Title:

An assessment of dietary adaptations and mandibular morphology in non-human primates, as comparative models for early hominins.

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A thesis submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

The University of Sheffield

Faculty of Arts and Humanities

Department of Archaeology

November 2019

Abstract

This thesis examines the association between diet and the mandibular morphology in non-human primates as a model for understanding the morphology present in hominins. The traditional explanations of the morphological differences present in *Paranthropus* and *Australopithecus* have been challenged due to revised interpretations of the mandibular morphology, and the application of stable carbon isotopes and dental microwear texture analysis, which have resulted in a reassessment of the relationship between diet and masticatory morphology.

The main aim was to explore the relationship between diet and mandibular/ dental morphology, whereby diet was analysed using a series of different diet classifications. Mandibular and dental traits were measured on a sample that included both extant non-human primate taxa (n = 37) and extinct hominin taxa (n = 6). The non-human primate species represent a diversity of dietary preferences, habitats and body sizes, while the hominin sample includes species from *Paranthropus, Australopithecus* and early *Homo.*

Morphological differences were identified between consumers of different diets, including between consumers of hard and tough foods. The strength of the association between diet and morphology was influenced by how diet was classified, with the more refined dietary classification techniques consistently and more successfully identifying morphological differences. Body size differences were also identified.

Results comparing the hominins to non-human primates of known-diet indicate that hominins were likely to have consumed quite varied (omnivorous) diets. The results also highlight how unique the hominin corpus robusticity is, whereby it is beyond the range of the extant non-human primates, thus diet interpretations in relation to extreme robusticity remain elusive.

While diet is not the only variable to contribute to masticatory form, this research demonstrates that it has a measurable influence on mandibular morphology. This research therefore offers a new perspective addressing the association between diet and morphology, providing additional evidence comparing hominin morphology to that of the non-human primates. This study contributes to an area of active research in palaeoanthropology, and forms a basis from which additional studies can proceed.

Acknowledgments

I would like to express my deepest gratitude to my supervisors Dr Kevin Kuykendall and Dr Pia Nystrom. For their guidance and advice, and seemingly infinite patience during times of difficulty and uncertainty, they helped me stay focussed and calm.

Thank you to the Faculty of Arts and Humanities for funding this research. It would not have been possible to pursue this project without the financial support provided.

Thank you to Dr Eleanor Stillman and the support team at Mathematics and Statistics Help (MASH), at the University of Sheffield. Your advice and support with the statistical procedures was invaluable.

To the curatorial staff at the museums who gave me access to visit their collections, made me feel welcome and ensured my visit was productive, Inbal Livne at the Powell Cotton Museum (Kent), Emmanuel Gilissen and Wim Wendelen at the Royal Museum of Central Africa (Tervuren), Christiane Funk at the Berlin Museum of Natural History (Berlin), Marcia Ponce de León, Ani Margvelashvili and Diego Fecker at the Adolph Schultz Anthropological Institute and Museum (Zurich), Alexander Bibl at the Vienna Museum of Natural History (Vienna), Michael Hiermeier at the Bavarian State Collection of Zoology (Munich), and Uta Olbrich-Schwarz at the Max Planck Institute for Evolutionary Anthropology (Leipzig). It has been a privilege to study in the museums/ collections, and I will always look back on the visits with great fondness. Thank you also to Max Fancourt at the IUCN for taking his time to create the distribution maps for *Pan* species.

For the teachers at my secondary school, who had faith that I could do well in school. You gave me the motivation and conviction that I could succeed in education.

To my friends, Laura, Miguel, Valentina, Beatrice, Giulia, Angela and Lucy, I am honoured to call you my friends. Thank you so much for the many happy adventures and memories we have shared over the years, and for your support throughout the PhD. A special mention to Laura for reading parts of my thesis, and for calming and reassuring me when things were not going right.

Finally, I could never have arrived at this point of submitting my PhD thesis without the love, help, support and encouragement of my family throughout the years. Helping me with my homework at school, never giving up on my education and latterly when I became engaged with my studies supporting my choices and reassuring me when I needed you. Thank you for always being there for me.

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Chapter 1 : Introduction

This study was borne out of recent challenges to the traditional interpretations of the masticatory morphology of *Paranthropus* and *Australopithecus*. Upon the discovery of the first specimens to be taxonomically classified *Paranthropus*, Broom emphasised the morphological distinctions between those specimens and those attributed to the genus *Australopithecus* (Broom, 1938). The craniofacial morphology present in the *Paranthropus* specimens was argued to be so different from the *Australopithecus* specimens that they could not possibly be part of the same genus. Features such as very large, heavily buttressed and highly robust craniofacial architecture, with inferred relatively massive muscles of mastication, and post-canine megadontia, characterised by hyper-thick dental enamel and molarised premolars (Broom, 1938; Dean, 1988; Grine & Martin, 1988; Wood & Strait, 2004; Wood & Constantino, 2007), all distinguished *Paranthropus* from the more gracile *Australopithecus* and earned *Paranthropus* the nickname: The Nutcracker Man (Lee-Thorp, 2011). A comparison of the craniofacial morphologies of *Paranthropus*, *Australopithecus* and early *Homo* is demonstrated in Figure 1.1.

Image removed due to copyright

Figure 1.1: Comparison of the morphological differences present in the cranium, maxilla and mandible of *Australopithecus africanus*, *Paranthropus boisei* and *Homo habilis* (image courtesy of Ungar & Sponheimer, 2011)

When describing the *Paranthropus* dental morphology Robinson (1954a: 328) highlighted the overall disparity of the size of the small anterior dentition in relation to the extremely massive postcanine dentition, the flattening of the postcanine dentition, and the thickening of the bone around the corpus, and compared these features with those of other hominins. He suggested that these traits were indicative of a diet of “crushing and grinding… vegetable materials”. In contrast, *Australopithecus* presented a more balanced and proportionate dentition, with larger canines and smaller postcanine dentition, indicative of a more omnivorous diet (Robinson, 1954a). Robinson (1963: 391-392) stated that these features in *Paranthropus* were dietary specialisations that “point[ed] to a prime dietary function of crushing and grinding”. This concept became known as the Dietary Hypothesis, and it was long assumed that the extreme morphological differences between *Australopithecus* and *Paranthropus* were the result of very different diets. This functional morphological hypothesis prevailed and indeed for many years after researchers attempted to identify the types of food to which *Paranthropus* was adapted, including seed eating (Jolly, 1970), hunting and scavenging (Szalay, 1975), nut-cracking (Kay, 1981), and frugivory (Walker, 1981).

Most adaptive explanations of masticatory morphology are related in some way to diet, with comparative studies determining that variation in the size and shape of the masticatory morphology is associated with stress (Hylander, 1979a, b, 1984, 1985, 1988; Bouvier, 1986a, b; Ravosa, 1991; Hylander & Johnson, 1994). Mandibular and dental features in non-human primates were analysed to determine their potential biomechanical importance, in particular their potential to resist high-stress loads. An increase in the width or depth of either the symphysis or the corpus of the mandible correspond to particular strains on the mandible during mastication and ingestion, and are considered to be necessary adaptations to resist those strains (Hylander, 1979a, b, 1984, 1985, 1988; Bouvier, 1986a, b; Ravosa, 1991; Hylander & Johnson, 1994). The presence of enlarged postcanine dentition (postcanine megadontia) and hyper-thick dental enamel are also considered to be important biomechanical adaptations to resist hard or tough foods (Dean, 1988; Hylander, 1988; Daegling, 1992; Macho & Spears, 1999; Lambert *et al.,* 2004; Macho, 2004; Lucas *et al.,* 2008a; Constantino *et al*., 2011; Ungar, 2011; Pampush *et al*., 2013; Grine & Daegling, 2017). These were some of the features that previously led Robinson (1954a, 1963) to propose the Dietary Hypothesis, whereby *Australopithecus* and *Paranthropus* were distinguished from one another on the basis that they were each adapted to consume strongly divergent diets, with *Paranthropus* in particular adapted to diets of mechanically challenging foods.

For *Paranthropus,* the large, flat molars would have been able to crush hard foods, while their thick enamel would have resisted the material properties of the foods consumed, and their robust masticatory apparatus would have been able to generate the high forces required to consume these foods, while at the same time resisting failure when masticating hard foods (Teaford & Ungar, 2000; Lucas *et al*., 2008a, b). These traits are often interpreted as dentognathic features adapted to the consumption of hard food items (Grine *et al*., 2006a). All of which led to the conclusion that the morphology present in *Paranthropus* were specialist adaptations to diet (Robinson, 1963).

A combination of a reinterpretation of the morphology by Wood & Strait (2004), and the application of dental microwear analysis and stable carbon isotope analysis challenged the original grounds for separating *Paranthropus* and *Australopithecus*. The review by Wood & Strait (2004) led to the conclusion that rather than interpreting the extreme morphology present in *Paranthropus* as an adaptation to being a dietary specialist, the morphology would instead facilitate consumption of a wide variety of foods, thus making this genus a dietary generalist. The results from both dental microwear texture analysis and stable carbon isotope analysis supported this reinterpretation of the morphology by Wood & Strait (2004). Furthermore, the dental microwear texture analysis and stable carbon isotope analysis also established that overlap existed between *P. robustus* and *A. africanus*, and that distinctions were present between *P. boisei* and *P. robustus.*

The results from the dental microwear analysis on *P. robustus* and *A. africanus* indicated that the two species consumed very similar diets, demonstrating a high degree of overlap between the anisotropy (long, parallel striations which form on the surface as a result of consuming tough foods, e.g., leaves and stems (Ungar *et al*., 2006, 2008)) and complexity (heavily pitted surface textures which form as a result of consuming hard and brittle foods, e.g., seeds (Silcox & Teaford, 2002; Ungar *et al.*, 2006, 2008; Scott *et al*., 2009)) of the microwear patterns (Scott *et al*., 2005; Peterson *et al*., 2018). It was suggested that where the microwear patterns did not overlap this was the result of the two genera consuming different foods on a seasonal basis (Scott *et al*., 2005). Overall, the high level of dietary overlap between the two genera was supported by analysis of the stable carbon isotopes in the two species; evidence suggests that both species' diets predominantly included C_3 based foods (plants from forest understory), but also a significant non-C_3 derived component, each consuming 35-40% C_4 foods (grass seeds, roots, sedges and underground storage organs (tropical grasses)) (Sponheimer & Lee-Thorp, 1999; Sponheimer *et al*., 2005a, 2006a). This represents an unexpected degree of overlap in the same isotopic dietary regime for the two South African hominin species, who based on their masticatory morphology were assumed to have consumed very different diets.

Further analysis and comparison between *P. boisei* and *P. robustus*, congeners from East and South Africa provided evidence of further complexity. These species express similar patterns of masticatory robusticity and on this basis were classified into the genus *Paranthropus* and historically considered to demonstrate a morphological adaptation to a common dietary habitat. Evidence now suggests that they consumed diets from different isotopic regimes: *P. boisei* predominantly consumed C_4 foods, while *P. robustu*s consumed a varied diet consisting of both C_3 and C_4 foods (Sponheimer *et al*., 2006a, 2013; Ungar *et al*., 2008; Cerling *et al*., 2011; Wynn *et al*., 2013).

The results from the studies using stable carbon isotopes and dental microwear texture analysis indicate they are at odds with the traditional interpretations of the hominins based on comparative morphology. There are morphological differences between *Australopithecus* and *Paranthropus* that can no longer be easily explained by clear dietary differences, but there are also dietary differences between the South and East African *Paranthropus* species that do not appear to correspond to expected morphological differences. These results counter the conventional notion that *Paranthropus* species were ‘specialist’ hard object feeders and indicate that more caution should be applied before attempting to reconstruct hominin palaeodietary ecology based only on the morphological data available (Lee-Thorp, 2011).

In an attempt to explain the morphology in a way that would complement the microwear and stable carbon isotope analyses, a concept based on seasonality of resources was invoked. As the microwear results indicated that the diets of *A. africanus* and *P. robustus* differed on a seasonal basis, it was suggested that their diets differed not in terms of the “preferred foods” consumed, but instead on those foods consumed during the period of resource scarcity, termed “fallback foods” (Laden & Wrangham, 2005; Scott *et al*., 2005; Lambert, 2007; Marshall & Wrangham, 2007; Marshall *et al*., 2009). Fallback foods are suggested to be abundant and low in quality and as a result, may require morphological adaptations in order to process them (Lambert, 2007; Marshall & Wrangham, 2007; Constantino & Wright, 2009). Based on this final point, it was suggested that the derived morphology present in *Paranthropus* was a reflection of their fallback foods (Scott *et al*., 2005; Ungar *et al*., 2008). The Fallback Food Hypothesis essentially replaced the Dietary Hypothesis of Robinson (1954a, 1963) as the proposed explanation for the divergent morphology present in *Australopithecus* and *Paranthropus.*

There are, however, problems with the hypothesis. While it cannot be doubted that non-human primates alter their diets during the seasons, or for that matter that there would have been a seasonal change in food resources during the Plio-Pleistocene, it has not been straightforward to test its effects in extant species (McGraw & Daegling, 2012). Therefore, the association between fallback foods and morphology has not been established. Consequently, it is perhaps too soon to rule out the possibility of diet in general (not only fallback foods) corresponding to morphology.

This study therefore sought to elucidate the potential evolutionary stimuli responsible for *Paranthropus* masticatory morphology. The potential factors that could influence morphology that were focussed on include: diet and body size, and to a lesser extent, sex dimorphism and taxonomy. This was done through the comparison of the mandible and its associated dentition from wide selection of haplorhine primate species, comprising Catarrhines and Platyrrhines, chosen with the intention of developing a greater insight of the interplay between masticatory morphology and diet, which would greatly enhance existing models of early hominin palaeobiology. By exploring patterns of variation using this strategy, it was possible to postulate on the strength of the influence of such specific factors. As highlighted by Ungar & Sponheimer (2011), in order to further palaeodietary research it is necessary for the results from microwear and stable carbon isotope analyses to be integrated with data of primate ecology and more focus is needed on the underlying processes, not just the outcomes.

The hominin sample for this project included *A. afarensis*, *A. africanus*, *P. boisei*, *P. robustus*, *Homo habilis sensu lato*, and *H. ergaster*. The *Australopithecus* species were important to include as they pre-date the emergence of *Paranthropus* and thus present the ancestral features, while the early *Homo* species were important as they overlapped and post-dated the presence of *Paranthropus*.

1.1 Research aims

The general focus of this research project was to determine if there are cranio-dental morphological differences present in consumers of different diets. In particular, whether there are morphological differences between those species that consume frugivorous-based diets from those that consume folivorous-based diets, or those containing granivorous contents in the diets. Comparison of dietary categories such as these is based on the knowledge that the mechanical properties of foods vary. In theory, a species with a diet dominated by fruit pulp, as a predominantly frugivorous species would be, should be very different morphologically from one dominated by leaves, as a folivorous species would be, or one that contains seeds, as a granivorous species would. Fruit pulp is soft and requires very little mastication prior to consumption, while tough foods such as bark and mature leaves, and hard foods such as immature seeds are more obdurate and thus more difficult to process (Lambert *et al*., 2004; Lucas, 2004; Wright, 2005; Taylor, 2006a).

To take this exploration a step further, it was expected that the quantity of any specific food category would be important. Thus, species that consume high quantities of seeds or leaves will be morphologically different to those that consume low quantities of these foods. This is because greater consumption of obdurate foods places the masticatory apparatus under greater mechanical loading strains, which should thus result in biomechanical adaptations to help resist such loads (Taylor, 2006a; Grine & Daegling, 2017; Daegling & Grine, 2017). Depending on where the stresses and strains occur, the mandible is predicted to respond by increasing bone growth in the corpus and symphysis to improve resistance to the increased loading, this can include making the corpus or symphysis deeper or wider.

A relatively **deeper mandibular corpus** was suggested to be the best way of resisting parasagittal bending loads (Hylander (1979a). These loads increase the tension and compression of the alveolar and basilar elements of the non-biting side of the corpus during mastication and incision. Previous comparative studies have highlighted that those species regularly consuming a diet that routinely requires forceful biting present deeper corpora than those species that do not consume such foods (Bouvier, 1986a, b; Ravosa, 1991; Daegling, 1992).

A relatively **thicker mandibular corpus** was proposed to be the best way of resisting axial torsion (Hylander, 1979a). Axial torsion is said to occur on the working side of the mandible during mastication and incision.

A relatively **deeper symphysis** was proposed to resist vertical bending of the symphysis (Hylander, 1984, 1985; Taylor, 2002). The same parasaggital bending stress and torsional load placed on the mandibular corpus during mastication also produces vertical bending of the symphysis (Hylander, 1985). During the vertical bending, the alveolar symphysis is compressed and the basilar symphysis is placed under increased tension.

A relatively **thicker mandibular symphysis** was proposed to resist lateral transverse bending (wishboning) (Hylander, 1985; Taylor, 2002). Wishboning is the result of a combination of bite force components that are at their maximum for stress and strain from both the working side and the balancing side occurring late in the power-stroke (Hylander, 1985; Hylander *et al*., 1987; Hylander & Johnson, 1994; Vinyard & Ravosa, 1998). A thicker mandibular symphysis can be achieved through the presence of a “simian shelf” or a superior transverse torus, which provide the necessary buttressing to the wishboning (Hylander, 1984).

The mandibular morphology of *Paranthropus* displays many of the above traits, which reinforced the idea that it was morphologically adapted to resist the stresses and strains of a hard or tough food diet (Hylander, 1979a, 1988; Daegling & Grine, 1991). However, recent studies have questioned the proposed dietary differences between *Australopithecus* and *Paranthropus*, and thus the traditional explanation of their morphological differences (Scott *et al*., 2005; Sponheimer *et al*., 2005a, 2006a, 2013; Ungar *et al*., 2008; Cerling *et al*., 2011; Ungar & Sponheimer, 2011). Based on this, it is clear that this topic is still of importance in palaeoanthropology today. It is for this reason that the main aim of this project is to explore the association between diet and the masticatory morphology of the mandible and associated dentition. In order to explore the potential association between diet and morphology, it was necessary to analyse non-human primates of known diet as comparative analogues. The first step was to explore the following questions:

1. *Are there morphological differences present between consumers of different diets?*
2. *Are there morphological differences between consumers of low quantities of particular foods to consumers of higher quantities of the same foods?*
3. *How much does diet contribute towards morphological variation?*

Once morphological variation of non-human primates in relation to diet was understood the next step was to compare hominins to non-human primates. The following questions were explored:

4. *Is the hominin morphology comparable to that present in non-human primates?*
5. *Is it possible to associate the morphological features of the hominins with dietary categories analogous to non-human primates?*
6. *Can the way hominins compare with known-diet non-human primates be used to frame hypotheses about diet variation in relation to morphological patterns in early hominins?*

1.1.1 Sub-aim

- To assess the potential viability of the Fallback Food Hypothesis as an explanation for the morphological differences present in *Paranthropus* and *Australopithecus*.

