove	-1.100	0.817	2.983	7.634
width-Hycnld	-0.895	0.444	-1.285	0.948
Mesial length-Bucc groove	0.129	0.132	-0.216	1.370
Dist length-Bucc groove	-0.066	0.613	0.084	0.745
ratio-MD:BL	-0.207	-1.398	-0.530	-0.989
ratio-MD:bucc groove	-0.165	0.091	1.705	4.488
ratio-Mesial:distal	0.566	-1.371	1.286	0.523
ratio-hypcnld	0.388	-0.982	0.814	-1.625

Canonical loadings (for both a normal DFA and a stepwise DFA) contributing to Function 1 (the x-axis) of the DFA plot (Figure 5 and Table 12) were primarily weighted towards raw breadth measurements across the crown (mesial versus distal cusp measurements) and the angle of the distal cusps in relation to the MD axis as well as to that of the mesial cusps. The breadth of tooth across the distal cusps was negatively weighted along Function 1, while the breadth across the mesial cusps was positively weighted. Along Function 2, mesial cusp lengths were positively weighted and distal cusp lengths were negatively weighted. In addition to the loadings accounted for by lengths and angles of the mesial and the distal cusps, the length of the mesiodistal axis and its ratio with buccolingual measurements contributed more heavily towards the

coefficients along Function 2. These features of the molars are presented visually in Figure 6: red lines show mesial and distal cusp length-and-angle differences between *H. sapiens, P. troglodytes* and *G. gorilla,* while the bounding boxes around the images (not to scale) show the basic differences in MD:BL proportion between these molars (*H. sapiens* being on average relatively broad across the crown, and *G. gorilla* generally narrow by comparison, with *P. troglodytes* in between). The average ratios between the angles across the mesial cusps versus the angles across the distal cusps (both relative to the longitudinal axis) are 1:1.002 for *H. sapiens;* 1:0.974 for *P. troglodytes* and 1:0.906 for *G. gorilla.* Mean distal cusp angles in raw form (relative to the longitudinal axis, measured in radians) are 1.651 for *H. sapiens,* 1.712 for *P. troglodytes* and 1.926 for *G. gorilla.* Mesiodistal:buccolingual ratios (relative breadth of molar, irrespective of size) are 1:1.118 for *H. sapiens,* 1:1.183 for *P. troglodytes,* and 1:1.240 for *G. gorilla.* In addition to these relative angles and ratios, the raw size variables contribute to discrimination between groups (raw length and breadth measurements). A summary of all mean measurements for the extant species is given in Appendix 3.

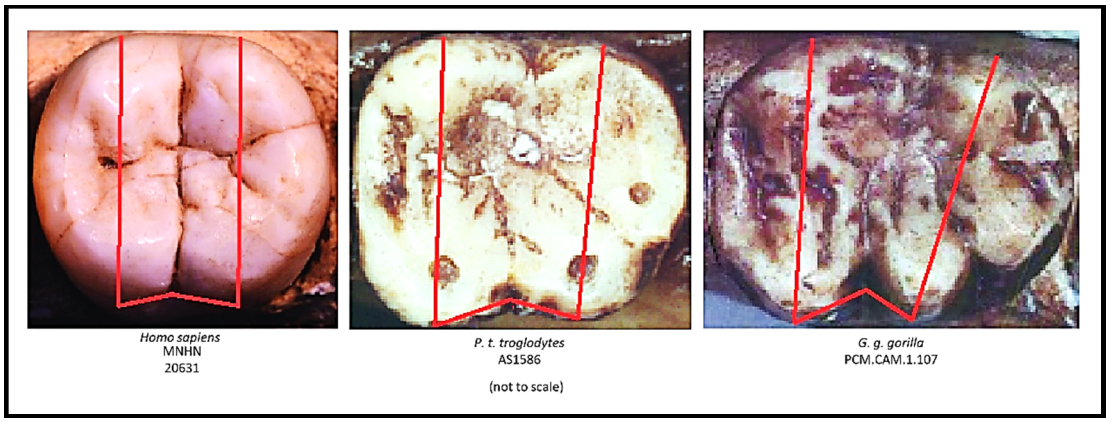


Figure 6. Images of molars belonging to *H. sapiens, P. troglodytes* and *G. gorilla*, illustrating mesial and distal cusp angles and general proportions of molars

4.1.2 Classification accuracy of lower second molars – extant species – subspecies level

At the subspecies level, classification was also reasonably accurate (82.9%; 79.2% jackknifed), with most misclassifications of individuals again being between subspecies of the same species (*G. g. diehli* and *G. g. gorilla; P. t. ellioti, P. t. troglodytes, P. t. schweinfurthii,* for instance). There was also again some overlap at the genus level between *G. beringei* species and *G. gorilla,* consistent with the previously-noted percentage misclassification at the species level.

Table 13. DFA classification accuracy of five extant species to the subspecies level

		Predicted Group Membership										
		G. b. beringei	*G. b. graueri*	*G. g. diehli*	*G. g. gorilla*	*P. t. verus*	*P. t. ellioti*	*P. t. troglodytes*	*P. t. schweinfurthii*	*P. paniscus*	*H. sapiens*	Total
Count	*G. b. beringei*	16	2	0	7	0	0	0	0	0	0	25
	G. b. graueri	1	38	0	11	0	0	0	0	0	0	50
	G. g. diehli	0	0	4	6	0	0	0	0	0	0	10
	G. g. gorilla	4	9	7	149	0	0	0	0	0	0	169
	P. t. verus	0	0	0	0	38	0	4	1	0	0	43
	P. t. ellioti	0	0	0	0	0	0	3	1	0	1	5
	P. t. troglodytes	0	0	0	0	4	2	83	10	5	4	108
	P. t. schweinfurthii	0	0	0	0	4	0	22	25	6	1	58
	P. paniscus	0	0	0	0	0	1	1	4	35	0	41
	H. sapiens	0	0	0	0	2	0	3	0	2	234	241
%	*G. b. beringei*	64.0	8.0	0.0	28.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	G. b. graueri	2.0	76.0	0.0	22.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	G. g. diehli	0.0	0.0	40.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	G. g. gorilla	2.4	5.3	4.1	88.2	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	P. t. verus	0.0	0.0	0.0	0.0	88.4	0.0	9.3	2.3	0.0	0.0	100.0
	P. t. ellioti	0.0	0.0	0.0	0.0	0.0	0.0	60.0	20.0	0.0	20.0	100.0
	P. t. troglodytes	0.0	0.0	0.0	0.0	3.7	1.9	76.9	9.3	4.6	3.7	100.0
	P. t. schweinfurthii	0.0	0.0	0.0	0.0	6.9	0.0	37.9	43.1	10.3	1.7	100.0
	P. paniscus	0.0	0.0	0.0	0.0	0.0	2.4	2.4	9.8	85.4	0.0	100.0
	H. sapiens	0.0	0.0	0.0	0.0	0.8	0.0	1.2	0.0	0.8	97.1	100.0

82,9% of original grouped cases correctly classified. 79,2% of cross-validated grouped cases correctly classified.

Once again, the canonical loadings were heavily weighted towards mesial and distal cusp breadths, angles and proportions of these relative to each other. At the subspecies level, there are additional loadings for the length of the mesiodistal axis along Function 1, breadth measurements along Function 2. The hypoconulid measurement plays a more prominent role in discriminating between groups at the subspecies level along Function 1 (see Table 14 and Figure 7).

Table 14. Discriminant Function Coefficients - subspecies level

Standardized Canonical Discriminant Function Coefficients									
	Function								
	1	2	3	4	5	6	7	8	9
LnCentroid	0.520	0.507	-4.319	-3.320	0.473	0.761	-0.893	-0.346	0.558
Angle-Bucc grv	-0.348	0.444	0.293	0.142	0.488	-0.111	-0.142	-0.617	-0.445
Angle-Hypcnld	-0.255	-0.198	-0.019	-0.694	0.000	0.084	0.712	-0.003	-0.690
Angle-Mesial	0.934	1.713	-0.280	2.748	1.378	0.077	0.994	-0.500	2.291
Angle-Distal	1.746	3.355	-0.380	2.969	2.927	-0.011	1.161	0.708	3.320
Angle-BL groove	-0.067	-0.731	0.108	0.335	-0.100	-0.048	0.531	-0.808	0.113
angle ratio-Mes:dist	1.437	2.659	-0.389	2.202	2.495	0.668	1.280	0.378	3.513
length-MD	1.540	2.086	2.340	-3.994	-4.127	0.262	0.629	-1.270	1.146
length-BL	-0.322	-2.448	-0.986	-0.747	5.548	2.012	-2.081	3.996	-2.162
breadth-Mesial	-1.011	2.227	-0.743	-2.041	-0.345	-2.896	1.487	-6.929	0.739
breadth-Distal	0.972	-2.698	0.977	2.280	-0.748	2.774	-1.100	4.746	-1.858
breadth-BL groove	-0.947	0.282	3.359	7.468	-0.681	-2.409	1.314	-0.226	1.859
width-Hycnld	-0.968	0.463	-1.246	0.846	0.059	-0.934	0.143	1.033	-2.022
Mesial length-Bucc groove	0.157	0.139	-0.083	1.226	-0.367	-0.651	0.696	-0.447	0.105
Dist length-Bucc groove	-0.063	0.512	0.243	0.729	0.219	-0.750	0.020	0.266	0.467
ratio-MD:BL	-0.482	-1.546	-0.923	-0.787	1.979	0.344	-1.260	1.746	-0.696
ratio-MD:bucc groove	-0.155	-0.242	1.733	4.383	0.321	-0.845	0.654	-1.207	-0.040
ratio-Mesial:distal	0.469	-1.374	0.443	0.754	-0.138	1.844	-1.232	3.160	0.028
ratio-hypcnld	0.451	-0.957	0.913	-1.543	-0.072	0.437	0.353	-0.925	1.539

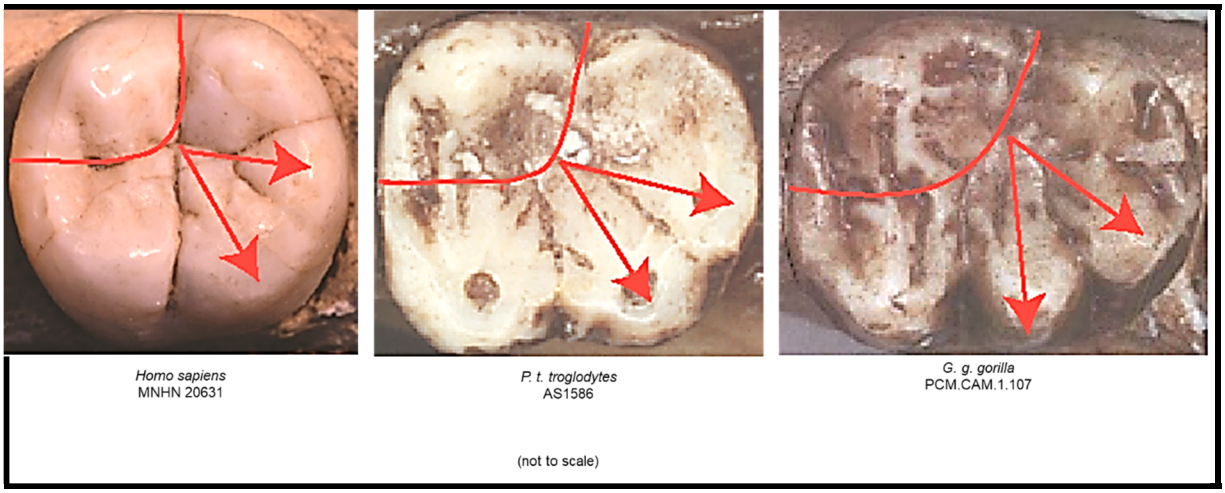


Figure 7. Illustration showing relative positioning of hypoconulid/hypoconid and its relevance in discriminating between groups

A near-neighbour joining tree (Figure 8), based on a distance matrix created from the squared Mahalanobis' distances of the functions at group centroids of the DFA at the subspecies level (see Table 15), largely confirms that lower second molar measurements, relative cusp lengths and angles and overall morphology are capable of

distinguishing between groups at the subspecies level. *Gorilla* is well-separated from the *Pan* and *Homo* clade. The squared Mahalanobis' distance method was used in a step-wise DFA to produce a table of pairwise F values between groups, and the average statistical significance of these inter-group values was calculated for each pairwise distance. Pairwise group values that were found to be non-significant at the 95% significance level were the values between *P. t. ellioti* and both *P. t. troglodytes* and *P. t. schweinfurthii.* This is a function of the small sample size for *P. t. ellioti* (n=5). The p values for the inter-group comparisons are shown in green font, with non-significant values highlighted, in Table 15.

Table 15. Proximity matrix - squared Euclidian distances between functions at group centroids, with significance values

Proximity Matrix

	Squared Euclidian distance with *significance values*									
Case	*1: G. b. beringei*	*2: G. b. graueri*	*3: G. g. diehli*	*4: G. g. gorilla*	*5: P. t. verus*	*6: P. t. ellioti*	*7: P. t. troglodytes*	*8: P. t. schweinfurthii*	*9: P. paniscus*	*10: H. sapiens*
1:G. b. beringei		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
2:G. b. graueri	16.688		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
3:G. g. diehli	23.794	30.011		*0.026*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
4:G. g. gorilla	9.884	16.862	5.425		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
5:P. t. verus	120.210	155.667	90.608	102.139		*0.047*	*0.000*	*0.001*	*0.000*	*0.004*
6:P. t. ellioti	138.830	176.842	113.862	122.638	9.774		*0.355*	*0.211*	*0.050*	*0.029*
7:P. t. troglodytes	121.917	159.410	97.823	107.551	8.433	4.182		*0.018*	*0.000*	*0.001*
8:P. t. schweinfurthii	126.869	162.543	98.751	109.366	8.870	5.105	1.891		*0.000*	*0.026*
9:P. paniscus	164.186	200.429	136.227	145.422	30.140	14.331	15.377	12.382		*0.000*
10:H. sapiens	160.102	197.583	136.506	148.153	17.855	17.877	22.167	25.849	40.862	

This is a dissimilarity matrix

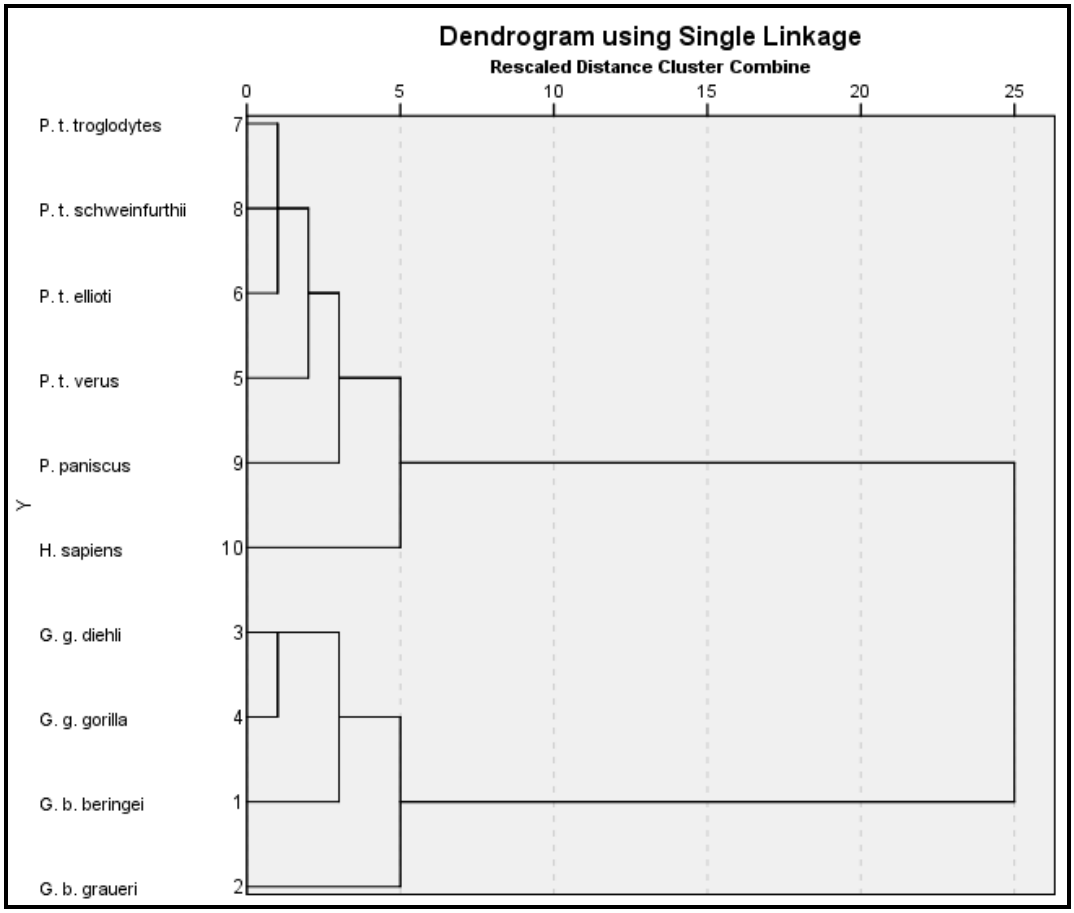


Figure 8. Near-neighbour joining tree (dendrogram) of squared Mahalanobis' distances in Euclidean space between group centroids of subspecies of extant species

4.1.3 Classification of lower second molars of *Gorilla*

A DFA carried out in PAST® on the four subspecies of *Gorilla* produced a general separation in the distribution of lower second molars in DF space, indicating a split between *G. gorilla* and *G. beringei,* with the two *beringei* subspecies to the right of the y-axis generally and the two *gorilla* subspecies mostly towards the left of the y-axis (Figure 9). Sexual dimorphism within each subspecies is generally evident, with females grouping towards the left along the x-axis, which mainly accounts for size, and males grouping towards the positive end of the axis, relative to their group (Figure 9).

Classification accuracy for *Gorilla* subspecies was 72.8% (65% jackknifed).

Table 16. DFA classification accuracy for *Gorilla* at the subspecies level

	G. b. beringei	*G. b. graueri*	*G. g. diehli*	*G. g. gorilla*	Total
G. b. beringei	92%	4%	0%	4%	25
G. b. graueri	12%	74%	4%	10%	50
G. g. diehli	0%	0%	90%	10%	10
G. g. gorilla	5%	7%	19%	69%	169
Total	38	50	43	123	254
72.8% correctly classified (65% jackknifed)					

A further DFA classified *Gorilla* species at the population level. The classification accuracy was 70.9% for all 14 populations (per Pilbrow, 2010) represented in this study (table not shown).

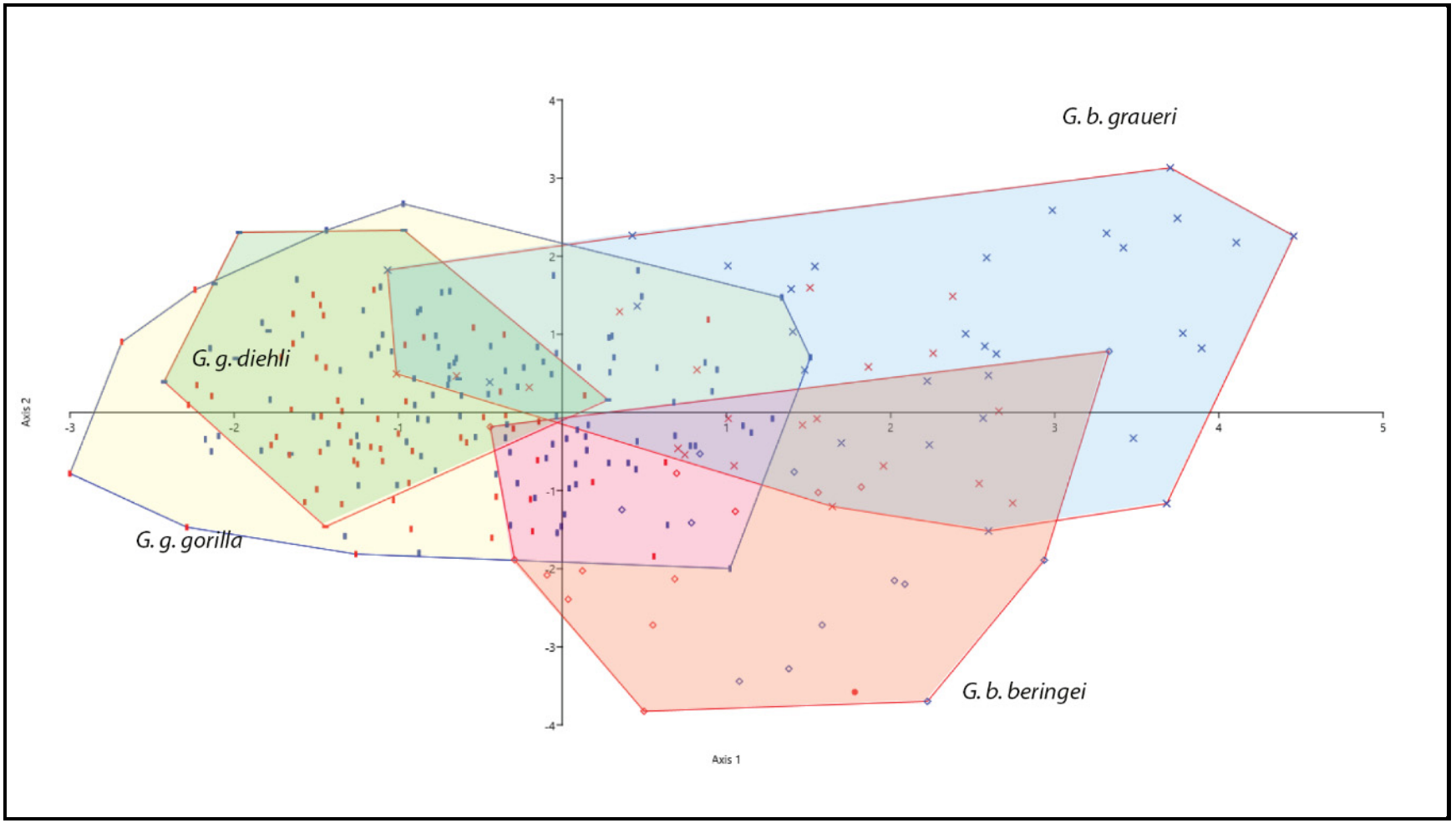


Figure 9. DFA plot of *Gorilla* subspecies

Axis 1: 70.06% of variance; Axis 2: 26.33% of variance. Legend: x crosses: *G. b. beringei;* circles: *G. b. graueri;* horizontal dashes: *G. g. diehli;* upright dashes: *G. g. gorilla.* Red=female; blue=male.

4.1.4 Classification of lower second molars of *Pan*

Similarly, with chimpanzees, lower second molars of *P. paniscus* group in a DFA plot most clearly away from those of *P. troglodytes*, but the western subspecies (*P. t. verus*) is highly distinct in lower second molar shape from the other three subspecies (see Figure 10). There is considerable overlap between all three subspecies east of the Sanaga River, with nesting of *P. t. schweinfurthii* evident within *P. t. troglodytes.* No sexual dimorphism is evident: females appear as likely as males to group more positively along the x-axis (mainly loaded for size). Classification accuracy was similar to that of *Gorilla* subspecies (Table 17).

Table 17. DFA classification accuracy of lower second molars of *Pan* species/subspecies

	P. t. verus	*P. t. ellioti*	*P. t. troglodytes*	*P. t. schweinfurthii*	*P. paniscus*	Total
P. t. verus	88%	7%	2%	2%	0%	43
P. t. ellioti	0%	100%	0%	0%	0%	5
P. t. troglodytes	5%	11%	64%	18%	3%	108
P. t. schweinfurthii	3%	17%	16%	60%	3%	58
P. paniscus	0%	5%	2%	7%	85%	41
Total	45	32	80	58	40	255
71.4% correctly classified (60,8% jackknifed)						

Classification accuracy to the population level of 15 populations represented in this study, out of 16 populations listed by Pilbrow (2006) was 54.5% for *Pan* (table not shown here).

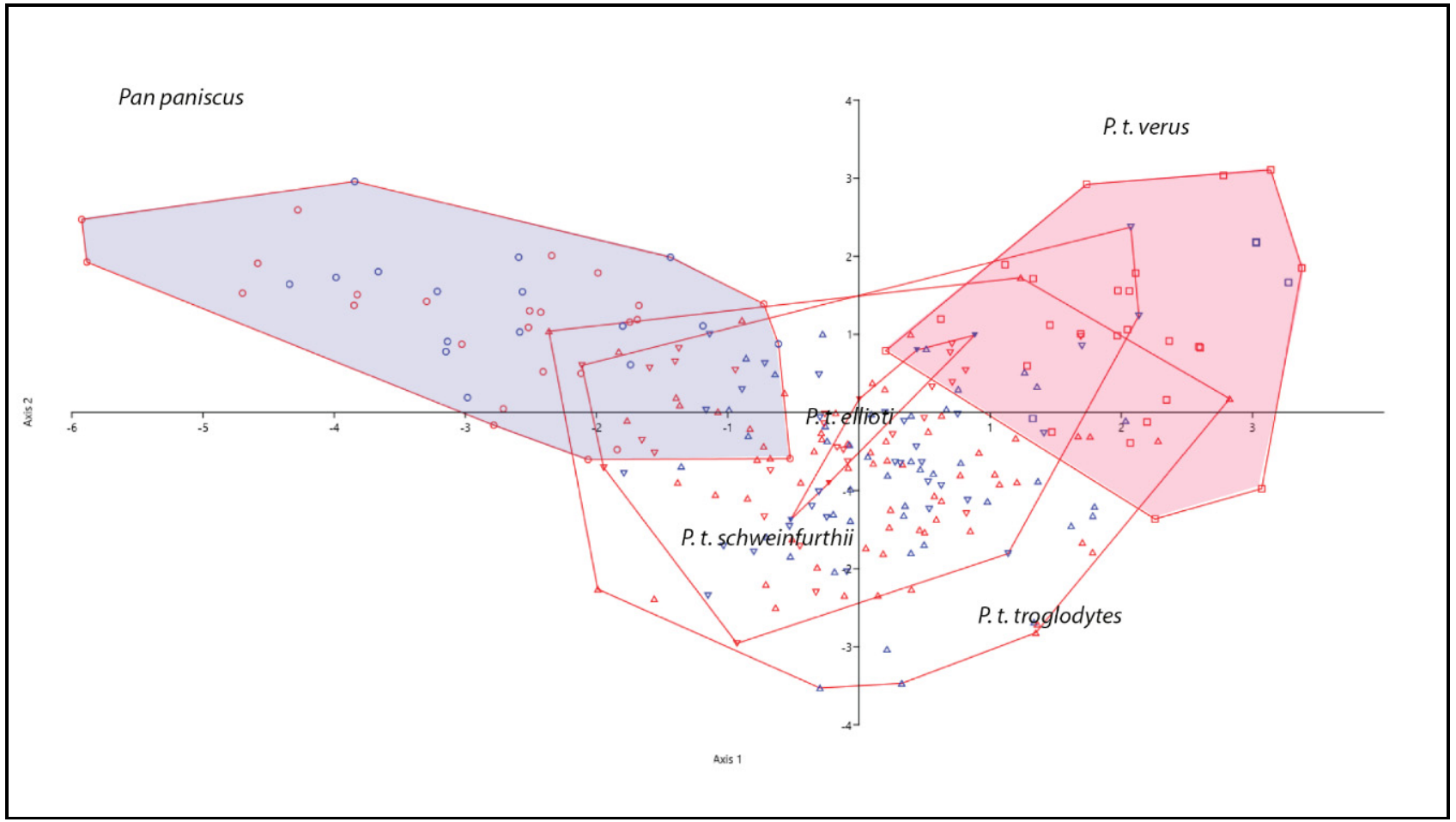


Figure 10. DFA plot of *Pan* species / subspecies

Axis 1: 63.26% of variance; Axis 2: 25.65% of variance. Legend: circles: *P. paniscus* enclosed in blue convex hull*;* squares: *P. t. verus* (enclosed in pink convex hull)*;* triangles: *P. t. troglodytes;* open inverted triangles: *P. t. schweinfurthii;* closed inverted triangles: *P. t. ellioti.* Red: female; blue: male

4.1.5 Classification of lower second molars: *Homo sapiens*

A DFA was carried out in SPSS® on modern humans at the population level. A total of 241 individual lower second molars represent (recent) modern *H. sapiens* in this analysis, divided into 16 population groups as set out in Table 3. These were classified with an accuracy of 95% for 16 groups (See Table 18). Of particular interest is the question of whether lower second molars group together in DF space according to subsistence strategy divergences since the Neolithic period. A general contrast is noted between groups that have remained with a hunter-gatherer lifestyle and those groups exposed to an early transition to widescale agriculture, as shown in Figure 11. The main loadings along Function 1 relate to raw size values (ln centroid size, MD axis, BL measurements across the mesial and distal cusps). An important additional loading factor along Function 1, adding to discrimination between groups of modern *H. sapiens,* is the measurement of the curve (bulge) of the hypoconulid at the distal margin of the tooth. Examples of molars typifying hunter-gatherers and agriculturalists are pictured (to scale) on the DFA plot along Function 1, and these images show the difference in complexity and robusticity of molars and their hypoconulids. Function 2 was loaded principally for the MD diameter and the breadth measurement across the distal cusps. Table 19 presents the canonical discriminant function coefficients with the main loading factors highlighted for the first two functions.

Table 18. DFA classification accuracy for 16 populations of modern humans

		Predicted Group Membership																Total
		KhoeSan	Babinga	SA Bantu	Teita	Australian Aboriginal	Polynesian	New Guinean	East Asian	South Indian	South Asian	Balkan	Semitic	Mesopo-tamian /Turkish	W. European	Amerindian	Inuit	
Count	KhoeSan	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16
	Babinga	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
	SA Bantu	0	0	20	0	0	0	0	0	0	0	0	2	0	1	0	0	23
	Teita	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	8
	Australian Aboriginal	0	0	0	0	26	0	0	0	0	0	0	0	0	1	0	0	27
	Polynesian	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	11
	New Guinean	0	0	1	0	0	0	18	0	0	0	0	0	0	0	0	0	19
	East Asian	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	16
	South Indian	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	10
	South Asian	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	5
	Balkan	0	0	0	0	0	0	0	0	0	0	16	2	0	0	0	0	18
	Semitic	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	11
	Mesopotamian/Turkish	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	9
	W. European	0	0	2	0	0	0	0	0	1	0	0	0	0	28	1	0	32
	Amerindian	0	0	0	0	0	0	0	0	1	0	0	0	0	0	17	0	18
	Inuit	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	11
%	KhoeSan	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	Babinga	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	SA Bantu	0.0	0.0	87.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.7	0.0	4.3	0.0	0.0	100.0
	Teita	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	Australian Aboriginal	0.0	0.0	0.0	0.0	96.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	100.0
	Polynesian	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	New Guinean	0.0	0.0	5.3	0.0	0.0	0.0	94.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	East Asian	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	South Indian	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	South Asian	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	Balkan	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	88.9	11.1	0.0	0.0	0.0	0.0	100.0
	Semitic	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Mesopotamian/Turkish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	W. European	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0	87.5	3.1	0.0	100.0
	Amerindian	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	94.4	0.0	100.0
	Inuit	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0

a. 95.0% of original grouped cases correctly classified.

Table 19. Discriminant Function Coefficients - modern *H. sapiens* - 16 population groups. First 5 functions shown (80.3% of variance, significant at 95% level)

Standardized Canonical Discriminant Function Coefficients					
	Function				
	1	2	3	4	5
Hsap_LnCentroid	4.376	0.157	1.424	1.739	0.915
BuccGrooveAngle	0.061	0.263	-0.129	0.016	0.151
HypcnldAngle	-0.631	0.514	0.194	0.516	0.323
MesialAngle	0.027	1.015	1.527	5.497	1.490
DistalAngle	1.669	0.562	1.378	8.041	2.254
BLGrooveAngle	-1.025	0.926	0.459	-0.368	0.088
MesDistAngleRatio	0.917	1.453	2.169	6.285	1.765
MD	-2.033	2.171	-0.300	3.210	-6.552
BL	-1.696	-0.006	-0.630	-1.434	4.859
MesialCusps	-3.372	1.323	-0.038	-1.640	3.423
DistalCusps	3.305	-3.660	0.494	-3.588	-5.852
BLGrooveBreadth	-0.676	-0.620	-0.475	0.615	2.408
HypcnldBreadth	1.523	0.117	2.940	2.771	2.778
BuccGrooveMesialSide	-0.410	0.298	-0.608	-0.300	-0.020
BuccGrooveDistalSide	-0.407	-0.339	-0.832	0.746	-0.444
MDBLRatio	-0.401	-1.037	0.372	-2.388	3.814
MesDistCuspRatio	1.916	-1.048	0.435	0.050	-1.827
HypcnldRatio	-2.605	0.621	-3.240	-2.021	-2.119

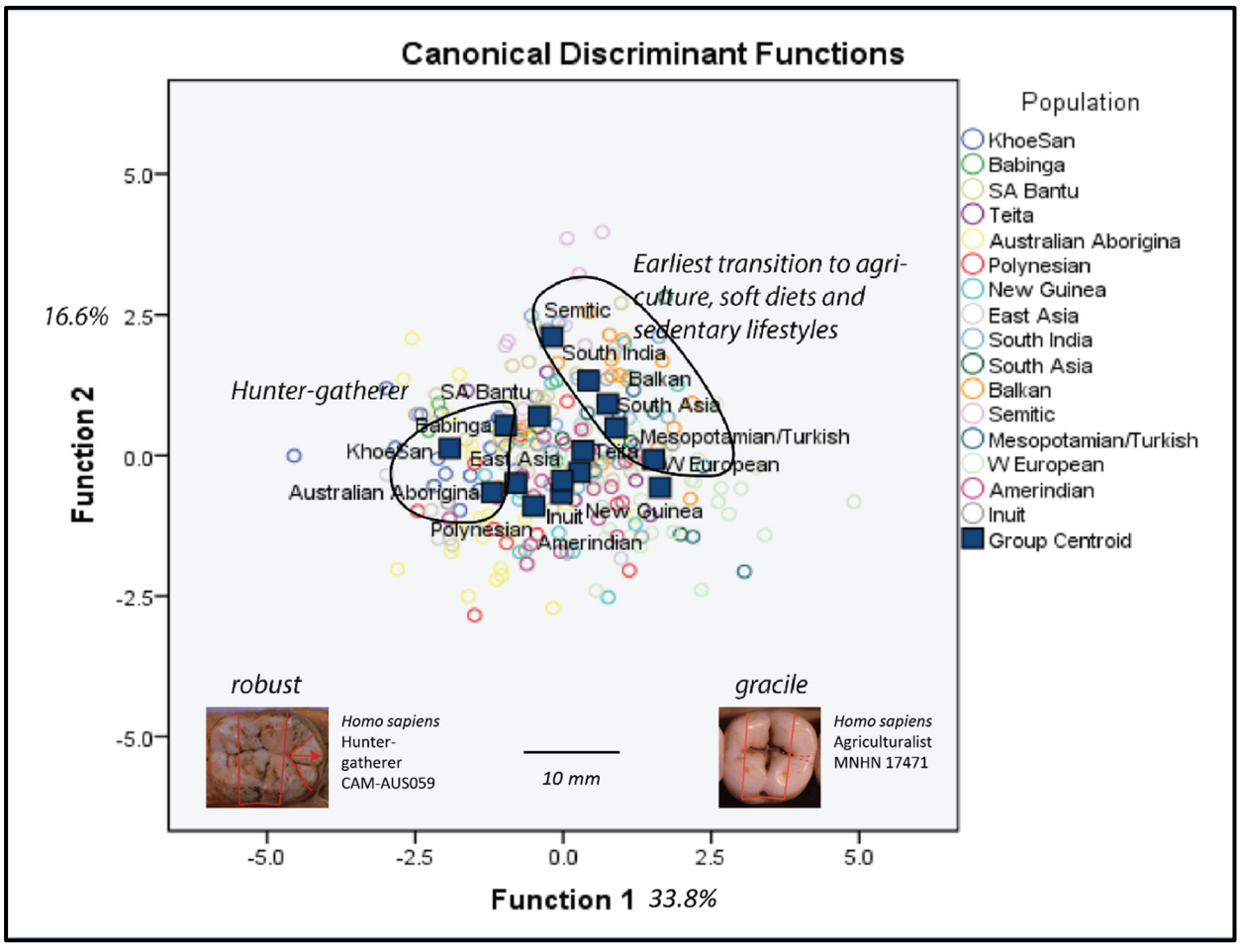


Figure 11. DFA plot of 16 groups of modern *H. sapiens*

The factors identified by the canonical loadings as being responsible for discriminating between groups within *H. sapiens* thus have largely to do with size of tooth, mesiodistal length of tooth and the size and positioning of the hypoconulid. Comparing these results with the actual photographic images included in the study, it can be confirmed that (as pictured in Figure 11) a typical hunter-gatherer tooth retains a larger size and more complex crown with five well-defined cusps, while a typical West European "agriculturalist" tooth is reduced in size, particularly in mesiodistal length, and cusp simplification has resulted in the diminishing or loss of the fifth cusp (hypoconulid).

If tooth-size reduction and cusp simplification are, indeed, regional historical adaptations following a change in dietary composition due to the transition to widescale agriculture, a historical time series in one such region ought to be able to confirm this adaptation over the transition period. To test this, images of lower second molars from specimens taken from the same region (Great Britain) catalogued as dating to the Neolithic period from 6000-4500 years before present (Price, 2000; Gkiasta et al., 2003), the Anglo-Saxon period (410 to 1066 CE) and the Medieval period (1066 to 1485 CE), were landmarked, analysed and visualised in morphospace by means of a principal components analysis (PCA) in formspace (size is added back to the analysis and becomes the main factor of variance along the first principal component). The results are shown in Figure 12. Barring one outlier from the Neolithic period which groups in morphospace with molars from the Medieval period, there appears to be a general trend of grouping from the upper right quadrant to the lower left quadrant of the plot. Examining the plot, larger molars group towards the positive values along the x-axis and smaller teeth towards the negative side of the x-axis, as is expected with a

formspace PCA. The second PC, plotting along the y-axis, is the primary principal component loaded for variance in shape rather than size, and on examination of the wireframes, one of the main differences contributing to variance along this axis is the size and position of the hypoconulid (and of the hypoconid, as a result). The second main factor of variance that is immediately observable from the y-axis wireframes is that molars that are relatively narrower across the crown (relative to the MD axis) plot towards positive values of the y-axis, while molars that are relatively broader (relative to the MD axis) plot towards the negative values. These molars would appear to have larger buccal cusps than lingual cusps. On examination of actual images of lower second molars classified as Neolithic and Medieval, these features are apparent (Figure 12). The molar depicted from the Neolithic period (specimen # EU 1 5 0061 from the Duckworth Collection at Cambridge University) retains a robust size with a large MD diameter and five cusps well defined by deep grooves. The molar from the Medieval period (specimen # EU 1 1 0099 from the Duckworth Collection) has a short MD diameter by comparison to the molar from the Neolithic period: it appears relatively broad buccolingually as a result. It has flatter cusps with grooves that are poorly-defined as they approach the perimeter edges of the tooth, and an almost undetectable hypoconulid, due to the fusion of enamel between the hypoconid and hypoconulid and the reduction in size of the latter.

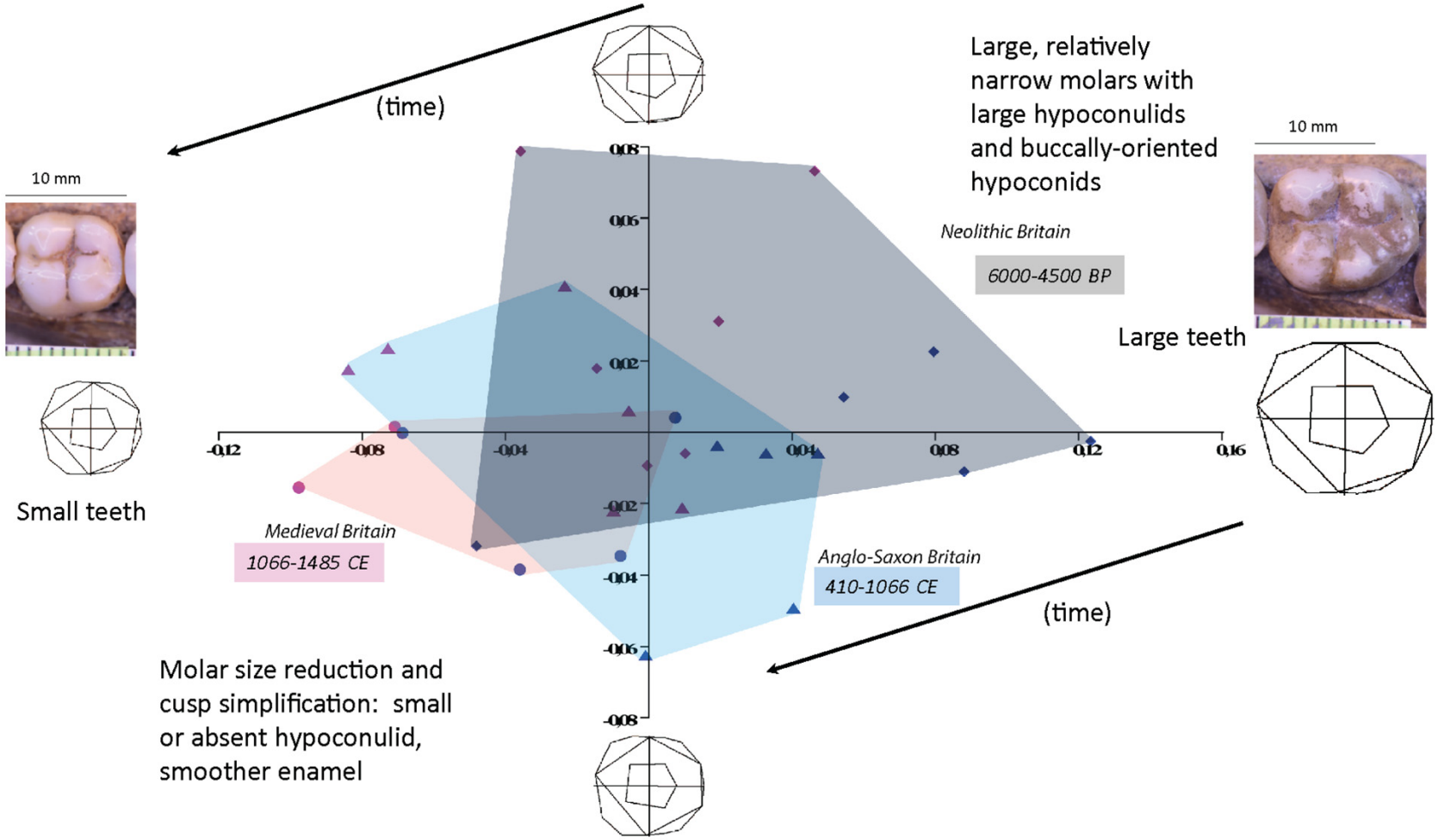


Figure 12. Time series showing tooth size reduction and shape change from Neolithic to Medieval times in Great Britain.

PC1 (x-axis) accounts for 51% of variance and mainly accounts for size differences – small molars at the negative end of the axis (later molars) and large molars at the positive end of the axis (Neolithic period). PC2 accounts for 18% of the variance and is mainly loaded for shape variability: teeth with large hypoconulids and buccally-oriented hypoconids (ancestral shape) and teeth with reduced or absent hypoconulids (derived/simplified shape). Legend: Neolithic period (6000 BP – 4500 BP): diamonds; Anglo-Saxon period (410-1066 CE): triangles; Medieval period: (1 066-1485 CE). Circles. Pink: female; blue: male. For eigenvalues, see App. 3

4.2 SPATIAL PATTERNING OF SEXUALLY DIMORPHIC SPECIES VERSUS SPECIES NOT DISPLAYING SEXUALLY-DRIVEN SIZE DIFFERENCES

Gorilla species are the only species showing general separation in the plots (Figure 5 and Figure 9) between males and females, and this differentiation is expressed primarily in size/length of teeth across the mesiodistal diameter rather than primarily across buccolingual breadth. This is an indication that there is generally more size variability than shape variability between the sexes in *Gorilla*. The other three species in the study (*P. paniscus, P. troglodytes, H. sapiens*) show general homogeneity of sexes in terms of size and shape (males and females group more or less together), and there is a higher degree of shape variability observed in the DFA plots, particularly for *P. troglodytes* and *H. sapiens.* In the case of *P. troglodytes,* the lower second molars of both male and female *P. t. verus* are typically broader across the buccolingual diameter relative to the mesiodistal axis than the other subspecies of *P. troglodytes.* In modern humans, lower second molars of both male and female individuals vary in both size and shape according to different population groups. For instance, lower second molars of Australian Aboriginals, both male and female, tend to have five well-defined cusps and have generally large centroid sizes. Lower second molars of Western Europeans, both male and female, tend to have smaller centroid sizes, and the teeth tend to be almost as broad buccolingually as they are long mesiodistally. Thus, size differences between molars are a factor of subspecies/population in *Pan* and of population group in modern *Homo sapiens,* rather than of sexual dimorphism. Sexual dimorphism at the species-subspecies level can be identified clearly by means of a box-and-whisker plot (Figure 13). After testing for normality of distribution (Shapiro-Wilk and Kolmogorov-Smirnov tests conducted in SPSS), a t-test was carried out on the log-transformed centroid size

data to assess whether males and females were distributed significantly differently for each species, and the results thereof are reported beneath the figure (Table 20).

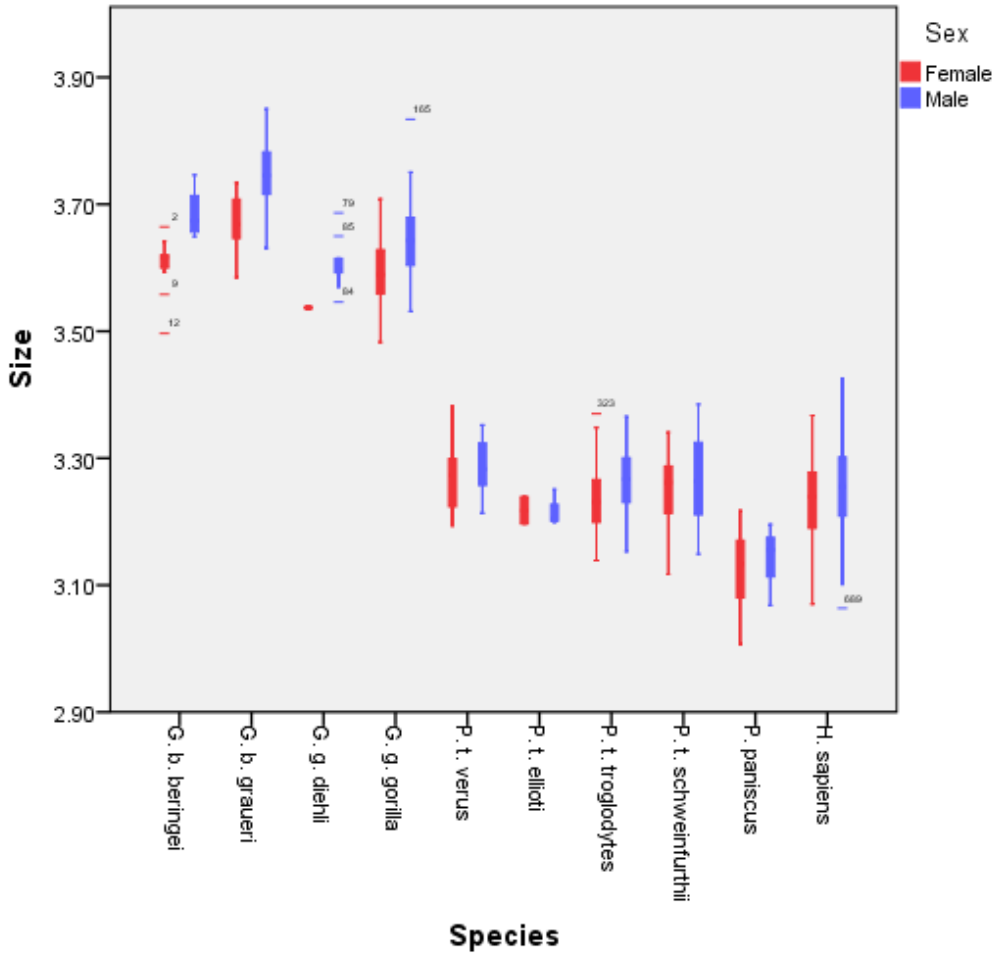


Figure 13. Species-subspecies level sexual dimorphism plot

Table 20. Statistics and t-test results: sexual dimorphism by species/subspecies

Species/subspecies	*G. b. beringei*	*G. b. graueri*	*G. g. diehli*	*G. g. gorilla*	*P. t. verus*	*P. t. ellioti*	*P. t. troglodytes*	*P. t. schweinfurthii*	*P. paniscus*	*H. sapiens*
Ln centroid size* mean (f)	3.607	3.670	3.540	3.595	3.270	3.220	3.235	3.253	3.128	3.236
Ln centroid size* mean (m)	3.682	3.745	3.607	3.644	3.286	3.217	3.266	3.263	3.145	3.257
F:M size ratio (mean CS)	0.93	0.93	0.94	0.95	0.98	1.00	0.97	0.99	0.98	0.98
Standard deviation (f)	0.040	0.009	0.000	0.006	0.010	0.020	0.006	0.011	0.011	0.007
Standard deviation (m)	0.034	0.009	0.014	0.005	0.010	0.017	0.008	0.012	0.010	0.006
Observations (f)	13	20	1	63	25	2	66	27	25	86
Observations (m)	12	30	9	106	18	3	42	31	16	135
Minimum value (f)	3.50	3.59	3.54	3.48	3.19	3.20	3.14	3.12	3.01	3.07
Maximum value (f)	3.66	3.73	3.54	3.71	3.38	3.24	3.37	3.34	3.22	3.37
Minimum value (m)	3.65	3.63	3.55	3.53	3.21	3.20	3.15	3.15	3.07	3.06
Maximum value (m)	3.75	3.85	3.69	3.83	3.35	3.25	3.37	3.38	3.20	3.43
Range of values (f)	0.16	0.14	0.00	0.23	0.19	0.04	0.23	0.22	0.21	0.30
Range of values (m)	0.10	0.22	0.14	0.30	0.14	0.05	0.22	0.23	0.13	0.37
Hyp. Mean Difference	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
df	23	48	8	167	41	3	106	56	39	219
t Stat	-5.002	-5.783	-1.512	-5.729	-1.026	0.127	-3.093	-0.632	-1.093	-2.297
P(T<=t) two-tail	0.000	0.000	0.169	0.000	0.311	0.907	0.003	0.530	0.281	0.023
t Critical two-tail	2.069	2.011	2.306	1.974	2.020	3.182	1.983	2.003	2.023	1.971
(Ln centroid size/centroid size (CS) calculated from 29 landmark centroid)										

For the four subspecies of *Gorilla,* females invariably have lower average centroid sizes than do their male counterparts (F:M mean size ratios of 0.93:1 - 0.95:1), with statistically-significant values for all but *G. g. diehli,* which had only one female in the sample. For other species and subspecies, there is more overlap between the sexes (ratios of centroid sizes between males and females closer to 1:1). *Homo sapiens* notably also shows significant overall size **ranges** for both males and females, although on **average** there is very little divergence in size ranges between the sexes.

Size differences are therefore apparent (and statistically significant) between gorilla males and females; less so for the other species. To establish whether sexes are differentiated by molar *shape* as well as by molar size, a further analysis was carried out on the relative breadth (buccolingual) measurements in relation to the mesiodistal lengths of molars, by sex and by species, since these relative measurements had been established via the DFA as accounting for additional shape variance that differentiated between groups, particularly at the species-subspecies level. Mesiodistal:buccolingual (MD:BL) ratios by species are presented in Table 21.

Table 21. Mean and range of MD:BL ratios for males and females of extant species at the subspecies level

G. b. beringei	*Females*	*G. b. beringei*	*Males*
Mean	1.21	Mean	1.21
Standard Deviation	0.05	Standard Deviation	0.04
Range	0.18	Range	0.12
Minimum	1.10	Minimum	1.14
Maximum	1.28	Maximum	1.26
Count	13	Count	12

G. b. graueri	*Females*	*G. b. graueri*	*Males*
Mean	1.27	Mean	1.27
Standard Deviation	0.04	Standard Deviation	0.05
Range	0.17	Range	0.18
Minimum	1.18	Minimum	1.19
Maximum	1.35	Maximum	1.37
Count	20	Count	30

G. g. gorilla	*Females*	*G. g. gorilla*	*Males*
Mean	1.24	Mean	1.24
Standard Deviation	0.05	Standard Deviation	0.05
Range	0.27	Range	0.25
Minimum	1.12	Minimum	1.12
Maximum	1.39	Maximum	1.36
Count	63	Count	106

P. t. verus	*Females*	*P. t. verus*	*Males*
Mean	1.13	Mean	1.13
Standard Deviation	0.04	Standard Deviation	0.03
Range	0.14	Range	0.10
Minimum	1.05	Minimum	1.08
Maximum	1.19	Maximum	1.18
Count	25	Count	18

P. t. troglodytes	*Females*	*P. t. troglodytes*	*Males*
Mean	1.20	Mean	1.19
Standard Deviation	0.05	Standard Deviation	0.04
Range	0.21	Range	0.20
Min+O60imum	1.10	Minimum	1.09
Maximum	1.31	Maximum	1.29
Count	66	Count	42

P. t. schweinfurthii	*Females*	*P. t. schweinfurthii*	*Males*
Mean	1.20	Mean	1.20
Standard Deviation	0.05	Standard Deviation	0.05
Range	0.20	Range	0.15
Minimum	1.13	Minimum	1.12
Maximum	1.33	Maximum	1.27
Count	27	Count	31

P. paniscus	*Females*	*P. paniscus*	*Males*
Mean	1.19	Mean	1.20
Standard Deviation	0.05	Standard Deviation	0.05
Range	0.20	Range	0.17
Minimum	1.12	Minimum	1.12
Maximum	1.32	Maximum	1.29
Count	25	Count	16

H. sapiens	*Females*	*H. sapiens*	*Males*
Mean	1.12	Mean	1.12
Standard Deviation	0.05	Standard Deviation	0.04
Range	0.24	Range	0.18
Minimum	1.01	Minimum	1.03
Maximum	1.25	Maximum	1.21
Count	89	Count	138

(*G. g. diehli* and *P. t. ellioti* were omitted from this analysis due to small sample sizes, with molars from female specimens within the samples of only one or two individuals)

There was no difference in relative mean breadth of molars in the sexually dimorphic *Gorilla* species, so it can be suggested that while males and females do differ noticeably between them in relative size, there is no average differentiation in relative proportions of the molars by sex. In other words, both males and females in one subspecies would have very narrow molars buccolingually (as is the case with typical lower second molars of *G. b. graueri*), and these molars would differ in size mainly by sex; both males and females in another group would have relatively broader molars buccolingually (*G. b. beringei* lower second molars are generally broader across the buccolingual axis), and again these would be grouped by sex when it came to size. On average, males and females are therefore equally well represented in terms of the relative breadth of their teeth, but in the case of *Gorilla,* teeth belonging to males and females will be differentiated by sex when it comes to size of molar (this is most evident at the subspecies level). In *Pan* and *H. sapiens,* there was likewise little or no differentiation between relative breadth measurements by sex. In *Pan,* the most noteworthy MD:BL values are those of *P. t. verus*, which is distinctive in its relative breadth, representing the broadest molars buccolingually of all the *P. troglodytes* subspecies. In this study, the broadest teeth across the crown belong to modern *H. sapiens,* although on average, these teeth are not significantly broader across the crown than those of *P. t. verus.*

4.3 EXTINCT HOMININ SPECIES – PATTERNS OF VARIABILITY

Because of low sample sizes for some of the fossil hominin species (holotypes and proxies of holotypes being included in this study for very basic comparative purposes), an initial DFA was run in PAST® on the four species with the largest sample sizes (*A. afarensis* – n=16; *A. africanus* – n=16; *P. robustus* – n=12; and *H. naledi* – n=7). DFA outputs and the plot along Functions 1 and 2 are given in Appendix 3. Thereafter, the other species were added to the DFA and the results compared. The classification accuracy for the DFA of the four largest species groups alone was 88.2%, with two of the *A. afarensis* specimens (AL 333-59 and AL 333-W57) classifying with *A. africanus,* two of the *A. africanus* specimens (StW 540 and MLD 18) classifying with *A. afarensis* and one (StW 308) classifying with *P. robustus,* and one *P. robustus* (the "gracile" TM 1517 from Kromdraai) classifying with *A. africanus* rather than with specimens from Swartkrans). The results of the DFA including all of the fossil hominin species in the study rendered a classification accuracy of lower second molars representing the attributed species of 88.9% correctly classified at the species level. When jackknifed, the classification accuracy reduced to 36.5% due to small sample size numbers in some instances. As can be seen from the classification accuracy table (Table 22) and from a plot of the first two canonical axes (Figure 14), most overlap again exists between *A. afarensis, A. africanus* and *P. robustus,* with one of the two *H. habilis* specimens (OH 16) classifying more closely with *A. afarensis.* The same specimens misclassified in the DFA with all the fossil specimens as had misclassified in the DFA with only four species. AL 333-59 again classified with *A. africanus,* but AL 333-W57 this time classified with *H. ergaster*; StW 540 and MLD 18 classify again with *A. afarensis*; TM 1517 also, as before, classifies with *A. africanus.* SK 5 classifies with *P. boisei.* (See Appendix 3 for full details).

Table 22. Classification accuracy of a DFA for the fossil hominin species

	A afarensis	*A africanus*	*P robustus*	*P boisei*	*A sediba*	*H naledi*	*H habilis*	*H rudolfensis*	*Early Homo*	*H ergaster*	Total
A afarensis	88%	6%	0%	0%	0%	0%	0%	0%	0%	6%	16
A africanus	13%	88%	0%	0%	0%	0%	0%	0%	0%	0%	16
P robustus	0%	8%	83%	8%	0%	0%	0%	0%	0%	0%	12
P boisei	0%	0%	0%	100%	0%	0%	0%	0%	0%	0%	2
A sediba	0%	0%	0%	0%	100%	0%	0%	0%	0%	0%	2
H naledi	0%	0%	0%	0%	0%	100%	0%	0%	0%	0%	7
H habilis	50%	0%	0%	0%	0%	0%	50%	0%	0%	0%	2
H rudolfensis	0%	0%	0%	0%	0%	0%	0%	100%	0%	0%	1
Early Homo	0%	0%	0%	0%	0%	0%	0%	0%	100%	0%	2
H ergaster	0%	0%	0%	0%	0%	0%	0%	0%	0%	100%	3
Total	17	16	10	3	2	7	1	1	2	4	63
88.9% correctly classified (36.5% jacknifed)											

Canonical loadings for both DFAs (see Appendix 3) were weighted very similarly, with Function 1 (x-axis) being loaded in both instances firstly for the breadth across the tooth measured along the buccolingual groove, secondly for variability in the mesial cusp breadth measurements (broad in *A. afarensis,* narrow by comparison in *P. robustus*), thirdly for other breadth measurements (BL diameter and distal cusp breadth) and fourthly for the MD diameter length. Along Function 2 (y axis) in both analyses, the MD diameter length accounted for the most significant canonical loading, followed by variability in the breadth of the tooth across the distal cusps (relatively broader in *Paranthropus,* relatively narrower in *Australopithecus,* compared to other breadth measurements). The other main canonical loadings of significance along Function 2, in order of importance for both DFAs, were the breadth of the tooth along the buccolingual groove, the BL diameter and, to a smaller extent, the breadth of tooth across the mesial cusps. The measurement of the curvature/length of the hypoconulid also contributed to loadings along the y-axis in both cases. The main difference between the two DFAs is that the main canonical loadings along Function 1 for the 4-species DFA are positive values, while the fully inclusive DFA values are negative. The plots are therefore extremely similar but appear as mirror images (horizontally) of each other (See Appendix 3 for full details and plot of the DFA of 4 species only). A plot of the first two canonical axes of the DFA including all the species is presented in Figure 14.

