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# Does tooth size matter?: A dental measurement analysis on StW 252 from Sterkfontein, South Africa

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## Recommended Citation

Mayer, Caitlin, "Does tooth size matter?: A dental measurement analysis on StW 252 from Sterkfontein, South Africa." Thesis, Georgia State University, 2016.
doi: https://doi.org/10.57709/8684853

# DOES TOOTH SIZE MATTER?: A DENTAL MEASUREMENT ANALYSIS ON STW 252 FROM STERKFONTEIN, SOUTH AFRICA

by

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Under the Direction of Frank L'Engle Williams, Ph.D.

## ABSTRACT

Sterkfontein West Pit, dated to 1.7-1.9 Ma, has yielded a number of fossils that are difficult to classify, such as StW 252, which comprises cranial bone fragments, and a full set of robust maxillary anterior and posterior teeth. The purpose of this study is to ascertain whether dental measurements of StW 252 more closely align with those of *Australopithecus africanus*, *Australopithecus robustus, Homo sapiens* or the African apes. For M1 and M2, StW 252 is distinct from the comparative samples, and is particularly large buccolingually for M1 and mesiodistally for M2, partly resembling the dimensions of *A. africanus*, whereas for M3, StW 252 is mesiodistally and buccolingually large. Canonical scores axes show StW 252 as extreme in terms of size and polarized from *A. robustus* in terms of shape. StW 252 is distinct from both *A. africanus* and *A. robustus*, indicating an additional hominin taxon may be represented at Sterkfontein West Pit.

INDEX WORDS: Human evolution, dental measurements, *Australopithecus,* Sterkfontein, Paleoanthropology, South Africa

# DOES TOOTH SIZE MATTER?: A DENTAL MEASUREMENT ANALYSIS ON STW 252 FROM STERKFONTEIN, SOUTH AFRICA

by

Caitlin Elizabeth Mayer

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

in the College of Arts and Sciences

Georgia State University

2016

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by

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August 2016

# DEDICATION

This thesis is dedicated to the late Alun Hughes. His discovery of StW 252 inspired me to conduct this research.

# ACKNOWLEDGEMENTS

I would like to thank the Chicago Field Museum for providing the specimens used for the dental measurement analysis comparative sample and the Transvaal Museum and the University of Witwatersrand for providing access to the fossil hominins.

I would like to thank my thesis committee for providing insight throughout this process, starting with my comprehensive examinations. Thanks to Dr. Frank Williams for his guidance throughout this process and providing his field journal and dental measurements. Without this information this research project would have not happened.

Dr. Bethany Turner for reminding me that writing discussions for research projects can be fun and encouraging me to never just study people, but actually be one. Thanks to Dr. Jason Heaton for joining my committee even though he did not know me previously. His help has proved to be invaluable and I greatly appreciate it.

Thanks for Dr. Arthur Durband for sticking with me throughout my undergraduate research and graduate research. My passion for South African australopiths began in his Human Evolution course. I have been obsessed ever since.

Thanks to Dr. Nicola Sharratt for letting me isolate myself in her lab office for the entire semester while I completed this thesis.

I would like to thank my family, especially my parents, for never pushing me to get a Master’s degree, but for supporting me in every decision I have made, William Cawley for being so encouraging for the past two years, and Ben Schaefer and Brittaney Hundman for always being available for proof reading.

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# 1 INTRODUCTION

South Africa is home to the Sterkfontein cave located about 50 km from Johannesburg, South Africa (Clarke, 2013; Pickering and Kramers, 2013; Partridge et al., 1999; Figure 1). This cave is situated among other evolutionarily significant sights within the Cradle for Humankind World Heritage Site. These sites include Sterkfontein, Swartkrans, Kromdraai, and Drimolen (Kuman and Clarke, 2008; Pickering and Kramers, 2010; Herries and Shaw, 2011; Clarke, 2013; Gibbon et al., 2014). Sterkfontein West Pit is made up of 6 Member deposits (Herries and Shaw, 2011; Clarke, 2013).

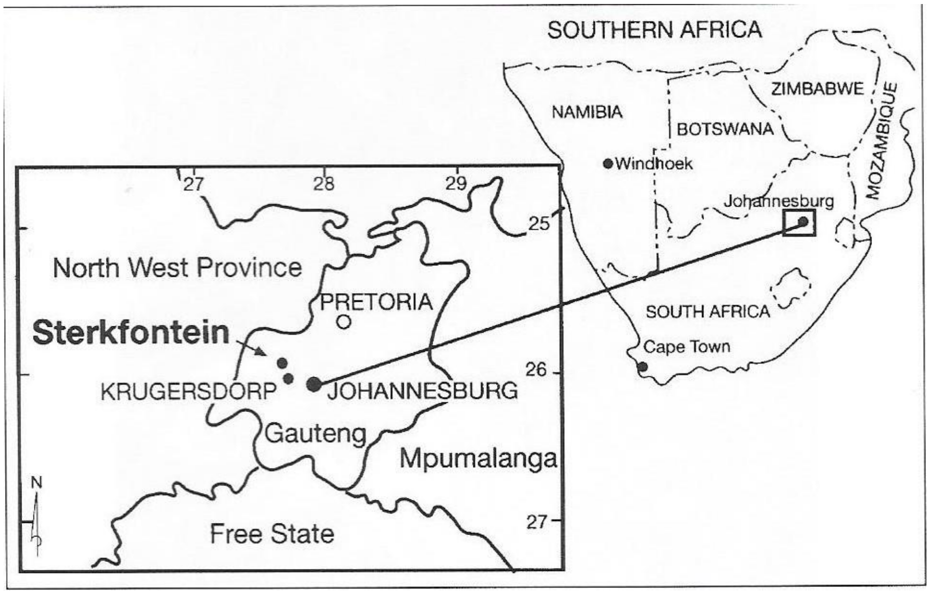

*Figure 1: Locality Map of South Africa courtesy of Partridge et al. 1999*

Sterkfontein cave has yielded a number of fossils that have been difficult to classify. One of these fossils, dated around 1.7-1.9 Ma, is StW 252. StW 252 is comprised of occipital, temporal, parietal, frontal, and maxillary fragments, and a full set of robust maxillary anterior and posterior teeth (Clarke, 2013). Craniofacial analyses on StW 252 have concluded that StW 252 combines morphological attributes of *A. africanus* and *A. robustus*.

Member 4 of the Sterkfontein cave has been interpreted as representing a wetter environment due to the faunal skeletal remain and fossil remains of woody plants, such as lianas, found in this deposit (Kuman and Clarke, 2008). In contrast, the Member 5 deposit shows evidence of a drier environment based on the faunal remains excavated at this site (Kuman and Clarke, 2008).

A number of sophisticated stone tools (Developed Oldowan and Acheulian) have been found in infills of Member 5 (Kuman and Clarke, 2000; Clarke, 2013). The inclusion of stone tools in some of the Member 5 infills, but not others, suggests that they were deposited at different times. The unique morphological attributes of some specimens, such as StW 53 (Williams et al., 2012) indicate that Member 5 deposits witnessed a radiation of different taxa.

## 1.1 Purpose of the Study

This study will focus on a dental analysis of StW 252 with a large comparative sample of non-human primate and modern human teeth coupled with a sample of unpublished fossil australopith dental measurements. This research is significant because StW 252 from the Sterkfontein West Pit is difficult to classify due to peculiar morphological characteristics. Although others have investigated the cranial morphology and the geometric morphometrics of this specimen, the tooth measurements of StW 252 have not yet been analyzed. This investigation will contribute to the debate about whether StW 252 is indeed representative of a new hominin species from Sterkfontein West Pit.

### *1.1.1 Research questions*

The sample will be used to address the theory that there is indeed a 4th *Australopithecus* specimen in South Africa as Clarke (1998; 2008; 2013), and Fornai (2010) have argued.

This project will also test the hypothesis that sexual dimorphism is attributed to the morphological differences observed in these larger toothed individuals as argued by Lockwood (1999) and Conroy et al. (2000).

Lastly, this research project will address if StW 252 and the other large tooth individuals are from a transitional species leading to *A. robustus* as stipulated by the Second Species Hypothesis (Clarke, 2013; Fornai, 2010) through interpretation of the statistical analysis.

### *1.1.2 Hypotheses*

The following hypotheses that will be investigated using quantitative and qualitative research methods include

1. StW 252 represents another species alongside *A. africanus* seen in Member 4 of the Sterkfontein Caves
2. Sexual dimorphism account for differences among the South African australopiths
3. StW 252 is among a transitional species from *A. africanus* into *A. robustus*

## 1.2 Chapter Preview

Chapter 2 discusses the background information on StW 252 as well as the cave sites near Sterkfontein. In this chapter, a more detailed discussion regarding the dating techniques used to date these sites will follow. This chapter will also cover sexual dimorphism and the implications this has on species classification of StW 252. The Second Species Hypothesis will be further defined.

Chapter 3 will begin with the theoretical background on the species concept to conceptualize species classification. This chapter will also discuss the different ways in which species are classified through cranial, postcranial, and dental morphology.

Chapter 4 will discuss the measurement error analysis and the statistical methods used to determine the margin of error. The comparative sample of dental measurements from The Field Museum of Natural History, Chicago will be discussed in this chapter. This section will also discuss the analytical methods used to test each hypothesis as stated in Chapter 1.

Chapter 5 will outline the analytical analysis used to address each hypotheses introduced in Chapter 1 including discriminant function analysis, bivariate comparisons, analysis of variance, Tukey's post-hoc significance test, and a cluster tree analysis.

The implications of the results will be discussed in this Chapter 6. This section will explore how the literature review holds up to the dental measurement results. This chapter will also discuss the results in the context of the hypotheses investigated.

# 2 BACKGROUND

## 2.1 StW 252

StW 252 was excavated by A. R. Hughes and his team of scientists on June 21st, 1984 from a talus cone (a deposit of fallen rocks) within the Member 4 deposit tucked far inside the Sterkfontein cave (Clarke, 1988). StW 252 consists of a full set of upper dentition. The distal portion of the right $I^1$ and the right $I^2$ are isolated from the other teeth (Clarke, 1988). Both left and right canines and all four premolars were found in each socket (Clarke, 1988). Both left and right $M^1$ and $M^2$ fit within the sockets next to the respective premolars (Clarke, 1988). The third molar position was estimated relative to the $M^2$ positon; the third molars are not erupted (Clarke, 1988). Among the cranial bones, there exists the medial portion of the face, anterior palate, portion of the frontal bone, a fragment of the left parietal, and the superomedial portion of the occipital (Clarke, 1988). The maxillary suture is mostly preserved which makes the placement of the two halves of the palate appropriate (Clarke, 1988). Clarke (1988) and Lockwood and Tobias (2000) classify StW 252 as an immature specimen due to the lack of dental wear on the teeth and the $M^3$ not being fully erupted (Figure 3).


*Figure 2: Cast of StW 252*

The craniofacial analysis shows the large toothed australopith, StW 252, has a thinner brow ridge when compared to the smaller toothed *A. africanus*, Sts 5 (Clarke, 2013). Among extant non-human primates and humans, males, on average, that have robust teeth tend to have larger brow ridges when compared to females. (Clarke, 2013). StW 252 also has forward facing cheekbones and a vertical, rounded occipital region (Clarke, 2013). Broom et al. (1950)

*Figure 3: StW 252 dentition*

attributed the morphological differences in individuals, such as Sts 71 in the cranium, possibly to crushing during the fossilization process, however, StW 252 is observed to have the same morphological differences, suggesting that crushing deformation was unlikely (Clarke, 2013). Characteristics of *A. robustus* include "sagittal and compound temporal/nuchal extracranial crests in males, a zygomatic arch positioned high above the occlusal plane, a forward placement of the zygoma, and a robust mandible with absolutely and relatively tall ramus and a correspondingly tall posterior face" (McCollum, 1999: 301).

The morphological differences between *A. robustus, A. africanus,* and StW 252 can be seen in other fossilized remains including Sts 71, Sts 1, StW 183, StW 498, StW 384, Sts 36, and StW 505 (Clarke, 2013). Even though the variation among the aforementioned individuals is vast, these fossils have been previously attributed to *A. africanus* (Brian, 1981; Lockwood, 1999; Lockwood and Tobias, 1999). Clarke (2013) categorizes StW 505 as one of the larger toothed individuals, however, Lockwood and Tobias (1999) categorize StW 505 and StW 252 both as *Australopithecus africanus*. Since Sts 71 and StW 252 are often grouped together in the Second Species Hypothesis due to morphological similarities, these two specimens could represent male and female of this second species (Fornai, 2010). Fornai (2010) concluded after conducting geometric morphometric analyses on StW 252 and specimens from other sites (Kromdraai, Swartkrans, Sterkfontein, and Makapansgat) that there are distinct morphological differences that suggests the possibility of another South African species similar to *A. robustus* (Fornai, 2009).

Lockwood and Tobias (1999) argue that the morphological differences among StW 252 and the other large toothed individuals can be attributed to sexual dimorphism.

### ***2.1.1 Sexual dimorphism***

Sexual dimorphism is defined as pronounced physical differences among males and females and is suggestive of social behavior (Lockwood, 1999; Balolia, 2010; Plavcan, 2012). In non-human primates, when sexual dimorphism is observed, a thick supraorbital torus is coupled with large canines in males. In a specimen with smaller canines (female), thinner supraorbital tori are observed (Clarke, 1988). StW 252 expresses the exact opposite of these known dimorphic features when compared to *A. africanus* (Clarke, 1988). StW 252 has thin supraorbital tori, but large canines. Sexual dimorphism is not expressed in every species, like gibbons (Plavcan, 2012). Canine size in male humans is about 10% larger than in females which is considered a small percentage on the scale of non-human primates (Plavcan, 2012). Male human skeletons are much more robust than female skeletons. For individuals with unknown sex, sex estimations can be made by using the os coxae. Sex estimations using the os coxae are accurate 95% of the time (Plavcan, 2012).

Males weigh about 15% more than females and are 7% taller than females, suggesting that body mass differs significantly between the sexes (Plavcan, 2012). Humans are more dimorphic than gibbons but less dimorphic than *Pan* and *Gorilla* (Plavcan, 2012). Sexual dimorphism among the non-human primates is not always universal (Plavcan, 2012). For example, Plavcan (2012) notes that there are cases where female body size is greater than male body size and cases where sexual dimorphism is not expressed at all. This is important to consider when analyzing the size differences among australopiths, because sexual dimorphism is highly variant (Plavcan, 2012). StW 252 and Sts 71 express traits in common that are distinct from *A. africanus* and *P. robustus* which may indicate an additional South African australopith species (Clarke, 2013). If StW 252 and Sts 71 indeed represent a male and female of a novel species, there should be an overall size difference in the canines, brow ridge, zygomatic arch, and molars. Regarding what is expressed in sex differences among *Pan troglodytes*, there should be a difference in canine morphology between StW 252 (male) and Sts 71 (female).

Determining the role sexual dimorphism played in social behavior among hominins is difficult because the hominin sample size is small and almost always fragmentary (Plavcan, 2012). Sexual dimorphism expressed in non-human primates is typically suggestive of male-male competition for sexual partners and food (Plavcan, 2012). If sexual dimorphism can indicate social behavior in non-human primates (Balolia, 2014) and if StW 252 and Sts 71 represent male and female of the same taxon, it is possible that sexual selection among these australopiths occurred similar to that observed in nonhuman primates.

To understand how sexual size dimorphism played a role in the behavior of StW 252 and the larger toothed individuals, the time line of the sites in which the australopiths have been found must be determined. Dating techniques vary from site to site. Figuring out how old a Member deposit is at Sterkfontein and other evolutionarily significant sites can help researchers address hominin phylogeny.

### *2.1.2 Dating*

Since there is no volcanic ash inside the cave, $^{40}Ar/^{39}Ar$ dating cannot be done (Pickering and Kramers, 2010). The oldest deposit is Member 1, and the youngest deposit is Member 6 (Clarke, 2013). In previous studies, faunal remains found in the Sterkfontein deposits were utilized in an attempt to date the subsequent Member deposits (Herries and Shaw, 2011). Member 2 was dated to 4.52-3.72 Ma using cosmogenic nuclide burial dating, but U-Pb dating (uranium-lead dating) has yielded an age of 2.33-2.06 Ma (Herries and Shaw, 2011). A reverse polarity analysis on Member 2 indicates the site cannot be older than 2.8 Ma (Herries and Shaw, 2011). Member 2 deposits are significant because StW 573 was discovered there and the fossil is thought to be part of the second species (Herries and Shaw, 2011). If the uranium-lead dates are correct, two australopith species were present in Sterkfontein as far back at 2.6 Ma (Herries and Shaw, 2011). Date estimates of Member 4 were based on a cache of hundreds of liana fossils found scattered throughout the deposit that shows evidence of the extent of the East African drying period at about 2.5 Ma (Herries and Shaw, 2011). Among these cave sites, other remains were found in Sterkfontein West Pit Member 4. Paleomagnetic dating, on speleothems in Member deposits 1-4, was used to determine the date range of the Sterkfontein sites (Herries and Shaw, 2011). Member 4 deposits were dated using paleomagnetic dating that yielded an age of 2.3-2.2 Ma, and the StW 53 infill is dated to 1.78-1.49 Ma (Herries and Shaw, 2011). Member 5 yields tool technology, early *Homo sp.,* and *A. robustus* and is now dated to about 1.4-1.07 Ma (Herries and Shaw, 2011).

The Swartkrans site in South Africa has yielded *A. robustus* and *Homo sp.* remains and evidence of tool use and animal butchering during the early Pleistocene (Pickering et al., 2000; Pickering et al., 2012). The Member 1 deposits at Swartkrans were dated using cosmogentic dating techniques (Gibbon et al., 2014). These date estimates are 2.18-.08 Ma and 1.8-.09 Ma (Gibbon et al., 2014). Since animal bones were found in Member 1 of the Swartkrans site with evidence of butchering, the dates indicate this is the earliest period stone tools were used in South Africa (Gibbon et al., 2014). However, a study conducted by Pickering et al. (2000) indicates that StW 53 bearing Member 5 has evidence of butchering. Therefore, tool technology may have shown up earlier than Member 1 at Swartkrans. Date estimates of Member 3 are 0.96

Ma based on the U-Pb analysis of dental enamel found in this deposit (Balter et al., 2008). Member 3 yields the last appearance of bone tools in South Africa (Gibbon et al., 2014). Bone tools found at Swartkrans appear to have been used by *A. robustus* to dig up tubers and roots (Brain, 2000) The paleoenvironment of Swartkrans during this time is described as an open grass area situated almost always near a source of water (Kuman and Clarke, 2000).