1.2 Research objectives:

In order to achieve these aims the following objectives were established:

- Review and discuss the background of the project: the traditional interpretations of the functional morphological differences between *Paranthropus* and *Australopithecus*, and the more recent challenges to conventional wisdom.
- To establish a non-human primate database of relevant species to analyse the mandible in the context of dietary variation and morphology. Other factors, such as sex dimorphism and taxonomy were also considered.
- To run statistical tests to assess the variation of the mandible in the different species, and to determine if there is significant association between diet and the mandibular morphology.
- To assess the results obtained in this study in the context of the traditional Dietary Hypothesis and the Fallback Food Hypothesis invoked today.

1.3 Remaining chapters

In this project the morphology of *Paranthropus* and *Australopithecus* was discussed, both in relation to the traditional Dietary Hypothesis and the more recent challenges to these interpretations. Extant non-human primates were explored to determine those that make suitable comparative analogues to the extinct hominin condition. Measurements were taken of the adult mandible of carefully selected species and analysed in the context of how the morphology corresponds to known diet, sex dimorphism and taxonomic information. Graphs based on known information from the non-human primates were created and hominins were interpreted in light of the morphological information gathered. The traditional Dietary Hypothesis and the Fallback Food Hypothesis were analysed in light of the information obtained using non-human primates.

Chapter 2: Evidence of diet adaptation in hominins

The morphological features of *Paranthropus* and *Australopithecus* are presented in the context of the traditional Dietary Hypothesis, the challenges to this hypothesis based on biomechanical reinterpretations of the morphology, the introduction of stable carbon isotopes and dental microwear texture analysis. The proposed resolution to the apparent discontinuity between the morphology and the stable carbon isotopes and dental microwear texture analyses is briefly introduced.

Chapter 3: Dietary adaptation in non-human primates

Diet variation and seasonality of resources in non-human primates and their responses to them are presented in this chapter. The Fallback Food Hypothesis and its potential applicability to explain behavioural and morphological differences in non-human primates and potentially hominins are further discussed.

Chapter 4: Materials and Methods

This chapter details the sample used for this study, including hominins and non-human primates, and the measurements obtained for each species and why. It finishes off detailing the statistical analyses used in this study and why they were selected.

Chapter 5: Statistical analysis of non-human primates and hominins

This chapter includes the results from the various statistical analyses chosen to test the research questions. The focus of the chapter is divided into two sections, with the first part analysing the variation present in apes, Old World and New World monkeys in relation to their diets and body size, and the second part analysing how hominins compare to known-diet non-human primates.

Chapter 6: Discussion

This chapter discusses the results in relation to the research questions, and how they compare to previous studies exploring similar questions. The chapter further discusses what the results could mean for interpreting *Paranthropus* morphology. Limitations of the study are discussed, as are future recommendations for this research.

Chapter 7: Conclusion

The main conclusions reached regarding the research questions answered and any other key points addressed in the discussion chapter are summarised here.

Bibliography

This chapter includes the complete list of references used in the thesis.

Appendix

All of the background information from the hominins analysed in this thesis is included in this chapter. This includes the environmental reconstructions, dental and mandibular measurements, the element analysed and its state of preservation. Also included in this chapter are the *t*-test/ ANOVA results that were not directly relevant to the results chapter.

Chapter 2 : Evidence of diet adaptation in hominins

This chapter introduces a brief summary of the hominins analysed, the Dietary Hypothesis of Robinson (1954a, 1963), the historical interpretations of the morphology present in *Paranthropus*, and how the interpretations of the morphology have changed assisted by the introduction of stable carbon isotope and dental microwear analyses. The application of stable carbon isotope and dental microwear analyses appears to have challenged the traditional grounds upon which Robinson's (1954a, 1963) Dietary Hypothesis was laid out, and the suggested resolution to these challenges is addressed briefly in this chapter, to be discussed in greater detail in the following chapter.

2.1 A brief history of hominins

As the focus of this project is centred on the morphological adaptations of *Paranthropus* in relation to *Australopithecus*, the study sample included species from both genera and early *Homo* (Table 2.1).

Table 2.1: *Australopithecus, Paranthropus* and early *Homo* species analysed in this project

Species	**Date of presence**	**Type specimen (element)**	**Locations**	**First descriptors**
A. afarensis	3.9 - 2.8 mya	LH 4 (mandible)	**Ethiopia:** Belohdelie; Dikika; Fejej; Galili; Hadar; Laetoli; Ledi-Gararu; Maka; Omo; Woranso-Mille. **Kenya:** Koobi Fora and West Turkana; Lothagam	Johanson *et al*. (1978)
A. africanus	3.5 - 2.0 mya	Taung 1 (cranium and mandible)	**South Africa**: Gladysvale; Makapansgat; Sterkfontein; Taung.	Dart (1925)
P. boisei	2.3 - 1.2 mya	OH 5 (cranium)	**Ethiopia:** Omo Shungura and Konso-Gardula. **Kenya:** Chesowanja; Koobi Fora, West Turkana. **Tanzania:** Olduvai; Peninj	Leakey (1959)
P. robustus	2.31 - 0.6 mya	TM 1517 (partial cranium and mandible)	**South Africa:** Coopers; Drimolen; Gondolin; Kromdraai; Swartkrans	Broom (1938)
H. habilis sensu stricto	2.3 - 1.4 mya	OH 7 (cranial, dental, postcranial elements of a juvenile)	**Kenya:** Koobi Fora; **Tanzania:** Olduvai; **Malawi**: Uraha; **South Africa:** Sterkfontein	Leakey *et al*. (1964)
H. ergaster	1.8 - 1.3 mya	KNM-ER 992 (mandible)	**Kenya:** Koobi Fora; **South Africa**: Swartkrans	Groves & Mazák (1975) – cited in Wood & Leakey (2011)

*mya = millions of years ago

Australopithecus afarensis is widely purported to be the common ancestor of all hominins postdating 2.6 million years ago, including *A. africanus, Paranthropus* and

Homo (Johanson & White, 1979; Ungar, 2004; Grine *et al*., 2012). Considering this proposed phylogenetic history, *A. afarensis* should then represent the morphology from which all descendants derive, as indeed is suggested from its occlusal morphology (Ungar, 2004; Wood & Strait, 2004). *A. afarensis* is therefore an appropriate species to include as they are widely considered to represent the more primitive earlier australopithecine condition (Johanson & White, 1979; White *et al*., 1981; Ungar, 2004; Wood & Strait, 2004; Grine *et al*., 2012). The two species of early *Homo* (*H. habilis sensu lato* and *H. ergaster*) formed the out-group comparison.

The environments, habitats and time range of *A. afarensis* do not overlap with those of *Paranthropus*. *A. afarensis*, does however, still provide insight into how the nature of diets changed over the millions of years leading up to and during the existence of *Paranthropus*.

As well as forming the out-group comparison, early *Homo* has been included in this study as it overlapped with the East African *Paranthropus boisei*, both in temporal and geographic distribution (Leakey *et al*., 2012; Cerling *et al*., 2013) (Table A.1 in Appendix A details the exact hominin specimens used and their condition). To be consistent with the microwear and isotopic studies conducted, the *H. habilis* sample also included *H. rudolfensis* and is referred to as *H. habilis sensu lato.* The inclusion of *H. ergaster* provided a clearly distinguished species to compare to *Australopithecus* and *Paranthropus. H. ergaster* is analysed as the African sample of *H. erectus* (if classified *sensu lato*), as it was not considered useful or pertinent to include the Asian samples of *H. erectus*, as they lived in a very different environment to the australopithecines and any differences in their morphology would likely reflect this environmental difference.

Postcranial evidence support that all of the hominins in question were adapted to bipedal locomotion, although this became more efficient over time (Leakey & Hay, 1979; Day & Wickens, 1980; Stern & Susman, 1983; Rose, 1984; Brown *et al*., 1985; Hunt, 1994; Ward *et al*., 2001, 2012; Pontzer *et al*., 2009; Haile-Selassie *et al*., 2010a; Raichlen *et al*., 2010; DeSilva *et al*., 2012; Drapeau & Harmon, 2013; Prang, 2015; Fernández *et al*., 2016). The craniofacial morphological differences between the hominin genera analysed ranges from more gracile (*Australopithecus*, early *Homo*) to more robust (*Paranthropus*) (Wood & Strait, 2004). This difference is present in almost all cranial features, although variation is present in the degree of difference for each species. Where each species is described as having possessed megadont postcanine dentition (large, flat molars), with thick dental enamel, pronounced facial prognathism and large overall mandibular corpus shape relative to extant hominoids, each trait is greatest in *Paranthropus* relative to *Australopithecus* or early *Homo* (Chamberlain & Wood, 1985; Dean, 1988; Grine & Martin, 1988; Teaford & Ungar, 2000; Ward *et al*., 2001; Ungar, 2004; Wood & Strait, 2004). A size reduction in the morphological features occurred during the time of *Homo*, where *H. habilis sensu lato* retained many of the ancestral features of earlier hominins, while *H. ergaster* did not, instead demonstrating a sizable reduction in the size of its cranial and dental traits (Wood & Collard, 1999; Ungar, 2004; Wood & Strait, 2004).

The reduction in size of morphological features in *Homo* was postulated to be due to the use of Oldowan stone tools[1] to acquire and process foods, which in turn reduced the selective pressures acting on their craniofacial morphology (Ungar, 2004; Wood & Strait, 2004). While this last suggestion could be doubted given that the advent of Oldowan stone tools appears to have preceded the emergence of *Homo*, dating back to 2.5 Ma – around the time of both *A. garhi* and *P. aethiopicus* (Walker *et al*., 1986; Asfaw *et al*., 1999) – it is also possible that it is accurate given the time it takes for morphology to adapt to behavioural change (Bock & von Wahlert 1965; Gailer *et al*., 2016; Ungar & Hlusko, 2016).

Early hominins were also characterised by varying degrees of sexual dimorphism, presenting little canine dimorphism, but in some species very strong body mass dimorphism (Plavcan & van Schaik, 1997; Plavcan *et al*., 2005). *A. afarensis* (although see Reno *et al*., 2003, 2010 for an alternative interpretation), *P. boisei*, *H. habilis* and *H. ergaster* were all described as having had large body mass dimorphism (Stern & Susman, 1983; McHenry, 1988, 1991a, 1992; Ward *et al*., 2001; Plavcan *et al*., 2005; Gordon *et al*., 2008; Gordon, 2013; Grabowski *et al*., 2015). *A. africanus* and *P. robustus,* in contrast had more moderate levels of body mass dimorphism (McHenry, 1991b, 1992; McHenry & Berger, 1998; Susman *et al*., 2001; Gordon, 2013). These body mass dimorphism differences highlight that even within the same genera, morphological differences occurred.

Considerable attention has been focussed on the types of habitats the early hominins would have inhabited, with various techniques having been applied to reconstruct the past environments and the dates during which the hominins existed. Through gaining a more comprehensive understanding of the environment, it could potentially put into context the morphological adaptation of the hominins, as well as provide indications of their behavioural and social adaptations (Reed, 1997). General reconstructions of the

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[1] Oldowan stone tools represent the earliest stone tool industry identified. They originated from Olduvai Gorge, and are primarily represented by simple artefacts, such as choppers, hammerstones and flakes (Leakey, 1971).

hominins are as follows: *Australopithecus* existed mostly in regions of woodland with good water supply, likewise *Paranthropus* lived in similar habitats, but with increasingly open landscapes, and early *Homo* followed this environmental shift towards more open and arid environments (Reed, 1997, 2008; Potts, 1998; Wood & Strait, 2004; Behrensmeyer, 2006; Behrensmeyer & Reed, 2013) (detailed information on the different palaeoenvironments reconstructed for each of the hominin species analysed in this project is available in Appendix A, Tables A.2-A.3). This change in environment is a reflection of a changing climate between 4 – 2 million years ago (Reed, 1997; Behrensmeyer, 2006).

2.2 The Dietary Hypothesis as a theory for the derived masticatory morphology

When the craniofacial morphology of *Paranthropus* was first described by Robinson (1954a) the derived morphological features observed in *Paranthropus* relative to *Australopithecus* were explained as specialist adaptations to diet. Wherein, *Paranthropus* and *Australopithecus* were adapted to consume strongly divergent diets - the Dietary Hypothesis.

Robinson (1963) observed that the morphology of *Paranthropus* was very different from the hominins that both preceded it (*Australopithecus*) and followed it (*Homo*). The derived features of *Paranthropus* (Table 2.2) were assumed to be of adaptive significance. The traits, relating in particular to the dentition (postcanine megadontia, including molarised premolars, hyper-thick enamel, large crowns and large occlusal surfaces) and superrobust mandible were suggested to be part of a suite of specialised adaptations to crushing and grinding (Robinson, 1954a, 1963). A viewpoint shared by many researchers, with the consensus that *Paranthropus* was adapted to the frequent consumption of unusually hard or tough objects, which would most likely have been small, thus not necessitating much incisal preparation (Hylander, 1979b, 1988; Demes & Creel, 1988; Rak, 1988; Daegling & Grine, 1991; Teaford & Ungar, 2000; Constantino *et al*., 2009, 2010, 2011; Smith *et al*., 2015). Hylander (1988: 233) referred to the masticatory apparatus as one that was “especially designed to generate and dissipate large forces during powerful postcanine biting and/ or mastication”.

Table 2.2: Features distinguishing *Paranthropus* and *Australopithecus* according to Robinson (1954a, b, 1963)

Cranial feature	***Paranthropus***	***Australopithecus***
Sagittal crest	Present	Normally absent
Maxillary prognathism	Reduced due to poor development of anterior dentition	More pronounced
Mastoid region	Projects laterally	Less pronounced
Post-orbital constriction	Well-developed	Less pronounced
Zygomatic bone/ processes	Well-developed	Slender
Mandibular/ dental feature		
Permanent canine	Crown is small, more symmetric, little relief on the lingual surface, but substantial root.	Crown is large and highly asymmetric
Anterior dentition	Canines and incisors smaller than in *Australopithecus*	Canines and incisors are relatively large for a hominin
Postcanine dentition	Massive postcanine dentition, including molarised premolars set in massive bone	Postcanine dentition in proportion and less robust bone
Postcanine dentition	Strongly developed root systems	Weaker root system
Enamel	Hyper-thick	Thick
Muscle markings		
Temporalis	Clearly large relative to brain-case	Less pronounced
Masseter	Muscle attachments clearly marked and extensive	Less pronounced
Pterygoid muscles	Relatively great development of the lateral pterygoid plate indicates a large and powerful pterygoid muscles	Less pronounced
Nuchal muscles	Robust	Less pronounced

Robinson (1963) did concede that the massive postcanine dentition in *Paranthropus* could simply be a reflection of body size difference. A point reinforced by Pilbeam (1972) and Pilbeam & Gould (1974), who suggested that *Paranthropus* was a larger allometrically[2] scaled equivalent of *Australopithecus* that required a larger postcanine dentition in order to masticate more of the same food during each chewing cycle to support its larger body size. Scaling is observed in extant non-human primates, e.g., in the mandibular symphysis of *Papio* species (Koyabu & Endo, 2009; Daegling *et al*., 2013), and in terms of diet and size differences, with larger species observed to consume a more fibrous diet than smaller ones (Jarman-Bell principle) (Gaulin, 1979; Daegling & McGraw, 2001). However, scaling arguments to explain the differences in morphology of these hominins were dismissed on the grounds that: 1) *Paranthropus* could not have consumed more of the same food than *Australopithecus* because their microwear patterns (discussed later in the chapter) indicated that dietary differences were present (Kay & Grine, 1988), 2) *Paranthropus* was estimated to be a similar size to *Australopithecus* (Kay & Grine, 1988; Daegling & Grine, 1991; Daegling *et al*.,

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[2] Allometry is defined as the "study of size and shape in relation to ontogenetic, evolutionary, and static intra- and interspecific series" (Shea, 1983: 275)

2013), and 3) the anterior dentition of *Paranthropus* was much reduced in size relative to that of *Australopithecus* (Robinson, 1954a).

The size and shape of the dentition of *Australopithecus* was closer to that of the other hominins than was *Paranthropus*. Indeed, differences in tooth size were proposed as an explanation for the derived mandibular morphology in *Paranthropus*. The influence of the growth of the dentition on the form of the mandible – first proposed by Dart (1948) – was developed further by Wolpoff (1975), Kay (1981), Leuteneger (1982), and Chamberlain & Wood (1985). Wolpoff (1975) suggested that the megadont postcanine teeth were responsible for the robust mandibular morphology on the grounds that the larger the teeth the larger the surrounding jaw would need be to house the teeth. While the reduced size of the canines were indicative of reduced sexual dimorphism, meaning that the corpus did not need to accommodate long canine roots, which in the process made the corpus appear wider relative to its height, and thus, “more robust” (Kay, 1981; Leuteneger, 1982; Chamberlain & Wood, 1985).

Evidence does not support these proposals. No association has been found between canine size or molar tooth size and mandibular robusticity in catarrhines, platyrrhines and hominins (Daegling & Grine, 1991; Teaford & Ungar, 2000; Plavcan & Daegling, 2006). In fact, when differences have been identified in the mandible between human populations there has been very little difference in tooth size (Holmes & Ruff, 2011). Studies investigating the possible link between sexual dimorphism and mandibular robusticity in haplorrhines (Daegling, 1989; Daegling & Grine, 1991; Plavcan & Daegling, 2006; Taylor, 2009) and strepsirrhines (Daegling & McGraw, 2001) did not find a correlation. Thus, the proposed correlation between dental allometry, sexual dimorphism and mandibular robusticity are not supported (Plavcan & Daegling, 2006). Instead, it was maintained that differences in postcanine tooth size in early hominins were more likely a reflection of dietary differences as Robinson (1963) suggested (Hylander, 1988; Brace *et al*., 1991; McHenry & Coffing, 2000; Teaford & Ungar, 2000; Ungar, 2011).