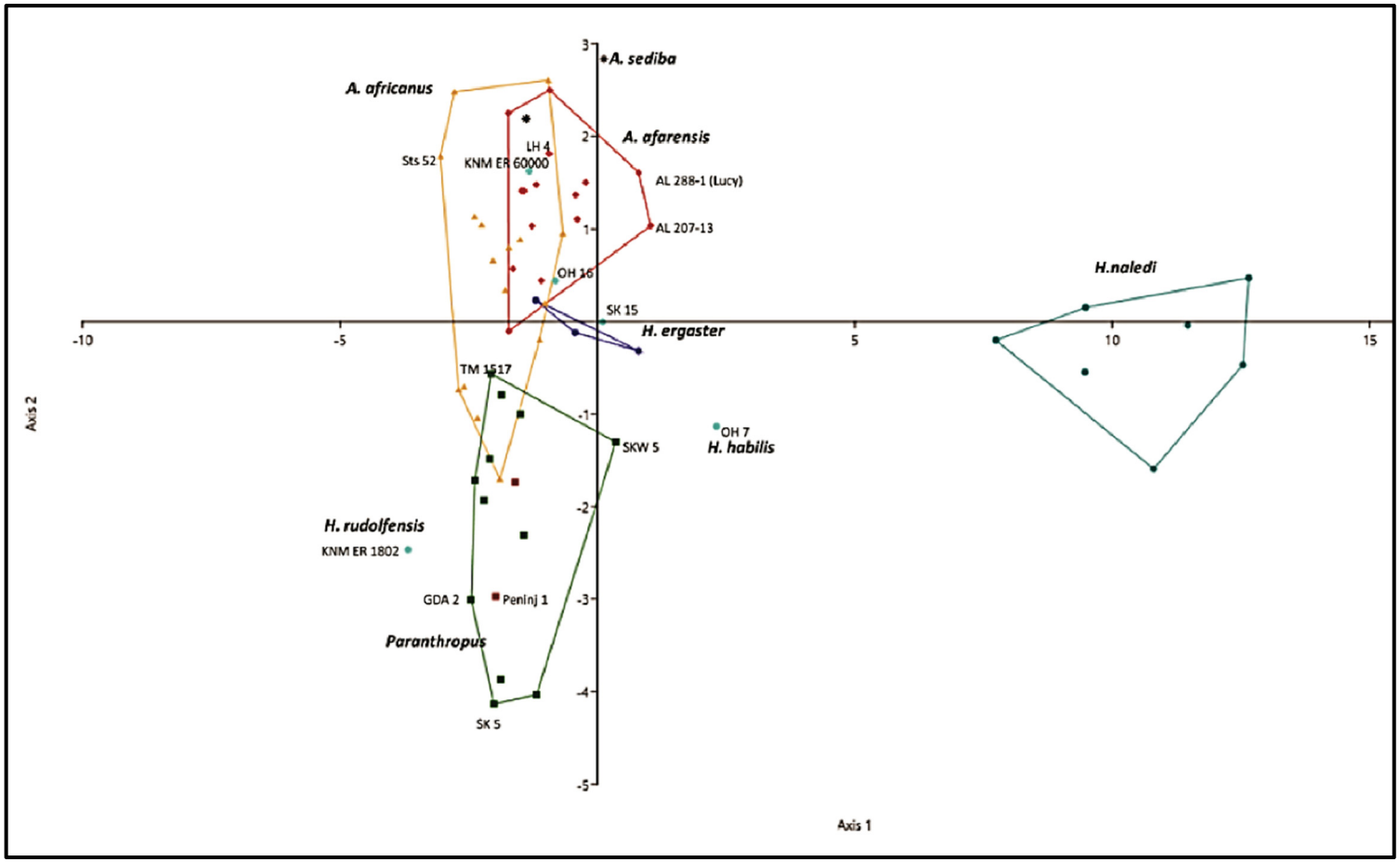


Figure 14. DFA plot of variability of lower M2s of fossil hominin species

Axis 1 accounts for 72.1% of variability, and is mainly loaded for raw measurements accounting for buccolingual breadth of the lower second molars (broader molars towards the negative range of the axis, narrower molars towards the positive side). Axis 2 accounts for 9.6% of variability, and is mainly loaded for a) mesiodistal length of the tooth – longer molars plot negatively; as well as b) the ratio of buccolingual breadth measurements between the mesial side and the distal side: there is a shift along the axis from molars that are broader distally (below the x-axis in negative values of PC2), to molars broader mesially (above the x-axis in positive values of PC2).

At the species level, it can be seen that specimens attributed to *A. africanus* show the greatest size variability (as measured along the y-axis). There is also a shift within this group between specimens with BL measurements that are broader across the mesial cusps and those that are broader across the distal cusps: the larger specimens from this group with broader distal cusps than mesial cusps (i.e. Stw 308, Stw 327, Stw 498 and Stw 555) plot alongside the more gracile teeth from *P. robustus* with less pronounced distal cusps (i.e. TM 1517, SK 1 and SK 843). The type specimen of *A. afarensis,* LH 4, has a very pronounced metaconid, so the measurement across the mesial cusps is larger than that across the distal cusps and it plots well inside the expected area. Two specimens appear to be slightly narrower across the buccolingual dimension for this group: AL 288-1 ("Lucy") and AL 207-13. *Paranthropus robustus* overlaps with *P. boisei*, and the very large specimen from Gondolin (GDA 2) plots directly alongside Peninj 1, a proxy for the type specimen of *P. boisei* (OH 5). The five specimens falling into the broad category of early *Homo* do not group together, which may reflect the fact that the group comprises specimens attributed to several different species. KNM ER 60000, in particular, groups towards *A. sediba* (black stars on the plot), and OH 16 groups with *Australopithecus*. OH 7, the type specimen of *H. habilis,* plots well away from KNM-ER 1802, which is attributed to *H. rudolfensis.* Middle Pleistocene *Homo* is represented by *H. naledi*, which groups well away from other species. A principal components analysis (PCA) in Procrustes Formspace ("shape-and-size" analysis) largely confirmed these groupings (Figure 15).

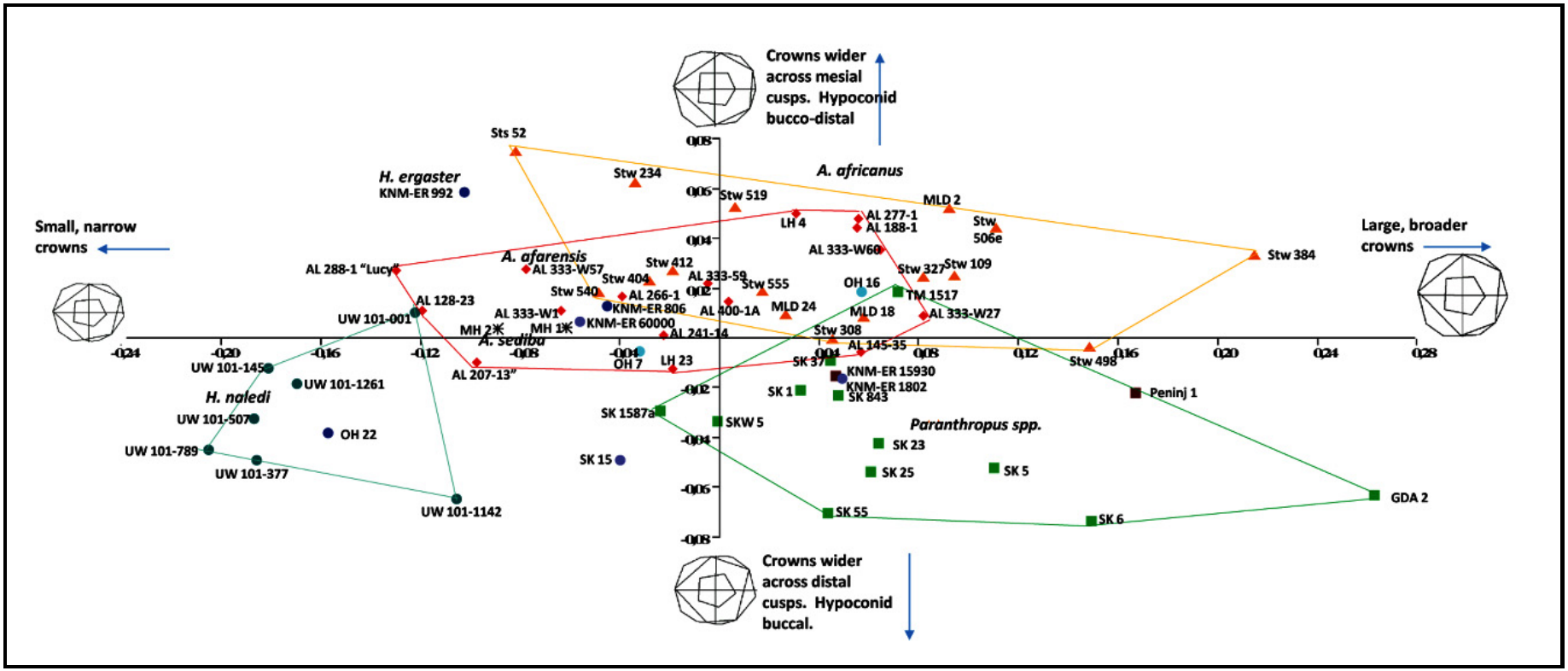


Figure 15. PCA plot in Procrustes Formspace of variability of lower M2s of fossil hominin species

Axis 1 accounts for 73.4% of variability and is mainly loaded for size and breadth of tooth across the crown (small, narrow molars towards the negative side of the axis, large, broad molars towards the positive). Axis 2 accounts for 9.3% of variability and is mainly loaded for the orientation of the hypoconid (from buccodistal to buccal as y decreases), as well as ratio of the breadth of the molar across the mesial versus the distal cusps (shift from molars wider mesially – above the x-axis - to molars wider distally – below the x-axis). Eigenvalues provided in Appendix 3.

In a Formspace PCA plot, because the natural log of the centroid is added back as a variable for each specimen, the first principal component (PC1: x-axis) is strongly correlated to the size of the tooth, and the second principal component (PC2) accounts for major shape differences. The PC1 in this instance also accounted for a change in the breadth across the molar from narrow (negative range of the axis) to broad (positive range of the axis). The PC2 shape differences, as in the DFA, indicate the relative shift from molars that are broader buccolingually across the mesial cusps (positive range of the y-axis) to molars that are broader buccolingually across the distal cusps (negative range of the y-axis). Additional shape variation measured along PC2 involves changes in the way the cusps are arranged: in this case, the orientation of the hypoconid. The hypoconid is buccally oriented toward the negative end of the y-axis, and bucco-distally oriented toward the positive end. As noted previously, molars belonging to *Australopithecus* species tend to be broader across the mesial cusps than the distal cusps (see also statistics in Appendix 3), which explains why most specimens attributed to this genus group plot along positive values of y (above the x-axis). *Paranthropus* species typically have lower second molars that are broadest across the distal cusps, partly because their hypoconid is buccally oriented rather than bucco-distally oriented. One notable exception in this group is TM 1517, which is the type specimen of *P. robustus*, and which groups with the mesially broad *Australopithecus* specimens. In this instance, however, this may be an anomaly due to the fact that when this partial mandible was discovered, the mesial half of the crown of the lower second molar was missing and was reconstructed using plaster of Paris. The reconstructed mesial cusps are extremely broad across the crown in proportion to the distal cusps, and this pattern is not evident in the lower first or third molar in this partial mandible. This specimen was retained in the study because it is the original type specimen, and because it is still

possible to make qualified comments about the specimen. Even if the proportions of the reconstruction had been more realistic (with a wider buccolingual measurement distally, a narrower measurement mesially), the fact remains that this molar is relatively "gracile" (relatively small and narrow) as compared to some other specimens attributed to *P. robustus.* The close grouping of this specimen with some of the more robust specimens of *A. africanus* is therefore a valid grouping, even if the mesial-distal proportions of the tooth are erroneous.

With the exception of *H. naledi* molars, which group cohesively together in the PCA plot as they do in the DFA plot, other molars attributed to various species of *Homo* group most readily with other species (even other genera) rather than with their own presumed holotype specimens. OH 16, currently attributed to *H. habilis* groups more readily with *A. africanus.* OH 7, the type specimen of *H. habilis,* groups most closely with LH 23, which is currently attributed to *A. afarensis.* The type specimen of *H. ergaster,* KNM-ER 992, is well separated and plots on its own in the expected quadrant (teeth with small, narrow crowns, as is the case with this specimen), but plotting nearby it are AL 288-1 (currently attributed to *A. afarensis*) and Sts 52 (currently attributed to *A. africanus*). KNM-ER 806, currently attributed to *H. ergaster,* plots well away from the type specimen and clusters more readily with *A. afarensis/A. africanus.* KNM-ER 60000 (currently attributed to *H. rudolfensis*) plots alongside *A. sediba* and *A. afarensis,* as it had done in the DFA plot (Figure 14). SK 15 (currently designated as "Early *Homo*") plots closely with SK 1587a, which is attributed to *P. robustus*. OH 22, variously attributed to *H. ergaster* or to *H. heidelbergensis* plots with the *H. naledi* cluster.

4.4 EXTINCT SPECIES COMPARED TO EXTANT SPECIES IN MORPHOSPACE

4.4.1 PRINCIPAL COMPONENTS ANALYSES

All specimens from the five species of extant hominoids included in this study (i.e. *G. beringei, G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens*) were analysed together with the specimens from the fossil species in a "Procrustes formspace" ("shape-and-size") principal components analysis. The results are shown in the form of a PCA plot in Figure 16. The main factor contributing to the loadings along PC1 (x-axis) is the centroid size, since this is a formspace PCA. PC1 accounts for 89.2% of the variance and is 99.6% correlated with centroid size, with small molars plotting towards the negative range of the axis and large teeth plotting to the positive side. While PC2 (y-axis) accounts for only 4.11% of variance, since PC1 is loaded almost completely for size variance, PC2 becomes the first principal component loading for shape variance (Mitteroecker, 2004). The relative warps wireframe images at each extremity of the y-axis show the significant shape variance along the axis. The main shape variability is accounted for by the breadth of the tooth, with extremely narrow molars plotting towards the positive end of the axis (*Gorilla, Pan* and some unusually narrow modern *Homo sapiens* molar outliers); relatively broad teeth buccolingually will plot along the negative side of the axis. The broadest teeth of the extant species belong to modern *Homo sapiens.* Some specimens of *Pan* also plot at negative values along PC2, these being predominantly individuals from *P. t. verus*, which typically have relatively broad lower second molars. There are two outliers of *G. g. gorilla* that are also atypically broad across the crown.

A second PCA, based on a reduced sample size for each extant hominoid species, is presented in Figure 17. The rationale for this "reduced-size, representative" sample analysis is explained in paragraph 3.2.5.2, but it bears repeating here, for clarity of interpretation of the results. 1000 randomly-selected samples of 16 individuals each was examined for each species, and a single "representative" sample from these was identified for the five extant species that had CV (coefficients of variation) values closest to the average CV values for that species, as calculated from the randomisation analysis. Being a single sample, it must be emphasised that the results from the reduced-size sample analyses are mainly for illustrative purposes, providing a "most probable" range of variation for a typical sample of 16 from a larger population. In Figure 17, extant species samples therefore match the sample size of *A. afarensis* and *A. africanus* (n=16 each). In this plot, the ranges of variability for 16 specimens per species is close to a more "realistic" (expected) range for such limited samples. With the reduction in the number of specimens per species, the presentation is far less visually confusing than the plot showing the maximised samples of the extant species, which is one of the main purposes for including this second analysis. The distribution of males and females for each extant species can also now be examined, and from this it can be seen which species exhibit sexual dimorphism and which do not. It will be noticed that molars belonging to females of *G. gorilla* generally plot at more negative values along PC1 (size-related variance) than do the males; in *Pan* and *H. sapiens,* males and females plot equally frequently together at lower values and at higher values along PC1.

Table 23 presents the numeric ranges of size and shape variability observed in morphospace along the first and second principal components axes for both PCA

analyses (maximised samples and reduced-size representative samples of n=16 each for the extant species). Ratios of size-versus-shape variability per species are calculated by examining variability along PC1 (predominantly size variability) and PC2 (predominantly shape variability, manifested mainly in buccolingual measurements across the mesial and distal cusps, relative to the mesiodistal axis).

Table 23. Ranges of variability along PC1 and PC2 of the PCA plot of extant species and fossil hominin species

	FULL SAMPLE				RANDOM LIMITED SAMPLE (n=16)			
	Range along PC1 (x-axis)	**Range along PC2 (y-axis)**	**Ratio along axes PC1:PC2**	**Sexual Dimorphism ratio**	**Range along PC1 (x-axis)**	**Range along PC2 (y-axis)**	**Ratio along axes PC1:PC2**	**Sexual Dimorphism ratio**
	(Main variance: size)	(Main variance: breadth)	(Main variance: size/breadth)	(F:M Centroid size)	(Main variance: size)	(Main variance: breadth)	(Main variance: size/breadth)	(F:M Centroid size)
G. beringei	0.35	0.11	3.30	0.92	0.20	0.06	3.26	0.95
G. gorilla	0.32	0.15	2.13	0.95	0.24	0.06	4.00	0.90
P. troglodytes	0.28	0.14	2.09	0.98	0.18	0.09	2.01	0.96
P. paniscus	0.21	0.10	2.20	0.98	0.11	0.09	1.28	1.00
H. sapiens	0.33	0.22	1.51	0.98	0.27	0.12	2.15	0.99
	FOSSIL SAMPLE COMPARISONS				FOSSIL SAMPLE COMPARISONS			
A. afarensis (n=16)	0.20	0.11	1.81		0.20	0.11	1.81	
A. africanus (n=16)	0.28	0.12	2.34		0.28	0.12	2.34	
P. robustus (n=12)	0.24	0.16	1.51		0.24	0.16	1.51	
A. sediba (n=2)	0.04	0.02	2.53		0.04	0.02	2.53	
H. naledi (n=7)	0.09	0.06	1.53		0.09	0.06	1.53	
H. habilis (n=2)	0.06	0.08	0.71		0.06	0.08	0.71	
Early "*Homo*" *(n=3)*	0.11	0.03	3.28		0.11	0.03	3.28	
H. ergaster/erectus (n=3)	0.15	0.08	1.80		0.15	0.08	1.80	

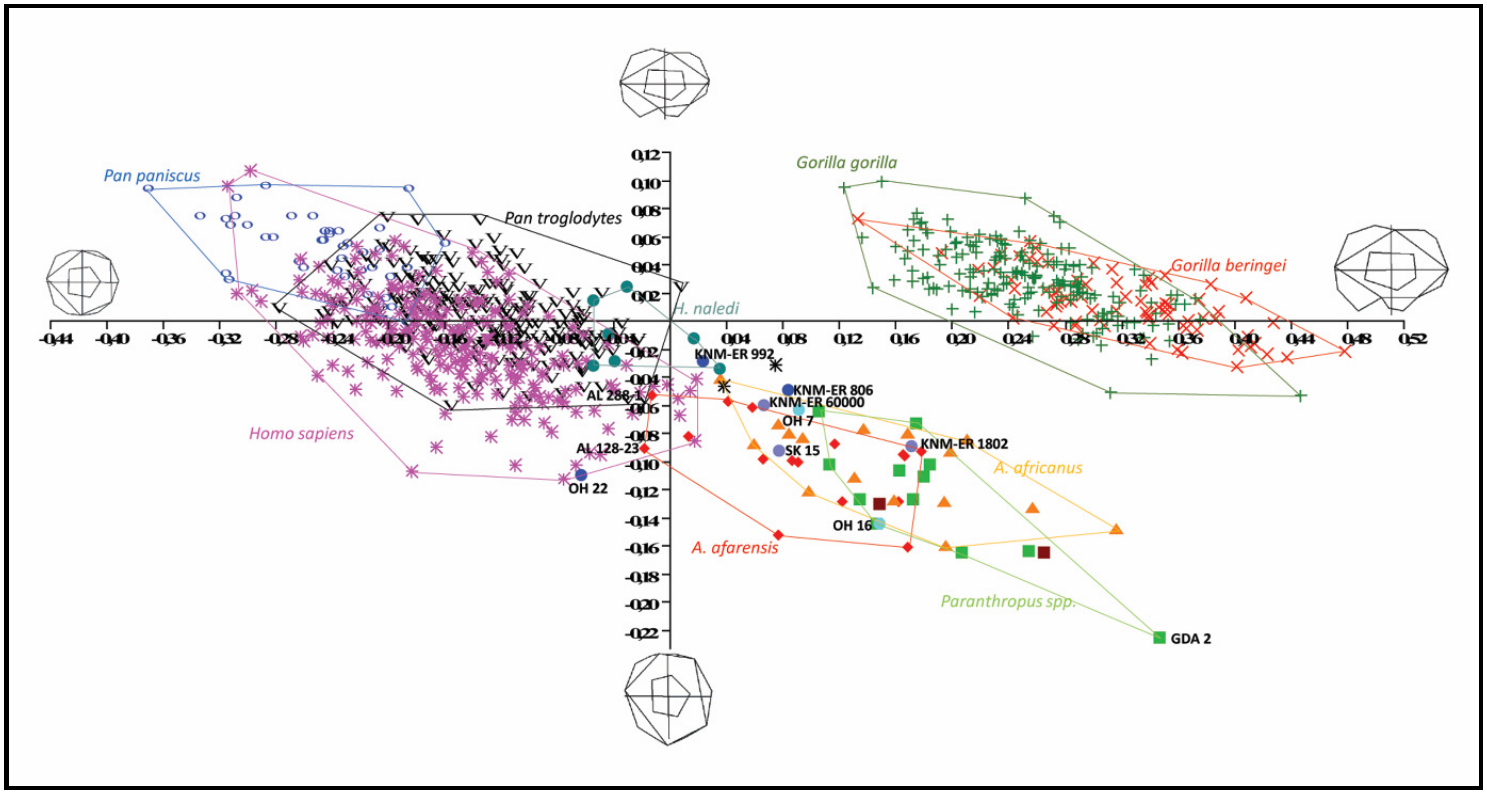


Figure 16. PCA results at the species level for five extant species (maximised samples) and extinct hominin species in the study

PC1 accounts for 89.2% of variance and is 99.6% correlated with centroid size; PC2 accounts for 4.11% of variance. The main factors contributing to PC1 are size and the length of the mesiodistal axis. The main factors contributing to PC2 (as illustrated by relative warps wireframes) are the buccolingual measurements across the breadth of the tooth in relation to the mesiodistal axis. Thus, small, narrow teeth will be found in the top left quadrant (i.e. positive PC1 and negative PC2 loadings); large, narrow teeth in the top right quadrant (i.e. positive PC1 and PC2 loadings); small, broad teeth in the bottom left quadrant (i.e. negative PC1 and PC2 loadings) and large broad teeth in the bottom right quadrant (negative PC1 and positive PC2 loadings). (Legend: blue circles: *P. paniscus;* pink stars: *H. sapiens;* black "V": *P. troglodytes;* green "+": *G. gorilla;* red "X": *G. beringei*; teal/dark turquoise circles: *H. naledi;* black stars: *A. sediba;* dark blue circles: *H. ergaster/erectus* or Later Pleistocene *Homo;* light turquoise circles: *H. habilis;* lilac circles: Early *Homo;* red diamonds: *A. afarensis;* orange triangles: *A. africanus;* green rectangles: *P. robustus;* brown rectangles: *P. boisei*)

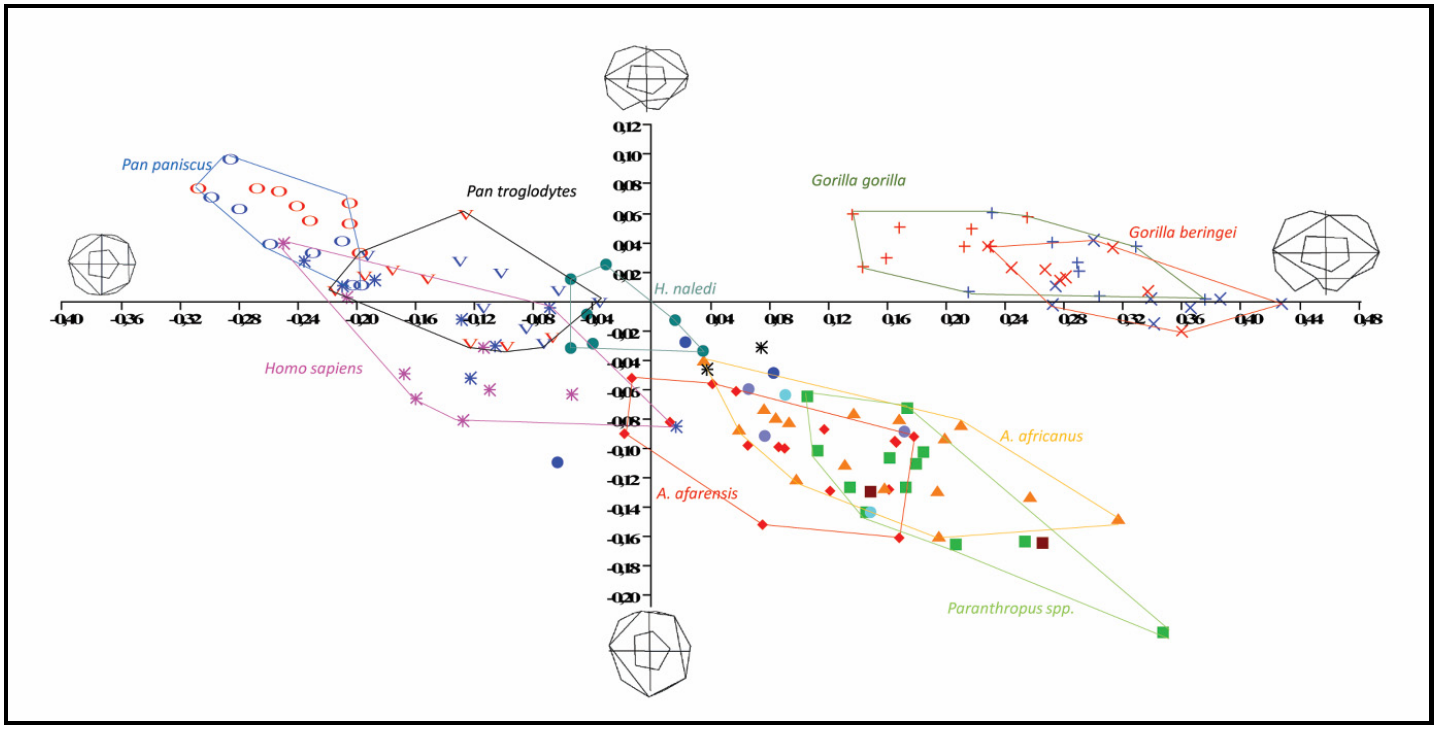


Figure 17. PCA results at the species level for five extant species (randomly selected matched-size samples, sexes indicated in blue and pink/red) and extinct hominin species in the study

PC1 represents 89.2% of variance and is 99.6% correlated with centroid size; PC2 represents 4.11% of the variance. The main factors contributing to the variance along the x-axis (PC1) are size and the length of the mesiodistal axis. The main factors contributing to variance along the y-axis (PC2) are buccolingual dimensions of the tooth. Thus, small, narrow teeth will be found in the top left quadrant (positive PC1, negative PC2); large, narrow teeth in the top right quadrant (positive PC1 and PC2); small, broad teeth in the bottom left quadrant (negative PC1 and PC2) and large broad teeth in the bottom right quadrant (negative PC1 and positive PC2). (Legend: blue circles: *P. paniscus;* pink stars: *H. sapiens;* black "V": *P. troglodytes;* green "+": *G. gorilla;* red "X": *G. beringei*; teal/dark turquoise circles: *H. naledi;* black stars: *A. sediba;* dark blue circles: *H. ergaster/erectus* or Later Pleistocene *Homo;* light turquoise circles: *H. habilis;* lilac circles: Early *Homo;* red diamonds: *A. afarensis;* orange triangles: *A. africanus;* green rectangles: *P. robustus;* brown rectangles: *P. boisei*).

In the all-inclusive, "maximised samples" PCA plot (Figure 16), *G. beringei* molars differ significantly more in morphospace by size than by shape/breadth of crown: the size:shape variability ratio is well over 3:1 in this analysis. *G. gorilla* molars exhibit almost as much as size variability as *G. beringei* molars, but differ more in terms of shape. However, based on clustering visualised in Figure 16, if a few outliers of *G. gorilla* are ignored, the main specimens in this large sample group also more horizontally than vertically (size again being the main contributor to variability in this sexually dimorphic species, rather than shape). *P. paniscus* and *P. troglodytes* molars vary less in terms of size and more proportionally in their shape/breadth (the ratio is closer to 2:1 in terms of size:shape variability). *P. troglodytes* molars (from four subspecies comprised of 13 identified populations spanning far western Africa to eastern Africa) show more variability than those of *P. paniscus* (no subspecies, and comprised of three populations spanning a limited geographical range). Modern *H. sapiens* lower second molars vary as much as those of *Gorilla* in size (although smaller ranges would be expected due to allometry) and almost twice as much in shape. In sum, based on the way that the molars of extant species plot in morphospace (Figure 16, Figure 17 and Table 23), it is possible to make some comments about the visual "patterning" of species clusters.

Size verus shape – sexually dimorphic species

Size-versus-shape variability in sexually dimorphic species is characterised by large size variance compared to shape variance. In morphospace, clustering is generally spread along PC1 (size-related axis) and relatively less along PC2 (shape-related axis), giving sexually dimorphic species a more "horizontal" clustering in morphospace. Moreover, on analysis of the clustering along PC1 (size axis), molars belonging to females plot predominantly at lower values along the axis than do molars belonging to males,

particularly at the subspecies level. The ratio of size to shape (PC1:PC2 ranges), would be between about 3.3:1 and 4:1, as calculated on the basis of observed ranges of variability along these axes (the ratio for *G. gorilla* might be lower, but five outliers out of a total of 179 specimens account for a disproportional amount of shape variance, and a more realistic distribution is, on average, more weighted towards size variability than shape variability, similar to that observed in *G. beringei*).

Size verus shape – non-sexually dimorphic species

Size-versus-shape variability in non-sexually dimorphic species is characterised by both size and shape variance, giving these species a more "diagonal" clustering in morphospace. Narrow molars with small centroid sizes belonging to both males and females will cluster towards more negative values along PC1 and more positive values along PC2; larger, broader molars across the crown, belonging to both males and females, will cluster towards more positive values along PC1 and more negative values along PC2. The size:shape ratios (PC1:PC2 ranges) for non-sexually dimorphic species would therefore be expected to be lower than those for sexually-dimorphic species, for which size is a more important factor of variance. Ratios of around 2:1 to 2.2:1 might probably be expected for non-sexually dimorphic species, based on values calculated from this study.

Size verus shape – summary: extant species

Thus, on examination of Figure 16, Figure 17 and Table 23, size-shape clustering patterns describing the ranges of variability of lower second molars for the five extant species can be summarised in preparation for comparison with the patterns of clustering observed for specimens attributed to the extinct hominin species. With the

exception of five unusually narrow molars and two unusually broad molars within the *G. gorilla* group, both species of *Gorilla* group in a generally horizontal pattern in morphospace (predominantly size variability, less shape variability by comparison). The molars of *Pan* species group proportionally more along PC2 than do those of *Gorilla* species, i.e. less "horizontally" along the size axis, and more "vertically-diagonally" along both size and shape axes, indicating that shape variability is more pronounced within the former species, relative to size variability. *Pan* species exhibit about half as much variability in shape compared to size, while *G. beringei* exhibits about a third as much.

Modern human variability as visualised in morphospace is also represented by a "diagonal" clustering pattern, but there is a significant increase in the measurable ranges of variability for this species. Size variability as plotted in morphospace is almost as much as the highly sexually dimorphic *G. beringei,* which includes two species characterised by size differences, so that there is not just sexual dimorphism but subspecies size differences that factor in to the range of size variability within this species (*G. b. graueri* has the largest molars in the *Gorilla* genus, meaning that the difference in size between the smallest female *G. b. beringei* molar and the largest male *G. b. graueri* molar is wider than the difference would be between the smallest female *G. g. diehli* molar and the largest male *G. g. gorilla* molar). Size variability in modern *H. sapiens* is therefore not able to be explained by sexual dimorphism, nor as a result of the existence of differently-sized subspecies, as would be the case for *G. beringei,* the species with the most size variance in this study. In terms of shape variability as well, no other extant species in this study exhibits the same extent of the range of variance exhibited by modern *H. sapiens,* especially taking into account the generally small size of *H. sapiens* teeth, compared to those of *G. beringei*. In fact, the shape variance in modern *H.*

sapiens molars is double that of *G. beringei* molars, in both analyses (maximised-size samples and representative limited-size samples; Table 23, left-hand and right-hand sides). In the maximised-sample analysis (Figure 16 and Table 23, left-hand side), the excessive shape variability exhibited by *H. sapiens* outweighs even the excessive size variability in morphospace, giving the clustering a much more "vertical-diagonal" pattern on the plot, and the lowest size:shape ratio of all the extant species (1.51:1 size-to-shape ratio for the maximised sample of *H. sapiens* – Table 23, left-hand side). This is partially due to two very "narrow" molar outliers, which rival the relative proportions of the narrowest *G. gorilla* and *P. paniscus* molars and which cluster with *P. paniscus* molars in terms of their size (Figure 16). When an illustrative, "representative" sample of 16 (with average CV values for a limited-sized sample for this species) is plotted in morphospace, these outliers are absent and the size:shape variability ratio rises to 2.15:1 (Table 23, right-hand side).

Allometric scaling

Singleton (2011) noted that in the absence of allometry, *P. paniscus* and *P. troglodytes* lower molars are virtually indistinguishable. This was observed in Dykes (2014) between small samples of *P. paniscus* and *P. t. schweinfurthii,* as well as between male and female *G. g. gorilla* teeth; other researchers (Pilbrow, 2006, 2010, for instance) have also noted that raw size measurements provide improved discrimination between species and subspecies. In the absence of comprehensive body weight data, it has not been possible in this present study to control for allometric scaling, particularly given the large sample sizes. A relevant allometric study (e.g. Singleton, 2011) involves randomised sampling and comparison of wireframes, linking shape variability (or the absence thereof) to body size. The findings of Paragraph 4.1 of this present study indicate that discriminant function analyses did not identify purely raw measurements

and size as factors discriminating (in isolation) between groups at the species and subspecies level. In fact, it was not raw measurements in isolation from each other that provided the best discrimination between groups, but these measurements (and angles) taken in relation to each other that seems to provide good discrimination between groups – these being predominantly the distal and the mesial cusp measurements, which should therefore be considered together, rather than in isolation. What can be proposed is that allometry does not account for all variation between groups, and that there must be other factors at play. Indeed, taking into account the size clusterings of the molars of modern *H. sapiens* groups in Figure 21 and Figure 22, where molars of small-bodied hunter-gatherer communities (e.g. Babinga pygmies) group with those of larger-bodied hunter-gatherer communities (e.g. Australian Aboriginals) at the "large, robust molar" side of the x-axis ("size" axis), and noting that groups with extremely reduced-size molars in populations that transitioned early to agriculture do not all typically have reduced body sizes, it might be concluded that the wide shape variance in modern *H. sapiens* would not be directly related to allometric scaling, and that something more adaptive in nature is the cause of variance in tooth size and shape – in this instance, primarily subsistence strategies and the proportions of hard:soft foods in the diet. Likewise, among populations of *Pan,* it would be important to study diets and other factors that might drive tooth shape change in *P. paniscus* and *P. troglodytes,* down to the individual population, level before confirming that allometric scaling fully explains morphological variance (or lack thereof) between lower second molars from different groups. The Singleton study (2011) used a small sample of *Pan* molars, at a species level. However, at the population level, it would seem that body size does not necessarily scale with overall size of tooth, and that tooth crown proportions are not necessarily homogenous across similarly-sized population groups, even within the same

subspecies. Some groups with small body size have lower second molars whose overall shape (relative breadth of tooth) falls outside the norm for their species/subspecies (Table 24). For instance, *P. paniscus* is distributed across three population groups with evenly matched lower second molar size; however, population 14 (as categorised in Pilbrow, 2006) has extremely narrow molars by comparison to the other two groups, followed by population 9 (*P. t. schweinfurthii*), whose molars are the second largest of all the populations of *Pan*. Likewise, population 12 (per Pilbrow, 2006) comprises individuals of *P. t. schweinfurthii* mainly from Gombe, which have small body size (Morbeck & Zihlman, 1989). Yet their molar size is average for their subspecies (tooth size is not scaled to match more closely with bonobos, whose body proportions the Gombe chimpanzees match more closely), and the molars are unusually broad by comparison to the generally narrow *P. t. schweinfurthii* molars. Clearly, something other than pure allometry must be driving tooth size and shape, in certain cases at least.

Table 24. *Pan*: regional breakdown of relative breadth, size and cusp breadths of lower second molars

Region	AVG MD:BL	Region	AVG CENTROID	Region	AVG MESIAL	Region	AVG DISTAL
14	1.226264	16	3.098833	16	8.508861	16	8.259292
9	1.2229121	14	3.126303	14	8.620551	14	8.465525
10	1.2160066	15	3.143411	15	8.955998	15	8.574108
5	1.2082387	4	3.217876	8	9.499571	4	9.505161
13	1.2077853	8	3.224107	4	9.547413	8	9.518514
8	1.2061921	7	3.235254	13	9.749854	13	9.690577
11	1.1951548	6	3.24409	6	9.811725	7	9.726089
6	1.1881239	13	3.244487	7	9.833139	11	9.737414
16	1.1870993	12	3.247328	5	9.922143	12	9.793638
15	1.1814437	11	3.25788	10	9.967337	6	9.801772
7	1.1768958	5	3.262827	11	10.00876	10	9.866465
4	1.1762778	10	3.26596	12	10.06346	5	9.935474
12	1.1762508	1	3.271571	1	10.39821	1	10.08168
2	1.1324408	9	3.304464	9	10.4686	9	10.21582
1	1.1302841	2	3.316065	2	10.96861	2	10.51095

Colour/region key: Blue (populations 1-2): *P. t. verus;* Pink (4): *P. t. ellioti;* Mauve (5-8): *P. t. troglodytes;* Light orange (9-13): *P. t. schweinfurthii;* Green (14-16): *P. paniscus*

What can be said, when comparing fossil hominin lower second molars to those of extant species, is that raw measurements of size (per species) should be considered of great importance, even if allometry does not completely account for the variability being measured, particularly shape variability. *Paranthropus robustus* teeth might vary in size in a range more closely matched to that of *Gorilla* species, rather than that of *P. paniscus,* and comparisons of size range must certainly bear this in mind. It is, however, the relationship between shape and size variability that is mainly considered in this study: expressed as a ratio ("size" axis range versus "shape" axis range) or a coefficient of variation (CV), it is possible to gain a better insight into comparative/relative patterns of size-shape variability rather than raw measurement ranges taken in isolation. Mesial cusp measurement variability taken together with distal cusp measurement variability will also be important in providing additional insights into expected ranges of shape variability in fossil hominin species' lower second molars.

Size verus shape – comparison: extinct hominin species

Comparing size and shape variability of molars of the fossil hominin taxa, at first glance, most extinct hominin species fall within the same numeric range of size/shape variability as those of most extant species. The hominin species exhibiting the greatest size variability of lower second molars along PC1 was *A. africanus,* with *P. robustus* and *A. afarensis* exhibiting a similar size variation range (Figure 16 and Table 23). These ranges (Table 23, left-hand side) for *A. africanus, A. afarensis* and *P. robustus* were not dissimilar to the size ranges exhibited in morphospace by *P. troglodytes.* When comparing size and shape variability together, however, there are differences between variability patterns of fossil hominin species and the extant species, as visualised in morphospace and as calculated in Table 23. The size-to-shape variability ratios of *P.*

robustus and *A. afarensis* lower second molars are lower than those observed for any of the African great ape species. This is explained by the fact that there are high levels of shape variability between specimens attributed to these groups, in relation to their size variability: more so than are evident for species of *Pan.* *A. africanus* shows similar shape:size variation to that of *P. troglodytes*, at least when the full range of variability of the extant species is included in the analysis. The actual measured range of size variability for *A. africanus* is the highest among the fossil species.

When comparing the ranges of variability of these three hominin species to the illustrative "representative" size-matched samples of extant species in morphospace (Figure 17 and Table 23, right-hand side), size variability of all three species (especially *A. africanus*) exceeds that of the representative limited-sized sample variability of *Pan* species, and the only extant species with a similar range of size variability is modern *H. sapiens.* In respect of shape variability, *A. afarensis* and *A. africanus* have similar ranges to that of modern *H. sapiens* but these ranges are well in excess of the expected ranges for a typical sample of 16 individuals of *Pan* species. They have, furthermore, approximately double the expected shape ranges for a typical sample of 16 individuals of both *Gorilla* species. On examination of the size:shape variability ratios of *A. afarensis, A. africanus* and *P. robustus.,* compared to the expected ranges for samples of 16 individuals of the extant species, there would appear to be excessive size-to-shape variability in *A. africanus* by comparison to *Pan* and *H. sapiens*, and excessive shape-to-size variability in *P. robustus*, compared to all of the extant species. However, on closer inspection of Figure 17, much of the shape variability measured for *P. robustus* along the second PC axis (y axis) is accounted for by the unusually large and unusually broad molar belonging to the specimen from Gondolin, GDA 2. Should this single outlier be

excluded from the analysis, the range of variation along PC2 (shape variation) for *P. robustus* would be less than that measured for *A. africanus,* and closer to that measured for *A. afarensis.* In terms of their size-to-shape patterning as visualised in morphospace, none of these three species (*A. afarensis*, *A. africanus, P. robustus*) cluster, as currently attributed to their species groups, in a "horizontal" pattern, as would be the case for a typically sexually-dimorphic species with high size-shape variance ratios.

Other species of fossil hominins are less well-represented in terms of their sample size, but some groups appear more cohesive as "species" than do others, even accounting for small sample sizes. *A. sediba* is represented by two specimens only, which might be from the same family group (Berger et al., 2010). There is some size variability in *A. sediba* (e.g. MH 1, the male specimen, has larger molars than MH 2, the female specimen), but there is extremely limited shape variability between the specimens. Small as this sample is, there is a "horizontal" clustering pattern between the larger male molar and the smaller female molar, with little shape variability measured along the y-axis. This patterning would fit with the conclusion already made, that sexually dimorphic species differ in size but not by shape (within species/subspecies), but with only two specimens in the sample, no firm conclusions about the wider population from which these two individuals are from can be made. This is in contrast to *H. habilis,* which is also represented by two individuals in this study, and which are both differently sized and differently shaped. Specifically, OH 16 groups more readily within the area of overlap between the australopith and paranthropine groups while OH 7 (the type specimen for *H. habilis*) groups closer to other specimens attributed to the genus *Homo.* *Homo naledi* is represented by seven individuals, which show good cohesion as a group. The three

specimens attributed to *H. erectus/ergaster* are poorly grouped, on the other hand, with OH 22 plotting with smaller, modern human molars, in a similar size range to that of *H. naledi* lower second molars.

In sum, what is confirmed from these PCA analyses is that the more sexually dimorphic a species is, the more size becomes the principal factor in describing variability between individuals in the species, with males and females varying in shape more or less equally, but varying by sex according to size. The shape:size ratio of variability (y:x axis ranges, or PC2:PC1 range ratio) decreases as sexual dimorphism increases (otherwise stated, the size:shape variability ratio, as measured by PC1:PC2 ranges of values, increases as sexual dimorphism increases). Clustering is therefore principally along the x-axis in highly dimorphic species. In species where size does not vary as greatly between individuals due to less sexual dimorphism, shape then becomes the main distinguishing factor in describing intra-species/inter-population variability in a mixed-sex sample. This is expressed in morphospace by a more vertical-diagonal spatial distribution than is the case for sexually dimorphic species. The vertical (shape) versus horizontal (size) distribution in morphospace becomes even more evident when sample sizes are reduced.

When comparing these patterns of size-shape groupings in morphospace based on reduced-size samples of extant species, only modern *H. sapiens* molars exhibit sufficient variance (even after reduction in sample size) in terms both of size and shape to be favourably comparable to variance exhibited by the two largest species samples of fossil hominins in the study, namely *A. afarensis* and *A. africanus*. The pattern of variance

exhibited by these extinct hominin species' molars, including wide ranges of both size and shape variability, does not match the pattern of variability exhibited by the molars belonging to individuals of sexually dimorphic species (i.e. *G. beringei* and *G. gorilla*). The variance exhibited by *H. sapiens* also exceeds the expected ranges of shape and size ranges of *Pan* species, despite the fact that *P. troglodytes* consists of four subspecies, one of which (*P. t. verus*) is highly distinct in molar shape and size from the other subspecies, and *H. sapiens* is a single species with no subspecies and low genetic diversity. The pattern and magnitude of size-shape variance of lower second molars of *P. robustus* likewise fail to follow the expected size-shape pattern and degree of variance exhibited by extant *Gorilla* and *Pan* species (Figure 17 and Table 23). Shape variability exhibited by the 12 *P. robustus* molars exceeds that of a random sample of 16 modern *H. sapiens* molars. Much of the shape variability, however, is accounted for by an outlier in the *P. robustus* group, GDA 2.

4.4.2 RANDOMISATION AND CV ANALYSIS

The PC analyses established that the ranges of morphospace (shape/size) variability expressed by lower second molar size and shape of specimens attributed to *A. africanus* (n=16)*, A. afarensis* (n=16), and *P. robustus,* (n=12) (and some of the less well-represented species groups in the analysis) seem high or at least differently spatially distributed in morphospace, by comparison to extant species groups. This difference in ranges of shape and size variability is most evident when comparing the extinct hominin species groups with similarly-sized representative samples of 16 specimens per extant species groups (with average coefficients of variation for this size of sample). The results of the randomisation and CV analyses that gave rise to the selection of the matched-size samples for the extant species are presented here.

CV ratios of key measurements for randomised samples of extant species

The three main raw length measurements that had been identified from DFA and PCA analyses as having contributed to the main loadings of variance between groups (MD length, BL breadth across the mesial cusps, BL breadth across the distal cusps – in relation to each other) formed the basis for the CV analysis between the extant species and the fossil species groups. Expected ranges of CV values are calculated for MD lengths, BL breadths across the mesial cusps and BL breadths across the distal cusps for any sample of 16 specimens for each extant species, as measured 1000 times by randomly selecting (with replacement) 16 specimens per sample at a time and calculating these CVs for each sample (Table 25). The average of 1000 CVs is calculated for each sample of 16 for each measurement and for each species (Table 25, third measurement cited in each case for each species).

Table 25. CV values for 1000 random samples of 16 specimens each of *G. beringei, G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens*

CV Values	1000 samples of 16	*MD length*	*Mesial breadth*	*Distal breadth*
G. beringei	Range: minimum value	*4.49*	*3.89*	*3.68*
	Range: maximum value	*10.12*	*9.73*	*9.47*
	Average	*7.39*	*6.82*	*6.36*
G. gorilla	Range: minimum value	*3.23*	*3.72*	*2.77*
	Range: maximum value	*8.98*	*11.86*	*11.02*
	Average	*5.77*	*7.01*	*6.60*
P. troglodytes	Range: minimum value	*3.29*	*2.77*	*3.22*
	Range: maximum value	*8.74*	*9.68*	*8.33*
	Average	*5.89*	*6.29*	*5.83*
P. paniscus	Range: minimum value	*2.78*	*2.95*	*3.05*
	Range: maximum value	*7.48*	*6.86*	*7.05*
	Average	*5.36*	*4.92*	*5.24*
H. sapiens	Range: minimum value	*3.59*	*2.48*	*3.28*
	Range: maximum value	*11.41*	*9.60*	*11.24*
	Average	*7.10*	*6.26*	*7.16*

In line with the size:shape patterns identified in morphospace, *G. beringei* shows more variability in molar length (MD length) rather than in either of the breadth measurements. *G. gorilla* shows higher variability in breadth measurements than does *G. beringei*, particularly across the mesial cusps. *P. paniscus* shows very limited variability in all three raw measurements, returning the lowest average randomised sample CVs of any of the five extant species in the study. *P. troglodytes* consists of four subspecies, one of which has generally much broader molars than the other three subspecies, and this is reflected in the wider range of CV values over 1000 randomised samples, particularly across the mesial cusps. Modern *H. sapiens* molars show extremely high variability across all three dimensions. For MD lengths, CV ranges (minimum to maximum value) measured over 1000 samples of modern *H. sapiens* molars are the highest of all five species, and the average randomised CV values for MD length variability approach the values for *G. beringei*, which is the species that exhibits the most variability in lengths of molars due to sexual dimorphism and because this species

consists of two subspecies with markedly different body sizes. The mesial cusp measurements for *H. sapiens* molars vary much in line with the same measurements in *P. troglodytes,* even though *H. sapiens* is comprised of different populations rather than subspecies, versus the four variable subspecies representing *P. troglodytes.* Variability across distal cusps exceeds that of all other extant species in the study, as indicated by the very high range of CV values returned from the analysis, as well as the high average CV value for randomised samples. Comparing results between *P. paniscus* and *H. sapiens*, which are the only two species in the study that have no subspecies, average randomised CV values for *H. sapiens* exceed those of *P. paniscus* by about 30% across the board, and the maximum values observed are up to 60% higher. Overall, the patterns observed in morphospace are again reflected in the randomised CV values for all five species.

Comparisons between average/probable CV ratios for samples of n=16 per extant species with actual CV ratios for samples representing fossil hominin species

The three most well-represented fossil samples were compared in turn to A) the two sexually dimorphic species in the study (*G. beringei* and *G. gorilla*), B) the two species of *Pan* (*P. troglodytes* and *P. paniscus*) and C) to modern *H. sapiens.* Frequency distributions of predicted CV ranges (1000 random samples, n=16) for each extant genus are presented in Figure 18, Figure 19 and Figure 20, respectively. The CVs of *A. afarensis, A. africanus* and *P. robustus* are plotted on the respective histograms where they fall. Thereafter, the probability (p) of encountering such a level of variability in the same-sized, or a similarly-sized, sample are presented in the following paragraphs, and summarised in Table 26**.**

Table 26. Probabilities that fossil species' CVs fall within the range of extant species' CVs.

Species	Sample size	CV	probability (p) of fossil species' CV falling within range of CVs of extant species				
		MD length	*G. beringei*	*G. gorilla*	*P. troglodytes*	*P. paniscus*	*H. sapiens*
A. afarensis	*n=16*	*6.28*	0.86	0.29	0.38	0.11	0.78
A. africanus	*n=16*	*8.17*	0.25	0.01	0.01	0.00	0.22
Paranthropus spp.	*n=14*	*7.21*	0.58	0.09	0.07	0.00	0.48
P. robustus	*n=12*	*7.33*	0.53	0.06	0.07	0.00	0.43
P. rob minus Gondolin	*n=11*	*4.35*	1.00	0.97	0.99	0.93	0.99
A. sediba	*n=2*	*3.83*	1.00	0.99	0.99	0.99	1.00
H. naledi	*n=7*	*3.56*	1.00	1.00	1.00	1.00	1.00
H. hab/rudolf.	*n=4*	*6.06*	0.89	0.40	0.45	0.21	0.83
H. erectus	*n=3*	*6.01*	0.91	0.40	0.45	0.21	0.83
Species	**Sample size**	**CV**	**probability (p) of fossil species' CV falling within range of CVs of extant species**				
		Mesial breadth	*G. beringei*	*G. gorilla*	*P. troglodytes*	*P. paniscus*	*H. sapiens*
A. afarensis	*n=16*	*7.53*	0.28	0.36	0.14	0.00	0.12
A. africanus	*n=16*	*8.47*	0.08	0.15	0.03	0.00	0.02
Paranthropus spp.	*n=14*	*7.39*	0.34	0.36	0.18	0.00	0.16
P. robustus	*n=12*	*7.43*	0.28	0.36	0.18	0.00	0.16
P. rob minus Gondolin	*n=11*	*5.17*	0.95	0.92	0.85	0.38	0.84
A. sediba	*n=2*	*1.91*	1.00	1.00	1.00	1.00	1.00
H. naledi	*n=7*	*4.92*	0.97	0.96	0.92	0.50	0.94
H. hab/rudolf.	*n=4*	*7.01*	0.44	0.48	0.27	0.00	0.27
H. erectus	*n=3*	*5.75*	0.87	0.87	0.70	0.10	0.72
Species	**Sample size**	**CV**	**probability (p) of fossil species' CV falling within range of CVs of extant species**				
		Distal breadth	*G. beringei*	*G. gorilla*	*P. troglodytes*	*P. paniscus*	*H. sapiens*
A. afarensis	*n=16*	*7.34*	0.22	0.26	0.04	0.00	0.47
A. africanus	*n=16*	*8.14*	0.07	0.12	0.00	0.00	0.25
Paranthropus spp.	*n=14*	*8.81*	0.01	0.07	0.00	0.00	0.13
P. robustus	*n=12*	*9.22*	0.00	0.04	0.00	0.00	0.07
P. rob minus Gondolin	*n=11*	*5.75*	0.69	0.76	0.59	0.26	0.88
A. sediba	*n=2*	*1.81*	1.00	1.00	1.00	1.00	1.00
H. naledi	*n=7*	*3.87*	1.00	1.00	0.99	0.98	1.00
H. hab/rudolf.	*n=4*	*5.10*	0.88	0.92	0.85	0.63	0.95
H. erectus	*n=3*	*6.55*	0.47	0.49	0.19	0.02	0.68

The CVs calculated for *A. afarensis* were 6.28%, 7.53% and 7.34%, respectively, for MD length, BL breadth across the mesial cusps and BL breadth across the distal cusps. For *A. africanus,* these figures were 8.17%, 8.47% and 8.14%, and for *P. robustus*, these figures were 7.33%, 7.43% and 9.22%.

CV Comparisons – *Gorilla* species (sexually dimorphic species)

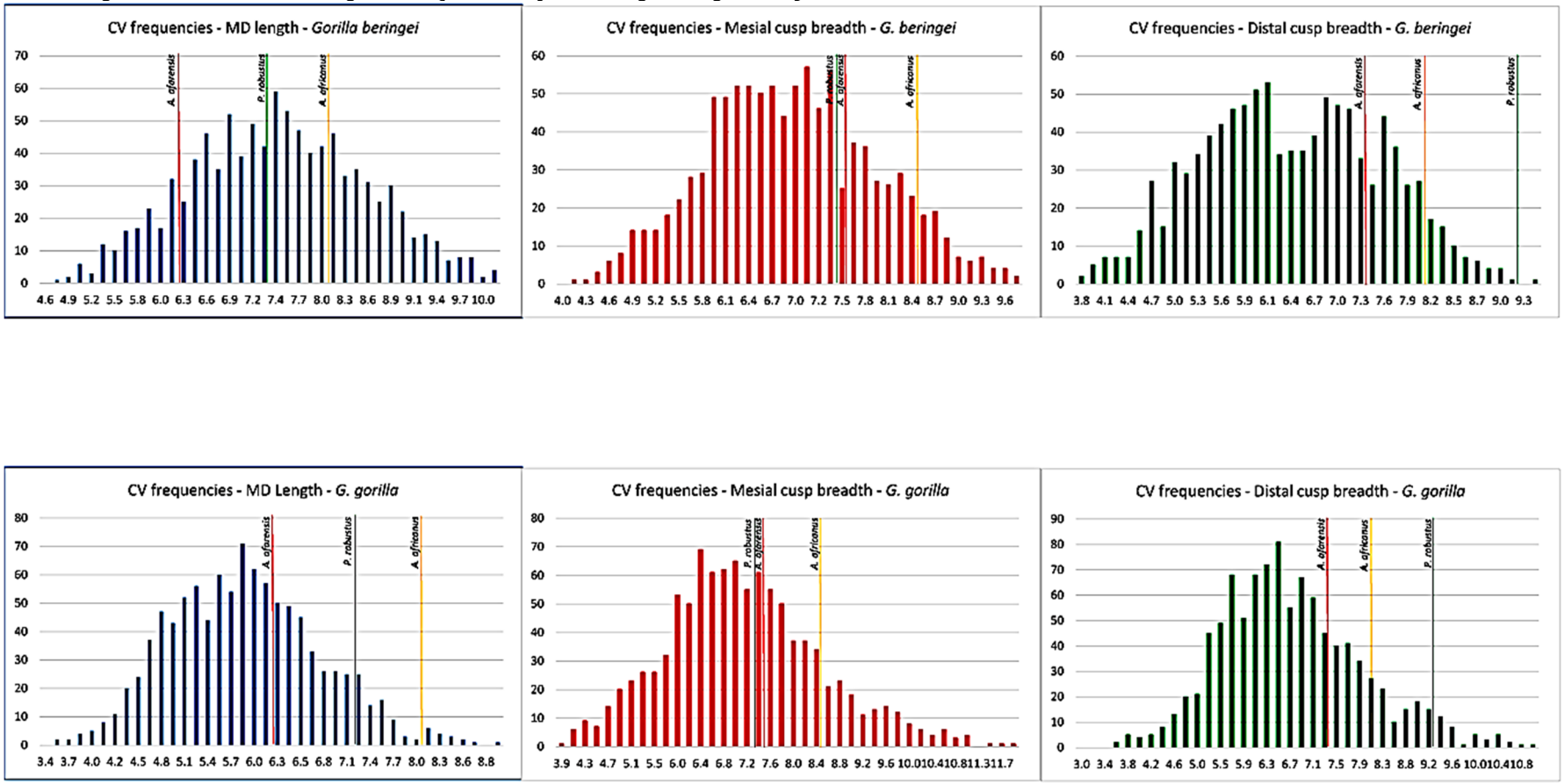


Figure 18. Frequency distributions of CVs of molar dimensions of *G. beringei* (top) and *G. gorilla* (bottom).

CVs of a) MD length (blue bars); b) BL breadth across mesial cusps (red bars); and c) BL breadth across distal cusps (green bars). Actual samples of *A. afarensis* (red line), *A. africanus* (orange line) and *P. robustus* (green line) are inserted where applicable onto the frequency distributions.

Australopithecus afarensis – Gorilla beringei

It was previously noted from the DFA and PCA results that *G. beringei* exhibits a great deal of size/length variability and less shape/breadth variability compared to *G. gorilla.* For this reason, all three species that exhibit considerable variability both in size/length and shape/breadth show higher probabilities of CVs falling within the expected MD length CVs of *G. beringei,* and higher probabilities of their breadth-related CVs matching expected patterns of frequencies of *G. gorilla* histograms. There was a probability of p=0.86 that the CV of *A. afarensis'* molar MD lengths would fall within the range of size-matched samples of *G. beringei* molars for the same variable. However, the probability that the breadth measurements (mesial and distal cusps) would be within the same CV ranges as those of *G. beringei* fell to p=0.28 and p=0.22, respectively. All three CV values for *A. afarensis*, therefore, fall within probable ranges of CVs for this species; however, the pattern of variability does not quite match the expected size:shape variability of this highly dimorphic species (i.e. size variability is well within range, but shape variability is higher than expected if the taxon were to match size:shape variability of *G. beringei*).

Australopithecus afarensis – Gorilla gorilla

Comparisons with *G. gorilla* were slightly more within the same expected patterning for the length and breadth CV values since this species showed more variability in the breadth of molars, along with the dimorphism-driven MD length variability. Probabilities that the CVs for MD length, mesial cusp breadth and distal cusp breadth of *A. afarensis* would fall within the range of the equivalent CVs for size-matched samples of *G. gorilla* were p=0.29, p=0.36 and p=0.26, respectively. In this analysis, therefore, *A.*

afarensis not only falls within the range of CV values for both size and shape, but within the same proportional variability between size and shape.

Australopithecus africanus – Gorilla beringei

A. africanus CVs were higher for all three measurements than those of *A. afarensis,* particularly compared to the CV for MD lengths. Probabilities of *A. africanus* specimens falling within the same range of CV values for equally-matched samples of *G. beringei* were p=0.25, p=0.08 and p=0.07 for the MD lengths, the BL (mesial) breadths and the BL (distal) breadths, respectively. This implies that crown breadth measurements across the sample representing *A. africanus* are certainly more variable than the average molars selected for any random sample of 16 *G. beringei* molars.