*A. robustus* was first discovered at the Kromdraai site (Herries et al., 2009). Kromdraai is split between two locations based on the remains found: A (faunal) and B (hominid) (Herries et al., 2009). Kromdraai has three member deposits numbered 1-3 and has yielded evidence of *A. robustus* and *Homo sp.* remains (Herries et al., 2009). Members 1-3 were dated using paleomagnetic dating and yielded an age of 1.95-1.78 Ma for Members 1-2 and age older than 1.78 for Member 3 (Herries et al., 2009).

The Drimolen site is located about 7 km from Sterkfontein cave sites (Keyser et al., 2000). The Drimolen site yielded more than 80 hominin specimens and is the site of the most well-preserved skull of a female *A. robustus* (DNH 7) and a male (DNH 8) mandible (Keyser, 2000; Keyser et al., 2000). The Drimolen collection consists mostly of dental remains belonging to *A. robustus* and *Homo* (Moggi-Cecchi et al., 2010). This site is dated at about 2.0-1.5 Ma based on a biostratigraphic analysis (Moggi-Cecchi et al., 2012).

The dates at which these sites are assigned are integral when interpreting the paleoclimate. The paleoclimate can help researchers understand and infer behavior by understanding what ecological factors influenced individuals in the past.

### *2.1.3 Paleoclimate*

Changes in the floral and faunal remains found in Member 4 deposits have been interpreted as representing a wetter climate (Kuman and Clarke, 2008). Member 5, which is more consistent with a drier environment, may provide context for the appearance of these new taxa (Kuman and Clarke, 2008).

Pickering et al. (2004) noted the minimum number of australopiths found in the Member 4 deposit totals to about 45 (Pickering et al., 2004). There have been no artifacts found in any deposits where australopiths have been discovered (Kuman and Clarke, 2000). Sterkfontein, known for being a massive underground area filled with a mass of rocks has yielded a number of fossilized fauna and flora remains of which are indicative of the paleo-climate (Kuman and Clarke, 2000). The Sterkfontein Member 4 deposit is filled with 300+ fossilized wood fragments that are most commonly known as lianas (Kuman and Clarke, 2000). Lianas need strong, robust trees as a brace since this plant species is a thick vine that is rooted deep in the soil (Kuman and Clarke, 2000). The fossilized fragments of lianas are not present toward the northern end of the cave, which signify the presence of lianas at the southern-most end as being the cave opening (Kuman and Clarke, 2000). The Member 5 deposit is considered drier due to the absence of lianas and the presence of *Equus* (ancestral to horses), *Pedetes* (ancestral to rodents), and *Struthio* (ancestral to ostriches) found in this deposit (Kuman and Clarke, 2000). In addition to lianas, the Sterkfontein Member 4 also yields *Makapania broomi*, related to the musk-ox, and fossil colobus monkey remains that are not found in the later Member 5 deposits (Kuman and Clarke, 2000). These faunal remains were found in the younger deposits at Kromdraai and Swartkrans (Kuman and Clarke, 2000). Since *M. broomi* and colobus monkey remains are found in younger deposits at Kromdraai and Swartkrans, these sites could be positioned closer to a large body of water, like a river (Kuman and Clarke, 2000).

A number of sophisticated stone tools (developed Oldowan and Acheulian) have been found throughout deposits of Member 5 (Kuman and Clarke, 2000; Clarke, 2013). The fact that there are stone tools in some of the Member 5 infills, but not others, suggests that they were deposited at different times (Clarke, 2013). *Parapapio broomi* and *Parapapio jonesi* inhabited the same area and were fossilized in Member 4 (Brian, 1981). *Pp. broomi* has medium-sized molars and *Pp. jonesi* has smaller molars and a squared-shaped muzzle (Brain, 1981) which suggests two different species of the same genus expressing different morphologies. The preserved fossils of *Panthera leo* and *Panthera pardalisi* are both found in Sterkfontein Member 4 deposits, again showing the possibility for two species of the same genus to have overlapping home ranges (Clarke, 2013). Since this is so common throughout the animal kingdom, it is possible that overlapping ranges might also be found among the australopiths. This is indicative of overlapping ecological niches as seen in the same genus and different species. The possibility of more than one species of the genus *Australopithecus* can be explained by the Second Species Hypothesis.

## 2.2 The Second Species Hypothesis

The Second Species hypothesis accounts for the number of these australopiths, the craniofacial morphology, and the sexual size dimorphism (Fornai, 2010). Sts 71 and StW 252 are classified as a possible second species because both specimens show signs of morphological differences that are not the result of a slow taphonomic deformation process (Fornai, 2010; Clarke, 2013). The defining features of this second species include large anterior and posterior teeth, bulbous cusps on the posterior teeth, a thin brow ridge, a flatter face compared to *A africanus*, a very vertical, round occipital region, and a sagittal crest (Clarke, 2013). Sexual dimorphic traits common to StW 252 and Sts 71 provides an argument against sexual dimorphism as an explanation for the differences among known *A. africanus* specimens (Clarke, 1988). After conducting geometric morphometric analyzes on StW 252 and specimens from other sites (Kromdraai, Swartkrans, Sterkfontein, Makapansgat), Fornai (2010) determined that there are distinct morphological differences that indicate the possibility of another South African species similar to *A. robustus* (Fornai, 2010).

## 2.3 Discussion

StW 252 being so unlike other individuals found within the Member 4 deposit was influenced by the paleoclimate. The faunal and floral remains found scattered throughout the deposits help researchers understand the conditions in which individuals such as StW 252 lived. Knowing the conditions and how old the Member deposits are can help determine the phylogenic placement of StW 252 and the other large toothed individuals found alongside *A. africanus* in the Sterkfontein cave. The possible placement of this robust group of unknown individuals can be supported by the Second Species Hypothesis. A way to explain how the divergence between StW 252 and *A. africanus* is through the Species Concept. The Species Concept is made up of many different theories to explain the mechanics of species divergence.

# 3 THEORY

## 3.1 Species Classification

Charles Darwin argued that every species, both extinct and living, descended from a single common ancestor and that a consistent avenue of change is explained by natural selection (Darwin, 1859). As well as the concept of evolution, the species concept underwent multiple and prominent revisions to classify the vast amount of organisms found in the past and present (Groves, 2012; Singh, 2012). Classification of biological species has been accounted for as far back as ancient Greece, with Aristotle who created a natural classification for introducing the notion of growing complexity among species known as the "ladder of life” (Singh, 2012). The biological classification system became the foundation for Charles Linnaeus' downward taxonomy that classified every species using nomenclature and sorted each into a series of categories and subcategories to build taxonomies (Szalay, 1993). Linnaeus created a binomial nomenclature system whereby each "kind" was defined as a species which “reflects the existence of fixed, unchangeable type” (Singh, 2012: 784). Species is, however, more accurately defined as a group of individuals that share the same fertilization system (Groves, 2012; Singh, 2012). Linnaeus’ proclamation of the “unchangeable type” provided the foundation of the Typological Species Concept during the latter half of the 17th century (Mayr, 1966; Singh, 2012). The Typological Species Concept (TSC) sometimes referred to as essentialism, stipulates that there is a limited amount of individuals that comprise a class (Mayr, 1966). TSC is influenced by the differences in morphologies used by taxonomists to group species, and this concept does not consider species change (Mayr, 1966; Szalay, 1993; Singh, 2012). The strict parameters of the TSC established by Linnaeus resulted in the rejection of this idea (Singh, 2012). The nominalistic species concept was hypothesized by Occam in 18th century France (Singh, 2012).

Occam argued that species is a mental concept, and that nature creates individuals; therefore, only individuals exist (Singh, 2012).

## 3.2 Species Concept

Dobzhansky determined that since individuals within a species must be genetically compatible, the typological and nominalistic species concepts are not sufficient enough to accurately classify an organism (Szalay, 1993). As more and more fossilized remains are being discovered, more complex explanations of their characteristic differences are needed to account for these distinct changes. Four species concepts are used when discussing hominins, but there exist 22 species concepts (Holliday, 2003). The biological, evolutionary, phylogenetic, and cohesion concepts are regularly applied to human evolution (Holliday, 2003).

### *3.2.1 The Biological Species Concept*

The Biological Species Concept (BSC) replaced the typological species concept and the nominalistic species concept during the 20th century and was described by Ernst Mayr and Theodosius Dobzhansky (Holliday, 2003). Mayr defined species as reproductively isolated groups that can interbreed (Cartmill and Smith, 2009). As a geneticist, Dobzhansky focused his definition of the BSC as a “reproductive community of sexually and cross-fertilizing individuals who share a common gene pool” (Singh, 2012: 785). Although the biological species concept is widely accepted, this concept does have practical problems such as the lack of recognition of “sexual dimorphism, age differences, and polymorphism” (Singh, 2012: 786).

### *3.2.2 The Evolutionary Species Concept*

As noted by paleontologist, George Simpson during the 1960s, the Biological Species Concept does not account for evolutionary change among species (Holliday, 2003; Singh, 2012). The evolutionary species concept accounts for evolutionary change and should approach a species as a lineage "evolving separately and with its evolutionary role and tendencies" (Singh, 2012: 787). The evolutionary species concept appears to satisfy both the definition of a species as well as the evolutionary trajectory of a species.

### *3.2.3 The Phylogenetic Species Concept*

Promoted by Joel Cracraft in the 1980s, the phylogenetic species concept accounts for the removal of reproductive isolation as a defining factor of a species (Holliday, 2003). The Phylogenetic Species Concept is defined as a group of individuals that share a portion of phylogeny that is genetically different, but is not reproductively isolated (Holliday, 2003; Groves, 2012). Through this concept, a species is defined by having the same common ancestor. This concept was created to account for hybridization and allopatric populations that are ignored by the biological species concept (Holliday, 2003).

### *3.2.4 The Cohesion Species Concept*

The Cohesion Species Concept was defined by Alan Templeton, a geneticist, at the end of the 1980s (Holliday, 2003). Under this concept, a species is defined by "genetic and phenotypic cohesion" (Templeton, 1989: 12). The cohesion species concept combines principles of the biological species concept and the evolutionary species concept (Templeton, 1989; Holliday, 2003). Through evolution, species are defined by the mechanisms leading to cohesion instead of reproductive isolation (Templeton, 1989).

### *3.2.5 Discussion*

Typological and Nominalistic Species Concepts (TSC and NSC) are examples of the scientific endeavor. The TSC and the NSC challenged scientists like Mayr, Dobzhansky, and Simpson to revisit the way species are classified to account for the variation that makes up complex ecosystems. Recent literature on the species concept has been quite critical in regards to applying the theoretical implications to actual populations.

Groves (2012) argues that the Biological Species Concept is not always applicable in cases of sympatry. Sympatry occurs when a new species evolves separately from an ancestral one while occupying the same habitat, thus rendering each species reproductively isolated (Groves, 2012; Singh, 2012). There have been some cases of sympatric species interbreeding which is consistent with speciation as a process (Groves, 2012). In Ethiopia, for example, *Theropithecus gelada* and *Papio anubis* have been observed interbreeding in the wild (Groves, 2012). DNA testing has also confirmed that other sympatric species such as *Rungwecebus kipunji* has mitochondrial DNA from the *P. cynocephalus* population that occupies the same habitat of *R. kipunji* (Groves, 2012). Another mode of speciation is parapatry, which is observed when a populations of a species that once inhabited the same geographic region as the entire species becomes isolated due to a sudden extreme change in habitat geography (Singh, 2012). During the time this emerging species is geographically isolated, subtle variations occur (Groves, 2012; Singh, 2012). Once the geographical barrier is removed (though not always the case) and separated populations inhabit the same region once again, these variations prevent individuals from reproducing, as “hybrids” may not be reproductively fit (Holliday, 2003). Therefore, individuals from the two populations do not mate. Allopatric speciation occurs when a species diverges so much from the ancestral species because of geographical isolation that different mechanisms of evolution occur, such as mutation or natural selection, that shape each species separately (Holliday, 2003). In cases of allopatric speciation, classification of a species is determined by the taxonomist, since the Biological Species Concept, which does not account for the evolutionary change of a species, cannot be tested (Holliday, 2003; Groves, 2012). Since this type of species classification has been argued to be based on intuition, the biological species concept as an explanatory model to understand the evolution of allopatric populations is of questionable scientific value (Groves, 2012).

Godfrey and Marks (1999) argue that a species is difficult to define because universalities cannot be applied to every case (Godfrey and Marks, 1991). Ideally, individuals must be similar and must also "occupy a particular niche, or have a unique way of life in the natural world" to be reproductively compatible (Godfrey and Marks, 1991).  Reproductive isolation is seen among groups that appear physically similar but are genetically different, and are, therefore, sometimes misclassified (Godfrey and Marks, 1991; Bearder, 1999). For instance, amongst the nocturnal primates in Africa, there exists considerable diversity throughout the galagos (Bearder, 1999). Since galago populations are identical in physical appearance, eat the same foods, and occupy the same habitat, based on the biological species concept these galagos would be classified as the same species (Bearder, 1999). However, mate recognition among the different galago populations is seemingly non-existent due to “anatomical, biochemical, physiological, and behavioral differences” (Bearder, 1999: 268). An example of species misclassification based on physical appearance is seen in the case of *Otolemur crassicaudatus* and *Otolemur garnettii* (Bearder, 1999). Even though *O. crassicaudatus* and *O. garnettii* occupy the same tree canopies in Tanzania at the same time and have the same body mass, the differences among these two organisms are so vast that mate recognition is impossible (Bearder, 1999). Skull size and shape, penis shape, and gestation period are some of the differences that make *O. crassicaudatus* and *O. garnettii* unable to reproduce (Bearder, 1999).

## 3.3 Methods of Species Classification

Based on the theoretical foundation of the species concept and modes of speciation, paleotaxa are identified based on dental morphology, craniofacial morphology, postcranial form, and genes. Assigning a newly discovered fossilized hominin to a species is often done by comparing various morphological traits to the type specimen (Clarke, 2013). Not every fossil hominin is found with a full skeleton. Therefore, it is important to have many different classification techniques.

### *3.3.1 Dental Morphology*

An example of classification of a hominin using dental analysis was completed by Kramer et al. (2005). Consisting of a single incisor, RH1 is the first fossilized hominin discovered in West Java (Kramer et al., 2005). Identification of RH1 was based on morphological similarities of a comparative sample comprising of *Homo erectus*, orangutan, and macaque lower incisors (Kramer et al., 2005). Enamel thickness was measured at 1 mm, the height of the tooth is 10 mm, and there is apparent shoveling on the lingual surface (Kramer et al., 2005). RH1 exhibited no wear on the mesial and distal surfaces, and the crown shape is oval (Kramer et al., 2005). Due to these features, the comparative studies suggest that RH1 is very similar to *Homo* (Kramer et al., 2005).

### *3.3.2 Craniofacial Morphology*

In cases in which skull fragments are found, craniofacial morphological comparisons can be made to identify a species. Typical facial features of *A. africanus* includes absent nuchal and temporal crests, absent or weak sagittal creating, hominin-positioned foramen magnum, sub-nasal prognathism, small supraorbital tori, and the presence of anterior pillars (Broom, 1936; Berger and Clarke, 1995; Clarke, 1998; Lockwood and Tobias, 1999; Clarke, 2008; Larsen et al., 1998; Rak, 1983). Craniofacial morphology observed in Sts 5 resembles the type specimen of *A. africanus* which is the Taung Child (Clarke, 2013). The Sterkfontein Member 4 collection has yielded many fossilized cranial, mandibular, and dental remains. Sterkfontein Member 5 has also yielded multiple remains, including StW 505. Lockwood and Tobias (1999) have stated that the remains found at the cave site have been argued to not fit within the classification of *A. africanus.* However, Lockwood and Tobias (1999) have used craniofacial morphology in an attempt to classify StW 505. At the time, StW 505 was the most preserved complete skull found in Member 4 (Lockwood and Tobias, 1999). Although the skull is robust, StW 505 does not resemble any of the robust australopithecines (Lockwood and Tobias, 1999). For example, the glabella and brow ridge present on StW 505 are consistent with what is found on some human males (Lockwood and Tobias, 1999). Lockwood and Tobias (1999) argue that, although StW 505 is estimated as being a male, the slight sagittal crest is more posteriorly placed, similar to that in "male chimpanzees, *A. afarensis,* and one specimen of early *Homo*" (Lockwood and Tobias, 1999: 681). Although the sagittal cresting is similar to the aforementioned specimens, the facial characteristics are different and much more similar to *A. africanus.* Therefore, Lockwood and Tobias (1999) classify StW 505 as *A. africanus*.

### *3.3.3 Postcranial Morphology*

Similar to identification using craniofacial morphology, postcranial form can be used to determine a species. A sample of fossilized remains excavated from the Swartkrans site (Members 1-3) was identified by comparing these unknown specimens against the already identified *A. robustus* and *Homo* specimens from Swartkrans, as well as at other sites in South and East Africa (Susman et al., 2001). This study included a large comparative sample of *Pan paniscus, Pan troglodytes, Gorilla gorilla*, multiple populations of *Homo sapiens,* and *A.*

*afarensis* (Susman et al., 2001). The right proximal femur identified as SK 3121, was once identified as a carnivore femur (Susman et al., 2001). The diameter of the femoral head of SK 3121 is 28.8 mm and the compressed femoral neck length is 23 mm, which is comparable to known australopiths SK 82 and SK 97 (Susman et al., 2001). A long compressed femoral neck is a common characteristic of the australopiths (Susman et al., 2001). The femoral head of SK 3121 is relatively small when compared to SK 82 and SK 97, which are argued to represent male *A. robustus*, and is close in size to East African specimen AL 288-1 (Susman et al., 2001). Due to these morphological characteristics and size, SK 3121 can be classified as a probable female robust australopith (Susman et al., 2001).

All three of these identification techniques have multiple similarities. Each technique had measurements from an extensive comparative sample that included the type specimen of the suspected species and non-human primates and humans. These studies also employed statistical analysis.