To support the Dietary Hypothesis Robinson (1963) highlighted the fact that the hominin formerly known as *Telanthropus* (presently *H. erectus*) was able to co-exist with *Paranthropus* in South Africa. If both were consuming the same foods then continued coexistence would be extremely unlikely, but if both were adapted to different ecological requirements then coexistence is entirely possible (Robinson, 1963). Thus, dietary specialisations distinguished *Paranthropus* from *Australopithecus* and *Homo* in both morphology and the types of foods consumed.

It is possible that the robust features present in the early hominin mandibles were the result of inheritance from a robust ancestor (Daegling & Grine, 1991). *A. afarensis* for example presents many of the same features of *Paranthropus*, but not to the same degree of expression. *A. afarensis* is therefore considered to have been less efficient at countering stresses in the corpus and symphysis (Hylander, 1988). This notion is consistent with the gradual increase of the mandible and postcanine size in the early hominins, increasing from *A. anamensis* > *A. afarensis* > *A. africanus* > *P. robustus* > *P. boisei* (Teaford & Ungar, 2000). For these reasons, the absolutely greater robusticity present in *Paranthropus* relative to *Australopithecus* is considered to be the result of factors other than simply inheritance. In fact, the increasing masticatory robusticity in each species led to suggestions that each species were better able to consume mechanically resistant foods than their predecessor (Teaford & Ungar, 2000).

Australopithecus, with their less-derived features were not viewed as being adapted to any particular food, but a consumer of a generalised diet that could include hard foods (Robinson, 1963). In contrast, the extremely large and flat postcanine dentition, and the overall size and robustness of the craniofacial architecture of *Paranthropus* were consistent with a specialist diet (Robinson, 1963; Hylander, 1988; Teaford & Ungar, 2000). Robinson (1963) suggested the diet to be one of tough foods requiring a large amount of mastication and low on nutritive value. This would comprise vegetable foods, such as “shoots and leaves, berries, tough wild fruits, roots and bulbs” (Robinson 1954a: 328), and would help to explain the presence of grit-related damage to the occlusal surfaces of the teeth (Robinson, 1963).

Through analysis of extinct and extant animals the morphology of *Paranthropus* was scrutinised. Based on these results the notion that *Paranthropus* was a dietary specialist was generally accepted, but the idea that their diet was one of tough foods was not. Du Brul (1977) analysed the specialist herbivore, the giant panda and the generalist omnivore, the grizzly bear. Of the two, the giant panda had the most derived morphology and these morphological differences combined with their dietary proclivities served to reinforce Robinson’s Dietary Hypothesis (1954a, 1963). Other researchers analysed the morphology present in *Gigantopithecus* (once considered an ancestor to hominins), which displayed a similarly robust and derived masticatory morphology to *Paranthropus* (Frayer, 1973; Miller *et al*., 2008; Dickson, 2011). Based on the robust masticatory morphology, it was suggested that *Gigantopithecus* were hard-object feeders, and so too were *Paranthropus*.

Other researchers focussed on attempting to identify the types of food that could have shaped the morphology of *Paranthropus* and several explanatory hypotheses have been presented with dentition being the focus. Based on the presence of the hyper-thick enamel in *Paranthropus*, it was suggested that the genus were best adapted to the consumption of small, hard objects, such as grass seeds (Jolly, 1970), bone crushing (Szalay, 1975), nut-cracking (Tobias, 1976), similar to *Ramapithecus* (formerly suggested as an ancestor, and known today as *Sivapithecus*) (Kay, 1981), or a frugivorous diet, based on hard-shelled fruits (Walker, 1981).

The various dietary theories suggested by Jolly (1970), Szalay (1975), Tobias (1976), and Walker (1981) were not readily accepted for various reasons. For example, bone crushing and seed consumption were not consistent with the dental microwear patterns present in *Paranthropus* (Walker, 1981). Regular consumption of nuts would not have driven the morphology because they are only seasonally available resources (Peters, 1987).

Hylander (1988) addressed the suggestion by Robinson (1954a, 1963) that *Paranthropus* could have consumed large quantities of highly fibrous roots that were high in structural carbohydrates. Observation of the molar morphology of *Paranthropus* is not consistent with a tough/ fibrous diet as its primary food-type, but Hylander (1988) conceded that the morphology would not prevent consumption of these types of foods. In fact, the mandibular morphology of *Paranthropus* could have been adapted to resist fatigue strain from prolonged chewing cycles of tough foods as suggested by Bouvier & Hylander (1981). The quality of the diet that *Paranthropus* consumed is not clear but regardless of hard or tough, high-quality or low-quality foods the unique features of the mandible and cranium of *Paranthropus* indicates it was well adapted for all types of foods, and capable of powerful repetitive loads (Hylander, 1979b, 1988; Daegling & Grine, 1991). In fact, *Paranthropus* was so well adapted to different foods it was considered “overdesigned” (Ward, 1991: 475). Such adaptations would have been beneficial for hominins during this time, for it is regarded that the diets of hominins during the Pliocene (the time of *Australopithecus* and *Paranthropus*) were shifting towards harder foods (Teaford & Ungar, 2000).

2.3 Biomechanics: mandibular and dental form

2.3.1 Mandibular form

The majority of the research on *Paranthropus* focussed on the potential biomechanical importance of the masticatory apparatus. Studies that concentrate on the biomechanical adaptations of the masticatory morphology are based on the premise that the mandibular and dental morphology represent functional adaptations to diet (Szalay, 1975; Happel, 1988; Kinzey, 1992; Kinzey & Norconk, 1993; Wright, 2005; Ravosa *et al*., 2010; Ruff, 2018). For the mandible it is assumed that there is a "functional association between plasticity in mammalian mandibular morphology and response to dietary-related manipulation of jaw-loading patterns" (Ravosa *et al*., 2010: 558). The functional adaptation of the mandible to the stresses of a hard-food or fracture-resistant diet is imperative, for it reduces the risk of fracture to the mandibular or cranial elements through unusual loading patterns (Ravosa *et al*., 2010).

Analysis of the biomechanical adaptations of non-human primates has focussed on different regions of the masticatory apparatus, but of particular interest for this thesis is the mandible and its dentition. This is partly because the mandible and its associated dentition are the most commonly available remains in the fossil record (for both human and non-human remains) (Szalay, 1975; Daegling, 1993a; Lucas *et al*., 2008a; Louys *et al*., 2011, 2015a), and because the mandibular morphology of *Paranthropus* is so derived it is logical to focus attention on this region. Researchers have analysed the responses of the mandibular corpus, symphysis, and temporomandibular joint (TMJ) to stress and strain, the effect of body size on the masticatory apparatus, along with variation in dental features including tooth cusp shape and size.

Studies that focussed on the mandibular corpus and symphysis analysed how these regions responded to the generation of stresses and strains and how they are dissipated during mastication (e.g., Hylander, 1979a, 1979b, 1984, 1985). During mastication the mandible is put under intense stress, but this stress is not evenly distributed (Hylander, 1979b; Daegling, 1993b). There are bending, twisting and shearing loads acting on the different regions of the mandible during mastication, and as a result, it is necessary for the mandible to be suitably adapted to resist such strains (Hylander, 1979b). There are two peak areas of stress located on the mandible, and these are in the corpus and the symphysis (Daegling, 1993b). The degree of loading, stresses and deformations are governed by the mechanical properties of the foods consumed, with harder or tougher foods resulting in higher stresses and strains on the mandible than softer, more pliable foods (Ravosa, 1991; Taylor *et al*., 2008). It is assumed that higher magnitude loads require structural adaptations to resist the stress (Taylor *et al*., 2008).

Stresses that have been observed in the mandible, include parasagittal bending (located on the corpus of the non-biting side), axial torsion (biting side corpus), vertical bending of the symphysis, and wishboning of the symphysis (Hylander, 1979a, b, 1984, 1985, 1988; Hylander & Johnson, 1994). Adaptations to these stresses are manifested by: 1) a deep corpus to resist parasagittal bending, 2) a thick corpus to resist axial torsion, 3) deeper symphysis and presence of a transverse torus to resist vertical bending of the symphysis, and 4) a fused/ thick symphysis and presence of a transverse torus to resist wishboning (Hylander, 1979a, b, 1984, 1985, 1988; Hylander & Johnson, 1994; Taylor, 2002, 2006a; Vinyard *et al*., 2006).

When these biomechanical principles are applied to *Paranthropus* the following adaptations are observed: 1) with its deep corpus *Paranthropus* could resist sagittal bending on the balancing side, 2) with its transversely thick corpus it could resist twisting loads on the working side, 3) with its large cross-sectional area it could resist direct shearing loads on the working side, and 4) with its thick symphysis is could resist wishboning and powerful torsion during mastication (Hylander, 1979b, 1988; Daegling, 1989). The large muscle attachment sites combined with the aforementioned large corpus dimensions of the mandible were interpreted as indications that the muscle forces acting on the mandible were unusually large in this genus (Hylander, 1988). It was suggested that these features were most likely related to the mechanical properties of the food consumed, with larger masticatory muscle forces associated with the consumption of hard and tough foods (Hylander, 1988).

Hylander (1979b) highlighted the importance of the transversely thick corpus and related it to the massive postcanine dentition, with particular focus on the premolars. The overall size and shape of the premolars indicates that they would have been of greater importance during mastication, and as a result would have increased the stress acting on this area of the mandibular corpus, which in turn would have required greater structural adaptations to resist the increased stress and strain (Hylander, 1988). The transversely thick corpus in the premolar region was highlighted as being particularly important because normally stresses acting in the premolar region are much smaller and less significant than in the molar region (Daegling, 1993b). The unique morphology present in the postcanine dentition and corpus indicates that the majority of the masticatory stresses occurred in the distal regions of the mandible/ tooth row. Indeed, it is in this region that torsion, parasagittal bending and direct shear strains are at their greatest (Daegling & Grine, 1991).

While there are some studies that have identified instances where there is a clear relationship between masticatory stress and strain and mandibular morphology, there are other studies that have obtained either mixed results or no correlation (Daegling & Hylander, 1997; Daegling & McGraw, 2001; Taylor, 2005; McGraw *et al.*, 2011; Terhune, 2011; Ross *et al.*, 2012, 2016). The potential correlation between TMJ morphology and diet was one area analysed with mixed results. Taylor (2005) established that the mandibular ramal and condylar heights in African apes appear to be correlated with folivory. While Terhune (2011) found that both body size and diet were influential variables that appeared to affect the anteroposterior dimensions of the TMJ morphology in atelines, cebines and pitheciines. Yet both studies found variables, such as the condylar area and width (Taylor, 2005), and the variation in entoglenoid and articular tubercle height (Terhune, 2011) that did not appear to be correlated to diet.

It has been suggested that the imprecise link between diet and morphology is due to the usage of traditional dietary classifications, such as folivore or frugivore (Smith, 1983; Ankel-Simons, 2007; McGraw & Daegling, 2012; McGraw *et al.*, 2016). These generic classifications of diet may be of little relevance and they potentially ignore components of the diet that are more influential, for within each category there is much variation of consistency and texture (Smith, 1983; Yamashita, 1996, 1998; Ankel-Simons, 2007). Indeed, the mechanical properties of foods can overlap from one dietary classification to another, meaning that these dietary groupings are not biomechanically informative but are vague and coarse-grained (Kinzey & Norconk, 1993; Yamashita, 1996, 1998; Taylor *et al.*, 2008; McGraw & Daegling, 2012; Vogel *et al.*, 2014; Coiner-Collier *et al.*, 2016; McGraw *et al.*, 2016). For example, within the leaf category there are variations in terms of maturity, with mature leaves being higher in fibre and therefore tougher than young leaves, thus requiring more force to masticate them (Yamashita, 1996; Koyabu & Endo, 2009; Talebi *et al.*, 2016). Once leaf maturity is accounted for, the mechanical properties can vary in relation to water content, venation and thickness (Yamashita, 1998). This means that not all leaves are tough (Grine *et al.*, 2006b, 2012; Coiner-Collier *et al.*, 2016; Talebi *et al.*, 2016). Similarly, not all seeds are hard and not all fruits are soft (Yamashita, 1998; Grine *et al.*, 2006b, 2012; Taylor, 2006b; Vogel *et al.*, 2014; Smith *et al.*, 2015; Coiner-Collier *et al.*, 2016). A diet comprising soft seeds will probably require different adaptations to one made up predominantly of hard seeds. This is a point raised to explain the lack of morphological robusticity in the seed-eating *Chlorocebus aethiops, Cercopithecus campbelli* and *Erythrocebus patas* (Happel, 1988). In addition, diet categories do not take into account extra-oral processing, or factors of diet, which are out of the control of the consumer, e.g., seasonality of resources, or the geographic variation affecting the types of food available (Smith, 1983).

Consequently, it is not sufficient or adequate to classify diets as folivorous or frugivorous when attempting to make correlations between diet and morphology (Yamashita, 1996, 1998). New dietary categories were proposed that addressed the types of food mechanical properties that the species predominantly consumed (Lucas 1979; Lucas & Luke 1984; Freeman 1988). The proposed dietary categories were hard (durophagus), tough (elastophagus), and soft, brittle (jusophagus) (Yamashita, 1996). Hardness and toughness are often opposite characteristics used to describe the resistance of foods. Hard foods possess a brittle, external, protective shell that requires peak-loads to fracture, e.g., nuts, while tough foods require more energy and repetitive loading to fracture, e.g., bark and pith (Taylor *et al.*, 2008; Koyabu & Endo, 2009; Berthaume *et al*., 2010; Lee *et al*., 2010; Vinyard *et al.*, 2011; Constantino *et al*., 2011, 2012; Wood & Schroer, 2012; Ungar, 2015; Berthaume, 2016). Studies of extant non-human primates and the extinct hominins predominantly focus on durophagy (hard-object feeding) (McGraw & Daegling, 2012). This is because it is generally associated with morphological adaptations such as powerful jaws and enlarged posterior teeth (Norconk & Veres, 2011), the same characteristics that define *Australopithecus* and especially, *Paranthropus*.

The incorporation of food mechanical properties provides further information upon which to understand how the morphology responds to the various physical properties of foods (Taylor, 2005; Wright, 2005; Koyabu & Endo, 2009). Investigation of food mechanical properties requires an understanding of fracture mechanics, about whether a food is hard or tough to fracture, or stiff or compliant (definitions in Table 2.3) (Wood & Schroer, 2012; Berthaume, 2016). There are two internal mechanical characteristics of foods that are commonly observed, these are: fracture toughness (R) and elastic modulus (Young’s modulus, E) (Taylor *et al*., 2008; Reed & Ross, 2010) (but see Berthaume, 2016 for the additional mechanical properties that should also be explored). It is expected that differences in food mechanical properties would result in different loads being applied to the mandible during mastication, and consequently, adaptations to reflect an ability to resist increased loads (Taylor, 2006a, b, 2009). Therefore, resistance to loads can vary with each food and highlights that this can result in the exact same morphology appearing to be “over- or under-designed” (Taylor *et al*., 2008: 611).

Table 2.3: Definitions of the physical properties of foods according to Lucas (2004); Lucas *et al*. (2008b); Taylor *et al,* (2008); McGraw & Daegling (2012: 205-206) and Wood & Schroer (2012). Table removed due to copyright.

A recent shift in research focus has occurred with studies no longer analysing only what a primate is eating, but rather the food mechanical properties, the overall feeding behaviour (how frequently foods are consumed) and how foods are most efficiently broken down, but much work still remains to be done (Reed & Ross, 2010; McGraw *et al*., 2011, 2012, 2016; McGraw & Daegling, 2012; Ross *et al*., 2012, 2016; Berthaume, 2016; van Casteren *et al*., 2016; Chalk-Wilayto *et al*., 2016; Talebi *et al*., 2016). This is because there is currently not enough known about food mechanical properties or the feeding behaviours of apes, and by extension other non-human primates (Taylor, 2002; Foster *et al*., 2006; Vogel *et al*., 2014; Coiner-Collier *et al*., 2016; McGraw *et al*., 2016).

Of the studies that incorporate food mechanical properties, results have been somewhat consistent with the idea that food mechanical properties and morphology are connected, thus supporting the research of Hylander (1979a, 1979b, 1984, 1985, 1988) on stress and strain. Researchers established that feeding behaviours that involve high stress and strain appear to be more important determinants of dental and mandibular form and muscular action than are those of low strain (Hylander, 1979b, 1984, 1985; Bouvier, 1986; Ravosa, 1991, 1996; Yamashita, 1996, 1998; Bouvier & Ravosa, 1998; Lambert *et al*., 2004; Foster *et al*., 2006; Dominy *et al*., 2008; Norconk *et al*., 2009; Daegling *et al*., 2011; McGraw *et al*., 2016; Ross *et al*., 2016). For example, the fruit-eating cercopithecines were compared to the more folivorous colobines and more obdurate-food consumers, papionins. Results consistently demonstrated that colobines and papionins (with the tougher and more obdurate diets) exhibited more symphyseal corpus robusticity than the cercopithecines (Bouvier, 1986a; Ravosa, 1996; Vinyard & Ravosa, 1998). Similar results were reported in *Pongo abelii* and *Pongo pygmaeus* – *P. pygmaeus* is known to consume a more obdurate diet than *P. abelii* – with *P. pygmaeus* observed to possess a more robust corpus and symphysis than *P. abelii* (Taylor, 2006a).

It also appears that feeding behaviours that require repetitive chewing on a regular basis, e.g., daily, illicit influences on the mandible that are as strong as high-stress feeding behaviours (Williams *et al*., 2011 (on goats); Ross *et al*., 2016). This is because, large stress levels are experienced by leaf-eating species during mastication due to the repetitive chewing and large bite forces required to break foods down that are tough and consist of large quantities of structural carbohydrates (Ravosa, 1991). Through this, there also exists a correlation between morphology, diet and body size, this is because generally as body size increases so too does jaw length and folivory (positive allometry) (Hylander, 1985; Terhune, 2011). Indeed, Beecher (1983) found a correlation between symphyseal fusion, increased body size and leaf eating. However, it remains unknown which food type and consumption frequency exerts the greater selection pressure on non-human primates (Coiner-Collier *et al*., 2016).