Australopithecus africanus – Gorilla gorilla

In comparisons with *G. gorilla*, CV values for *A. africanus* specimens do not match well. The probability (p) that CVs of the shape/width variables of *A. africanus* would fall within the expected range of probable CV values of size-matched samples of molars from *G. gorilla* were 0.15 and 0.12 for the CVs of the BL breadths across the mesial and distal cusps, respectively. However, there was a negligible probability that the CV value for this fossil species returned for MD length measurements would fall into the range of probable CV values for *G. gorilla* (p= 0.01). Great variability in the MD lengths of teeth in this sample make it unlikely that the sample follows the same size:shape levels of variability as exhibited by a sexually dimorphic species such as *G. gorilla.*

Paranthropus robustus – Gorilla beringei and *Gorilla gorilla*

P. robustus lower second molars used for this analysis exhibit great variability both in size and shape, showing particular shape differences between mesial and distal cusp BL measurement ratios. Specimens representing *P. robustus* in this analysis matched the similarly-sized sample CVs for the highly length-variable *G. beringei,* but had a probability of only 0.06 of falling within the range of CVs for MD lengths of *G. gorilla.* Across mesial cusps, ranges matched the expected ranges of both extant species a little better, with probabilities of 0.28 and 0.36 of the mesial BL breadth CVs falling within the range of *G. beringei* and *G. gorilla*, respectively. Distal cusp measurements, as expected, were much more variable than should be expected for similarly-sized samples from the sexually dimorphic species represented in the analysis. Raw distal cusp BL measurements varied greatly between the gracile type specimen from Kromdraai, TM 1517, and the substantially more massive lower second molar from Gondolin, GDA 2. The CV for *P. robustus* measured for buccolingual breadth across distal cusps fell almost out of the range for similarly-sized samples of *G. beringei* ($p = 0.001$), and exhibited less than a probability of $p=0.04$ of falling within the range of distal cusp variability of *G. gorilla.* Given that this comparison is not using exactly matched sample sizes in this instance (this analysis has been based on 1000 randomly-selected samples of 16 specimens each for the extant species, while the sample representing *P. robustus* consists of only 12 specimens and random draws are not possible), the probability that any given sample of 12 randomly chosen *G. beringei* or *G. gorilla* specimens would show this level of variability in its distal cusp measurements would therefore be significantly less than $p=0.001$ and $p=0.04$ for *G. beringei* and *G. gorilla* respectively. Surprisingly, when *P. boisei* specimens were added to the *P. robustus* specimens, CVs for all three

measurements fell marginally better within the ranges of CVs for both species. While this did not improve the probability of paranthropines as a whole falling within the range of variability of measurements across the distal cusps by comparison to *G. beringei* (the probability of 0.001 rose to 0.01 with the inclusion of *P. boisei* within the sample, and the probability of the distal cusp CVs falling within the range of *G. gorilla* closely-matched samples rose from 0.04 to 0.07), the other probabilities rose by 3-6%. The inclusion of *P. boisei* specimens (n=2) increases the *Paranthropus spp.* sample size to n=14, so the comparisons with samples of n=16 *G. beringei* and n=16 *G. gorilla* are more relevant than comparisons with a sample size of n=12 for *P. robustus* alone. What is more interesting to note is that if the Gondolin specimen were omitted from the specimens representing *P. robustus*, CV values for this species would fall substantially across the board, as this specimen is an outlier contributing significantly to both size and shape variance. If GDA 2 is omitted, *P. robustus* would have only 11 specimens in the sample (which is being compared with randomised samples of 16 each for the *Gorilla* species). However, in the absence of this outlier, with CVs reduced to 4.35%, 5.17% and 5.75% for the MD, BL (mesial) and BL (distal) measurements, respectively, the probabilities that this sample (*P. robustus* minus GDA 2), consisting mainly of specimens from Swartkrans, would fall well within the range of expected CVs for *G. beringei* were p=1 (100% probability), p=0.95 and p=0.69, respectively, and for *G. gorilla* these probabilities were p=0.97, p=0.92 and p=0.76.

To summarise, in comparison to the two sexually-dimorphic species of *Gorilla, A. afarensis* falls within the ranges of expected CVs of *G. beringei,* particularly in the MD length of molars, and seems to follow the length:breadth patterning of *G. gorilla.* The

high variability exhibited by specimens attributed to *A. africanus* result in this species, or at least the specimens representing the species in this study, being a poor candidate for comparisons with *G. beringei* coefficients of variation. Variability in the MD length measurement of these fossil lower second molars also seems to preclude this species from the expected range of variability exhibited by lower second molars of *G. gorilla. Paranthropus* specimens represented in this study exhibit excessive variability across the distal cusps, falling outside of the expected range of similarly-sized sample variability of either of the *Gorilla* species. If, however, the Gondolin molar is excluded from *P. robustus,* the remaining specimens from two different sites show good cohesion as a group. Specifically, the CVs for all three measurements of this fossil group would, in the absence of GDA 2, fall well within the expected ranges of CVs exhibited by similarly-sized samples of both *Gorilla* species.

CV Comparisons – *Pan* species – not sexually dimorphic

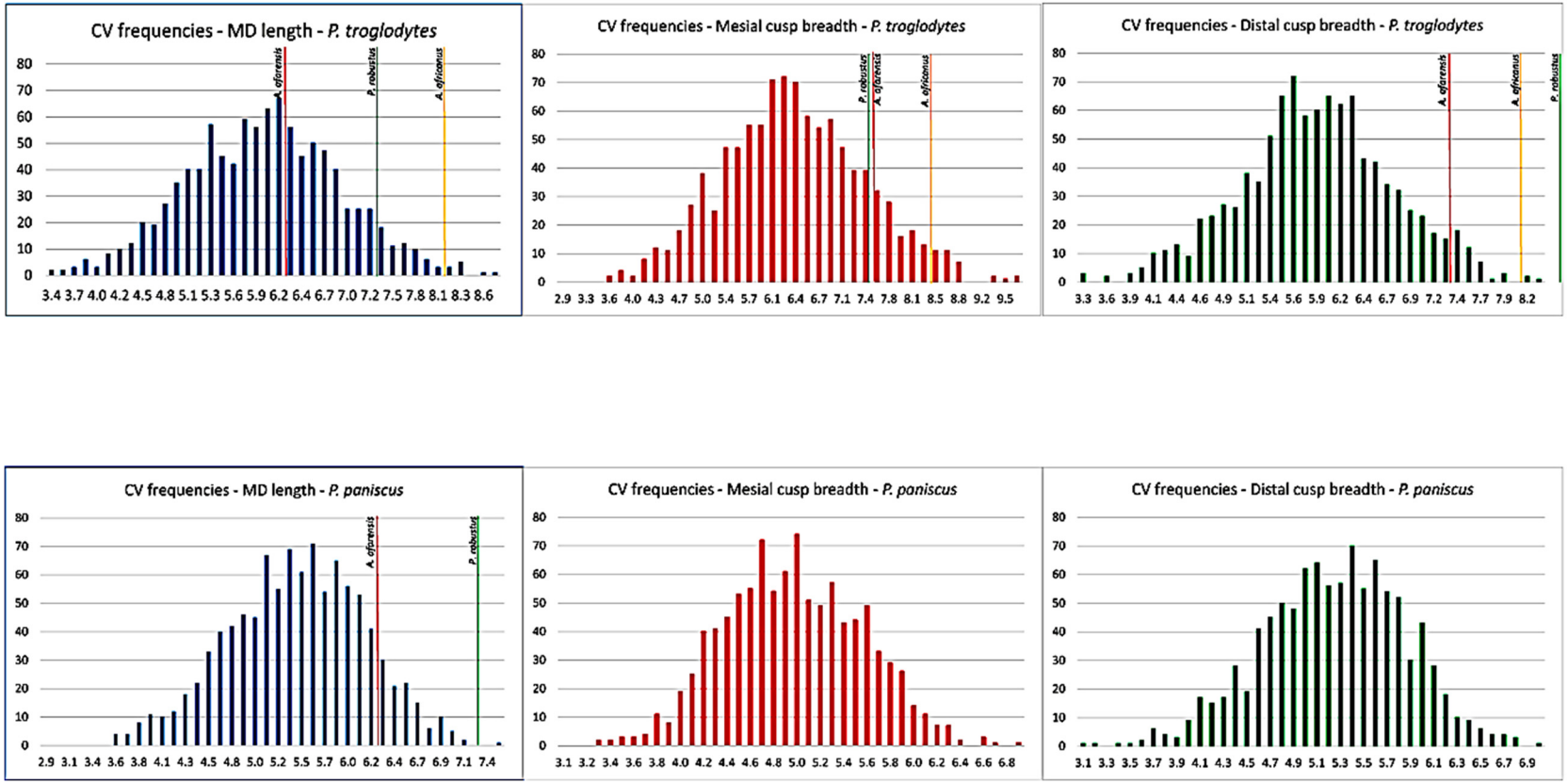


Figure 19. Frequency distributions of CVs of molar dimensions of *P. troglodytes* (top) and *P. paniscus* (bottom).

CVs of a) MD length (blue bars); b) BL breadth across mesial cusps (red bars); and c) BL breadth across distal cusps (green bars). Actual samples of *A. afarensis* (red line), *A. africanus* (orange line) and *P. robustus* (green line) are inserted where applicable onto the frequency distributions.

Australopithecus afarensis – *Pan* species

The CVs of the three raw measurement dimensions of the specimens attributed to *A. afarensis* have probabilities (p) of falling within the range of size-matched samples of *P. troglodytes* of 0.38, 0.14 and 0.04 for the MD lengths, the BL breadths across the mesial cusps, and the BL breadths across the distal cusps, respectively. There is, therefore, a probability (p) of less than 0.05 that the range of variability of distal cusp measurements of the group of 16 specimens attributed to *A. afarensis* in this study would be within the range of a typical sample of 16 *P. troglodytes* molars. When compared to *P. paniscus,* CVs of the breadth measurements (both mesial and distal) of *A. afarensis* fall well outside of the expected range of CVs for this species (p=0.00 in both cases). The CV of MD length measurements for this sample have a 0.11 probability of being within the expected range of CVs for *P. paniscus.*

Australopithecus africanus – *Pan* species

The CVs of all three raw measurements of *A. africanus* lower second molars in the study fail to fall within a probable range of CVs for either *Pan* species. In comparison with *P. troglodytes* size-matched samples, probabilities (p) of finding CVs as high as those calculated for this sample of *A. africanus* molars were 0.01, 0.03, and 0.0, respectively. These probabilities were reduced to zero for all three dimensions in comparisons with size-matched samples of *P. paniscus.*

Paranthropus robustus – *Pan* species

Variability within the specimens making up the sample of *P. robustus* again render it unlikely that the observed high CVs would be found in a similarly-sized sample of either species of *Pan.* CVs for the MD length, the BL breadth across the mesial cusps and the BL breadth across the distal cusps for *P. robustus* were 7.33%, 7.43%, and 9.22% respectively. The probability (p) of finding such high CVs for these measurements in a random sample of 16 specimens of *P. troglodytes* were 0.07, 0.18, and 0, respectively. Variability across the distal cusps therefore precludes *P. robustus* from falling within an expected range of variability for a sample of 16 *P. troglodytes.* There was zero probability of finding such high CVs (across all three dimensions) among similarly-sized samples of *P. paniscus.* If, however, the Gondolin molar is removed from the *P. robustus* sample, the remaining eleven specimens in the sample have much reduced CVs for the three measurements (4.35%, 5.17%, and 5.75%, respectively) and the probabilities (p) of finding CVs as high as these in similarly matched samples of *Pan* become 0.99, 0.85, and 0.59 for *P. troglodytes*, and 0.93, 0.38, and 0.26 for *P. paniscus.*

In summary, if all the specimens selected for this study are correctly allocated according to their fossil hominin species groups, none of the three extinct species' molars demonstrate similar levels of variability to those shown by numerically similarly-sized samples of *P. paniscus. A. africanus* shows excessive variability across all three raw measurements, which precludes this particular sample of specimens from falling within the observed range of variability for *P. troglodytes.* The other two species' samples show such variability in their distal cusp measurements that they, too, are unlikely to fall

within the range of variability of *P. troglodytes*, even though there are very small probabilities of the other dimensions falling within expected ranges for this species.

The exception to this observation would be *P. robustus,* if the Gondolin molar were excluded from the sample. If that were the case, the remaining 11 specimens, from two different sites, would fall easily within the expected range of variability of similarly-sized samples of both *P. troglodytes* and *P. paniscus.*

CV Comparisons – modern *Homo sapiens*

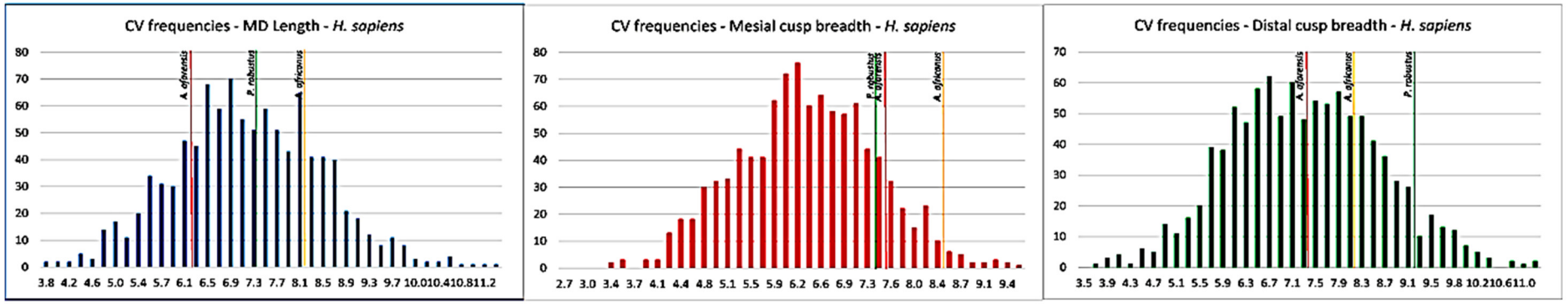


Figure 20. Frequency distributions of CVs of molar dimensions of Homo sapiens

CVs of a) MD length (blue bars); b) BL breadth across mesial cusps (red bars); and c) BL breadth across distal cusps (green bars). Actual samples of *A. afarensis* (red line), *A. africanus* (orange line) and *P. robustus* (green line) are inserted where applicable onto the frequency distributions.

Although, like *P. paniscus,* modern *H. sapiens* is a single species comprised of populations rather than subspecies, ranges of variability in CVs for all three dimensions that account for most of the variability within and between groups in this study are considerably higher than for any of the other extant species studied here. Unlike the comparisons with *Pan* species, and with the exception of *A. africanus* in one of the dimensions measured (i.e. mesial cusp breadth variability), there is a reasonably high likelihood of the CVs of all three hominin species examined here (*A. afarensis, A. africanus* and *P. robustus*) falling within the probable ranges of variability of CVs measured for modern *H. sapiens.* For *A. afarensis* CVs for MD length, mesial cusp breadth and distal cusp breadths are 6.28%, 7.53%, and 7.34%, respectively, and the probabilities (p) of finding such levels of variation in a random sample of 16 *H. sapiens* were 0.78, 0.12 and 0.17 respectively, so this species falls well within the expected range of variability for size-matched samples of modern *H. sapiens* molars. For specimens attributed to *A. africanus,* the CVs were as high as 8.17%, 8.47%, and 8.14% for MD length, BL (mesial) and BL (distal) breadths respectively, and the respective probabilities (p) of finding such high variance in a random sample of 16 *H. sapiens* molars were 0.22, 0.02 and 0.25 respectively. This would imply that variability across the mesial cusp measurements (CV = 8.47%, p=0.02) of the specimens representing *A. africanus* in this study is at too high a level to be within the expected range of matched-size samples of modern *H. sapiens* molars. *Paranthropus robustus,* on the other hand, falls within the expected ranges of variability of modern *H. sapiens* molar dimensions, even with the inclusion of the Gondolin specimen. Probabilities (p) of similarly-sized samples of modern *H. sapiens* molars displaying the level of variability as displayed by the specimens attributed to *P. robustus* in this study were 0.43, 0.16, and 0.07,

respectively, so even the highly variable distal cusp measurements that were remarked upon previously still fall within the 5% confidence level of the frequency distribution plotted for the CVs of this particular measurement in *H. sapiens.* If the Gondolin molar is excluded, then these probabilities (p) rise to 0.99, 0.84, and 0.88, respectively. To summarise, both size and shape variability displayed by any typical sample of 16 modern *H. sapiens* molars is so high that all three of the fossil hominin species' molar variability, as measured by CV ratios in this study, fall within the expected range of variability.

CV Comparisons – brief comments on the variability of other fossil hominin groups included in this study

CV values for all of the fossil hominin species, including those species that were not represented by large sample sizes, are given in Table 26. These results are included for the sake of interest and of completion: each of the samples is represented by a holotype or a proxy for a holotype of the taxa into which they are categorised. No firm conclusions are, however, drawn from such small samples.

Australopithecus sediba

The two specimens attributed to *A. sediba* are extremely similar to each other in all dimensions and therefore reflect low coefficients of variation. The CVs returned for the two specimens were 3.83%, 1.91%, and 1.81%, for the MD length, the mesial cusp breadths, and distal cusp breadths, respectively. This is very much in keeping with two individuals belonging to a sexually dimorphic species, e.g. one being male and one being female (i.e. the CV for MD length/size of molar differentiated the two molars more than did the CVs for the breadth/shape measurements).

Homo naledi

The sample representing *H. naledi* consisted of seven specimens. These molars had low CVs for all raw measurements (3.56%, 4.92%, and 3.87% for the MD length, the mesial cusp breadth, and the distal cusp breadth, respectively), reflecting low variability between all three molar dimensions in this group. The probabilities (p) of these low CVs falling within the ranges of variability of the expected CVs for samples of 16 specimens of the extant species in the study were 1 (100% probability) for the MD measurements in all cases, between 0.94 and 0.97 for the mesial cusp measurements (in all cases except *P. paniscus,* where the probability dropped to 0.5), and between 0.98 and 1 for the distal cusp measurements.

Early *Homo* and *Homo ergaster*

While *A. sediba* and *H. naledi* therefore show a lack of variability in their shape and size measurements, variability shown in the small samples of specimens attributed to Early *Homo* (consisting of at least two species) and *H. ergaster/erectus* (with possibly all three specimens belonging to *H. erectus,* but possibly a second, Mid-Pleistocene, species represented in this sample) are comparably less cohesive in their size and shape dimensions, particularly when these groups are compared to randomised samples of *P. paniscus.* Despite there only being four specimens representing *H. habilis* and *H. rudolfensis* (grouped as "Early *Homo*"), the CVs in these four specimens alone were high at 6.06% for the MD length, fairly high at 5.10% for the BL measurement across the distal cusps, and very high at 7.01% for the BL measurement across the mesial cusps. The probability (p) of a random sample of 16 specimens each of *G. beringei, G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens* having such high CVs for the mesial BL measurements are 0.44, 0.48, 0.27, 0.00 and 0.27 respectively. These probabilities were

expected for random samples of 16. If the probabilities were recalculated for sample sizes of 4 for each of these species, then the mesial cusp size variability represented by these four specimens of Early *Homo* appears high, and not only by comparison to *P. paniscus.* A similar situation arises with the three specimens representing *H. erectus* in this study. CVs, particularly for the distal cusp measurement variability in just these three specimens, were high. The probability (p) of finding a CV as high as 6.55% for the distal cusp breadth measurements of a random sample of 16 molars of *G. beringei, G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens* is 0.47, 0.49, 0.19, 0.02 and 0.68 respectively. If, instead of random samples of 16, the sample size were reduced to n=3, the resultant coefficients of variation would be drastically lower and the probabilities that a sample of 3 of any of these extant species having CVs as high as that for the distal breadth measurement reported here for the three *H. erectus* specimens would be reduced considerably.

CHAPTER FIVE – DISCUSSION

This chapter aims to address the questions set out in Chapter One, with the aim of addressing the main hypotheses proposed, namely, a) whether all extant species are equally as suitable for use as analogue species in comparative studies of molar morphometrics of extant hominoid and extinct hominin species, and b) whether hominin species, as currently attributed, follow similar patterns of variability in size and shape as do analogous extant species.

To recap, the principal questions being asked in this thesis are as follows:

1) Are lower second molars successful in delineating diagnostic differences between genera, species, subspecies and even populations of living hominoids?
2) What patterns of both size *and* shape variability of lower second molars are identifiable in the context of extant hominoid species, and can these be attributed to specific causes (e.g., sexual dimorphism)?
3) Do specimens attributed to certain African Plio-Pleistocene fossil hominin species exhibit the same patterns and ranges of shape and size variability?
4) Does the pattern of variability in lower second molars of modern humans confirm studies of patterns of variability in other skeletal elements, concluding that variability might be due to historically divergent subsistence lifestyle strategies between groups?
5) Is there shape variability over and above tooth-size reduction in certain modern human populations?
6) Can a historical time-series analysis of modern *Homo sapiens*' lower second molars confirm tooth-size reduction over time?

7) Should any of the extant species, particularly modern *Homo sapiens,* traditionally used as comparative analogues to provide expected limits for species variability in fossil hominins ideally be excluded as analogues in these comparative studies?

5.1 DIAGNOSTIC CAPACITY OF LOWER SECOND MOLARS

Most taxonomic assessments of hominin fossils, many of which are dental remains, are made at the level of species. In this study, large samples of lower second molars of five known extant species *(G. beringei, G. gorilla, P. troglodytes, P. paniscus* and *H. sapiens)* were tested for accuracy of classification using a discriminant function analysis. At the species level, 92.3% of the 750 specimens were correctly classified, with most of the misclassifications being incorrectly assigned to a species within the same genus (incorrect classifications between *G. beringei* and *G. gorilla*, and between *P. troglodytes* and *P. paniscus*). When performing a discriminant function analysis at the level of subspecies, classification accuracy dropped to 82.9%. Most of the additional misclassifications occurred within *P. t. ellioti, P. t. troglodytes* and *P. t. schweinfurthii*. It is perhaps unsurprising that misclassifications occurred amongst these three subspecies because they are known to have continued interbreeding until very recently (Guy et al., 2003; Won and Hey, 2004; Fischer et al., 2011; Gonder et al., 2011), which is also evident in genetic studies that show *P. t. schweinfurthii* forms a nested hierarchy within *P. t. troglodytes* (Gagneux et al., 1999, Bjork et al., 2011). The exception to the additional misclassifications in the DFA at the subspecies level is *P. t. verus*, in which nearly 90% of the individuals were classified correctly, with only about 10% of these misclassifying with the other *P. troglodytes* subspecies.

The genetic substructure of *Pan* would place the split between *Pan troglodytes* and *Pan paniscus* at about 1 million years ago (Hey, 2010; Prüfer, 2012), followed by a split by *P. t. verus* from the other three subspecies of *P. troglodytes* at about 500 000 years ago (Gonder et al. 2011). Gene flow is indicated between the other subspecies until about 100 000 years ago (Gonder et al., 2011). This genetic distance is mirrored in the morphological distances calculated from the DFA, as shown in the near-neighbour joining tree based on squared Mahalanobis' distances in Euclidian space between group centroids at the subspecies level (Figure 8).

Similar DFAs on subspecies of *Gorilla* (Figure 9), together with the dendrogram at the subspecies level, Figure 8) confirmed that molar morphological distances again reflected genetic substructures in the order in which divergences occurred, starting with the initial split between *G. beringei* and *G. gorilla* (Thalmann et al., 2007), with a subsequent split between *G. b. beringei* and *G. b. graueri* (Thalmann et al., 2007; Scally et al., 2012; Prado-Martínez et al., 2013; Roy et al., 2014; Xue et al., 2015). Figure 8 also shows a close morphological distance of the molars of *G. g. gorilla* and *G. g. diehli,* again reflective of genetic substructures, with research indicating that there was gene flow between these two subspecies until much more recently - about 18 000 years ago - (Thalmann et al., 2011).

The DFA classification seems to confirm what would be expected from genetic, behavioural and other studies, and although the present study only includes lower

second molars, it is also in line with results from Pilbrow (2003, 2006, 2010) who investigated population systematics of chimpanzees and gorillas using upper and lower first, second, and third molars (6 tooth types).

5.2 SIZE-SHAPE VARIABILITY OF MOLARS IN EXTANT SPECIES

Results from DFAs, statistical MD:BL ratio analyses, PCAs, and randomisation analyses all indicate that in the case of *G. beringei* and *G. gorilla,* which are the two most sexually dimorphic species in the extant sample, size variability of lower second molars accounts for the majority of variance between individuals at the species level. Shape variability, by comparison, is proportionally less significant and emphasises intraspecific variability, not variability according to sex. This is particularly evident when a limited sample is randomly selected from the larger available sample of lower second molars. Size variability exceeded shape variability in morphospace (Figure 16, Figure 17and Figure 21) by 3.26 times amongst *G. beringei*, and by 4 times amongst *G. gorilla,* with males and females plotting in morphospace homogeneously along the y-axis (PC2, accounting mainly for variability in the breadth of teeth across the buccolingual axis, relative to the mesiodistal axis). In morphospace of a PCA in Procrustes formspace, where centroid size is strongly correlated with the first principal component (x-axis), and where the main shape-related principal component is plotted along the y-axis (PC2), the observed distribution includes more "horizontal" scatter amongst *Gorilla* species, especially *G. beringei,* which consists of a smaller-bodied subspecies, *G. b. beringei*, and the largest-bodied subspecies in the genus, *G. b. graueri.* Variability of the lower second molars within *G. beringei* is increased due to the fact that lower second

molars of small-bodied, *G. b. beringei* females fall at one end of the range and those of large-bodied *G. b. graueri* males fall at the other end.

For other species, namely those whose male and female molars cluster together within the size and shape range of the species as a whole, it is shape as well as size that contributes significantly to the variance between individuals in the group, resulting in a more "vertical-diagonal" scatter in morphospace, rather than the "horizontal" size-related scatter observed for the sexually dimorphic *Gorilla* species. Small, narrow molars belonging to both males and females alike plot (Figure 16, Figure 17 and Figure 21) at positive values along PC2 and negative values along PC1, while the largest, broadest teeth would plot more positively along PC1 and negatively along PC2. The most variable species included in this study is modern *H. sapiens.* This species rivals the range of size variability displayed by *Gorilla* taxa, although males and females overlap in size in *H. sapiens,* unlike within *Gorilla* species where primarily sexual dimorphism appears to drive size variability. Shape variability of modern humans, which mainly reflects buccolingual measurements and proportions between mesial and distal cusp breadth measurements, is double that observed in *Gorilla* species. *Pan paniscus* exhibited the least variable molars in this study. This corresponded to both size and breadth/shape variability. *Pan troglodytes*, by comparison, displays a high level of shape variability, exceeding that of *G. beringei* and rivalling the variability expressed by *G. gorilla.*

5.2.2 CONTRIBUTION OF SUBSPECIES AND POPULATION VARIABILITY TO SIZE AND/OR SHAPE VARIABILITY WITHIN SPECIES

The two *Gorilla* species in this study comprise two subspecies each; *Pan paniscus* is a single species with no subspecies, as is modern *H. sapiens. P. troglodytes,* on the other hand, consists of four subspecies, one of which, *P. t. verus,* is so distinctive from the other three subspecies in behaviour, genetics and morphology, that a proposal has been made to elevate this taxon to the species level (Morin et al., 1994). That the extant comparative species are comprised of variable numbers of subspecies is an important issue for comparative studies featuring extinct taxa that display size and/or shape variability.

If an assemblage of fossils attributed to a single hominin species shows considerable size variability, but little shape variability, the present study joins previous work (e.g. Pilbrow, 2006, 2010; Dykes, 2014) in demonstrating that such a pattern of variability would mirror that of a sexually dimorphic species. But the question naturally arises as to whether all size (as opposed to shape) variability is due to sexual dimorphism alone: it has already been noted that, in addition to sexual dimorphism at the subspecies level, size variability of *G. beringei* at the species level is driven by the size differences between the two subspecies. If, however, the assemblage of fossils exhibits considerable shape variability, the indications from the results of this study and previous research (Dykes, 2014) would indicate that species with both size and shape variability, plotting diagonally in morphospace, are more likely to be non-sexually dimorphic. Table 27 summarises the points for discussion when analysing size-shape variability of lower second molars of the five extant species in this study.

Table 27. Summary of size-shape analyses for extant species (PCA)

Species	Subspecies	Comments	Sexual dimorphism	Expected shape variability (range along PC2) (matched samples)	Observed size:shape variance (uneven samples)	Expected size:shape variance (matched samples)	Pattern in morphospace	Comments
G. beringei	2	*G. beringei* subspecies vary by size	Yes, particularly noticeable at the suspecies level. 8% F:M difference at the species level	0.06	3.3:1	3.3:1	Mostly horizontal (size-related)	Size variability increased by the differences in size between the two subspecies
G. gorilla	2	Recent split	Yes, though high intra-species variability masks the effect of this. 5% difference between males and females at the species level	0.06	2.1:1	4.0:1	Mostly horizontal (size-related)	Extreme variability within this subspecies, magnified by the large sample size compared to other species
P. troglodytes	4	*P. t. verus* is significantly different from the other subspecies	Not significant (2% difference on average at the species level)	0.09	2.1:1	2.0:1	Horizontal and vertical (size and shape)	Extreme shape variability within this species, especially with the addition of *P. t. verus,* which might be reclassified as a separate species
P. paniscus	1		Not significant (2% difference on average at the species level)	0.09	2.2:1	1.3:1	Horizontal and vertical (size and shape)	Size and shape variability
H. sapiens	1		Not significant (2% difference on average at the species level)	0.12	1.5:1	2.2:1	Horizontal and vertical (size and shape)	Excessive size and shape variability for a single species. Shape variability up to double that observed in other species

(Observed size and shape variance based on Figure 16, Figure 17 and Figure 21of this study). The "recent split" in *G. gorilla* refers to the recent divergence of *G. g. gorilla* and *G. g. diehli.* The "pattern in morphospace" is a description of the relative size-shape ratio. The higher the ratio, the more "horizontal" or size-related the patterning would be.

Special case: modern *Homo sapiens* – shape and size variability – PCA

The expected range of shape variability (distribution along PC2 in Figure 16, Figure 17 and Figure 21 of this study) is low in *Gorilla* species, moderate in *Pan* species, but high in *H. sapiens*. In fact, *H. sapiens* exhibits approximately twice the amount of shape variability exhibited by *Gorilla* species, each of which consist of two subspecies. *H. sapiens*, which is a genetically cohesive species without subspecies, also exhibits shape variability that exceeds that of *P. troglodytes*, which consists of four subspecies. It appears, therefore, that *H. sapiens* presents an exception to the expected ranges of variability for a single species with no subspecies, based on patterns exhibited by the African ape species. Further principal components analyses give additional insight into factors which might be uniquely driving the substantial variability exhibited by *H. sapiens.*

Research into the effects of different subsistence lifestyles on the robusticity of femora (Siddiqi, 2012; Püschel and Benítez, 2014) has suggested that individuals who adopt a hunter-gatherer lifestyle strategy have more robust femora/femoral heads than individuals who lead a sedentary lifestyle. Research into mandibular and dentognathic morphology (von Cramon-Taubadel, 2011; Pinhasi et al, 2015) cited similar contrasts due to subsistence strategies, with more robust mandibles and dental dimensions being retained by individuals maintaining a hunter-gatherer lifestyle with harder, less-processed foods to masticate, and with reduced-size mandibles and smaller teeth being found in individuals from areas where there was an early transition to agriculture (see, for instance, Dahlberg, 1960; Pinhasi et al., 2008; Emes et al., 2011 and other examples

of research into dental reduction as cited in Chapter One of this study). The transition to agriculture and softer, more processed foods has also brought with it a certain level of simplification of molar cusp arrangements, with fewer cusps in some cases, and a consequent shape change (see, for example, Hanihara and Ishida, 2005). This transition to agriculture began in the Near East, North Africa and Anatolia around 12 000 years ago, so that these first populations to adopt this subsistence strategy would presumably have more extreme differences apparent in molar morphology by comparison with groups that have retained a hunter-gather strategy. When a distinction is made between hunter-gatherer individuals and individuals from other populations on the PCA plot (see Figure 22), there is a general distinction between molars belonging to hunter-gatherers (larger molars, plotting at higher values along PC1) and population groups that have had the longest exposure to agriculture (mainly smaller molars, plotting at lower values along PC1).

The smallest, narrowest modern human molars (grouping with *P. paniscus*) belong to individuals from Europe, whose ancestors transitioned to widescale agriculture and the consumption of soft, starchy cereals, together with the use of more widespread use of cooking technology for softening food as the Neolithic culture spread from the Near East, from about 10 000 years ago (Gkiasta et al., 2003). On the other side of the size range, seven of the eight largest teeth in the modern *H. sapiens* sample belong to individuals from Australia, specifically from communities that have retained a hunter-gatherer lifestyle to the present.

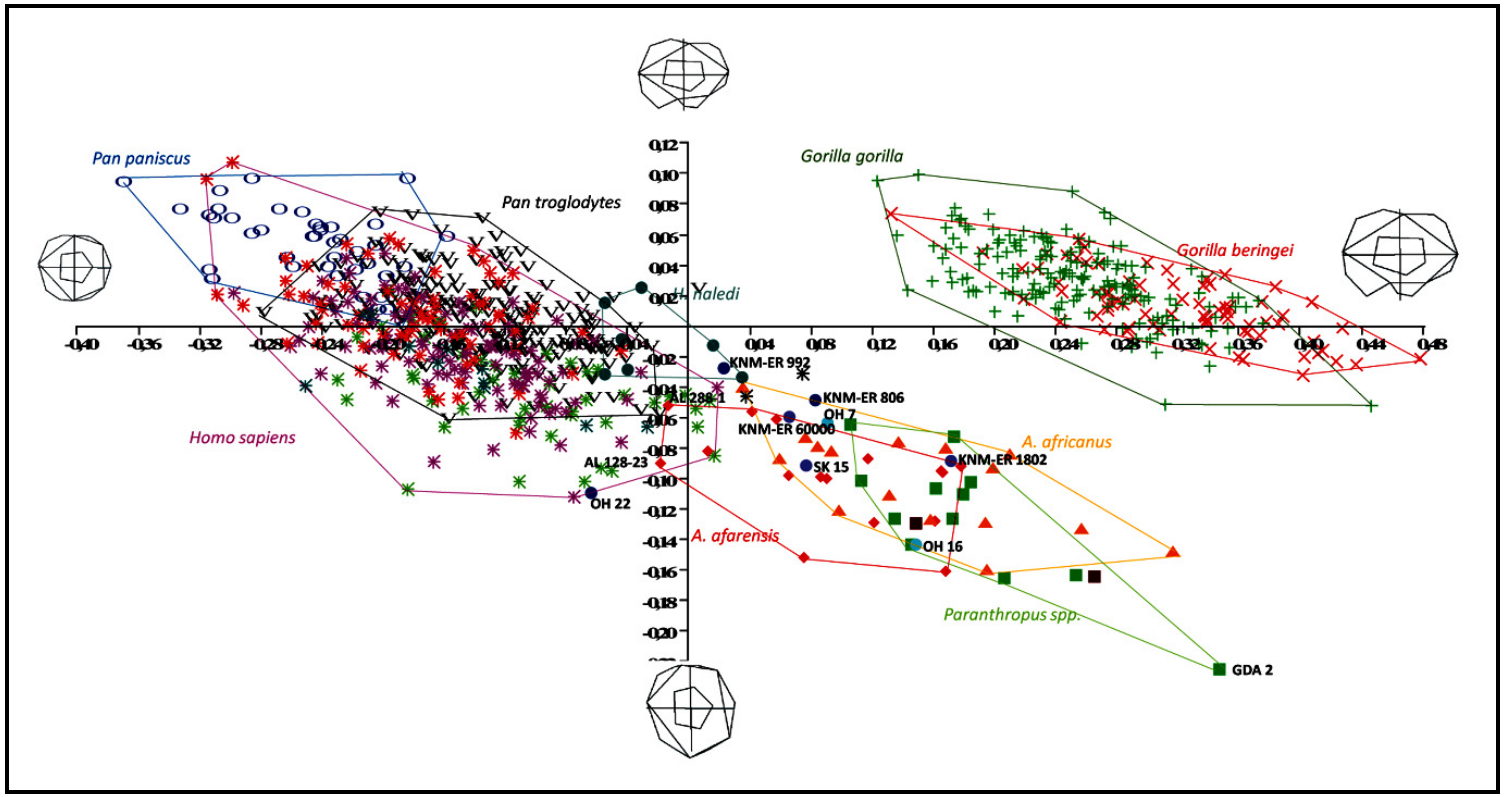


Figure 21. PCA results at the species level for five extant species (full samples) and extinct hominin species in the study, with modern *H. sapiens* groups sorted by basic subsistence lifestyle differences

Axis 1 represents 89.2% of variance and is 99.6% correlated with centroid size; Axis 2 represents 4.11% of the variance. The main factors contributing to the variance along the x-axis (PC1) are size and the length of the mesiodistal dimension. The main factors contributing to variance along the y-axis (PC2) are the buccolingual dimensions. Thus, small, narrow teeth will be found in the top left quadrant (negative PC1, positive PC2); large, narrow teeth in the top right quadrant (positive PC1 and PC2); small, broad teeth in the bottom left quadrant (negative PC1 and PC2) and large broad teeth in the bottom right quadrant (positive PC1 and negative PC2). (Legend: blue circles: *P. paniscus;* black "V": *P. troglodytes;* green "+": *G. gorilla;* red "X": *G. beringei*; teal/dark turquoise circles: *H. naledi;* black stars: *A. sediba;* dark blue circles: *H. ergaster/erectus* or Later Pleistocene *Homo;* light turquoise circles: *H. habilis;* lilac circles: Early *Homo;* red diamonds: *A. afarensis;* orange triangles: *A. africanus;* green rectangles: *P. robustus;* brown rectangles: *P. boisei*; *H. sapiens* divided by coloured stars as follows: green stars: hunter-gatherer communities; teal stars: fisher-gatherer groups; pink stars: horticulturalists, pastoralists and small-scale farmers; red stars: widescale farmers/sedentary groups whose transition to agriculture was the earliest.)

Figure 22 recapitulates the information shown in Figure 21, but the area on the plot occupied by the cluster of modern *H. sapiens* is enlarged and simplified to enable a better observation of this distinction in the morphology of molars between hunter-gatherer groups and communities that experienced an early transition to agriculture, widespread cooking and softer diets.

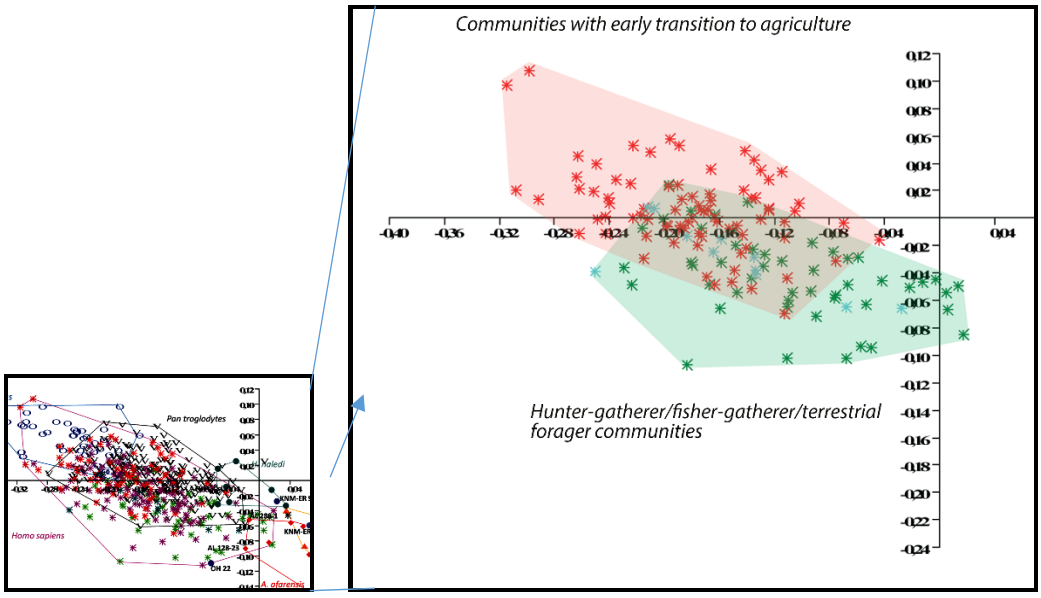


Figure 22. PCA results taken from Figure 21, showing only selected modern *H. sapiens* groups sorted by basic subsistence lifestyle differences

Hunter-gatherer/terrestrial forager groups shown as green stars; "fisher-gatherer" (Inuit) groups in teal/turquoise stars; communities with the earliest transition to agriculture shown in red stars. Other groups (pastoralists; horticulturalists; small-scale farmers; groups with later transition to agriculture) not shown in the enlarged diagram. Small, narrow teeth will group top left; larger, broader teeth will group bottom right.

Modern *H. sapiens* as a single species with no subspecies is characterised by extremely low genetic diversity compared to that of chimpanzees and other apes (Gagneux et al., 1999; Gonder et al., 2006; Prado-Martínez *et al.,* 2013). Despite this, morphological variability in lower second molars far exceeds that in chimpanzees and gorillas. The PCA

(Figure 21 and Figure 22) would seem to confirm that the high level of variability in tooth morphology appears to be driven, at least in part, by historical divergences in subsistence strategies that go back 12 000 years or more. There is clearly some overlap in tooth size and shape between these two clusters of groups whose subsistence economies are the most divergent (populations that have retained a hunter-gatherer subsistence strategy versus populations living in areas that transitioned to agriculture since the onset of the Neolithic period). However, the general trend shows that traditional hunter-gatherer/terrestrial forager communities (green stars) have retained larger, broader, more robust molars, designed for strong jaws that are suited for mastication of tough foods that are not subject to high degrees of food processing (milling, for instance) or cooking. Communities that are catalogued in collections specifically as "fisher-gatherers" (represented by Inuit individuals, shown as turquoise stars in Figure 22) have molars that are intermediate in breadth across the crown. The diet of Inuit communities comprises high levels of Omega 3 fats and proteins (Fumagalli et al., 2015) which, together with fish-based proteins, the main staple food for these communities, produce lower levels of stress on the dentognathic apparatus than does the diet of traditional hunter-gatherer/terrestrial forager communities such as Australian Aboriginal or KhoeSan groups.

Communities that have been exposed for the longest period to the transition to agriculture have undergone a change to very starchy, soft cereals, domesticated cattle with more tender meat, and high levels of food processing – the use of more frequent cooking of foodstuffs and finer milling of grains – which both lead to a different balance in hard:soft ratios in the foods consumed. These populations have generally

experienced the most significant levels of tooth-size reduction and narrowing, supporting earlier work by Brace and others (Campbell, 1925; Brace, 1963; Brace and Mahler, 1971; Brace, 1976; Keiser, 1990; Hanihara and Ishida, 2005; Emes et al., 2011). The remaining groups (smaller-scale agriculturalists, horticulturalists, pastoralists and groups that experienced a later transition to agriculture) generally fall in between the two extremes. It should be noted additionally that two out of the three communities representing hunter-gatherer / terrestrial forager societies in the sample also have relatively small body sizes (Babinga pygmy community; KhoeSan community) compared to the third group (Australian Aboriginal individuals), so it is perhaps surprising that there is not greater overlap of these two groups with the communities that transitioned earliest to agriculture. Specifically, the communities who transitioned earliest to agriculture exhibit greater mandibular size reduction (von Cramon-Taubadel, 2011; Pinhasi et al., 2015) and thus presumably exhibit smaller molars due to these dietary shifts rather than due to generally small body size. The pattern of clustering in morphospace shown in Figure 21 and Figure 22 almost exactly matches the pattern observed by von Cramon-Taubadel (2011), who used geometric morphometrics to compare mandibular shape and size in a PCA (von Cramon-Taubadel, p. 19550, Figure 3) and linked this with masticatory behaviour according to subsistence economies. Her conclusion was that hunter-gatherers generally retained longer and narrower mandibles than agriculturalists. Groups that transitioned earlier to agricultural subsistence economies tended to exhibit greater lower facial reduction, associated with decreases in masticatory stresses. Dental reduction has occurred as a result of the shift to intensive agriculturalism and sedentism, although these mandibular and dental size reductions are not always congruent, leading to dental malocclusions and tooth crowding in certain instances (Pinhasi et al., 2015).

The pattern of group separation identified by the PCA confirms the discrimination between groups already noted from the DFA of *H. sapiens* at the population level (Figure 11). Hunter-gatherer groups (Australian Aboriginal, KhoeSan and Babinga) cluster together at the lower value range of the first canonical function (large molars), while groups from Europe, the Near East and the Balkans cluster at the higher value range of the first canonical function (small molars). SA Bantu-speaking groups cluster along the same axis as the Teita Bantu-speaking group from East Africa. Inuits and Amerindians cluster close together. The East Asian group includes Chinese (normally catalogued as intensive agriculturalists) as well as Mongolians (pastoralists), so there is a mixture of subsistence lifestyle economies represented in the region as a whole. Some of the specimens included in the sample had missing population data, although they were listed as originating from East Asia, so their subsistence economies remain unknown. The grouping pattern observed from Figure 11 seems to confirm what was observed from the PCA (Figure 22), in that traditional hunter-gatherer communities plot separately from populations living in areas that have been exposed to intensive agriculture for longer periods, and would be in agreement with expectations from research into biological changes that have occurred due to a transition to soft-cereal and domestic meat eating, with foods being heavily processed (fine milling of grains, tenderising of meat, cooking and softening of foodstuffs) before consumption.

Thus, in the case of lower second molars of modern *H. sapiens*, there is confirmation that not only molar size reduction, but also molar shape change, associated with cusp simplification due to non-challenging diets (Emes et al., 2011), has occurred primarily in

communities that have transitioned to agriculture in the early stages of the Neolithic period. This matches the pattern observed in lower second molars analysed in the historical time-series PCA (Figure 12). Molars from the Neolithic period, which spanned approximately 1 500 years as Britain transitioned to agriculture, are variable in size and shape, but tend to be by far the largest teeth in the analysis. Barring one outlier, these molars generally do not overlap significantly with the much smaller teeth from the Medieval period, while molars belonging to males tend to be larger in size in both the Neolithic and the Anglo-Saxon groups, than those belonging to females. Beyond the size trend, some tooth cusp simplification is observable from the PCA. The relative warps along the y-axis (PC2 or "shape" axis in Figure 12) indicate that the Neolithic tooth state was one with a large hypoconulid and a buccally-oriented hypoconid. Over time, the more recent teeth show a tendency to shift to a reduced or absent hypoconulid (with the hypoconid taking up the space buccodistally that had previously been occupied by the larger hypoconulid). This pattern of tooth simplification (i.e. reduction of cusps, grooves and fissures), alongside tooth reduction, has been observed since the Nubian transition to agriculture (3400-1100 BCE) and is postulated to be a selective compromise favouring reduced risk of caries in the face of increased starch consumption (Greene, 1972; Calcagno and Gibson, 1988; Emes, 2011). Bermúdez de Castro and Nicolas (1995) note that even as early as the Middle Pleistocene, tooth simplification was occurring (loss of the hypoconulid in *Homo heidelbergensis* at the Atapuerca site in Spain, similar to that observed in modern humans with soft diets), and they postulate that soft diets are presumed to have created selective pressures for smaller, less complicated teeth. This would make sense in light of research into the formation of molar cusps (e.g. Jernvall and Jung, 2000), which has found that later-developing molars in the dental cascade are "evolvable" and homoplastic (developing

separately), relying on the activation of specific "dental modules". According to these researchers, structures called enamel knots play a key role in determining how the precursor tissue to the enamel-forming tissue folds into what will become the dental cusps. If a smaller tooth forms and enamel knots have a minimum size threshold for formation, fewer enamel knots can form, which leads to reduced numbers of cusps. In the case of mice, soft diets lead to reductions in the size of mandibles, which is likely heritable (Anderson et al., 2014), and small mandibles are genetically and developmentally linked to small teeth (Workman et al., 2002). It follows that both size reduction and reduction in complexity might be a direct consequence of the consumption of soft, non-challenging diets in humans as well. This would then be a structural, non-random cause of excessive size and shape variability within a single species.

Gorilla and *Pan* underwent no such equivalent transition in diet as humans from hunter-gatherer to agriculture subsistence strategies, nor did the former adopt high levels of food processing, cooking, or consumption of domesticated starchy grains. Since extinct hominin species were unlikely to have experienced similarly substantial shifts as modern humans, the range of variability exhibited by molars of modern humans should not be treated as a simple numeric value that requires no qualification in comparisons with fossil hominin teeth. With this in mind, the range of lower second molar size and morphology exhibited by different groups of modern humans characterised by such diverse subsistence strategies and such differences in the hard:soft consistency of diet between groups must inform comparisons of ranges of size-shape variability for the

lower second molars of modern human groups and those of presumed extinct hominin species.

In sum: modern *H. sapiens* exhibits extremely high ranges of variability in both size and shape of lower second molars by comparison with extant African great ape species. Modern *H. sapiens* is not significantly sexually dimorphic in lower second molar size, and in all analyses, small, buccolingually-narrow molars belong equally probably to males as to females, and large, robust molars belong equally probably to males as to females. Wide ranges of size variability in lower second molars of modern *H. sapiens* should therefore not be attributed to sexual dimorphism. Further to this, structural, non-random factors such as differences in hard:soft ratios in dietary intake resulting from different populations following divergent subsistence strategies have caused tooth reduction and molar cusp simplification in some populations, while those populations retaining a hunter-gatherer strategy have retained more robust teeth, capable of masticating a diet containing more hard-textured and less processed food elements. Since these highly divergent lifestyle strategy differences (starting around 12500 BP) do not exist among African apes and would not have existed in extinct fossil hominin species, extreme caution should be exercised before comparing ranges of lower second molar size and shape variability in the modern human sample to those of fossil hominin species.

5.3 SIZE-SHAPE VARIABILITY PATTERNS AND RANGES OF SPECIMENS ATTRIBUTED TO FOSSIL HOMININ SPECIES: COMPARISONS WITH EXTANT SPECIES

Most of the groups of specimens attributed to African Plio-Pleistocene fossil hominin species in this study seem to group in morphospace generally along a diagonal trajectory (Figure 16, Figure 17 and Figure 21), which is similar to the patterning in morphospace exhibited by *Pan* species and *H. sapiens*. The PCA indicates that *A. afarensis, A. africanus* and *P. robustus* (the three most well-represented fossil hominin species in this study with sample sizes of n=16, n=16 and n=12 respectively) do not group along a horizontal orientation, which suggests that they might not necessarily be following the "pattern" of a typical sexually dimorphic species such as *G. beringei. G. gorilla* displays more variability along the y-axis than would be expected by comparison with *G. beringei*, but if three unusually narrow outliers and two unusually broad outliers are removed from the large sample of 179 *G. gorilla* specimens, the morphospace patterning would be qualitatively more horizontal and appear more similar to that of *G. beringei.* These five outlier specimens should not be discounted, but it needs to be remembered that the fossil hominin species samples in this study consist of a maximum of sixteen per group. When comparing these limited groups of fossil hominin specimens to the full range of variability shown by a sample of *G. gorilla* that is over eleven times the size of the fossil hominin samples, it should be the overarching, more horizontal, patterning of *G. gorilla* in morphospace against which these limited samples should ideally be compared, not the outliers, which account for a disproportionate part of the range. Variability within *G. gorilla* does exist, but the probability that any random sample of sixteen specimens taken from the full sample of 179 individuals would happen to include all five outliers in the sample would be negligible. Likewise, a group

of sixteen specimens representing a larger population of a fossil hominin species is not likely to comprise all of the "outliers" in the larger population – teeth that are outside of the size or shape range of the bulk of the population from which they originate: although it is conceivable that the specimens that have been recovered may include one or two outliers, the expectation would remain that the majority of specimens in the sample would be within "normal" ranges for that species. Even in the case of a sample bias in the fossil assemblage towards smaller-bodied individuals (at an identified leopard's prey accumulation site, for instance) it would be unusual then to have outliers at both ends of the size range, and the sampling bias, if known or suspected, can always be taken into consideration when drawing conclusions about ranges of variability in the fossil molars representing that species.

For each sample of specimens attributed to each fossil hominin group, therefore, the questions being asked are whether the specimens as a group fit within an expected range of variability of an extant species, and secondly whether the relative "patterning" – the size-versus-shape variability – also matches the expected pattern of variability of that extant species. If there is one group within the fossil hominin species sample that consists of large, broad molars, and a second group that comprises only small, narrow molars, a simple, unqualified, numerical analysis will show that as a group, this sample has a size range of "x" from small to large, and a shape range of "y" from narrow to broad across the crown. These ranges may fall within the observed/expected ranges of an extant species group. However, the simple statistical analysis tells us nothing about the fact that in this example there might be one or two (or more) perceptibly differently shaped and sized groups of molars within the sample, which would cluster separately in

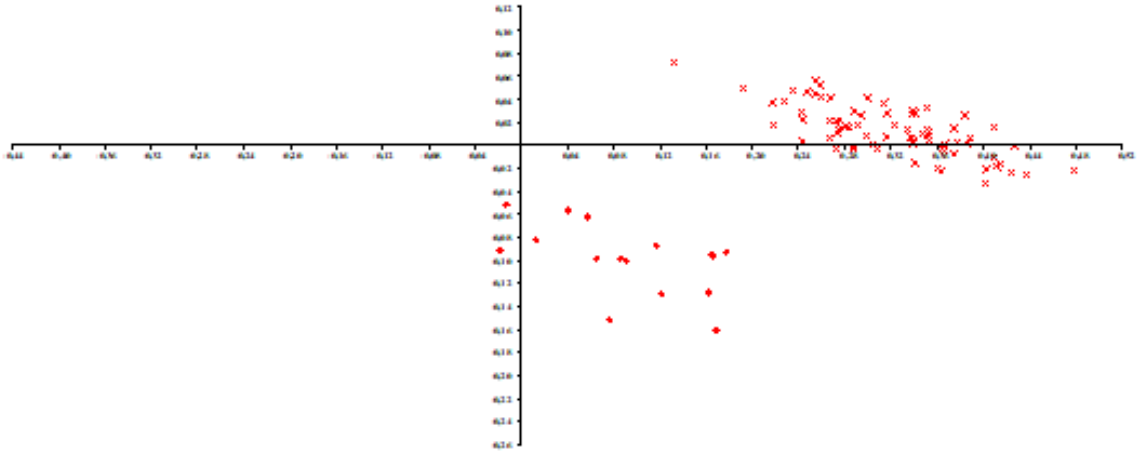
morphospace, and which could either be representative of two different species, or at the very least to two different subspecies, as is the case with *P. t. verus* (typically broad molars across the crown) and *P. t. schweinfurthii* (typically narrower molars). If the fossil hominins comprising the two subgroups (small, narrow molars and large, broad molars) exceed the size variability of *P. troglodytes,* and instead exhibit the size range of *G. beringei,* then there might be the temptation to conclude that the small molars belong to females and the large molars belong to males. Here again, patterning in morphospace is important. While molars belonging to male gorillas tend to group along the positive x-axis and females tend to exhibit smaller PC1 scores than males, the same cannot be said of male and female dispersion with respect to PC2 (i.e. along the y-axis). Not all *Gorilla* molars that are relatively narrower in shape belong to females and not all buccolingually broad *Gorilla* molars belong to males. There are molars belonging to both male and female gorillas that are narrow buccolingually and the same is true for molars that are broad buccolingually. Relative shapes of molars vary within the species, but not in a sexually dimorphic way. In the example above, there is one group of fossil molars that are both small in size and narrow buccolingually, and another group of fossil molars that are both large in size and broad buccolingually. While it might be postulated that these differences represent expected ranges of variability within a species (particularly one that has several different subspecies), caution would be advised before attributing the size differences between the two groups to simple sexual dimorphism, no matter how wide the size range is between the largest and the smallest of these molars.

Further to this: if size and shape variability within a fossil hominin sample matches the expected pattern and statistical range of any given extant hominoid species, additional considerations must be taken into account, regarding the underlying population structures of each extant species itself. *Pan paniscus* has a limited range of shape and size variability of lower second molars, reflective of the fact that it is a species with no subspecies, and relatively little variability between populations. If specimens attributed to a fossil hominin group fit within the range of *P. paniscus,* then there would be little hesitation in concluding that the specimens belong to a single species. If there are different clusterings of the molars (size and shape differences) in morphospace, such as in the hypothetical example cited above, but if the measured ranges of variability of the fossil sample fall within the expected range of variability of a species like *P. troglodytes* (wider ranges along both axes, and visible shape differences between groups, manifested by the buccolingually broad molars of *P. t. verus* and the buccolingually narrower molars of the other three subspecies of *P. troglodytes*), then an assessment might be made that the fossil hominin specimens belong to a single species that has several morphotypes included in its subspecies. If, on the other hand, the specimens representing a fossil hominin species show ranges of variability that exceed the size and shape variability of a species like *Pan troglodytes,* matching only the exceedingly wide ranges of variability in molar size and shape shown by modern *H. sapiens,* then further qualification might be required in light of identifiably non-random causes of variability identified in *H. sapiens* molar shape and size, as discussed above. *Australopithecus afarensis* (sample size n=16), *A. africanus* (sample size n=16) and *P. robustus* (sample size n=12) are good candidates for such a discussion. In this chapter, however, rather than refer back, repeatedly, to tables and figures presented in the preceding chapter, the clusters of salient species groups are extracted in turn for comparison purposes from

Figure 16 and Figure 17, together with the relevant CV data from Table 25 and Table 26, for ease of reference. In each graphic presentation that follows, the fossil species plot, as on Figure 16 and Figure 17, in the bottom right-hand quadrant of the plot (clustering below the x-axis) and the extant species being compared with the fossil species in question will plot at more positive values along the y axis. Identical colour-coded symbols are used as before.

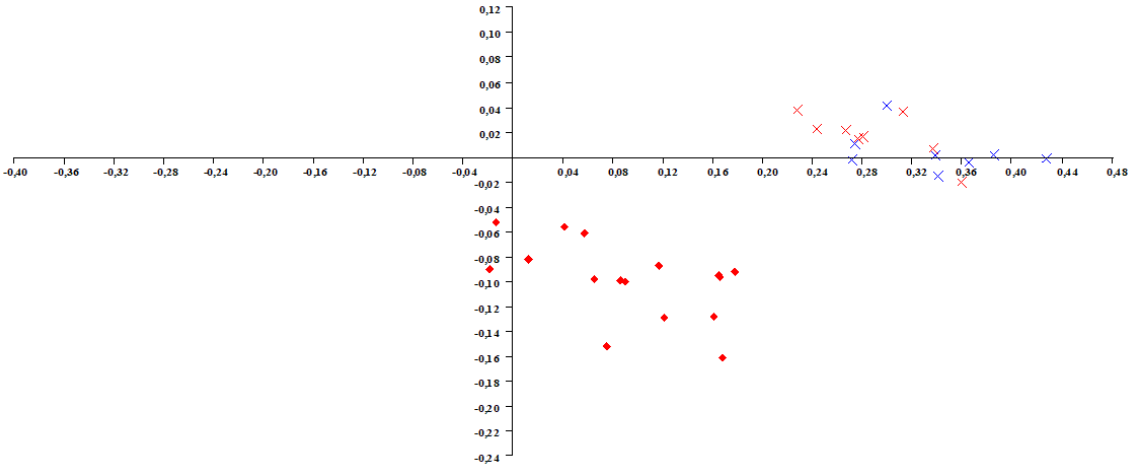
5.3.1 *Australopithecus afarensis.* Recap of results and initial discussion:

A. afarensis size and shape variability (red diamonds) compared to the full sample of *G. beringei* (red crosses).



Size (range along x-axis) : *A. afarensis* – 0.20; *G. beringei:* 0.35
Shape (range along y-axis) : *A. afarensis* – 0.11; *G. beringei:* 0.11

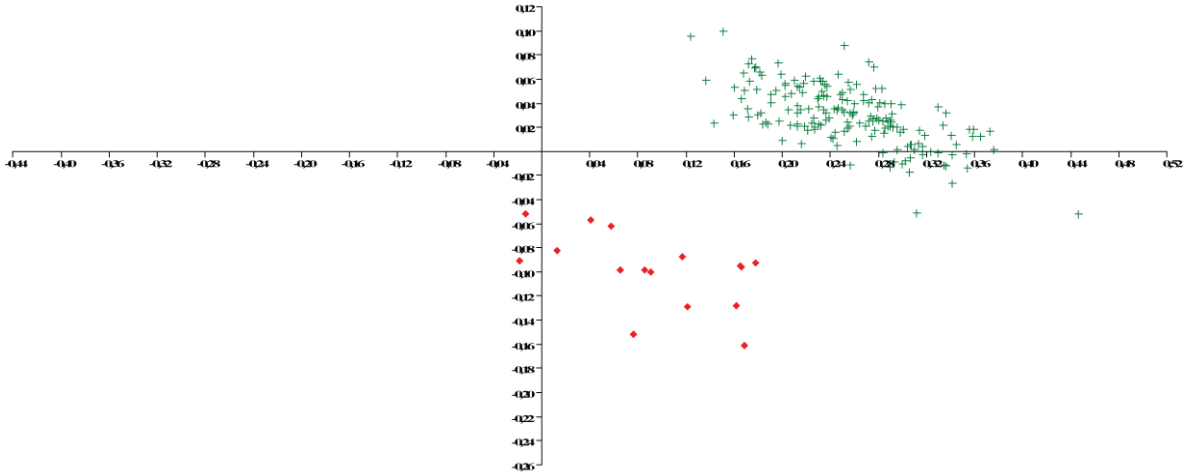
A. afarensis versus a randomly-selected, matched-size sample of *G. beringei*



Size (range along x-axis) : *A. afarensis* – 0.20*; G. beringei:* 0.20
Shape (range along y-axis) : *A. afarensis* – 0.11; *G. beringei*: 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.86; 0.28; 0.22
Patterning match: too vertical to match the pattern in morphospace of *G. beringei. G. beringei* consists of 2 subspecies, differentiated more by length (x-axis) than by shape (y- axis). This is why the probability that the MD measurement would be in range would be higher than the breadth probabilities. Examining the pattern in morphospace, the possibility of two subspecies (or two species) should not be ruled out. The larger specimens tend to be broader across the crown. The smaller specimens are also the narrowest. Two specimens fall into a different quadrant and a third is close to the y-axis (AL 288-1; AL 128-23; AL 207-13).
Conclusion: patterning in morphospace does not fit the horizontal pattern of this sexually dimorphic species but the ranges of size-shape variability in this fossil sample still fall within the range of *G. beringei*. A second species (due to shape *and* size differences between the smaller specimens and the larger specimens) or at least two subspecies within *A. afarensis* might be considered.