#### ***3.3.4 Other Methods of Identification***

When using dental measurements to classify an unknown species, Plavcan (1993) states that the focus should be on $P^4$-$M^2$ size differences. The best statistics test to determine tooth-size variation is using a bivariate analysis, especially when testing size differences among fossil samples because the number of individuals is often very few (Plavcan, 1993). Dental measurements should also only be compared to species that have already been identified (Plavcan, 1993). When interpreting statistical data plots for both bivariate and multivariate tests, if a group separated from the majority, then the group is from a distinct species (Plavcan, 1993). Dental measurements can be used to determine if there is a second species when the variation among living species is high (Plavcan, 1993).

DNA testing can be utilized to determine if two organisms are genetically similar to one another (Bearder, 1999). As mentioned previously, *O. crassicaudatus* and *O. garnettii* were once classified as the same species due to physical similarities. However, genetic tests revealed significantly different chromosomal and mitochondrial DNA among *O. crassicaudatus* and *O. garnettii*, indicating these organisms are indeed from two separate species (Bearder, 1999). Another example of two different species occupying the same habitat is seen in StW 252 and the recently discovered *Australopithecus sediba*. *A. sediba* and StW 252 have an overlapping time interval, and *A. sediba* may even help discern the phylogenetic placement of StW 252.

## 3.4 Conclusion

The theoretical background for species classification informs researchers about the diversity of life. When it comes to human evolution and, more specifically, StW 252 a “one size fits all” scenario may not work. A mix between two species concepts, the Biological Species Concept and the Evolutionary Species Concept, may work when trying to define a species such as StW 252 for classification and the Evolutionary Species Concept can account for evolutionary change. These concepts and theories can be tested in many ways, but for this project specifically, species classification will be tested through dental measurements.

# 4 MATERIALS AND METHODS

The sample consists of *Gorilla gorilla* (n= 27), *Pan troglodytes* (n= 16), *Homo sapiens* (n=44) from The Field Museum in Chicago, and *Australopithecus africanus* (n=24), and *Australopithecus robustus* (n=9) (Table 1) dental measurements from Dr. Frank Williams' research in South Africa (Table 2). Each of the individuals from The Field Museum are associated with sex and age estimations. The measurements obtained during the trip to The Field Museum have been utilized to test if there is a dental size difference among StW 252, *Australopithecus africanus,* and *Australopithecus robustus* with a much larger more diverse comparative sample.

*Table 1. Sample size and location*

| Taxa | Number of Individuals | Location |
|---|---|---|
| *Gorilla gorilla* | 27 | Chicago Field Museum |
| *Pan troglodytes* | 16 | Chicago Field Museum |
| *Homo sapiens* | 44 | Chicago Field Museum and Georgia State University |
| *Australopithecus africanus* | 24 | University of Witwatersrand and Transvaal Museum |
| *Australopithecus robustus* | 9 | Transvaal Museum |

*Table 2. A. africanus and A. robustus measurements used in study*

| Taxa | Specimen # |
|---|---|
| *A. africanus* | StW 53, MLD 9, MLD 6, MLD 45, MLD 28, MLD 11, StW 40, StW 73, StW 404, StW 14, StW 183, StW 138, StW 126, StW 127, StW 188, StW 287, StW 189, StW 133, StW 140, StW 132, StW 131, StW 56, TM 1511, TM 1512 |
| *A. robustus* | Sk 46, Sk 48, Sk 52, Sk 83, Sk 47, Sk, 13/14, Sk 11, Sts 52, TM 1517 |

### *4.1.1 Measurement Methods*

Seven modern humans from the Georgia State University skeletal collection were measured to collect preliminary sample dental measurements. These individuals are included in the larger comparative sample increasing the number of *H. sapiens* individuals to 44 (Table 1). Dental measurements were acquired from both left and right side of the modern human sample to document a full set of measurements. The dental measurements consisted of buccolingual and mesiodistal measurements of the maxillary teeth using digital calipers. The maxillary teeth were measured because these are the only teeth present for StW 252. Each tooth was individually measured three times beginning with the buccolingual angle and then the mesiodistal angle on incisor$^1$, incisor$^2$, canine, premolar$^3$, premolar$^4$, molar$^1$, molar$^2$, and molar$^3$. The fossil hominin sample used for this study is a collection of unpublished dental measurements collected by Dr. Frank Williams from his research in South Africa (Table 2). His field journal contains measurements of both mandible and immature dentition, but these measurements were omitted since there is no mandible found in association with StW 252 and the maxillary dentition is nearly fully erupted. This process was repeated during data collection for the larger comparative sample at The Field Museum Chicago. However, each individual was only measured once instead of three times.

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### *4.1.2 Measurement Error Analysis*

To control for measurement error, each individual was measured in three trials. Each trial was recorded in an Excel spreadsheet and then transferred to SPSS to test for inter-observer error. The anticipated measurement error was less than 0.5 mm. To calculate the measurement error, each of the three trials was averaged. To estimate measurement error, the mean for each dental measurement must be calculated and compared to each of the three trials using the absolute value (ABS). The equation used to calculate the mean of each tooth is:

ABS (Trial 1 –X) + ABS (Trial 2 –X) + ABS (Trial 3 – X)/ 3.

“X” is the average of the 3 trials. For specimen GSU 57.1 which totaled 7.53 mm, the equation is now:

ABS (7.9-7.53) + ABS (7.38-7.53) + ABS (7.3- 7.53)/3

The values for each individual were then compared using a one-way ANOVA test to determine if the variation between trials exceeded the variation between individuals (Appendix 1; Table 9 and 10). The p-value of the ANOVA is 0.05.

### *4.1.2.1 Measurement Error Analysis Results*

The significance value of each ANOVA is < 0.900 indicating no real groups. In other words, the differences between trials was less than the differences between individuals. To further estimate measurement error, the minimum and maximum absolute mean deviations were identified. The highest mean deviation is the 3$^{rd}$ molar buccolingual measurement at 3.84 mm and the highest absolute mean deviation is 0.95 mm. The lowest absolute mean deviation is 0.23 mm for the fourth premolar with a minimum deviation of 0.04 mm and a maximum deviation at 0.59 mm. For each tooth measurement, the average measurement error was calculated by taking the average of the deviations of each of the three measurements from the mean of all three measurements (Table 4). The average of all of the averages was found by taking 16 numbers in Table 3 and adding them together followed by dividing the numbers by the number of variables (16). As mentioned previously, the absolute mean measurement error is 0.3853 mm. This measurement fails to show a meaningful difference between each measurement. The maximum amount of deviation between future measurements is anticipated to be less than 0.3853 mm. It is expected that measurement precision will improve as this study progresses.

## 4.2 Analytical Methods

The analytical analysis includes a univariate sex specific analysis of each measurement angle for each tooth except for the three molars for which the geometric mean was utilized. The bivariate scatterplots were completed to determine to which group StW 252 most closely align using 95% confidence ellipses around group centroids to demarcate taxa. This method was modified from a study conducted on RH1, a single $I_2$, done by Kramer et al. (2005). For this project, the variables tested are the buccolingual (BL) and mesiodistal (MD) angles for each dental measurement. Eight charts were completed for each dental measurement set. The charts were separated by MD (y axis) and BL (x axis) measurements for $I^1$, $I^2$, C, $P^3$, $P^4$, $M^1$, $M^2$, and $M^3$ for each specimen. An ANOVA was conducted to determine if the groups differed for each dental measurement. Additionally, a Tukey's Post-hoc test was executed to see if there exists a pair-wise difference among groups. A principal components analysis using the five dental dimensions most often preserved in *A. africanus* and *A. robustus* was calculated and the first two PC axes plotted using 95% confidence ellipses around group centroids to identify where StW 252 would fall with respect to the comparative taxa. The discriminant function analysis coupled with the Mahalanobis' Distances and Jackknifed and Non-Jackknifed classification rates includes only the molar measurements scaled to the geometric mean to classify StW 252 with the comparative sample. The p-value for these tests are 0.05. The means for each taxon were taken for the cluster analysis using all dental traits except $I^2$ BL as this was not preserved for *A. robustus.* The data were scaled to the geometric mean of all 15 dental measurements before the cluster analysis was conducted to remove the effects of size. Lastly, a qualitative analysis of StW 252 and Sts 71 craniofacial morphology was conducted.

# 5 RESULTS

## 5.1 Statistical analysis

### *5.1.1 Univariate Analysis*

#### *5.1.1.1 $I^1$ BL*

With respect of the $I^1$ BL measurements StW 252 falls on the larger end of the *H. sapiens* male measurements and on the smaller side of *P. troglodytes* male measurements (Figure 4). *P. troglodytes* female BL measurements are similar to that of the *P. troglodytes* male measurements (Figure 4). Both *H. sapiens* male and female BL measurements fall on the smaller end of all of the $I^1$ BL measurements (Figure 4). *A. robustus* is not represented in this chart, however two *A. africanus* individuals are represented and fall closer to *H. sapiens* male BL measurements and are similar to that of StW 252. (Figure 4).

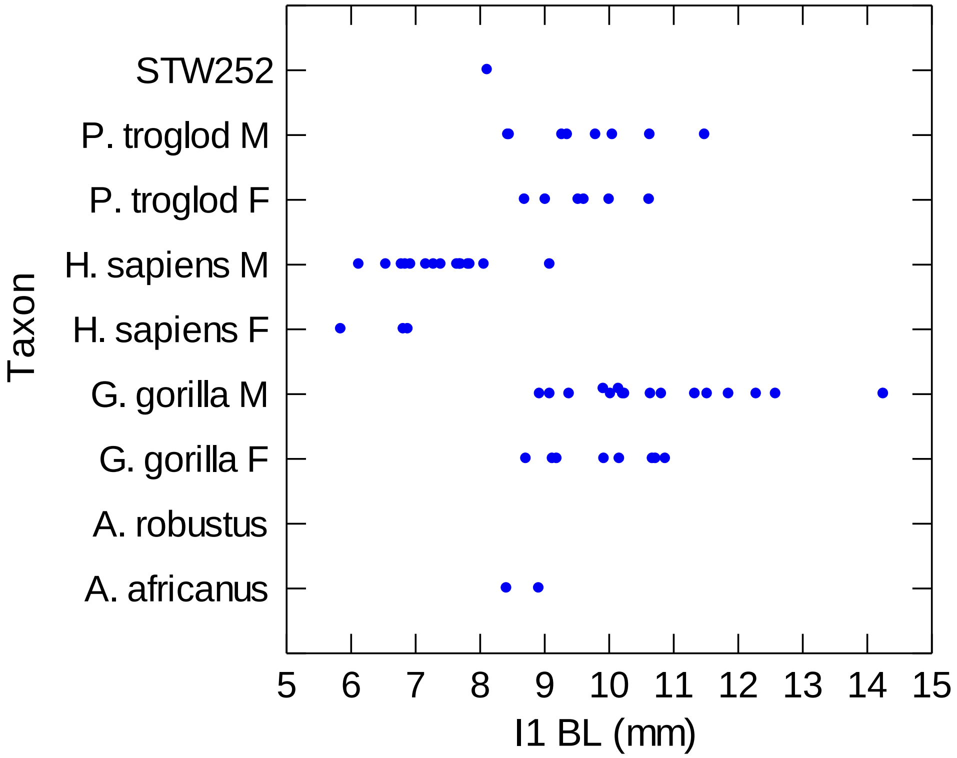

*Figure 4: Univariate analysis of* $I^1$*BL. P. troglod means P. troglodytes*

### *5.1.1.2 $I^1$ MD*

When $I^1$ MD measurements are considered, StW 252 falls on the lower end of *P. troglodytes* and *G. gorilla* male MD measurements (Figure 5). *A. africanus* falls on the lower end of the $I^1$ MD measurements closer to that of *H. sapiens* males and females and smaller than StW 252 (Figure 5). *G. gorilla* male and female measurements seem to be the most variable when compared to the other individuals, which means that the other individuals cluster more closely together whereas *G. gorilla* male and females are more spread out (Figure 5). Similar to that of $I^1$ BL measurements, *A. robustus* is not represented in this chart (Figure 5).

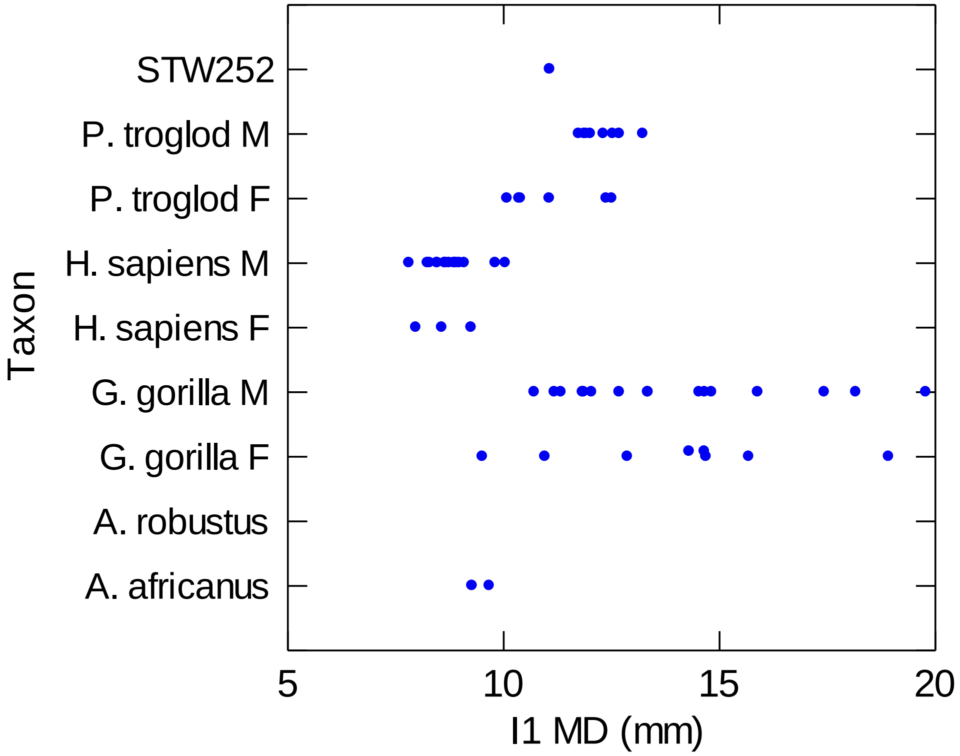

*Figure 5: Univariate analysis of* $I^1$ *MD*

#### 5.1.1.3 $I^2$ BL

For $I^2$ BL measurements, StW 252 falls on the lower end of *P. troglodytes* and *G. gorilla* male and female measurements (Figure 6). StW 252 is larger than that of *A. africanus* and *A. robustus* for $I^2$ BL measurements (Figure 6). *H. sapiens* falls on the smaller end of all of the measurements, however StW 252 is within range of the male I2 BL measurements (Figure 6). *A. robustus* and *A. africanus* $I^2$ BL measurements are similar to that of *H. sapiens* measurements with one *A. africanus* individual falling on the lower end being more similar to *H. sapiens* female I2 BL measurements (Figure 6).

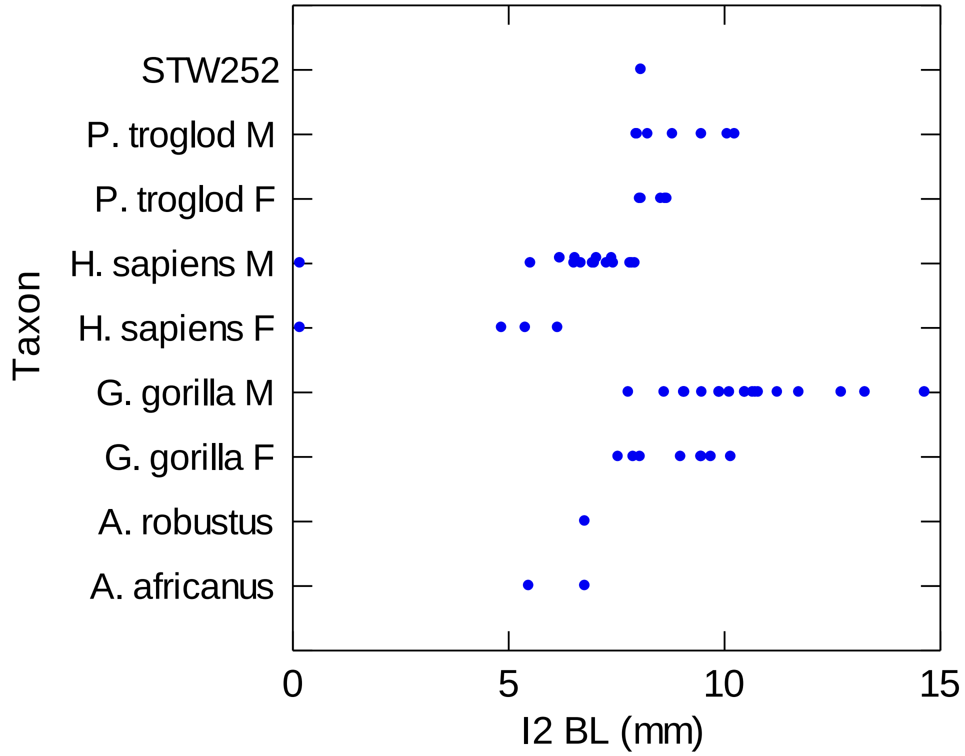

*Figure 6: Univariate analysis of $I^2$ BL*

### 5.1.1.4 $I^2$ MD

All individuals are shifted down the chart on the lower end for I2 MD measurements (Figure 7). StW 252 is situated on the lower end of *P. troglodytes* and *G. gorilla* male measurements and is found situated in the middle of *H. sapiens* male I2 MD measurements (Figure 7). One *A. africanus* individual is placed on the smaller end of the chart smaller than that of *H. sapiens* female measurements, however both *A. africanus* and *A. robustus* MD measurements fall within range of the *H. sapiens* male and female MD measurements (Figure 7).