Evidence once indicated that there is a greater correlation between dietary behaviour, food mechanical properties and morphology in platyrrhine primates (Norconk *et al*., 2009; Thompson *et al*., 2014; Ross *et al*., 2016), than in catarrhine primates (McGraw & Daegling, 2012). However, recent analysis of *Pongo pygmaeus*, *Cercocebus atys* and *Colobus polykomous* indicates that the correlation between form and function in catarrhines is stronger than once considered. Indeed, studies indicate their dental (*C. atys, P. pygmaeus*) and craniofacial morphologies (*Co. polykomos*) are reflections of accessing hard foods (Vogel *et al*., 2008; Daegling *et al*., 2011; McGraw *et al*., 2016). In the case of *Co. polykomos*, the craniofacial morphology reflects the crushing of the outer shells of seeds before mastication, not the mastication of the inner seeds themselves (McGraw *et al*., 2016), a feature that was missed in an earlier study of this species (Daegling & McGraw, 2001).

While the correlation between dietary ecology and masticatory morphology remains incompletely understood (Vogel *et al*., 2014; Ross *et al*., 2016), further data on feeding behaviours, food mechanical properties and the frequency of ingestion and mastication should improve the understanding of how the different factors relate to one another

(Foster *et al*., 2006; Berthaume, 2016; Coiner-Collier *et al*., 2016; McGraw *et al*., 2016). Indeed, Daegling & McGraw (2001) and Berthaume (2016) suggest that where the studies do not find correlations it is because there are errors with the hypotheses, data collection, with the method to assess biomechanical function (as seen with the revisions made for the *Co. polykomos* feeding behaviour), or the wrong food mechanical properties have been investigated. Alternatively, it is possible that the diets observed to be consumed today are not the same as the diets to which a species was morphologically adapted, e.g., colobines are commonly referred to as leaf-eating monkeys, yet their ancestors were most likely seed eaters (Lucas & Teaford, 1994). It is also possible that the potential correlation between food mechanical properties and morphology are not apparent in every feature or to the same extent for all species (Daegling & McGraw, 2001; Taylor *et al*., 2008; Ross *et al*., 2012; Vogel *et al*., 2014).

Despite the success of many studies in establishing a correlation between stress and strain, according to some researchers it is not possible to distinguish between a morphology shaped by hard or tough-object eating (Smith, 1983; Ravosa, 1996; Daegling & McGraw, 2001; Hogue, 2008; McGraw & Daegling, 2012; Daegling *et al*., 2013; Grine & Daegling, 2017). That is because both loading regimes result in changes to the osseous architecture, along with an increase in bone mass (Grine & Daegling, 2017). Thus, attempts to interpret morphology can be clouded by similar morphological responses to stress and strain (Ross *et al*., 2012). To confound the situation further there is a great diversity of mandibular morphologies associated with hard-object feeding in non-human primates[3] (Daegling & Grine, 1991; Daegling, 1992; Taylor, 2006; Daegling & McGraw, 2007; Grine & Daegling, 2017). As a result, studies on the biomechanics of the masticatory morphology of non-human primates did not always reveal strong correlations between diet and morphological form (e.g., Daegling & McGraw, 2001, 2007; Taylor, 2002, 2005, 2006b; Koyabu & Endo, 2009; McGraw & Daegling, 2012; Ross *et al*., 2012; Vogel *et al*., 2014; Grine & Daegling, 2017).

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[3] A situation not shared by cichlid and centrarchid species of fish that are characterised by divergent evolutionary histories, with examples in both of species being morphologically convergent, adapted for the consumption of small prey using the same modes of jaw movement (Montaña & Winemiller, 2013). Similarly, bovines and hippotragines convergently evolved features of their dentition to assist with grazing, which makes distinguishing the two based on their dental morphology difficult (Gailer *et al*., 2016).

2.3.2 Dental form

While the correlation between mandibular form and diet cannot be determined beyond high-stress diets from hard or tough foods, or low stress diets from soft foods, the correlation between dentition and different types of diets appears to be more straightforward. Conventional wisdom pertaining to tooth form generally concludes that a tooth is adapted to the external physical characteristics and the internal mechanical properties of the foods consumed (Rosenberger & Kinzey, 1976; Kinzey, 1978; Kinzey & Norconk, 1990; Yamashita, 1996; Swindler, 2002; Lucas *et al.*, 2008b; Constantino *et al.*, 2012; Ungar, 2015). This assumed correlation is because their primary relationship is a physical one, with the occlusal surface of the tooth being the point of contact between the food consumed and the masticatory apparatus (Yamashita, 1998; Norconk *et al.*, 2009). To comminute the foods, the teeth must apply enough pressure (stress) to the food in order for it to fracture so that it is either easier to masticate further or more digestible (Yamashita, 1998). Teeth therefore need to be adapted to both break down foods and resist potential stress and strain from foods without fracturing (Lee *et al.*, 2010; Constantino *et al.*, 2012; Ungar, 2015; Gailer *et al.*, 2016). The physical properties of a food (its resistance to fracture) and the tooth form (suitable adaptations to fracture food) will determine how much effort is required during mastication and therefore, how successful the breakdown of the food is (Yamashita, 1998; Norconk *et al.*, 2009; Gailer *et al.*, 2016).

Teeth are assumed to be biological structures that have evolved to perform their functions with the maximum of efficiency (Ungar, 2015; Gailer *et al.*, 2016). That is to mechanically break down foods to assist the subsequent biochemical digestion (Kinzey, 1978; Swindler, 2002). In so doing, teeth should enable the consumption of more of the relevant foods in order to increase the intake of energy required for their high metabolic demands (Gailer *et al.,* 2016). It is also expected that the tooth will wear in such a way to keep it functionally efficient throughout life (Ungar, 2015). Various aspects of a tooth’s morphology provide information regarding the physical properties of the foods consumed (Ungar, 2011, 2015). Morphological features include: tooth size, thickness of the dental enamel and occlusal morphology (Ungar, 2011, 2015). Variation of tooth size is reflective of the external characteristics of foods, e.g., their overall size and shape, along with their properties, e.g., abrasiveness (Teaford & Ungar, 2000). Variation of tooth shape on the other hand is a reflection of the internal characteristics of foods, e.g., their resistance to fracture (hardness or toughness) (Teaford & Ungar, 2000).

The first mineralised tissue to interact with foods is the enamel, its primary responsibility is to protect the tooth from the mechanical properties of foods, resisting the stresses and strains and reducing wear (Shellis *et al*., 1998; Macho, 2004; Macho & Shimizu, 2009; Ungar, 2015). As a result, it is commonly considered that the thickness and distribution of enamel over the tooth crown are adaptations to diet (Shellis *et al*., 1998; Macho, 2004; Pampush *et al*., 2013; Ungar, 2015). Thick enamel is associated with high stress diets that include hard and/ or tough foods (Happel, 1988; Shellis *et al*., 1998; Yamashita, 1998; Macho & Spears, 1999; Teaford & Ungar, 2000; Lambert *et al*., 2004; Macho, 2004; Constantino *et al*., 2011; Ungar, 2011; McGraw *et al*., 2012; Pampush *et al*., 2013; Grine & Daegling, 2017). In contrast, thin enamel is generally associated with a soft food diet (Kay, 1981; Kinzey, 1992; Lucas *et al.*, 2008a; Vinyard *et al*., 2011). The adaptive benefit of thick enamel for hard or tough-object feeders is the protection and extended lifetime of the tooth, a feature perhaps not selected for in a consumer of soft foods with little wear (DeGusta *et al*., 2003; King *et al*., 2005; Lucas *et al*., 2008a; Constantino *et al*., 2011; Pampush *et al*., 2013; Grine & Daegling, 2017), although, it must be acknowledged that occlusal morphology and how it resists fracture is complex (Berthaume *et al.*, 2010).

Each part of the dentition has a particular function to perform, where the anterior dentition is for the initial preparation, puncture and incision of foods; the postcanine dentition is responsible for mastication of the foods and as a result is adapted to the physical and chemical properties of foods (Happel, 1988; Kinzey & Norconk, 1990; Norconk *et al*., 2009). Depending on the nature of the diet consumed the size and shape of the anterior and posterior dentition varies (Scott, 2012). The anterior and posterior dentition can therefore provide indications about the general dietary classification or the hardness/ toughness of the diets consumed (Kay, 1975; Happel, 1988; Yamashita, 1998; Lucas *et al*., 2008b; Vinyard *et al*., 2011). Folivores (generally consumers of tough foods) have large teeth relative to their body size, and relatively long molar shearing blades in order to divide leafy materials more efficiently. Insectivores also have relatively long and sharp molar shearing blades but this is to puncture and reduce the brittle exoskeleton of invertebrates. Frugivores generally have larger incisors than folivores as they require a larger surface area to prepare fruits, with small postcanine teeth relative to their body size and more rounded molar cusps adapted for grinding. Granivores in contrast (generally consumers of hard foods) have low, blunt cusps (bunodonty) that correspond to opposing basins to prevent cracks from propagating

(Kay, 1975; Kinzey, 1978; Happel, 1988; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Lucas *et al*., 2008b; Lee *et al*., 2010; Ungar 2011, 2015).

Australopithecus and *Paranthropus* dental morphology was analysed in light of the above patterns of tooth form. The large, megadont postcanine teeth present in the australopithecines, and particularly the derived *Paranthropus*, have been suggested to provide a greater surface area to evenly distribute the occlusal load and increase the probability of fracturing small food particles or to assist with the processing of more obdurate foods, thus maximising the efficiency of oral food processing (Rak, 1988; Teaford & Ungar, 2000; Lucas *et al*., 2008b; Constantino *et al*., 2011; Norconk & Veres, 2011; Ungar, 2011; Scott, 2012). The presence of hyper-thick enamel, enamel chips and short shearing crests on *Paranthropus* are suggestive of a diet consisting of hard objects (Teaford & Ungar, 2000; Lucas *et al*., 2008b; Koyabo & Endo, 2009; Constantino *et al*., 2010, 2011). Greater occlusal relief and larger shearing crests in *Australopithecus* are suggestive of a tougher-food diet, while the short shearing crests on *Paranthropus* are suggestive of a diet consisting of hard objects (Teaford & Ungar, 2000; Koyabo & Endo, 2009).

Of course, attempting to reconstruct past diets based on dental morphology does have its weaknesses. As previously mentioned, thick dental enamel can be a characteristic of both hard and tough object feeders (Happel, 1988; Shellis *et al*., 1998; Yamashita, 1998; Macho & Spears, 1999; Teaford & Ungar, 2000; Lambert *et al.*, 2004; Macho, 2004; Constantino *et al*., 2011; Ungar, 2011; McGraw *et al*., 2012; Pampush *et al*., 2013; Grine & Daegling, 2017). In addition to this, larger teeth can be reflections of both small, hard objects, or tough objects, or abrasive objects (Ungar, 2011). Similarly, consistent with previously described molar size and shape patterns, the molars of insectivorous lorisids resemble the folivorous pattern (see Kinzey, 1978; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Ungar, 2011, 2015), while the molars of insectivorous galagids follow the frugivorous pattern (Scott, 2012). Generally folivorous species are associated with having relatively larger molars than frugivores (Kay, 1975; Kinzey, 1978; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Ungar, 2011, 2015), but in the case of the folivorous colobines and frugivorous cercopithecines this pattern has been reversed (Ungar, 2011; Scott, 2012). The latter point is perhaps a reflection that the dietary focus on foliage is only a recent occurrence in the evolutionary history of colobines (Lucas & Teaford, 1994).

Given that there is overlap between species consuming diets of different mechanical properties and species’ morphology not conforming to expected patterns, it is clear that there is a need for caution when attempting to make inferences on diet based on morphology (Yamashita, 1996; Berthaume *et al.*, 2010; Scott *et al.*, 2012). Indeed, because diet is so complex it would perhaps be naïve to expect one morphological solution to each diet type (Yamashita, 1998). Thus, it appears that the majority of studies confirm that there are some generalised morphologies associated with certain diets and basic inferences can be made based on them.

2.4 Challenges to the conclusion that Paranthropus was a dietary specialist

2.4.1 Specialist and generalist morphologies

A reappraisal by Wood & Strait (2004) of the morphology present in *Paranthropus*, *Australopithecus* and early *Homo* led to questions being raised about whether *Paranthropus* was a dietary specialist. The question follows on from studies that have explored the form-function relationship with regards to what it means to be morphologically specialised or generalised.

A specialised feeding morphology is one that is adapted to and enables the efficient exploitation of a particular type of food that would otherwise be inaccessible, while also reducing the dietary diversity (Saldaña-Vázquez *et al*., 2015; deVries *et al*., 2016). For example, large rounded molars and fusion of pharyngeal plates in *Lepomis microlophus* (redear sunfish) enables the species to crush hard-bodied prey such as molluscs (Lauder, 1983), while long-tongued bees (e.g., *Bombus hortorum*) have a narrow dietary breadth, specialising on the red clover (*Trifolium pratense*) (Goulson & Darvill, 2004). In contrast, a generalised dietary morphology is not adapted to any particular food and reflects a wide dietary intake, such as bees with shorter tongues (Goulson & Darvill, 2004).

Through analysis of supposedly morphologically specialised cichlid fish, the understanding of what it means to be a dietary specialist was challenged. Liem (1980) analysed the morphology of *Petrotolapia tridentiger*, a species described as a highly specialised rock scraper, while Cosandey-Godin *et al*. (2008) and Binning *et al*. (2009) analysed *Astatoreochromis alluaudi*, a species with massive pharyngeal jaws assumed to be a hard-bodied prey specialist, but each of the studies found the cichlid fish were capable of consuming a more diverse range of foods than expected based on their feeding morphology. The apparent morphological specialism in the fish did not equate to dietary or behavioural specialism, but instead enabled the species to act as ecological generalists (Liem, 1980; Robinson & Wilson, 1998; Liem & Summers, 2000; Cosandey-Godin *et al*., 2008; Binning *et al*., 2009). These species appeared to be morphologically specialised yet behaved as ecological generalists, thus becoming examples of Liem’s Paradox (Robinson & Wilson, 1998).

This paradox was resolved by an optimal foraging strategy (Robinson & Wilson 1998), which is based on the principle that less preferred foods would be ignored when other, more preferred foods were available. Competition for food during periods of resource shortage drove the morphological specialisations, but these adaptations would not prevent organisms from exploiting more preferred resources when they were available (Robinson & Wilson, 1998). In this case, a species would act as dietary specialists during the period of food abundance by focussing on the preferred foods, and become generalists during the period of food scarcity by switching to less preferred foods (Robinson & Wilson, 1998). This theory opposes the traditional assumption that a specialist trait is one that would enable the frequent consumption of a particular food rather than one that enables the occasional exploitation of a food resource and rests upon the assumption that the preferred food resources are also easier to access and use (Robinson & Wilson, 1998). Based on this, what it is to be a specialist was questioned (Liem, 1980).

Robinson & Wilson (1998) proposed three different areas of specialisation: diet, morphology and prey utilisation efficiency, while Liem & Summers (2000) proposed two types of specialists: stenotopic and eurytopic. A stenotopic species is specialised morphologically and functionally to a narrow dietary niche, and a eurytopic species is morphologically specialised, but with the capacity to consume a wide variety of foods (Liem & Summers, 2000).

A key aspect of the Dietary Hypothesis (Robinson, 1954a, 1963) was that the morphology of *Paranthropus* appeared to be specialised. The derived masticatory features present in *Paranthropus* were specialist adaptations to a diet of “crushing and grinding” (Robinson, 1963: 392). As previously discussed, Liem’s Paradox brings into question what it is to be a dietary specialist (Liem, 1980). According to Wood & Strait (2004) the question of whether a morphology is a generalist one or a specialist one can be broken down into two factors: 1) what does the morphology enable an organism to do? and 2) what does it restrict an organism from doing? Applying this to the studies of Liem (1980), Cosandey-Godin *et al*. (2008) and Binning *et al*. (2009) it is clear that the apparent specialisations of the cichlid fish enabled them to consume the foods they were adapted to, but did not prevent them consuming other foods when they were available. This supposed specialist adaptation had the effect of broadening the dietary repertoire available to the fish; this is the sign of a generalist adaptation (Wood & Strait, 2004).

Further examples of species that appear to be morphologically specialised but display generalist behaviours come from platyrrhine primates (Wood & Strait, 2004; Wright, 2005; Norconk *et al.*, 2009; Norconk & Veres, 2011). Features commonly interpreted as specialist adaptations to hard-object feeding in *Cebus* and *Sapajus* have been revised and are now viewed as enabling a broadening of the dietary niche (Wright, 2005; Norconk *et al.*, 2009; Norconk & Veres, 2011). Similarly, the morphological adaptations that enable leaf consumption in *Alouatta* once considered specialised are now regarded as generalised, as they do not prevent the consumption of other foods (Wood & Strait, 2004).

In the above instances, the features enabled the monkeys to consume harder-food objects or leaves when there was little else available (Wright, 2005; Norconk *et al.*, 2009). The morphology of these platyrrhine monkeys have not been shaped by one food type, but rather by a range of mechanically demanding foods (Wright, 2005). Researchers have observed that dental and behavioural adaptations of many non-human primates have bypassed the accessibility problems posed by mechanically protected foods, such as seeds (Daegling *et al.*, 2011, 2013; Norconk & Veres, 2011; McGraw & Daegling, 2012; Pampush *et al.*, 2013). This essentially follows Liem & Summers' (2000) definition of a eurytopic species, as it appears that a morphological specialisation does not equate to a behavioural specialisation.

In order to overcome the lack of morphological adaptations suited to hard-object feeding, species such as *Colobus polykomos*, *Cacajao calvus* and *Chiropotes satanas* have been observed to fracture foods in different areas of the mouth to increase efficiency (Daegling & McGraw, 2001; McGraw & Daegling, 2012; Pampush *et al.*, 2013; McGraw *et al.*, 2016). Each species are suggested to process the hard seeds with their incisors instead of their molars, and then masticate the softer, more pliable seeds with their postcanine dentition (Daegling & McGraw, 2001; McGraw & Daegling, 2012; Pampush *et al.*, 2013; McGraw *et al.*, 2016). Mastication of foods to different degrees across the mandible would result in different loading conditions and potentially different biomechanical solutions (Daegling & McGraw, 2001; Vinyard *et al.*, 2011).

Other behaviours can include pounding mechanically resistant foods against rocks, as *Cebus* do (Wright, 2009; McGraw & Daegling, 2012), or the use of tools, as *Pan, Papio* and *Pongo* are observed to do (Goodall, 1965; van Lawick-Goodall *et al.*, 1973; Sugiyama, 1994; van Schaik & Knott, 2001; Fox *et al.*, 2004; Hicks *et al.*, 2005; Gruber *et al.*, 2010; McLennan, 2011; Smith *et al.*, 2012). These behaviours have the capacity to bypass the potential lack of masticatory robusticity in order to enable access to otherwise inaccessible foods and thus provide access to relatively high quality resources throughout the year (Norconk & Veres, 2011; McGraw & Daegling, 2012).