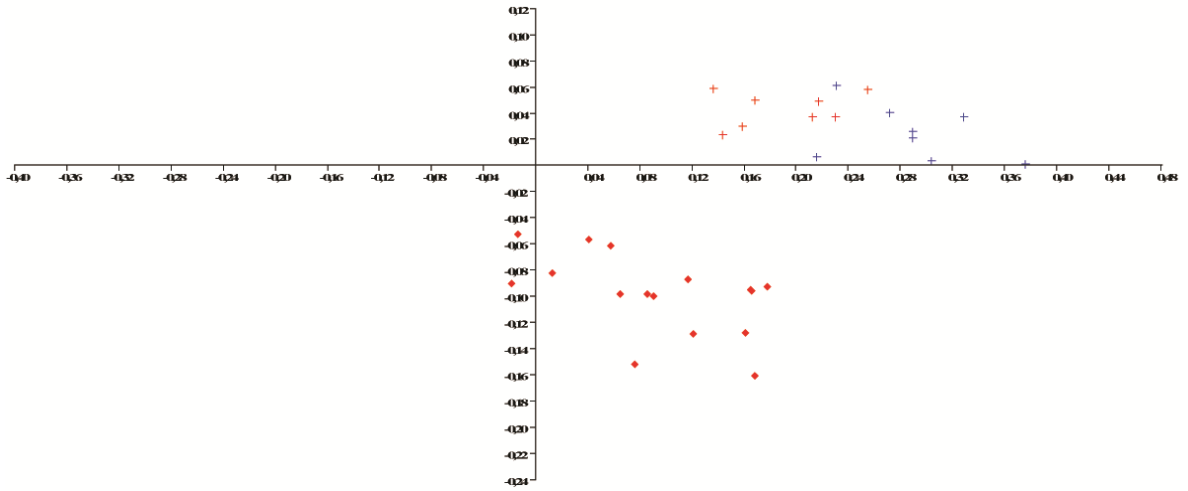
Figure 23. Comparisons in morphospace of specimens attributed to *A. afarensis* with *G. beringei*

A. afarensis (red diamonds) size and shape variability compared to the full sample of *G. gorilla* (green crosses)



Size (range along x-axis) : *A. afarensis* – 0.20; *G. gorilla:* 0.32
Shape (range along y-axis) : *A. afarensis* – 0.11; *G. gorilla*: 0.15

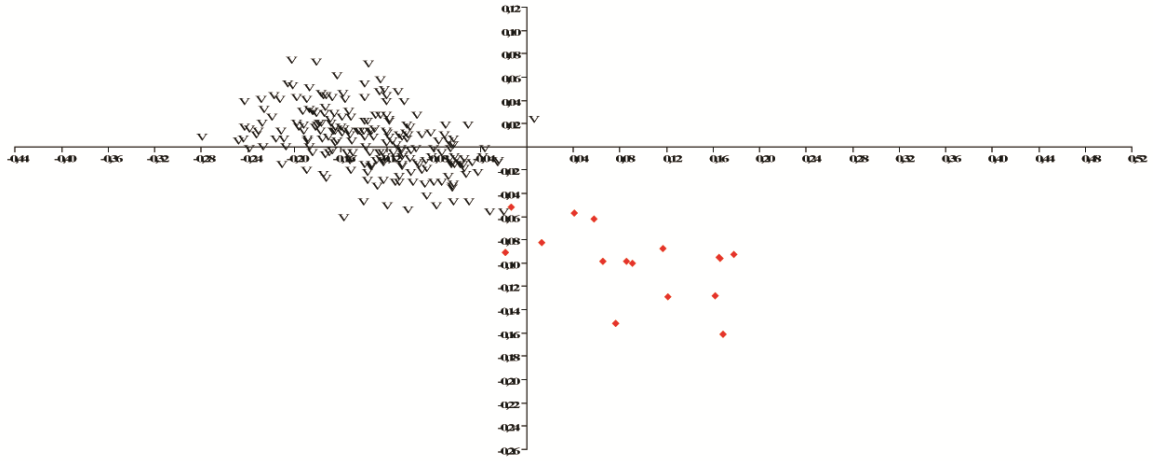
A. afarensis versus a randomly-selected, matched-size sample of *G. gorilla*



Size (range along x-axis) : *A. afarensis* – 0.20; *G. gorilla*: 0.24
Shape (range along y-axis) : *A. afarensis* – 0.11; *G. gorilla:* 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.29; 0.36; 0.26
Patterning match: again too vertical to match the sexually-dimorphic (horizontal) pattern in morphospace of *G. gorilla,* which again consists of 2 subspecies. Examining the pattern in morphospace, the possibility of two subspecies (or two species) should not be ruled out. The larger specimens tend to be broader across the crown. The smaller specimens are all the narrowest. Two specimens fall into a different quadrant and a third is close to the y-axis (AL 288-1; AL 128-23; AL 207-13).
Conclusion: patterning in morphospace does not fit the horizontal pattern of a sexually dimorphic species but the probabilities fall within this 2-subspecies range. A second species or at least two subspecies within *A. afarensis* might be considered.

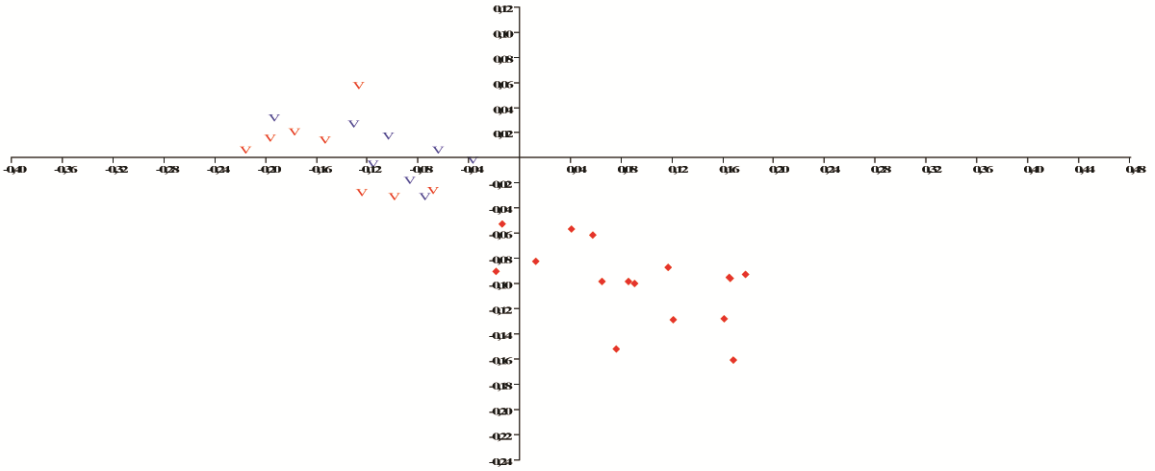
Figure 24. Comparisons in morphospace of specimens attributed to *A. afarensis* with *G. gorilla*

A. afarensis (red diamonds) size and shape variability compared to the full sample of *P. troglodytes* (black V)



Size (range along x-axis) : *A. afarensis* – 0.20; *P. troglodytes:* 0.28
Shape (range along y-axis) : *A. afarensis* – 0.11; *P. troglodytes:* 0.14

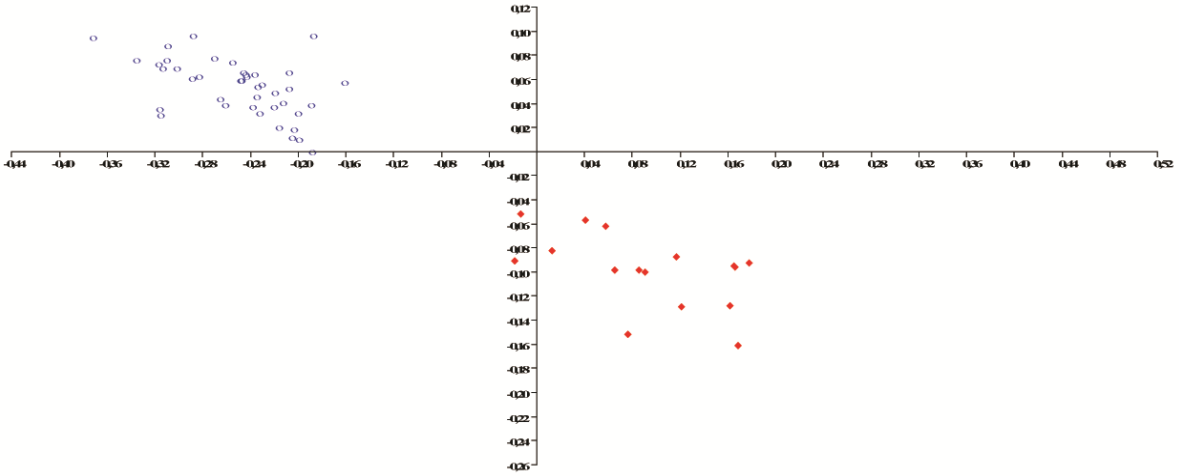
A. afarensis versus a randomly-selected, matched-size sample of *P. troglodytes*



Size (range along x-axis) : *A. afarensis* – 0.20; *P. troglodytes:* 0.18
Shape (range along y-axis) : *A. afarensis* – 0.11; *P. troglodytes:* 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.38; 0.14; 0.04
Patterning match: Very similar pattern in morphospace with 4 subspecies of *P. troglodytes,* one of which is morphologically distinct and may be elevated to the level of species. The variability across the distal cusps of *A. afarensis* is so high that it is unlikely to find a match in a random sample of 16 *P. troglodytes* individuals, however.
Conclusion: patterning in morphospace fits this 4-subspecies group, although variability across the distal cusps of *A. afarensis* is more extreme than expected for *P. troglodytes*. A second species or several subspecies within *A. afarensis* might be considered, based on this comparison.

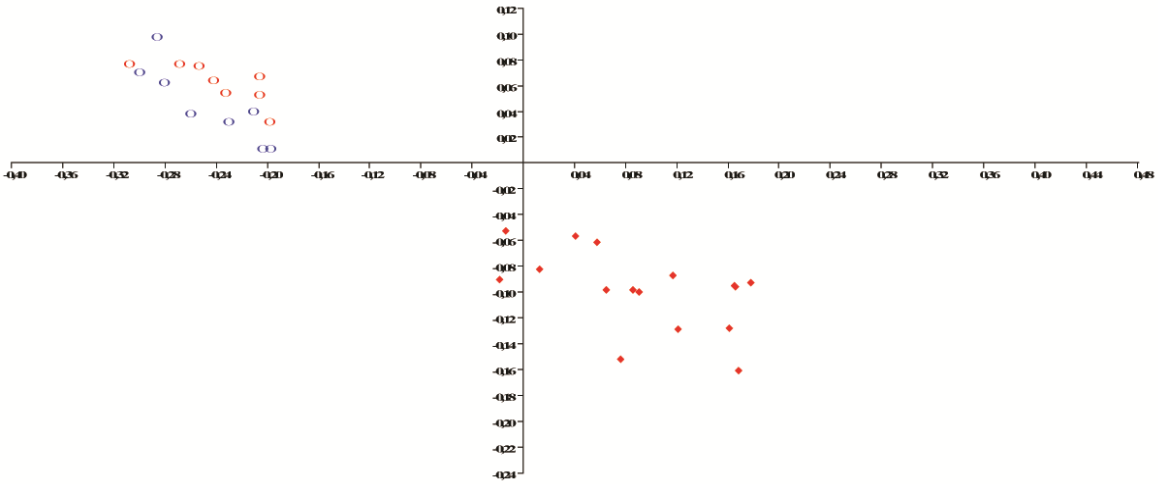
Figure 25. Comparisons in morphospace of specimens attributed to *A. afarensis* with *P. troglodytes*

A. afarensis (red diamonds) size and shape variability compared to the full sample of *P. paniscus* (blue circles)



Size (range along x-axis) : *A. afarensis* – 0.20; *P. paniscus:* 0.21
Shape (range along y-axis) : *A. afarensis* – 0.11; *P. paniscus:* 0.10

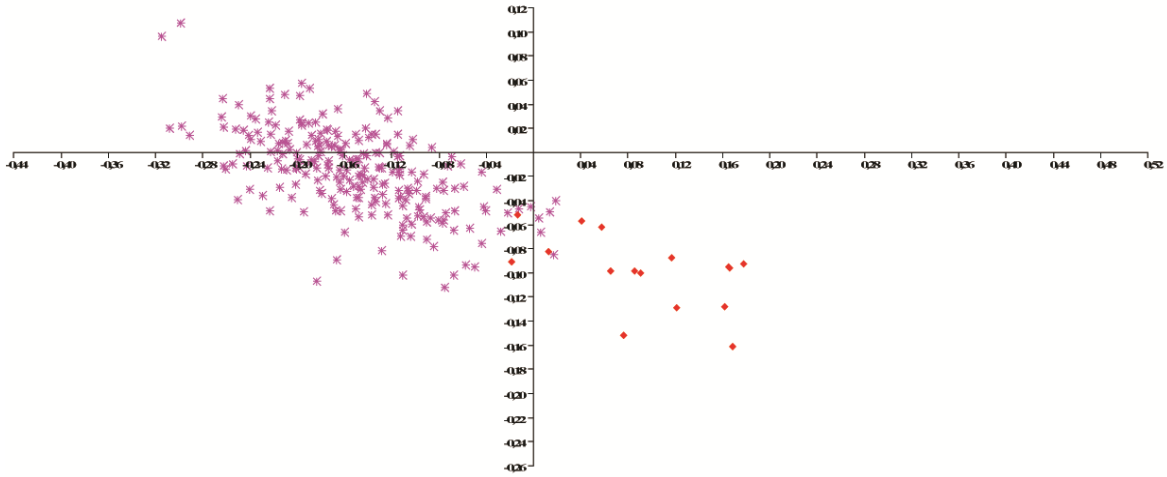
A. afarensis versus a randomly-selected, matched-size sample of *P. troglodytes*



Size (range along x-axis) : *A. afarensis* – 0.20; *P. paniscus:* 0.11
Shape (range along y-axis) : *A. afarensis* – 0.11; *P. paniscus:* 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.11; 0.00; 0.00
Patterning match: Broadly similar pattern in morphospace with single species, *P. paniscus.* However, even with the full sample, variability in morphospace of the shape component of *A. afarensis* exceeds that of *P. paniscus.* Randomisation analyses indicate that there is no probability at all of this type of variability in breadth of crown matching any random sample of 16 *P. paniscus* individuals.
Conclusion: patterning in morphospace barely fits within this group even when the *P. paniscus* sample is maximised. Variability across the breadth of the crown of *A. afarensis* precludes it from matching any 16-specimen sample of *P. paniscus.* More than one species, or several subspecies, should be considered for *A. afarensis.*

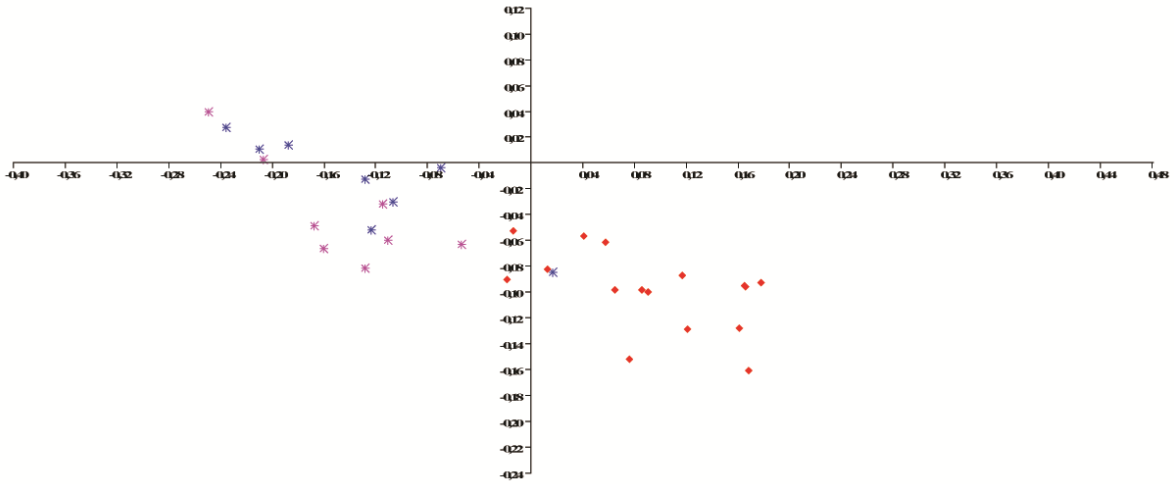
Figure 26. Comparisons in morphospace of specimens attributed to *A. afarensis* with *P. paniscus*

A. afarensis (red diamonds) size and shape variability compared to the full sample of *H. sapiens* (pink stars)



Size (range along x-axis) : *A. afarensis* – 0.20; *H. sapiens:* 0.33
Shape (range along y-axis) : *A. afarensis* – 0.11; *H. sapiens*: 0.22

A. afarensis versus a randomly-selected, matched-size sample of *H. sapiens*



Size (range along x-axis) : *A. afarensis* – 0.20; *H. sapiens:* 0.27
Shape (range along y-axis) : *A. afarensis* – 0.11; *H. sapiens:* 0.12
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.78; 0.12; 0.47
Patterning match: Similar pattern in morphospace with single species, *H. sapiens.* Surprisingly, although size variability is well within the probabilities, the shape variability of *A. afarensis* is slightly out of proportion, especially across the mesial cusps. There is some overlap between the smaller narrower group of *A. afarensis* and larger, broader molars of *H. sapiens* in morphospace.
Conclusion: patterning in morphospace fits well within the range of modern *H. sapiens*, especially as far as length variability is concerned. The eligibility of *H. sapiens* as a valid analogue will, however, be discussed further.

Figure 27. Comparisons in morphospace of specimens attributed to *A. afarensis* with *H. sapiens*

General Discussion – *A. afarensis*:

On initial inspection of the grouping of *A. afarensis* in morphospace, there appears to be two groups: one group of large-sized molars that are broad across the crown and cluster horizontally around the holotype, LH 4 (indicating perhaps males and females in the same group), and another smaller group that clusters horizontally at more positive values along PC2 (narrower teeth) and along both sides of zero along PC1 (smaller teeth):

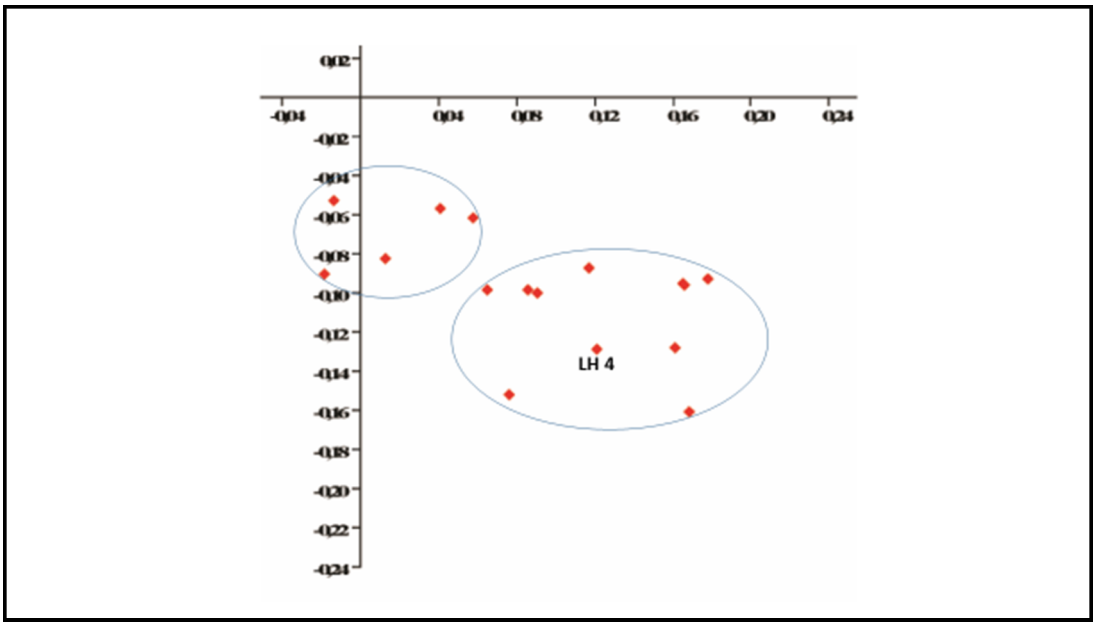


Figure 28. Clustering in morphospace of specimens attributed to *A. afarensis*. (Recap/detail of clustering pattern shown in Figure 16 and Figure 17)

Two of the specimens from the large AL 333 assemblage are present in the "narrow molar" group illustrated in Figure 28. This suggests that at least some "small, narrow molar" group members were from the same sites as some "large, broad molar" group members.

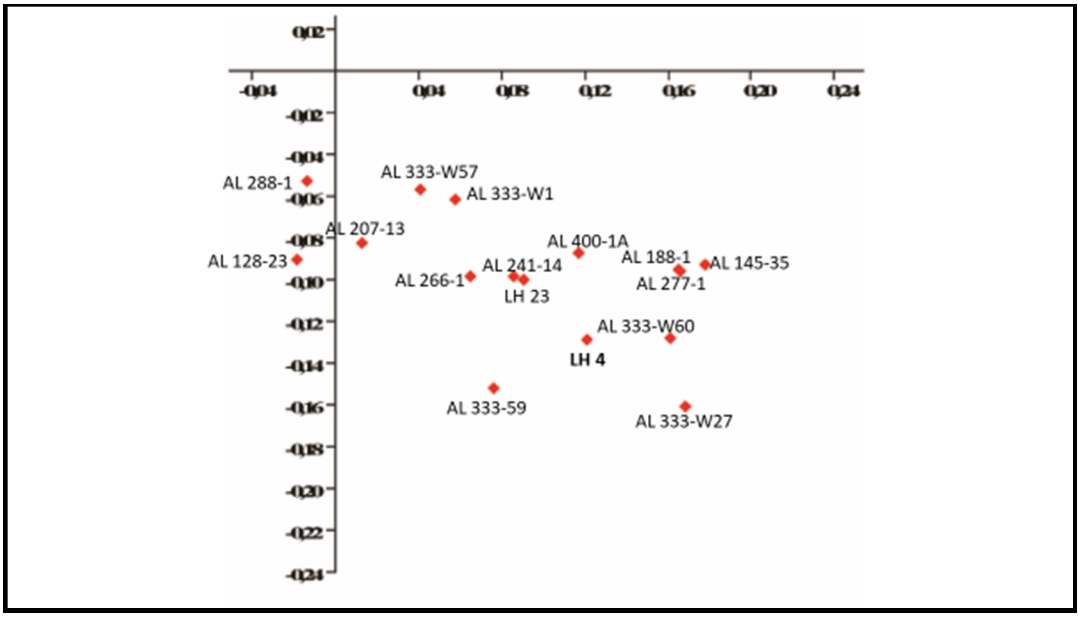


Figure 29. Clustering in morphospace of specimens attributed to *A. afarensis* (specimen number labels added)

Initial descriptions of skeletal elements of Hadar specimens indicated possibly three morphotypes within the sample, some showing affinities with robust australopiths (*Paranthropus*), some with *A. africanus* and some with *Homo* (including OH 7 and KNM-ER 1802) (Johanson & Taieb, 1976). However, after the discovery of the AL 333 assemblage – consisting mainly of surface finds on two hillsides with drainage gullies, that were "littered with hominin fossils" (Kimbel and Delezene, 2009) – the assumption that these specimens all belonged to a single, variable species gained more traction. Nevertheless, such is the mix of primitive and derived traits in various skeletal elements and dental features between specimens attributed to this species that the single species hypothesis for this group of specimens has often been challenged, and this current study, as well as the previous research (Dykes, 2014), based on lower molar morphology, seems to add support to the idea that perhaps more than one species may be present in the various assemblages attributed to *A. afarensis*. Ferguson (1989) in particular made a case for more than one species based on lower premolar morphology.

It is hard to imagine a single species having specimens with very "primitive" premolars (lacking a metaconid or lingual cusp) and fully "derived" premolars (fully molarised), particularly if the individuals with the "primitive" premolars post-date those with the "derived" premolars. AL 288-1 is notable in this regard: although one of the later-dated specimens attributed to *A. afarensis,* it lacks a P_3 metaconid, so it retains the "primitive" form. It also has a "Tomes" root, which is a single root with two canals, whereas most other specimens in the *A. afarensis* hypodigm possess two distinct roots. Its V-shaped, gracile mandible, together with small molars that have been called "chimp-like" (Johanson and Edey, 1990) all point to a primitive state. Using lower second molars in the current study, and lower first molars (Dykes, 2014), this particular specimen (A.L. 288-1) plots in different quadrants of a PCA from the bulk of the specimens within the *A. afarensis* hypodigm, and in particular, the holotype (in this present study, the other specimen grouping in the "y-negative; x-negative" quadrant is AL 128-23, which also lacks a metaconid on its lower P3). It is not just the premolars and the mandible that seem "primitive" in some specimens and "more derived" in others: other skeletal elements have drawn the attention of researchers because of their morphological differences. Schmid (1989) makes the point that the skull reconstructed by Kimbel et al. (1984) is purportedly that of a male, but in comparisons with the reconstruction of the presumed female skull of AL 288-1 ("Lucy"), there are such differences in shape as well as in size of certain of the features in the skull that the polymorphism cannot be explained by sexual dimorphism. Schmid rightly points out that within the same hominoid group, males and females differ by allometry – size differences relative to body size – not in morphology.

The present study and others (e.g., Uchida, 1998a, b; Pilbrow 2006, 2010; Dykes, 2014) would suggest that shape differences, in the context of lower molars, are not easily explained by sexual dimorphism, yet sexual dimorphism remains a typical response to claims that more than one species is present in the *A. afarensis* hypodigm (e.g. Leonard and Hegmon, 1987; Johanson and Edey, 1990; Leonard, 1991; Lockwood et al., 2000; Reno et al., 2003, 2010). Reno et al (2003, 2010) use modern *H. sapiens* as the template for measuring variability in *A. afarensis* and conclude that it falls within the same range of "dimorphism" as their comparative human sample. Kimbel and Delezene (2009), however, state that the observed variation in their human sample does not support this hypothesis. These researchers (Kimbel and Delezene), however, also reject the idea of multiple species within the hypodigm, claiming instead that dental variation "reflects a structural and functional transition within an early hominin lineage" (p. 24), and that what is being observed is "a prime example of how temporal variation can bias analyses of variation in a fossil taxon" (p. 38). Such a suggestion is difficult to resolve, however, since the "primitive" AL 288-1 ("Lucy") is dated to 3.2 Ma (toward the later period for the *A. afarensis* hypodigm), as are the specimens in the AL 333 group, including specimens that have "derived" lower third molars (Ferguson, 1989). Another issue that confounds the idea of cohesion within this species is the variability in diet, ranging widely from C3 to C4/CAM components, with no temporal trend nor any cohesive pattern observable, even in the same geological layers (Wynn, 2016). This apparent dietary flexibility within a single species has been described as "unusual".

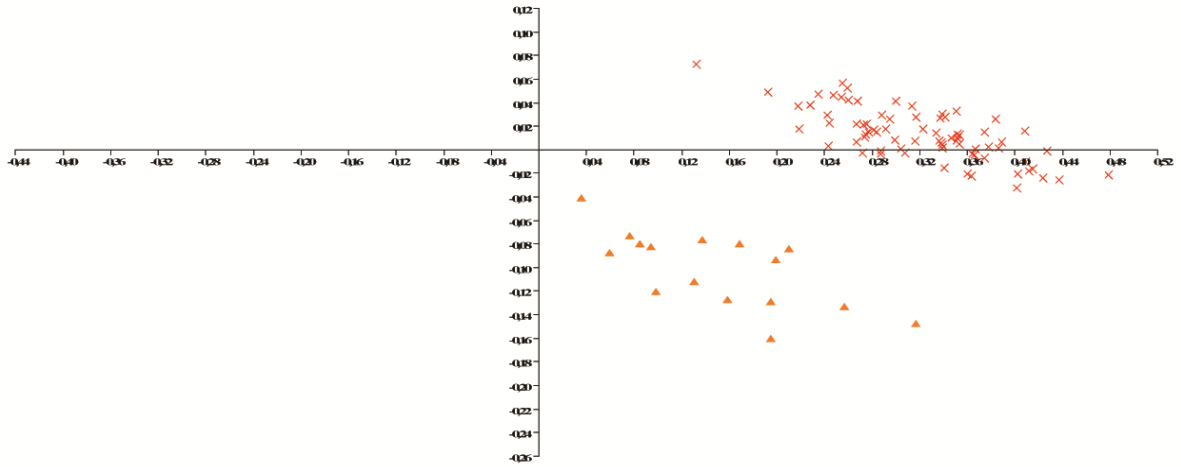
Patterning in morphospace exhibited by *A. afarensis* lower second molars does not preclude a one-species hypothesis in the assemblage, although certainly the existence of

multiple subspecies with different morphologies ought to be considered if a one-species hypothesis is preferred. However, on close inspection of the unexplainable dietary variability (Wynn, 2016), and particularly the craniodental data that indicate "primitive" and "derived" features co-exist at the same geological date, the question of multiple sympatric species, exploiting different niches, should be re-examined. Chimpanzees and gorillas both coexist today with several species of monkey and baboon (Reynolds, 1965), and there are several areas in Africa where chimpanzees and gorillas also live in sympatry (see, for example, Tutin and Fernandez, 1993). There has already been a claim that one of the vertebrae of "Lucy" belonged to a baboon (Meyer et al., 2015). This is not to suggest that palaeoanthropologists have completely misidentified the taxonomy of AL 288-1 (the authors stress that only one bone, not the others, have been misclassified): the point here is that clearly AL 288-1 lived in sympatry with at least one other species, whose skeletal elements are similar enough to have been misidentified and put together, not just within one taxon but within one individual from that taxon. The elements of AL 288-1 were not discovered together in one exact spot – the site has been described as a "sinusoidal stream deposit and crevasse splay deposit that spilled out across the floodplain" (Yemane, 1997, as quoted in Meyer et al., 2015), and Donald Johanson made the assumption that these elements were all from the same individual largely based on their colouration (Johanson and Edey, 1990). The idea that two or more species might be present at the same site should never be ruled out: within a single cave system in South Africa (Sterkfontein, arguably the same member of the cave – Clarke, 2008), there are now considered to be not one but two different species of *Australopithecus* (one robust, one gracile – Clarke, 1988, 2008, 2013), as well as at least one early *Homo* cranium (Hughes and Tobias, 1977). Early *Homo* and *Paranthropus* have been found together at Swartkrans. Perhaps, in the

context of this kind of research that does not rule out the coexistence of more than one species within any one assemblage, the variability seen between specimens attributed to *A. afarensis,* even those from the AL 333 site, might be better explained in the context of sympatric species living in the same area.

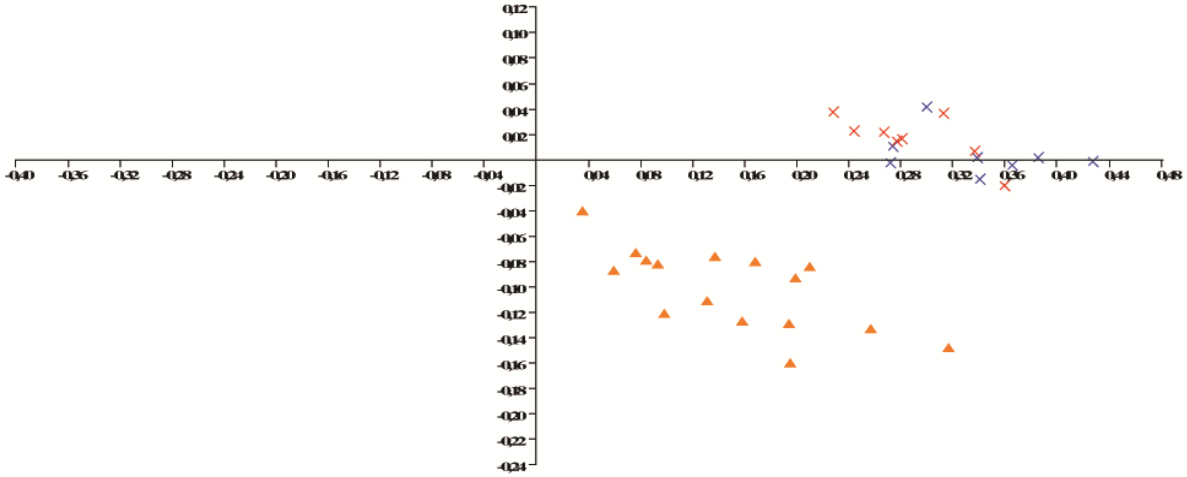
5.3.2 *Australopithecus africanus.* Recap of results and preliminary discussion

A. africanus (orange triangles) size and shape variability compared to the full sample of *G. beringei* (diagonal crosses)



Size (range along x-axis) : *A. africanus* – 0.28; *G. beringei* – 0.35
Shape (range along y-axis) : *A. africanus* – 0.12; *G. beringei* - 0.11

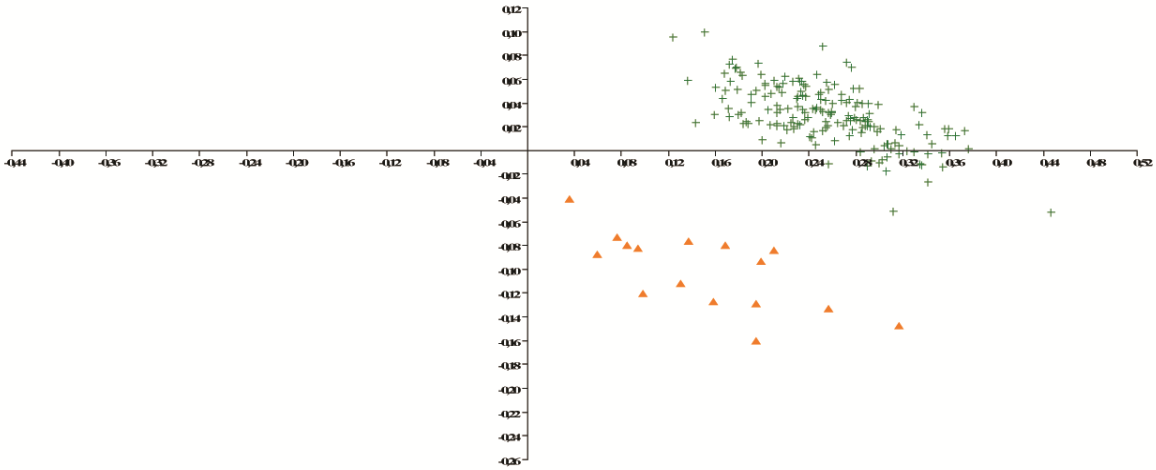
A. africanus versus a randomly-selected, matched-size sample of *G. beringei*



Size (range along x-axis) : *A. africanus* – 0.28; *G. beringei* – 0.20
Shape (range along y-axis) : *A. africanus* – 0.12; *G. beringei* - 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.25; 0.08; 0.07
Patterning match: Slightly too much variability in breadth/shape to fit well with the horizontal pattern of sexually dimorphic *G. beringei*, consisting of two species of differing average size. The randomised MD probability is higher than the probabilities of the breadth measurements matching this species' range for that reason. MD length measurements are a better "fit" with *G. beringei,* but the size differences between *G. b. graueri* and *G. b. beringei* inflate the size range of *G. beringei.*
Conclusion: there is a small possibility that this group of specimens matches the shape variability of *G. beringei,* which consists of two subspecies. Possibly more than one species or more than one subspecies is represented in this sample.

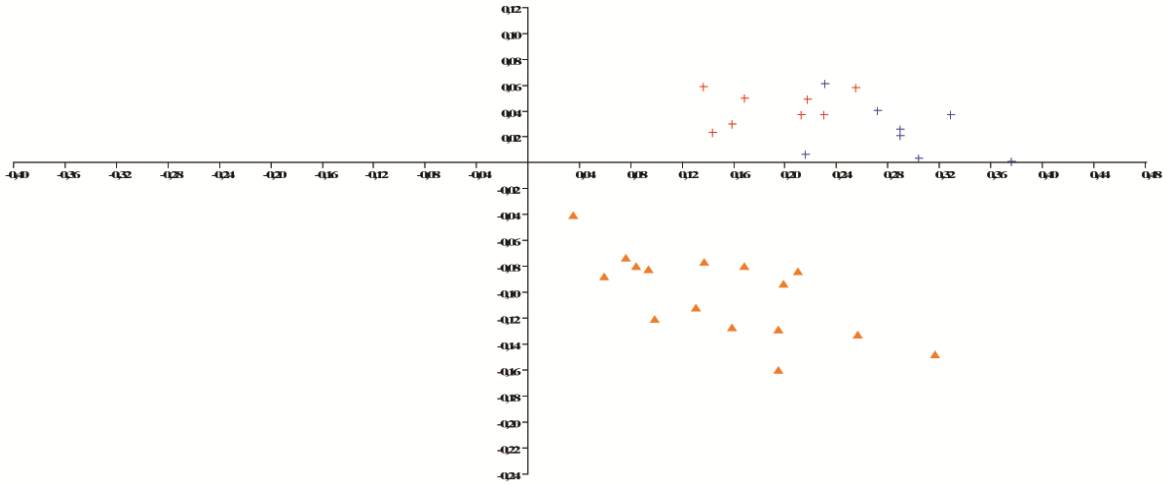
Figure 30. Comparisons in morphospace of specimens attributed to *A. africanus* with *G. beringei*)

A. africanus (orange triangles) size and shape variability compared to the full sample of *G. gorilla* (upright crosses)



Size (range along x-axis) : *A. africanus* – 0.28*; G. gorilla* – 0.32
Shape (range along y-axis) : *A. africanus* – 0.12*; G. gorilla* - 0.15

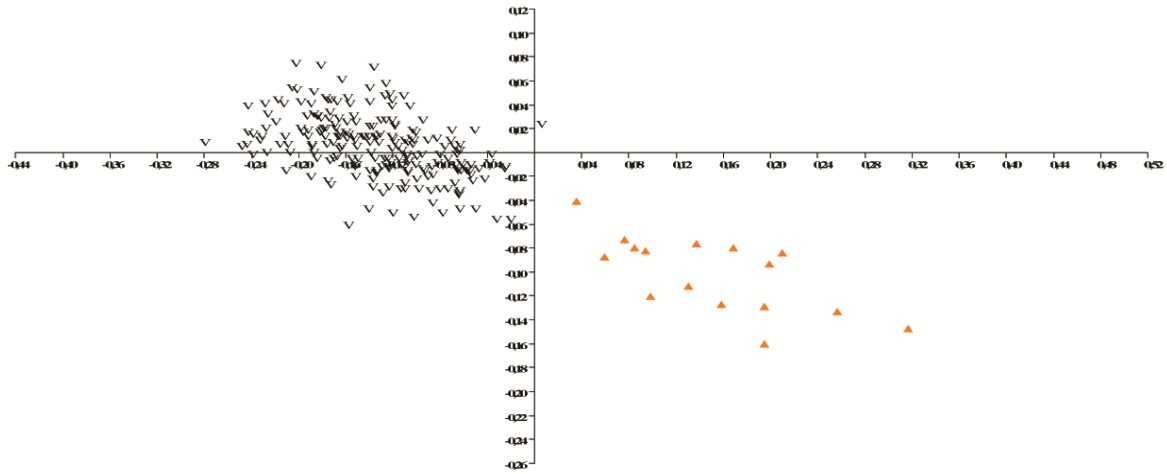
A. africanus versus a randomly-selected, matched-size sample of *G. gorilla*



Size (range along x-axis) : *A. africanus* – 0.28; *G. gorilla* – 0.24
Shape (range along y-axis) : *A. africanus* – 0.12; *G. gorilla* - 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.01; 0.15; 0.12
Patterning match: In this comparison, it is the variability in MD length of *A. africanus* that precludes it from probably falling within the range of *G. gorilla,* which consists of two subspecies. Shape variability does not match with the horizontal patterning of this sexually dimorphic species, although there are fairly low probabilities of shape variance being within the range of this species.
Conclusion: the specimens representing *A. africanus* in this study are variable in both size and shape. The explanation is not likely to be sexual dimorphism, but rather that there may be different subspecies or species present in this group. If so, size variability between the subspecies should match that of the two *G. beringei* subspecies.

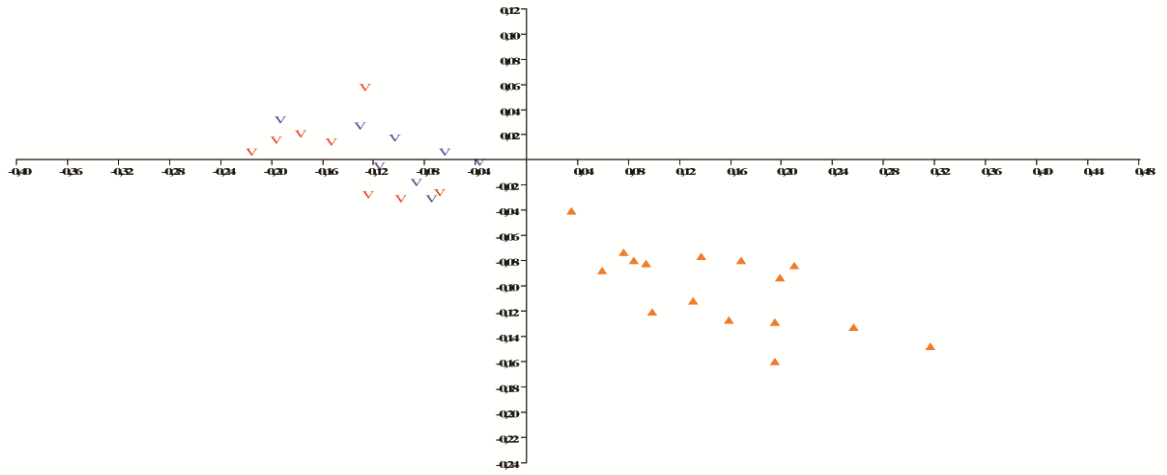
Figure 31. Comparisons in morphospace of specimens attributed to *A. africanus* with *G. gorilla*

A. africanus (orange triangles) size and shape variability compared to the full sample of *P. troglodytes* (V-shapes)



Size (range along x-axis) : *A. africanus* – 0.28; *P. troglodytes* – 0.28
Shape (range along y-axis) : *A. africanus* – 0.12; *P. troglodytes* - 0.14

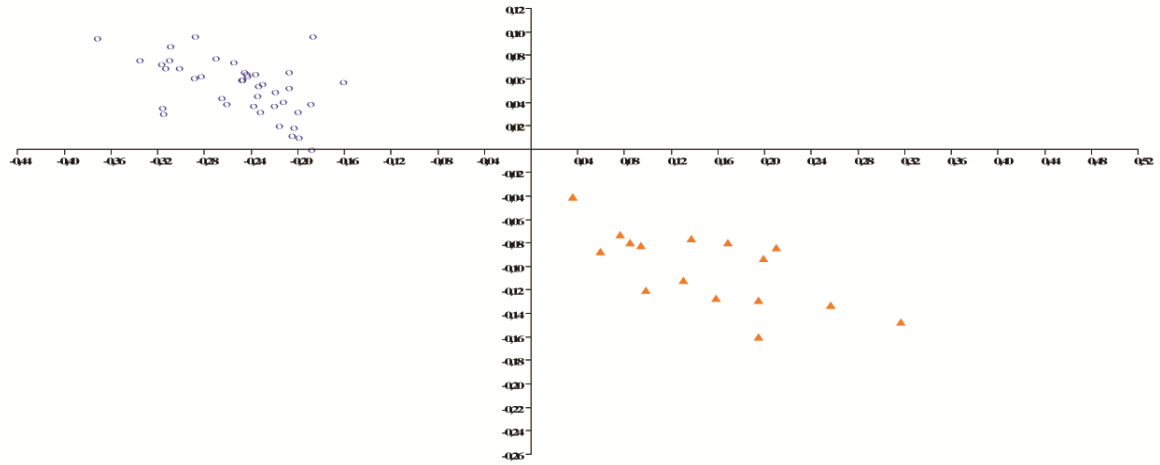
A. afarensis versus a randomly-selected, matched-size sample of *P. troglodytes*



Size (range along x-axis) : *A. africanus* – 0.28; *P. troglodytes* – 0.18
Shape (range along y-axis) : *A. africanus* – 0.12; *P. troglodytes* - 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.01; 0.03; 0.00
Patterning match: The directionality of the patterning of specimens attributed to *A. africanus* matches that of *P. troglodytes.* However, the level of variability within this sample barely falls within the range of the full sample of *P. troglodytes,* which consists of four subspecies, one of which is morphologically very distinct from the others. The probabilities of finding a matched-size sample with the amount of variability displayed by these specimens is negligible.
Conclusion: the specimens representing *A. africanus* in this study are too variable in shape even to fall within the range of the 4-subspecies *P. troglodytes.* The directionality of the patterning in morphospace is similar to this non-dimorphic species; however, a second species represented within this sample might be considered to explain the excessive variability.

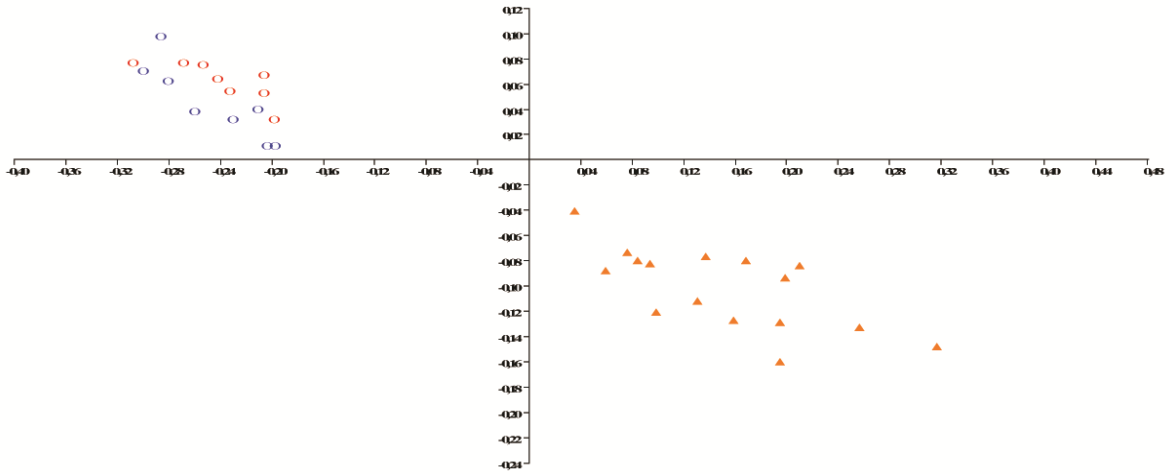
Figure 32. Comparisons in morphospace of specimens attributed to *A. africanus* with *P. troglodytes*

A. africanus (orange triangles) size and shape variability compared to the full sample of *P. paniscus* (open circles)



Size (range along x-axis) : *A. africanus* – 0.28; *P. paniscus* – 0.21
Shape (range along y-axis) : *A. africanus* – 0.12; *P. paniscus* - 0.10

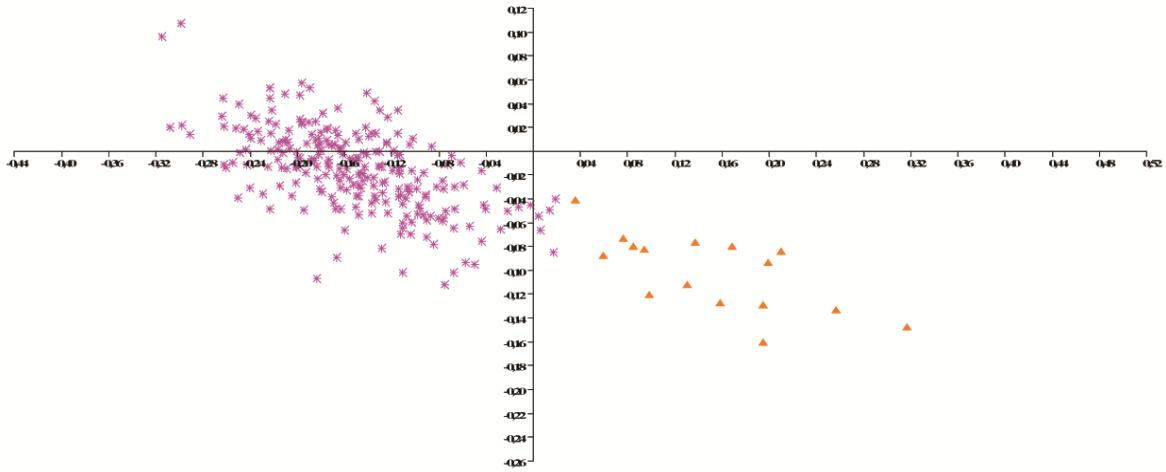
A. africanus versus a randomly-selected, matched-size sample of *P. paniscus*



Size (range along x-axis) : *A. africanus* – 0.28; *P. paniscus* – 0.11
Shape (range along y-axis) : *A. africanus* – 0.12; *P. paniscus* - 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.00; 0.00; 0.00
Patterning match: The directionality of the patterning of specimens attributed to *A. africanus* matches that of *P. paniscus.* However, the level of variability within this sample exceeds the size and shape variability of even the full sample of *P. paniscus.* There is zero probability of the length and breadth measurement variability of *A. africanus* matching any randomly selected matched-size sample of *P. paniscus.*
Conclusion: *P. paniscus* is a single species with no subspecies. The range of variability of the specimens representing *A. africanus* in this study is excessive. This result is highly suggestive of the inclusion of two or more subspecies, perhaps two or more species, represented in the *A. africanus* sample.

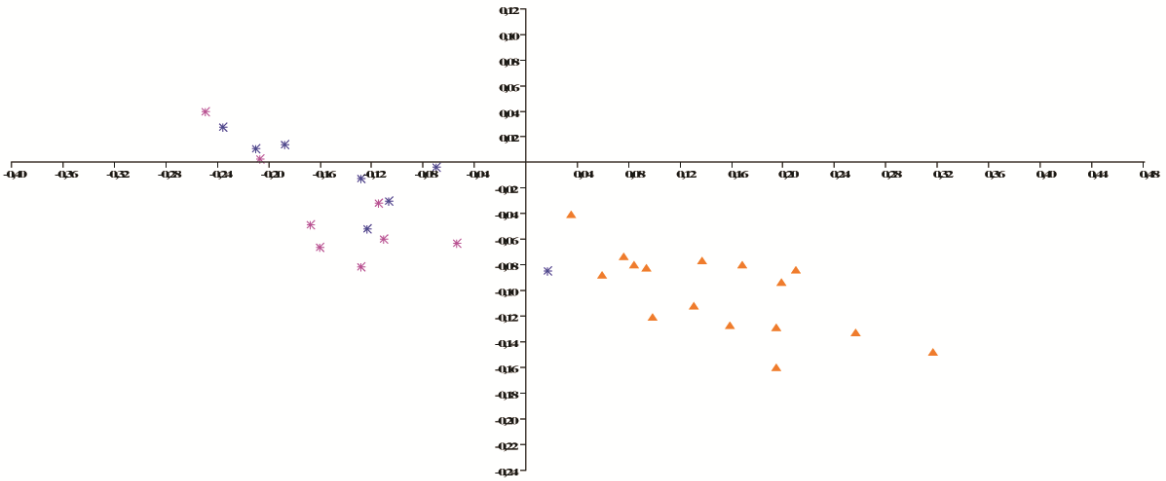
Figure 33. Comparisons in morphospace of specimens attributed to *A. africanus* with *P. paniscus*

A. africanus (orange triangles) size and shape variability compared to the full sample of *H. sapiens* (stars)



Size (range along x-axis) : *A. africanus* – 0.28; *H. sapiens* – 0.33
Shape (range along y-axis) : *A. africanus* – 0.12; *H. sapiens* - 0.22

A. africanus versus a randomly-selected, matched-size sample of *H. sapiens*



Size (range along x-axis) : *A. africanus* – 0.28; *P. H. sapiens* – 0.27
Shape (range along y-axis) : *A. africanus* – 0.12; *H. sapiens* - 0.12
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.22; 0.02; 0.25
Patterning match: The directionality of the patterning of specimens attributed to *A. africanus* matches that of *H. sapiens.* The ranges of size and shape variability fit comfortably within the full range of variability of *H. sapiens,* but when the sample size is reduced, it only just matches the range. More specifically, variability of breadth across the mesial cusps of these specimens is too high to fit within the probable range of any sample of 16 *H. sapiens* individuals.
Conclusion: Specimens representing *A. africanus* are so variable, especially across the mesial cusps, that there is only a slight probability that this sample would match the range of any randomly chosen sample of modern *H. sapiens,* which, given the huge ranges of variability in both size and shape of *H. sapiens* molars is rather surprising.

Figure 34. Comparisons in morphospace of specimens attributed to *A. africanus* with *H. sapiens*

General discussion: *A. africanus*

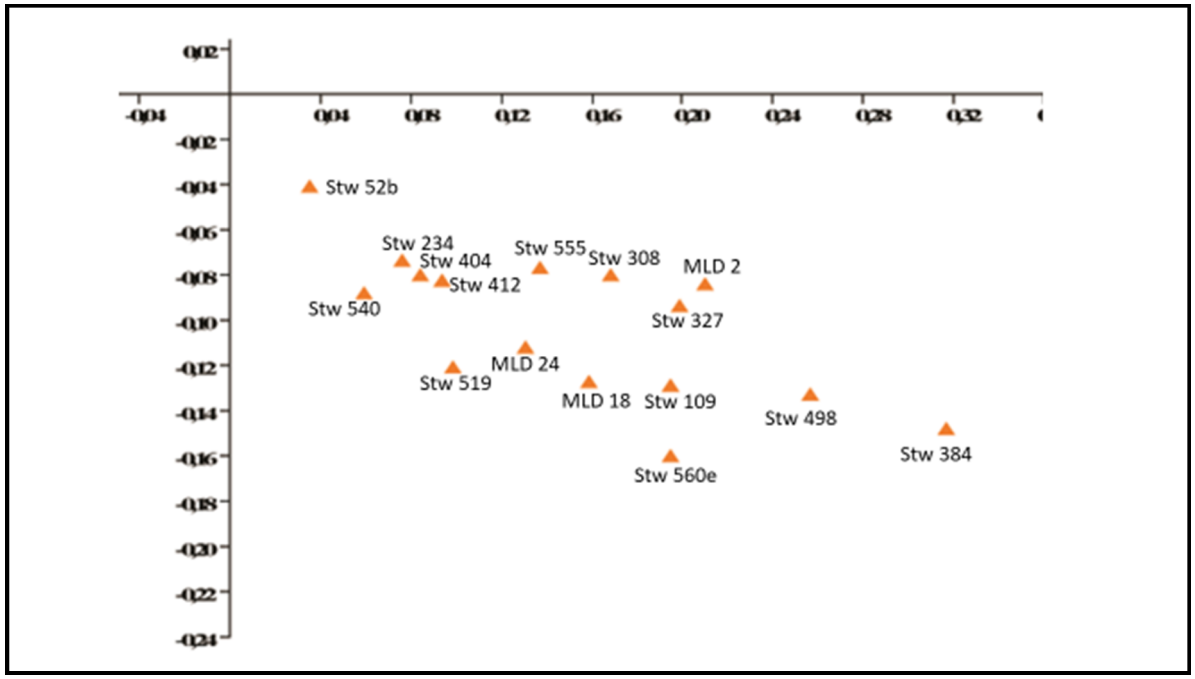


Figure 35. Clustering in morphospace of specimens attributed to *A. africanus*, extracted from Figure 16 and Figure 17, with labels.

Patterning in morphospace ("diagonal" – along PC1 and PC2) with high ranges of variability, suggests that more than one species is also present within this hypodigm. Substantial variability, even between specimens from the same Member in the same cave (Member 4, Sterkfontein), has led researchers to suggest that the specimens cannot be accommodated into one species (e. g. Clarke, 1988, 2008, 2013; Calcagno et al., 1997; Lockwood, 1997). Calcagno et al. (1997) used average weighted coefficients of variation from numerous reference samples of two sexually dimorphic species to compare variability within teeth from Member 4. They suggested that the probability was low that these specimens could have been sampled from a population as variable as either of the two reference species. In a seminal paper describing in detail many of the remains from Members 4 and 5 of Sterkfontein, Moggi-Cecchi et al. (2006) argued that these specimens did not exhibit more variability than other hominin samples, citing, for

example, *H. habilis sensu lato* and *A. afarensis*. However, these two hypodigms themselves are often challenged themselves from the point of view of there being more than one species included within them. Kimbel and White (1988) note that *A. africanus* is more variable than *P. robustus,* a point which had already been made by Robinson (1956) who noted that "*Australopithecus* is more variable than *Paranthropus,* even though sample numbers are highest in the latter" (p. 151). Similar levels of variability for both *A. africanus* and *P. robustus* were observed in the present study. Kimbel and White (1988) offer two hypotheses to explain the observed variability. Either Member 4 includes temporally-mixed specimens from an "evolving lineage", or there is more than a single species represented in this Member. Clarke (1988) takes the latter approach. He had previously noted (1985) that the talus cone of Member 4 must have accumulated over a considerable time span, since there were indications of temporally-mixed faunal assemblages within it. This might support both hypotheses, but the second is more parsimonious: remains of several hominin species, over a long period, could become mixed in the talus cone. Indeed, Clarke proposed that at least two species of *Australopithecus* were represented in Member 4, with the second species being larger-toothed and similar to that represented by MLD 2 from Makapansgat. Dart (1948) originally attributed MLD 2 to *A. prometheus.* Clarke (2013) revived *A. prometheus* to accommodate these specimens, and StW 573 from Member 2, which has been named "Little Foot" (Granger et al., 2015).

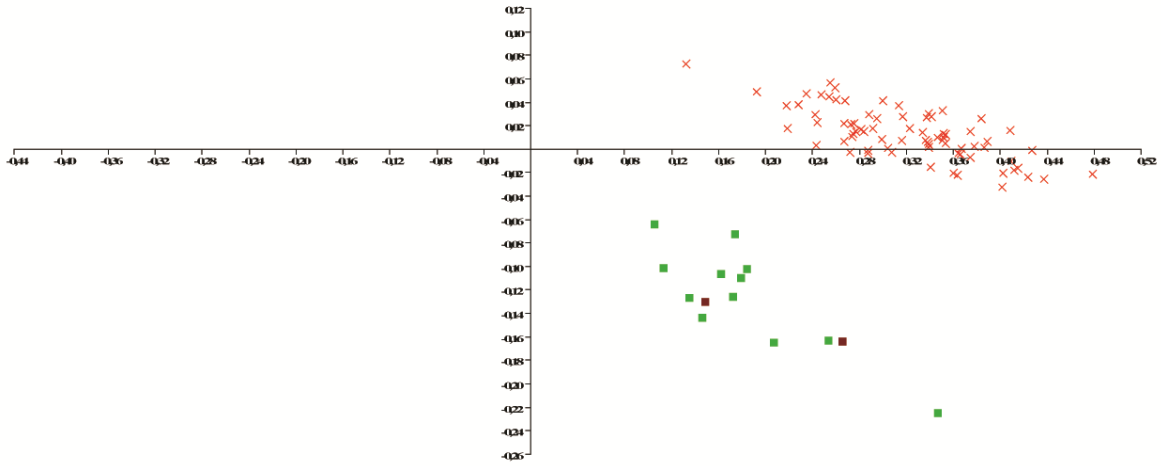
Attributed to *A. africanus*, Clarke (1988) grouped Sts 52 with other small-toothed specimens, stating that these had characters "trending toward *Homo".* In the present study, Sts 52 does not group with the remainder of the *A. africanus* lower second molars

(Figure 15). In fact, it is the only specimen in the *A. africanus* group that overlaps with *Homo* on the PCA that incorporates all extant and extinct species (Figure 21). It plots closest to the holotype of *H. ergaster,* KNM-ER 992. In a comparison of lower first molars (Dykes 2014), Sts 52 also appears "anomalous". Thus, both the first and second lower molars corroborate other research suggesting that Sts 52 does not fall into *A. africanus*, but appears to fall into another hominin species (Kimbel and White, 1988; Clarke, 2008; Fornai et al., 2013).