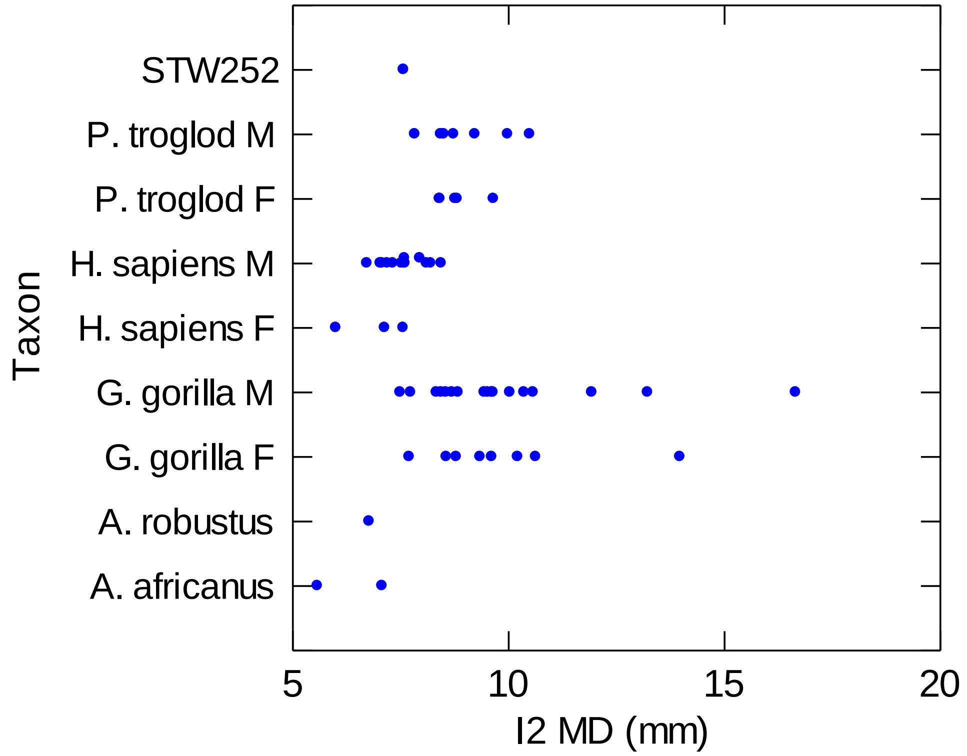

*Figure 7: Univariate analysis of I$^2$ MD*

### *5.1.1.5 Canine BL*

When canine BL measurements are considered, StW 252 falls within range of *P. troglodytes* and *G. gorilla* (Figure 8). *H. sapiens* male and female BL measurements cluster more closely with *P. troglodytes* female BL measurements and even cluster with some *G. gorilla* male BL measurements (Figure 8). StW 252 is positioned away from *A. africanus* and *A. robustus* canine BL measurements toward the larger end with male *P. troglodytes* and *G. gorilla* measurements (Figure 8).

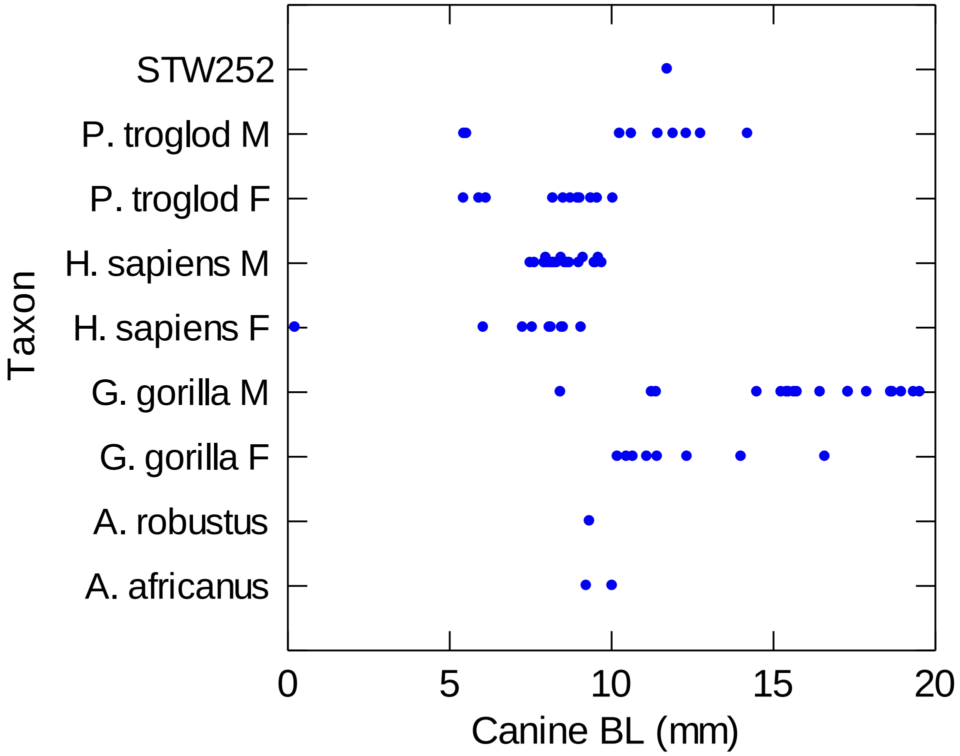

*Figure 8: Univariate analysis of Canine BL*

### *5.1.1.6 Canine MD*

When canine MD measurements are considered, *H. sapiens* male and females are clustered closely and align (Figure 9). StW 252 falls in the middle of the *P. troglodytes* male MD measurements and on the smaller end for the male *G. gorilla* measurements (Figure 9). *H. sapiens* is within the smaller sizes of the *G. gorilla* canine measurements, but fall within the canine MD measurements of *A. robustus* (Figure 9).

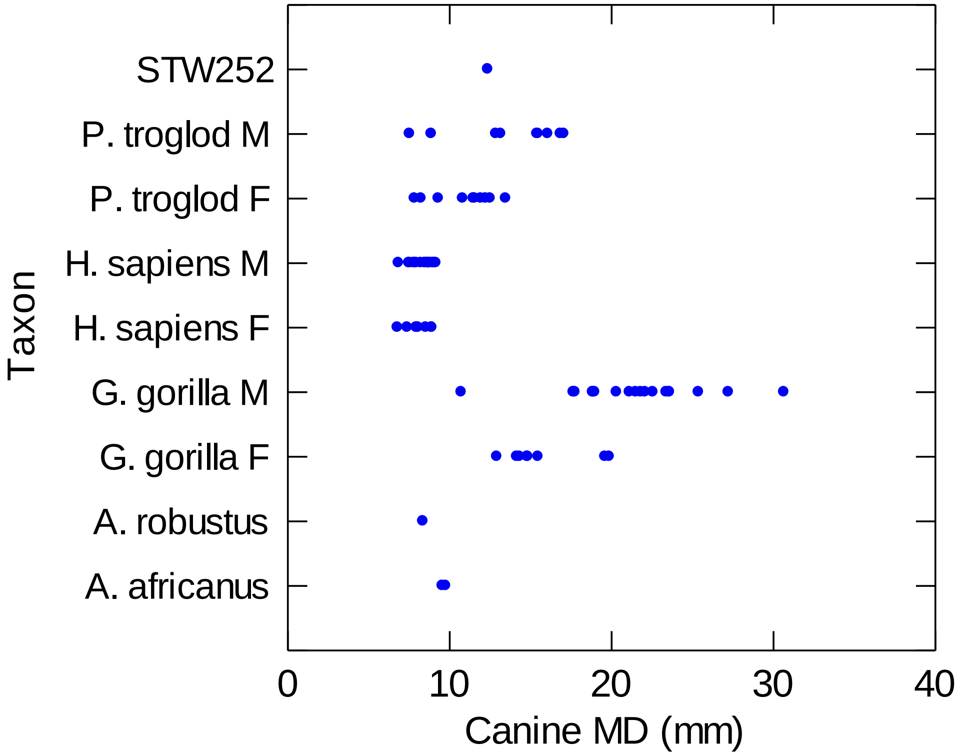

*Figure 9: Univariate analysis of canine MD*

#### 5.1.1.7 P$^3$ BL

When P$^3$ BL measurements are considered, StW 252 is positioned away from both *P. troglodytes* and *H. sapiens* male and female dimensions (Figure 10). StW 252 falls more within range of that of *G. gorilla*, *A. robustus*, and *A. africanus* for P$^3$ measurements (Figure 10). *A. robustus* is projected larger than *A. africanus* and all of the individuals that comprise the *A. robustus* collection cluster more tightly and closer to StW 252 in contrast to *A. africanus* (Figure 10). StW 252, *A. robustus*, and *A. africanus* are situated on the smaller end of the *G. gorilla* measurements and are more closely positioned with the female *G. gorilla* P$^3$ BL dimensions (Figure 10).

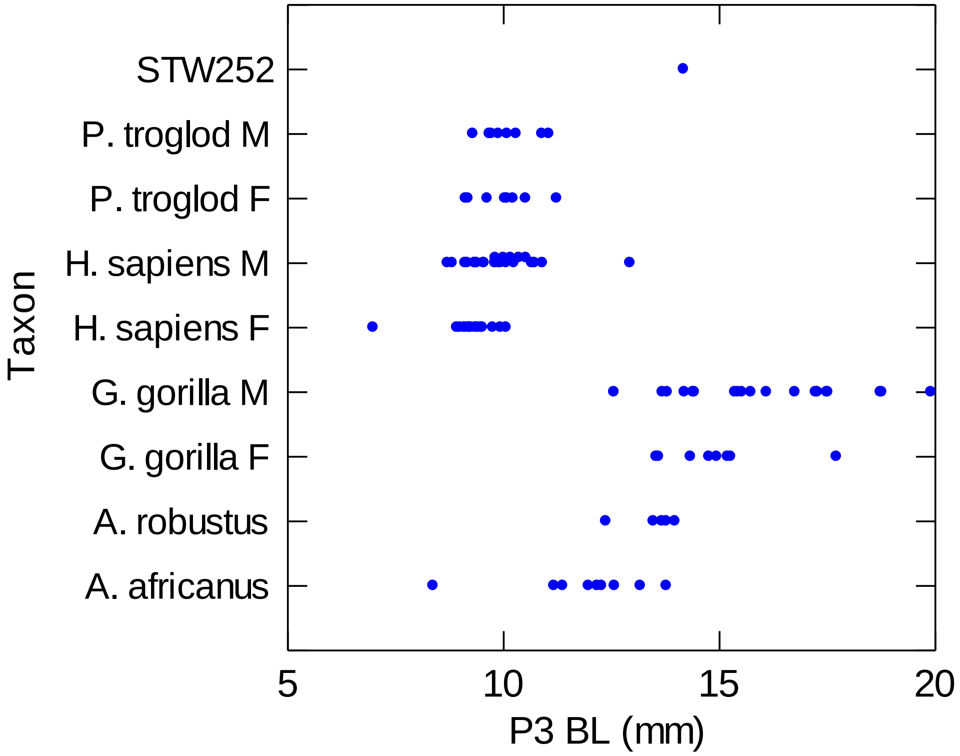

*Figure 10: Univariate analysis of $P^3$ BL*

### ***5.1.1.8 $P^3$ MD***

Similar to the $P^3$ BL measurements, StW 252 is positioned away from *H. sapiens* and *P. troglodytes* for $P^3$ MD measurements (Figure 11). *G. gorilla* males and females align and some female measurements are larger than some male measurements (Figure 11). *A. robustus* and *A. africanus* are clustered on the smaller end of the *G. gorilla* measurements. *A. africanus* overlap with *H. sapiens* male and female measurements for the $P^3$ MD (Figure 11). StW 252 falls on the larger end of the $P^3$ MD measurements with *A. robustus* and is situated away from *A. africanus* (Figure 11).

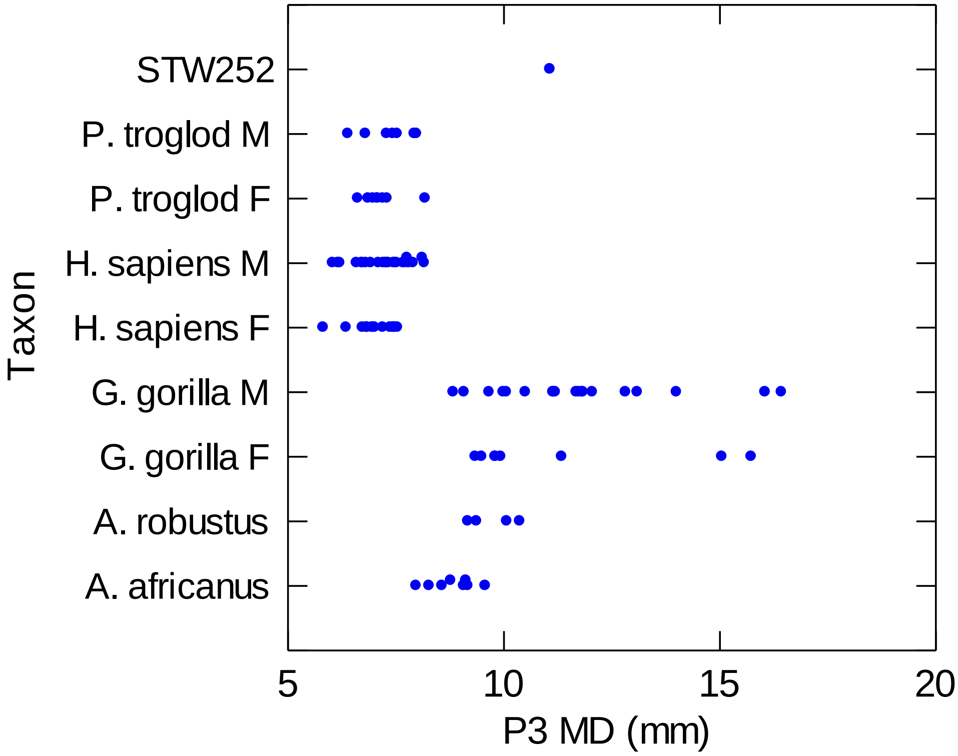

*Figure 11: Univariate analysis of $P^3$ MD*

### *5.1.1.9 $P^4$ BL*

StW 252 is situated away from *P. troglodytes* and *H. sapiens* for $P^4$ BL measurements and aligns more closely with *G. gorilla* male and female measurements as well as with *A. robustus* measurements (Figure 12). *A. africanus* has the most variability for $P^4$ BL measurements because these measurements have the most distance between each other in contrast to *H. sapiens* male measurements that are clustered very tightly together (Figure 12).

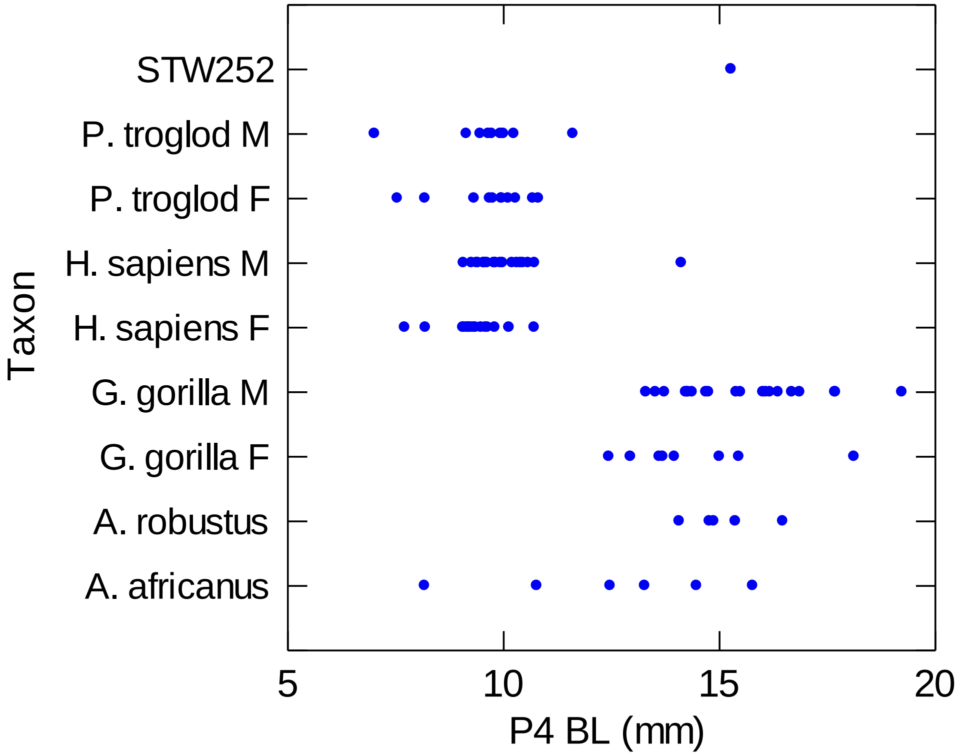

*Figure 12: Univariate analysis of $P^4$ BL*

### *5.1.1.10 P4 MD*

When $P^4$ MD measurements are considered, StW 252 is positioned away from *P. troglodytes* and *H. sapiens* measurements (Figure 13). StW 252 is more similar with *G. gorilla* male and *A. robustus* $P^4$ MD measurements. *A. africanus* overlaps some with *A. robustus*/ However, three *A. africanus* individuals fall outside of the smallest measurement for *A. robustus*. *A. robustus* measurements align closely with *G. gorilla* female measurements.

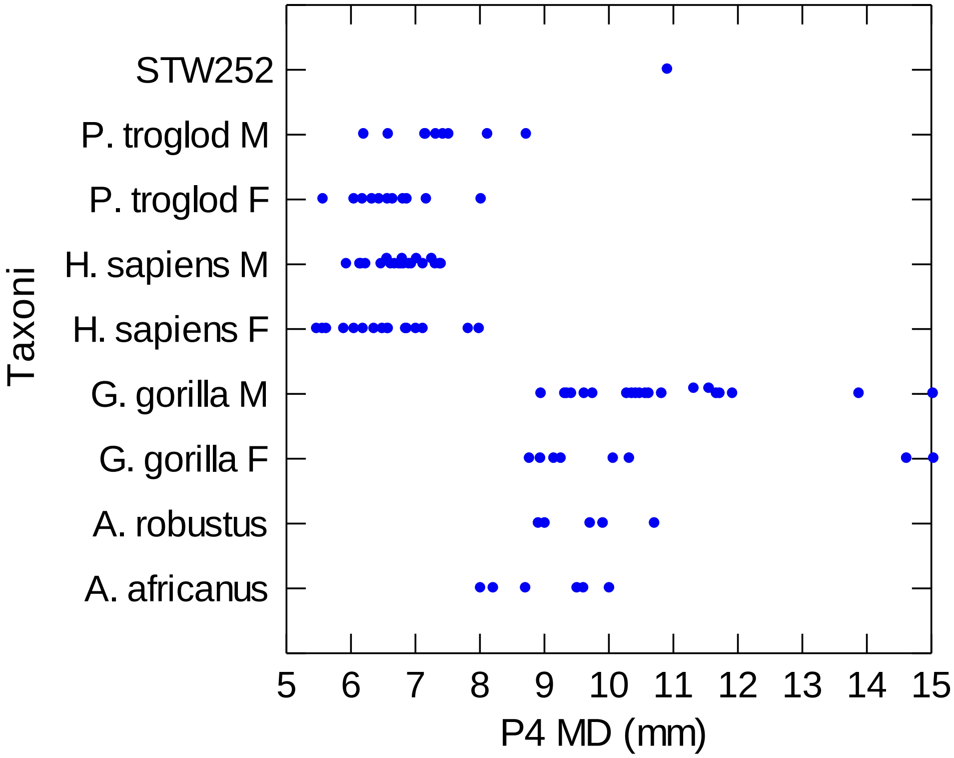

*Figure 13: Univariate analysis of* $P^4$ *MD*

### 5.1.1.11 Geometric Mean of $M^1$-$M^3$

When the molar measurements are scaled to the geometric mean, StW 252 is positioned away from *P. troglodytes* and *H. sapiens* and falls in the range of *G. gorilla*, *A. africanus,* and *A. robustus* measurements (Figure 14). *A. africanus* and *A. robustus* are similar in that they cluster on the smaller end of the *G. gorilla* male and female $M^1$-$M^3$ measurements (Figure 14). StW 252 falls directly outside of the M1-M3 measurements of *A. robustus* and *A. africanus* (Figure 14).