2.4.2 How revisions of what it means to be morphologically specialised affects the interpretations of hominin morphology

Based on the questions raised with regard to what it means to be a dietary specialist, Wood & Strait (2004) analysed how congruent the morphology of *Paranthropus* is to the interpretation that they were dietary specialists. The conclusion was that the morphology of *Paranthropus* was quite clearly derived, but while a specialised feature is derived, it does not mean that a derived feature is specialised. The key variables to consider when classifying a species as a specialist or generalist and how they apply to *Paranthropus* are in Table 2.4.

Table 2.4: Definitions of stenotopy and eurytopy according to Eldredge (1979) and Vrba (1980), as detailed in Table 1 from Wood & Strait (2004), and how the terms can be applied to *Paranthropus* summarised from Wood & Strait (2004). Table removed due to copyright.

Analysis of *Paranthropus* morphology reveals that the features so often identified as specialist adaptations could in fact represent generalist adaptations (Wood & Strait, 2004). For example, the robust masticatory morphology, megadont postcanine dentition, and hyper-thick enamel do not preclude other foods from being consumed, so they do not necessarily indicate a specialist adaptation (Wood & Strait, 2004). The robust mandibular morphology shows that it is capable of resisting high loads and stresses being placed on it by various diets, but biomechanical analyses of extant non-human primates cannot distinguish between a hard food and a tough food diet (Hylander, 1988; Daegling & McGraw, 2001; Daegling *et al*., 2013). The enamel might be hyper-thick to prevent fracture from hard food items, or to prevent wear and extend the tooth-life from an extremely abrasive diet (Happel, 1988; Shellis *et al*., 1998; Teaford & Ungar, 2000; Wood & Strait, 2004; Pampush *et al*., 2013; Grine & Daegling, 2017). The premolars might have undergone expansion to increase the chewing surface area so as to masticate more food per bite, or to extend the life of the postcanine dentition by including premolars in the molar row (Wood & Strait, 2004). According to researchers the only morphological feature that is consistent with specialist adaptations is the occlusal surface, a feature considered to be a poor design for leaf consumption (Hylander, 1988; Wood & Strait, 2004; Wood & Shroer, 2012; Strait *et al*., 2013). Based on the majority of the above traits Wood & Strait (2004) concluded that rather than excluding foods from the diet of *Paranthropus* these adaptations had the potential to broaden it, by enabling the frequent or seasonal consumption of hard or tough foods to go along with the softer foods that are available (Wood & Strait, 2004).

The morphology of *Paranthropus* is therefore consistent with euryphagy, but the derived features may be more important for the seasonal consumption of hard foods (Peters, 1987; Wood & Strait, 2004). Following on from the morphological analyses by Wood & Strait (2004), dental microwear texture analysis and stable carbon isotope analysis on the hominin fossils have combined to challenge the grounds upon which the original dietary reconstructions were based. In so doing, the analyses served to provide support for the revisions that Wood & Strait (2004) advocated.

2.4.3 Dental Microwear Texture Analysis

2.4.3.1 What it is and how it works

Microscopic wear patterns on the occlusal surface of molar teeth have received considerable attention (Yamashita *et al*., 2016). The method is based on the understanding that food mechanical properties, abrasives attached to the foods (such as exogenous grit, phytoliths and enamel prisms) and the chemical properties of foods are known to have a direct impact on the microwear surface texture of teeth (Nystrom *et al*., 2004; Ungar *et al*., 2006; Scott *et al*., 2009; Grine *et al*., 2012). Microwear patterns are predominantly interpreted as the result of foods masticated at a specific moment in time (Nystrom *et al*., 2004; Ungar, 2011). As a result, it is suggested that analysis of dental microwear texture analysis provides direct evidence about the qualitative traits and fracture mechanics of the different food items consumed, which thus reflects the nature of the dietary ecology of the specimens analysed (Scott *et al*., 2005, 2009).

Microwear can distinguish between a diet of hard-brittle foods and tough-pliable foods (Kay & Grine, 1988; Ungar, 2011). These food mechanical properties produce two main feature-types on the occlusal surfaces of the dentition: striations and pitting. Pits produce a complexity signal on the occlusal surfaces and are formed from abrasives being crushed between the teeth and into facets; these are commonly associated with a hard food diet. Striations give an anisotropic signal, and are formed from abrasives being dragged along the tooth surface by the opposing tooth; these are associated with a tough food diet (Ungar *et al*., 2006; Grine *et al*., 2012; Ungar, 2015; Percher *et al*., 2018). The latter category is more a reflection of the abrasives attached to the foods, because in order for microwear patterns to form the object must be as hard as or harder than the enamel itself (Nystrom *et al*., 2004). A tough food by its very nature is not hard, but should exogenous grits, phytoliths or enamel particles be attached to the food, their interaction with the occlusal surfaces will create the microwear patterns (Nystrom *et al*., 2004; Scott *et al*., 2012). A microwear surface pattern intermediate of 'anisotropic' and 'complex' (a balance of pits and scratches) reflects a soft fruit diet (Ungar *et al*., 2006). Microwear can also provide an indication on the size of the foods, with large, hard foods creating larger pits, and similarly small, hard foods creating smaller pits (Ungar, 2011; Grine *et al*., 2012). Feature sizes can be informed based on the scale of maximal complexity and fill volume (Ungar, 2011, 2015).

In general, hard-object feeders will have high complexity values and low anisotropy, whereas tough-object feeders tend to have high anisotropy and low complexity values (Scott *et al*., 2012). Frugivorous species often fall midway between the two microwear types (Ungar, 2011, 2015). In other words, dental microwear texture analysis will not define the exact diet consumed, but it will provide a general indication of the fracture properties of the foods consumed (Grine *et al.*, 2012; Wood & Shroer, 2012), so it can distinguish between diets focussed on hard-foods, tough-foods or soft-foods (Scott *et al*., 2012; Grine *et al*., 2012; Daegling *et al*., 2013; Ungar, 2015).

2.4.3.2 Limitations of Dental Microwear Texture Analysis

There are very clear benefits to using dental microwear texture analysis as it provides information on the physical properties of the foods consumed and it can identify subtle and seasonal differences in diet. In terms of hominins it is an essential resource to understand more about the nature of the foods consumed (Grine *et al*., 2012), but there are limitations associated with the method too.

As dental microwear texture analysis provides information about the physical properties of the foods consumed in the days or weeks prior to death this can be very informative (Ungar, 2011). By itself it can be a problem as it is recording only a very short period of dietary history and thus it informs very little about overall diet of a species and therefore little about their overall dietary adaptations (Ungar, 2011; Wood & Schroer, 2012; Strait *et al*., 2013). This is because the more attrition/ wear/ hardness involved in the diet the faster the turnover of the microwear features (Nystrom *et al*., 2004; Ungar, 2011; Scott *et al*., 2012; Percher *et al*., 2018). The turnover of features means that a diet that normally involves non-complex foods can be rapidly altered to appear as though hard foods are present, even after a short time consuming such foods (Scott *et al.*, 2012; Wood & Schroer, 2012). The effect of which potentially results in an overestimation of the consumption of hard foods (Scott *et al*., 2012; Wood & Schroer, 2012). Attempting to establish the abrasiveness or fibrousness of a diet based on tooth wear is not straightforward, for the two with their different mechanical properties/ fracture requirements could result in a similar morphology (Ungar, 2015). The question then becomes, does a species have a "steep wear gradient because it chews a little with a very abrasive diet, or a lot, with less abrasive one" (Ungar, 2015: 33).

The accuracy of dental microwear texture analysis has also been questioned in recent years. Doubt was raised due to a study exploring a wide range of non-human primate microwear patterns, which revealed that it is not always possible to distinguish species with different diets using dental microwear texture analysis (Scott *et al*., 2012). Based on the research of Scott *et al*. (2012) it was suggested that dental microwear texture analysis studies are not perhaps as clear cut as they appear, and that therefore, the dietary signal identified in microwear samples might only be indirect (Strait *et al*., 2013; Smith *et al.,* 2015).

The problem that many comparative studies have, including that of Scott *et al*. (2012) is that their studies are not based on samples that have been directly observed when feeding in the wild. Any inferences made about diet are therefore based on other field studies and not necessarily about the sample analysed. The studies by Nystrom *et al*. (2004), Yamashita *et al*. (2016) and Percher *et al*. (2018) recognised this weakness and incorporated direct observation of the dietary habits of their samples of *Papio hamadryas* (*sensu lato*), *Mandrillus sphinx,* and *Lemur catta* into their analysis of the dental microwear texture analysis and dental topographic analysis. The results of the studies highlighted seasonal differences in the nature of the foods consumed, which were reflected by changes in the microwear patterns and dental topography (Nystrom *et al.*, 2004; Yamashita *et al.*, 2016; Percher *et al.*, 2018). These studies highlight the potential that dental microwear texture analysis has; specifically when the sample and data gathered (the method) is carefully controlled. A factor not possible to control for in hominins, but through a more comprehensive understanding of microwear patterns in extant non-human primates it is possible to generate more accurate comparisons for hominins.

2.4.4 Stable Carbon Isotope Analysis

2.4.4.1 What it is and how it works

Stable isotope analysis using strontium/ calcium (Sr/Ca), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) are additional methods used to reconstruct past diets (Copeland *et al.*, 2011; Klein, 2013). Nitrogen isotopes are extracted from protein retained in fossil bones; strontium/calcium can be extracted from bone and dental enamel; while oxygen and carbon isotopes are extracted from tooth enamel (Sponheimer *et al.*, 2005b; Balasse *et al.*, 2012; Klein, 2013).

Stable carbon isotopes and strontium/ calcium isotopes can reflect the dietary ecology, the chemistry of the foods consumed and the plant communities available to the specimen analysed, while oxygen isotopes can establish patterns of seasonality and determine if a species is a frugivore, faunivore or herbivore (Sillen, 1992; Cerling *et al.*, 2004; Sponheimer *et al.*, 2006a; Ungar, 2011; Balasse *et al.*, 2012; Grine *et al.*, 2012). A more complete picture of the diet of an individual would be generated if the above isotopes and what they inform were used in conjunction (Balasse *et al.*, 2012; Grine *et al.*, 2012). This is because, the dental enamel stores carbon and oxygen isotope information that is laid down during the early years (during enamel and tooth development), while the strontium isotopes taken from the bone present information from both the early and later years (during bone remodelling) (Grine *et al.*, 2012).

The current understanding of oxygen isotopes and their foodweb patterns is limited, while strontium/ calcium isotopes are inhibited by problems relating to diagenesis[4], and nitrogen isotopes are restricted by the short lifespan of proteins present in nitrogen (with a maximum lifespan of 200,000 years, depending on location) (Sillen, 1992; Sponheimer *et al.*, 2005b; Grine *et al.*, 2012; Klein, 2013). Unlike nitrogen isotopes,

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[4] Diagenesis is chemical alteration over time. The effects of which have been known to obscure or even obliterate strontium/calcium in the fossil remains (Sillen, 1992; Sponheimer *et al.*, 2005b; Grine *et al.*, 2012)

carbon isotopes do not face the same limitations of time, for they persist and are protected in dental enamel, and unlike strontium/ calcium isotopes from bone, carbon isotopes do not face the same limitations of diagenesis, because enamel is denser and more crystalline, so the bioapatites are better protected and are less likely to be affected by post-mortem chemical alteration (Lee-Thorp *et al*., 1989; Sponheimer *et al*., 2005a; Grine *et al*., 2012). The highly crystalline nature and resistance to postdepositional diagenesis in tooth enamel means that the antemortem stable carbon isotope signal is retained for millions of years. Stable carbon isotopes are therefore considered to be the most reliable sample material used to extract dietary information (Lee-Thorp *et al.*, 2000; Sponheimer *et al*., 2005a, 2013; van der Merwe *et al*., 2008; Grine *et al*., 2012; Klein, 2013).

Animal tissues contain the degree of dietary carbon in the system, which derives from the particular “photosynthetic pathways at the base of the foodweb” utilised (Lee-Thorp *et al*., 2000: 567; Sponheimer *et al*., 2006a). In other words, the isotope signals from the plants are carried over into the consumers (animals), and based on this; it is possible to identify the photosynthetic pathways that the animals’ diets were derived from (Grine *et al*., 2012). The pathways explored are C_3, C_4 and CAM (although the latter is not as common) (Lee-Thorp *et al.,* 2000; van der Merwe *et al.,* 2003; Sponheimer *et al*., 2006a; Grine *et al*., 2012). Plants that follow the C_3 pathway are derived mainly from trees, shrubs, bushes and grasses of forested environments (the resultant diets would consist of nuts, fruits and leaves) (Lee-Thorp *et al.,* 2000; van der Merwe *et al.,* 2003; Sponheimer *et al*., 2006a; Grine *et al*., 2012). Plants that follow the C_4 pathway are derived mostly from grasses and sedges, which could perhaps reflect a more open environment (Lee-Thorp *et al.,* 2000; van der Merwe *et al.,* 2003; Sponheimer *et al*., 2006a; Grine *et al*., 2012). So not only are stable carbon isotopes useful in identifying fundamental dietary differences, they also provide information about the environment an individual was from, which is particularly useful for reconstructing hominin habitats (see Table 2.5 for an environmental breakdown according to photosynthetic pathways) (Lee-Thorp *et al.,* 2000; van der Merwe *et al.,* 2003, 2008; Sponheimer *et al*., 2006a; Grine *et al*., 2012).

The two pathways (C_3 and C_4) are distinguished based on the levels of ^{13}C in their tissues, where C_3 plant tissues are relatively depleted in ^{13}C, C_4 plant tissues are relatively enriched in ^{13}C (Lee-Thorp *et al*., 2000; Sponheimer *et al*., 2006a, 2013). As a result, the composition of carbon isotopes in C_3 and C_4 plants does not overlap (photosynthetic pathway ranges detailed in Table 2.5) (Sponheimer *et al*., 2013).

Table 2.5: Environmental breakdown of the plants using the various photosynthetic pathways, according to Cerling *et al.*, 2013

$\delta^{13}C$ range	C_3 pathway (range between 24% - 32%)	C_4 pathway (range between 10% - 14%)
Positive values	Xeric (dry) environments	Mesic (moderately moist) environments
Intermediate values	Mesic (moderately moist) environments	
Negative values	Closed canopy environments	Xeric (dry) environments

Typically stable carbon isotope data are dominated by C_3 and C_4 based food resources, but it is not a straightforward dichotomous system, as there exists a third photosynthetic pathway extracted from succulent plants, the crassulacean acid metabolism (CAM) pathway (Cerling *et al.*, 2013; Sponheimer *et al*., 2013). They form minor, but potentially important elements of the plant biomass in most woodland and savannah ecosystems (Cerling *et al.*, 2013; Sponheimer *et al*., 2013). However, depending on where a species lives, the majority of foods follow C_3 or C_4 photosynthetic pathways, and as such most diets are distinguished accordingly.

2.4.4.2 Limitations of Stable Carbon Isotope Analysis

A potentially important limitation of stable carbon isotope analysis involves the pre-treatment methods used. Recent studies employing these analyses appear to be using a consistent amount of chemicals and for a similar period of time (e.g., Cerling *et al*., 2011, 2013; Sponheimer *et al*., 2013; Wynn *et al*., 2013). There is slight variation with those of the earlier studies (e.g., Sponheimer & Lee-Thorp, 1999; Sponheimer *et al*., 2005a), but in theory as most of the earlier samples/ specimens have been reanalysed later using a consistent method the results should be accurate.

Sponheimer *et al*. (2006a) report on seasonal variation within the enamel, but Strait *et al*. (2013) highlight that this might not be entirely accurate, as it could take weeks or months for the mineralisation of the enamel to be complete. In addition, as the stable carbon isotopes are extracted from the dental enamel, which grows during development, this means that the stable carbon isotopes are not reflective of an individual’s whole life, but rather they are snapshots of their diets when they were juveniles (Strait *et al*., 2013). It is possible that the diet consumed during early life differed from that during adulthood (Strait *et al*., 2013; Chalk-Wilayto *et al*., 2016).

The difference between the diet of a juvenile and that of an adult therefore requires different teeth be used for the extraction of stable carbon isotope analysis. The deciduous dentition or the earlier erupting permanent teeth are likely to reflect weaning, whereas, the M_2 or M_3 are more reflective of an adult diet (van der Merwe *et al*., 2008). Observation of those teeth that are recorded for their stable carbon isotopes in the hominins reveals that of the 149 recorded, 72 are from the M_2 or M_3, while 77 are not (information available in Cerling *et al.*, 2013 Supplementary Information). In generally the results are quite consistent across the dentition, but it is preferable that the specimens are extracted from the later developing teeth to generate a more thorough understanding of the adult dietary variation.

A further limitation of using stable carbon isotopes for the interpretation of hominin diets, is that if they were predators it is possible that their prey's consumption of foods from one pathway (e.g., C_4) obfuscated their actual diet, by overestimating a particular food source (Grine *et al*., 2012). The isotopes do not actually inform the exact nature of the diet, just the photosynthetic pathway, as a result it is hard to rule out foods that were not consumed (Strait *et al*., 2013). Isotope data are therefore useful to provide information on the abundance of resources that were exploited (Strait *et al*., 2013).

2.4.5 Application of Dental Microwear Texture Analysis and Stable Carbon Isotope Analysis to hominins

While there are limitations associated with the methods of dental microwear texture analysis and stable carbon isotope analysis – as there are with any method – their strengths outweigh their weaknesses, and their potential importance to palaeoanthropological research cannot be overlooked, particularly if they are used in conjunction. As stable carbon isotope analysis reflects the early years of life during tooth formation, and dental microwear texture analysis represent the days/ weeks prior to death, the two methods provide a more complete picture of diet during different time periods (Grine *et al*., 2012; Percher *et al*., 2018).

Dental microwear texture analysis and stable carbon isotope analysis have both been applied to various specimens from the majority of hominin genera and species. The two methods have produced results that largely correspond, which thus increased their reliability (Grine *et al*., 2012). The results of stable carbon isotope analysis and dental microwear texture analysis when compared with the traditional comparative morphological interpretations are summarised in Table 2.6.