It appears that the variability in lower first and second molars observed within the *A. africanus* hypodigm, and even within Member 4 of Sterkfontein, represents multiple species. In addition to *A. africanus, A. prometheus* and the *Homo*-like specimen, Sts 52, another possible specimen belonging to "Early *Homo",* probably *H. habilis,* is also represented within Member 4 (and not Member 5, according to Clarke, 1994), in the form of Stw 53 (Hughes and Tobias, 1977). Oldowan tools have also been discovered at Sterkfontein, dating to less than 2 million years in age, which would suggest an association with *H. habilis* rather than *A. africanus* and *A. prometheus*. At other sites, such as Swartkrans and Drimolen, early *Homo* is also believed to be present (Curnoe, 2008), so the coexistence of possibly more than one species in an assemblage is perhaps not such an unusual idea.

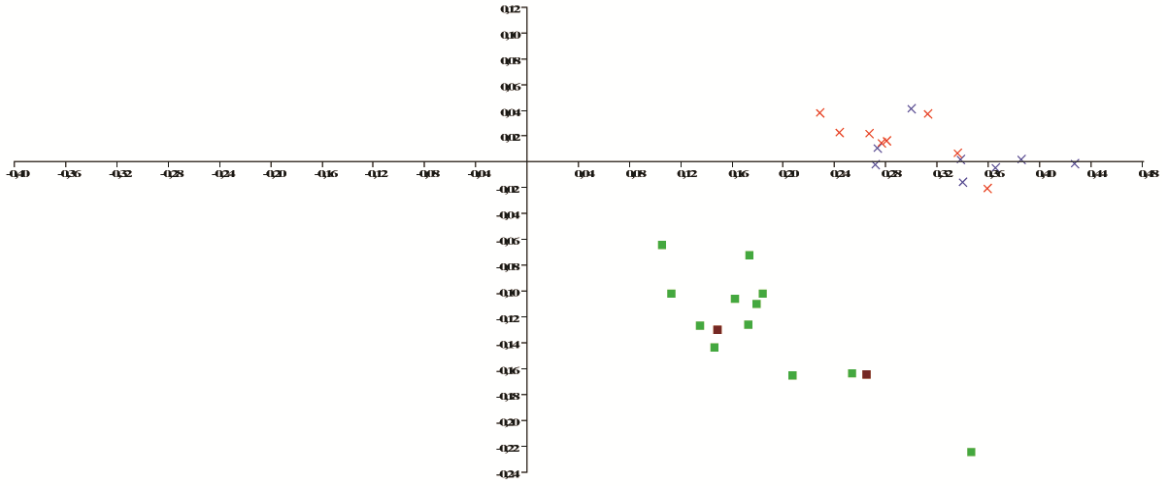
5.3.3 *Paranthropus robustus.* Recap of results and preliminary discussion:

P. robustus (green squares) size and shape variability compared to the full sample of *G. beringei* (diagonal crosses). Brown squares represent *P. boisei.*



Size (range along x-axis) : *P. robustus* – 0.24; *G. beringei* – 0.35
Shape (range along y-axis) : *P. robustus* – 0.16*; G. beringei* - 0.11

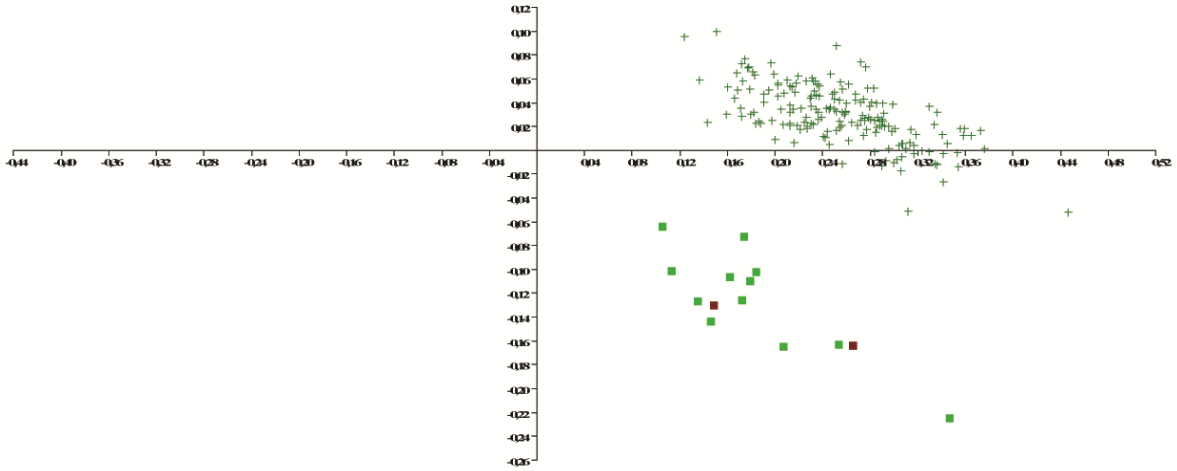
P. robustus versus a randomly-selected, similarly-sized sample of *G. beringei*



Size (range along x-axis) : *P. robustus* – 0.24*; G. beringei* – 0.20
Shape (range along y-axis) : *P. robustus* – 0.16; *G. beringei* - 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.53; 0.28; 0.00
Patterning match: The vertical and horizontal patterning of *P. robustus* (green squares) does not follow the more horizontal clustering of the sexually dimorphic *G. beringei.* The main shape component that influences the range of variability along the x-axis is the measurement across the distal cusps in *P. robustus*, and this excessive variability precludes the probability that this group of specimens would fall within the range of *G. beringei*. Excluding the massive Gondolin molar would markedly increase the probabilities of being within range, to 1.00; 0.95; 0.69, respectively.
Conclusion: If only the Kromdraai and Swartkrans molars were included here, this group of specimens would easily fall within the range of *G. beringei,* even though the patterning does not resemble the horizontal grouping of a sexually dimorphic species.

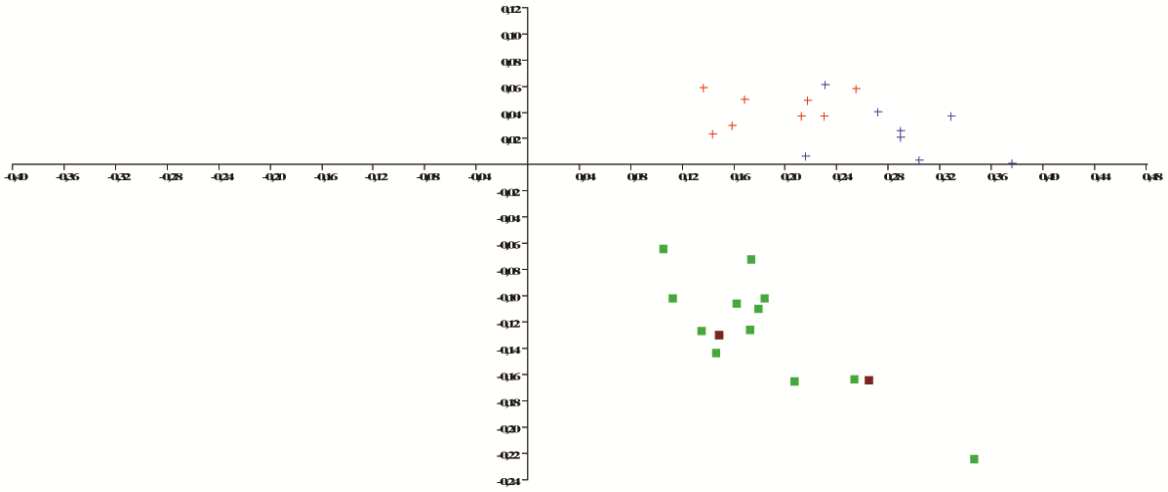
Figure 36. Comparisons in morphospace of specimens attributed to *P. robustus* with *G. beringei*

P. robustus (green squares) size and shape variability compared to the full sample of *G. gorilla* (upright crosses). Brown squares represent *P. boisei.*



Size (range along x-axis) : *P. robustus* – 0.24; *G. gorilla* – 0.32
Shape (range along y-axis) : *P. robustus* – 0.16; *G. gorilla* - 0.15

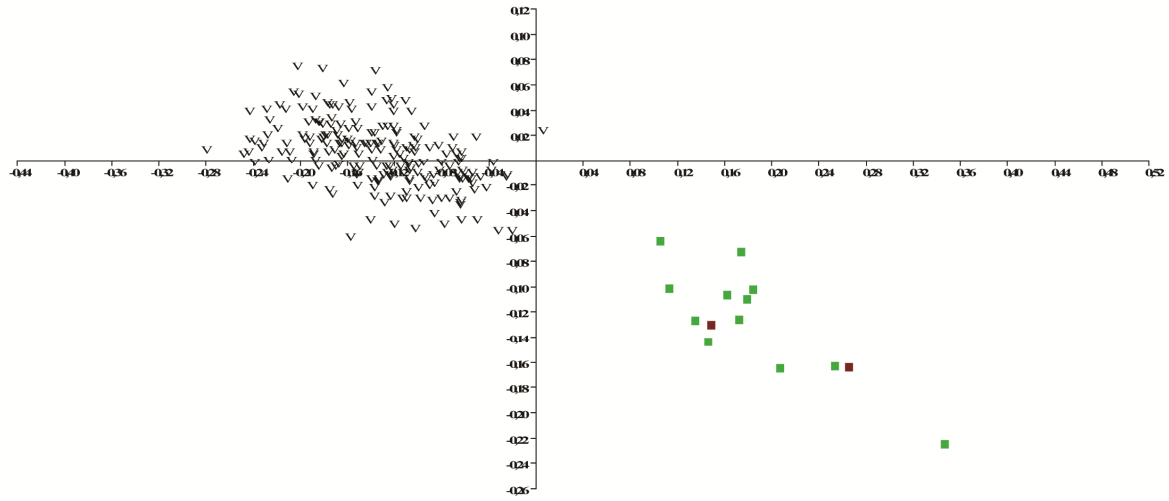
P. robustus versus randomly-selected, similarly-sized sample of *G. gorilla*



Size (range along x-axis) : *P. robustus* – 0.24; *G. gorilla* – 0.24
Shape (range along y-axis) : *P. robustus* – 0.16; *G. gorilla* - 0.06
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.06; 0.36; 0.04
Patterning match: The vertical and horizontal patterning of *P. robustus* (green squares) does not follow the more horizontal clustering of the sexually dimorphic *G. gorilla.* Again, the variability in breadth across the distal cusps in *P. robustus*, makes it improbable that this group of 16 specimens would fall within the range of *G. gorilla*. Excluding the massive Gondolin molar would markedly increase the probabilities of being within range, to 0.97; 0.92; 0.76, respectively.
Conclusion: If only the Kromdraai and Swartkrans molars were included here, this group of specimens would easily fall within the range of *G. gorilla,* even though the patterning does not resemble the horizontal grouping of a sexually dimorphic species.

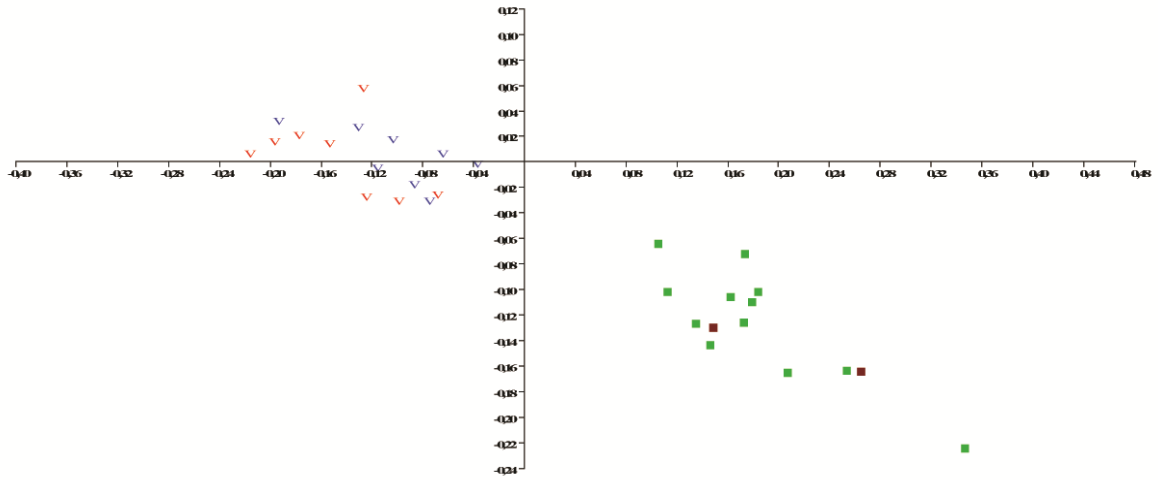
Figure 37. Comparisons in morphospace of specimens attributed to *P. robustus* with *G. gorilla*

P. robustus (green squares) size and shape variability compared to the full sample of *P. troglodytes* (V-shapes). Brown squares represent *P. boisei.*



Size (range along x-axis) : *P. robustus* – 0.24; *P. troglodytes* – 0.28
Shape (range along y-axis) : *P. robustus* – 0.16; *P. troglodytes* - 0.14

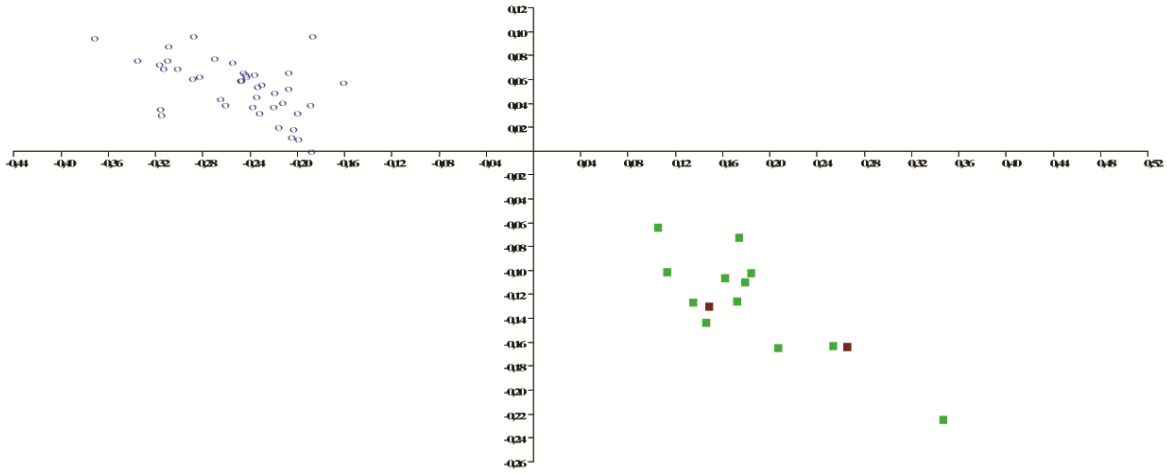
P. robustus versus a randomly-selected, similarly-sized sample of *P. troglodytes*



Size (range along x-axis) : *P. robustus* – 0.24; *P. troglodytes* – 0.18
Shape (range along y-axis) : *P. robustus* – 0.16; *P. troglodytes* - 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.07; 0.18; 0.00
Patterning match: The vertical range (shape variability) of *P. robustus* (green squares) is excessive by comparison even to a 4-subspecies species group like *P. troglodytes.* Again, the variability in the measurement across the distal cusps in *P. robustus* is so excessive that there is no probability that this group of specimens would fall within the range of *P. troglodytes*. Excluding the massive Gondolin molar would again increase the probabilities of being within range, to 0.99; 0.85; 0.59, respectively.
Conclusion: If only the Kromdraai and Swartkrans molars were included here, this group of specimens would easily fall within the range of *P. troglodytes,* even though there is considerably more variability in distal cusp breadth to make it a perfect match in morphospace.

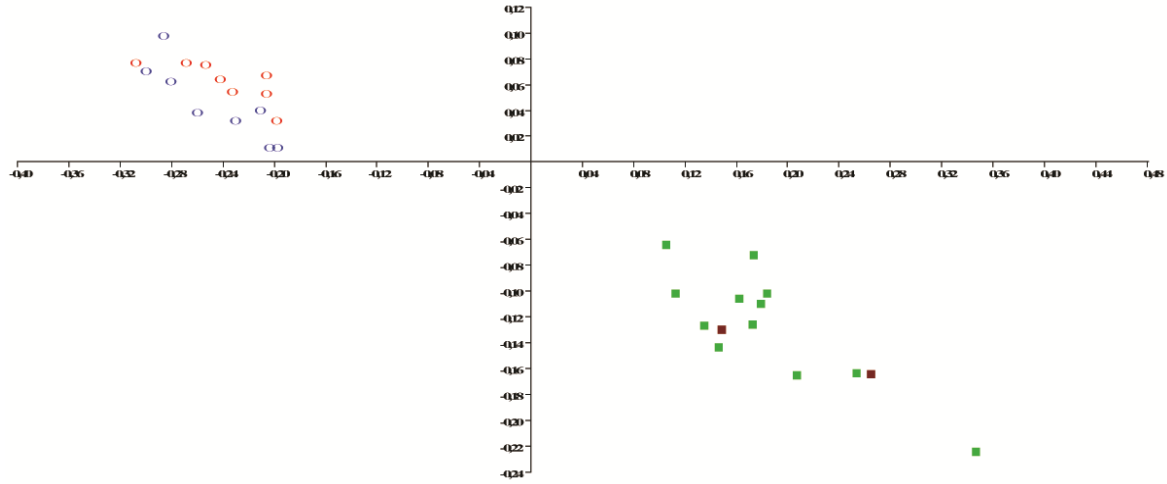
Figure 38. Comparisons in morphospace of specimens attributed to *P. robustus* with *P. troglodytes*

P. robustus (green squares) size and shape variability compared to the full sample of *P. paniscus* (circles). Brown squares represent *P. boisei.*



Size (range along x-axis) : *P. robustus* – 0.24*; P. paniscus* – 0.21
Shape (range along y-axis) : *P. robustus* – 0.16*; P. paniscus* - 0.10

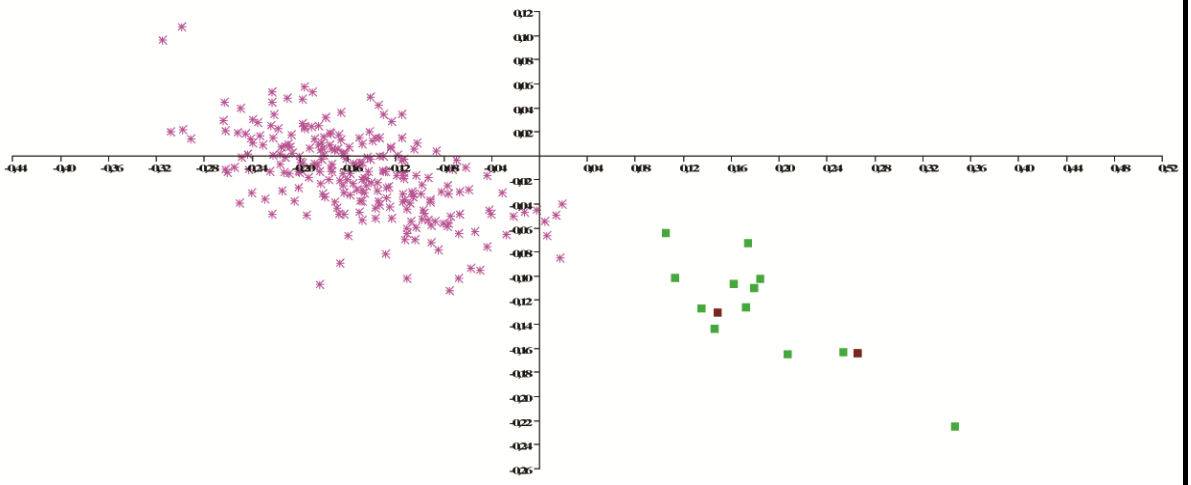
P. robustus versus a randomly-selected, similarly-sized sample of *P. paniscus*



Size (range along x-axis) : *P. robustus* – 0.24; *P. paniscus* – 0.11
Shape (range along y-axis) : *P. robustus* – 0.16; *P. paniscus* - 0.09
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.00; 0.00; 0.00
Patterning match: The vertical range (shape variability) of *P. robustus* (green squares) is excessive and well outside of the range of variability of *P. paniscus.* In this instance, the horizontal range is also too high, even when the whole *P. paniscus* sample is included. In all three dimensions (MD; BL-Mes; BL-Dis), there is no probability whatsoever of this group of specimens falling within the range of *P. paniscus.* Excluding the massive Gondolin molar, however, would increase the probabilities of being within range, to 0.93; 0.38; 0.26, respectively.
Conclusion: If only the Kromdraai and Swartkrans molars were included here, this group of specimens would easily fall within the range of *P. paniscus,* even though there is considerably more variability in distal cusp breadth to make it a perfect match in morphospace.

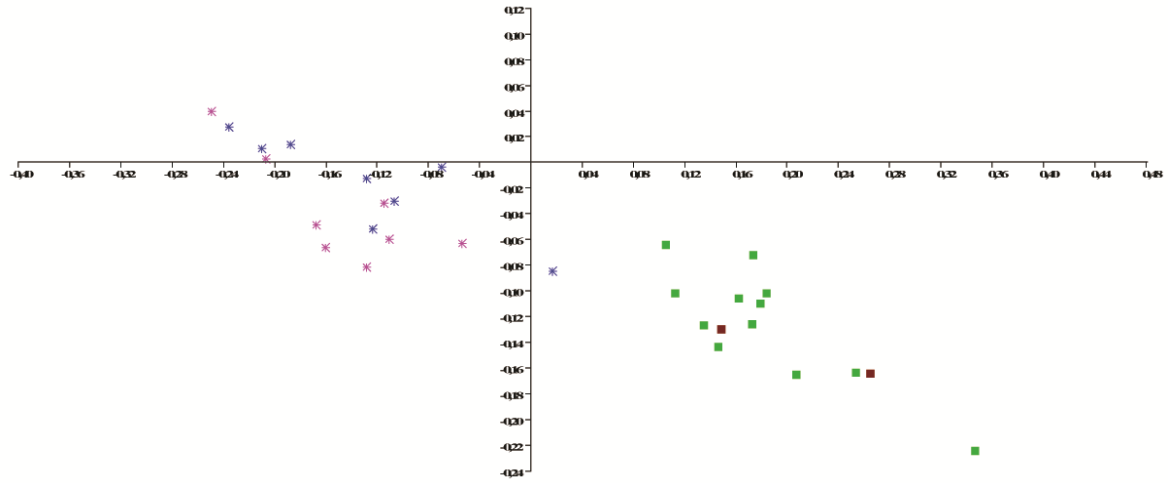
Figure 39. Comparisons in morphospace of specimens attributed to *P. robustus* with *P. paniscus*

P. robustus (green squares) size and shape variability compared to the full sample of *H. sapiens* (stars). Brown squares represent *P. boisei.*



Size (range along x-axis) : *P. robustus – 0.24; H. sapiens – 0.33*
Shape (range along y-axis) : *P. robustus – 0.16; H. sapiens - 0.22*

P. robustus versus a randomly-selected, similarly-sized sample of *H. sapiens*



Size (range along x-axis) : *P. robustus* – 0.24; *H. sapiens* – 0.27
Shape (range along y-axis) : *P. robustus* – 0.16; *H. sapiens* – 0.12
Randomisation probabilities MD; BL (Mesial); BL (Distal) in range: 0.43; 0.16; 0.07
Patterning match: There is considerable size and shape variability within *H. sapiens* molars, and there is a good match in the pattern of clustering between *P. robustus* (green squares) and *H. sapiens,* even when the sample size is limited to n=16 (*P. robustus,* n=12). The probabilities of encountering a sample of 16 human molars which have as much, or more, variability than the 12 *P. robustus* molars in this sample are quite within the realm of probability. Excluding the Gondolin molar would raise these probabilities to 0.99; 0.84; 0.88, respectively.
Conclusion: This species matches the pattern of variability of *H. sapiens* in shape and size. If the Gondolin molar were excluded, the match would be much better. However, the variability within *H. sapiens* requires discussion.

Figure 40. Comparisons in morphospace of specimens attributed to *P. robustus* with *H. sapiens*

General discussion – *P. robustus*

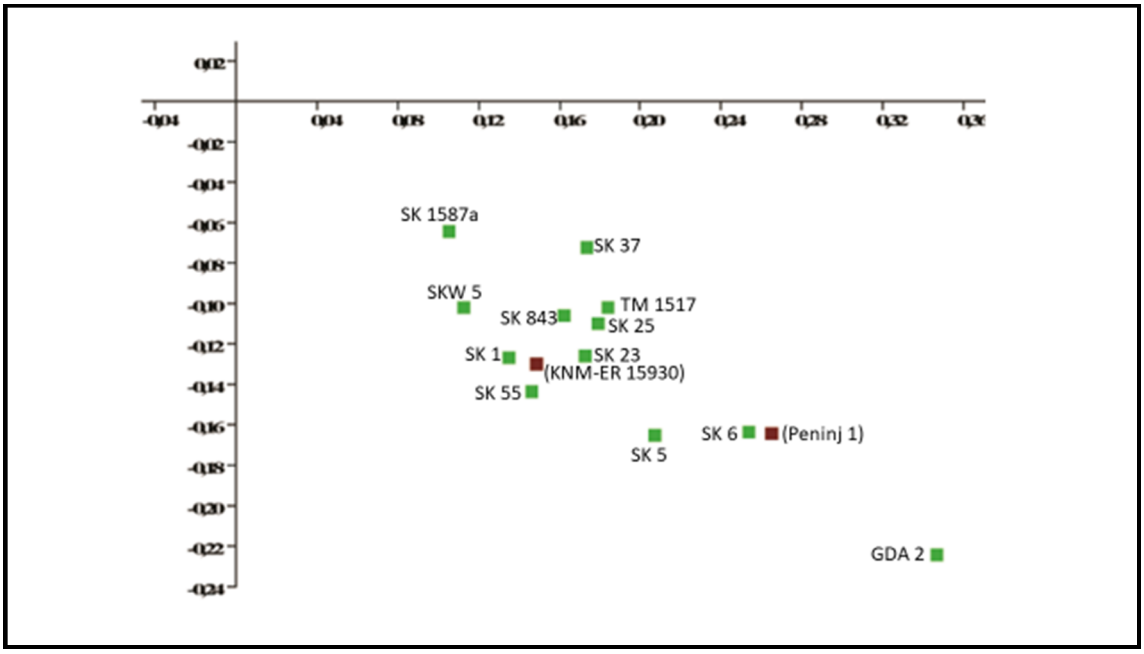


Figure 41. Clustering in morphospace of specimens attributed to *P. robustus* (green squares) (*P. boisei* in brown squares) (extract from Figure 16 and Figure 17 with specimen labels)

With the exception of the "enigmatic" molar from Gondolin, 20km to the northwest of Swartkrans (Menter et al., 2000; Grine et al., 2012), there is a reasonably close clustering of the specimens attributed to *P. robustus.* Most of the specimens in the current study that are attributed to *P. robustus* are from Swartkrans, a site where both *P. robustus* and Early *Homo* have been discovered (in this study, Early *Homo* from Swartkrans is represented by SK 15). There is one specimen from nearby Kromdraai (TM 1517, the holotype of the species).

Grine (1982, 1988) recognised differences between "*P. robustus*" from Kromdraai and "*P. crassidens*" (as named by Howell, 1978) from Swartkrans, suggesting that the more gracile Kromdraai specimens were intermediate between *A. africanus* and *P. crassidens.* However, the Swartkrans specimens originally attributed to *P. crassidens* have been subsumed under *P. robustus,* and the taxon *P. crassidens* has fallen into disuse. Despite

the differences in lower second molar robusticity between these two sites, the Kromdraai and Swartkrans lower second molars form a cohesive group with limited variability (Figure 41), and as such the present analyses support their attribution to the same species, falling well within the range, even of *P. paniscus,* despite allometric differences, provided that the Gondolin molar is excluded from the analysis.

Inclusion of the Gondolin molar in *P. robustus* increases intraspecific variability exhibited by *P. robustus* such that it exceeds intraspecific variability exhibited by *G. beringei*, *P. troglodytes* or *P. paniscus* (Figure 36, Figure 38 and Figure 39). There is only a negligible probability that the *P. robustus* sample with the Gondolin molar included could represent a species with similar intraspecific variability to *G. gorilla,* and the patterning in morphospace of this fossil hominin sample follows a "diagonal" (shape-and-size variation) trajectory rather than a "horizontal" (more size than shape variation), as would be more typical of the sexually dimorphic *G. gorilla* clustering. Although the probabilities were low of being sampled from a species with a similar range of variability to *H. sapiens* (p=0.07 for one of the measurements, bearing in mind that n=12 for *P. robustus* but n=16 for the randomised samples of *H. sapiens,* on which this probability was based), the variability within this latter species is inflated by non-random structural factors, as discussed above, which might imply that *H. sapiens* is not a good candidate for comparison to *P. robustus*. Thus, based on the current study, it is questionable whether the Gondolin molar is reasonably included within *P. robustus.* The Gondolin molar falls within the range of dimensions of *P. boisei,* but outside the range of dimensions of *P. robustus* (Menter et al., 1999; Grine et al., 2012). The published range of MD measurements for *P. boisei* is 16.4 mm to 20.3 mm and BL

measurements range from 14.7 mm to 18.5 mm. The average MD and BL dimensions of *P. robustus* lower second molars are 16.21mm and 14.7 mm, respectively, with a range of 13.8 mm to 17.7 mm for the MD and 13.0 mm to 16.5 mm for the BL dimensions. The average MD:BL ratio is 1:1.102 for *P. robustus.* Therefore the Gondolin molar, at 19.3 mm for the MD diameter and 17.9 mm for the BL diameter, with a relatively broader crown (MD:BL = 1:1.078) appears, from these data, quite simply too large in dimension and broader in overall shape to be a likely candidate for inclusion into the *P. robustus* hypodigm. Grine et al. (2012) suggest, however, that the fairly large assemblages of fossils from Kromdraai, Swartkrans and Drimolen that are attributed to *P. robustus* must be heavily skewed towards females and juvenile males, because it is believed that these specimens were accumulated by carnivores (particularly leopards) who might have favoured juveniles and small adults as prey.

Nevertheless, this assessment overlooks the extreme sexual dimorphism exhibited by the DNH 7 skull and the DNH 8 mandible (from Drimolen), which have been suggested as belonging to a *P. robustus* female and male respectively (Keyser, 2000). The male mandible cannot belong to a juvenile, however, since the third molars had fully erupted (Keyser, 2000). The published MD measurements for the lower second molars of the female *P. robustus,* DNH 7, are 13.4 mm for the left molar and 14.2 mm for the right. For DNH 8 (male), these are 15.9 mm and 15.5 mm, respectively. The BL measurements are: DNH 7 (female) – 13.5 mm for both the left and the right LM2s; DNH 8 (male) – 15.0 mm for the left LM2 and 14.8 mm for the right LM2. The dimensions of the molar belonging to the male mandible are clearly more massive, and this is reflected in the size of the mandible itself. The combined lengths of the premolar and molar tooth rows are 55.1

mm for the left and right sides of the mandible belonging to the female, DNH 7, and 67.7 mm and 68.5 mm for the left and right sides, respectively, of the mandible belonging to the male. The overall differences (full length and full width) are striking, and are presented visually (Keyser, 2000, p. 191). Calculating crown area as a simple product of MD*BL, the left molar of the female specimen is 0.76 times the size of that of the male and the right molar is 0.84 times the size. Since the sexual dimorphism ratios calculated from lower second molars of gorillas in this present study were no lower than 0.90 (F:M), even when sample sizes were reduced (Table 23), calculating the equivalent ratio of sexual dimorphism for DNH 7 and DNH 8 gives a value that is above average for *Gorilla* species.

It is difficult to test the possibility that DNH 8 may have been a "small" adult male, because there is not a comprehensive sample from Drimolen that would provide an idea of the full range of size variability in typical males of this species. However, these two specimens provide evidence of considerable size differences within specimens of *P. robustus,* which is confirmed by the existence of other larger specimens in the sample, such as SK 6 from Swartkrans, the lower second molar of which rivals Peninj 1 (from the large-bodied *P. boisei* subspecies) in size. Thus this study, together with published measurements on specimens from Drimolen, would suggest that the assemblages of *P. robustus* at Swartkrans and Drimolen might not be confined to the smallest individuals from *P. robustus,* as suggested by Grine et al. (2012). Lockwood et al. (2007) has calculated a level of sexual dimorphism in *P. robustus,* excluding the Gondolin molar from the sample that is similar to that exhibited by *Gorilla,* which would seem to fit the pattern observed at Drimolen. The inclusion of the Gondolin molar would increase the

range of variability within *P. robustus* to levels that significantly exceed that of *Gorilla.* It may, of course, be that fossil species exhibited a higher range of sexual dimorphism than do the most sexually dimorphic species today, but this would only account for the massive size variability, not its shape variability.

Grine et al., (2012) have described this molar as representing a very large, presumptive male *P. robustus*, that must be "rare", in other words, it represents in their eyes a single, significant outlier, with its massive size and unusually broad crown. The results of this present study would rather seem to indicate that this molar belongs to another species, or perhaps another subspecies of *Paranthropus,* similar to *P. boisei.* Grine et al. (2012) suggest that an attribution to *P. robustus* is more plausible than an attribution to *P. boisei* since only "15%" of the fauna found in East African sites are also found in South African sites. These counts were taken from 13 localities in East Africa versus 8 localities in South Africa, and perhaps if more sites were examined in South Africa, more species common to both areas might be discovered. From a taphonomic viewpoint there may be a bias, in view of the fact that all 8 localities in South Africa were cave sites, and some of the more open-habitat species from East Africa, particularly large-bodied species, might not be expected to be found fossilised in caves (although interestingly, one infant elephant was among the South African fauna). Over and above this possible bias, the fact that even 15% of East African fauna, and more importantly, certain hominin species (e.g. *H. habilis* and *H. erectus*) are already recognised in South Africa as well as in East Africa, implies at least the possibility that nothing need prevent a species from being present in both areas.

Tobias (2000) suggested three possible attributions to consider for the Gondolin molar. He suggested it could be a) an extremely large molar of *P. robustus*, b) the initial presence of *P. boisei* in South Africa, or c) a representative of a third, hitherto unrecognised species of robust australopith. Based on the present study, an attribution to *P. robustus,* i.e. scenario a), is considered unlikely because it would be necessary to increase the level of variation observed within a fossil species to a degree well in excess of that observed in a living species. This leaves the most parsimonious explanations as either scenario b) or c). Since the Gondolin molar fails to cluster with the Peninj 1 molar (this specimen is considered to be a mandibular proxy for the holotype of *P. boisei,* OH 5, as it is very similar in dimension), perhaps scenario c) might be considered a possibility. Certainly, if there is a possibility to conduct isotope analyses on the Gondolin molar, it will be possible to ascertain whether the diet of this specimen was similar to that of other specimens of *P. robustus* in South Africa, *P. boisei* in East Africa, or something else entirely.

5.3.4 *Australopithecus sediba*

Recapping results for this small sample (n=2) from a juvenile male with fully-erupted second molars, MH 1 (the holotype), and an adult female, MH 2, there might be evidence of sexual dimorphism as evidenced by the lower second molars, which exhibit some size variability but little shape variability, and therefore cluster in morphospace in a "horizontal" pattern (Figure 16 and Figure 17). The *A. sediba* grouping in morphospace confirms Berger et al.'s (2010) observations that these teeth are smaller and narrower than other South African australopiths, and generally cluster towards the early *Homo/H. erectus* range (i.e. they are closest to KNM-ER 992 in Figure 16). The lack of shape

variability evident between the two specimens, indicates that perhaps these two individuals might be from the same family group, as initially suggested by Berger. The taphonomic analysis for Malapa (Val et al., 2015), and the initial analyses of the fossil assemblage (Berger, 2010) and the geological context (Dirks et al., 2013), suggest a death trap scenario occurred at the site with rapid burial.

5.3.5 *Homo naledi*

Despite more recent discoveries in other parts of the Rising Star cave system, the specimens included in this study were all from the Dinaledi Chamber of the Rising Star Cave System (Berger et al., 2015, 2017; Dirks et al., 2015, 2017). Fossils from the Dinaledi Chamber were found within a terminal chamber in the cave system, very close to each other and to the near exclusion of other faunal life. Craniodental and other skeletal elements suggest low ranges of within-species shape variability between the individuals in this particular chamber, and it is therefore not surprising that the grouping of their lower second molars in morphospace is very close (Figure 16), nor that CVs for all three measurements (MD, BL-mesial cusps, BL-distal cusps) were extremely low (Table 26). The probabilities that this fossil aggregate expressed the level of variability that would be expected within the ranges of any of the five extant species were 1.00, or close to 100% probability. One dimension, the buccolingual measurement across the mesial cusps, was slightly more variable than other two measurements, but even when this was compared with the least variable extant species (*P. paniscus*), the probability of finding such variability in that dimension was still 0.5, and it can probably be safely concluded that all the specimens from this assemblage

belonged to a single species with very little variability in the size and shape of lower second molars. The DFA plot shows this group clusters distinctly apart from all other fossil hominin groups (Figure 14), which is interesting because of the recently-announced geological age dates for this species (Dirks et al., 2017), placing the species in the Mid-Pleistocene, at a much later date than other species represented in the study. Perhaps the "distance" in time between the species is being reflected in the morphological distance on the DFA plot.

5.3.6 *Homo habilis*

OH 7 and OH 16, both attributed to *H. habilis,* did not plot closely together in any of the analyses carried out, confirming the shape variability observed in a previous study of their lower first molars (Dykes, 2014). OH 7 plots distinctly away from any other specimen (including OH 16) on the DFA plot (Figure 14). OH 16 groups instead with lower second molars attributed to the genus *Australopithecus,* and this is true also of both of the PCA plots (Figure 15 and Figure 16). The lower second molar of OH 16, like the lower first molar (Dykes, 2014) is more robust in its dimensions and is relatively broader across the crown. Tobias (1965, p. 392) likened this specimen to an australopithecine. Indeed, the OH 16 lower second molar is unusual for a *Homo* specimen in that the protoconid has a protostylid (i.e. a ridge of enamel), which is a feature exhibited by some *A. africanus* specimens such as Sts 52b (Tobias, 1965). The occurrence of *A. africanus* in East Africa has not been widely accepted, but in this instance the geological age of the specimen, at approximately 1.74 Ma (Wood, 2011) or 1.8 Ma (Spoor et al., 2015) is worth mentioning. Given this was a surface find on a slope, its geological setting was inferred. Thus, while the date is too recent to be considered

for the *A. africanus* hypodigm, some doubt about the accuracy of the data exists for surface finds such as this (Wood, 2011). According to Wood (2011), "some researchers have suggested OH 16 samples a second *Homo* taxon at Olduvai Gorge". In this instance, the extremely narrow molar that is the holotype of the species (OH 7) is paired with a large, broad molar (OH 16). Sexual dimorphism would not account for the observed variability in the present study because the relative breadths and different shapes of the teeth differentiate them, more than size per se, and because both OH 7 and OH 16 are putative males (Tobias 1991). OH 7 is also dated to around 1.84 Ma (Wood, 2011). Being the smaller and more gracile of the two molars, OH 7 would appear more "derived" than OH 16, so it seems unlikely that this pair of fossils might represent a temporal difference in an evolving lineage. Rather, if these two individual teeth belong to the same species, perhaps a species with two or more morphotypes (i.e. subspecies) would explain the observed variability in both size and shape.

5.3.7 Other "Early *Homo" / Homo rudolfensis*

A discussion of the variability shown between specimens attributed to "Early *Homo"* needs to be contextualised by the fact that although three specimens have been grouped together for purposes of this study, it is not clear that they all belong to the same species. KNM-ER 1802 is catalogued as *H. rudolfensis* at the National Museum in Nairobi, Kenya. Dated at around 1.88-1.95 Ma, it is close in age to *A. sediba.* The morphology of the KNM-ER 1802 lower second molar is distinct from that of OH 7, the type specimen of *H. habilis*. According to Spoor et al. (2015), the mandible shapes of these two specimens are similar. Others (e.g. Wood, 2011), have described the KNM-ER 1802 mandible as

"relatively robust". The dimensions of this specimen's relatively large and broad lower second molar result in it plotting in an area of overlap in this study (Figure 17) between *P. robustus, A. africanus*, and even the small *P. boisei* specimen, KNM-ER 15930. This corroborates an earlier comparison of the lower first molars belonging to these same specimens (Dykes, 2014).

KNM-ER 60000 has been associated with *H. rudolfensis* (Leakey et al., 2012), but Spoor et al. (2015) disagree and suggest that it has greater affinities with *H. erectus,* specifically those from Dmanisi, Georgia. It is dated at 1.78 to 1.87 Ma (Leakey et al., 2012). In the present study, this specimen clusters with *H. erectus* (KNM-ER 806) and *H. habilis* (OH 7) and with *Australopithecus* in the PCAs (Figure 15 and Figure 16), and with *A. sediba* and other australopiths in the DFA (Figure 14). However, Leakey et al. (2012) note that while the lower second molar is small in size, other teeth in the arcade (e.g. anterior teeth and the lower M3) differ from those of *H. erectus.* In their view, KNM-ER 60000 is a better match for *H. rudolfensis* (e.g. KNM-ER 1470). Leakey et al. (2012) suggest that KNM-ER 1802 is not a good match for *H. rudolfensis*. Although the two papers mentioned here were both authored/co-authored by Spoor, the results seem at odds with each other, one paper attributing KNM-ER 60000 to *H. rudolfensis* and the other, to *H. erectus*.

SK 15 is a specimen attributed to "Early *Homo*" from Swartkrans. Different researchers have suggested taxonomic allocations to be *H. erectus* (Robinson, 1961), *H. habilis* (Blumenberg and Lloyd, 1983), and *Homo sp. indet.* (Grine, 2001). Curnoe (2006) finds that crown sizes fall outside ranges of variability of both *A. africanus* and, more

importantly, *P. robustus*, which makes up the bulk of the hominin fossil assemblage from Swartkrans. Crown size and cusp size analyses resulted in this specimen's attribution to *H. habilis* or *H. erectus.* In the present study, SK 15 groups closest to *P. robustus* (albeit slightly smaller than the remaining specimens), as there is little shape variability between it and other *P. robustus* specimens, based on the PCA plots (Figure 15 and Figure 21). In the plot consisting of all the extant and extinct species (Figure 21), it arguably falls between OH 7 and OH 16 (attributed to *H. habilis*). In the DFA (Figure 14), SK 15 plots closest to *H. ergaster.*

5.3.8 "Later *Homo" / Homo ergaster* (*erectus*)

KNM-ER 992 is the holotype for *H. ergaster,* the African equivalent of *H. erectus* (Leakey and Wood, 1973). In this study, it plots on its own in the expected quadrant in morphospace (small, narrow teeth) in the PCA including the fossil species alone (Figure 15), and between specimens of Early *Homo* and *H. naledi* in the PCA including fossil species with the extant species (Figure 21). Unlike the other specimens examined in this "Later *Homo"* grouping, it does not group in an unexpected area of the fossil PCA plot (Figure 15) and certainly does not overlap with other genera.

KNM-ER 806 is relatively broader across the crown. This specimen plots alongside *A. africanus* (Figure 15), and confirms a slightly anomalous grouping also observed in previous research on lower first molars (Dykes, 2014), in which it also grouped with *A. africanus*.

OH 22 was originally allocated to *H. erectus* (Rightmire, 1980), and has been dated to the Early or Middle Pleistocene. Rightmire (1998) later suggested that it should be reallocated to *H. heidelbergensis,* and Bräuer (1984) has suggested its allocation should be to "early archaic *H. sapiens".* In the present study, it groups well away from the *H. ergaster/erectus* type specimen in morphospace. In the PCA including fossil hominin species alone (Figure 15), OH 22 plots within the cluster of *H. naledi*, which has recently also been dated to the Middle Pleistocene era (Dirks et al., 2017). In the PCA including the fossil hominin species and the extant hominoid species (Figure 21), OH 22 plots with modern *H. sapiens*, specifically the larger, broader molars belonging to the hunter-gatherer/terrestrial forager group of Aboriginal Australians. This present study would therefore support the conclusion that OH 22 might be classified as a "later *Homo"* or "Pre-modern *Homo".*

5.4 HYPOTHESES TESTED IN THIS THESIS

Extant species and their potential as analogue species for fossil hominin comparisons of post-canine dental morphology

$H1_0$: Gorilla species are appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

$H1_1$: Gorilla species are not appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

The null hypothesis cannot be rejected. This study confirms that lower second molars describe a pattern of sexual dimorphism evidenced primarily by size (rather than shape) differences between the sexes, as well as some general shape differences between subspecies (variability evidenced in males and females alike). These species are useful to include in comparative studies of the post-canine dental morphology of African Plio-Pleistocene fossil hominin species, particularly as certain of these species are presumed to display sexual dimorphism, due to large size variation between specimens.

$H2_0$: Pan species are appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.
$H2_1$: Pan species are not appropriate for use as analogue species (proxies) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

The null hypothesis cannot be rejected. *Pan troglodytes* reflects shape and size morphological differences by subspecies and/or by region, which can provide comparisons for cases in the African Plio-Pleistocene fossil hominin record where variability within a presumed species might suggest several "morphotypes" included within a single species, in a situation where shape variability is most pronounced, relative to size variability. *Pan troglodytes* includes a subspecies, *P. t. verus,* which is molecularly, behaviourally and, with relevance for fossil comparative studies, morphologically quite distinct from other subspecies of *P. troglodytes,* in that its lower second molars are typically far broader across the crown than that of the majority of its

counterparts to the east of the Sanaga River. This provides researchers with an analogue species that is far less sexually dimorphic than *Gorilla* species, yet which exhibits a wide range of shape variability against which to measure ranges of variability in hominin species' lower molars, particularly those with similar habitats (ranging from Savanna to forest, with mosaic environments in between). *Pan paniscus* is an example of a single species with no subspecies. Its molars are small by comparison to *P. troglodytes,* and certainly to *Gorilla,* and allometric considerations need to be taken into account before comparing numerical ranges of variability in raw form, particularly when the species being compared has generally large molars (e.g. *Paranthropus*). However, in comparisons that use size-shape range ratios or CV values, and for comparisons with fossil hominin species with generally smaller teeth (e.g. *Homo*), this is a species that still displays some size and shape variability for comparative purposes and is an appropriate analogue for such fossil hominin species.

$H3_0$: *Homo sapiens* is appropriate for use as an analogue species (proxy) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.
$H3_1$: *Homo sapiens* is not appropriate for use as an analogue species (proxy) for comparisons of variability in the post-canine dental morphology of African Plio-Pleistocene fossil hominin species.

The null hypothesis should be rejected. This study confirms, in lower second molars, not only the well-documented tooth-size reduction that has occurred in areas known to have been exposed to radical changes in diet as a result of a transition to widescale agriculture many millennia ago, but also molar cusp simplification and overall

morphological change which can be observed to have occurred during history, again according to subsistence strategy groupings. Ranges of variability, both in size and shape, are therefore quantifiably "extended" in *H. sapiens,* one could argue "artificially" so, due to adaptive responses to non-random dietary change and modifications in some areas at the expense of other areas where no such changes have been made to the original hunter-gatherer dietary strategy. Although diet may vary between region to region in African great apes, and although there may have been a shift towards more meat eating and the cooking of food during the Pleistocene period in hominin species, only *H. sapiens* has ever experienced major adaptive modifications to this degree, caused by this shift to agriculture (and only in certain areas) since the Neolithic period. Therefore the degree of variability (size and shape) in the postcanine dentition of modern *H. sapiens* is not a good proxy for dental comparisons with African Plio-Pleistocene hominin species. What is more, size variability in the lower second molars of modern *H. sapiens* is not linked to sexual dimorphism, and although there is, numerically at least, a "wide" range of variability in size of molars belonging to this species, *H. sapiens* is not a good proxy for comparisons with presumed sexually dimorphic species in the fossil hominin record.

$H4_0$: Specimens attributed to single African Plio-Pleistocene hominin species will exhibit similar ranges of variability in size and shape of lower second molars to those exhibited by analogous extant hominoid species.

$H4_1$: Specimens attributed to single African Plio-Pleistocene hominin species may exceed ranges of variability in size and shape of lower second molars to those exhibited by analogous extant hominoid species.

The null hypothesis cannot be fully rejected, based on the findings from this study, particularly as some species (such as *H. naledi*) appear to be well grouped within narrow ranges of size and shape variability. By comparison with sexually dimorphic analogous extant hominoid species (*Gorilla* species), *A. afarensis, A. africanus* and *P. robustus* all exhibit high levels of both shape and size variability in lower second molars, if the specimens currently attributed to these species is correct, and more interestingly, the ratio of shape variability to size variability does not seem to reflect the shape-to-size variability expected for a sexually dimorphic species, based on *Gorilla*. The large size variability might not, therefore, be attributed to sexual dimorphism, according to this study, unless the extant species used here to stand proxy for "sexually dimorphic species" (*Gorilla* species) might themselves be poor proxies for the degree of sexual dimorphism that may have existed in past hominin species. There is, for instance, an excessive range of variability in size and in shape of lower second molars currently attributed to *P. robustus.* If sex-related size variability were greater in the past than is evident in *Gorilla* today, *P. robustus* could be considered to be a highly sexually dimorphic species within parameters that no longer exist. However, *P. robustus* also exhibits too high a range of shape variability in lower second molars for it to conform to the shape-versus-size variability ratios expected for a sexually dimorphic species, if the Gondolin molar is included in the *P. robustus* paradigm. Similar observations apply to *A. afarensis* and *A. africanus*, wherein certain specimens appear to be unusual in both size and in shape by comparison with the "typical" lower second molars of the species. On the basis of high shape-and-size variability measured for fossil hominin species in this study, it is suspected that more than one species may be represented among the specimens currently attributed to *A. afarensis, A. africanus, P. robustus, H. habilis* and *H. erectus,* which would either imply that there might be an argument to be made for

reclassification of certain existing single species into two or more separate species (still to be described), or perhaps that certain specimens are simply misclassified, and should be classified into more appropriate (already existing) taxa.

5.5 SCOPE FOR FURTHER WORK

While the use of a single molar type to discuss variability within and between species is not ideal, lower second molars have proven useful in distinguishing between groups at the genus, species, subspecies and even population levels. However, further analyses, for instance, into the link between subsistence strategies in modern *H. sapiens* and tooth size and shape, should ideally include other molar types (an expanded sample of lower first and possibly third molars; upper molars). Molars of other hominoid species, particularly the sexually-dimorphic orang-utan, would be useful to add to future comparative analyses. A study of large samples of gibbon teeth might also provide a useful outlier group for such studies. Fossil hominin species represented in this study were often poorly represented in terms of sample size and the issue of permits and access should be addressed for future studies. A study into allometry and the degree to which it affects the shape of molars should be attempted, ideally at a population level (rather than species or subspecies level) wherever body weight data is available, to inform further discussions of the factors driving shape change in molars over time (size-related shape change versus shape change driven by diet or other factors).

CHAPTER 6 – CONCLUSIONS

This study sought to establish whether patterns of both size *and* shape variability observable in the lower second molars of five extant hominoid species are useful for comparisons with specimens attributed to fossil hominin species. Patterns were identified in morphospace for typically sexually dimorphic species of *Gorilla,* where clustering in morphospace was inclined to be predominantly along a horizontal orientation in PCA plots where size accounts for the variance along the first principal component (x-axis), with molars differentiating between male and female individuals by size rather than by shape. By comparison, the less-dimorphic species (e.g. *Pan*) exhibited clusters that were more vertical-diagonal in trajectory, implying more shape differentiation in relation to size variation without implicating sex of the individual.

Modern *H. sapiens* also followed a clustering pattern in morphospace similar to that of *Pan,* but exhibited a higher degree of variability along both axes. Hunter-gatherer groups clustered generally separately from populations in which an agriculturalist subsistence had emerged, possibly because high-starch foods and high levels of food processing and cooking had radically altered masticatory requirements. The transition to agriculture appears to be associated with both a reduction in tooth size and some reduction in crown enamel complexity. The large differences in molar size and in molar shape, between communities that have retained a hunter-gatherer subsistence strategy and populations living in areas that transitioned to agriculture up to 12500 years ago effectively create an expansion of the range of size and complexity of molar cusp arrangements, with lower second molars of hunter-gatherers remaining large in size

and retaining five cusps, and at the other end of the spectrum teeth belonging to communities that have adopted very soft, highly processed diets having small molars with reduced numbers of cusps in some cases.

Size and shape-related changes over time were tracked in human lower second molars using a more temporally and geographic constrained 'control' sample. In this subsample, a trend was observed from large, complex molars to small, relatively broad molars from Neolithic to Medieval periods of Great Britain, respectively. The actual mechanism for this tooth size reduction and reduction in complexity is not fully understood, but the link with the transition to agriculture and the adoption of a diet consisting of starchy, soft grains, often highly-milled, and foods that have been softened by cooking, is indisputable and widely recognised. Along with diet-driven accelerations in genetic mutations starting 12500 years ago, there has been additional variability introduced via massive population increases until modern *H. sapiens* which now exceeds 7 billion individuals. There would also have been a serial founder effect as *H. sapiens* migrated around the world. For these reasons, the resultant very high variability observed in the human dentition (both size *and* shape variability) in the present study should be considered as non-analogous to any extant hominoid species, and likely not a representative model for any fossil hominin species. For this reason, modern *H. sapiens* should be excluded as an analogue species for comparative purposes of ranges of variability in lower second molars of fossil hominin species, and should particularly not be cited in comparative studies of ranges of variability attributed to sexual dimorphism.

Gorilla and *Pan* still remain useful as analogue species for testing intraspecific or intrageneric ranges of morphological (lower second molar) variability. Different patterns of variability are observed in morphospace and confirmed by imbalances in coefficients of variation and variability probabilities based on crown length and relative breadth measurements. Such differences can inform assessments of the contributions of sexual dimorphism to the variability observed in fossil hominin species.

Comparisons of lower second molars between extant groups and specimens attributed to *A. afarensis, A. africanus* and *P. robustus* revealed that the specimens attributed to these groups did not conform to the typical size-shape variability pattern observed for sexually dimorphic species of *Gorilla*. The pattern of variability expressed by species of *Pan* in morphospace also was typically exceeded by the ranges of size variability in these hominin species. For all three of these hominin taxa, very high shape and size variability suggests the possible existence of a second species intermixed within each of them. Temporal variation is not discounted, but in key cases, (e.g. *A. afarensis* and *A. africanus*), evidence points to "primitive" specimens existing concurrently with "derived" specimens, or to great periods of time of deposition of the assemblage, allowing for more than one species to accumulate. In the case of *A. afarensis*, patterning in morphospace and the coefficients of variability suggest that at least two species are intermixed, or at least two distinct morphotypes (equivalent to subspecies) occur within one single hypodigm. *A. africanus* molars are extremely variable, even from the same Member (4) of Sterkfontein, but the known presence of more than one species already (*H. habilis*) in this Member lends support to the idea proposed by R. Clarke (2013) that two species of australopith *(A. africanus* and *A. prometheus)* form part of the

hypodigm originally allocated to *A. africanus.* The present study confirms this proposal, and identifies a further specimen that may not belong to *A. africanus* – Sts 52 – which is a small molar trending towards early *Homo* in size and shape. *P. robustus* lower second molars are fully compatible with the range of variability of all the extant species in this study, until the exceptionally large and buccolingually relatively broad molar found at Gondolin is included within the hypodigm. This molar readily falls within the size range of *P. boisei*, but when included within the range of *P. robustus,* the level of sexual dimorphism exhibited by the hominin species well exceeds the levels currently observed in *Gorilla* species.

Other specimens included in this study are considered to be from a single fossil hominin species (e. g. *A. sediba* and *H. naledi*), and this study would seem to confirm this. Specimens attributed to these two species cluster extremely tightly together manifesting very little intraspecific variability within each taxon. Some slight sexual dimorphism appears to be confirmed between known male and female specimens of *A. sediba,* although small sample sizes preclude the ability to make firm conclusions. For the purposes of this study, some specimens of *Homo* were grouped together, even though they are not necessarily attributed to the same species – for instance, the "Early *Homo"* category included specimens attributed to *H. habilis* and other less-well categorised molars. The lack of cohesion between these specimens as they plotted in morphospace confirmed that it was unlikely that these specimens all belong to a single species, even in light of small sample sizes.

Summary of the main three potential contributions of this study:

- Wide ranges of variability in both the size and the shape of lower second molars of modern *H. sapiens* are largely driven by factors arising from divergent lifestyle subsistence strategies and the adoption of starchy, soft and processed diets in certain areas. These factors are unique to the human species since the Neolithic period and do not apply to *Gorilla* and *Pan* species, nor to any fossil hominin species. It is therefore preferable to exclude modern *H. sapiens* as an analogue species for purposes of comparative studies on the morphology of molars of fossil species and extant hominoid species.
- Very high variability in lower second molar size and shape in *A. afarensis, A. africanus* and *P. robustus* may indicate the presence of more than one species within each species group, as currently attributed. Of particular interest is the extremely large and relatively broad molar from Gondolin, GDA 2. This specimen is of interest for future research, ideally isotope analyses to assess its diet compared to data obtained from specimens attributed to *P. robustus,* to *P. boisei*, or to another species altogether.
- A mathematical landmarking methodology, designed to allow for the inclusion of heavily worn teeth in the analysis, was tested against a traditional methodology and the classification accuracy on a DFA was almost identical between the two methods. This methodology can be applied to lower molars belonging to all hominoid and hominin species, it is adaptable for odontometric studies, for CV analyses, DFAs, PCAs and other analyses. It is able to make use of low resolution photographs, so that images of teeth from papers published before high resolution photography was available may also be included in an analysis, thereby increasing sample sizes. It is quick and easily repeatable.