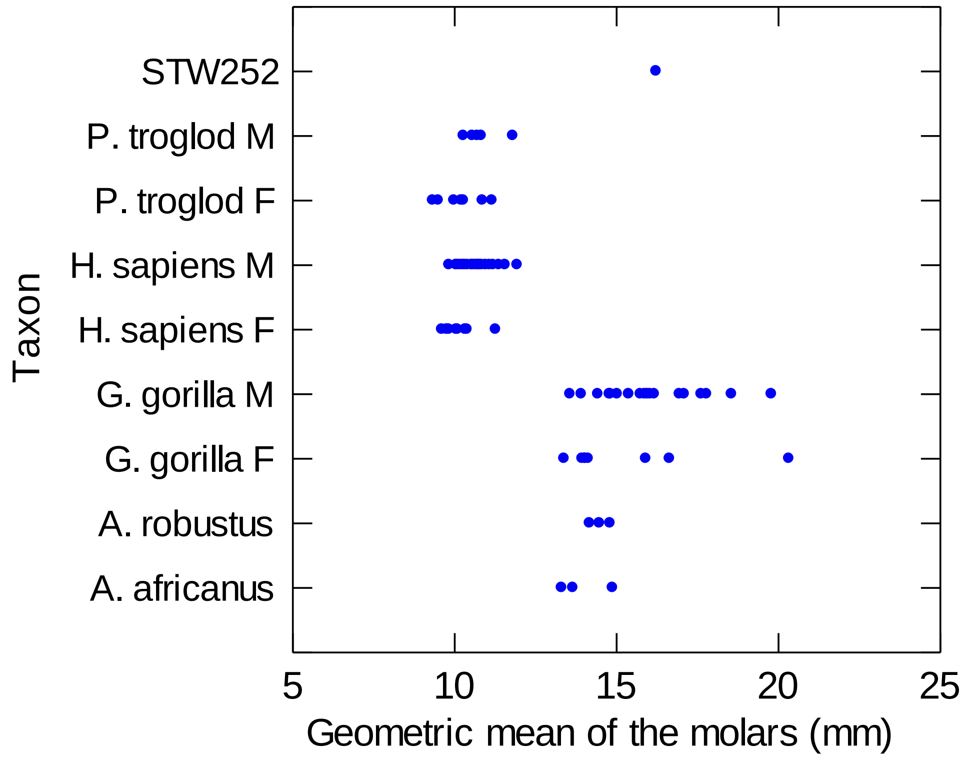

*Figure 14: Geometric Mean of* $M^1$-$M^3$

### **5.1.2 Bivariate scatterplot analysis**

#### **5.1.2.1 $I^1$ MD-BL**

StW 252 falls just outside of the 95% confidence ellipse around the group centroid of *P. troglodytes* and *G. gorilla*. *A. africanus* is not well represented in this chart due to the lack of $I^1$ measurements, however, the one *A. africanus* individual that is on the chart is right on the 95% ellipse of *H. sapiens* dimensions (Figure 15). None of the *A. robustus* individuals represented in this study are present on the chart due to a lack of $I^1$ measurements. One of the *H. sapiens* falls within the 95% confidence ellipse around the group centroid for *G. gorilla*.

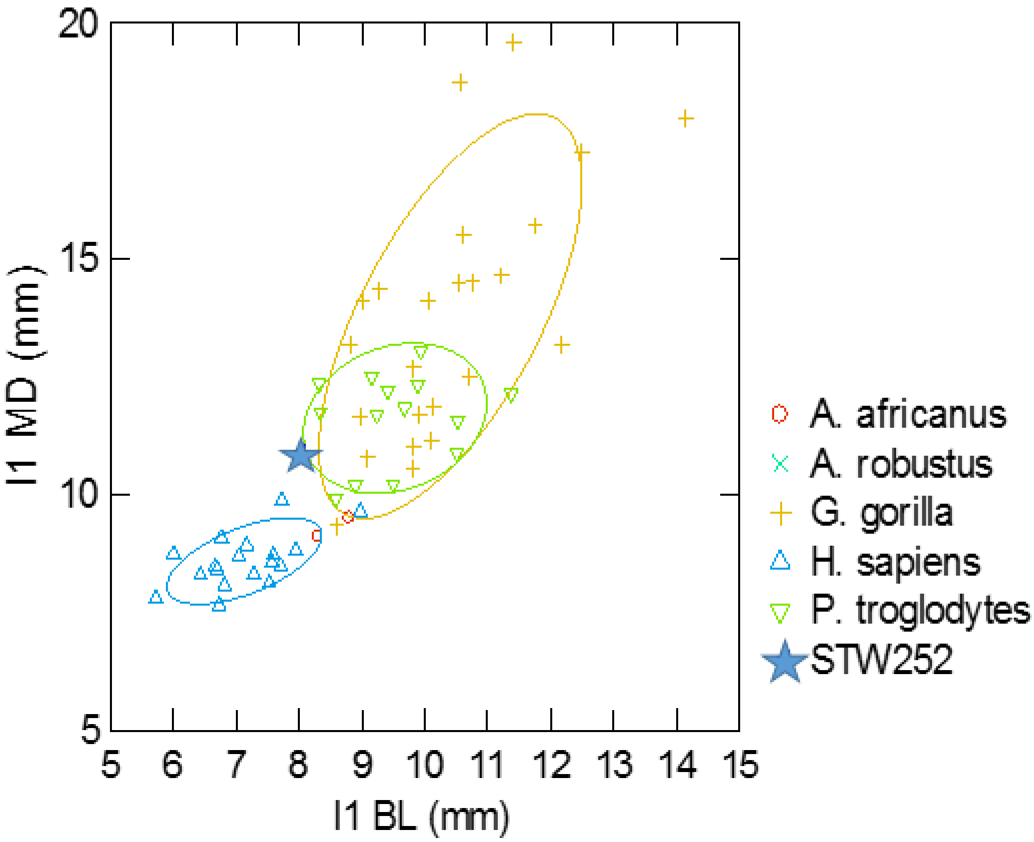

*Figure 15: I$^1$ MD-BL dimensions*

### 5.1.2.2 I$^2$ MD-BL

For I$^2$, *H. sapiens*, *P. troglodytes*, *A. robustus*, and StW 252 fall completely within the 95% confidence ellipse around the group centroid of *A. africanus*. One *A. robustus*, SK 52, clusters among *H. sapiens* with two *A. africanus*, Sts 52 and StW 126. StW 252 is more closely positioned on the smaller side of *P. troglodytes* and the larger side of *H. sapiens*. One *A. robustus*, Sk 52, individual falls within the 95% confidence ellipse of *H. sapiens* (Figure 16).

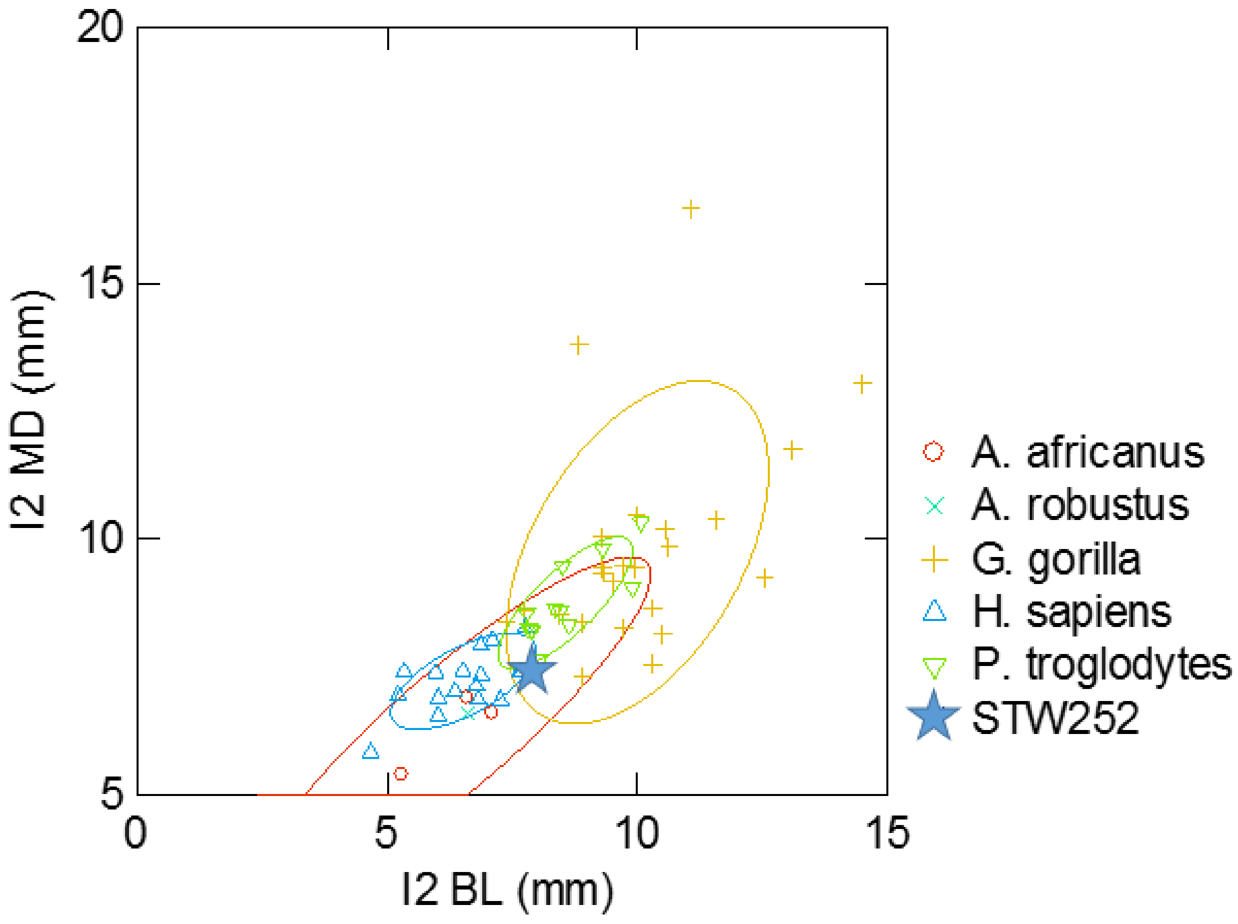

*Figure 16: $I^2$ MD-BL dimensions*

### ***5.1.2.3 Canine MD-BL***

When canine dimensions are considered, StW 252 is found outside of the 95% confidence ellipses around group centroids of the comparative samples (Figure 17). StW 252 is positioned in between the confidence ellipse for *A. africanus* and *G. gorilla*. The one *A. robustus* individual, SK 48, is found close to the distribution of humans and is distant from StW 252. *Pan troglodytes* is a scaled-down version of *G. gorilla* and is not similar to StW 252.

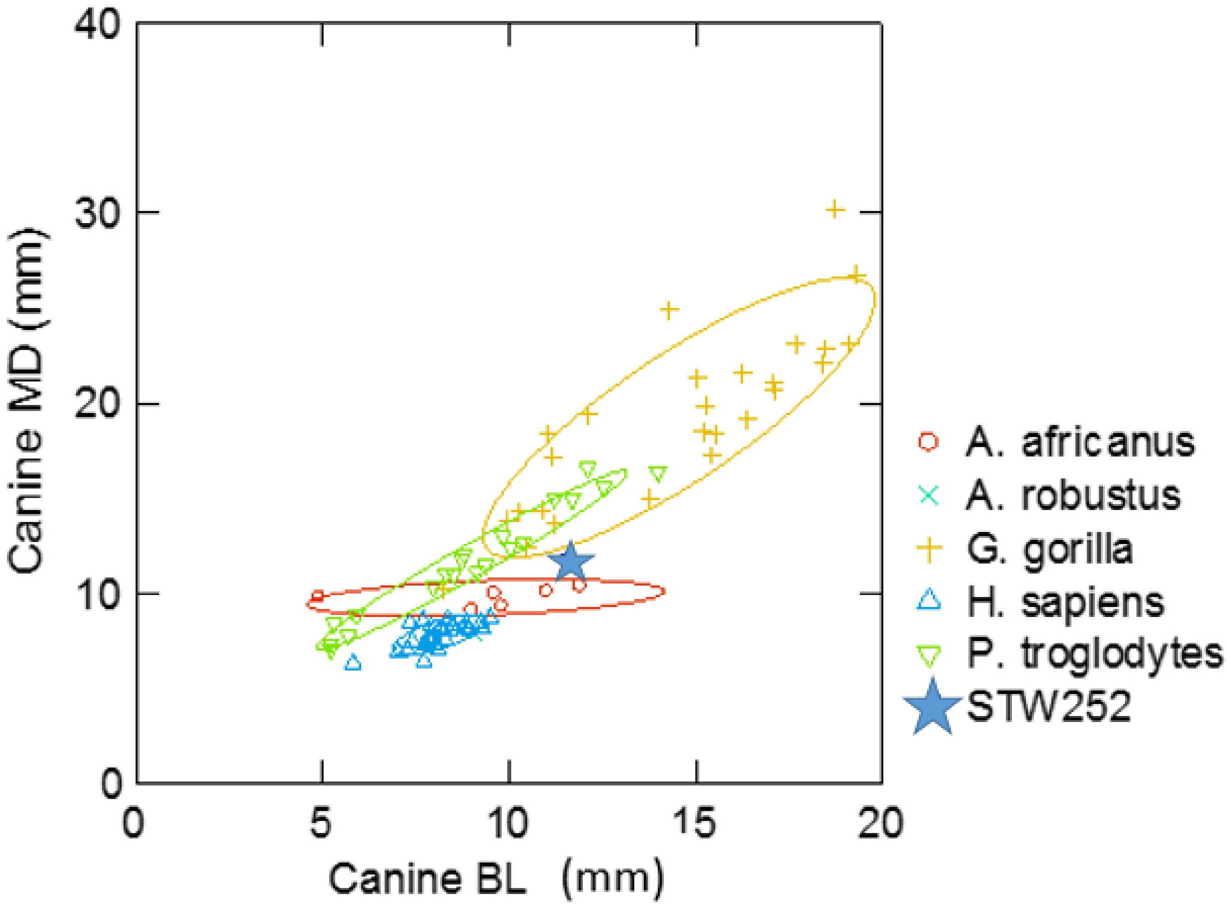

*Figure 17: Canine MD-BL dimensions*

### *5.1.2.4 P³ MD-BL*

When $P^3$ is examined, StW 252 with its molariform premolars is situated on the margin of the 95% confidence ellipse of the group centroid for *A. robustus*; this confidence ellipse overlaps with that of *G. gorilla* which also has relatively large premolars (Figure 18). The 95% confidence ellipse around the group centroid for *A. africanus* overlaps extensively with that for *A. robustus* and is smaller suggesting less variability (Figure 18). Meanwhile, the $P^3$ for *H. sapiens* and *P. troglodytes* is positioned away from the other taxa due to the relatively small dimensions of this tooth.

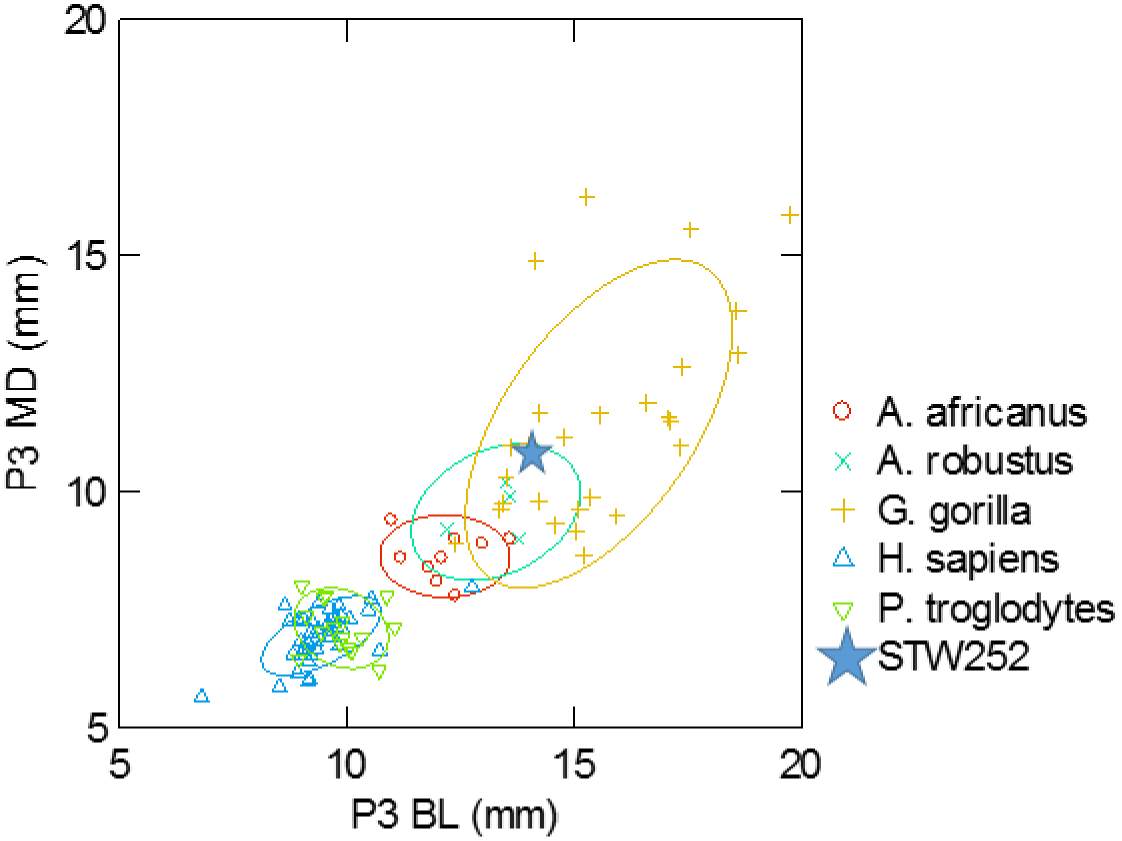

*Figure 18: $P^3$ MD-BL dimensions*

### 5.1.2.5 $P^4$ MD-BL

When $P^4$ is considered, StW 252 falls within the 95% confidence ellipse of *G. gorilla* and just outside of the 95% confidence ellipse of *A. robustus* (Figure 19). Both StW 252 and *A. robustus* are within range of or completely clustered with *G. gorilla*. $P^4$ measurements for *P. troglodytes* and *H. sapiens* are positioned away from StW 252, *A. robustus*, and *G. gorilla* measurements, but fall within the 95% confidence ellipse of *A. africanus*.