Table 2.6: Dietary interpretations based on morphological analysis, Stable Carbon Isotope Analysis and Dental Microwear Texture Analysis

Species	Comparative Morphological Analysis	Stable Carbon Isotope Analysis	Dental Microwear Texture Analysis
A. anamensis	Thick enamel, but thinner mandibular corpora compared to *Paranthropus* suggest it was able to consume a relatively broad diet. [1, 2]	C_3 consumer. [3, 4]	Microwear patterns lacking both complexity and anisotropy signals, suggestive of a diet consisting predominantly of softer foods. [5, 6]
A. afarensis	Similar features to *Australopithecus anamensis*, but greater mandibular robusticity. Able to consume a broad diet. [1]	C_3 - C_4/ CAM consumer. [4, 7]	Microwear patterns lacking both complexity and anisotropy signals, suggestive of a diet consisting predominantly of softer foods. [6, 8]
A. africanus	An increase in postcanine size compared to those above, indicates diet breadth was emphasised. [1]	Highly mixed and varied diet. Consuming more than 50% of C_3 foods and further substantial quantities of C_4 foods. [4, 9, 10, 11, 12]	Highly varied diet, with more anisotropy than complexity patterns present suggestive of more tough than hard foods being consumed. [13, 14, 15, 16]
P. aetheopicus	Highly derived craniofacial morphology. [17]	Diet dominated by C_4 resources. [3]	No microwear information available
P. boisei	• Traditional interpretation: Highly derived, specialist hard-object feeder. [1] • Alternative interpretation: Derived morphology enables the consumption of a broader range of foods and thus makes this species a dietary generalist. [18]	Diet heavily dominated by C_4 resources, with a slight increase over time. Values do not overlap with *Paranthropus robustus.* [4, 12, 19]	Microwear patterns not consistent with hard-object feeding, but instead predominantly one of softer foods - similar to *A. anamensis* and *A. afarensis.* [12, 15, 20, 21]
P. robustus	• Traditional interpretation: Highly derived, specialist hard-object feeder. [1] • Alternative interpretation: Derived morphology enables the consumption of a broader range of foods and thus makes this species a dietary generalist. [18]	Highly mixed and varied diet, with seasonal and annual variation. Consuming more than 50% of C_3 foods and further substantial quantities of C_4 foods. [4, 9, 11, 12, 22, 23]	Highly varied diet, with some overlap with *A. africanus*. High complexity and low anisotropy suggestive of a diet that included hard, brittle foods. [12, 13, 16, 24, 25, 26]
*H. habilis (sensu lato)**	Relatively large cheek teeth, robust mandibles compared to non-hominins and moderate prognathism. Morphology consistent with ability to consume tough foods. [18, 27]	A largely C_3 based diet, but variable consumption of C_4 based foods is present (between 23 - 49% C_4). Consumption of C_4 resources increased over time. [3, 4, 28]	Varied diets, but no strong microwear patterns consistent with hard or tough object feeding, suggestive of consuming soft foods predominantly. [29]
H. ergaster	Reduction in the size of dentition and mandible compared to other *Homo* species and the earlier *Australopithecus* and *Paranthropus*. Morphological reduction could potentially restrict what this species can consume - most likely offset by tool use. [18]	Results are indistinguishable from *P. robustus*. Consumer of a highly mixed and varied diet. Consuming more than 50% of C_3 foods and further substantial quantities of C_4 foods (approximately 20-25%). [12, 30]	Microwear patterns consisting of both complexity and anisotropy, suggestive of varied diets. Presents greater microwear complexity than any other hominin analysed, except for *P. robustus*. [12, 29]

[1] Teaford & Ungar, 2000; [2] Ward *et al*., 2001; [3] Cerling *et al*., 2013; [4] Sponheimer *et al*., 2013; [5] Grine *et al*., 2006a; [6] Ungar *et al*., 2010; [7] Wynn *et al*., 2013; [8] Grine *et al*., 2006b; [9] Sponheimer & Lee-Thorp, 1999; [10] van der Merwe *et al*., 2003; [11] Sponheimer *et al*., 2005a; [12] Ungar & Sponheimer, 2011; [13] Scott *et al*., 2005; [14] Ungar, 2011; [15] Grine *et al*., 2012; [16] Peterson *et al*., 2018; [17] Walker *et al*., 1986; [18] Wood & Strait, 2004; [19] Cerling *et al*., 2011; [20] Ungar *et al*., 2008; [21] Ungar *et al*., 2012; [22] Lee-Thorp *et al*., 1994; [23] Sponheimer *et al*., 2006a; [24] Grine, 1981; [25] Grine, 1986; [26] Kay & Grine, 1988; [27] Ungar, 2004; [28] van der Merwe *et al*., 2008; [29] Ungar *et al*., 2006; [30] Lee-Thorp *et al*., 2000

* Referred to here as *Homo habilis sensu lato* following the convention established by other studies that analyse the stable carbon isotopes in Early *Homo* and do not distinguish *Homo habilis* from *Homo rudolfensis* due to the small sample sizes available for these species (e.g., Cerling *et al*., 2013).

The key results from Table 2.6 that are of interest to this study are from *Paranthropus robustus* in relation to *P. boisei* and *A. africanus,* and *P. boisei* in relation to early *Homo.* In their review of *Paranthropus* morphology, Wood & Strait (2004) suggested that features once considered indicative of specialisms (per Robinson, 1954a, 1963), might be better considered as generalist adaptations to broaden *Paranthropus* dietary repertoires (Sponheimer & Lee-Thorp, 2003; Wood & Strait, 2004). Application of dental microwear texture analysis and stable carbon isotope analysis on *P. robustus* provided support for the latter conclusion, as both dental microwear texture analysis and stable carbon isotope analysis indicate a highly varied diet that included hard objects, from both C_3 and C_4 resources, similar to that of *A. africanus* (Scott *et al.,* 2005; Sponheimer *et al*., 2006a, 2013; Cerling *et al*., 2011; Wynn *et al*., 2013). The highly derived and robust craniofacial morphology present in *P. robustus* was extremely different to that of *A. africanus,* yet the isotopic range and microwear patterns of the two hominins indicate some overlap. However, overlap between *Paranthropus* and *Australopithecus* in their dental microwear texture analysis and stable carbon isotope analysis results do not mean that their diets were the same (Lee-Thorp *et al*., 2000). Rather, the overlap means that both genera consumed some foods with similar material properties and derived from the same isotopic pathways.

Comparison of the dental microwear texture analysis and stable carbon isotope analysis of *P. boisei* and *P. robustus,* congeners from East and South Africa revealed further problems with Robinson’s (1954a, 1963) Dietary Hypothesis. Historically they were considered to demonstrate a morphological adaptation to hard-object feeding that required powerful bite forces and the ability to withstand powerful bending moments (Hylander, 1988; Ungar *et al*., 2008). Yet the evidence from the dental microwear texture analysis and stable carbon isotope analysis suggests that the two species consumed diets of different mechanical properties and from different isotopic regimes (Grine, 1981; Walker, 1981; Scott *et al.,* 2005; Sponheimer *et al*., 2006a, 2013; Ungar *et al*., 2008, 2012; Cerling *et al*., 2011, 2013). The dental microwear texture analysis patterns present in *P. robustus* are, at least occasionally, consistent with hard object feeding, while those present in *P. boisei* are not (Scott *et al*., 2005; Ungar *et al*., 2008, 2012; Ungar & Sponheimer, 2011; Grine *et al*., 2012). The stable carbon isotope analysis signals present in *P. robustus* are derived from both C_3 and C_4 resources, while *P. boisei* are dominated by C_4 resources (both isotopic regimes are consistent with environmental reconstructions – information available in Appendix A Tables A.2-A.3) (Lee-Thorp *et al*., 1994; Sponheimer & Lee-Thorp, 1999; Sponheimer *et al*., 2005a, 2006a, 2013; Cerling *et al*., 2011). These results indicate that *P. robustus* were not dietary specialists (Lee-Thorp *et al*., 1994; Sponheimer & Lee-Thorp, 1999; Scott *et al*., 2005; Sponheimer *et al*., 2005a, 2006a). *P. boisei* could have been a dietary specialist, but not on hard-object foods (Cerling *et al*., 2011, 2013; Daegling *et al*., 2011, 2013). It appears clear that the two species were not adapted to consume foods with the same mechanical properties.

The stable carbon isotope analysis results from early *Homo* compared to *P. boisei* are also of interest, particularly as they demonstrate change over time (information available in Cerling *et al*., 2013 Supplementary Information). The diets of both early *Homo* species were largely dominated by C_3 resources (>50%), and supplemented by C_4 resources (~25%), yet the percentage of both resources changes over 500kys (Lee-Thorp *et al*., 2000; van der Merwe *et al*., 2008; Ungar & Sponheimer, 2011; Cerling *et al*., 2013; Sponheimer *et al*., 2013). From 1.99-1.67 Ma and 1.65-1.46 Ma the stable carbon isotope analysis results change from a dominance of C_3 resources in the earlier time period (a ratio of C_3/C_4-based resources of 65/35) to a diet dominated slightly by C_4 resources in the latter period (ratio of C_3/C_4-based resources of 45/55) (Cerling *et al*., 2013). Stable carbon isotope analysis results of *P. boisei* specimens taken from the same periods and locations analysed for early *Homo*, consistently recorded a diet based on C_4 resources (Cerling *et al*., 2013). These results indicate that early *Homo* species were dietary generalists, while *P. boisei* could have been dietary specialists, as *P. boisei* were predominantly consuming C_4 resources when C_3 resources were available. This ability of *P. boisei* and *Homo* sp. to coexist during these time periods is in-keeping with Wood & Strait’s (2004) definition of a stenotopic species.

Based on these results, it was questioned why the different *Paranthropus* species had such similarly derived morphologies when they were consuming very different diets, and what could have been the selective force that drove such a derived morphological adaptation in these species. In contrast, the morphological differences between *Homo* sp. and *P. boisei* appear to correspond to dietary differences (Cerling *et al*., 2013). Overall, these results indicate that diet could be an important factor driving morphological form, but not the only one. Together dental microwear texture analysis and stable carbon isotope analysis and biomechanical studies are seen to have questioned the foundations upon which the Dietary Hypothesis had been built, and call into question the existing models regarding current understanding of the nature of the diet consumed by the early hominins.

In an attempt to explain the highly derived morphology of *Paranthropus* relative to *Australopithecus*, it was suggested that *Paranthropus* were better adapted to foods they eat on an infrequent basis, when their preferred foods were unavailable (thus becoming examples of Liem's Paradox). The idea that the hominins may switch to less preferred foods during periods of resource scarcity is commonly referred to as the Fallback Food Hypothesis (this is discussed in greater detail in the next chapter) (Lambert *et al*., 2004; Laden & Wrangham, 2005; Scott *et al*., 2005, 2014; Marshall & Wrangham, 2007; Marshall *et al*., 2009; Strait *et al*., 2009; Ungar, 2011; Grine *et al*., 2012; Scott *et al*., 2014). It is assumed that fallback foods are low quality, tougher and more resistant to deformation than the preferred foods (Marshall & Wrangham, 2007; Marshall *et al*., 2009; Harrison & Marshall, 2011). It is due to these assumed mechanical properties that fallback foods are suggested to have imbued selective pressures and influenced the different trophic morphologies observed in extant non-human primates (Lambert *et al*., 2004), and indeed, have been proposed as a viable explanation for the more robust masticatory morphology present in the hominin species (Vogel *et al*., 2014). The Fallback Food Hypothesis represents a shift in emphasis, where morphology previously considered to have been influenced by foods consumed frequently; it is now proposed to be influenced by high-stress foods consumed infrequently.

The concept of seasonally available resources is not new to this discussion. Indeed, when Robinson (1963) proposed the Dietary Hypothesis as the reason for the clear morphological differences between *Paranthropus* and *Australopithecus*, he suggested the climate would have been undergoing changes, where over millennia there would have been a gradual shift towards a longer and drier dry season. Robinson (1963) suggested that the critical period would have been towards the end of the dry period, which would have been the trough in food shortage. During this critical time other foods, including vertebrates and invertebrates would have been consumed to supplement the diets of both hominins. As the climate changed the critical periods would have extended and the once short periods of exploiting other foods would have become much longer. Competition for resources would have increased, and as a result population levels would have dropped. According to Robinson (1963) the distinction between the two genera would have arisen during this time of extended food shortage, wherein the more generalised *Australopithecus* exploited their environments in a way that *Paranthropus* could not.

Seasonally available resources were therefore clearly acknowledged when the Dietary Hypothesis was first proposed. It is perhaps other researchers' interpretations of

Robinson's (1963) work where it appears that the description of *Paranthropus* being a dietary specialist has been misconstrued to mean that *Paranthropus* ***only*** ate particular foods.

The idea that there are morphological adaptations beyond what might be required of a routine diet as suggested by the Fallback Food Hypothesis is not a recent concept. Indeed, Bock & von Wahlert (1965) suggested that most organisms possess features that appear to be overdesigned for their routine needs and were suggested as potential adaptations to overcome the harshest extremes of their environments. Rosenberger & Kinzey (1976) and Kinzey (1978) called these morphological adaptations critical functions, which would enable the consumption of different foods during the resource scarce periods. Support for critical functions was found in studies of non-human primate dentition (e.g., by Happel, 1988; Anapol & Lee, 1994; Yamashita, 1996, 1998; Lambert *et al.*, 2004; Norconk *et al*., 2009).

In the extant non-human primate literature seasonal diet variation was first called Keystone Resources (*sensu* Terborgh, 1983, 1986), which has now been revised and replaced by the Fallback Foods Hypothesis (*sensu* Wrangham *et al*., 1998), and is commonly invoked to explain seasonal diet variation. While seasonal diet variation is a concept that has been recognised for many years, it is only with the recent challenges to the proposed diets of *Paranthropus* and *Australopithecus* that the concept has been applied to hominins. This is due to other studies not identifying overlap and variability in the hominin diets at an earlier time and as a result, continued with the assumption that a robust morphology indicates a unique, specialised diet (Laden & Wrangham, 2005; Scott *et al*, 2005).

The Fallback Food Hypothesis has been invoked to explain the increasingly robust masticatory morphology of hominins and the differences between them (Ungar, 2004, 2011; Laden & Wrangham, 2005; Scott *et al*., 2005, 2014; Grine *et al*., 2006a, 2006b, 2012). Indeed, the mechanical properties of the fallback foods were suggested to have applied a selective pressure to influence the masticatory morphology of the following hominins: *A. anamensis, A. afarensis, A. africanus, P. robustus, P. boisei* and early *Homo* (Ungar, 2004, 2011; Laden & Wrangham, 2005; Scott *et al*., 2005, 2014; Grine *et al*., 2006a, 2006b, 2012). These morphological features would enable the consumption of hard or tough foods during periods of resource scarcity (Scott *et al*., 2005; Grine *et al*., 2006a, 2006b).

The overlap in the microwear and stable carbon isotopes present between *A. africanus* and *P. robustus* was interpreted as the hominins consuming the same preferred foods, but diverging in their use of fallback foods on a seasonal basis (Scott *et al*., 2005). *A. africanus* displayed greater anisotropy and were suggested to exploit tough fallback resources, while, *P. robustus* displayed greater complexity and were suggested to exploit hard fallback resources (Scott *et al*., 2005). The fallback foods for *Paranthropus* could have been underground storage organs (USOs), such as corms and tubers or the seeds of grasses (as Jolly, 1970 proposed), as both can be hard and brittle (depending on the time of the year) and can follow the C_4 photosynthetic pathway (depending on location) (Dominy *et al.*, 2008; Lucas *et al*., 2008b).

The hyper-thick dental enamel and hyper-robust masticatory apparatus of *P. robustus* is suggested to be consistent with a hard-food diet, be it frequently or infrequently consumed (Lucas *et al*., 2008a; Constantino *et al*., 2010, 2011; Pampush *et al*., 2013; Strait *et al*., 2013; Smith *et al*., 2015). However, while the morphology of *P. boisei* is further derived than that of *P. robustus*, the nature of foods consumed and their frequency of consumption are still debated for *P. boisei*. Ungar *et al*. (2008) suggested that the morphology reflected a hard-object adaptation to fallback foods, although this is weakened by the lack of any hard-object signals in any of the 9 *P. boisei* specimens sampled (Ungar, 2011). To account for this lack of hard-object signal, Strait *et al*. (2013) and Scott *et al*. (2014) suggested that the specimens did not perish during the fallback time and that the seasonal use of different resources has been missed. Grine *et al*. (2012) and Pampush *et al*. (2013) instead proposed that the morphology might better reflect the repetitive mastication of tough, fibrous foods, rather than hard objects, yet such a diet would not correspond to the occlusal surfaces of the dentition, which are poorly designed for tough food eating (Strait *et al*., 2013).

According to some researchers it is illogical to assume that as the mandibular morphology of *Paranthropus* became better adapted to consume tough foods (*sensu* Grine *et al*., 2012; Pampush *et al*., 2013) its dentition became better adapted to consume hard foods (Wood & Schroer, 2012; Strait *et al*., 2013; Smith *et al*., 2015). The arguments of Wood & Schroer (2012); Strait *et al*. (2013) and Smith *et al*. (2015) are based on the idea that morphological features are optimal solutions. Such an assumption is erroneous (Bock, 1980; Daegling *et al*., 2013; Elton *et al*., 2016; Grine & Daegling, 2017). Just because something might not be “ideally” suited to a particular function does not mean that it cannot perform the job efficiently (Daegling *et al*., 2013; Elton *et al*., 2016; Gailer *et al*., 2016). As Ungar & Hlusko (2016: 30) stated “evolution tends to follow the path of least resistance”. After all, there can be multiple functions for a given form, and multiple forms can perform the same function (Bock & von Wahlert, 1965; Bock, 1980; Taylor, 2002; McGraw & Daegling, 2012; Ungar & Hlusko, 2016).

Based on examples of extant animals they sometimes consume foods that would not be expected based on their morphologies. As an example *Cercocebus atys* frequently consume extremely hard seeds, and grazing bovids frequently consume tough plant materials, yet the morphology in both appears to be sub-optimally suited to those foods (Daegling *et al*., 2011, 2013; McGraw & Daegling, 2012; Gailer *et al*., 2016). *C. atys* lack the expected craniofacial buttressing of a hard-object feeder, while *Kobus ellipsiprymnus* (bovid) appear to lack the occlusal complexity suitable for grazing (as observed in other bovines and hippotragines) (Daegling *et al*., 2011, 2013; McGraw & Daegling, 2012; Gailer *et al*., 2016). When applied to *P. boisei*, the rest of its masticatory apparatus could have compensated for the apparent sub-optimal dental adaptation by generating and transmitting the high, repetitive loads required when grinding tough foods (Ungar & Hlusko, 2016). Analysis of the mechanical properties of foods reveals that young leaves in their membranous state are similar to ripe fruits in their composition and would not require dental adaptations to masticate (Talebli *et al*., 2016). Thus, should *P. boisei* have been consuming the leaves of grasses and sedges in their membranous state (as is consistent with their C_4 isotopic range) their dental morphology would not need to be reflective of a typical folivore (Talebli *et al*., 2016).