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APPENDIX 1 DETAILED LIST OF SPECIMENS INCLUDED IN THE STUDY

Main analyses:

	SPECIMEN NAME (Subspecies-image#-region-sex)	SPECIES / SUBSPECIES	SPECIMEN DETAILS (Collection + number if applicable)(List of collection abbreviations in Table 5)
1	Gbb157+1911+F	*G. b. beringei*	Z 6194
2	Gbb180+1911+F	*G. b. beringei*	RG 2258
3	Gbb182+1911+F	*G. b. beringei*	RG 2263
4	Gbb188+1911+F	*G. b. beringei*	RG 8607
5	Gbb196+1911+F	*G. b. beringei*	USNM 396935
6	Gbb197+1911+F	*G. b. beringei*	USNM 396936
7	Gbb200+1911+F	*G. b. beringei*	USNM 397356
8	Gbb202+1911+F	*G. b. beringei*	USNM 545026
9	Gbb203+1911+F	*G. b. beringei*	USNM 545027
10	Gbb205+1911+F	*G. b. beringei*	USNM 545029
11	Gbb206+1911+F	*G. b. beringei*	USNM 545030
12	Gbb207+1911+F	*G. b. beringei*	USNM 545031
13	Gbb179+1911+M	*G. b. beringei*	RG 2257
14	Gbb189+1911+M	*G. b. beringei*	RG 8608
15	Gbb194+1911+M	*G. b. beringei*	USNM 395636
16	Gbb199+1911+M	*G. b. beringei*	USNM 397351
17	Gbb201+1911+M	*G. b. beringei*	USNM 397358
18	Gbb204+1911+M	*G. b. beringei*	USNM 545028
19	Gbb208+1911+M	*G. b. beringei*	USNM 545032
20	Gbb209+1911+M	*G. b. beringei*	USNM 545034
21	Gbb210+1911+M	*G. b. beringei*	USNM 545036
22	Gbb211+1911+M	*G. b. beringei*	USNM 545037
23	Gbb224+1911+M	*G. b. beringei*	FMNH 26065
24	Gbb234+A12+F	*G. b. beringei*	BMNH ZD 1922.2.10.2
25	Gbb233+A12+M	*G. b. beringei*	BMNH ZD 1922.2.10.1
26	Gbg257+1608+F	*G. b. graueri*	RG 27755
27	Gbg259+1608+F	*G. b. graueri*	RG 27840
28	Gbg263+1608+F	*G. b. graueri*	RG 86044M7
29	Gbg267+1608+F	*G. b. graueri*	RG 86044M20
30	Gbg268+1608+F	*G. b. graueri*	RG 86044M22
31	Gbg269+1608+F	*G. b. graueri*	RG 86044M23
32	Gbg270+1608+F	*G. b. graueri*	RG 86044M24
33	Gbg186+1608+M	*G. b. graueri*	RG 29101
34	Gbg192+1608+M	*G. b. graueri*	RG 15234
35	Gbg225+1608+M	*G. b. graueri*	FMNH 27550
36	Gbg226+1608+M	*G. b. graueri*	FMNH 27551
37	Gbg246+1608+M	*G. b. graueri*	RG 9424
38	Gbg247+1608+M	*G. b. graueri*	RG 10051

39	Gbg249+1608+M	*G. b. graueri*	RG 17770
40	Gbg250+1608+M	*G. b. graueri*	RG 18191
41	Gbg253+1608+M	*G. b. graueri*	RG 24001
42	Gbg255+1608+M	*G. b. graueri*	RG 27108
43	Gbg256+1608+M	*G. b. graueri*	RG 27495
44	Gbg260+1608+M	*G. b. graueri*	RG 86044M1
45	Gbg262+1608+M	*G. b. graueri*	RG 86044M5
46	Gbg264+1608+M	*G. b. graueri*	RG 86044M15
47	Gbg266+1608+M	*G. b. graueri*	RG 86044M18
48	Gbg243+1709+F	*G. b. graueri*	RG 833
49	Gbg244+1709+F	*G. b. graueri*	RG 881
50	Gbg304+1709+F	*G. b. graueri*	ZMB 31626
51	Gbg184+1709+M	*G. b. graueri*	RG 27841
52	Gbg242+1709+M	*G. b. graueri*	RG 804
53	Gbg245+1709+M	*G. b. graueri*	RG 998
54	Gbg312+1709+M	*G. b. graueri*	ZMB 31624
55	Gbg318+1709+M	*G. b. graueri*	ZMB 31619
56	Gbg191+1810+F	*G. b. graueri*	RG 14615
57	Gbg272+1810+F	*G. b. graueri*	RG 11725
58	Gbg273+1810+F	*G. b. graueri*	RG 15352
59	Gbg274+1810+F	*G. b. graueri*	RG 15353
60	Gbg275+1810+F	*G. b. graueri*	RG 15354
61	Gbg276+1810+F	*G. b. graueri*	RG 15355
62	Gbg277+1810+F	*G. b. graueri*	RG 15356
63	Gbg278+1810+F	*G. b. graueri*	RG 15357
64	Gbg283+1810+F	*G. b. graueri*	RG 21537
65	Gbg027+1810+M	*G. b. graueri*	MCZ 38017
66	Gbg271+1810+M	*G. b. graueri*	RG 8187
67	Gbg281+1810+M	*G. b. graueri*	RG 18739
68	Gbg284+1810+M	*G. b. graueri*	RG 22903
69	Gbg285+1810+M	*G. b. graueri*	RG 22905
70	Gbg235+1911+M	*G. b. graueri*	BMNH ZE.1961.4.5.1
71	Gbg001+B13+M	*G. b. graueri*	MNHN 1929-503
72	Gbg251+B13+M	*G. b. graueri*	RG 22761
73	Gbg252+B13+M	*G. b. graueri*	RG 23958
74	Gbg254+B13+M	*G. b. graueri*	RG 26206
75	Gbg241+C14+F	*G. b. graueri*	RG 102
76	Ggd118+0101+F	*G. g. diehli*	BMNH ZD.1939.914
77	Ggd039+0101+M	*G. g. diehli*	BMNH ZD.1948.435
78	Ggd115+0101+M	*G. g. diehli*	BMNH ZD.1948.436
79	Ggd116+0101+M	*G. g. diehli*	BMNH ZD.1936.7.14.1
80	Ggd117+0101+M	*G. g. diehli*	BMNH ZD.1939.913
81	Ggd239+0101+M	*G. g. diehli*	BMNH ZD.1935.3.19.2
82	Ggd314+0101+M	*G. g. diehli*	ZMB 12789
83	Ggd325+0101+M	*G. g. diehli*	ZMB 83573A
84	Ggd333+0101+M	*G. g. diehli*	ZMB 83565
85	Ggd341+0202+M	*G. g. diehli*	ZMB 18516
86	Ggg319+0101+M	*G. g. gorilla*	ZMB 30261

87	Ggg057+0202+F	*G. g. gorilla*	PCM Z.VI.33
88	Ggg061+0202+F	*G. g. gorilla*	PCM Z.V.91
89	Ggg065+0202+F	*G. g. gorilla*	PCM CAM.I.42
90	Ggg330+0202+F	*G. g. gorilla*	ZMB 14647
91	Ggg036+0202+M	*G. g. gorilla*	BMNH ZD.1939.908(A)
92	Ggg038+0202+M	*G. g. gorilla*	BMNH ZD.1939.910
93	Ggg041+0202+M	*G. g. gorilla*	PCM Z.II.65
94	Ggg056+0202+M	*G. g. gorilla*	PCM Z.II.64
95	Ggg060+0202+M	*G. g. gorilla*	PCM Z.III.31
96	Ggg064+0202+M	*G. g. gorilla*	PCM CAM.I.41
97	Ggg066+0202+M	*G. g. gorilla*	PCM CAM.I.48
98	Ggg099+0202+M	*G. g. gorilla*	PCM Z.VI.30
99	Ggg146+0202+M	*G. g. gorilla*	AS 1444
100	Ggg150+0202+M	*G. g. gorilla*	Z 7117
101	Ggg151+0202+M	*G. g. gorilla*	Z 5684
102	Ggg347+0202+M	*G. g. gorilla*	ZMB 83581
103	Ggg349+0202+M	*G. g. gorilla*	ZMB 83561
104	Ggg153+0303+F	*G. g. gorilla*	Z 5563
105	Ggg154+0303+F	*G. g. gorilla*	Z 7118
106	Ggg155+0303+F	*G. g. gorilla*	Z 12499
107	Ggg156+0303+F	*G. g. gorilla*	Z 12500
108	Ggg158+0303+F	*G. g. gorilla*	Z 7145
109	Ggg167+0303+F	*G. g. gorilla*	Z 6840
110	Ggg168+0303+F	*G. g. gorilla*	Z 6896
111	Ggg171+0303+F	*G. g. gorilla*	Z 6699
112	Ggg172+0303+F	*G. g. gorilla*	Z 7225
113	Ggg173+0303+F	*G. g. gorilla*	Z 7488
114	Ggg174+0303+F	*G. g. gorilla*	Z 7510
115	Ggg175+0303+F	*G. g. gorilla*	Z 7604
116	Ggg176+0303+F	*G. g. gorilla*	Z 7667
117	Ggg177+0303+F	*G. g. gorilla*	Z 7690
118	Ggg178+0303+F	*G. g. gorilla*	Z 7693
119	Ggg309+0303+F	*G. g. gorilla*	ZMB 6965
120	Ggg002+0303+M	*G. g. gorilla*	MNHN 1936-1982
121	Ggg148+0303+M	*G. g. gorilla*	Z 7079
122	Ggg149+0303+M	*G. g. gorilla*	Z 7081
123	Ggg152+0303+M	*G. g. gorilla*	Z 7144
124	Ggg160+0303+M	*G. g. gorilla*	Z 7204
125	Ggg161+0303+M	*G. g. gorilla*	Z 7649
126	Ggg162+0303+M	*G. g. gorilla*	Z 7666
127	Ggg163+0303+M	*G. g. gorilla*	Z 7692
128	Ggg164+0303+M	*G. g. gorilla*	Z 6672
129	Ggg165+0303+M	*G. g. gorilla*	Z 6878
130	Ggg166+0303+M	*G. g. gorilla*	Z 7203
131	Ggg169+0303+M	*G. g. gorilla*	Z 6720
132	Ggg170+0303+M	*G. g. gorilla*	Z 6877
133	Ggg306+0303+M	*G. g. gorilla*	ZMB 31277
134	Ggg307+0303+M	*G. g. gorilla*	ZMB 31275

135	Ggg308+0303+M	*G. g. gorilla*	ZMB 7157
136	Ggg217+0404+F	*G. g. gorilla*	USNM 174711
137	Ggg129+0404+M	*G. g. gorilla*	MNHN 1987.250
138	Ggg218+0404+M	*G. g. gorilla*	USNM 174712
139	Ggg219+0404+M	*G. g. gorilla*	USNM 174715
140	Ggg221+0404+M	*G. g. gorilla*	USNM 174720
141	Ggg223+0404+M	*G. g. gorilla*	USNM 220325
142	Ggg230+0404+M	*G. g. gorilla*	FMNH 18401
143	Ggg289+0504+F	*G. g. gorilla*	RG 23136
144	Ggg126+0504+M	*G. g. gorilla*	MNHN 1966.222
145	Ggg130+0504+M	*G. g. gorilla*	MNHN 1963.275
146	Ggg286+0504+M	*G. g. gorilla*	RG 63
147	Ggg346+0504+M	*G. g. gorilla*	ZMB 14644
148	Ggg106+0604+F	*G. g. gorilla*	PCM F.C.120
149	Ggg108+0604+F	*G. g. gorilla*	PCM F.C.146
150	Ggg030+0604+M	*G. g. gorilla*	AMNH 214107
151	Ggg032+0604+M	*G. g. gorilla*	AMNH 214111
152	Ggg033+0604+M	*G. g. gorilla*	AMNH 214112
153	Ggg034+0604+M	*G. g. gorilla*	AMNH 214113
154	Ggg035+0604+M	*G. g. gorilla*	AMNH 214114
155	Ggg107+0604+M	*G. g. gorilla*	PCM F.C.123
156	Ggg109+0604+M	*G. g. gorilla*	PCM F.C.115
157	Ggg110+0604+M	*G. g. gorilla*	PCM F.C.133
158	Ggg122+0604+M	*G. g. gorilla*	BMNH ZD.1923.11.29.6
159	Ggg123+0604+M	*G. g. gorilla*	BMNH ZD.1986.534
160	Ggg124+0604+M	*G. g. gorilla*	BMNH ZD.1986.535
161	Ggg127+0604+M	*G. g. gorilla*	MNHN 1964.1540
162	Ggg133+0604+M	*G. g. gorilla*	MNHN 1962.1492
163	Ggg139+0604+M	*G. g. gorilla*	MNHN 1962.1491
164	Ggg140+0604+M	*G. g. gorilla*	MNHN 1948.639
165	Ggg212+0705+F	*G. g. gorilla*	USNM 252575
166	Ggg213+0705+F	*G. g. gorilla*	USNM 252576
167	Ggg214+0705+F	*G. g. gorilla*	USNM 252579
168	Ggg215+0705+F	*G. g. gorilla*	USNM 252580
169	Ggg344+0705+F	*G. g. gorilla*	ZMB 20306
170	Ggg287+0705+M	*G. g. gorilla*	RG 9291
171	Ggg300+0705+M	*G. g. gorilla*	RG 77032M16
172	Ggg301+0705+M	*G. g. gorilla*	RG 77032M18
173	Ggg302+0705+M	*G. g. gorilla*	RG 77032M20
174	Ggg342+0705+M	*G. g. gorilla*	ZMB 20318
175	Ggg345+0705+M	*G. g. gorilla*	ZMB 83537
176	Ggg112+0805+M	*G. g. gorilla*	PCM F.C.112
177	Ggg113+0805+M	*G. g. gorilla*	PCM F.C.196
178	Ggg114+0805+M	*G. g. gorilla*	PCM 206
179	Ggg105+0905+F	*G. g. gorilla*	PCM F.C.224
180	Ggg051+1006+F	*G. g. gorilla*	PCM M.716
181	Ggg052+1006+F	*G. g. gorilla*	PCM M.729
182	Ggg054+1006+F	*G. g. gorilla*	PCM CAM.II.315

183	Ggg058+1006+F	*G. g. gorilla*	PCM M.03
184	Ggg063+1006+F	*G. g. gorilla*	PCM M.281
185	Ggg074+1006+F	*G. g. gorilla*	PCM M.798
186	Ggg075+1006+F	*G. g. gorilla*	PCM M.799
187	Ggg078+1006+F	*G. g. gorilla*	PCM M.856
188	Ggg079+1006+F	*G. g. gorilla*	PCM M.878
189	Ggg080+1006+F	*G. g. gorilla*	PCM M.696
190	Ggg083+1006+F	*G. g. gorilla*	PCM M.847
191	Ggg085+1006+F	*G. g. gorilla*	PCM M.460
192	Ggg088+1006+F	*G. g. gorilla*	PCM M.470
193	Ggg092+1006+F	*G. g. gorilla*	PCM M.688
194	Ggg228+1006+F	*G. g. gorilla*	FMNH 18397
195	Ggg068+1006+M	*G. g. gorilla*	PCM M.204
196	Ggg071+1006+M	*G. g. gorilla*	PCM M.119
197	Ggg073+1006+M	*G. g. gorilla*	PCM M.372
198	Ggg076+1006+M	*G. g. gorilla*	PCM M.835
199	Ggg077+1006+M	*G. g. gorilla*	PCM M.854
200	Ggg081+1006+M	*G. g. gorilla*	PCM M.720
201	Ggg082+1006+M	*G. g. gorilla*	PCM M.729(A)
202	Ggg084+1006+M	*G. g. gorilla*	PCM M.962
203	Ggg086+1006+M	*G. g. gorilla*	PCM M.464
204	Ggg087+1006+M	*G. g. gorilla*	PCM M.462
205	Ggg089+1006+M	*G. g. gorilla*	PCM M.505
206	Ggg090+1006+M	*G. g. gorilla*	PCM M.320
207	Ggg091+1006+M	*G. g. gorilla*	PCM M.687
208	Ggg350+1006+M	*G. g. gorilla*	ZMB 83530
209	Ggg043+1107+F	*G. g. gorilla*	PCM M.35
210	Ggg044+1107+F	*G. g. gorilla*	PCM M.57
211	Ggg045+1107+F	*G. g. gorilla*	PCM M.89
212	Ggg046+1107+F	*G. g. gorilla*	PCM M.136
213	Ggg047+1107+F	*G. g. gorilla*	PCM M.138
214	Ggg048+1107+F	*G. g. gorilla*	PCM M.139
215	Ggg049+1107+F	*G. g. gorilla*	PCM M.174
216	Ggg050+1107+F	*G. g. gorilla*	PCM M.177
217	Ggg295+1107+F	*G. g. gorilla*	RG 75056M2
218	Ggg042+1107+M	*G. g. gorilla*	PCM M.20
219	Ggg069+1107+M	*G. g. gorilla*	PCM M.342
220	Ggg070+1107+M	*G. g. gorilla*	PCM M.502
221	Ggg229+1107+M	*G. g. gorilla*	FMNH 18396
222	Ggg297+1107+M	*G. g. gorilla*	RG 75056M9
223	Ggg339+1107+M	*G. g. gorilla*	ZMB 83546
224	Ggg098+1207+M	*G. g. gorilla*	PCM M.212
225	Ggg348+1207+M	*G. g. gorilla*	ZMB 17802
226	Ggg014+1307+F	*G. g. gorilla*	MCZ 37264
227	Ggg017+1307+F	*G. g. gorilla*	MCZ 38326
228	Ggg093+1307+F	*G. g. gorilla*	PCM CAM.I.95
229	Ggg094+1307+F	*G. g. gorilla*	PCM CAM.I.96
230	Ggg009+1307+M	*G. g. gorilla*	MCZ 20038

231	Ggg010+1307+M	*G. g. gorilla*	MCZ 20039
232	Ggg011+1307+M	*G. g. gorilla*	MCZ 20043
233	Ggg012+1307+M	*G. g. gorilla*	MCZ 37261
234	Ggg013+1307+M	*G. g. gorilla*	MCZ 37262
235	Ggg040+1307+M	*G. g. gorilla*	PCM CAM.I.107
236	Ggg055+1307+M	*G. g. gorilla*	PCM CAM.I.208
237	Ggg095+1307+M	*G. g. gorilla*	PCM CAM.I.99
238	Ggg096+1307+M	*G. g. gorilla*	PCM CAM.I.105
239	Ggg097+1307+M	*G. g. gorilla*	PCM CAM.I.134
240	Ggg334+1307+M	*G. g. gorilla*	ZMB 30892
241	Ggg100+1407+F	*G. g. gorilla*	PCM CAM.I.149
242	Ggg101+1407+F	*G. g. gorilla*	PCM CAM.I.150
243	Ggg103+1407+F	*G. g. gorilla*	PCM M.II.2
244	Ggg294+1407+F	*G. g. gorilla*	RG 73029M3
245	Ggg021+1407+M	*G. g. gorilla*	MCZ 29049
246	Ggg022+1407+M	*G. g. gorilla*	MCZ 23160
247	Ggg023+1407+M	*G. g. gorilla*	MCZ 23161
248	Ggg062+1407+M	*G. g. gorilla*	PCM Z.VI.32
249	Ggg102+1407+M	*G. g. gorilla*	PCM CAM.I.230
250	Ggg227+1407+M	*G. g. gorilla*	FMNH 57201
251	Ggg303+1407+M	*G. g. gorilla*	ZMB 11642
252	Ggg291+1507+F	*G. g. gorilla*	RG 73018M3
253	Ggg290+1507+M	*G. g. gorilla*	RG 33467
254	Ggg293+1507+M	*G. g. gorilla*	RG 73018M8
255	Ptv073+0101+F	*P. t. verus*	AS 1'745
256	Ptv074+0101+F	*P. t. verus*	AS 1'763
257	Ptv087+0101+F	*P. t. verus*	Z 6533
258	Ptv159+0101+F	*P. t. verus*	RG 31490
259	Ptv202+0101+F	*P. t. verus*	USNM 282763
260	Ptv218+0101+F	*P. t. verus*	MCZ 9493
261	Ptv223+0101+F	*P. t. verus*	PM N/6908
262	Ptv226+0101+F	*P. t. verus*	PM N/6914
263	Ptv228+0101+F	*P. t. verus*	PM N/6918
264	Ptv231+0101+F	*P. t. verus*	PM N/6925
265	Ptv237+0101+F	*P. t. verus*	PM N/6945
266	Ptv238+0101+F	*P. t. verus*	PM N/6946
267	Ptv239+0101+F	*P. t. verus*	PM N/6950
268	Ptv242+0101+F	*P. t. verus*	PM N/6954
269	Ptv262+0101+F	*P. t. verus*	PM N/7254
270	Ptv264+0101+F	*P. t. verus*	PM N/7265
271	Ptv267+0101+F	*P. t. verus*	PM N/7272
272	Ptv268+0101+F	*P. t. verus*	PM N/7282
273	Ptv270+0101+F	*P. t. verus*	PM N/7286
274	Ptv271+0101+F	*P. t. verus*	PM N/7288
275	Ptv288+0101+F	*P. t. verus*	PM N/7561
276	Ptv289+0101+F	*P. t. verus*	PM N/7562
277	Ptv075+0101+M	*P. t. verus*	AS 1595
278	Ptv158+0101+M	*P. t. verus*	RG 31489

279	Ptv160+0101+M	*P. t. verus*	RG 35122
280	Ptv230+0101+M	*P. t. verus*	PM N/6923
281	Ptv232+0101+M	*P. t. verus*	PM N/6936
282	Ptv245+0101+M	*P. t. verus*	PM N/6959
283	Ptv247+0101+M	*P. t. verus*	PM N/6962
284	Ptv248+0101+M	*P. t. verus*	PM N/6968
285	Ptv260+0101+M	*P. t. verus*	PM N/7252
286	Ptv261+0101+M	*P. t. verus*	PM N/7253
287	Ptv263+0101+M	*P. t. verus*	PM N/7257
288	Ptv266+0101+M	*P. t. verus*	PM N/7271
289	Ptv269+0101+M	*P. t. verus*	PM N/7283
290	Ptv282+0101+M	*P. t. verus*	PM N/7550
291	Ptv287+0101+M	*P. t. verus*	PM N/7556
292	Ptv290+0101+M	*P. t. verus*	PM N/7565
293	Ptv066+0102+F	*P. t. verus*	MNHN 1932.95
294	Ptv067+0102+F	*P. t. verus*	MNHN 1949.149
295	Ptv299+0102+F	*P. t. verus*	AMNH 89351
296	Ptv297+0102+M	*P. t. verus*	AMNH 89407
297	Ptv298+0102+M	*P. t. verus*	AMNH 89406
298	Pte035+0204+F	*P .t. ellioti*	PCM M.279
299	Pte351+0204+F	*P .t. ellioti*	ZMB 83632
300	Pte034+0204+M	*P .t. ellioti*	PCM M.278
301	Pte349+0204+M	*P .t. ellioti*	ZMB 83642
302	Pte356+0204+M	*P .t. ellioti*	ZMB 83647
303	Ptt002+0205+F	*P. t. troglodytes*	PCM Z.VII.23
304	Ptt011+0205+F	*P. t. troglodytes*	PCM Z.VII.26
305	Ptt014+0205+F	*P. t. troglodytes*	PCM Z.VIII.10
306	Ptt018+0205+F	*P. t. troglodytes*	PCM Z.IX.51
307	Ptt033+0205+F	*P. t. troglodytes*	PCM Z.V.83
308	Ptt070+0205+F	*P. t. troglodytes*	MNHN 1944.227
309	Ptt072+0205+F	*P. t. troglodytes*	AS 1'586
310	Ptt089+0205+F	*P. t. troglodytes*	Z 7688
311	Ptt090+0205+F	*P. t. troglodytes*	Z 7691
312	Ptt097+0205+F	*P. t. troglodytes*	ZSM 1908.36
313	Ptt098+0205+F	*P. t. troglodytes*	ZSM 1962.330
314	Ptt207+0205+F	*P. t. troglodytes*	FMNH 18404
315	Ptt208+0205+F	*P. t. troglodytes*	FMNH 18413
316	Ptt219+0205+F	*P. t. troglodytes*	MCZ 15312
317	Ptt355+0205+F	*P. t. troglodytes*	ZMB 83654
318	Ptt365+0205+F	*P. t. troglodytes*	ZMB 83669
319	Ptt366+0205+F	*P. t. troglodytes*	ZMB 83619
320	Ptt003+0205+M	*P. t. troglodytes*	PCM Z.VII.24
321	Ptt012+0205+M	*P. t. troglodytes*	PCM CAM.II.62
322	Ptt013+0205+M	*P. t. troglodytes*	PCM Z.VI.34
323	Ptt065+0205+M	*P. t. troglodytes*	MNHN 1962.1480
324	Ptt071+0205+M	*P. t. troglodytes*	AS 1'443
325	Ptt076+0205+M	*P. t. troglodytes*	Z 6876
326	Ptt077+0205+M	*P. t. troglodytes*	Z 6938

327	Ptt080+0205+M	*P. t. troglodytes*	Z 6839
328	Ptt081+0205+M	*P. t. troglodytes*	Z 7080
329	Ptt092+0205+M	*P. t. troglodytes*	ZSM 1968.522
330	Ptt362+0205+M	*P. t. troglodytes*	ZMB 19071
331	Ptt363+0205+M	*P. t. troglodytes*	ZMB 83610
332	Ptt005+0206+F	*P. t. troglodytes*	PCM M.105
333	Ptt007+0206+F	*P. t. troglodytes*	PCM M.148
334	Ptt008+0206+F	*P. t. troglodytes*	PCM M.158
335	Ptt009+0206+F	*P. t. troglodytes*	PCM M.172
336	Ptt010+0206+F	*P. t. troglodytes*	PCM M.873
337	Ptt015+0206+F	*P. t. troglodytes*	PCM M.169
338	Ptt016+0206+F	*P. t. troglodytes*	PCM .181
339	Ptt017+0206+F	*P. t. troglodytes*	PCM M.576
340	Ptt020+0206+F	*P. t. troglodytes*	PCM M.702
341	Ptt021+0206+F	*P. t. troglodytes*	PCM M.706
342	Ptt025+0206+F	*P. t. troglodytes*	PCM M.720
343	Ptt026+0206+F	*P. t. troglodytes*	PCM M.743
344	Ptt031+0206+F	*P. t. troglodytes*	PCM M.803
345	Ptt032+0206+F	*P. t. troglodytes*	PCM M.814
346	Ptt036+0206+F	*P. t. troglodytes*	PCM M.574
347	Ptt037+0206+F	*P. t. troglodytes*	PCM M.664
348	Ptt039+0206+F	*P. t. troglodytes*	PCM M.967
349	Ptt040+0206+F	*P. t. troglodytes*	PCM M.986
350	Ptt041+0206+F	*P. t. troglodytes*	PCM M.184
351	Ptt042+0206+F	*P. t. troglodytes*	PCM M.254A
352	Ptt043+0206+F	*P. t. troglodytes*	PCM M.299
353	Ptt045+0206+F	*P. t. troglodytes*	PCM M.449
354	Ptt046+0206+F	*P. t. troglodytes*	PCM M.450
355	Ptt047+0206+F	*P. t. troglodytes*	PCM M.474
356	Ptt048+0206+F	*P. t. troglodytes*	PCM M.501
357	Ptt049+0206+F	*P. t. troglodytes*	PCM M.504
358	Ptt050+0206+F	*P. t. troglodytes*	PCM M.655
359	Ptt051+0206+F	*P. t. troglodytes*	PCM CAM.I.147
360	Ptt055+0206+F	*P. t. troglodytes*	PCM CAM.I.203
361	Ptt056+0206+F	*P. t. troglodytes*	PCM CAM.I.204
362	Ptt057+0206+F	*P. t. troglodytes*	PCM CAM.I.205
363	Ptt058+0206+F	*P. t. troglodytes*	PCM CAM.I.216
364	Ptt059+0206+F	*P. t. troglodytes*	PCM CAM.I.217
365	Ptt083+0206+F	*P. t. troglodytes*	Z 6523
366	Ptt152+0206+F	*P. t. troglodytes*	RG 75056M23
367	Ptt216+0206+F	*P. t. troglodytes*	MCZ 23167
368	Ptt342+0206+F	*P. t. troglodytes*	ZMB 83639
369	Ptt357+0206+F	*P. t. troglodytes*	ZMB 15848
370	Ptt364+0206+F	*P. t. troglodytes*	ZMB 7872
371	Ptt367+0206+F	*P. t. troglodytes*	ZMB 83623
372	Ptt001+0206+M	*P. t. troglodytes*	PCM Z.IX.49
373	Ptt004+0206+M	*P. t. troglodytes*	PCM M.78
374	Ptt006+0206+M	*P. t. troglodytes*	PCM M.144

375	Ptt019+0206+M	*P. t. troglodytes*	PCM M.254
376	Ptt022+0206+M	*P. t. troglodytes*	PCM M.707
377	Ptt023+0206+M	*P. t. troglodytes*	PCM M.712
378	Ptt024+0206+M	*P. t. troglodytes*	PCM M.719
379	Ptt027+0206+M	*P. t. troglodytes*	PCM M.401
380	Ptt028+0206+M	*P. t. troglodytes*	PCM M.984
381	Ptt029+0206+M	*P. t. troglodytes*	PCM M.988
382	Ptt030+0206+M	*P. t. troglodytes*	PCM M.347
383	Ptt044+0206+M	*P. t. troglodytes*	PCM M.440
384	Ptt060+0206+M	*P. t. troglodytes*	PCM CAM.I.219
385	Ptt147+0206+M	*P. t. troglodytes*	RG 73018M14
386	Ptt153+0206+M	*P. t. troglodytes*	RG 75056M26
387	Ptt209+0206+M	*P. t. troglodytes*	FMNH 18406
388	Ptt212+0206+M	*P. t. troglodytes*	MCZ 19187
389	Ptt213+0206+M	*P. t. troglodytes*	MCZ 20041
390	Ptt214+0206+M	*P. t. troglodytes*	MCZ 23163
391	Ptt215+0206+M	*P. t. troglodytes*	MCZ 23164
392	Ptt344+0206+M	*P. t. troglodytes*	ZMB 15846
393	Ptt353+0206+M	*P. t. troglodytes*	ZMB 83594
394	Ptt358+0206+M	*P. t. troglodytes*	ZMB 30846
395	Ptt359+0206+M	*P. t. troglodytes*	ZMB 30755
396	Ptt082+0207+F	*P. t. troglodytes*	Z 5196
397	Ptt339+0207+F	*P. t. troglodytes*	ZMB 83686
398	Ptt348+0207+F	*P. t. troglodytes*	ZMB 7156
399	Ptt352+0207+F	*P. t. troglodytes*	ZMB 83687
400	Ptt068+0207+M	*P. t. troglodytes*	MNHN 1899.17
401	Ptt144+0208+F	*P. t. troglodytes*	RG 178
402	Ptt195+0208+F	*P. t. troglodytes*	USNM 174701
403	Ptt198+0208+F	*P. t. troglodytes*	USNM 220062
404	Ptt199+0208+F	*P. t. troglodytes*	USNM 220064
405	Ptt340+0208+F	*P. t. troglodytes*	ZMB 83685
406	Ptt063+0208+M	*P. t. troglodytes*	MNHN 1886.104
407	Ptt145+0208+M	*P. t. troglodytes*	RG 179
408	Ptt196+0208+M	*P. t. troglodytes*	USNM 174703
409	Ptt200+0208+M	*P. t. troglodytes*	USNM 220327
410	Ptt373+0208+M	*P. t. troglodytes*	ZMB 27049
411	Pts180+0309+F	*P. t. schweinfurthii*	RG 9931
412	Pts166+0309+M	*P. t. schweinfurthii*	RG 1942
413	Pts191+0309+M	*P. t. schweinfurthii*	RG 14219
414	Pts164+0310+F	*P. t. schweinfurthii*	RG 928
415	Pts165+0310+F	*P. t. schweinfurthii*	RG 929
416	Pts170+0310+F	*P. t. schweinfurthii*	RG 4188
417	Pts171+0310+F	*P. t. schweinfurthii*	RG 7000
418	Pts172+0310+F	*P. t. schweinfurthii*	RG 7002
419	Pts173+0310+F	*P. t. schweinfurthii*	RG 8341
420	Pts182+0310+F	*P. t. schweinfurthii*	RG 10071
421	Pts184+0310+F	*P. t. schweinfurthii*	RG 10448
422	Pts185+0310+F	*P. t. schweinfurthii*	RG 10800

423	Pts190+0310+F	*P. t. schweinfurthii*	RG 13716
424	Pts194+0310+F	*P. t. schweinfurthii*	RG 20480
425	Pts295+0310+F	*P. t. schweinfurthii*	AMNH 51376
426	Pts296+0310+F	*P. t. schweinfurthii*	AMNH 51392
427	Pts174+0310+M	*P. t. schweinfurthii*	RG 8369
428	Pts183+0310+M	*P. t. schweinfurthii*	RG 10447
429	Pts292+0310+M	*P. t. schweinfurthii*	AMNH 51377
430	Pts293+0310+M	*P. t. schweinfurthii*	AMNH 51382
431	Pts294+0310+M	*P. t. schweinfurthii*	AMNH 51204
432	Pts327+0310+M	*P. t. schweinfurthii*	RG 10732
433	Pts169+0311+F	*P. t. schweinfurthii*	RG 2665
434	Pts175+0311+F	*P. t. schweinfurthii*	RG 9246
435	Pts177+0311+F	*P. t. schweinfurthii*	RG 9249
436	Pts334+0311+F	*P. t. schweinfurthii*	RG 83006M26
437	Pts336+0311+F	*P. t. schweinfurthii*	RG 83006M32
438	Pts163+0311+M	*P. t. schweinfurthii*	RG 730
439	Pts179+0311+M	*P. t. schweinfurthii*	RG 9576
440	Pts187+0311+M	*P. t. schweinfurthii*	RG 11987
441	Pts328+0311+M	*P. t. schweinfurthii*	RG 83006M14
442	Pts329+0311+M	*P. t. schweinfurthii*	RG 83006M15
443	Pts331+0311+M	*P. t. schweinfurthii*	RG 83006M17
444	Pts332+0311+M	*P. t. schweinfurthii*	RG 83006M19
445	Pts333+0311+M	*P. t. schweinfurthii*	RG 83006M21
446	Pts335+0311+M	*P. t. schweinfurthii*	RG 83006M30
447	Pts061+0312+F	*P. t. schweinfurthii*	PCM C.370
448	Pts168+0312+F	*P. t. schweinfurthii*	RG 2523
449	Pts204+0312+F	*P. t. schweinfurthii*	USNM 236971
450	Pts307+0312+F	*P. t. schweinfurthii*	BMNH ZD 1920.4.13.2
451	Pts318+0312+F	*P. t. schweinfurthii*	RG 29074
452	Pts326+0312+F	*P. t. schweinfurthii*	RG 30845
453	Pts062+0312+M	*P. t. schweinfurthii*	PCM C.372
454	Pts162+0312+M	*P. t. schweinfurthii*	RG 688
455	Pts308+0312+M	*P. t. schweinfurthii*	BMNH ZD 1922.12.19.2
456	Pts310+0312+M	*P. t. schweinfurthii*	RG 25534
457	Pts319+0312+M	*P. t. schweinfurthii*	RG 29078
458	Pts370+0312+M	*P. t. schweinfurthii*	ZMB 31647
459	Pts189+0313+F	*P. t. schweinfurthii*	RG 12090
460	Pts193+0313+F	*P. t. schweinfurthii*	RG 15238
461	Pts178+0313+M	*P. t. schweinfurthii*	RG 9277
462	Pts186+0313+M	*P. t. schweinfurthii*	RG 11362
463	Pts320+0313+M	*P. t. schweinfurthii*	RG 29082
464	Pts324+0313+M	*P. t. schweinfurthii*	RG 29089
465	Pts341+0313+M	*P. t. schweinfurthii*	ZMB 24838
466	Pts369+0313+M	*P. t. schweinfurthii*	ZMB 31649
467	Pts371+0313+M	*P. t. schweinfurthii*	ZMB 13749
468	Pts372+0313+M	*P. t. schweinfurthii*	ZMB 31640
469	Ppan101+0414+F	*P. paniscus*	RG 9388
470	Ppan103+0414+F	*P. paniscus*	RG 11352

471	Ppan105+0414+F	*P. paniscus*	RG 13201	
472	Ppan109+0414+F	*P. paniscus*	RG 20881	
473	Ppan110+0414+F	*P. paniscus*	RG 20882	
474	Ppan126+0414+F	*P. paniscus*	RG 29040	
475	Ppan138+0414+F	*P. paniscus*	RG 84036M4	
476	Ppan104+0414+M	*P. paniscus*	RG 11354	
477	Ppan106+0414+M	*P. paniscus*	RG 14738	
478	Ppan112+0414+M	*P. paniscus*	RG 23509	
479	Ppan127+0414+M	*P. paniscus*	RG 29044	
480	Ppan128+0414+M	*P. paniscus*	RG 29047	
481	Ppan114+0415+F	*P. paniscus*	RG 26945	
482	Ppan115+0415+F	*P. paniscus*	RG 26947	
483	Ppan117+0415+F	*P. paniscus*	RG 26993	
484	Ppan118+0415+F	*P. paniscus*	RG 26994	
485	Ppan120+0415+F	*P. paniscus*	RG 27002	
486	Ppan121+0415+F	*P. paniscus*	RG 27012	
487	Ppan122+0415+F	*P. paniscus*	RG 27698	
488	Ppan123+0415+F	*P. paniscus*	RG 29033	
489	Ppan131+0415+F	*P. paniscus*	RG 29057	
490	Ppan140+0415+F	*P. paniscus*	RG 88041M3	
491	Ppan141+0415+F	*P. paniscus*	RG 88041M4	
492	Ppan142+0415+F	*P. paniscus*	RG 88041M5	
493	Ppan143+0415+F	*P. paniscus*	RG 88041M12	
494	Ppan221+0415+F	*P. paniscus*	MCZ 38019	
495	Ppan222+0415+F	*P. paniscus*	MCZ 38020	
496	Ppan107+0415+M	*P. paniscus*	RG 15294	
497	Ppan108+0415+M	*P. paniscus*	RG 15295	
498	Ppan113+0415+M	*P. paniscus*	RG 26944	
499	Ppan116+0415+M	*P. paniscus*	RG 26971	
500	Ppan119+0415+M	*P. paniscus*	RG 26996	
501	Ppan124+0415+M	*P. paniscus*	RG 29036	
502	Ppan125+0415+M	*P. paniscus*	RG 29037	
503	Ppan130+0415+M	*P. paniscus*	RG 29050	
504	Ppan137+0415+M	*P. paniscus*	RG 84036M3	
505	Ppan139+0415+M	*P. paniscus*	RG 88041M2	
506	Ppan132+0416+F	*P. paniscus*	RG 29060	
507	Ppan134+0416+F	*P. paniscus*	RG 29066	
508	Ppan136+0416+F	*P. paniscus*	RG 84036M2	
509	Ppan100+0416+M	*P. paniscus*	RG 888	
510	Hsap518-1A2-F	*H. sapiens*	Iziko	278
511	Hsap519-1A2-F	*H. sapiens*	Iziko	1871
512	Hsap583-1A2-F	*H. sapiens*	Iziko	6252
513	Hsap584-1A2-F	*H. sapiens*	Iziko	6260
514	Hsap587-1A2-F	*H. sapiens*	Iziko	5050
515	Hsap620-1A2-F	*H. sapiens*	Iziko	6313

516	Hsap506-1A2-M	*H. sapiens*	Iziko	1142
517	Hsap514-1A2-M	*H. sapiens*	Iziko	1473
518	Hsap520-1A2-M	*H. sapiens*	Iziko	6075
519	HSap521-1A2-M	*H. sapiens*	Iziko	6020
520	Hsap523-1A2-M	*H. sapiens*	Iziko	5048
521	Hsap529-1A2-M	*H. sapiens*	Iziko	1441
522	Hsap558-1A2-M	*H. sapiens*	Iziko	5049
523	Hsap645-1A2-F	*H. sapiens*	Dart*	A0320
524	Hsap647-1A2-F	*H. sapiens*	Dart*	A0028
525	Hsap646-1A2-F	*H. sapiens*	Dart*	A0173
526	Hsap291-1B2-F	*H. sapiens*	MNHN	18446-1
527	Hsap296-1B2-F	*H. sapiens*	MNHN	23641-1
528	Hsap299-1B2-F	*H. sapiens*	MNHN	18849-1
529	Hsap292-1B2-M	*H. sapiens*	MNHN	17980
530	Hsap294-1B2-M	*H. sapiens*	MNHN	4653
531	Hsap295-1B2-M	*H. sapiens*	MNHN	4577
532	Hsap300-1B2-M	*H. sapiens*	MNHN	9598
533	Hsap621-1E3A-F	*H. sapiens*	Dart*	A0863
534	HSap623-1E3A-F	*H. sapiens*	Dart*	A1319
535	Hsap624-1E3A-F	*H. sapiens*	Dart*	A0381
536	Hsap627-1E3A-F	*H. sapiens*	Dart*	A0900
537	Hsap629-1E3A-F	*H. sapiens*	Dart*	A1954
538	HSap631-1E3A-F	*H. sapiens*	Dart*	A0084
539	Hsap633-1E3A-F	*H. sapiens*	Dart*	A0263
540	Hsap635-1E3A-F	*H. sapiens*	Dart*	A0935
541	Hsap637-1E3A-F	*H. sapiens*	Dart*	A1263
542	HSap638-1E3A-F	*H. sapiens*	Dart*	A3376
543	Hsap641-1E3A-F	*H. sapiens*	Dart*	A1483
544	HSap643-1E3A-F	*H. sapiens*	Dart*	A1903
545	Hsap622-1E3A-M	*H. sapiens*	Dart*	A0973
546	Hsap625-1E3A-M	*H. sapiens*	Dart*	A3360
547	Hsap626-1E3A-M	*H. sapiens*	Dart*	A3770
548	Hsap628-1E3A-M	*H. sapiens*	Dart*	A1570
549	Hsap630-1E3A-M	*H. sapiens*	Dart*	A0927
550	Hsap632-1E3A-M	*H. sapiens*	Dart*	A0861
551	Hsap634-1E3A-M	*H. sapiens*	Dart*	A0924
552	Hsap636-1E3A-M	*H. sapiens*	Dart*	A1860
553	Hsap639-1E3A-M	*H. sapiens*	Dart*	A0281
554	Hsap640-1E3A-M	*H. sapiens*	Dart*	A0691
555	HSap644-1E3A-M	*H. sapiens*	Dart*	A0821
556	Hsap440-1E3B1-F	*H. sapiens*	CAM-DL	Af.21.0.080
557	Hsap447-1E3B1-F	*H. sapiens*	CAM-DL	Af.21.0.142
558	Hsap449-1E3B1-F	*H. sapiens*	CAM-DL	Af.21.0.150
559	Hsap438-1E3B1-M	*H. sapiens*	CAM-DL	Af.21.0.046

560	Hsap439-1E3B1-M	*H. sapiens*	CAM-DL	Af.21.0.052
561	Hsap442-1E3B1-M	*H. sapiens*	CAM-DL	Af.21.0.099
562	Hsap444-1E3B1-M	*H. sapiens*	CAM-DL	Af.21.0.138
563	Hsap446-1E3B1-M	*H. sapiens*	CAM-DL	Af.21.0.140
564	Hsap001-2C4-F	*H. sapiens*	MNHN	1503
565	Hsap003-2C4-F	*H. sapiens*	MNHN	4665
566	Hsap007-2C4-F	*H. sapiens*	MNHN	4767
567	Hsap010-2C4-F	*H. sapiens*	MNHN	1509
568	Hsap016-2C4-F	*H. sapiens*	MNHN	5329
569	HSAP310-2C4-F	*H. sapiens*	CAM-DL	AUS 046
570	Hsap312-2C4-F	*H. sapiens*	CAM-DL	AUS 047
571	Hsap314-2C4-F	*H. sapiens*	CAM-DL	AUS 061
572	Hsap333-2C4-F	*H. sapiens*	CAM-DL	AUS 131
573	Hsap004-2C4-F?	*H. sapiens*	MNHN	3638
574	HSAP311-2C4-ND	*H. sapiens*	CAM-DL	Aus 057/37
575	Hsap313-2C4-F?	*H. sapiens*	CAM-DL	Aus 026/76
576	Hsap315-2C4-ND	*H. sapiens*	CAM-DL	AUS 059
577	Hsap316-2C4-F?	*H. sapiens*	CAM-DL	AUS 066
578	Hsap322-2C4-F?	*H. sapiens*	CAM-DL	AUS 083
579	Hsap009-2C4-M	*H. sapiens*	MNHN	3637
580	Hsap013-2C4-M	*H. sapiens*	MNHN	1505
581	Hsap307-2C4-M	*H. sapiens*	CAM-DL	AUS 027
582	Hsap308-2C4-M	*H. sapiens*	CAM-DL	AUS 028
583	Hsap319-2C4-M	*H. sapiens*	CAM-DL	AUS 080
584	Hsap328-2C4-M	*H. sapiens*	CAM-DL	AUS 106
585	Hsap005-2C4-ND	*H. sapiens*	MNHN	4763
586	Hsap008-2C4-M?	*H. sapiens*	MNHN	4759
587	Hsap012-2C4-M?	*H. sapiens*	MNHN	4768
588	Hsap014-2C4-M?	*H. sapiens*	MNHN	3628
589	Hsap019-2C4-M?	*H. sapiens*	MNHN	35347
590	Hsap330-2C4-M?	*H. sapiens*	CAM-DL	AUS 109
591	Hsap081-3C2A-F	*H. sapiens*	MNHN	34805
592	Hsap066-3C2A-ND	*H. sapiens*	MNHN	24285
593	Hsap067-3C2A-ND	*H. sapiens*	MNHN	557
594	Hsap070-3C2A-ND	*H. sapiens*	MNHN	4854
595	Hsap072-3C2A-ND	*H. sapiens*	MNHN	551
596	Hsap077-3C2A-ND	*H. sapiens*	MNHN	4875
597	Hsap078-3C2A-ND	*H. sapiens*	MNHN	20530
598	Hsap370-3C2A-F?	*H. sapiens*	CAM-DL	POL 40
599	Hsap368-3C2A-M	*H. sapiens*	CAM-DL	POL 15
600	Hsap366-3C2A-M?	*H. sapiens*	CAM-DL	POL 09
601	Hsap371-3C2A-M?	*H. sapiens*	CAM-DL	POL 44
602	Hsap335-4M-F	*H. sapiens*	CAM-DL	MEL 067
603	Hsap337-4M-F	*H. sapiens*	CAM-DL	MEL 071/099
604	Hsap340-4M-F	*H. sapiens*	CAM-DL	MEL 080
605	Hsap341-4M-F	*H. sapiens*	CAM-DL	MEL 082
606	Hsap346-4M-F	*H. sapiens*	CAM-DL	MEL 120/131
607	Hsap347-4M-F	*H. sapiens*	CAM-DL	MEL 153

608	Hsap352-4M-F	*H. sapiens*	CAM-DL	MEL 212
609	Hsap363-4M-F	*H. sapiens*	CAM-DL	MEL 310
610	Hsap336-4M-M	*H. sapiens*	CAM-DL	MEL 069
611	Hsap343-4M-M	*H. sapiens*	CAM-DL	MEL 085
612	Hsap350-4M-M	*H. sapiens*	CAM-DL	MEL 169
613	Hsap353-4M-M	*H. sapiens*	CAM-DL	MEL 217
614	Hsap354-4M-M	*H. sapiens*	CAM-DL	MEL 249
615	Hsap356-4M-M	*H. sapiens*	CAM-DL	MEL 255
616	Hsap357-4M-M	*H. sapiens*	CAM-DL	MEL 262
617	Hsap360-4M-M	*H. sapiens*	CAM-DL	MEL 232
618	Hsap227-5O3-F	*H. sapiens*	MNHN	17575
619	Hsap244-5O3-F	*H. sapiens*	MNHN	3428
620	Hsap239-5O3-M	*H. sapiens*	MNHN	17787
621	Hsap241-503-M	*H. sapiens*	MNHN	7788
622	Hsap242-5O3-M	*H. sapiens*	MNHN	7789
623	Hsap245-5O3-M	*H. sapiens*	MNHN	7791
624	Hsap246-5O3-M	*H. sapiens*	MNHN	7792
625	Hsap254-5O3-M	*H. sapiens*	MNHN	35498-1
626	Hsap256-5O3-M	*H. sapiens*	MNHN	35481-1
627	Hsap262-5O3-M	*H. sapiens*	MNHN	33600
628	Hsap264-5O3-M	*H. sapiens*	MNHN	33612
629	Hsap267-5O3-M	*H. sapiens*	MNHN	33598
630	Hsap222-5O3-M?	*H. sapiens*	MNHN	4822
631	Hsap231-5O3-M?	*H. sapiens*	MNHN	4826
632	Hsap268-5O3-M?	*H. sapiens*	MNHN	33593
633	Hsap270-5O3-M?	*H. sapiens*	MNHN	4378
634	Hsap196-6R2-F	*H. sapiens*	MNHN	6188
635	Hsap187-6R2-F?	*H. sapiens*	MNHN	33344
636	Hsap192-6R2-F?	*H. sapiens*	MNHN	33494
637	Hsap185-6R2-M	*H. sapiens*	MNHN	33325
638	Hsap190-6R2-M	*H. sapiens*	MNHN	33362
639	Hsap193-6R2-M	*H. sapiens*	MNHN	33508
640	Hsap186-6R2-M?	*H. sapiens*	MNHN	33346
641	Hsap189-6R2-M?	*H. sapiens*	MNHN	33358
642	Hsap194-6R2-M?	*H. sapiens*	MNHN	35350
643	Hsap195-6R2-M?	*H. sapiens*	MNHN	35251
644	Hsap450-6R1A-F	*H. sapiens*	CAM-DL	SAS08
645	Hsap451-6R1A-M	*H. sapiens*	CAM-DL	SAS10
646	Hsap452-6R1A-M	*H. sapiens*	CAM-DL	SAS11
647	Hsap454-6R1A-M	*H. sapiens*	CAM-DL	SAS25
648	Hsap455-6R1A-M	*H. sapiens*	CAM-DL	SAS36
649	Hsap126-7I2A-F	*H. sapiens*	MNHN	17462
650	Hsap127-7I2A-F	*H. sapiens*	MNHN	17465
651	Hsap128-7I2A-F	*H. sapiens*	MNHN	17466
652	Hsap129-712A-F	*H. sapiens*	MNHN	17467
653	Hsap108-712A-M	*H. sapiens*	MNHN	17475
654	Hsap110-712A-M	*H. sapiens*	MNHN	17491
655	Hsap114-7I2A-M	*H. sapiens*	MNHN	17499

656	Hsap115-7I2A-M	*H. sapiens*	MNHN	17686
657	Hsap116-7I2A-M	*H. sapiens*	MNHN	17692
658	Hsap118-7I2A-M	*H. sapiens*	MNHN	17494
659	Hsap119-7I2A-M	*H. sapiens*	MNHN	17477
660	Hsap120-7I2A-M	*H. sapiens*	MNHN	17418
661	Hsap121-7I2A-M	*H. sapiens*	MNHN	17423
662	Hsap122-7I2A-M	*H. sapiens*	MNHN	17426
663	Hsap130-7I2A-M	*H. sapiens*	MNHN	17436
664	Hsap302-7I2A-M	*H. sapiens*	MNHN	17442
665	Hsap303-7I2A-M	*H. sapiens*	MNHN	17450
666	Hsap304-7I2A-M	*H. sapiens*	MNHN	17683
667	Hsap219-8J1-F	*H. sapiens*	MNHN	19235
668	Hsap209-8J1-M	*H. sapiens*	MNHN	7253
669	Hsap208-8J1-ND	*H. sapiens*	MNHN	4706
670	Hsap210-8J1-ND	*H. sapiens*	MNHN	24526
671	Hsap211-8J1-ND	*H. sapiens*	MNHN	24527
672	Hsap215-8J1-ND	*H. sapiens*	MNHN	24533
673	Hsap216-8J1-ND	*H. sapiens*	MNHN	24532
674	Hsap477-8J1-F	*H. sapiens*	CAM-DL	NU062
675	Hsap480-8J1-F	*H. sapiens*	CAM-DL	NU094
676	Hsap483-8J1-F	*H. sapiens*	CAM-DL	NU146
677	Hsap478-8J1-M	*H. sapiens*	CAM-DL	NU063
678	Hsap277-8J2-M	*H. sapiens*	MNHN	17471
679	Hsap278-8J2-M	*H. sapiens*	MNHN	17468
680	Hsap279-8J2-M	*H. sapiens*	MNHN	17469
681	Hsap197-8J2-ND	*H. sapiens*	MNHN	27269
682	Hsap199-8J2-ND	*H. sapiens*	MNHN	27276
683	Hsap202-8J2-ND	*H. sapiens*	MNHN	27289
684	Hsap203-8J2-ND	*H. sapiens*	MNHN	27290
685	Hsap204-8J2-ND	*H. sapiens*	MNHN	27296
686	Hsap207-8J2-ND	*H. sapiens*	MNHN	27295
687	Hsap133-9R1B-F	*H. sapiens*	MNHN	24672
688	Hsap138-9R1B-F	*H. sapiens*	MNHN	35080-2
689	Hsap151-9R1B-F	*H. sapiens*	MNHN	5578
690	Hsap161-9R1B-F	*H. sapiens*	MNHN	347
691	Hsap162-9R1B-F	*H. sapiens*	MNHN	350
692	Hsap180-9R1B-F	*H. sapiens*	MNHN	35071-2
693	Hsap182-9R1B-F	*H. sapiens*	MNHN	35079-2
694	Hsap183-9R1B-F	*H. sapiens*	MNHN	35047-2
695	Hsap132-9R1B-M	*H. sapiens*	MNHN	24672b
696	Hsap135-9R1B-M	*H. sapiens*	MNHN	35390
697	Hsao136-9R1B-M	*H. sapiens*	MNHN	35389
698	Hsap152-9R1B-M	*H. sapiens*	MNHN	29279
699	Hsap154-9R1B-M	*H. sapiens*	MNHN	29278
700	Hsap155-9R1B-M	*H. sapiens*	MNHN	29280
701	Hsap163-9R1B-M	*H. sapiens*	MNHN	348
702	Hsap1739R1B-M	*H. sapiens*	MNHN	35013-2
703	Hsap174-9R1B-M	*H. sapiens*	MNHN	32020-2

704	Hsap177-9R1B-M	*H. sapiens*	MNHN	35026-2
705	Hsap401-9R1B-F	*H. sapiens*	CAM-DL	EU 1 1 0099
706	Hsap410-9R1B-F	*H. sapiens*	CAM-DL	EU 1 2 0292
707	Hsap412-9R1B-F	*H. sapiens*	CAM-DL	EU 1 2 0295
708	Hsap415-9R1B-F	*H. sapiens*	CAM-DL	EU 1 2 0305
709	Hsap416-9R1B-F	*H. sapiens*	CAM-DL	EU 1 2 0306
710	Hsap424-9R1B-F	*H. sapiens*	CAM-DL	WOR 018(1)W56
711	Hsap425-9R1B-F	*H. sapiens*	CAM-DL	WOR 053W44 NONSUCH 012
712	Hsap427-9R1B-F	*H. sapiens*	CAM-DL	C/U12/8
713	Hsap402-9R1B-M	*H. sapiens*	CAM-DL	EU 1 1 0102
714	Hsap404-9RB1-M	*H. sapiens*	CAM-DL	EU 1 2 0022
715	Hsap405-9R1B-M	*H. sapiens*	CAM-DL	EU 1 2 0029
716	Hsap417-9R1B-M	*H. sapiens*	CAM-DL	EU 1 2 0319
717	Hsap420-9R1B-M	*H. sapiens*	CAM-DL	EU 1 2 0448
718	Hsap426-9R1B-M	*H. sapiens*	CAM-DL	WOR 071W8 NONSUCH 026
719	Hsap429-9R1B-M	*H. sapiens*	CAM-DL	C/U/12/8 NONSUCH 068
720	Hsap432-9R1B-M	*H. sapiens*	CAM-DL	C/VI/5
721	Hsap436-9R1B-M	*H. sapiens*	CAM-DL	EU 1 1 0083
722	Hsap08410Q3-F	*H. sapiens*	MNHN	34218
723	Hsap104-10Q3-F?	*H. sapiens*	MNHN	20531
724	Hsap08510Q3-M	*H. sapiens*	MNHN	34224
725	Hsap093-10Q3-M	*H. sapiens*	MNHN	4962
726	Hsap103-10Q3-M	*H. sapiens*	MNHN	18891
727	Hsap083-10Q3-M?	*H. sapiens*	MNHN	34222
728	Hsap086-10Q3-M?	*H. sapiens*	MNHN	34211
729	Hsap089-10Q3-M?	*H. sapiens*	MNHN	3001
730	Hsap094-10Q3-M?	*H. sapiens*	MNHN	4957
731	Hsap095-10Q3-M?	*H. sapiens*	MNHN	12290
732	Hsap050-10Q3-F	*H. sapiens*	MNHN	10253
733	Hsap020-10Q3-M?	*H. sapiens*	MNHN	10438
734	Hsap023-10Q3-M?	*H. sapiens*	MNHN	7015
735	Hsap024-10Q3-M?	*H. sapiens*	MNHN	7038
736	Hsap027-10Q3-M?	*H. sapiens*	MNHN	1247
737	Hsap033-10Q3-M?	*H. sapiens*	MNHN	10435
738	Hsap038-10Q3-M?	*H. sapiens*	MNHN	7074
739	Hsap039-10Q3-M?	*H. sapiens*	MNHN	7090
740	Hsap056-11Q1-F?	*H. sapiens*	MNHN	20407
741	Hsap057-11Q1-F?	*H. sapiens*	MNHN	20413
742	Hsap381-11Q1-F?	*H. sapiens*	CAM-DL	NA142
743	Hsap061-11Q1-M	*H. sapiens*	MNHN	19230
744	Hsap064-11Q1-M	*H. sapiens*	MNHN	1697
745	Hsap373-11Q1-M	*H. sapiens*	CAM-DL	NA123
746	Hsap059-11Q1-M?	*H. sapiens*	MNHN	9726
747	Hsap063-11Q1-M?	*H. sapiens*	MNHN	1691
748	Hsap372-11Q1-M?	*H. sapiens*	CAM-DL	NA122

749	Hsap374-11Q1-M?	*H. sapiens*	CAM-DL	NA132
750	Hsap376-11Q1-M?	*H. sapiens*	CAM-DL	NA134
751	LH_4	*A. afarensis*	KNM	
752	LH_23	*A. afarensis*	U-Wits	
753	AL_207-13	*A. afarensis*	U-Wits	
754	AL_333-59	*A. afarensis*	U-Wits	
755	AL_333-W27	*A. afarensis*	U-Wits	
756	AL_241-14	*A. afarensis*	U-Wits	
757	AL_333-W57	*A. afarensis*	U-Wits	
758	AL_333-W60	*A. afarensis*	U-Wits	
759	AL_145-35	*A. afarensis*	U-Wits	
760	AL_277-1	*A. afarensis*	U-Wits	
761	AL_288-1	*A. afarensis*	U-Wits	
762	AL_400-1A	*A. afarensis*	U-Wits	
763	AL_128-23	*A. afarensis*	U-Wits	
764	AL_188-1	*A. afarensis*	U-Wits	
765	AL_266-1	*A. afarensis*	U-Wits	
766	AL_333-W1	*A. afarensis*	U-Wits	
767	Stw_404	*A. africanus*	U-Wits	
768	Stw_560e	*A. africanus*	U-Wits	
769	Stw_519	*A. africanus*	U-Wits	
770	Stw_412	*A. africanus*	U-Wits	
771	Stw_109	*A. africanus*	U-Wits	
772	Stw_327	*A. africanus*	U-Wits	
773	Stw_384	*A. africanus*	U-Wits	
774	Stw_540	*A. africanus*	U-Wits	
775	Stw_308	*A. africanus*	U-Wits	
776	Stw_555	*A. africanus*	U-Wits	
777	Stw_234	*A. africanus*	U-Wits	
778	Stw_498	*A. africanus*	U-Wits	
779	MLD_18	*A. africanus*	U-Wits	
780	MLD_2	*A. africanus*	U-Wits	
781	Sts_52b	*A. africanus*	Ditsong	
782	MLD_24	*A. africanus*	U-Wits	
783	TM_1517	*P. robustus*	Ditsong	
784	SK_37	*P. robustus*	Ditsong	
785	SK_6	*P. robustus*	Ditsong	
786	SK_23	*P. robustus*	Ditsong	
787	SK_25	*P. robustus*	Ditsong	
788	SK_55	*P. robustus*	Ditsong	
789	SK_1587a	*P. robustus*	Ditsong	
790	SK_1	*P. robustus*	Ditsong	
791	SK_5	*P. robustus*	Ditsong	
792	SK_843	*P. robustus*	Ditsong	
793	SKW_5	*P. robustus*	Ditsong	
794	GDA_2	*P. robustus*	U-Wits	
795	Peninj_1	*P. boisei*	NMTanz	
796	KNM-ER_15930	*P. boisei*	KNM	

797	MH_1	*A. sediba*	U-Wits
798	MH_2	*A. sediba*	U-Wits
799	UW_101-1261	*H. naledi*	U-Wits
800	UW_101-001	*H. naledi*	U-Wits
801	UW_101-377	*H. naledi*	U-Wits
802	UW_101-1142	*H. naledi*	U-Wits
803	UW_101-507	*H. naledi*	U-Wits
804	UW_101-145	*H. naledi*	U-Wits
805	UW_101-789	*H. naledi*	U-Wits
806	OH_7	*H. habilis*	NMTanz
807	OH_16	*H. habilis*	NMTanz
808	KNM-ER_1802	*H. rudolfensis*	KNM
809	KNM-ER_60000	*H. rudolfensis?*	KNM
810	SK_15	*"Early Homo"*	Ditsong
811	KNM-ER_992	*H. erectus*	KNM
812	KNM-ER_806b	*H. erectus*	KNM
813	OH_22	*H. erectus?*	NMTanz

* Blanket Ethics Waiver Number W-CJ-14064-1

Analysis of molars from Great Britain (Time Series)

Specimen name	*Species, period*	Collection	Specimen #
Hsap388-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0031?
Hsap390-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0040
Hsap392-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0059
Hsap393-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0060
Hsap394-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0073
Hsap399-NEO-F	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0100
Hsap385-NEO-M	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0061
Hsap391-NEO-M	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0041
Hsap397-NEO-M	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0083
Hsap398-NEO-M	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0090
Hsap400-NEO-M	*H. sapiens (Neolithic)*	CAM-DL	EU 1 5 0092
Hsap401-MED-F	*H. sapiens (Medieval)*	CAM-DL	EU 1 1 0099
Hsap410-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0292
Hsap412-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0295
Hsap415-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0305
Hsap416-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0306
Hsap424-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	WOR 018(1)W56
Hsap425-ASAX-F	*H. sapiens (Anglo Saxon)*	CAM-DL	WOR 053W44
Hsap427-MED-F	*H. sapiens (Medieval)*	CAM-DL	NONSUCH 012 C/U12/8
Hsap402-MED-M	*H. sapiens (Medieval)*	CAM-DL	EU 1 1 0102
Hsap404-ASAX-M	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0022
Hsap405-ASAX-M	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0029
Hsap417-ASAX-M	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0319
Hsap420-ASAX-M	*H. sapiens (Anglo Saxon)*	CAM-DL	EU 1 2 0448

Hsap426-ASAX-M	*H. sapiens (Anglo Saxon)*	CAM-DL	WOR 071W8 NONSUCH 026
Hsap429-MED-M	*H. sapiens (Medieval)*	CAM-DL	C/U/12/8
Hsap432-MED-M	*H. sapiens (Medieval)*	CAM-DL	NONSUCH 068 C/VI/5
Hsap436-MED-M	*H. sapiens (Medieval)*	CAM-DL	EU 1 1 0083

APPENDIX 2 ADDITIONAL DETAILS REGARDING IMAGE PROCESSING

For purposes of repeatability of results, additional details are provided here in respect of image capture, processing and landmarking.