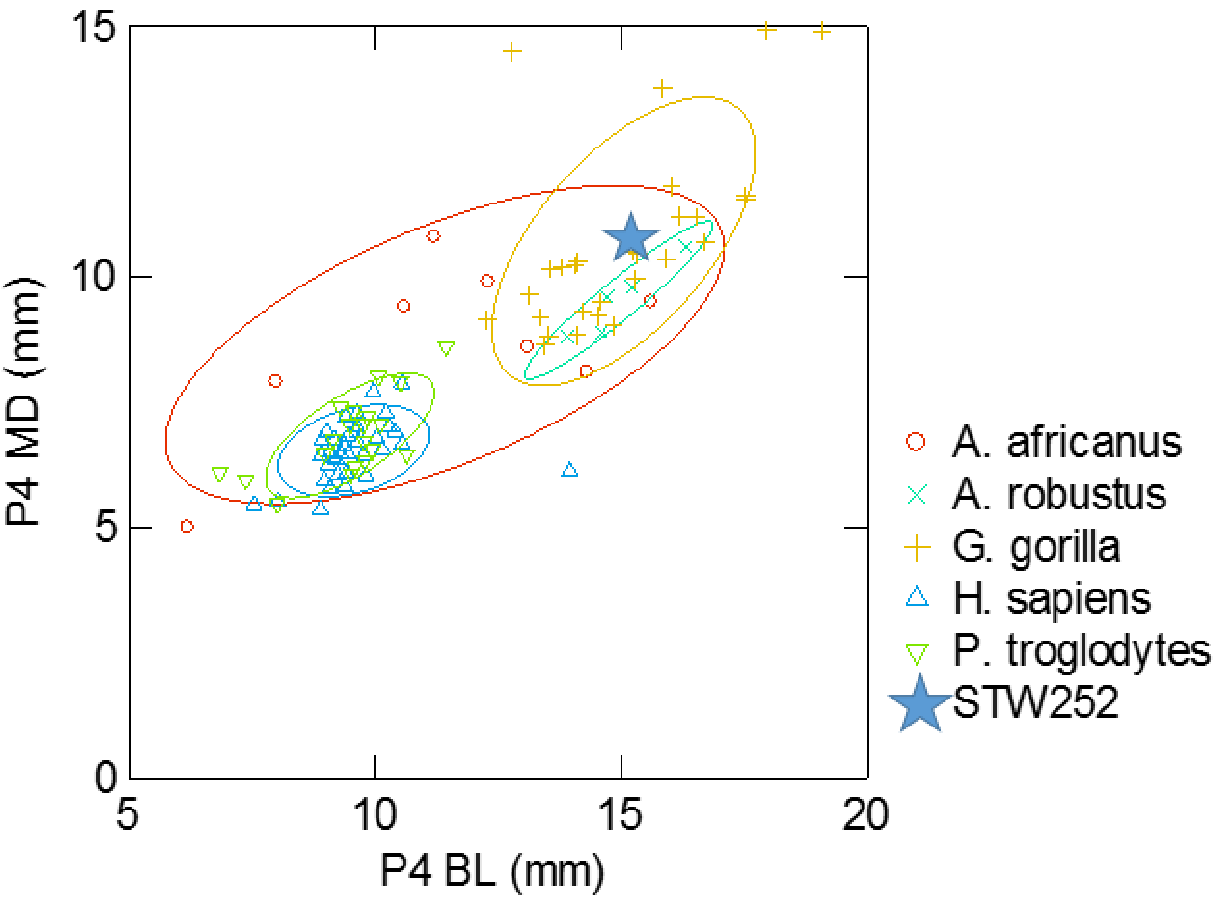

*Figure 19: P$^4$ MD-BL dimensions*

### *5.1.2.6 M$^1$ MD-BL*

StW 252 falls within the range of *G. gorilla* M$^1$ dimensions and close to the 95% confidence ellipse for *A. africanus* (Figure 20). The 95% confidence ellipses around group centroids of *A. africanus* and *A. robustus* overlap with those of *G. gorilla* (Figure 7). M$^1$ dimensions of *P. troglodytes*, which are much smaller than StW 252, overlap and cluster more closely with *H. sapiens*. Unlike the P$^3$ dimensions (Figure 19), *H. sapiens* and *P. troglodytes* both overlap with *A. robustus*.

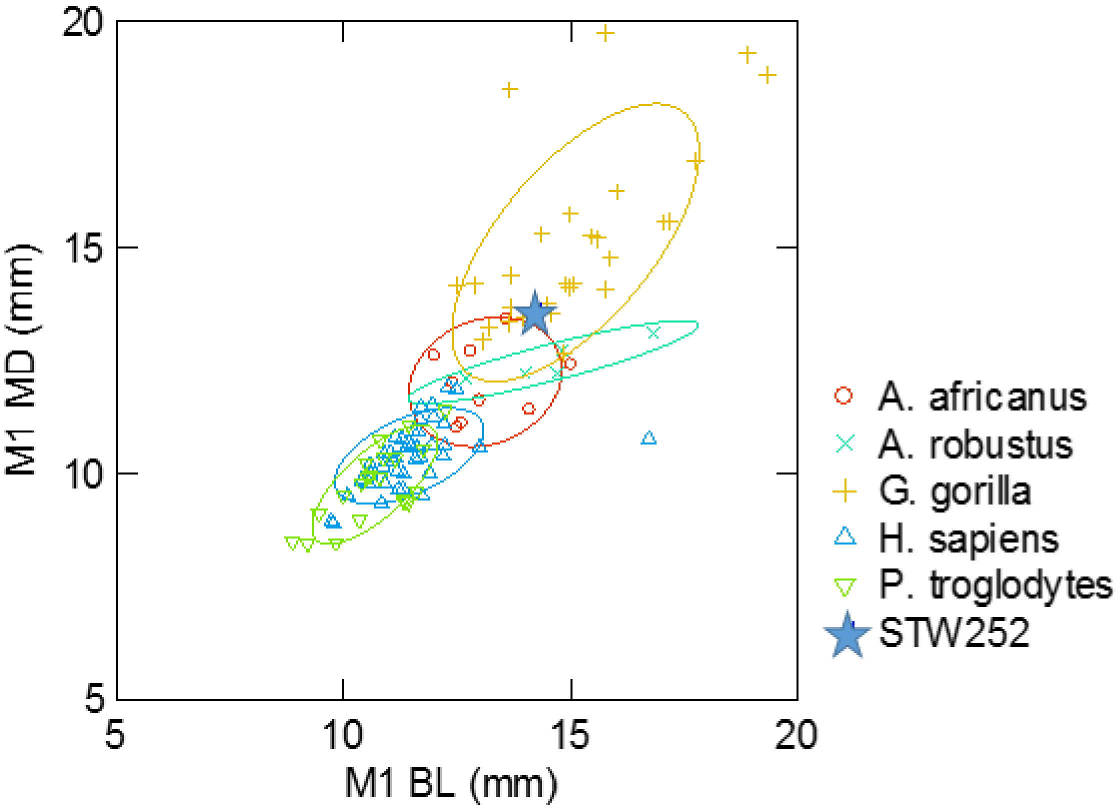

*Figure 20: M$^1$ MD-BL dimensions*

### *5.1.2.7 M$^2$ MD-BL*

StW 252 is on the cusp of the 95% confidence ellipse around the group centroid of *G. gorilla* for M$^2$ dimensions (Figure 21). StW 252 has relatively large buccolingual measurements whereas *G. gorilla* M$^2$ measurements gradually increase mesiodistally as a function of buccolingual size. *A. robustus* and *A. africanus* are clustered with *G. gorilla*, however, *G. gorilla* measurements are increasing mesiodistally rather than buccolingually as size increases which is not observed in *A. africanus* and *A. robustus*.

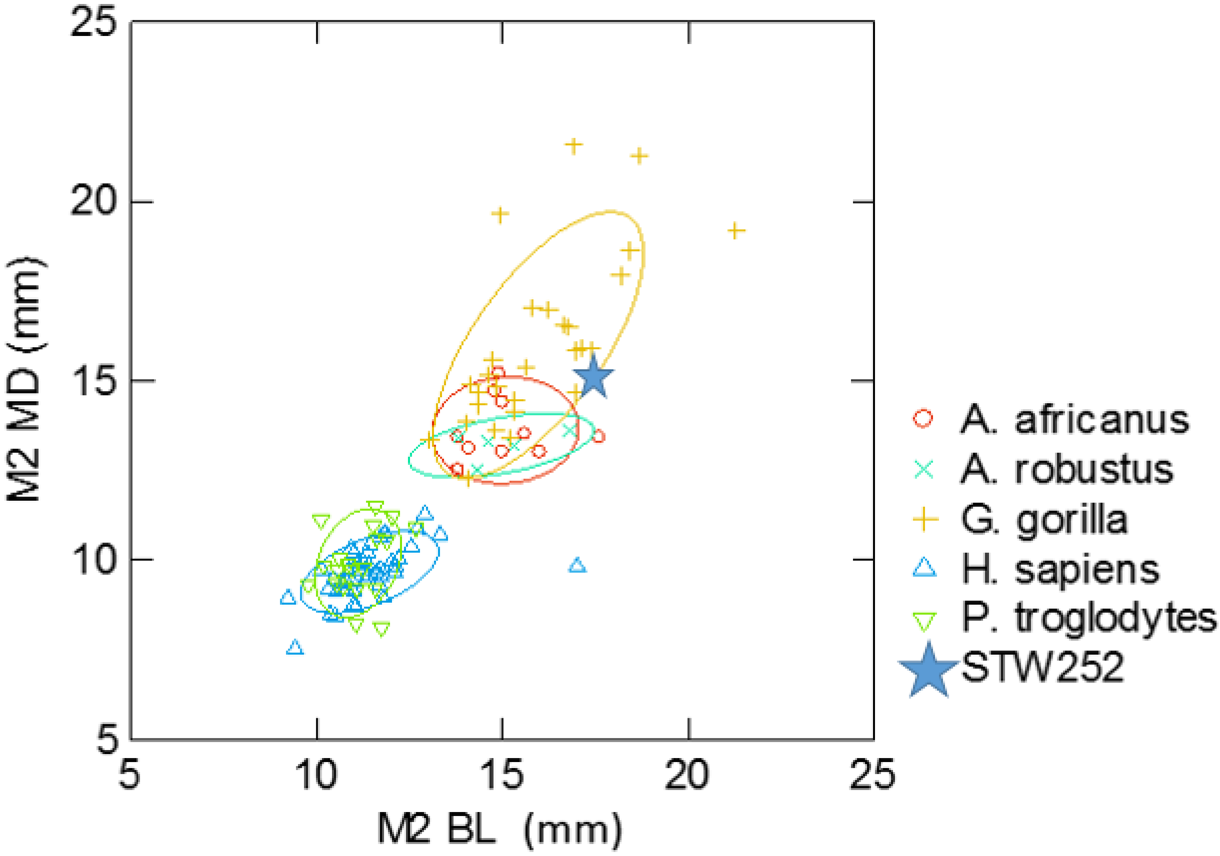

*Figure 21: M$^2$ MD-BL dimensions*

### **5.1.2.8 M$^3$ MD-BL**

For M$^3$ measurement, *P. troglodytes* and *H. sapiens* are positioned away from *G. gorilla, A. africanus, A. robustus*, and StW 252 (Figure 22). The position of *H. sapiens* and *G. gorilla* is similar to that seen in the M$^1$ measurements. StW 252 is situated on the 95% confidence ellipse around the group centroid of *G. gorilla* and near the 95% confidence ellipse of *A. africanus* and *A. robustus.*

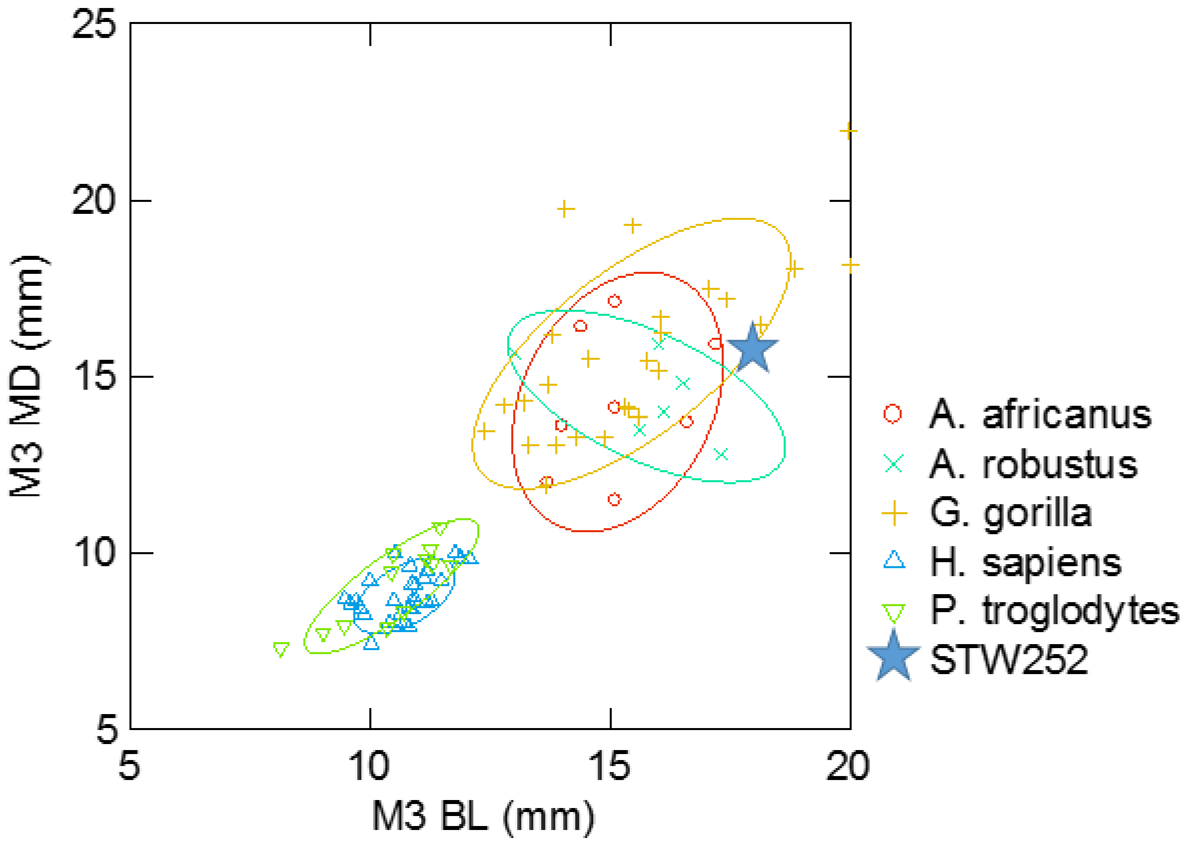

*Figure 22: M$^3$ MD-BL dimensions*

### *5.1.3 ANOVA Results*

When an analysis of variance is considered, more between-group variation for some traits is seen when compared to others. The canines BL have a low F-value at 26.232 whereas the lowest F-value for all of the BL values is in the second incisor at 16.249 (Table 3). The F-values are strong in M$^2$. The highest F-values for the BL dimensions is 106.737 for P$^3$ (Table 3). The lowest F-value for the MD values is 9.400 for I$^2$. The highest F-value the MD values is 105.244 for M$^2$ .

When I$^2$ BL measurements are considered, StW 252 is not as large as *G. gorilla*. Rather, StW 252 is somewhat *P. troglodytes*-like and not very australopith-like. With respect to canine measurements, StW 252 is unlike any of the comparative sample and is positioned in between *G. gorilla* and *P. troglodytes*. The $P^3$ measurements of StW 252 appear to be more similar to *A. robustus*, whereas the $P^4$ measurements tend to be more like *A. robustus* and *G. gorilla*. $M^1$ measurements for StW 252 fall within the parameters of *A. robustus* and *G. gorilla* which means the molars for StW 252 are relatively large. StW 252 canine mesiodistal measurements are unlike *G. gorilla* and are closer to *P. troglodytes*. $M^3$ measurements are similar to that of *A. robustus* and *G. gorilla*.

For the pairwise comparison, $I^1$ buccolingual measurements were not considered because *A. robustus* is inadequately represented.