The exploitation of fallback foods by the genus *Australopithecus* and *P. robustus* would make them eurytopic in nature (Wood & Strait, 2004). In contrast, it remains unclear if *P. boisei* did exploit fallback foods, and the clear divergence from *Homo* sp. in their isotopic regimes despite appearing to occupy the same locations at the same time (Cerling *et al*., 2013 Supplementary Information) is consistent with a stenotopic classification. The validity of Robinson’s (1954a, 1963) Dietary Hypothesis is therefore questioned.

2.5 Chapter summary

To summarise, it has long been assumed that there is an association between dietary ecology and morphological and behavioural diversity, and that diets with different mechanical demands will be reflected in different morphological adaptations in the mandible in predictable ways (Daegling & McGraw, 2007; McGraw & Daegling, 2012). However, in palaeoanthropology there is yet to be an agreement over how diet influenced the distinctive craniofacial morphology observed in the australopithecines (Berthaume *et al*., 2010). Assumptions regarding the morphology focussed on the necessity for the robust masticatory form to represent a dietary adaptation to hard object feeding (e.g., Strait *et al*., 2009, 2013), as that corresponded to the assumptions that the diet was shifting to one inclusive of hard foods (Teaford & Ungar, 2000).

The recent application of stable carbon isotope and dental microwear texture analyses and a continued exploration of biomechanics challenge how closely correlated form and function are (Ungar & Hlusko, 2016). The evidence from stable carbon isotope analysis and dental microwear texture analysis are not consistent with any of the previous assumptions of the hominin diets (Berthaume *et al*., 2010; Grine *et al*., 2012; Wood & Shroer, 2012; Scott *et al*., 2014). This results in two major issues for the traditional understanding of *Paranthropus* being dietary specialists: 1) *P. robustus* and *A. africanus* overlapped in certain aspects of their mechanical properties of the diets consumed and their photosynthetic pathways (Sponheimer & Lee-Thorp, 1999; Scott *et al*., 2005; Sponheimer *et al*., 2005a, 2006a), and 2) *P. boisei* and *P. robustus* did not consume the same type of diet (Sponheimer *et al*., 2006a, 2013; Ungar *et al*., 2008).

With regard to the biomechanics, there are examples where there appears to be a clear correlation between masticatory form and the stresses applied to them (e.g., Hylander, 1979a, 1979b, 1984; Taylor, 2005, 2006a). However, this is not a universal correlation and in fact, could reflect species-specific adaptations (Daegling & McGraw, 2001; Ross *et al*., 2012; Vinyard *et al*., 2016). Furthermore, it is not necessary to view an adaptation as an optimal solution to a problem (Bock, 1980; Grine & Daegling, 2017), for it must be remembered that natural selection acts over many generations with the adaptive modifications gradually coming into effect in each one (Bock & von Wahlert 1965; Elton *et al*., 2016; Gailer *et al*., 2016; Ungar & Hlusko, 2016). Rather, those features that do not represent the biomechanical "optimum" can still perform a given function, that is, even apparently maladaptive structures are able to efficiently perform a task (Daegling *et al*., 2011, 2013; McGraw & Daegling, 2012; Elton *et al*., 2016; Gailer *et al*., 2016). It may be that the rest of the morphology present is able to compensate for an apparent sub-optimal adaptation (Ungar & Hlusko, 2016). Indeed, there are examples of extant non-human primate species regularly masticating extremely hard foods but not necessarily having the morphological adaptations suited to do so (Daegling *et al.*, 2011, 2013; McGraw & Daegling, 2012). Therefore, the buttressed facial configuration observed in many of the australopithecines is not necessarily an adaptation to hard-object feeding (McGraw & Daegling, 2012). An additional problem with regard to morphology is the fact that there appears to be no singular solution to a diet, where hard or tough object feeding does not result in one morphological form (Bock, 1980; Daegling & McGraw, 2001; McGraw & Daegling, 2012; Daegling *et al*., 2013; Grine & Daegling, 2017). For example, both colobines and gorillas have tough diets, but colobines do not have thick mandibular corpora like gorillas do (Teaford & Ungar, 2000). Of course, a lack of correlation between diet and morphology could reflect the fact the morphology reflects an adaptation to a previous generations' diet.

Behavioural flexibility, such as tool use, or dietary switching, is proposed as a way in which organisms can mitigate the potential effects resulting from an adaptation not being optimally suited for a particular function (Grine & Daegling, 2017). Alternatively, a proposed resolution to the inconsistencies surrounding the dental microwear texture and stable carbon isotope analyses and the morphology is the Fallback Food Hypothesis (Norconk *et al.,* 2009; Berthaume *et al*., 2010; Wood & Shroer, 2012). It is suggested that fallback foods drive the morphological adaptations, wherein the adaptations are the result of the infrequent consumption of mechanically resistant foods during the fallback periods (Marshall & Wrangham, 2007; Marshall *et al*., 2009; Berthaume *et al*., 2010; Wood & Shroer, 2012). It is assumed that fallback foods are low quality, tougher and more resistant to deformation than the preferred foods (Marshall & Wrangham, 2007; Marshall *et al*., 2009; Harrison & Marshall, 2011; Vogel *et al*., 2014). They therefore require morphological adaptations to generate the necessary power to fracture these foods and also to resist potential deleterious effects of consuming these foods, thus fallback foods have been proposed as a viable explanation for the more robust masticatory morphology present in some species (Vogel *et al*., 2014). Fallback foods may not be observed in the microwear, which is a reflection of the fact that the specimens did not perish during the fallback period (Berthaume *et al*., 2010; Strait *et al*., 2013; Scott *et al*., 2014).

To maintain the necessity for the derived morphological adaptations in *Paranthropus* it was suggested that both *P. robustus* and *P. boisei* consumed hard foods as fallback foods (Scott *et al*., 2005; Ungar *et al*., 2008). While microwear evidence supported the consumption of hard foods in the diet of *P. robustus* (Scott *et al*., 2005), there is no evidence to support the presence of hard objects in the microwear of *P. boisei* (Ungar, 2011; Grine *et al*., 2012). Indeed, the morphological features once interpreted as hard-object feeding adaptations in *P. boisei* could be the result of the regular consumption of tough-objects (Grine *et al*., 2012). It remains unclear which factor (if any) is more important for determining masticatory form, be it from repetitive/

cyclical loads (average forces) or from peak masticatory forces (Happel, 1988; Yamashita, 1998; Taylor *et al*., 2008; McGraw & Daegling, 2012).

Application of this hypothesis to the extinct hominins is not without its critics though. Invocation of fallback foods as an explanation for the morphological adaptations present in hominins are considered to be extremely convenient, as they can be applied in almost any context as the explanation for a derived morphology (McGraw & Daegling, 2012; Grine & Daegling, 2017). It is expected that at least some of the fossils would present microwear traces consistent with hard-object feeding (Kimbel & Delezene 2009). Indeed, as Kimbel & Delezene (2009: 29) highlight "it would be a taphonomic anomaly that none do". To date, there is no microwear evidence identifying hard-object fallback foods in hominins. Since they cannot actually be identified in the fossil record they remain untestable and invocation of it to fossil hominins is erroneous (Strait *et al*., 2009; McGraw & Daegling, 2012; Grine & Daegling, 2017).

Chapter 3 : Dietary adaptation in non-human primates

Non-human primate diets has long been of interest to researchers, whereby studies spanning a few months, a year or more analyse what foods were consumed at certain times of the day, how the nature of these foods varied according to the season and year, and potential hierarchical differences associated with sex, age or dominance (Clutton-Brock, 1977; Watts *et al*., 2012a). In order to analyse the diets of the different species it is necessary to categorise them according to the nature of the foods they consume, for example, the primary dietary categories of non-human primates consist of “fruits”, “seeds”, “leaves” and “insects” (Clutton-Brock & Harvey, 1977; Fleagle, 1999). A diet that consists mostly of any one of these four food types would result in the classifications of frugivore, granivore, folivore, or insectivore (Clutton-Brock & Harvey, 1977; Fleagle, 1999; Robbins & Hohmann, 2006). In addition to these categories, there are further classifications to consider, these include omnivore (consumers of many different foods, with no one food type dominating completely), gummivore (consumer of gums), and nectivore (consumer of nectar) (Fleagle, 1999).

Dietary requirements are governed by internal and external factors that include physiological, chemical and social constraints (Ham, 1994; Tutin *et al*., 1997; Conklin-Brittain *et al*., 1998; Hohmann *et al*., 2006; Lambert & Rothman, 2015). Internal factors that can influence the type of diet consumed include body size, the need to reach a nutritionally balanced diet, and the ability to masticate and digest foods to gain nutrients (Terborgh, 1983; Barton *et al*., 1993; Mills *et al*., 1993; Ham, 1994; Tutin *et al*., 1997; Peres, 2000; Remis *et al*., 2001; Marshall & Leighton, 2006; Russon *et al*., 2009; Fernandez-Duque & Heide, 2013; Fleagle, 2013; McGraw *et al*., 2014; Vogel *et al*., 2014; Lambert & Rothman, 2015; Sengupta & Radhakrishna, 2016). All non-human primates must balance the nutritional components of their diets, meaning that there must be a variation in the types of food consumed (Hladik, 1977; Tutin *et al*., 1997; Altmann, 2009; Felton *et al*., 2009a, 2009b, 2009c; Norconk *et al*., 2009; Potts *et al*., 2011; Fleagle, 2013). Due to differences in digestive strategies how much a diet varies depends on a species’ nutritional demands, which means that the importance of certain foods appears to be species-specific (Hladik, 1977; Krishnamani, 1994; Hohmann *et al*., 2006; Doran-Sheehy *et al*., 2009).

According to the Jarman-Bell principle, body size, energy requirements and metabolic rates are all scaled to one another (Gaulin, 1979). Essentially, this scaled relationship means that body mass influences metabolic rates, which in turn influence energy requirements. For example, larger bodied non-human primates have slower metabolic rates, while smaller bodied non-human primates have faster metabolic rates (Clutton-Brock & Harvey, 1977; Walker, 1981; Conklin-Brittain *et al*., 1998; Remis *et al*., 2001; Lambert, 2002; Taylor, 2002, 2006b; Yamagiwa & Basabose, 2006a; Vogel *et al*., 2008; Fleagle, 2013; Hanya & Chapman, 2013). The slower metabolic rates of larger bodied non-human primates are facilitated by digestive adaptations and lower nutritional requirements per unit of their body weight, while smaller bodied non-human primates have faster gut passage times to assist with the fast metabolism (Clutton-Brock & Harvey, 1977; Walker, 1981; Conklin-Brittain *et al*., 1998; Remis *et al*., 2001; Lambert, 2002; Taylor, 2002, 2006b; Yamagiwa & Basabose, 2006a; Vogel *et al*., 2008; Fleagle, 2013; Hanya & Chapman, 2013).

Such digestive adaptations have a bearing on the types of diets that can be consumed. For example, large bodied non-human primates are generally more folivorous, while small bodied non-human primates are more insectivorous (Walker, 1981; Barton *et al*., 1993; Cardini & Elton, 2008a; Fleagle, 2013). Both foliage and insects provide protein, but large bodied non-human primates can best meet their nutritional requirements through consumption of foliage as it is readily available in large quantities, while there would not be enough insects to meet demand (Walker, 1981; Taylor, 2002, 2006b; Yamagiwa *et al*., 2005; Fleagle, 2013). Small bodied non-human primates can best meet their nutritional requirements through consumption of insects, as they are protein-rich and quickly digested, small non-human primates also do not need the same volume of insects to meet their nutritional requirements as larger bodied non-human primates do (Clutton-Brock & Harvey, 1977; Walker, 1981; Conklin-Brittain *et al*., 1998; Lambert, 2002; Vogel *et al*., 2008; Fleagle, 2013). In general, foliage would not be a suitable food source for a smaller bodied non-human primate as they do not have the digestive adaptations to process such fibrous foods as larger bodied non-human primates do (exceptions to this include bamboo and immature leaves) (Clutton-Brock & Harvey, 1977; Walker, 1981; Conklin-Brittain *et al*., 1998; Lambert, 2002; Vogel *et al*., 2008; Fleagle, 2013).

Foods are selected based on their appearance and the ability of the consumer to masticate and digest the food. The nutritional composition, appearance, material properties and chemical contents of foods influence how appealing the food is to the consumer (Barton *et al*., 1993; Mills *et al*., 1993; Tutin *et al*., 1997; Peres, 2000; Remis *et al*., 2001; Marshall & Leighton, 2006; Chancellor *et al*., 2012; Cooke, 2012; Fernandez-Duque & Heide, 2013; McGraw *et al*., 2014; Vogel *et al*., 2014; Lambert &

Rothman, 2015; Sengupta & Radhakrishna, 2016). While the ability to access certain foods is determined by the consumer's morphological or behavioural adaptations that can overcome the mechanical defences of the food (Fernandez-Duque & Heide, 2013; Fleagle, 2013; McGraw *et al.*, 2014; Vogel *et al.*, 2014; Lambert & Rothman, 2015).

Morphological adaptations to diet can include aspects of the craniofacial morphology, relating to the dentition and mandible/ maxilla (as discussed in the previous chapter), along with digestive adaptations (Clutton-Brock, 1977; Milton, 1993). Digestive adaptations vary in different species, whereby they can prevent a species' from consuming a particular food, or through increasing processing efficiency they can enable increased consumption of lower-quality foods[5] (Tutin *et al.*, 1997; Doran-Sheehy *et al.*, 2009; Hanya & Chapman, 2013). For example, lower-quality foods, such as mature leaves, bark and fibrous fruits can be consumed by *Gorilla* because they have longer gut retention times and entodiniomorph ciliates present in their colons, which means that they can better digest cellulose and maximise absorption of nutrients (Goussard *et al.*, 1983; Rogers et al., 1990; Tutin *et al.*, 1997; Remis 1997; Remis *et al.*, 2001; Morgan & Sanz, 2006; Taylor, 2009; Head *et al.*, 2011; Hanya & Chapman, 2013). While *Colobus* have compartmentalised stomachs that increase the amount of energy that can be extracted from fibre and detoxify secondary compounds present in seeds and leaves (Tutin *et al.*, 1997).

Behavioural adaptations to diet include differences in ranging behaviour, social organisation and tool use (discussed in this chapter) (Clutton-Brock, 1977; Fleagle, 1999, 2013; Newton-Fisher *et al.*, 1999). External factors that govern the nature of diet include habitat quality and location, season, and competition for resources from sympatric species (Goodall, 1977; Nishida *et al.*, 1983; Fleagle, 2013). The nature of the habitats occupied by non-human primates is important because the vegetative resources within will determine the quality and quantity of foods available.

3.1 Nutritional requirements of non-human primates

The nutritional requirements of non-human primates dictate what foods they eat and why. In general, fruits are consumed in preference by almost all non-human primates when they are available. Fruits alone do not, however, provide all of the required nutrients, as it is high in calories but low in protein (Hladik, 1977; Milton, 1993; Doran-Sheehy *et al.*, 2009; Norconk *et al.*, 2009; Fleagle, 2013; Lambert & Rothman, 2015).

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[5] Lower quality foods are defined as those that are harder or tougher to process/ digest, and may contain chemical deterrents within (Lahm, 1986; Milton, 1993).

Due to this, even when ripe fruit is available non-fruit foods continue to be consumed (Milton, 1993; Krishnamani, 1994; Nishihara, 1995; Tutin *et al*., 1997; Morgan & Sanz, 2006; Norconk *et al*., 2009; Taylor, 2009; Kanamori *et al*., 2010; Chancellor *et al*., 2012; Hanya & Chapman, 2013; Vogel *et al*., 2014). It is essential to obtain a balanced intake of the necessary macronutrients and energy, rather than focussing solely on one particular food type (Hladik, 1977; Hoshino, 1985; Happel, 1988; Milton, 1993; Nishihara, 1995; Tutin *et al*., 1997; Conklin-Brittain *et al*., 1998; Rothman *et al*., 2007; Felton *et al*., 2009a, b, c; Norconk *et al*., 2009; Potts *et al*., 2011). As no one food provides all of the required nutrients, a combination of food resources ensures that the necessary balance is met (Table 3.1 details the nutritional breakdown of foods) (Hladik, 1977; Hoshino, 1985; Happel, 1988; Mitani, 1989; Milton, 1993; Nishihara, 1995; Rothman *et al*., 2007; Altmann, 2009; Taylor, 2009; Vogel *et al*., 2014; Lambert & Rothman, 2015).

Other food resources include foods at the different phenological stages, such as leaf flush and young leaves, flowers, flower buds, shoots, herbs, and immature seeds, all of which provide protein, while also being low in fibre and plant secondary metabolites[6] (Clutton-Brock, 1977; Hladik, 1977; Peters, 1987; Wrangham *et al*., 1991; Nishihara, 1995; Tutin *et al*., 1997; Morgan & Sanz, 2006; Lappan, 2009; Kanamori *et al*., 2010; Hanya & Chapman, 2013; Lambert & Rothman, 2015). Even the inner parts of bark can be consumed in preference by some genera, e.g., *Pongo*, as it can be highly nutritious and an important source of energy, being similar to fruits in their non-structural carbohydrates composition and high in sodium (Vogel *et al*., 2014; Lambert & Rothman, 2015). Indeed, sometimes a species is not consuming bark or fruits (e.g., figs) *per se* but rather the highly nutritious grubs and larvae located within (Krishnamani, 1994; Remis *et al*., 2001; Felton *et al*., 2009a, b; Potts *et al*., 2011).

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[6] Plant secondary metabolites are digestion-inhibiting compounds and chemicals that form the chemical defences present in plants to prevent consumption by herbivorous animals (Makkar *et al*., 2007).