Image capture

Photos were taken using a Nikon D3200 digital SLR camera (24 Megapixels) with a macro lens and around-lens ring light, with the lens facing vertically downwards, orthogonal to the plane of the tooth enamel surface. An adjustable scale bar (height, x,y,z axes adjustable) was placed at the level of the occlusal plane of the tooth, so both tooth and scale bar were orthogonal to the lens and both in focus.

Image processing

Selection

Lower second molars were chosen for the study. All usable lower M2s were chosen from the available images from the Pilbrow image database (gorillas, common chimpanzees and bonobos) and from the modern human and fossil image database (Dykes database). Exclusions were made in cases where the outline of the teeth along interstitial wear-facets were difficult to infer, or in a few cases where the longitudinal axis of the tooth was ambiguous or too difficult to determine. For the modern human database, teeth were excluded on the following basis: no data regarding sex [although some whole populations had no sex data and were therefore included as "ND"("no

data") and marked with different colour or symbols on charts; the same applied to populations where there were only a few examples].

Where possible, right teeth were chosen (these were the predominant selection from the Pilbrow database), but to remain comparable to previous work (Dykes, 2014), all teeth were analysed as left-side teeth. In other words, all right molars were mirror imaged to appear as left teeth for the landmarking protocol.

Processing

After standardising teeth to appear as left-side teeth with the buccal edge facing downwards in the image and the mesiodistal axis running left to right in the image (mirror imaging used where necessary), the images were rotated (using Photoshop or Gimp) so that the longitudinal axis of the tooth was horizontal in the image. Wood (1991) and Goose (1963) both provide a comparable methodology wherein the axis runs along the centre of the tooth in normal occlusion. Goose (1963) suggests that the mesiodistal axis should be aligned between the contact points of the tooth crown with its neighbouring teeth in the occlusal view, in normal occlusion. In cases where the tooth is in malocclusion (in "rotation" relative to the general axis of the dental arcade), the positions of the contact points on the crown would be situated at the points on the tooth where contact would ordinarily be with the neighbouring teeth if it were in normal occlusion. The orientation of the mesial groove can often act as a guide for the correct rotation of the tooth in all the species analysed, including misaligned/rotated and asymmetrical teeth.

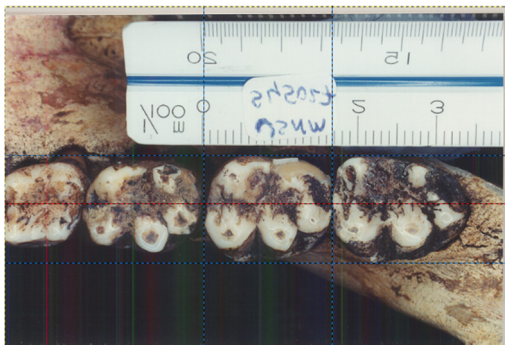


Figure 42. Teeth in "normal occlusion", showing the longitudinal axis.

(The red line signifies the longitudinal or mesiodistal axis. Image processed using GIMP® software)

To measure the mesiodistal (MD) diameter, the distance between the mesial-most point and the distal-most point of the tooth are measured, parallel to the longitudinal axis (Moorrees and Reed, 1954). Wood and Abbot (1983) suggest a corrected and an uncorrected measurement, depending on whether the tooth is used as it exists in the tooth row (with interstitial wear between teeth uncorrected), or whether corrections are made to the outline of the tooth in the image, to trace the inferred shape of the mesial and distal edges of the tooth before interstitial wear occurred due to damage from the teeth on each side (proximal and distal). For this study, because interstitial wear was variable (in extent and in directionality), it was decided to correct (via estimation) for the original inferred curvature of the outline of the tooth in the occlusal view, using Adobe Illustrator (AI).

Correction for interstitial damage/wear

In each case, the section of the outline of the tooth which showed damage due to interstitial wear was identified in the occlusal view of the image along its buccolingual extent, at the point of contact with each neighbouring tooth. Using the pencil tool in AI, the curvature of the outline of the tooth where the damage began on the buccal side was traced and continued along its trajectory towards the lingual side, as was the curvature of the outline from the start of the damaged area on the lingual side, continuing the trajectory towards the buccal side of the damaged area, until the two curved trajectories joined at the midpoint of the damaged section of the tooth. The 100% smoothing tool in AI was then used to ensure smoothing of the curvature where both curved lines met. Wood and Abbott (1983) present a diagram to illustrate correction of the interstitial wear facets (page 202, Figure 43 below).

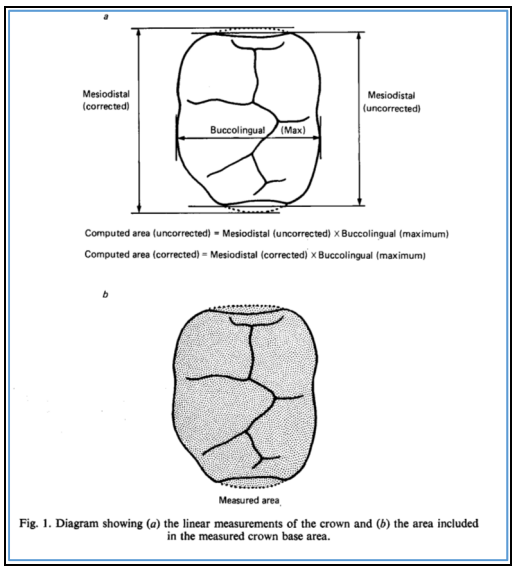


Fig. 1. Diagram showing (*a*) the linear measurements of the crown and (*b*) the area included in the measured crown base area.

Figure 43. Calculation of MD and BL axes, correction of interstitial wear facets.

Calculation of the MD and BL diameters using a "bounding box"

The "corrected" MD diameter, as defined by Wood and as described above for this study, was used for all teeth. For the buccolingual (BL) axis, this is taken at 90° to the MD axis. Wood suggests a minimum and a maximum BL diameter (the mesial cusps and the distal cusps are, in many species, different in size, and the two diameters may be useful in analyses) (Wood and Abbott, p. 202). For this study, I used the maximum BL diameter, which is equivalent to the measurement taken by callipers held as close to horizontal to the crown enamel as possible and opened until the full breadth of the tooth from the lingual side to the buccal side is measured, perpendicular to the longitudinal axis. The maximum BL diameter and the corrected MD diameter can be described for each tooth by enclosing the tooth visually into a "bounding box", using Adobe Illustrator. The sides parallel to the longitudinal axis of the tooth will be equivalent to the (corrected) MD diameter, and the sides running from the buccal to the lingual edges of the outline of the tooth, perpendicular to the longitudinal axis, will be equivalent to the (maximum) BL diameter. For the purposes of this study, the MD and BL axes themselves were additionally drawn onto the image in Adobe Illustrator by bisecting the edges of the bounding box and placing lines running vertically and horizontally through the centre of the bounding box superimposed on the image. The geometric centre point of the bounding box, at the intersection of the MD/BL diameters, then provides an approximation for the centre of the tooth, and this location is used for Landmark 1. Inter-observer tests to calculate the degree of error in calculating the longitudinal axis and the correction for the inferred curvature of the tooth are under way.

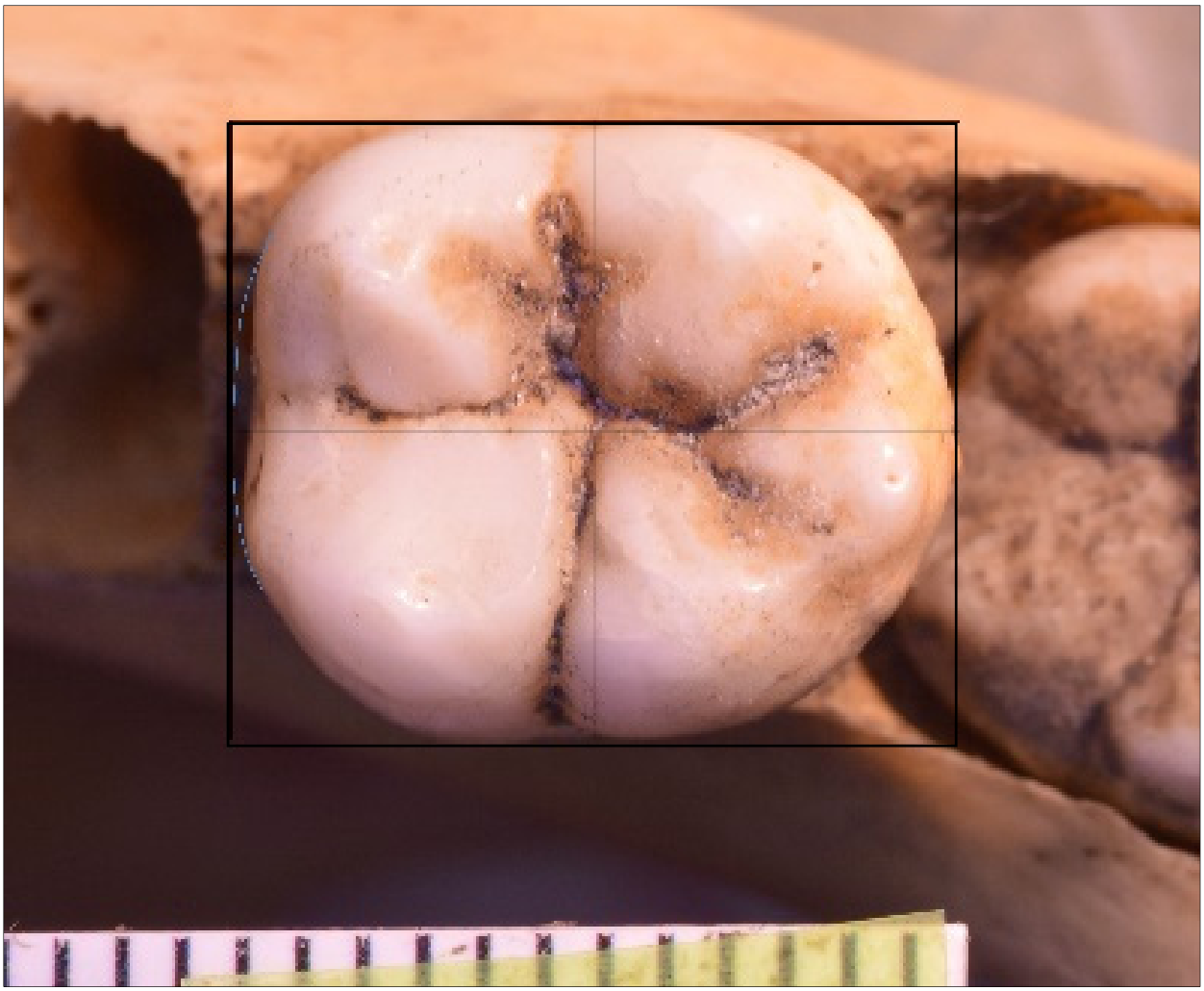


Figure 44. Superimposition of a "bounding box", MD/BL diameters, tooth centre.

Landmarking

ImageJ was used to draw landmark placement points (using the line tool and the paintbrush blob tool) on the image prior to landmarking. Once points were measured and marked on the image (as described below), the images were scaled and landmarks placed, to provide an output of Euclidian coordinates in millimetres for all 29 landmarks. The landmarks were placed as follows:

Landmarks 1-5 define, respectively, 1) the geometric centre of the bounding box/the tooth, where the MD and BL diameters intersect; 2) the point where the MD diameter intersects with the mesial edge of the bounding box; 3) the point where the BL diameter intersects with the lingual side of the bounding box; 4) the point where the MD diameter intersects with the distal edge of the bounding box; and 5) the point where the BL diameter intersects with the buccal edge of the bounding box:

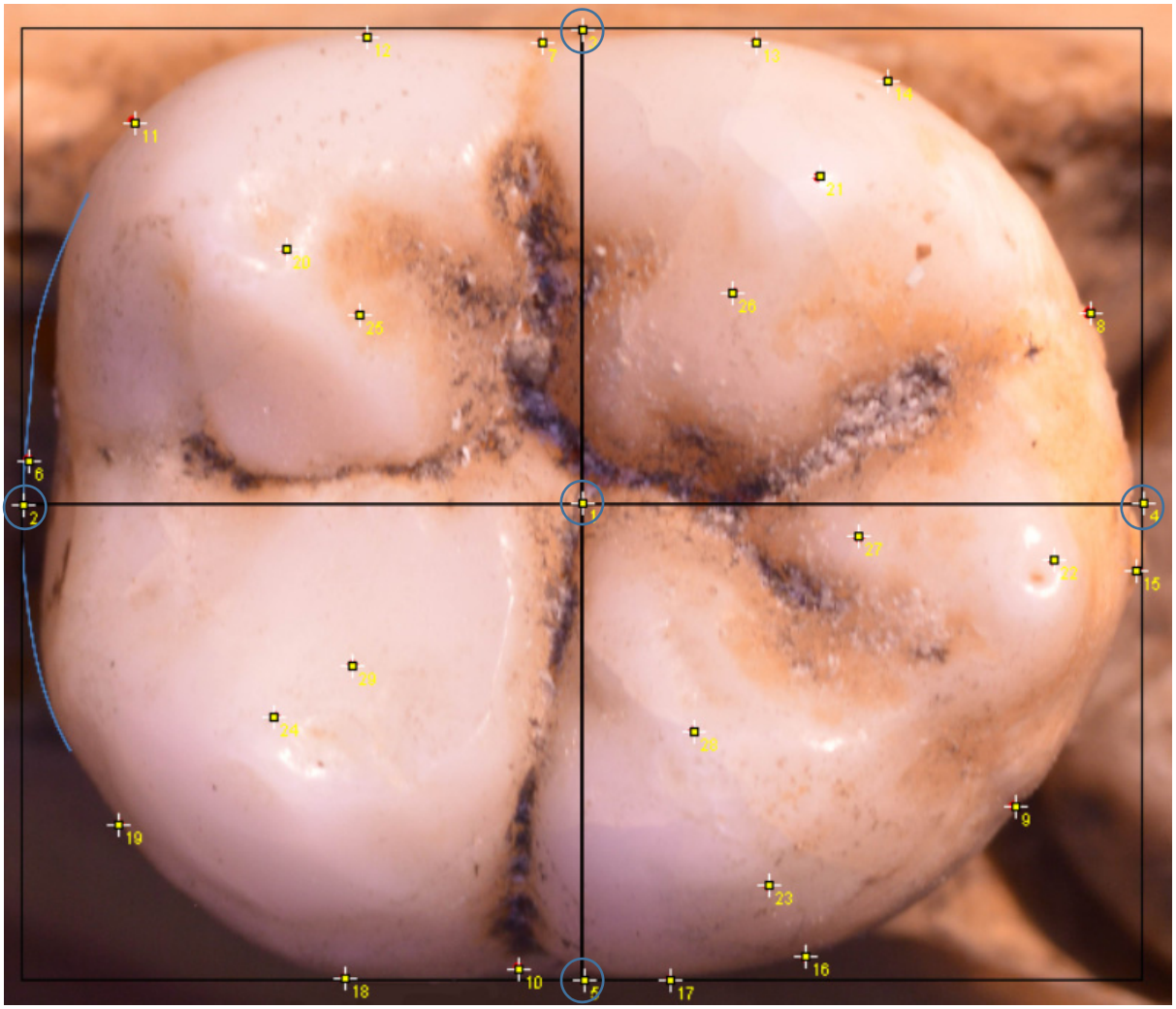


Figure 45. Landmarks 1 – 5.

Landmarks 6-10 are anatomical/homologous/Type I landmarks at the junctions where the five major cusps meet at the perimeter outline of the tooth in the occlusal view,

starting at 6) the mesial edge, where mesial groove is inferred to meet the mesial edge of the tooth (usually where it would intersect with the corrected curve of the tooth – as described previously, depicted in this image by the blue line), defining the intersection of the metaconid and the protoconid projected to the inferred (corrected) perimeter outline of the tooth; from there, proceeding clockwise around the tooth, landmarks are placed at: 7) the junction (at the perimeter outline of the tooth image) between the metaconid and entoconid on the lingual edge of the tooth outline; 8) the junction between the entoconid and hypoconulid; 9) the junction between the hypoconulid and hypoconid; and 10) the junction between the hypoconid and protoconid on the buccal side of the tooth:

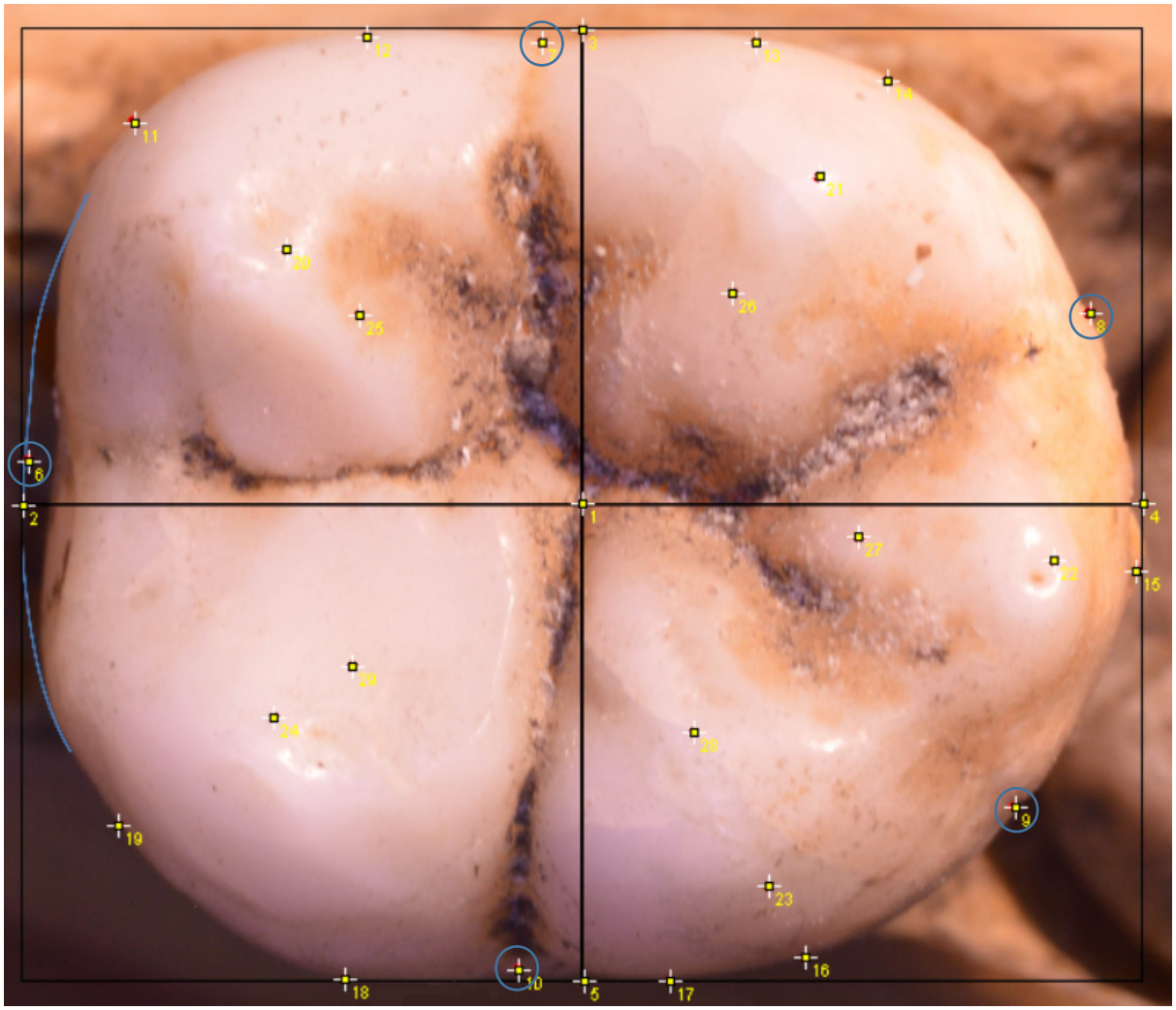


Figure 46. Landmarks 6 – 10.

Landmarks 20-24 denote the midpoints of the cords subtending the arcs of the perimeter outlines of each cusp, calculated by drawing a cord between the cusp junctions (landmarks 6-10 as already described). Landmark 20 is placed on the midpoint of the cord drawn between landmarks 6 and 7, denoting the "midline" orientation of the metaconid from the approximated centre of the tooth to the mid-point of the cusp arc at the perimeter outline. Progressing clockwise, 21 denotes the midline orientation of the entoconid; 22, the midline orientation of the hypoconulid; 23, the midline orientation of the hypoconid; and 24, the midline orientation of the protoconid.

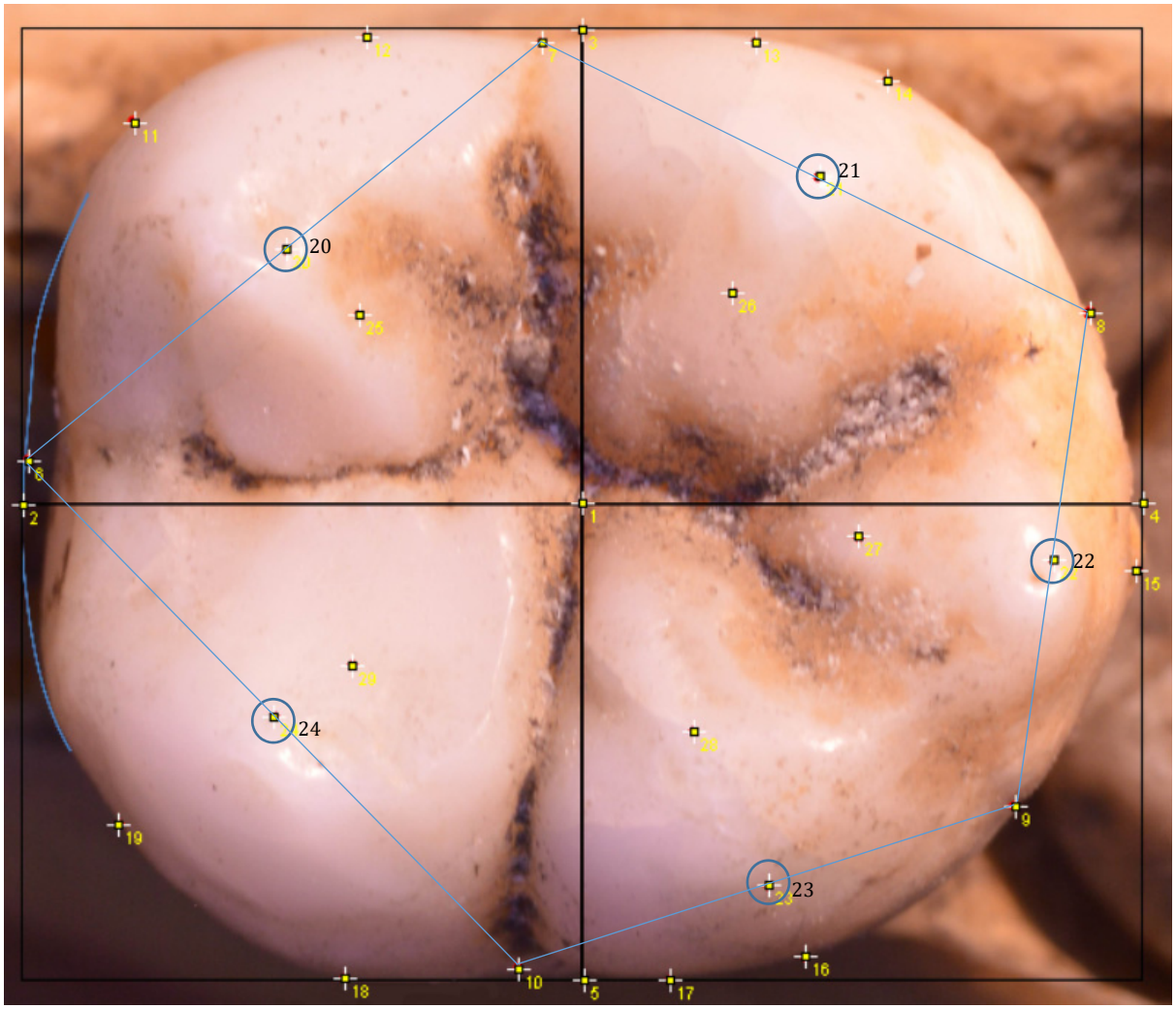


Figure 47. Landmarks 20-24.

Using these “midline” orientation points, lines are then drawn from the approximated centre point (landmark 1) to define two further landmarks for each cusp along their respective midlines from the approximated centre of the tooth: one at the perimeter of the tooth in line with the midline of each cusp (landmarks 11, 14, 15, 16 and 19 respectively, as depicted below), to define an approximated midpoint at the perimeter outline of each cusp arc. Landmark 11 denotes the midpoint of the perimeter outline of the cusp arc of the metaconid, and progressing clockwise, 14, 15, 16 and 19 mark the midpoints of the cusp arcs at the perimeter outline of the entoconid, hypoconulid, hypoconid and protoconid in turn. The second at the point for each cusp defines the midpoint between the approximated centre of the tooth (landmark 1) and the perimeter outline midpoint of each cusp as just described (landmarks 11, 14, 15, 16 and 18 as just described), to approximate the “centre” point of each cusp in relation to the geometric centre of the tooth. The landmarks produced thus form an inner pentagon, starting with the metaconid and rotating clockwise to the protoconid to produce landmarks 25 to 29.

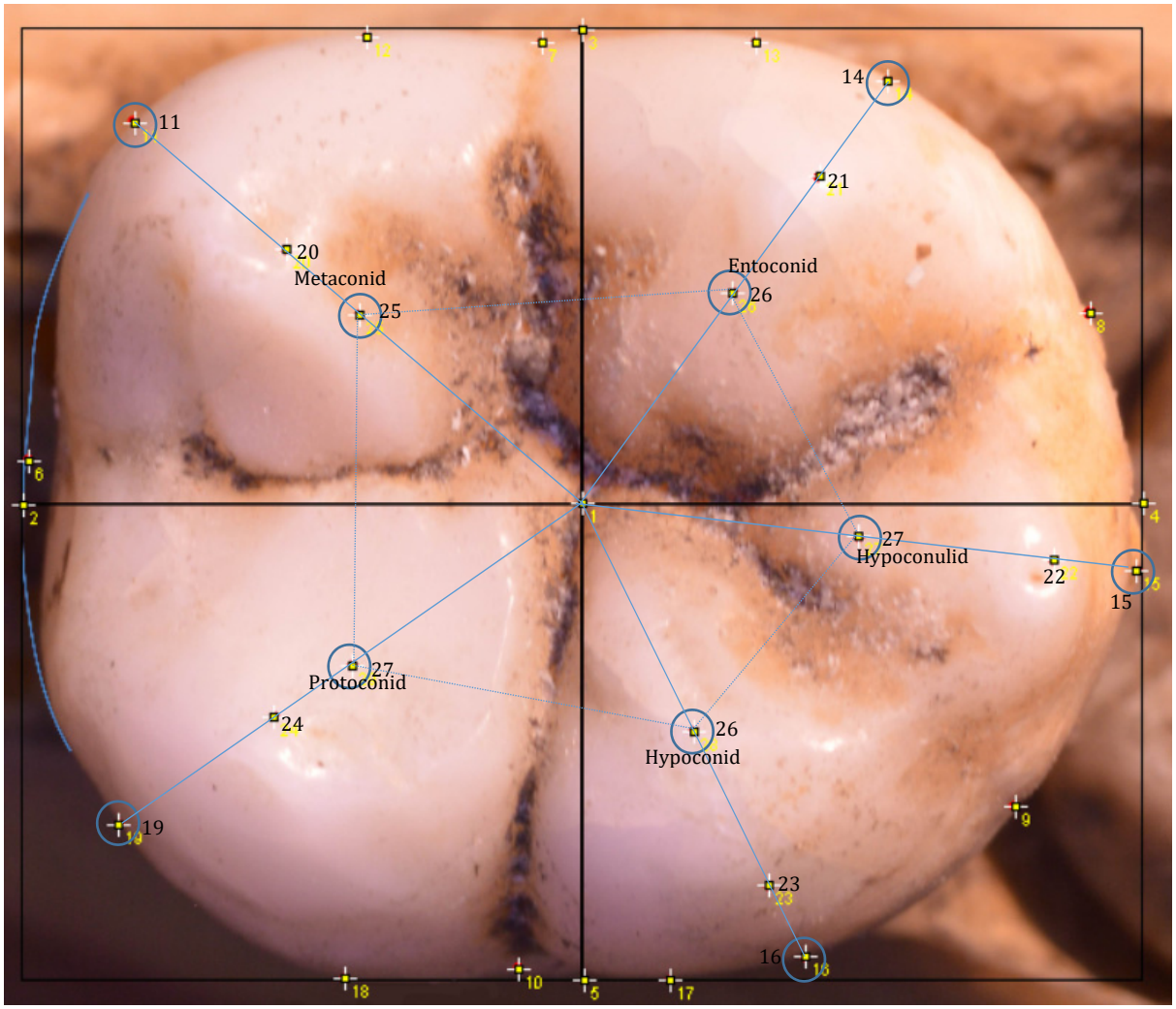


Figure 48. Landmarks 25-29 and 11, 14, 15, 16, 19.

Lastly, the general orientation of the mesial and the distal cusps relative to the longitudinal axis of the tooth is defined at the perimeter outline of the tooth by extending lines through the approximated centres of the two mesial cusps (metaconid and protoconid) and the two main distal cusps (entoconid and hypoconid). To achieve this, a line is extended through landmarks 25 and 29 (mesial cusp "centres") to the lingual-side perimeter edge of the metaconid and the buccal-side perimeter of the protoconid; and then the same procedure is used to extend a line through landmarks 26 and 28 (distal cusp "centres") to the lingual-side perimeter edge of the entoconid and the buccal-side perimeter edge of the hypoconid. These landmarks are numbered 12 (metaconid, lingual

edge), 13 (entoconid, lingual edge), 17 (hypoconid, buccal edge) and 18 (protoconid, buccal edge). These additional landmarks also capture four additional points around the perimeter of the tooth, allowing for a more complete reference shape to be used in the shape analysis (giving a clearer interpretation of relative warps along the axes of a principal components analysis, for example).

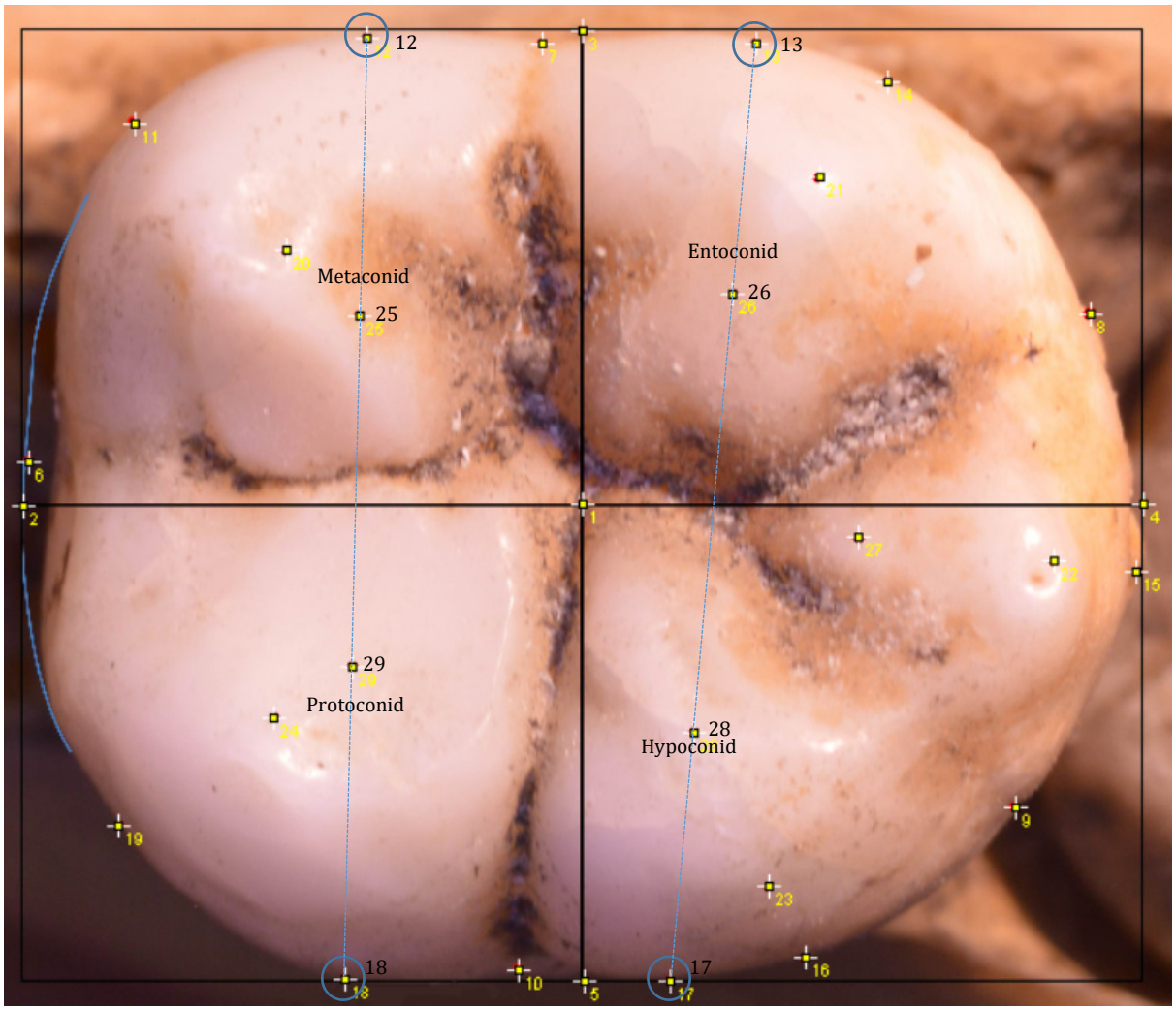


Figure 49. Landmarks 12, 13, 17, 18.

In this way, the perimeter is described via landmarks 6 – 10 (cusp intersections) and then 11-19, clockwise around the tooth. The cusp breadths and orientations are described by two pentagons: one joining the cusp arcs at landmarks 6-10 via the midline landmarks

20-24 and the second, inner pentagon, delineating the approximations of the centre points for each cusp, landmarks 25-29.

Notes for teeth with 4 or 6+ cusps

To keep the methodology as simple as possible, and bearing in mind that numerous species (fossil hominin species and extant hominoid species) are all being compared in an analysis that requires the same number of landmarks for each specimen, all teeth were considered to be five-cusp teeth. In the case of the gorilla, for instance, if additional cusps are present, they can usually be inferred to form part of a "split" entoconid. The hypoconulid is usually very distinct from the entoconid, even if the latter has additional cusp/cingulum areas attached to it. In the case of some chimpanzees and humans, the hypoconulid, rather than the entoconid, appeared to be split, with a groove close to the midline of the cusp. In some humans, there appear to be only four cusps. Unless there was an obvious partial groove between the hypoconid and the entoconid denoting a fifth cusp [where the enamel appears to have a degree of fusion towards the perimeter edge between the hypoconid and the hypoconulid (in which case five cusps could still be inferred, particularly when the pattern of the adjoining teeth indicates five distinct cusps with the same orientation as that of the partially fused cusps on the second molar between them)], the "fifth cusp" was marked at the centre of the groove between the entoconid and the hypoconid on the distal edge. This would mean that there would be no cusp arc to speak of, providing a curve for a hypoconulid. Examples are depicted below

a) Split hypoconulid:

Figure 50. Tooth with a split hypoconulid.

b) “Inferred” hypoconulid:

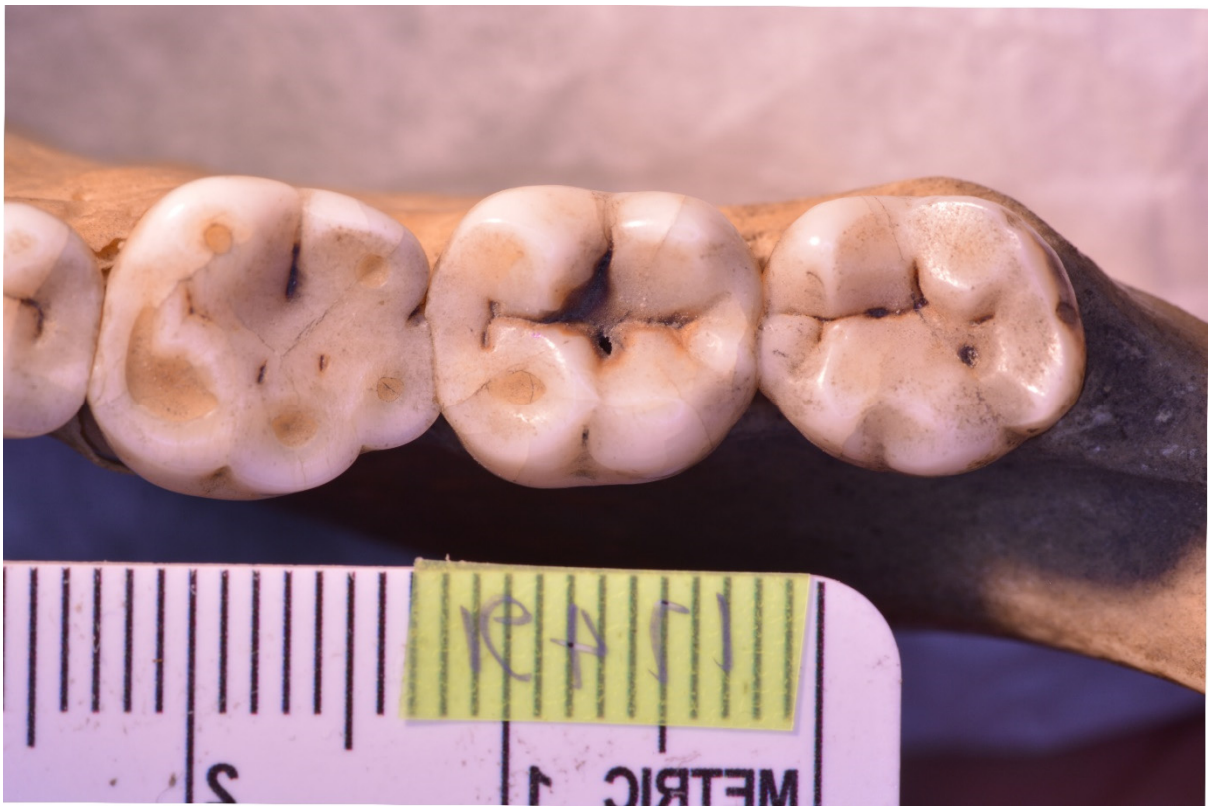


Figure 51. Tooth with an "inferred" hypoconulid.

c) Four cusps with centre of “groove” in between the curves of the entoconid and the hypoconid used to approximate the hypoconulid landmark site:

Figure 52. Tooth with four cusps: siting of landmark for “hypoconulid” between entoconid and hypoconid.

d) Split entoconid. The hypoconulid can clearly be defined, oriented bucco-distally. It can be observed that it is not the hypoconulid, in this instance, but the entoconid which is complex.

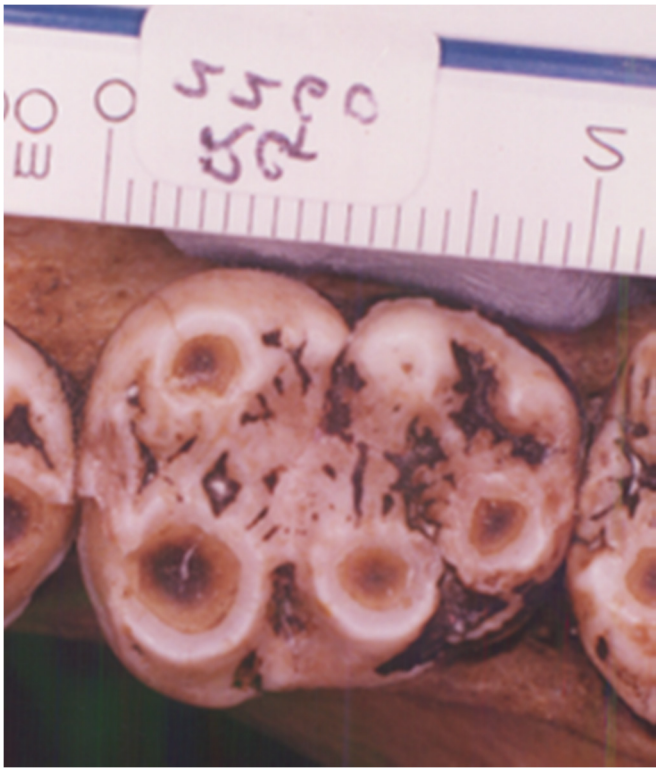


Figure 53. Tooth with a split entoconid.

APPENDIX 3 INPUT AND OUTPUT DATA RELEVANT TO ANALYSES
(Data in Excel format available from author).

Table 28. Extant Species - Descriptive Statistics at species level

	Species	Mean	Std. Deviation	Species	Mean	Std. Deviation	Species	Mean	Std. Deviation
LnCentroid	G. beringei (n=75)	3.691	0.066	P. troglodytes (n=214)	3.255	0.056	H. sapiens (n=241)	3.249	0.067
Angle-Bucc grv		1.913	0.169		2.598	0.165		3.036	0.085
Angle-Hypcnld		2.072	0.038		1.975	0.053		2.025	0.038
Angle-Mesial		1.368	0.055		1.476	0.047		1.489	0.052
Angle-Distal		1.956	0.055		1.712	0.069		1.651	0.073
Angle-BL groove		1.756	0.051		1.673	0.053		1.616	0.052
angle ratio-Mes:dist		0.907	0.033		0.974	0.037		1.002	0.039
length-MD		19.559	1.440		11.993	0.713		11.428	0.832
length-BL		15.685	1.114		10.146	0.618		10.224	0.685
breadth-Mesial		15.209	1.029		9.985	0.638		10.012	0.635
breadth-Distal		14.840	0.958		9.866	0.586		10.037	0.739
breadth-BL groove		12.544	0.906		9.225	0.594		9.948	0.684
width-Hycnld		1.438	0.377		1.422	0.395		0.847	0.361
Mesial length-Bucc groove		4.327	0.553		2.247	0.372		2.056	0.389
Dist length-Bucc groove		2.148	0.418		1.401	0.260		1.557	0.458
ratio-MD:BL		1.248	0.055		1.183	0.050		1.118	0.042
ratio-MD:bucc groove		1.561	0.069		1.302	0.064		1.149	0.047
ratio-Mesial:distal		1.025	0.042		1.012	0.034		0.999	0.030
ratio-hypcnld		0.161	0.039		0.240	0.062		0.147	0.059
LnCentroid	G. gorilla (n=179)	3.624	0.057	P. paniscus (n=41)	3.134	0.049	Total (n=750)	3.378	0.202
Angle-Bucc grv		1.842	0.153		2.617	0.175		2.491	0.504
Angle-Hypcnld		2.031	0.049		1.958	0.044		2.013	0.056
Angle-Mesial		1.398	0.052		1.502	0.052		1.452	0.069
Angle-Distal		1.926	0.060		1.700	0.073		1.767	0.140
Angle-BL groove		1.750	0.048		1.698	0.047		1.683	0.075
angle ratio-Mes:dist		0.906	0.038		0.966	0.042		0.960	0.055
length-MD		18.045	1.030		10.747	0.603		13.945	3.421
length-BL		14.579	1.024		8.995	0.429		11.720	2.450
breadth-Mesial		14.260	1.008		8.814	0.439		11.472	2.358
breadth-Distal		13.976	0.945		8.512	0.455		11.325	2.254
breadth-BL groove		11.684	0.847		8.100	0.432		10.315	1.452
width-Hycnld		1.498	0.371		1.251	0.301		1.247	0.466
Mesial length-Bucc groove		4.145	0.533		2.039	0.254		2.835	1.073
Dist length-Bucc groove		2.085	0.417		1.199	0.203		1.678	0.498
ratio-MD:BL		1.240	0.052		1.195	0.047		1.183	0.070
ratio-MD:bucc groove		1.548	0.078		1.328	0.053		1.339	0.177
ratio-Mesial:distal		1.021	0.040		1.036	0.037		1.013	0.037
ratio-hypcnld		0.173	0.038		0.234	0.049		0.186	0.066

Table 29. Extant Species - Descriptive Statistics at subspecies level

Group Statistics									
	Subspecies	Mean	Std. Deviation	Subspecies	Mean	Std. Deviation	Subspecies	Mean	Std. Deviation
LnCentroid	G. b. beringei (n = 25)	3.644	0.054	P. t. verus (n = 43)	3.277	0.048	P. paniscus (n = 41)	3.134	0.049
Angle-Bucc grv		1.973	0.176		2.601	0.129		2.617	0.175
Angle-Hypcnld		2.061	0.040		2.023	0.038		1.958	0.044
Angle-Mesial		1.362	0.059		1.495	0.039		1.502	0.052
Angle-Distal		1.963	0.054		1.661	0.059		1.700	0.073
Angle-BL groove		1.778	0.036		1.623	0.040		1.698	0.047
angle ratio-Mes:dist		0.907	0.039		0.993	0.033		0.966	0.042
length-MD		18.441	1.071		11.894	0.614		10.747	0.603
length-BL		15.285	0.993		10.526	0.558		8.995	0.429
breadth-Mesial		14.673	0.955		10.465	0.578		8.814	0.439
breadth-Distal		14.154	0.635		10.132	0.505		8.512	0.455
breadth-BL groove		12.018	0.779		9.572	0.555		8.100	0.432
width-Hycnld		1.374	0.393		1.023	0.326		1.251	0.301
Mesial length-Bucc groove		4.025	0.458		2.603	0.300		2.039	0.254
Dist length-Bucc groove		2.072	0.358		1.366	0.230		1.199	0.203
ratio-MD:BL		1.208	0.046		1.131	0.033		1.195	0.047
ratio-MD:bucc groove		1.537	0.067		1.244	0.041		1.328	0.053
ratio-Mesial:distal		1.037	0.049		1.033	0.028		1.036	0.037
ratio-hypcnld		0.161	0.044		0.174	0.052		0.234	0.049
LnCentroid	G. b. graueri (n = 50)	3.715	0.059	P. t. ellioti (n = 5)	3.218	0.025	H. sapiens (n = 241)	3.249	0.067
Angle-Bucc grv		1.883	0.158		2.731	0.216		3.036	0.085
Angle-Hypcnld		2.078	0.037		1.997	0.047		2.025	0.038
Angle-Mesial		1.371	0.053		1.504	0.015		1.489	0.052
Angle-Distal		1.953	0.056		1.705	0.045		1.651	0.073
Angle-BL groove		1.745	0.055		1.660	0.016		1.616	0.052
angle ratio-Mes:dist		0.907	0.030		0.961	0.021		1.002	0.039
length-MD		20.117	1.270		11.483	0.250		11.428	0.832
length-BL		15.886	1.126		9.775	0.461		10.224	0.685
breadth-Mesial		15.477	0.966		9.547	0.570		10.012	0.635
breadth-Distal		15.183	0.909		9.505	0.175		10.037	0.739
breadth-BL groove		12.806	0.856		8.874	0.526		9.948	0.684
width-Hycnld		1.470	0.369		1.217	0.336		0.847	0.361
Mesial length-Bucc groove		4.479	0.538		2.166	0.357		2.056	0.389
Dist length-Bucc groove		2.186	0.444		1.260	0.296		1.557	0.458
ratio-MD:BL		1.268	0.049		1.176	0.046		1.118	0.042
ratio-MD:bucc groove		1.573	0.067		1.296	0.055		1.149	0.047
ratio-Mesial:distal		1.020	0.038		1.004	0.052		0.999	0.030
ratio-hypcnld		0.160	0.037		0.215	0.057		0.147	0.059
LnCentroid	G. g. diehli (n = 10)	3.600	0.045	P. t. troglodytes (n = 108)	3.247	0.054	Total (n = 750)	3.378	0.202
Angle-Bucc grv		1.795	0.119		2.598	0.172		2.491	0.504
Angle-Hypcnld		2.005	0.056		1.968	0.048		2.013	0.056
Angle-Mesial		1.403	0.043		1.454	0.043		1.452	0.069
Angle-Distal		1.917	0.044		1.735	0.065		1.767	0.140
Angle-BL groove		1.721	0.037		1.697	0.046		1.683	0.075
angle ratio-Mes:dist		0.907	0.030		0.973	0.036		0.960	0.055
length-MD		17.544	0.769		11.957	0.701		13.945	3.421
length-BL		14.008	0.600		10.013	0.555		11.720	2.450
breadth-Mesial		13.726	0.703		9.813	0.561		11.472	2.358
breadth-Distal		13.915	0.878		9.808	0.574		11.325	2.254
breadth-BL groove		11.526	0.763		9.122	0.559		10.315	1.452
width-Hycnld		1.701	0.346		1.509	0.321		1.247	0.466
Mesial length-Bucc groove		3.893	0.458		2.160	0.339		2.835	1.073
Dist length-Bucc groove		2.078	0.318		1.429	0.280		1.678	0.498
ratio-MD:BL		1.253	0.041		1.195	0.044		1.183	0.070
ratio-MD:bucc groove		1.526	0.073		1.312	0.062		1.339	0.177
ratio-Mesial:distal		0.987	0.023		1.001	0.033		1.013	0.037
ratio-hypcnld		0.198	0.035		0.256	0.049		0.186	0.066
LnCentroid	G. g. gorilla (n = 169)	3.626	0.058	P. t. schweinfurthii (n = 58)	3.258	0.062			
Angle-Bucc grv		1.845	0.155		2.585	0.172			
Angle-Hypcnld		2.033	0.049		1.950	0.048			
Angle-Mesial		1.398	0.053		1.502	0.040			
Angle-Distal		1.926	0.060		1.707	0.064			
Angle-BL groove		1.751	0.048		1.668	0.046			
angle ratio-Mes:dist		0.906	0.038		0.962	0.037			
length-MD		18.075	1.037		12.179	0.793			
length-BL		14.612	1.035		10.143	0.672			
breadth-Mesial		14.291	1.016		9.986	0.645			
breadth-Distal		13.980	0.951		9.808	0.632			
breadth-BL groove		11.693	0.853		9.191	0.602			
width-Hycnld		1.486	0.370		1.573	0.377			
Mesial length-Bucc groove		4.159	0.534		2.153	0.327			
Dist length-Bucc groove		2.085	0.423		1.386	0.239			
ratio-MD:BL		1.239	0.053		1.202	0.047			
ratio-MD:bucc groove		1.549	0.078		1.326	0.057			
ratio-Mesial:distal		1.023	0.039		1.019	0.031			
ratio-hypcnld		0.172	0.037		0.262	0.059			

EXTANT SPECIES –DFA OUTPUTS – EIGENVALUES

Table 30. Extant species - DFA - Species level - Eigenvalues

Eigenvalues					Wilks' Lambda				
Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation		Wilks' Lambda	Chi-square	df	Sig.
1	28.817[a]	87.5	87.5	0.983	1 through 4	0.004	4166.608	76	0.000
2	3.061[a]	9.3	96.7	0.868	2 through 4	0.105	1664.423	54	0.000
3	.624[a]	1.9	98.6	0.620	3 through 4	0.424	631.652	34	0.000
4	.451[a]	1.4	100.0	0.557	4	0.689	274.143	16	0.000

a. First 4 canonical discriminant functions were used in the analysis.

Table 31. Extant Species - DFA - Subspecies level - Eigenvalues

Eigenvalues					Wilks' Lambda				
Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1	30.343[a]	84.9	84.9	0.984	1 through 9	0.002	4755.963	171	0.000
2	3.483[a]	9.7	94.7	0.881	2 through 9	0.048	2225.627	144	0.000
3	.837[a]	2.3	97.0	0.675	3 through 9	0.217	1123.704	119	0.000
4	.468[a]	1.3	98.3	0.565	4 through 9	0.398	677.122	96	0.000
5	.313[a]	0.9	99.2	0.488	5 through 9	0.584	395.286	75	0.000
6	.170[a]	0.5	99.7	0.381	6 through 9	0.766	195.487	56	0.000
7	.063[a]	0.2	99.9	0.243	7 through 9	0.896	80.307	39	0.000
8	.036[a]	0.1	100.0	0.187	8 through 9	0.953	35.694	24	0.059
9	.013[a]	0.0	100.0	0.113	9	0.987	9.506	11	0.575

a. First 9 canonical discriminant functions were used in the analysis.

EXTANT SPECIES: SPECIES-LEVEL DFA OUTPUTS

Table 32. Extant Species - Species level - Canonical Discriminant Function Coefficients

Standardized Canonical Discriminant Function				
	Function			
	1	2	3	4
LnCentroid	0.686	0.042	-4.101	-3.189
Angle-Bucc grv	-0.331	0.519	0.216	0.099
Angle-Hypcnld	-0.263	-0.265	-0.022	-0.695
Angle-Mesial	1.009	1.789	-0.002	2.885
Angle-Distal	1.907	3.553	0.051	3.068
Angle-BL groove	-0.074	-0.755	0.078	0.403
angle ratio-Mes:dist	1.544	2.699	0.137	2.255
length-MD	0.958	1.691	1.468	-4.056
length-BL	0.349	-1.919	0.387	-1.236
breadth-Mesial	-1.266	2.158	-2.375	-1.657
breadth-Distal	1.115	-2.716	2.338	1.952
breadth-BL groove	-1.100	0.817	2.983	7.634
width-Hycnld	-0.895	0.444	-1.285	0.948
Mesial length-Bucc groove	0.129	0.132	-0.216	1.370
Dist length-Bucc groove	-0.066	0.613	0.084	0.745
ratio-MD:BL	-0.207	-1.398	-0.530	-0.989
ratio-MD:bucc groove	-0.165	0.091	1.705	4.488
ratio-Mesial:distal	0.566	-1.371	1.286	0.523
ratio-hypcnld	0.388	-0.982	0.814	-1.625

EXTANT SPECIES: SUBSPECIES-LEVEL DFA OUTPUTS

Table 33. Extant Species - Subspecies level - Canonical Discriminant Function Coefficients

Standardized Canonical Discriminant Function Coefficients									
	Function								
	1	2	3	4	5	6	7	8	9
LnCentroid	0.520	0.507	-4.319	-3.320	0.473	0.761	-0.893	-0.346	0.558
Angle-Bucc grv	-0.348	0.444	0.293	0.142	0.488	-0.111	-0.142	-0.617	-0.445
Angle-Hypcnld	-0.255	-0.198	-0.019	-0.694	0.000	0.084	0.712	-0.003	-0.690
Angle-Mesial	0.934	1.713	-0.280	2.748	1.378	0.077	0.994	-0.500	2.291
Angle-Distal	1.746	3.355	-0.380	2.969	2.927	-0.011	1.161	0.708	3.320
Angle-BL groove	-0.067	-0.731	0.108	0.335	-0.100	-0.048	0.531	-0.808	0.113
angle ratio-Mes:dist	1.437	2.659	-0.389	2.202	2.495	0.668	1.280	0.378	3.513
length-MD	1.540	2.086	2.340	-3.994	-4.127	0.262	0.629	-1.270	1.146
length-BL	-0.322	-2.448	-0.986	-0.747	5.548	2.012	-2.081	3.996	-2.162
breadth-Mesial	-1.011	2.227	-0.743	-2.041	-0.345	-2.896	1.487	-6.929	0.739
breadth-Distal	0.972	-2.698	0.977	2.280	-0.748	2.774	-1.100	4.746	-1.858
breadth-BL groove	-0.947	0.282	3.359	7.468	-0.681	-2.409	1.314	-0.226	1.859
width-Hycnld	-0.968	0.463	-1.246	0.846	0.059	-0.934	0.143	1.033	-2.022
Mesial length-Bucc groove	0.157	0.139	-0.083	1.226	-0.367	-0.651	0.696	-0.447	0.105
Dist length-Bucc groove	-0.063	0.512	0.243	0.729	0.219	-0.750	0.020	0.266	0.467
ratio-MD:BL	-0.482	-1.546	-0.923	-0.787	1.979	0.344	-1.260	1.746	-0.696
ratio-MD:bucc groove	-0.155	-0.242	1.733	4.383	0.321	-0.845	0.654	-1.207	-0.040
ratio-Mesial:distal	0.469	-1.374	0.443	0.754	-0.138	1.844	-1.232	3.160	0.028
ratio-hypcnld	0.451	-0.957	0.913	-1.543	-0.072	0.437	0.353	-0.925	1.539

EXTANT SPECIES: DFA OUTPUTS – STRUCTURE MATRICES

Table 34. Extant species - Species level - DFA Structure Matrix

Structure Matrix

	Function			
	1	2	3	4
length-MD	.664*	0.224	0.088	-0.234
Angle-Bucc grv	-.614*	0.483	0.209	-0.116
LnCentroid	.582*	0.334	-0.158	-0.213
length-BL	.527*	0.334	0.020	-0.182
breadth-Mesial	.524*	0.318	-0.032	-0.169
breadth-Distal	.501*	0.365	-0.102	-0.187
ratio-MD:bucc groove	.473*	-0.399	0.080	0.035
Mesial length-Bucc groove	.419*	0.090	-0.031	0.079
Angle-Distal	.341*	-0.061	0.044	-0.013
angle ratio-Mes:dist	-.194*	0.114	-0.011	-0.090
Angle-Mesial	-.168*	-0.049	-0.039	0.151
breadth-BL groove	0.292	.459*	-0.026	-0.214
ratio-hypcnld	-0.023	-.403*	-0.069	-0.270
Angle-Hypcnld	0.078	.323*	0.143	-0.057
width-Hycnld	0.098	-.292*	-0.127	-0.224
ratio-MD:BL	0.176	-.251*	0.072	-0.063
Angle-BL groove	0.190	-.211*	0.101	0.046
Dist length-Bucc groove	0.142	.179*	-0.074	0.038
ratio-Mesial:distal	0.040	-0.111	.154*	0.077

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions
Variables ordered by absolute size of correlation within function.