*Table 3: ANOVA results for all individuals*

| ID | F-Value | P-Value |
|---|---|---|
| I1 BL | 34.287 | 0.000 |
| I2 BL | 16.249 | 0.000 |
| C BL | 26.232 | 0.000 |
| P3 BL | 106.737 | 0.000 |
| P4 BL | 70.429 | 0.000 |
| M1 BL | 56.600 | 0.000 |
| M2 BL | 73.686 | 0.000 |
| M3 BL | 55.836 | 0.000 |
| I1 MD | 21.608 | 0.000 |
| I2 MD | 9.400 | 0.000 |
| C MD | 48.328 | 0.000 |
| P3 MD | 58.329 | 0.000 |

| | | |
|---|---|---|
| P4 MD | 54.420 | 0.000 |
| M1 MD | 89.868 | 0.000 |
| M2 MD | 105.244 | 0.000 |
| M3 MD | 75.034 | 0.000 |

### ***5.1.4 Tukey's Pair-wise Comparisons***

#### ***5.1.4.1 BL Measurements***

When $I^2$ BL pairwise differences are considered, *G. gorilla* and *A. africanus* are the most distinct (Table 4). *H. sapiens* and *G. gorilla* are significantly different from each other and *P. troglodytes* and *H. sapiens* do not have the same BL measurements (Table 4). *A. africanus* and *A. robustus* are not significantly different for $I^2$ BL measurements (Table 4). With respects to canine BL measurements, *G. gorilla* and *A. africanus* are distinct. Typically, *H. sapiens* and *G. gorilla* are significantly different from each other in canine BL measurements (Table 4). *A. robustus* and *A. africanus* do not exhibit significant differences in canine BL measurements. *A. robustus* and *A. africanus* do not have significant differences for $P^3$ BL measurements (Table 4). *H. sapiens* show significant $P^3$, $P^4$, $M^1$, $M^2$, and $M^3$ BL measurement differences with *A. robustus* and *A. africanus. A. robustus* and *A. africanus* are significantly different in $P^4$ BL measurements. *A. robustus* and *A. africanus* do not exhibit significant differences in $M^1$, $M^2$, and $M^3$ BL measurements (Table 4).

*Table 4: Tukey's Pairwise Comparisons of BL Measurements*

| **I2 BL** | **P-value** |
|---|---|
| *G. gorilla- A. africanus* | 0.011 |
| *H. sapiens- G. gorilla* | 0.000 |

| | |
|---|---|
| *P. troglodytes- H. sapiens* | 0.001 |
| **C BL** | |
| *G. gorilla- A. africanus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **P3 BL** | |
| *A. robustus- A. africanus* | 0.039 |
| *G. gorilla- A. africanus* | 0.000 |
| *G. gorilla- A. robustus* | 0.002 |
| *H. sapiens- A. africanus* | 0.000 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.008 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **P4 BL** | |
| *A. robustus- A. africanus* | 0.001 |
| *G. gorilla- A. africanus* | 0.000 |
| *H. sapiens- A. africanus* | 0.017 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.022 |
| *P. troglodytes- A. robustus* | 0.000 |

| | |
|---|---|
| *P. troglodytes- G. gorilla* | 0.000 |
| **M1 BL** | |
| *G. gorilla- A. africanus* | 0.001 |
| *H. sapiens- A. africanus* | 0.003 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **M2 BL** | |
| *H. sapiens- A. africanus* | 0.000 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **M3 BL** | |
| *H. sapiens- A. africanus* | 0.000 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |

#### *5.1.4.2 MD Measurements*

For $I^1$ MD comparisons, *A. robustus* and *A. africanus* do not have significant differences (Table 5). *G. gorilla* is significantly different from *A. africanus* and *H. sapiens* and *P. troglodytes* differs from *H. sapiens* for this measurement. When $I^2$ MD measurements are considered, *A. africanus* and *A. robustus* do not differ significantly. Additionally, *G. gorilla* and *A. africanus* are different and so are *H. sapiens* and *G. gorilla* in $I^2$ MD. *H. sapiens* are not significantly different from *A. africanus* and *A. robustus* in $I^2$ MD. *G. gorilla* exhibits differences with both *A. africanus* and *A. robustus* in canine MD measurements. Similar to that in $I^1$ and $I^2$, *H. sapiens* do not differ significantly from *A. africanus* and *A. robustus* in canine MD measurements. With respect to $P^3$ MD measurements, *H. sapiens* differs significantly from *A. africanus* and *A. robustus*. *G. gorilla* shows significant differences with *A. africanus* and *A. robustus* in $P^3$ MD measurements. *H. sapiens* significantly differs from *A. robustus* and *A. africanus* in $P^4$, $M^1$, $M^2$, and $M^3$ MD measurements (Table 5).

*Table 5: Pairwise Comparison of MD Measurements*

| **I1 MD** | **P-Value** |
|---|---|
| *G. gorilla- A. africanus* | 0.015 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| *P. troglodytes- H. sapiens* | 0.000 |
| **I2 MD** | |

| | |
|---|---|
| *G. gorilla- A. africanus* | 0.004 |
| *H. sapiens- G. gorilla* | 0.000 |
| **C MD** | |
| *G. gorilla- A. africanus* | 0.000 |
| *G. gorilla- A. robustus* | 0.005 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| *P. troglodytes- H. sapiens* | 0.000 |
| **P3 MD** | |
| *G. gorilla- A. africanus* | 0.000 |
| *G. gorilla- A. robustus* | 0.049 |
| *H. sapiens- A. africanus* | 0.002 |
| *H. sapiens- A. robustus* | 0.001 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.020 |
| *P. troglodytes- A. robustus* | 0.006 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **P4 MD** | |
| *G. gorilla- A. africanus* | 0.001 |
| *H. sapiens- A. africanus* | 0.000 |
| *P. troglodytes- A. africanus* | 0.005 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |

| | |
|---|---|
| **M1 MD** | |
| *G. gorilla- A. africanus* | 0.000 |
| *G. gorilla- A. robustus* | 0.000 |
| *H. sapiens- A. africanus* | 0.001 |
| *H. sapiens- A. robustus* | 0.002 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **M2 MD** | |
| *G. gorilla- A. africanus* | 0.000 |
| *G. gorilla- A. robustus* | 0.001 |
| *H. sapiens- A. africanus* | 0.000 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |
| **M3 MD** | |
| *H. sapiens- A. africanus* | 0.000 |
| *H. sapiens- A. robustus* | 0.000 |
| *H. sapiens- G. gorilla* | 0.000 |
| *P. troglodytes- A. africanus* | 0.000 |

| | |
|---|---|
| *P. troglodytes- A. robustus* | 0.000 |
| *P. troglodytes- G. gorilla* | 0.000 |

### *5.1.5 Molar Only Statistical Analyses*

#### *5.1.5.1 Principal Components Analysis*

A principal components analysis of five molar dimensions (M$^1$ BL, M$^2$ BL, M$^2$ MD, M$^3$ BL, M$^3$ MD) yields only one axis with an eigenvalue over 1.0 suggesting that the first axis was primarily size-related (Figure 23). The component loadings confirm the size-related function of the first axis with values between 0.941 and 0.972 (Table 6). The first PC axis accounts for 91.1% of the variance explained, and separates *P. troglodytes* and *H. sapiens* with small molar dimensions from *G. gorilla* and australopiths with larger molars. StW 252 is positioned on the margin of the 95% confidence ellipse around the group centroid for *A. africanus* and exhibits larger molars than any of the individuals from the fossil taxa (Figure 23).

The second PC axis, accounting for 5.3% of the variance, partly contrasts *A. africanus* and *A. robustus* (Figure 23). The majority of *A. africanus* specimens are negatively projected on the basis of the negative loadings for M$^2$ and M$^3$ MD, whereas *A. robustus* and StW 52 are positioned in a positive direction on PC Axis 2 due to the positive loadings of the other dental traits, particularly M$^1$ BL (Figure 23; Table 6). This suggests that like *A. robustus*, StW 252 has a relatively large BL dimension of M$^1$ with respect to the sizes of the other molars.

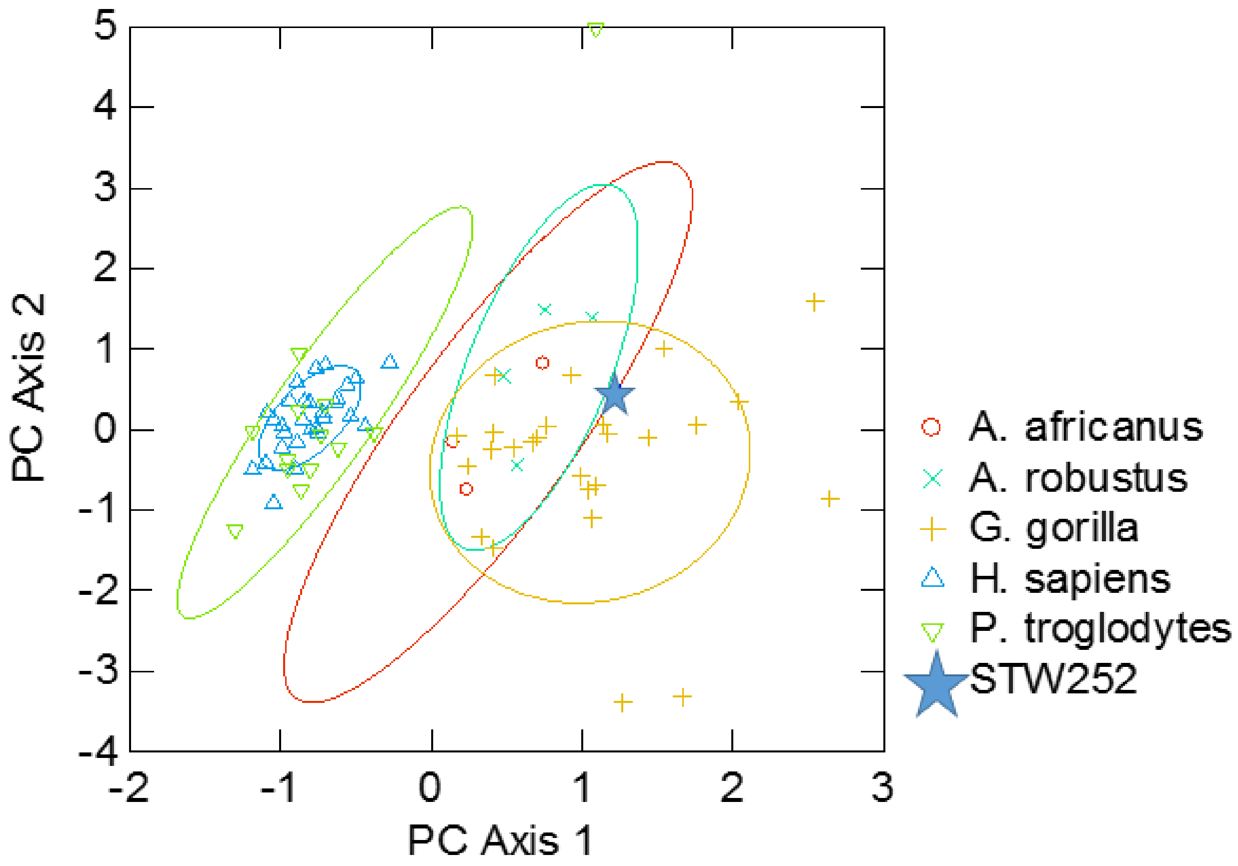

*Figure 23: Principal components analysis*

*Table 6: Principal Components Analysis Component Loadings*

| | **1** | **2** |
|---|---|---|
| M1 BL | 0.951 | 0.227 |
| M2 BL | 0.972 | 0.148 |
| M3 BL | 0.953 | 0.181 |
| M2 MD | 0.941 | -0.310 |
| M3 MD | 0.956 | -0.251 |
| Variance Explained by Components | 4.556 | 0.266 |
| Percent of Total Variance Explained | 91.129 | 5.318 |

### *5.1.5.2 Discriminant Function Analysis*

The jackknife test classifies StW 252 as *A. africanus* for the molars-only comparison (Table 7). This classification is a product of discriminant function analysis, which is the boot strapped version. The initial classification yielded 100% for *A. africanus* and 75% for *A. robustus* and StW 252 is classified in its own category (Table 8). The Jackknifed test misclassifies one *A. robustus* as *A. africanus* and another *A. robustus* as *G. gorilla.* To determine which individuals were misclassified, a Mahalanobis' Distance test was conducted. Mahalanobis' Distances show that SK 13/14 is misclassified as *A. africanus*, but only marginally given the small difference in Mahalanobis' Distances for *A. africanus* (9.5) compared to *A. robustus* (9.6) *A. robustus* respectfully. Additionally, TM 1517, the type specimen for *A. robustus* (Cofran and Thackery, 2010), was misclassified as *G. gorilla*, however the Mahalanobis' Distance for this individual (13.1) is actually lower than that for *G. gorilla* (13.4) so, TM 1517 should be correctly classified as *A. robustus*. This misclassification is most likely an artifact from the procedure to calculate the Jackknifed classification. *A. robustus* is different than *A. africanus* in having a lower classification rate.

*Table 7: Jackknifed Classification*

| | Correct Percentage |
|---|---|
| *A. africanus* | 100 |
| *A. robustus* | 50 |
| *G. gorilla* | 54 |
| *H. sapiens* | 66 |
| *P. troglodytes* | 67 |
| StW 252 | 0 |

| | |
|---|---|
| Total | 61 |

*Table 8: Classification Matrix*

| | Correct Percentage |
|---|---|
| *A. africanus* | 100 |
| *A. robustus* | 75 |
| *G. gorilla* | 58 |
| *H. sapiens* | 76 |
| *P. troglodytes* | 75 |
| StW 252 | 100 |
| Total | 71 |

#### ***5.1.5.3 Cluster Analysis Unscaled***

A cluster analysis links A. *africanus* and *A. robustus* by the shortest branch length and StW 252 is grouped to these taxa by a medium branch length (Figure 24). *Gorilla gorilla* is linked to the fossil taxa by a relatively long branch length and this cluster is distinct from both *P. troglodytes* and *H. sapiens* which are joined together by a medium branch length (Figure 24).

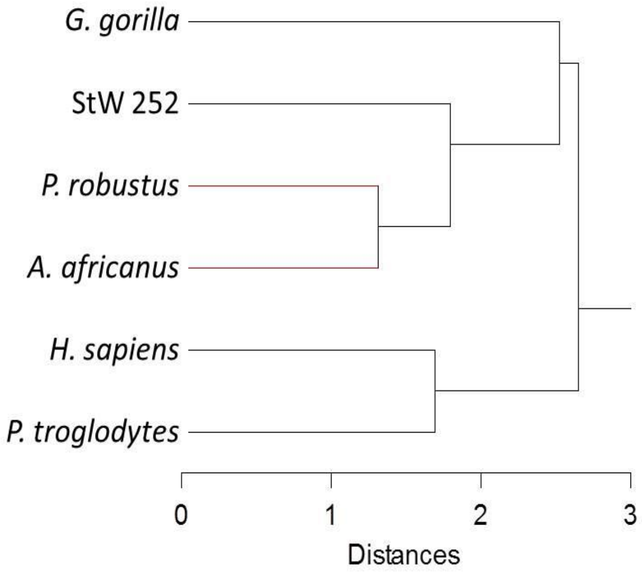

*Figure 24: Cluster Tree unscaled to account for taxonomic size differences*

#### *5.1.5.4 Cluster Analysis Scaled to Geometric Means*

The cluster tree analysis demonstrates that StW 252 and *A. africanus* are more similar. *A. robustus* clusters with the group containing StW 252 and *A. africanus* (Figure 25). *H. sapiens* is grouped to the branch including *A. africanus, A. robustus,* and StW 252. *G. gorillas* and *P. troglodytes* are grouped furthest away from StW 252, *A. africanus, A. robustus*, and *H. sapiens.* Out of every taxon represented in this project, StW 252 clusters closest to *A. africanus*. Since 15 out of 16 dental measurements were included and the data were scaled by the geometric mean, removing size as a factor, this cluster tree represents the most comprehensive analysis performed.

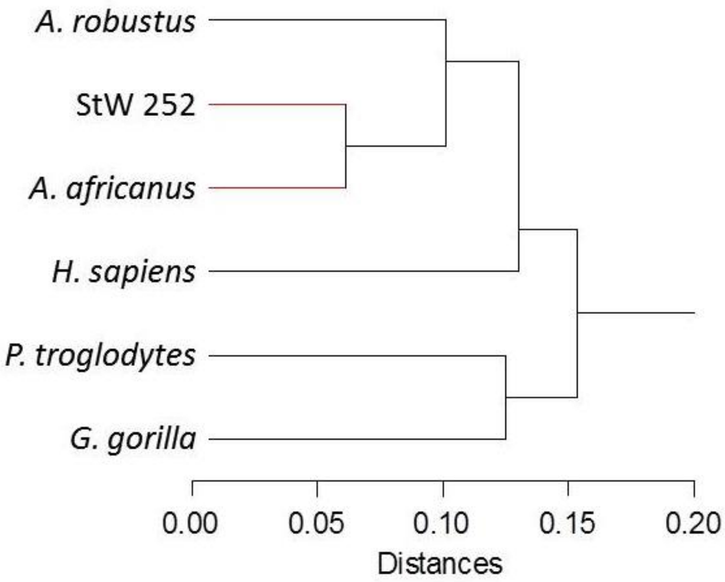

*Figure 25: Cluster tree*

## 5.2 Qualitative Analyses

Williams unpublished field notes state the following observations: “Sts 71 is comprised of a nearly complete right half cranium. The face is shorter than that of Sts 5, but also broader, particularly in the lower maxillary region including the nasal region. Actually the skull includes more than half of the cranium, the entire anterior portion of the palate, half of the lower inferior left orbit, and complete right orbit. The position of the glabella, nasion, and anterior nasal spine are intact.  Although both anterior and posterior halves of the left zygomatic arch are preserved, some distortion to the cranial vault does not permit their realignment. This is true to a lesser extent to the lateral orbital wall (frontomaxillary articulation).”

Williams unpublished field notes also state that “The temporal lines are more marked on Sts 71 (and more medially placed) than Sts 5. The lateral posterior portions of the cranial vault are largely contorted from separate, but adjoining pieces and although the mastoid process is largely complete, as cracking along its inferolateral border has artificially lengthened it mediolaterally. The mastoid is a bit larger and more pointed than in Sts 5 despite the damage exhibited by both crania. The posterior cranial vault appear much flatter and more vertical in Sts 71. With respect to Sts 5, the palate of Sts 71 is wider and shorter. The teeth are heavily worn, particularly in $M^1$ and $P^4$ and age is estimated at advanced adult. Not only are the teeth heavily worn, but they are cracked and partially shattered. Dentine is exposed on all of the preserved teeth ($RM^3$, $M^1$, $M^2$, and $P^4$) except for $M^3$. $LP^3$ is fragmented and so is $P^3$ and $P^4$. The premaxillary and median palatine sutures are completely obliterated. The two canines exhibit better preservation on the right rather than the left. Left $I^1$ and $I^2$ are preserved. Right $I^2$ and the lateral $I^1$ wall are absent. The space between the zygomatic arch and the neurocranium in Sts 71 is much shorter lengthwise, but perhaps similar in its depth to Sts 5. Although Sts 71 has a well preserved glabella and the midline of the cranial vault, at the apex of the cranium, the preservation line zig-zags around the midline of the cranium. The occipital squama is slightly better preserved although reconstructed on only slightly more than half its original size. The posterior aspect of the foramen magnum maybe preserved although its details are not. The basicranium except much of the palate is absent."