*. Largest absolute correlation between each variable and any discriminant function

Table 35. Extant species - Subspecies level - DFA Structure matrix

Structure Matrix

	Function								
	1	2	3	4	5	6	7	8	9
length-MD	.679*	0.190	0.162	-0.212	-0.082	-0.240	-0.425	-0.084	-0.008
Angle-Bucc grv	-.602*	0.467	0.272	-0.085	0.154	0.043	-0.207	-0.239	-0.066
LnCentroid	.583*	0.308	-0.089	-0.203	-0.051	-0.167	-0.419	-0.089	0.046
breadth-Mesial	.530*	0.302	-0.019	-0.150	-0.080	0.111	-0.336	-0.127	0.145
length-BL	.526*	0.307	0.025	-0.151	0.036	0.107	-0.344	-0.070	0.042
breadth-Distal	.503*	0.341	-0.030	-0.181	-0.093	-0.210	-0.230	0.061	-0.068
ratio-MD:bucc groove	.478*	-0.425	0.079	0.045	0.088	-0.257	-0.126	-0.157	-0.172
Mesial length-Bucc groove	.427*	0.097	-0.076	0.074	-0.233	0.269	0.208	-0.211	0.118
breadth-BL groove	0.294	.437*	0.042	-0.199	-0.097	-0.079	-0.336	0.028	0.123
Angle-BL groove	0.193	-0.238	0.102	0.037	.448*	-0.266	0.363	-0.069	0.292
Angle-Distal	0.341	-0.089	0.063	-0.011	.342*	-0.328	0.164	0.111	-0.146
ratio-Mesial:distal	0.040	-0.098	0.028	0.107	-0.036	.644*	-0.202	-0.241	0.371
ratio-MD:BL	0.183	-0.281	0.174	-0.073	-0.094	-.582*	-0.154	-0.024	-0.076
width-Hycnld	0.099	-0.314	-0.036	-0.244	0.064	-.573*	-0.326	0.161	-0.006
ratio-hypcnld	-0.026	-0.428	0.012	-0.299	0.108	-.534*	-0.240	0.123	0.031
Angle-Hypcnld	0.082	0.342	0.082	-0.050	-0.105	.498*	0.426	-0.121	-0.188
Dist length-Bucc groove	0.140	0.159	-0.021	0.032	0.060	-.236*	-0.060	0.023	0.214
Angle-Mesial	-0.169	-0.035	-0.056	0.178	-0.302	0.213	-.594*	-0.250	-0.268
angle ratio-Mes:dist	-0.191	0.128	-0.019	-0.109	-0.095	0.165	0.287	0.086	.364*

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions

*. Largest absolute correlation between each variable and any discriminant function

EXTANT SPECIES –SUBSPECIES LEVEL DFA OUTPUTS

Table 36. Extant species - Subspecies level - DFA - Proximity Matrix from squared Euclidean distances between group centroids

	Squared Euclidian distance with *significance values*									
Case	*1:G. b. beringei*	*2:G. b. graueri*	*3:G. g. diehli*	*4:G. g. gorilla*	*5:P. t. verus*	*6:P. t. ellioti*	*7:P. t. troglodytes*	*8:P. t. schweinfurthii*	*9:P. paniscus*	*10:H. sapiens*
1:G. b. beringei		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
2:G. b. graueri	16.688		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
3:G. g. diehli	23.794	30.011		*0.026*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
4:G. g. gorilla	9.884	16.862	5.425		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
5:P. t. verus	120.210	155.667	90.608	102.139		*0.047*	*0.000*	*0.001*	*0.000*	*0.004*
6:P. t. ellioti	138.830	176.842	113.862	122.638	9.774		*0.355*	*0.211*	*0.050*	*0.029*
7:P. t. troglodytes	121.917	159.410	97.823	107.551	8.433	4.182		*0.018*	*0.000*	*0.001*
8:P. t. schweinfurthii	126.869	162.543	98.751	109.366	8.870	5.105	1.891		*0.000*	*0.026*
9:P. paniscus	164.186	200.429	136.227	145.422	30.140	14.331	15.377	12.382		*0.000*
10:H. sapiens	160.102	197.583	136.506	148.153	17.855	17.877	22.167	25.849	40.862	

This is a dissimilarity matrix

EXTANT SPECIES/SUBSPECIES – SEXUAL DIMORPHISM STUDY BASED ON LN CENTROID SIZE

Table 37. Descriptive statistics at subspecies level for ln Centroid size in SPSS ®

			Statistic	Std. Error
G. b. beringei	Mean		3.6436	0.01077
	95% Confidence Interval for Mean	Lower Bound	3.6214	
		Upper Bound	3.6659	
	5% Trimmed Mean		3.6457	
	Median		3.6493	
	Variance		0.003	
	Std. Deviation		0.05383	
	Minimum		3.50	
	Maximum		3.75	
	Range		0.25	
	Interquartile Range		0.06	
	Skewness		-0.492	0.464
	Kurtosis		1.312	0.902
G. b. graueri	Mean		3.7150	0.00831
	95% Confidence Interval for Mean	Lower Bound	3.6983	
		Upper Bound	3.7317	
	5% Trimmed Mean		3.7154	
	Median		3.7150	
	Variance		0.003	
	Std. Deviation		0.05879	
	Minimum		3.59	
	Maximum		3.85	
	Range		0.26	
	Interquartile Range		0.08	
	Skewness		-0.104	0.337
	Kurtosis		-0.356	0.662
G. g. diehli	Mean		3.6001	0.01423
	95% Confidence Interval for Mean	Lower Bound	3.5679	
		Upper Bound	3.6323	
	5% Trimmed Mean		3.5988	
	Median		3.5957	
	Variance		0.002	
	Std. Deviation		0.04501	
	Minimum		3.54	
	Maximum		3.69	
	Range		0.15	
	Interquartile Range		0.06	
	Skewness		0.508	0.687
	Kurtosis		0.282	1.334
G. g. gorilla	Mean		3.6256	0.00445
	95% Confidence Interval for Mean	Lower Bound	3.6168	
		Upper Bound	3.6344	
	5% Trimmed Mean		3.6249	
	Median		3.6243	
	Variance		0.003	
	Std. Deviation		0.05784	
	Minimum		3.48	
	Maximum		3.83	
	Range		0.35	
	Interquartile Range		0.08	
	Skewness		0.261	0.187
	Kurtosis		0.203	0.371
P. t. verus	Mean		3.2767	0.00738
	95% Confidence Interval for Mean	Lower Bound	3.2618	
		Upper Bound	3.2916	
	5% Trimmed Mean		3.2756	
	Median		3.2767	
	Variance		0.002	
	Std. Deviation		0.04840	
	Minimum		3.19	
	Maximum		3.38	
	Range		0.19	
	Interquartile Range		0.08	
	Skewness		0.097	0.361
	Kurtosis		-0.725	0.709
P. t. ellioti	Mean		3.2179	0.01124
	95% Confidence Interval for Mean	Lower Bound	3.1867	
		Upper Bound	3.2491	
	5% Trimmed Mean		3.2172	
	Median		3.2037	
	Variance		0.001	
	Std. Deviation		0.02513	
	Minimum		3.20	
	Maximum		3.25	
	Range		0.05	
	Interquartile Range		0.05	
	Skewness		0.686	0.913
	Kurtosis		-2.572	2.000
P. t. troglodytes	Mean		3.2469	0.00515
	95% Confidence Interval for Mean	Lower Bound	3.2367	
		Upper Bound	3.2571	
	5% Trimmed Mean		3.2462	
	Median		3.2445	
	Variance		0.003	
	Std. Deviation		0.05351	
	Minimum		3.14	
	Maximum		3.37	
	Range		0.23	
	Interquartile Range		0.07	
	Skewness		0.125	0.233
	Kurtosis		-0.472	0.461
P. t. schweinfurthii	Mean		3.2584	0.00814
	95% Confidence Interval for Mean	Lower Bound	3.2421	
		Upper Bound	3.2747	
	5% Trimmed Mean		3.2596	
	Median		3.2626	
	Variance		0.004	
	Std. Deviation		0.06197	
	Minimum		3.12	
	Maximum		3.38	
	Range		0.27	
	Interquartile Range		0.11	
	Skewness		-0.213	0.314
	Kurtosis		-0.833	0.618
P. paniscus	Mean		3.1341	0.00771
	95% Confidence Interval for Mean	Lower Bound	3.1185	
		Upper Bound	3.1496	
	5% Trimmed Mean		3.1356	
	Median		3.1389	
	Variance		0.002	
	Std. Deviation		0.04938	
	Minimum		3.01	
	Maximum		3.22	
	Range		0.21	
	Interquartile Range		0.08	
	Skewness		-0.485	0.369
	Kurtosis		-0.401	0.724
H. sapiens	Mean		3.2488	0.00449
	95% Confidence Interval for Mean	Lower Bound	3.2400	
		Upper Bound	3.2577	
	5% Trimmed Mean		3.2481	
	Median		3.2488	
	Variance		0.004	
	Std. Deviation		0.06676	
	Minimum		3.06	
	Maximum		3.43	
	Range		0.36	
	Interquartile Range		0.09	
	Skewness		0.108	0.164
	Kurtosis		0.061	0.326

EXTANT SPECIES – SEXUAL DIMORPHISM STUDY BASED ON LN CENTROID SIZE

Table 38. Tests of normality of distributions by species/subspecies in SPSS ®

Tests of Normality

Species		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
		Statistic	df	Sig.	Statistic	df	Sig.
Size	G. b. beringei	0.123	25	.200*	0.962	25	0.460
	G. b. graueri	0.080	50	.200*	0.990	50	0.951
	G. g. diehli	0.171	10	.200*	0.959	10	0.769
	G. g. gorilla	0.034	169	.200*	0.992	169	0.525
	P. t. verus	0.093	43	.200*	0.971	43	0.349
	P. t. ellioti	0.314	5	0.121	0.821	5	0.120
	P. t. troglodytes	0.044	108	.200*	0.988	108	0.424
	P. t. schweinfurthii	0.102	58	.200*	0.966	58	0.106
	P. paniscus	0.102	41	.200*	0.963	41	0.205
	H. sapiens	0.028	221	.200*	0.996	221	0.799

*. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

MODERN *HOMO SAPIENS* DFA OUTPUTS

Table 39. Modern *H. sapiens* group statistics

Group Statistics												
	Population	Mean	Std. Deviation	Population	Mean	Std. Deviation	Population	Mean	Std. Deviation	Population	Mean	Std. Deviation
Hsap_LnCentroid	KhoeSan (n=16)	3.257774	0.0567191	Australian Aboriginal (n=27)	3.324312	0.0661014	South Indian (n=10)	3.210188	0.0397945	Mesopotamian/ Turkish (n=9)	3.251444	0.0219733
BuccGrooveAngle		3.066638	0.0697436		3.005851	0.1339912		3.061268	0.0499380		3.028915	0.0606512
HypcnldAngle		1.980114	0.0388033		2.007681	0.0388473		2.049604	0.0337185		2.066147	0.0147141
MesialAngle		1.516573	0.0434835		1.519869	0.0453135		1.449409	0.0547954		1.462894	0.0306069
DistalAngle		1.636734	0.0996103		1.622908	0.0555009		1.622070	0.0483284		1.644947	0.0447957
BLGrooveAngle		1.617486	0.0881933		1.601212	0.0482238		1.630999	0.0295294		1.629066	0.0301407
MesDistAngleRatio		0.995163	0.0446637		1.000026	0.0341918		1.043944	0.0431334		1.021027	0.0272569
MD		11.671260	0.6947228		12.424206	0.7863050		10.896512	0.4719917		11.261899	0.3671931
BL		10.369829	0.6411474		10.922470	0.8001303		9.824308	0.3142911		10.250354	0.1945066
MesialCusps		9.976060	0.5804540		10.584593	0.6761061		9.666965	0.3314625		10.143734	0.2233329
DistalCusps		10.202869	0.6454123		10.820544	0.8013003		9.574466	0.3955349		9.981116	0.2049042
BLGrooveBreadth		10.127903	0.6354697		10.575458	0.7754590		9.549565	0.3563560		9.999582	0.1570341
HypcnldBreadth		1.266113	0.3064639		1.078415	0.3606166		0.604190	0.2273135		0.405233	0.1840688
BuccGrooveMesialSide		1.682047	0.2870471		1.914365	0.3221735		2.259274	0.2661233		2.237913	0.3619293
BuccGrooveDistalSide		1.688310	0.4146685		1.903029	0.4412256		1.640198	0.3423391		1.715851	0.2472947
MDBLRatio		1.126690	0.0486788		1.139118	0.0447783		1.109069	0.0294737		1.098800	0.0333920
MDBuccGrRatio		1.153884	0.0547230		1.176734	0.0527116		1.141093	0.0272699		1.126581	0.0434014
MesDistCuspRatio		0.978311	0.0243024		0.979164	0.0239442		1.010062	0.0198607		1.016447	0.0203238
HypcnldRatio		0.217099	0.0492730		0.174309	0.0581267		0.112186	0.0444611		0.071443	0.0300801
Hsap_LnCentroid	Babinga (n=7)	3.270663	0.0448359	Polynesian (n=11)	3.277837	0.0530839	South Asian (n=5)	3.195595	0.0261293	W. European (n=32)	3.213090	0.0597928
BuccGrooveAngle		3.055037	0.0505579		3.048966	0.0619386		3.017178	0.0485251		3.040635	0.0732805
HypcnldAngle		1.993195	0.0427060		2.028918	0.0400805		2.048403	0.0187892		2.050373	0.0290318
MesialAngle		1.469685	0.0425794		1.519787	0.0441988		1.498932	0.0596694		1.481902	0.0457545
DistalAngle		1.658142	0.0714660		1.635042	0.0683146		1.628029	0.0482905		1.702529	0.0715100
BLGrooveAngle		1.646323	0.0570471		1.610324	0.0478679		1.606116	0.0347728		1.613477	0.0462094
MesDistAngleRatio		1.009030	0.0221959		0.992950	0.0364004		1.009833	0.0511361		0.975868	0.0336062
MD		11.772587	0.6966482		11.813650	0.7212797		10.751404	0.3064414		10.933434	0.6234945
BL		10.337734	0.4045823		10.448921	0.5426709		9.690854	0.3316808		9.913795	0.5855509
MesialCusps		10.222026	0.4546240		10.125158	0.4764555		9.625918	0.3219584		9.775698	0.5589084
DistalCusps		10.223998	0.3169641		10.303206	0.5925217		9.423179	0.3027450		9.632027	0.6456129
BLGrooveBreadth		10.128275	0.3573220		10.211888	0.4933000		9.366143	0.3556875		9.676585	0.6039758
HypcnldBreadth		1.169838	0.3484242		0.817193	0.4344601		0.610651	0.2559145		0.580546	0.2465254
BuccGrooveMesialSide		2.078952	0.4428704		1.601003	0.5212336		2.069796	0.3864059		2.173723	0.3227730
BuccGrooveDistalSide		1.591541	0.3298401		2.034896	0.5689782		1.464086	0.1624494		1.193378	0.4040106
MDBLRatio		1.138713	0.0473112		1.130567	0.0364068		1.109763	0.0216557		1.103545	0.0348086
MDBuccGrRatio		1.161745	0.0363497		1.156663	0.0385952		1.148408	0.0255962		1.130934	0.0385910
MesDistCuspRatio		0.999572	0.0211314		0.983683	0.0317364		1.021937	0.0334281		1.015970	0.0287156
HypcnldRatio		0.197163	0.0515180		0.137310	0.0686488		0.113588	0.0454805		0.105577	0.0425571
Hsap_LnCentroid	SA Bantu (n=23)	3.252708	0.0580008	New Guinean (n=19)	3.280187	0.0727552	Balkan (n=18)	3.215080	0.0571513	Amerindian (n=18)	3.271005	0.0407399
BuccGrooveAngle		3.012052	0.1114748		3.010843	0.0747344		3.067274	0.0793972		3.032065	0.0710732
HypcnldAngle		2.024291	0.0364819		2.038545	0.0301637		2.039307	0.0278831		2.007064	0.0310813
MesialAngle		1.492484	0.0465622		1.495658	0.0475802		1.474317	0.0483464		1.478056	0.0488016
DistalAngle		1.631214	0.0704767		1.633930	0.0867691		1.636946	0.0473289		1.702799	0.0522691
BLGrooveAngle		1.618748	0.0480609		1.625205	0.0499982		1.602237	0.0632775		1.623211	0.0379233
MesDistAngleRatio		1.012316	0.0412490		1.009418	0.0489728		1.018647	0.0162302		0.977214	0.0218208
MD		11.561682	0.7474687		11.704763	0.9610400		10.952290	0.6729274		11.688463	0.4043895
BL		10.126315	0.5817005		10.560958	0.7645110		9.947021	0.5407840		10.427852	0.5109474
MesialCusps		9.985430	0.6404906		10.402556	0.6997372		9.797800	0.5206482		10.220315	0.5313966
DistalCusps		9.948351	0.5643555		10.414726	0.7615858		9.610552	0.6158484		10.313736	0.5014390
BLGrooveBreadth		9.854688	0.5760096		10.286656	0.7701085		9.595144	0.5767399		10.191428	0.4886731
HypcnldBreadth		0.867164	0.3002047		0.699532	0.2643100		0.706892	0.2344555		1.040800	0.2673098
BuccGrooveMesialSide		2.236101	0.3695225		2.015805	0.2946894		2.359127	0.3348868		2.073326	0.2894831
BuccGrooveDistalSide		1.525743	0.3867917		1.817219	0.4308049		1.316786	0.3652785		1.324270	0.3541052
MDBLRatio		1.142122	0.0430238		1.108209	0.0424293		1.101118	0.0335322		1.122085	0.0352480
MDBuccGrRatio		1.173993	0.0526474		1.138315	0.0531816		1.142232	0.0464288		1.148028	0.0353267
MesDistCuspRatio		1.003593	0.0247698		0.999528	0.0255124		1.020294	0.0213460		0.991121	0.0282543
HypcnldRatio		0.149884	0.0488947		0.118089	0.0415288		0.128142	0.0376911		0.179196	0.0437997
Hsap_LnCentroid	Teita (n=8)	3.241629	0.0594693	East Asian (n=16	3.219876	0.0531673	Semitic (n=11)	3.178814	0.0498574	Inuit (n=11)	3.250405	0.0656599
BuccGrooveAngle		3.068722	0.0520542		3.002382	0.0929348		3.044371	0.0609536		3.075120	0.0498003
HypcnldAngle		2.041638	0.0279122		2.001411	0.0330536		2.025910	0.0201129		2.013924	0.0233635
MesialAngle		1.499835	0.0210617		1.515802	0.0399600		1.460302	0.0636430		1.436435	0.0684545
DistalAngle		1.658963	0.0802780		1.638298	0.0734585		1.615936	0.0351918		1.700425	0.0803611
BLGrooveAngle		1.622039	0.0330141		1.592896	0.0475073		1.622041	0.0450932		1.643789	0.0787733
MesDistAngleRatio		0.991286	0.0405294		0.993596	0.0347751		1.040500	0.0337714		1.003223	0.0173385
MD		11.322661	0.7048697		10.972270	0.6212249		10.792571	0.6332126		11.365012	0.9018064
BL		10.025261	0.6357949		10.094633	0.5966366		9.438562	0.3791730		10.344856	0.6615331
MesialCusps		9.926159	0.6118864		9.733370	0.5149932		9.270280	0.4432398		10.072877	0.6365007
DistalCusps		9.854472	0.5744459		9.998767	0.6061685		9.119435	0.4996109		10.298346	0.7182822
BLGrooveBreadth		9.853288	0.6228912		9.716004	0.5369536		9.088477	0.4091485		10.200578	0.6810369
HypcnldBreadth		0.735391	0.3030308		1.025936	0.3346193		0.780198	0.1590917		0.966455	0.2969189
BuccGrooveMesialSide		2.029850	0.2058399		1.755416	0.2818188		2.363338	0.4054018		2.015397	0.2819304
BuccGrooveDistalSide		1.463162	0.4545504		1.588370	0.4510856		1.404817	0.3902723		1.478819	0.2639269
MDBLRatio		1.129849	0.0320003		1.087701	0.0397037		1.143109	0.0385095		1.098165	0.0371690
MDBuccGrRatio		1.149400	0.0248487		1.129882	0.0414309		1.187577	0.0467374		1.113867	0.0375702
MesDistCuspRatio		1.007310	0.0214295		0.974052	0.0229634		1.017376	0.0333215		0.978938	0.0324544
HypcnldRatio		0.130150	0.0511109		0.186167	0.0551872		0.144231	0.0246047		0.170932	0.0462321

Table 40. Modern *H. sapiens* - DFA - Eigenvalues - Significance

Eigenvalues					Wilks' Lambda				
Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1	1.295[a]	33.8	33.8	0.751	1 through 15	0.050	667.415	270	0.000
2	.638[a]	16.6	50.4	0.624	2 through 15	0.115	482.126	238	0.000
3	.509[a]	13.3	63.7	0.581	3 through 15	0.189	372.081	208	0.000
4	.343[a]	8.9	72.6	0.505	4 through 15	0.284	280.394	180	0.000
5	.296[a]	7.7	80.3	0.478	5 through 15	0.382	214.668	154	0.001
6	.232[a]	6.1	86.4	0.434	6 through 15	0.495	156.897	130	0.054
7	.181[a]	4.7	91.1	0.391	7 through 15	0.610	110.284	108	0.421
8	.103[a]	2.7	93.8	0.306	8 through 15	0.720	73.188	88	0.872
9	.094[a]	2.5	96.3	0.293	9 through 15	0.795	51.230	70	0.955
10	.060[a]	1.6	97.8	0.238	10 through 15	0.869	31.207	54	0.995
11	.035[a]	0.9	98.8	0.184	11 through 15	0.922	18.228	40	0.999
12	.027[a]	0.7	99.5	0.162	12 through 15	0.954	10.521	28	0.999
13	.010[a]	0.3	99.7	0.099	13 through 15	0.980	4.587	18	0.999
14	.006[a]	0.1	99.9	0.075	14 through 15	0.989	2.379	10	0.993
15	.005[a]	0.1	100.0	0.071	15	0.995	1.120	4	0.891

a. First 15 canonical discriminant functions were used in the analysis.

Table 41. Modern *H. sapiens* - DFA - Canonical Discriminant Function Coefficients

Standardized Canonical Discriminant Function Coefficients															
	Function														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Hsap_LnCentroid	4.376	0.157	1.424	1.739	0.915	-2.868	-4.453	-6.338	-3.743	2.112	3.012	0.399	3.444	4.648	0.399
BuccGrooveAngle	0.061	0.263	-0.129	0.016	0.151	-0.025	0.174	-0.318	0.231	-0.189	0.148	0.060	0.321	-0.404	0.742
HypcnldAngle	-0.631	0.514	0.194	0.516	0.323	-0.109	-0.053	0.260	-0.416	-0.610	-0.122	0.918	-0.009	0.082	-0.600
MesialAngle	0.027	1.015	1.527	5.497	1.490	7.281	3.802	3.272	0.820	3.531	3.003	5.604	8.186	-0.463	-1.087
DistalAngle	1.669	0.562	1.378	8.041	2.254	8.911	5.843	4.137	1.149	5.205	3.949	7.476	12.900	-1.184	-2.725
BLGrooveAngle	-1.025	0.926	0.459	-0.368	0.088	0.833	0.203	0.255	0.014	0.165	0.210	0.053	-0.398	0.515	0.675
MesDistAngleRatio	0.917	1.453	2.169	6.285	1.765	8.360	5.611	3.231	1.750	3.206	5.299	5.776	10.347	-0.068	-3.295
MD	-2.033	2.171	-0.300	3.210	-6.552	-2.508	5.004	-2.041	0.093	-1.921	-0.525	15.531	-3.337	-10.391	-7.760
BL	-1.696	-0.006	-0.630	-1.434	4.859	2.603	-2.295	5.326	2.631	2.857	3.074	-17.249	1.424	5.521	5.171
MesialCusps	-3.372	1.323	-0.038	-1.640	3.423	15.075	5.707	-10.088	1.341	4.064	-0.188	-5.324	-5.491	-7.942	-6.480
DistalCusps	3.305	-3.660	0.494	-3.588	-5.852	-11.984	-5.305	13.245	0.909	-9.789	-1.852	5.400	6.160	6.902	8.290
BLGrooveBreadth	-0.676	-0.620	-0.475	0.615	2.408	-1.604	1.447	1.502	-1.521	0.987	-1.319	1.388	-2.068	0.775	0.006
HypcnldBreadth	1.523	0.117	2.940	2.771	2.778	1.792	0.358	-5.507	7.050	1.788	-4.980	1.316	-0.444	5.620	-0.553
BuccGrooveMesialSide	-0.410	0.298	-0.608	-0.300	-0.020	-0.382	-0.516	0.833	-0.705	1.785	-1.797	1.272	0.160	-0.611	1.494
BuccGrooveDistalSide	-0.407	-0.339	-0.832	0.746	-0.444	-0.923	-0.124	0.529	-1.047	1.625	-2.769	1.021	0.814	-1.145	1.317
MDBLRatio	-0.401	-1.037	0.372	-2.388	3.814	1.850	-1.695	3.566	0.378	-0.166	0.510	-9.575	0.897	4.012	3.795
MesDistCuspRatio	1.916	-1.048	0.435	0.050	-1.827	-5.951	-2.336	4.711	0.155	-3.465	-0.448	1.948	2.833	2.928	2.833
HypcnldRatio	-2.605	0.621	-3.240	-2.021	-2.119	-2.035	-0.801	4.988	-7.197	-1.690	3.779	-0.028	0.903	-5.228	0.300

Table 42. Great Britain Time Series Analysis - PCA Eigenvalues – Great Britain

		eigenvalue	percentage of total variance explained		cumulative variance explained	
PC 1		2879781571	51	2.36E+12	51	2.36E+12
PC 2		102593453	18	2.53E+12	69	4.89E+12
PC 3		592657921	10	5.44E+12	80	3.38E+10
PC 4		436115037	7	7.59E+13	87	7.93E+12
PC 5		190237403	3	3.85E+13	91	1.78E+12
PC 6		135397726	2	4.09E+13	93	5.87E+11
PC 7		106652333	1	8.98E+13	95	4.84E+12
PC 8		71423522	1	2.71E+13	96	7.55E+12
PC 9		42460219	0	7.55E+14	97	5.1E+12
PC 10		36422622	0	6.48E+14	98	1.58E+12
PC 11		2451406	0	4.36E+14	98	5.95E+10
PC 12		18971018	0	3.38E+14	98	9.32E+12
PC 13		14189066	0	2.52E+14	99	1.84E+12
PC 14		10191697	0	1.81E+14	99	3.66E+12
PC 15		8055479	0	1.43E+14	99	5.09E+11
PC 16		5474399	9	7.40E+11	99	6.07E+12
PC 17		4313982	0	7.68E+13	99	6.83E+11
PC 18		3904548	6	9.47E+11	99	7.53E+12
PC 19		2834353	5	4.28E+10	99	8.03E+12
PC 20		2447281	4	3.54E+11	99	8.47E+12
PC 21		2348444	4	1.78E+11	99	8.89E+12
PC 22		1767835	3	1.45E+11	99	9.2E+12
PC 23		1434312	2	5.52E+11	99	9.45E+12
PC 24		1153978	2	5.31E+10	99	9.66E+12
PC 25		923943	1	6.44E+11	99	9.82E+12
PC 26		601262	0	1.07E+13	99	9.93E+12
PC 27		385167	6	8.53E+10	100	53375

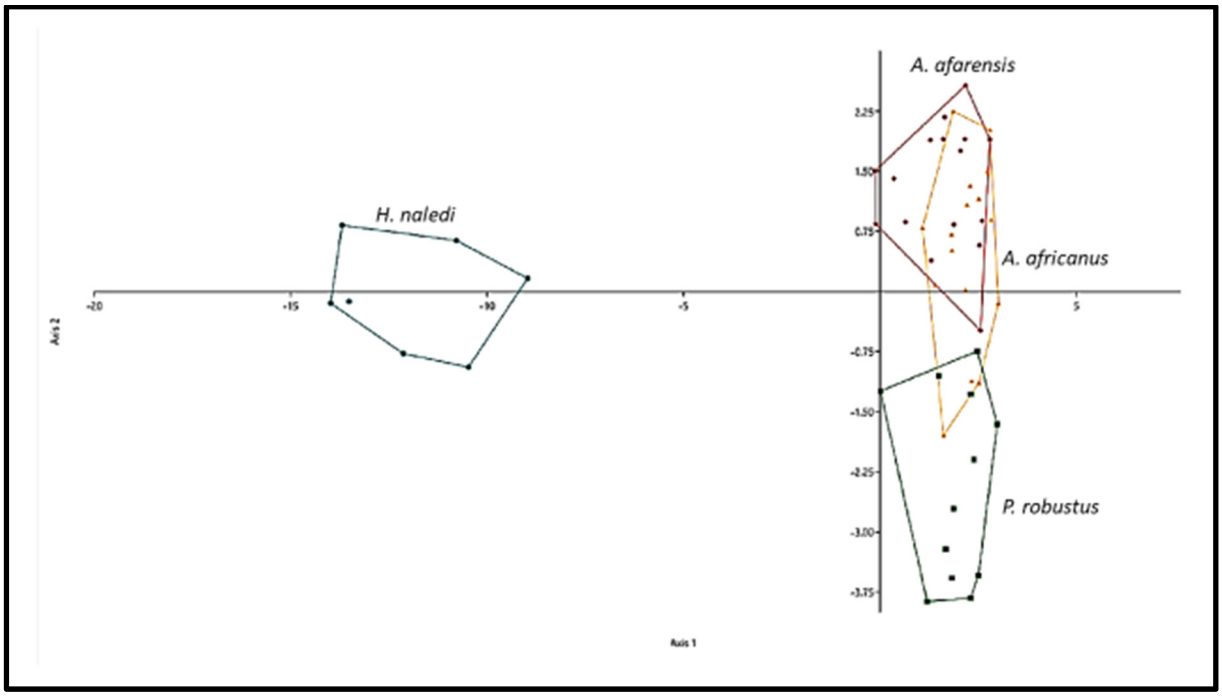
(Full Morphologika results available on request)

DFA – FOSSIL HOMININ SPECIES

Table 43. Fossil hominins - DFA - Group statistics

Group Statistics									
	Species	Mean	Std. Deviation	Species	Mean	Std. Deviation	Species	Mean	Std. Deviation
LnCentroid	A. afarensis (n=16)	3.5068	0.06870	P. boisei (n=2	3.6296	0.08617	H. habilis (n=2)	3.5364	0.05469
A_Bucc_Gr		2.9809	0.07725		3.0373	0.07243		2.9212	0.25726
A_Hypcnld		2.0223	0.03446		1.9411	0.02074		1.9731	0.07488
A_Mesial		1.5261	0.04367		1.5441	0.01818		1.4873	0.03219
A_Distal		1.6593	0.05823		1.6099	0.01790		1.6794	0.09287
A_BL_Grv		1.6062	0.03633		1.5632	0.02459		1.7013	0.12030
R_A_Mes_Dis		0.9744	0.03469		0.9923	0.00026		0.9860	0.03536
L_MD		14.8219	0.93077		16.9870	1.51040		15.8556	0.15752
L_BL		13.3178	1.00980		15.0130	1.22331		13.4955	1.41916
L_Mesial		13.1827	0.99251		14.3661	1.28956		13.1392	1.58466
L_Distal		12.8063	0.94032		14.8142	1.09236		12.8824	1.16582
L_BL_Grv		12.6840	0.93170		14.3671	1.31790		12.8953	1.47625
L_Hypcld		1.3643	0.26363		2.2394	0.49719		2.0174	0.58103
L_BcGrv_Mesial		2.9004	0.53717		2.8777	0.44609		2.8137	0.30487
L_BcGrv_Distal		1.4393	0.35089		2.0343	0.08256		1.7810	0.07302
R_MD_BL		1.1147	0.04314		1.1311	0.00844		1.1820	0.13597
R_MD_BLGrv		1.1704	0.04993		1.1825	0.00334		1.2384	0.15398
R_Mes_Dis		1.0299	0.03843		0.9692	0.01558		1.0185	0.03083
R_Hypcld		0.1879	0.03676		0.2616	0.03317		0.2559	0.07016
LnCentroid	A. africanus (n=16	3.5655	0.07959	A. sediba (n=2)	3.4537	0.02226	Early Homo (n=3)	3.5120	0.05908
A_Bucc_Gr		2.9921	0.12074		2.8219	0.00271		2.9960	0.10736
A_Hypcnld		2.0058	0.02680		2.0011	0.00572		1.9980	0.05134
A_Mesial		1.4940	0.03985		1.5182	0.00021		1.4619	0.02367
A_Distal		1.6641	0.04236		1.7868	0.03964		1.7685	0.03771
A_BL_Grv		1.6314	0.04284		1.7090	0.02092		1.7335	0.04499
R_A_Mes_Dis		0.9905	0.02857		0.9088	0.02004		0.9499	0.01343
L_MD		15.8575	1.29500		14.4610	0.55438		15.2960	1.25201
L_BL		13.9881	1.17061		12.2595	0.23829		12.9510	0.38552
L_Mesial		13.8222	1.17129		12.1751	0.23298		12.5785	0.41029
L_Distal		13.6031	1.10696		12.0102	0.21729		12.9162	0.43061
L_BL_Grv		13.5106	1.12407		11.9815	0.36857		12.5684	0.60994
L_Hypcld		1.4660	0.33182		1.4346	0.07801		1.7117	0.39060
L_BcGrv_Mesial		3.2233	0.45669		2.1585	0.32624		2.2890	0.46357
L_BcGrv_Distal		1.6923	0.37358		1.3352	0.36201		1.6829	0.45814
R_MD_BL		1.1345	0.04234		1.1794	0.02230		1.1799	0.06092
R_MD_BLGrv		1.1745	0.04389		1.2068	0.00915		1.2157	0.03962
R_Mes_Dis		1.0163	0.02697		1.0141	0.03774		0.9739	0.01071
R_Hypcld		0.1849	0.03613		0.1992	0.00360		0.2254	0.04970
LnCentroid	P. robustus (n=12)	3.5977	0.07380	H. naledi (n=7)	3.3668	0.03683	H. ergaster (n=3)	3.4219	0.06301
A_Bucc_Gr		3.0287	0.07836		2.6890	0.09959		3.0264	0.08388
A_Hypcnld		1.9666	0.03356		1.9528	0.03110		1.9816	0.10759
A_Mesial		1.5089	0.05027		1.5047	0.02587		1.4678	0.02947
A_Distal		1.7057	0.07039		1.7416	0.05823		1.6920	0.05213
A_BL_Grv		1.6295	0.06178		1.6498	0.03716		1.6897	0.03864
R_A_Mes_Dis		0.9579	0.02913		0.9406	0.02987		0.9897	0.02659
L_MD		16.6657	1.22093		13.6670	0.48621		14.1273	0.84967
L_BL		14.4129	1.28916		10.8993	0.37821		12.0614	0.74704
L_Mesial		13.8590	1.03010		10.4590	0.51417		11.7229	0.67365
L_Distal		14.2391	1.31227		10.9397	0.42367		11.6684	0.76388
L_BL_Grv		13.9225	1.09300		10.1758	0.32044		11.5397	0.71775
L_Hypcld		2.1747	0.53720		1.7213	0.31828		1.6123	0.99473
L_BcGrv_Mesial		2.4411	0.46590		1.9261	0.31341		2.4382	0.48867
L_BcGrv_Distal		1.8439	0.51856		1.7395	0.18325		1.6325	0.57624
R_MD_BL		1.1580	0.03256		1.2541	0.02084		1.1714	0.00329
R_MD_BLGrv		1.1979	0.03129		1.3432	0.02580		1.2245	0.02791
R_Mes_Dis		0.9749	0.03257		0.9560	0.02684		1.0052	0.02504
R_Hypcld		0.2624	0.04954		0.2524	0.04247		0.2348	0.15437

Table 44. DFA – 4 Fossil hominin species – Plot in PAST®



Axis 1: Eigenvalue – 24.7; 88.7% of variance; Axis 2: Eigenvalue 2.2; 7.7% of variance.

DFA – Fossils – Output in PAST ®

Table 45. Fossil hominins - DFA output - Left – DFA including 4 fossil hominin species; Right – including all species

	Axis 1	Axis 2	Axis 3
LnCentroid	0.014	-0.021	0.014
A_Bucc_Gr	0.022	-0.012	-0.005
A_Hypcnld	0.003	0.015	-0.003
A_Mesial	0.000	0.002	-0.013
A_Distal	-0.005	-0.013	-0.001
A_BL_Grv	-0.002	-0.005	0.009
R_A_Mes_Dis	0.003	0.006	0.008
L_MD	0.151	-0.439	0.250
L_BL	0.216	-0.250	0.143
L_Mesial	0.229	-0.132	0.167
L_Distal	0.187	-0.338	0.174
L_BL_Grv	0.231	-0.278	0.196
L_Hypcld	-0.007	-0.225	-0.031
L_BcGrv_Mesial	0.071	0.161	0.172
L_BcGrv_Distal	-0.006	-0.096	0.076
R_MD_BL	-0.009	-0.011	0.007
R_MD_BLGrv	-0.012	-0.008	0.002
R_Mes_Dis	0.004	0.015	-0.002
R_Hypcld	-0.003	-0.022	-0.008

	Axis 1	Axis 2	Axis 3
LnCentroid	-0.016	-0.022	-0.014
A_Bucc_Gr	-0.026	-0.016	-0.010
A_Hypcnld	-0.003	0.015	-0.002
A_Mesial	0.000	0.002	-0.009
A_Distal	0.005	-0.005	0.025
A_BL_Grv	0.002	0.000	0.030
R_A_Mes_Dis	-0.003	0.002	-0.009
L_MD	-0.183	-0.447	-0.115
L_BL	-0.247	-0.262	-0.268
L_Mesial	-0.258	-0.144	-0.281
L_Distal	-0.218	-0.340	-0.241
L_BL_Grv	-0.265	-0.274	-0.220
L_Hypcld	0.002	-0.212	0.044
L_BcGrv_Mesial	-0.076	0.105	-0.169
L_BcGrv_Distal	0.003	-0.112	-0.013
R_MD_BL	0.009	-0.011	0.014
R_MD_BLGrv	0.013	-0.010	0.011
R_Mes_Dis	-0.004	0.014	-0.003
R_Hypcld	0.003	-0.020	0.008

A_ = Angle; L_ = Length; R_ = Ratio. See **Table 7**

Table 46. Outputs DFA – 4 fossil hominin species (left) – All fossil hominin species (right) – Casewise classifications using PAST®

Point	Given group	Classification	Jackknifed
LH-4	A afarensis	A afarensis	A afarensis
LH-23	A afarensis	A afarensis	A africanus
AL-207-13	A afarensis	A afarensis	A afarensis
AL-333-59	A afarensis	A africanus	A africanus
AL-333-W27	A afarensis	A afarensis	A afarensis
AL-241-14	A afarensis	A afarensis	A afarensis
AL-333-W57	A afarensis	A africanus	A africanus
AL-333-W60	A afarensis	A afarensis	A africanus
AL-145-35	A afarensis	A afarensis	P robustus
AL-277-1	A afarensis	A afarensis	A africanus
AL-288-1	A afarensis	A afarensis	A afarensis
AL-400-1A	A afarensis	A afarensis	A afarensis
AL-128-23	A afarensis	A afarensis	A afarensis
AL-188-1	A afarensis	A afarensis	A afarensis
AL-266-1	A afarensis	A afarensis	A afarensis
AL-333-W1	A afarensis	A afarensis	A africanus
Stw-404	A africanus	A africanus	A afarensis
Stw-560e	A africanus	A africanus	A afarensis
Stw-519	A africanus	A africanus	A afarensis
Stw-412	A africanus	A africanus	A afarensis
Stw-109	A africanus	A africanus	A africanus
Stw-327	A africanus	A africanus	A africanus
Stw-284	A africanus	A africanus	A africanus
Stw-540	A africanus	A afarensis	A afarensis
Stw-308	A africanus	P robustus	P robustus
Stw-555	A africanus	A africanus	A africanus
Stw-234	A africanus	A africanus	A africanus
Stw-498	A africanus	A africanus	A africanus
MLD-18	A africanus	A afarensis	A afarensis
MLD-2	A africanus	A africanus	A africanus
Sts-52b	A africanus	A africanus	A africanus
MLD-24	A africanus	A africanus	A afarensis
TM-1517	P robustus	A africanus	A africanus
SK-37	P robustus	P robustus	A africanus
SK-6	P robustus	P robustus	P robustus
SK-23	P robustus	P robustus	P robustus
SK-25	P robustus	P robustus	P robustus
SK-55	P robustus	P robustus	P robustus
SK-1587a	P robustus	P robustus	A afarensis
SK-1	P robustus	P robustus	A africanus
SK-5	P robustus	P robustus	P robustus
SK-843	P robustus	P robustus	A africanus
SKW-5	P robustus	P robustus	A afarensis
GDA-2	P robustus	P robustus	P robustus
UW-101-1261	H naledi	H naledi	H naledi
UW-101-001	H naledi	H naledi	H naledi
UW-101-377	H naledi	H naledi	H naledi
UW-101-1142	H naledi	H naledi	H naledi
UW-101-507	H naledi	H naledi	H naledi
UW-101-145	H naledi	H naledi	H naledi
UW-101-789	H naledi	H naledi	H naledi

	Given group	Classification	Jackknifed
LH-4	A afarensis	A afarensis	Early Homo
LH-23	A afarensis	A afarensis	A africanus
AL-207-13	A afarensis	A afarensis	H ergaster
AL-333-59	A afarensis	A africanus	A africanus
AL-333-W27	A afarensis	A afarensis	A afarensis
AL-241-14	A afarensis	A afarensis	A afarensis
AL-333-W57	A afarensis	H ergaster	H ergaster
AL-333-W60	A afarensis	A afarensis	A africanus
AL-145-35	A afarensis	A afarensis	P robustus
AL-277-1	A afarensis	A afarensis	A africanus
AL-288-1	A afarensis	A afarensis	H ergaster
AL-400-1A	A afarensis	A afarensis	A afarensis
AL-128-23	A afarensis	A afarensis	A afarensis
AL-188-1	A afarensis	A afarensis	A afarensis
AL-266-1	A afarensis	A afarensis	A afarensis
AL-333-W1	A afarensis	A afarensis	A afarensis
Stw-404	A africanus	A africanus	A afarensis
Stw-560e	A africanus	A africanus	H ergaster
Stw-519	A africanus	A africanus	A afarensis
Stw-412	A africanus	A africanus	A afarensis
Stw-109	A africanus	A africanus	H habilis
Stw-327	A africanus	A africanus	A africanus
Stw-284	A africanus	A africanus	A africanus
Stw-540	A africanus	A afarensis	A afarensis
Stw-308	A africanus	A africanus	P robustus
Stw-555	A africanus	A africanus	P boisei
Stw-234	A africanus	A africanus	A africanus
Stw-498	A africanus	A africanus	A africanus
MLD-18	A africanus	A afarensis	A afarensis
MLD-2	A africanus	A africanus	A africanus
Sts-52b	A africanus	A africanus	A africanus
MLD-24	A africanus	A africanus	A afarensis
TM-1517	P robustus	A africanus	A africanus
SK-37	P robustus	P robustus	P boisei
SK-6	P robustus	P robustus	P robustus
SK-23	P robustus	P robustus	Early Homo
SK-25	P robustus	P robustus	P robustus
SK-55	P robustus	P robustus	P robustus
SK-1587a	P robustus	P robustus	H ergaster
SK-1	P robustus	P robustus	A africanus
SK-5	P robustus	P boisei	P boisei
SK-843	P robustus	P robustus	A africanus
SKW-5	P robustus	P robustus	A afarensis
GDA-2	P robustus	P robustus	P boisei
Peninj-1	P boisei	P boisei	P robustus
KNM-ER-15930	P boisei	P boisei	P robustus
MH-1	A sediba	A sediba	A africanus
MH-2	A sediba	A sediba	Early Homo
UW-101-1261	H naledi	H naledi	H naledi
UW-101-001	H naledi	H naledi	H naledi
UW-101-377	H naledi	H naledi	H naledi
UW-101-1142	H naledi	H naledi	H naledi
UW-101-507	H naledi	H naledi	H naledi
UW-101-145	H naledi	H naledi	H naledi
UW-101-789	H naledi	H naledi	H naledi
OH-7	H habilis	H habilis	H rudolfensis
OH-16	H habilis	A afarensis	A afarensis
KNM-ER-1802	H rudolfensis	H rudolfensis	P robustus
KNM-ER-60000	Early Homo	Early Homo	A sediba
SK-15	Early Homo	Early Homo	A afarensis
KNM-ER-992	H ergaster	H ergaster	H habilis
KNM-ER-806b	H ergaster	H ergaster	A afarensis
OH-22	H ergaster	H ergaster	A afarensis

Outputs PCA – Fossils only

Table 47. Eigenvalues - PCA - Fossils only

E 1 = eigenvalues, E 2 = Proportion, E 3 = Cumulative

	E 1	E 2	E 3
Prin	1 9,83E-03	7,34E-01	7,34E-01
Prin	2 1,24E-03	9,29E-02	8,27E-01
Prin	3 9,10E-04	6,80E-02	8,95E-01
Prin	4 4,04E-04	3,02E-02	9,25E-01
Prin	5 3,28E-04	2,45E-02	9,50E-01
Prin	6 1,59E-04	1,19E-02	9,62E-01
Prin	7 1,37E-04	1,03E-02	9,72E-01
Prin	8 9,35E-05	6,99E-03	9,79E-01
Prin	9 5,90E-05	4,40E-03	9,83E-01
Prin	10 4,88E-05	3,64E-03	9,87E-01
Prin	11 3,68E-05	2,75E-03	9,90E-01
Prin	12 3,25E-05	2,43E-03	9,92E-01
Prin	13 2,41E-05	1,80E-03	9,94E-01
Prin	14 2,22E-05	1,66E-03	9,96E-01
Prin	15 1,29E-05	9,66E-04	9,97E-01
Prin	16 8,63E-06	6,45E-04	9,97E-01
Prin	17 5,45E-06	4,07E-04	9,98E-01
Prin	18 4,15E-06	3,10E-04	9,98E-01
Prin	19 3,61E-06	2,69E-04	9,98E-01
Prin	20 3,25E-06	2,43E-04	9,99E-01
Prin	21 2,73E-06	2,04E-04	9,99E-01
Prin	22 2,48E-06	1,85E-04	9,99E-01
Prin	23 2,01E-06	1,50E-04	9,99E-01
Prin	24 1,86E-06	1,39E-04	9,99E-01
Prin	25 1,20E-06	8,98E-05	9,99E-01
Prin	26 1,16E-06	8,69E-05	9,99E-01
Prin	27 1,04E-06	7,79E-05	9,99E-01
Prin	28 8,94E-07	6,68E-05	1,00E+00
Prin	29 8,73E-07	6,52E-05	1,00E+00
Prin	30 7,93E-07	5,92E-05	1,00E+00
Prin	31 7,28E-07	5,44E-05	1,00E+00
Prin	32 5,22E-07	3,90E-05	1,00E+00
Prin	33 4,56E-07	3,40E-05	1,00E+00
Prin	34 3,95E-07	2,95E-05	1,00E+00
Prin	35 3,60E-07	2,69E-05	1,00E+00
Prin	36 3,51E-07	2,62E-05	1,00E+00
Prin	37 2,93E-07	2,19E-05	1,00E+00
Prin	38 2,47E-07	1,85E-05	1,00E+00
Prin	39 2,46E-07	1,83E-05	1,00E+00
Prin	40 2,11E-07	1,58E-05	1,00E+00
Prin	41 1,91E-07	1,42E-05	1,00E+00
Prin	42 1,56E-07	1,16E-05	1,00E+00
Prin	43 1,42E-07	1,06E-05	1,00E+00
Prin	44 1,29E-07	9,64E-06	1,00E+00
Prin	45 9,73E-08	7,27E-06	1,00E+00
Prin	46 7,91E-08	5,91E-06	1,00E+00
Prin	47 6,27E-08	4,68E-06	1,00E+00
Prin	48 5,48E-08	4,09E-06	1,00E+00
Prin	49 4,26E-08	3,18E-06	1,00E+00
Prin	50 3,60E-08	2,69E-06	1,00E+00
Prin	51 2,45E-08	1,83E-06	1,00E+00
Prin	52 1,99E-08	1,49E-06	1,00E+00
Prin	53 1,41E-08	1,05E-06	1,00E+00
Prin	54 8,53E-09	6,37E-07	1,00E+00
Prin	55 3,24E-09	2,42E-07	1,00E+00
Prin	56 0,00E+00	0,00E+00	1,00E+00
Prin	57 -1,00E-12	-7,47E-11	1,00E+00

Table 48. Outputs PCA – Fossils only - Eigenvectors: First four PCs

Eigenvectors

	Prin 1	Prin 2	Prin 3	Prin 4
variable 1	1,81E-02	5,03E-02	-5,40E-02	-3,97E-02
variable 2	1,82E-03	1,64E-02	-5,68E-02	1,66E-01
variable 3	-3,44E-02	-1,03E-01	1,16E-01	1,39E-02
variable 4	-1,77E-02	-6,69E-02	1,18E-01	-1,96E-01
variable 5	2,63E-02	7,07E-02	-6,38E-02	-5,02E-02
variable 6	6,92E-03	3,73E-01	-7,14E-02	-3,89E-01
variable 7	-4,45E-02	2,64E-02	3,85E-01	-3,26E-02
variable 8	9,67E-03	2,74E-01	5,95E-02	2,06E-01
variable 9	2,77E-02	2,30E-01	-8,90E-02	-2,05E-01
variable 10	3,30E-02	7,06E-02	-1,78E-01	-7,55E-02
variable 11	2,35E-02	6,18E-03	-1,31E-01	5,33E-02
variable 12	-3,59E-02	-3,54E-02	2,03E-01	-1,42E-01
variable 13	-3,53E-02	1,36E-01	2,70E-01	-1,66E-01
variable 14	-2,72E-02	-2,08E-01	4,02E-02	1,71E-01
variable 15	2,37E-02	3,06E-01	1,50E-02	1,36E-01
variable 16	2,24E-02	1,15E-01	-6,71E-02	1,89E-01
variable 17	-1,92E-03	-1,40E-01	-2,11E-02	-1,60E-01
variable 18	1,69E-02	-3,26E-02	-9,37E-02	-2,23E-01
variable 19	1,56E-02	9,23E-02	-9,96E-02	-1,53E-01
variable 20	-1,89E-02	1,02E-01	1,23E-01	-1,65E-01
variable 21	-2,08E-02	7,55E-02	2,01E-01	1,18E-01
variable 22	1,63E-02	1,88E-01	-1,95E-02	3,44E-02
variable 23	2,42E-02	4,24E-02	-1,01E-01	-7,49E-02
variable 24	1,51E-02	-6,43E-02	-1,13E-01	1,80E-02
variable 25	-2,05E-02	-2,61E-02	1,15E-01	-3,04E-02
variable 26	-1,74E-02	-2,01E-01	4,78E-03	1,30E-01
variable 27	8,05E-03	5,96E-02	-4,31E-03	1,18E-01
variable 28	5,39E-03	-1,04E-01	-6,45E-02	-6,44E-02
variable 29	-1,63E-02	-5,69E-02	9,89E-02	-1,34E-01
variable 30	-1,45E-02	1,38E-03	3,25E-02	9,81E-02
variable 31	3,29E-02	1,02E-01	-1,90E-01	2,14E-01
variable 32	2,22E-02	6,32E-02	-1,19E-01	-5,41E-02
variable 33	-3,92E-02	-1,40E-01	1,85E-01	-2,32E-01
variable 34	-1,60E-02	-2,95E-02	5,69E-02	8,88E-02
variable 35	-9,66E-03	1,43E-01	3,49E-01	6,17E-03
variable 36	7,70E-03	-3,50E-01	-2,19E-01	-2,39E-01
variable 37	4,27E-02	6,14E-02	-1,71E-01	-5,63E-02
variable 38	-3,73E-02	-2,37E-01	1,39E-01	9,71E-02
variable 39	-1,60E-02	-6,58E-02	8,41E-02	8,95E-02
variable 40	-6,13E-04	9,48E-02	-9,68E-04	5,96E-02
variable 41	6,57E-03	1,38E-01	2,78E-02	1,12E-02
variable 42	-4,99E-03	-1,14E-01	9,91E-02	-1,50E-01
variable 43	2,86E-02	-6,23E-02	-1,57E-01	6,61E-02
variable 44	2,65E-02	1,72E-02	-1,50E-01	9,91E-02
variable 45	2,33E-02	1,58E-01	-8,41E-02	-9,65E-02
variable 46	1,63E-02	1,16E-01	-1,29E-03	-1,80E-01
variable 47	-2,89E-02	-6,45E-02	1,03E-01	-3,87E-02
variable 48	-1,62E-02	8,76E-02	1,99E-01	9,10E-02
variable 49	-2,98E-03	-8,06E-02	6,59E-02	-9,05E-02
variable 50	2,62E-02	-1,26E-01	-1,92E-01	-1,42E-01
variable 51	1,26E-03	-1,15E-02	-8,61E-03	-1,19E-01
variable 52	-1,57E-02	-8,94E-02	3,15E-02	8,70E-02
variable 53	6,78E-03	9,37E-02	-1,91E-02	4,93E-02
variable 54	1,96E-04	-2,47E-02	2,41E-02	-3,43E-02
variable 55	1,86E-02	-8,34E-03	-1,03E-01	7,55E-02
variable 56	1,31E-02	8,82E-02	-3,24E-02	-5,02E-02
variable 57	9,86E-01	-6,41E-02	1,38E-01	-2,52E-03

(Full results available on request: 75 pages)

Outputs PCA – Full samples of extant species + Fossils

Table 49. PCA output - All extant + Fossils - Eigenvalues

E 1 = eigenvalues, E 2 = Proportion, E 3 = Cumulative

	E 1	E 2	E 3
Prin 1	4,35E-02	8,92E-01	8,92E-01
Prin 2	2,00E-03	4,11E-02	9,33E-01
Prin 3	1,33E-03	2,72E-02	9,60E-01
Prin 4	5,59E-04	1,15E-02	9,71E-01
Prin 5	4,16E-04	8,53E-03	9,80E-01
Prin 6	2,28E-04	4,68E-03	9,85E-01
Prin 7	1,67E-04	3,42E-03	9,88E-01
Prin 8	1,13E-04	2,31E-03	9,90E-01
Prin 9	8,71E-05	1,79E-03	9,92E-01
Prin 10	7,79E-05	1,60E-03	9,94E-01
Prin 11	5,28E-05	1,08E-03	9,95E-01
Prin 12	4,24E-05	8,70E-04	9,96E-01
Prin 13	3,62E-05	7,43E-04	9,96E-01
Prin 14	2,97E-05	6,09E-04	9,97E-01
Prin 15	2,45E-05	5,02E-04	9,97E-01
Prin 16	1,76E-05	3,61E-04	9,98E-01
Prin 17	1,57E-05	3,23E-04	9,98E-01
Prin 18	1,26E-05	2,59E-04	9,98E-01
Prin 19	1,04E-05	2,13E-04	9,99E-01
Prin 20	7,17E-06	1,47E-04	9,99E-01
Prin 21	6,38E-06	1,31E-04	9,99E-01
Prin 22	5,56E-06	1,14E-04	9,99E-01
Prin 23	5,19E-06	1,07E-04	9,99E-01
Prin 24	4,39E-06	9,01E-05	9,99E-01
Prin 25	3,45E-06	7,07E-05	9,99E-01
Prin 26	3,20E-06	6,56E-05	9,99E-01
Prin 27	3,12E-06	6,41E-05	9,99E-01
Prin 28	2,68E-06	5,49E-05	9,99E-01
Prin 29	2,44E-06	5,01E-05	1,00E+00
Prin 30	2,11E-06	4,33E-05	1,00E+00
Prin 31	1,57E-06	3,21E-05	1,00E+00
Prin 32	1,35E-06	2,78E-05	1,00E+00
Prin 33	1,20E-06	2,47E-05	1,00E+00
Prin 34	1,14E-06	2,33E-05	1,00E+00
Prin 35	1,11E-06	2,27E-05	1,00E+00
Prin 36	1,05E-06	2,15E-05	1,00E+00
Prin 37	9,92E-07	2,04E-05	1,00E+00
Prin 38	9,76E-07	2,00E-05	1,00E+00
Prin 39	9,04E-07	1,85E-05	1,00E+00
Prin 40	8,62E-07	1,77E-05	1,00E+00
Prin 41	8,47E-07	1,74E-05	1,00E+00
Prin 42	8,24E-07	1,69E-05	1,00E+00
Prin 43	8,15E-07	1,67E-05	1,00E+00
Prin 44	7,70E-07	1,58E-05	1,00E+00
Prin 45	7,66E-07	1,57E-05	1,00E+00
Prin 46	7,30E-07	1,50E-05	1,00E+00
Prin 47	7,00E-07	1,44E-05	1,00E+00
Prin 48	6,74E-07	1,38E-05	1,00E+00
Prin 49	6,46E-07	1,32E-05	1,00E+00
Prin 50	6,33E-07	1,30E-05	1,00E+00
Prin 51	6,02E-07	1,23E-05	1,00E+00
Prin 52	5,60E-07	1,15E-05	1,00E+00
Prin 53	4,70E-07	9,65E-06	1,00E+00
Prin 54	2,16E-07	4,43E-06	1,00E+00
Prin 55	1,71E-07	3,51E-06	1,00E+00
Prin 56	0,00E+00	0,00E+00	1,00E+00
Prin 57	0,00E+00	0,00E+00	1,00E+00

Table 50. PCA Output - All extant species + Fossils. Eigenvectors - First four PCs

Eigenvectors

	Prin 1	Prin 2	Prin 3	Prin 4
variable 1	-2,54E-02	-8,51E-02	8,40E-02	-5,92E-02
variable 2	-2,37E-02	-6,00E-02	2,66E-02	1,31E-01
variable 3	5,50E-02	1,77E-01	-1,62E-01	6,09E-02
variable 4	5,26E-02	1,48E-01	-1,02E-01	-1,33E-01
variable 5	-3,80E-02	-1,24E-01	1,36E-01	-1,05E-01
variable 6	-1,82E-02	6,75E-02	9,25E-02	3,31E-01
variable 7	6,07E-02	1,87E-01	9,43E-03	-7,44E-02
variable 8	-3,96E-02	-2,96E-02	4,70E-01	5,75E-02
variable 9	1,77E-02	8,52E-02	9,00E-02	-2,55E-03
variable 10	-6,32E-02	-1,93E-01	1,19E-01	-2,33E-02
variable 11	-3,04E-02	-1,07E-01	3,36E-02	5,31E-02
variable 12	7,67E-02	2,26E-01	-9,98E-02	-1,08E-01
variable 13	7,56E-02	2,78E-01	4,07E-02	-5,92E-02
variable 14	-3,80E-03	6,13E-03	-1,77E-01	1,88E-01
variable 15	-4,45E-03	6,85E-02	3,67E-01	1,12E-01
variable 16	-1,89E-02	-3,25E-02	1,74E-01	6,97E-02
variable 17	-1,33E-02	-8,38E-02	-1,11E-01	-2,23E-01
variable 18	-3,49E-02	-1,45E-01	-1,99E-02	-1,97E-01
variable 19	-2,83E-02	-6,11E-02	8,00E-03	8,59E-02
variable 20	1,96E-02	9,93E-02	-4,39E-02	1,21E-01
variable 21	1,10E-02	6,08E-02	1,61E-01	-1,31E-02
variable 22	-1,06E-02	1,56E-02	2,25E-01	2,39E-02
variable 23	-8,41E-03	-4,27E-02	2,77E-02	-7,42E-02
variable 24	-2,79E-02	-1,12E-01	-2,92E-02	-2,30E-02
variable 25	4,19E-02	1,26E-01	-6,82E-02	-4,36E-02
variable 26	2,88E-03	-6,10E-03	-1,76E-01	8,00E-02
variable 27	2,24E-03	2,59E-02	1,03E-01	4,10E-02
variable 28	-1,39E-02	-8,28E-02	-8,18E-02	-1,18E-01
variable 29	3,70E-02	9,83E-02	-5,87E-02	-1,13E-01
variable 30	-2,29E-02	-4,35E-02	8,32E-03	1,05E-01
variable 31	-6,05E-02	-1,67E-01	1,08E-01	1,68E-01
variable 32	2,06E-03	-1,88E-02	3,70E-02	-5,72E-02
variable 33	5,42E-02	1,61E-01	-1,63E-01	-9,73E-03
variable 34	7,10E-03	8,28E-02	-3,14E-02	1,57E-01
variable 35	9,26E-02	2,87E-01	3,14E-01	-4,52E-01
variable 36	-5,97E-02	-2,58E-01	-2,64E-01	-1,41E-01
variable 37	-9,68E-02	-3,00E-01	1,44E-01	-2,00E-01
variable 38	3,32E-02	7,09E-02	-1,33E-01	-1,88E-02
variable 39	4,59E-03	2,06E-02	-4,04E-02	4,98E-02
variable 40	-8,59E-04	5,03E-02	1,21E-02	1,52E-01
variable 41	2,36E-02	1,25E-01	1,24E-01	7,91E-02
variable 42	2,58E-02	2,83E-02	-5,66E-02	-2,98E-01
variable 43	-3,85E-02	-1,29E-01	1,82E-02	3,90E-02
variable 44	-5,17E-02	-1,62E-01	9,94E-02	9,71E-03
variable 45	5,31E-04	-1,49E-02	3,95E-02	-6,15E-02
variable 46	-2,39E-02	-6,20E-02	3,88E-02	-1,01E-01
variable 47	3,08E-02	1,25E-01	-1,08E-01	1,50E-01
variable 48	5,33E-02	2,02E-01	1,30E-01	-7,32E-02
variable 49	2,26E-02	3,90E-02	2,21E-02	-2,43E-01
variable 50	-7,26E-02	-2,65E-01	-6,92E-02	-1,35E-01
variable 51	-2,11E-02	-7,02E-02	-1,55E-02	-4,39E-02
variable 52	1,22E-02	2,20E-02	-6,21E-02	4,48E-02
variable 53	8,57E-03	5,31E-02	6,46E-02	1,02E-01
variable 54	9,35E-03	5,93E-03	-2,54E-02	-8,84E-02
variable 55	-2,20E-02	-7,32E-02	1,24E-02	7,28E-02
variable 56	-1,63E-02	-4,44E-02	2,63E-02	-2,61E-03
variable 57	9,57E-01	-2,81E-01	4,95E-02	5,25E-02

(Full results available on request : 610 pages).