The frontal fragment for StW 252 is observed with concavity of the frontal squama right above the glabella of which is similar to that expressed in Sts 71 (Clarke, 1988). StW 252 exhibits a rather thin, flattened supra-orbital margin and the glabella is not particularly protuberant (Clarke, 1988). The nasion on StW 252 is positioned above the frontomaxillary suture near the glabella (Clarke, 1988). Both StW 252 and Sts 71 exhibit very large molars and premolars (Clarke, 1988). Incisors and canines are rather large as well and larger than those of *A.*

*robustus* (Clarke, 1988). There exists diastemata between $I^2$ and the canine on StW 252 (Clarke, 1988). Other morphological similarities that StW 252 and Sts 71 share include a high rounded occipital region, large posterior teeth, and front facing zygomatic processes of the maxilla (Clarke, 1988). Sts 71 has less subnasal prognathism than Sts 5 (Williams, unpublished field notes).

# 6 DISCUSSION

Overall StW 252 falls closest to other fossil australopith taxa but is distinct in having both larger anterior and posterior dental dimensions. Yet, its canine dimensions are unique and do not fall within the distribution of the comparative taxa. The anterior premolar of StW 252 falls slightly outside the range of *A. robustus*, and the molars are slightly larger than those of *A. africanus* in both dimensions. The premolar and molar dimensions are somewhat gorilla-like. However, these teeth fall within the range of female gorillas, and StW 252 is suggested to be a male. This could mean that the dental measurements for StW 252 are not as drastically large as *G. gorilla* dental measurements especially if they are similar in size to female gorillas. If StW 252 is a male as suggested by Clarke (2013) and the dental measurements are closer in size to that of female gorillas, then this suggests that body size of StW 252 may have been closer in size to female gorillas or even smaller. The statistical analysis shows that StW 252 is relatively similar to *A. africanus* and *A. robustus*.

Sexual dimorphism is defined as pronounced physical differences between males and females (Lockwood, 1999; Balolia, 2010; Plavcan, 2012). The canine dimensions of StW 252 fall between *P. troglodytes* and *A. africanus* which could itself be indicative of social organization. However, the canine dimensions of *P. troglodytes* and *G. gorilla* are scaled versions on one another. The same could be said for *H. sapiens*, *A. robustus*, and *A. africanus*. In this way, StW 252 can be thought of as a scaled up version of other hominins in its canine dimensions, and distinct from canine crowns that characterize the African apes. If StW 252 and Sts 71 indeed represent a male and female of a novel species, as suggested by Clarke (2013), there should be an overall size difference in the canines, brow ridge, zygomatic arch, and molars. Regarding what is expressed in sex differences among *Pan troglodytes*, there should be a difference in canine morphology between StW 252 (male) and Sts 71 (female). However, for Sts 71 the dentition was so poorly preserved that canine morphology cannot be deciphered. The statistical results indicate that StW 252 expresses more uniqueness in regard to canine size rather than being similar in canine size to *P. troglodytes*.

The relatively large molars of StW 252 could be indicative of eating habits. Large molars are typically seen in mammals for grinding and chewing. Lucas et al. (1986) examined whether trends in post-canine dentition can suggest diet. This diet estimation was made by testing the M1 to M3 ratios to see if these ratios could indicate the percentage of leaves and flowers in the diet of arboreal and terrestrial non-human primates (Lucas et al., 1986). The sample was made up of cebids, arboreal cercopithecoids, and arboreal hominoids as well as terrestrial cercopithecoids (Lucas et al., 1986). The results yielded that for the arboreal species diet could be inferred by the M1 to M3 ratios. High ratios (r=0.75-0.87) suggest a higher percentage of leaves and fruits in the diet whereas a lower ratio (r=0.61- 0.82) indicated the opposite (Lucas et al., 1986). The ratio is calculated by finding the area of both M1 and M3 (BL X MD) and then dividing the numbers by each other (M1 Area/M3 Area) (Lucas et al., 1986; Teaford and Ungar, 2000). However, Lucas et al. (1986) concluded that for terrestrial species, a better way of calculating diet is based on relative body size. Is it possible to apply this ratio to hominins such as *A. africanus*?

In a study conducted by Teaford and Ungar (2000) the M1 to M3 ratios were modeled after the Lucas et al. (1986) study to provide insight into the diet of hominins. The sample size consisted of mandibular dental measurements and included measurements from *A. africanus* and *A. afarensis* (Teaford and Ungar, 2000). When the M1 to M3 ratio is calculated for StW 252, the number falls on the lower end at 0.687. Based on the results of Teaford and Ungar (2000), StW 252 is more similar to that of, in general, the australopiths. This suggests that the diet of the

South African australopiths is highly variable and may have included fruit and perhaps fewer leaves than folivorous monkeys. Dental microwear can show how individuals used their teeth and what foods they ate (Teaford and Ungar, 2000). Dental microwear analyses suggest that folivores have more long scratches on their molars whereas frugivores exhibit more pitting on their molars (Teaford and Ungar, 2000). Dental microwear on modern day non-human primates has been used to infer feeding behaviors and dietary strategies for fossils (Teaford and Ungar, 2000). Dental microwear for *A. robustus* suggests that there was more crushing and grinding of foods unlike the most gracile australopiths in South Africa (Grine, 1986). The robust australopiths found at Swartkrans and Kromdraai exhibited a diet that differed from their gracile counterparts from Sterkfontein, Taung, and Makapansgat (Grine, 1986; Scott et al., 2005).

The relatively large anterior dentition in StW 252 could indicate an adaptation for food preparation using the front teeth rather than tools as is possibly the case for *A. robustus*. These differences can be seen in the bivariate analysis of $I^2$ and canine buccolingual and mesiodistal dimensions. *A. africanus* and *A. robustus* are not significantly different in $I^1$, $I^2$, and canine BL and MD pairwise comparisons. However, this could be due to a lack of $I^1$ preservation in the *A. robustus* collection.

When the premolars are considered, StW 252 exhibits much larger sizes when compared to *A. africanus* and *A. robustus*. The premolar sizes are more similar to that of *G. gorilla* measurements. The robusticity of the premolars could be attributed to diet. This size difference could mean that StW 252 needed a large grinding surface while eating fall back foods. The preservation of the bicuspid morphology of the premolars for StW 252 could be interpreted as having a similar chewing pattern as humans. This chewing pattern starts the mastication of food with the anterior teeth, moves it toward the transitional premolars, and pushes food to the molars for the final grinding before swallowing occurs. Since the premolars are so large, perhaps the foods StW 252 was eating needed more grinding before being chewed by the molars.

The bivariate scatter plots for M1, M2, and M3 measurements plotted StW 252 either within the group centroid of the 95% confidence ellipse of *G. gorilla* or right on the margin of the 95% confidence ellipse of *G. gorilla* (Figure 20, 21, and 22). However, the cluster analysis (Figure 25) groups StW 252 more closely to that of *A. africanus* which partially supports Lockwood and Tobias (1999) classification of StW 252 as *A. africanus*. If StW 252 is more similar to that of *A. africanus*, then the diet should be made up of mostly soft fruit or leaves. However, if StW 252 molars are more similar to that of *A. robustus*, then the diet would include hard and tough to chew foods. The statistical analysis shows that StW 252 is a mix between *A. africanus* and *A. robustus*. This is evident when the bivariate analysis is considered. StW 252 falls either within *A. africanus* (Figure 15; Figure, 18) or right outside of *A. africanus* (Figure 17; Figure 20; Figure 21). With *A. robustus* StW 252 either falls within (Figure16; Figure 18) or close to the 95% confidence ellipse around the group centroid (Figure 19; Figure 20; Figure 21; Figure 22). Instances in which StW 252 is found between *A. africanus* and *A. robustus* can be seen in the bivariate scatter plots (Figure 16; Figure 19; Figure 20), and Principal Components Analysis (Figure 23). The cluster analysis on all the teeth is the most telling of the classification of StW 252 (Figure 25). The cluster analysis situates StW 252 closest to *A. africanus* suggesting that, when the 15 measurements are scaled by the geometric mean, StW 252 is more similar to *A. africanus*. However, following the similarities of *A. africanus*, *A. robustus* is the next closest to StW 252. The dental measurement similarities with both *A. africanus* and *A. robustus* coupled with the morphological similarities between the two could support the theory that StW 252 is a transitional species in South Africa that begins with *A. africanus* and leads into *A. robustus*. This transition can be supported by the phylogenetic placement of *A. sediba* and StW 53.

*A. sediba* was excavated about 15 km from the Sterkfontein deposits at the Malapa site by Lee Berger and his excavation team (Berger et al., 2010). *A. sediba* consists of juvenile (MH1) and adult (MH2) fossilized remains and dates to 1.95-1.78 Ma (Berger et al., 2010). MH1, a juvenile, is the type specimen of *A. sediba* (Berger et al., 2010). MH1 and MH2 have distinct morphological differences from *A. africanus, A. robustus,* and *Homo spp.* (Berger et al., 2010). Craniofacial morphology in *A. sediba* shows the following traits: "small cranial capacity, pronounced glabellar region, patent premaxillary suture, moderate canine jugum with canine fossa, small anterior nasal spine, steeply inclined zygomaticoalveolar crest, high masseter origin, moderate development of the mesial marginal ridge of the maxillary central incisor, and relatively closely spaced premolar and molar cusps" (Berger et al., 2010: 196). Craniofacial traits absent in *A. sediba* that are commonly seen in *A. robustus* include "pronounced cranial muscle markings, derived facial morphology, mandibular corpus robusticity, and post-canine megadontia" (Berger et al., 2010: 196). Berger et al. (2010) argue that the combination of primitive and derived craniofacial traits observed in *A. sediba* could indicate that *A. sediba* is a later version of *A. africanus* transitioning into *Homo* (Berger et al., 2010). *A. sediba* dentition differs from StW 252 in that *A. sediba* has a decrease in incisor and canine sizes and a slight increase in $M^1$ and $M^2$ and a subtle decrease distally in $M^3$, which aligns with size patterns seen in *H. habilis* (Berger et al., 2010). The morphological differences seen in both *A. sediba* and StW 252 indicates the existence of two different australopiths living in South Africa that are both dated to about 1.9-1.7 Ma (Berger et al., 2010; Fornai, 2010; Clarke, 2013). The differences seen in the dental morphology among *A. sediba* and StW 252 are similar to those that Clarke (2013) used to explain the differences in dental and craniofacial morphology between StW 252 and *A. africanus*.

It is possible that *A. sediba* and StW 252 are different species of *Australopithecus* that inhabited South Africa at the same time, which can be explained by sympatric speciation. Sympatric speciation occurs when species diverge from the parent species, and eventually the descendant forms become morphologically diverse while occupying the same habitat. In this case, the parent species is *A. africanus*, and the descendant species are *A. sediba* and StW 252. The morphological differences observed in *A. sediba* and StW 252 are probably related to dietary niches exploited after the divergence. Competition for food and sexual partners could also play a role in morphological differences, such as sexual size dimorphism.

The phylogenetic position of StW 53 may pertain to the placement and classification of StW 252 in the South African hominin fossil record. StW 53, a set of fragmented cranial bones, was discovered in 1976 by Alun Hughes and was originally thought to come from Sterkfontein Member 5 (Curnoe and Tobias, 2006; Clarke, 2013). StW 53 is dated to about 1.78-1.49 Ma (Williams et al., 2012). Initially, scholars agreed that StW 53 should be designated as *Homo habilis* (Curnoe and Tobias, 2006). Curnoe and Tobias (2006) completed a reconstruction of the StW 53 craniofacial fragments. The overall size of the face is small, which Curnoe and Tobias (2006) argue to be an important feature of *H. habilis.* The superior facial breadth falls within the range of *A. africanus* (Curnoe and Tobias, 2006). StW 53 has slight subnasal prognathism in contrast to a previous classification of severe subnasal prognathism (Curnoe and Tobias, 2006). Curnoe and Tobias (2006) argue that these features are diagnostic of *H. habilis*, but acknowledge that this classification should be continuously tested. The description of these features is similar to that of Sts 5, which is classified as *A. africanus*. Is it possible that StW 53 is a late *A. africanus* rather than representing a new species- *H. habilis?* When multivariate landmark-based linear distances from the mid-face are considered, StW 53 classifies as closest to *A. africanus* rather than early *Homo* (Williams et al., 2012).

A reconstruction of the cranial fragments of StW 53 supports the *A. africanus* classification. Clarke (2013) argued StW 53 to be reclassified as *A. africanus* instead of *Homo* (Clarke, 2013). StW 53 more closely resembles australopiths rather than *Homo*, because the morphological characteristics point to a "smaller brain size, larger teeth, ape-like nasal region and a size increase of the molars atypical of *Homo*" (Williams et al., 2012: 246). Clarke (2013) argues StW 53 shows no significant morphological differences from Sts 5 (Clarke, 2013).

The discovery of *A. sediba* could explain the differences in morphology between *A. africanus* and StW 53. It is important to keep in mind that both *A. sediba* and StW 53 are argued to be something other than *A. robustus*. If both *A. sediba* and StW 53 express a morphology more similar to *A. africanus* than *Homo spp.*, one can infer that these two individuals may represent the transition from *A. africanus* to *Homo spp.* A parallel example can be seen in the East African fossil record with *Australopithecus garhi*. Dated to about 2.5 Ma, *A. garhi* combines the canine to premolar and molar sizes of *A. afarensis*, *A. africanus*, and early *Homo* (Asfaw et al., 1999).

The cluster analysis places StW 252 closest to *A. africanus* and furthest away from *G. gorilla* and *P. troglodytes*, Geometric scaling of the measurements from all of the teeth indicates that StW 252 is more similar to that of *A. africanus* which is what Lockwood and Tobias (1999) have argued. The differences seen in StW 252 and other large toothed australopiths have been suggested to be caused by sexual dimorphism (Lockwood and Tobias, 1999). However, the larger size of StW 252 may not be related to sexual dimorphism with the known *A. africanus* individuals, but rather may be traits of another species as argued by Fornai (2010) and Clarke

(1988, 2013). The cluster analysis and Jack-knifed classification partially supports Lockwood and Tobias (1999) attribution of StW 252 as *A. africanus*. However, the cluster analysis showed that StW 252 is most similar to that of *A. africanus* but does not suggest that it should be referred to *A. africanus*.

# 7 CONCLUSION

Future research should encompass a larger sample of the unknown individuals being uncovered each field season in South Africa as well as a larger comparative sample. A resampling of the comparative measurements coupled with the statistical application known as R can provide probability distributions for the South African hominin fossil record.

The statistical analysis suggests that StW 252 is a highly unique South African specimen. The degree to which craniofacial morphological differences are seen in this unknown individual is indicative of the evolutionary changes occurring in South African during the Plio-Pleistocene. The difficulty of placing StW 252 into one of the previously recognized South African species is apparent when one looks at the dental measurement analysis. StW 252 exhibits both *A. africanus* and *A. robustus* dental traits but does not fit perfectly into one species. This may support the theory that there is more than one species of *Australopithecus* at Sterkfontein during this time. The dental measurement differences expressed among the larger toothed individuals when compared to *A. africanus* suggests that there was a shift in the environment in which all of the hominins were living. This shift may have caused individuals such as StW 252 to rely more on fall back foods which can explain the large molar size. StW 252 exhibiting larger anterior teeth suggests that these individuals relied more on teeth as tools rather than stone tools as seen in the more recent Swartkrans deposits.

In sum, this study supports the Second Species Hypothesis proposed by Clarke (2013). The placement of StW 252 within the timeline of the South African fossil record indicates a climatic event that caused feeding behaviors to change and species to diverge. The dental measurements of StW 252 coupled with the comparative sample only tell part of the story. The morphological traits expressed in StW 252 are what would be expected in a transitional form evolving from *A. africanus* into *A. robustus*. The dental measurement analysis supports this assessment.

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# APPENDICES

## Appendix A: Statistical analyses

### *Appendix A.1 Mean deviation and average mean deviation*

*Table 9: Measurement error averages*

| Variable | Min | Max | Average |
|---|---|---|---|
| Incisor One BL | 0.09 | 0.6 | 0.27 |
| Incisor Two BL | 0.21 | 0.63 | 0.3 |
| Canine BL | 0.07 | 0.9 | 0.34 |
| Premolar Three BL | 0.03 | 1.04 | 0.48 |
| Premolar Four BL | 0.04 | 0.59 | 0.23 |
| Molar One BL | 0.06 | 0.54 | 0.26 |
| Molar Two BL | 0.05 | 0.77 | 0.3 |
| Molar Three BL | 0.17 | 3.84 | 0.95 |
| Incisor One MD | 0.04 | 0.29 | 0.19 |
| Incisor Two MD | 0.1 | 1.14 | 0.38 |
| Canine MD | 0.09 | 0.51 | 0.34 |
| Premolar Three MD | 0.12 | 0.97 | 0.4 |
| Premolar Four MD | 0.16 | 0.84 | 0.4 |
| Molar One MD | 0.02 | 0.71 | 0.31 |
| Molar Two MD | 0.04 | 2.02 | 0.55 |
| Molar Three MD | 0.02 | 0.92 | 0.46 |

### *Appendix A.2 Measurement Error ANOVA Results*

*Table 10: ANOVA results*

| Species Number | F Value | Significant value |
|---|---|---|
| GSU 57.1 | 0.003 | 0.997 |
| GSU 51.1 | 0.064 | 0.938 |
| WC | 0.082 | 0.921 |
| GSU 511.1 | 0 | 1 |
| *A. ramidus* | 0.024 | 0.976 |
| HNE | 0.019 | 0.981 |
| *S. Indicus* | 0.009 | 0.991 |
| GSU 56.1 | 0.009 | 0.991 |
| GSU 510.1 | 0 | 1 |
| GSU 52.1 | 0.001 | 0.999 |