Table 3.1: General nutritional contents of foods consumed by non-human primates*

Food type	**Low**	**Moderate**	**High**	**Availability**	**References**
Ripe fruit pulp	Protein, insoluble fibre and PSMs**	Soluble fibre	Calories, lipids, sugar concentrations and easily digested carbohydrates	A few months during the period of fruit abundance	Hladik, 1977; Mitani, 1989; Wrangham *et al*., 1991; Milton, 1993; Krishnamani, 1994; Yamakoshi, 1998; Doran-Sheehy *et al*., 2009; Norconk *et al*., 2009; Lambert & Rothman, 2015
Unripe fruit pulp	Protein	Insoluble fibre, soluble fibre, sugars and PSMs	Fat	A few months leading up to the period of fruiting	Lambert & Rothman, 2015
Seeds	Concentrations of toxic compounds	Depending on stage of development can be moderate to high in physical defences	High quality and quantity of proteins, fat, lipids and energy. High mechanical defences and tannin content	After the fruiting season	Kinzey & Norconk, 1990; Reynolds *et al*., 1998; Norconk *et al*., 2009; Rosenberger, 2013
Young leaves and shoots	Energy, fats and tannin content	Insoluble and soluble fibre, sugars, PSMs	Protein	Half the year	Hladik, 1977; Kinzey, 1978; Mitani, 1989; Wrangham *et al*., 1991; Milton, 1993; Krishnamani, 1994; Reynolds *et al*., 1998; Doran-Sheehy *et al*., 2009; Norconk *et al*., 2009; Vogel *et al*., 2014; Lambert & Rothman, 2015
Mature leaves	Energy and fats	Protein and soluble fibre	Calcium, cellulose, insoluble fibre and PSMs	Throughout the year	Kinzey, 1978; Milton, 1993; Krishnamani, 1994; Reynolds *et al*., 1998; Lambert & Rothman, 2015
Flowers	Soluble fibre, fats and PSMs	Insoluble fibre and sugars	Protein	A few months	Clutton-Brock, 1977; Milton, 1993; Lambert & Rothman, 2015
Stems/ Piths	Energy, protein and PSMs	Insoluble fibre and sugars	Soluble fibre	Throughout the year, but more protein present during the wet season	Wrangham *et al*., 1991; Lambert & Rothman, 2015
Bark/ wood	Soluble fibre, fats, protein, sugars and PSMs		Insoluble fibre	Throughout the year	Lambert & Rothman, 2015
Gums	Insoluble fibre, fat and protein		Soluble fibre and sugars		Lambert & Rothman, 2015
Vertebrates		Fats	Protein		Lambert & Rothman, 2015
Invertebrates	Soluble fibre, sugars and PSMs	Insoluble fibre (chitin) and fats	Protein	Seasonal	Hladik, 1977; Krishnamani, 1994; Yamakoshi, 1998

* ***N.B.*** these represent generalisations of the nutritional qualities for each food type. In reality, the nutritional composition of all foods vary widely both within and between species (Lambert & Rothman, 2015). ** PSMs = plant secondary metabolites

While fruits are commonly preferred food items, many non-human primates search for particular fruit species rather than just opportunistically consuming any fruit available (Reynolds *et al*., 1998; Basabose, 2002; Yamagiwa & Basabose, 2006a). In the case of the great apes, selectivity of foods applies even more to foods such as mature fruits or leaves, terrestrial herbaceous vegetation (THV), seeds, pith, bark, etc., which are often carefully selected and only consumed from a select few species, and even then, not all elements of the food are consumed (Goodall, 1977; Rodman, 1977; Nishida & Uehara, 1983; Galdikas, 1988; Nishihara, 1995; Reynolds *et al*., 1998; Newton-Fisher, 1999; Remis *et al*., 2001; Taylor, 2006a, 2009; Altmann, 2009; Kanamori *et al*., 2010; Watts *et al*., 2012a; Hanya & Chapman, 2013).

Such discrimination of food is due to the fact that variation in quality exists within each food. For example, consumption of a particular leaf or part of a leaf is likely to be influenced by the nutrients present, such as sugar and protein, and its digestibility, with leaves from deciduous trees easier to digest due to containing lower levels of cellulose than leaves from evergreen trees (Clutton-Brock, 1977; Lambert & Rothman, 2015). Similarly, maturity level influences selection too, with younger leaves and immature seeds preferred while the more mature leaves and seeds are avoided. This preference reflects the fact that many of the younger versions are higher in protein and more nutritious than are the more mature versions, which are generally higher in fibre, plant secondary metabolites and mechanical defences (making them harder to masticate) (Goodall, 1977; Milton, 1979; Barton *et al*., 1993; Nishihara, 1995; Remis *et al*., 2001; Taylor, 2006a, 2009; Altmann, 2009; Kanamori *et al*., 2010; Hanya & Chapman, 2013).

Essentially what this food preference highlights is that all non-human primates modify their diets to reduce the negatives and focus on the positives, by selecting the most nutritious foods they can (Reynolds *et al*., 1998; Newton-Fisher, 1999; Taylor, 2006a; Rothman *et al*., 2007; Altmann, 2009). The negatives and positives are determined by the nutritional qualities of foods and correspondingly, the nutritional requirements of the consumer, with the latter point a factor that changes in different species, due to differences in digestive anatomy. A food or macronutrient important for one species may not hold the same value for another; similarly, different species have different responses to plant secondary metabolites (Clutton-Brock, 1977; Barton *et al*., 1993; Krishnamani, 1994; Conklin-Brittain *et al*., 1998; Remis *et al*., 2001; Worman & Chapman, 2005; Hohmann *et al*., 2006; Watts *et al*., 2012b; Lambert & Rothman, 2015). *G. g. gorilla* for example, appear to avoid the lipid-rich foods and non-pulpy fruits that are commonly consumed by *Pan* (Williamson *et al*., 1990; Head *et al*., 2011).

While *G. b. beringei* consume foods high in plant secondary metabolites (e.g., tannins) suggested to assist with the maintenance of a healthy population of gut microbes (Hladik, 1977; Remis *et al*., 2001). Species may avoid certain foods due to them containing high quantities of lignin and plant secondary metabolites, while some species exploit these resources for a few days and then shift to another food before being exposed to too high a concentration of plant secondary metabolites (Krishnamani, 1994; Conklin-Brittain *et al*., 1998; Reynolds *et al*., 1998; Wrangham *et al*., 1998; Worman & Chapman, 2005; Doran-Sheehy *et al*., 2009).

The nutritional contents of foods are not fixed throughout the year, but rather they change according to habitat, season, time of the day, positioning on a tree, and developmental stage in response to sunlight, rainfall and temperature (Wrangham *et al*., 1991; Altmann, 1998; White, 1998; Remis *et al*., 2001; Worman & Chapman, 2005; Doran-Sheehy *et al*., 2009; Lambert & Rothman, 2015). For example, the lipid content in tropical fruits can range from <0.1% (Matsumoto-Oda & Hayashi, 1999) to almost 90% (Galetti *et al*., 2000). Such a variation in lipid content influences the selection of a fruit (Williamson *et al*., 1990; Basabose, 2002; Head *et al*., 2011). For example, despite *Celtis durandii* fruit being abundant during the wet season they were only consumed by *Cercopithecus mitis, C. ascanius and Lophocebus albigena* during the dry season when their lipid contents were high (Worman & Chapman, 2005).

3.2 Seasonal availability of food resources

A key factor for why diet and nutritional properties of foods change is due to seasonal availability of food resources. Non-human primates occupy variations of tropical habitats throughout Africa, Central/ South America and Southeast Asia that range from rain forest to savannah (Tutin *et al*., 1997). The various habitat types and the plant species within them are subject to daily and seasonal changes in weather patterns (rainfall, solar radiation, cloud cover, etc.,) and temperature variation and, consequently, frequent changes in food availability (van Schaik *et al*., 1993; Boesch *et al*., 2006; Yamagiwa & Basabose, 2006a; Norconk *et al*., 2009; Taylor, 2009; van Doorn *et al*., 2010; Hanya *et al*., 2013; Diaz-Martin *et al*., 2014; Lambert & Rothman, 2015). Changes to any one of these factors could potentially have massive implications for the phenological behaviour of the plants and the volume of crop produced (van Schaik *et al*., 1993; Norconk *et al*., 2009; Diaz-Martin *et al*., 2014).

The presence of young leaves (including leaf flush), flowers, fruits, and seeds follow a yearly cycle, being produced in intervals, but generally in complete synchrony with other plant species within the forest habitat (although there are some species that fruit in asynchrony to the rest) (Hladik, 1977; Rodman, 1977; Galdikas, 1988; Gauiter-Hion & Michaloud, 1989; van Schaik *et al*., 1993; Tutin *et al*., 1997; Peres, 2000; Fox *et al*., 2004; Marshall & Leighton, 2006; Norconk *et al*., 2009; Lambert & Rothman, 2015). These foods represent different phenophases of plants, with the presence of one food type followed by another. Generally, the phenophase begins with leaves, then flowering and finishes with fruiting (Figure 3.1 details the breakdown of phenophases) (van Schaik *et al*., 1993; Fleagle & McGraw 2002; McGraw *et al*., 2011; Denny *et al*., 2014). The seasonality of resources means that young leaves, fruits and many of the reproductive plant parts (flowers and seeds) that are the preferred food choice of many non-human primates and exploited heavily when available can fluctuate between abundance and absence. In contrast, the more fibrous foods, such as mature leaves and bark are less affected by the seasonal changes and are thus present throughout the year (Sabater Pi, 1979; Galdikas, 1988; Tutin & Fernandez, 1993a; Tutin *et al*., 1997). The period when fruits, leaves that are young and in flush and reproductive plant parts are unavailable is known as resource scarcity (as shown in Figure 3.1).

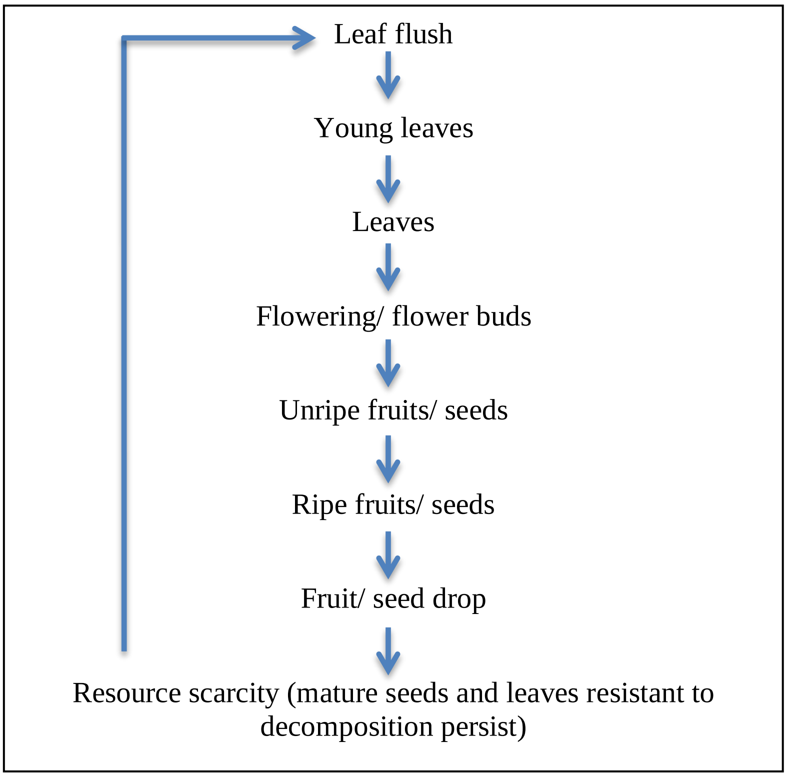

Figure 3.1: Plant phenophases according to van Schaik *et al*. (1993); Fleagle & McGraw (2002); McGraw *et al*. (2011); Denny *et al*. (2014).

Of course, habitats are different, and as a result, the nature of seasonal variation will vary in each location (van Schaik *et al*., 1993; Ganas *et al*., 2004; Ferriss *et al.*, 2005; Yamagiwa *et al*., 2005; Boesch *et al*., 2006; Hohmann *et al*., 2006; Robbins *et al*., 2006; Nystrom & Ashmore, 2008; van Doorn *et al*., 2010; Robbins, 2011). Habitat type is dependent on various factors, such as altitude, climatic conditions, forest-type, plant species composition, and soil fertility (Poulsen *et al*., 2001; Hanya *et al*., 2006; Hohmann *et al*., 2006; Morgan & Sanz, 2006; Yamagiwa & Basabose, 2006b; van Doorn *et al*., 2010; Lambert & Rothman, 2015). Given non-human primates inhabit vast areas of Africa, Asia and South/ Central America the environments inhabited – even at the subspecific level – are very different. For example, the subspecies of *Pan troglodytes* (*P. t. schweinfurthii*, *P. t. troglodytes* and *P. t. verus*) are distributed in habitats from east to west/ central Africa (Figure 3.2). This covers a range of habitats including more open and arid savannah habitats (e.g., Semliki, Uganda; Klainedoxa Bosquet, Gabon; Bossou, Guinea) and areas of evergreen/ mixed forest habitats within each subspecies (e.g., Kanyawara, Uganda; Lope Reserve, Gabon; Taï Forest, Ivory Coast) (Appendix Tables B.1-B.3 detail the environments and diets of subspecies by site) (Sugiyama & Koman, 1987; Tutin *et al*., 1991, 1997; Chapman *et al*., 1994; Wrangham *et al*., 1996; Jones *et al*., 1996; Doran, 1997; Yamakoshi, 1998; Tutin, 1999; Hunt & McGrew, 2002; Potts *et al*., 2011).

Image removed due to copyright

Figure 3.2: Distribution map of *Pan paniscus* and subspecies of *Pan troglodytes* (*Pan troglodytes ellioti* is not included in this study due to very small sample sizes in collections) (Image generated by the IUCN upon request, 2017)

Between different habitats the species of vegetation differ and can follow different trends, with some species providing high-quality and highly sought-after foods, such as young leaves, flowers and fruits in short concentrated spells, other species provide flowers and fruits when young leaves are unavailable, while other species provide fruits in short bursts throughout the year (van Schaik *et al*., 1993; Lambert & Rothman, 2015). As a result, there is inter-site variation in food source availability, with variability in the quantity and quality of foods produced during both the periods of resource abundance and scarcity (Boesch *et al*., 2006; Rothman *et al*., 2007; Kunz & Linsenmair, 2010; Watts *et al*., 2012b).

There are occasions where changes in the weather patterns (e.g., failure of rainfall) lead to prolonged periods of resource scarcity, beyond that of the annual resource-scarce periods (Tutin & Fernandez, 1993b; van Schaik *et al.*, 1993; Hafner *et al.*, 1994; Tutin *et al*., 1997; Muri, 1999). Extreme periods of resource scarcity are characterised by the failure of some trees to produce fruit (Tutin *et al*., 1997). Alternative foods are sought out during these periods of extreme resource scarcity; it is during such times that animals are most vulnerable to starvation and mass mortality can occur (Hamilton, 1985; Durham *et al*., 2008, 2010). How an animal responds to such extreme periods will determine their survival and thus affect their reproductive success (Nishida, 1976; Tutin *et al*., 1997; Poulsen *et al*., 2001).

An extreme example of swings between resource abundance and scarcity occurs in Southeast Asia. In addition to the annual periods of resource scarcity, islands such as Borneo and Sumatra are exposed to prolonged troughs in fruit availability on a more regular basis. These troughs can lead to years of little to no fruits being available, followed by years of extended periods of fruit abundance, so-called fruit masts (Knott, 1998; Wich & van Schaik, 2000; Taylor, 2006a; Wich *et al*., 2006a, b, 2011; Kanamori *et al*., 2010). Mast-fruiting events are not commonly associated with African rain forests, but they have been known to occur, for example, *Chrsyophyllum albidum*, a fruiting species present at Ngogo, Kibale National Park, was observed over multiple years to mast (Watts *et al*., 2012b). During the periods of fruit mast the population of *P. t. schweinfurthii* under analysis were seen to heavily exploit the fruits (Watts *et al*., 2012b).

3.2.1 How non-human primates react to resource scarcity

As fruits, young leaves and reproductive plant parts are the preferred food of many non-human primates they are heavily exploited when available. The diets of many sympatric species therefore overlap during the period of resource abundance, but given that these foods are seasonally available resources non-human primates must find other foods to eat when they are unavailable (Kinzey & Norconk, 1990; Tutin *et al*., 1997; Lambert, 1999; Marshall & Wrangham, 2007; Norconk *et al*., 2009; Harrison & Marshall, 2011; Smith *et al*., 2012). During periods of resource scarcity, competition for resources is greatest, so in order to reduce feeding competition sympatric species diets diverge, this was traditionally known as niche separation (Conklin-Brittain, 1977; Gautier-Hion, 1980; Terborgh, 1983, 1986; Cords, 1986; Ham, 1994; Tutin & Fernandez, 1993a; Remis, 1997; Tutin *et al*., 1997; Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998; Yamakoshi, 1998; Tutin, 1999; Remis *et al*., 2001; Stanford & Nkurunungi, 2003; Doran-Sheehy *et al*., 2006; Yamagiwa & Basabose, 2006b; Taylor, 2009; Head *et al*., 2011; Oelze *et al*., 2014).

Periods of resource scarcity has been known to influence various factors, which all appear to vary by location and population. The different reactions of species and even populations is likely to be a reflection of the different habitats occupied, which will then influence the length of resource scarcity and the quality of resources available at the different sites (Clutton-Brock, 1977; Furuichi *et al*., 2001; Hohmann *et al*., 2006; Morgan & Sanz, 2006; Harrison & Marshall, 2011; Potts *et al*., 2011; Chancellor *et al*., 2012; Watts *et al*., 2012b; Webster *et al*., 2014). During resource scarcity non-human primates can increase their home range to seek out specific preferred foods or they can reduce ranging distance to conserve energy and subsist on alternative food sources available (Reynolds & Reynolds, 1965; Clutton-Brock, 1977; Goodall, 1977; Hoshino, 1985; van Schaik *et al*., 1993; Tutin & Fernandez, 1993a; Tutin *et al.,* 1997; Yamakoshi 1998; Pruetz, 2006; Wich *et al*., 2006a; Vogel *et al*., 2009; Chancellor *et al*., 2012). Some species, such as *Pan troglodytes* fission into smaller foraging parties to reduce competition for resources (Sugardjito *et al*., 1987; Sakura, 1994; Doran, 1997; Tutin *et al.*, 1997; White, 1998; Wrangham *et al*., 1998; Newton-Fisher *et al*., 1999; Tutin, 1999; Hohmann *et al.,* 2006; Morgan & Sanz, 2006; Pruetz, 2006; Chancellor *et al*., 2012).

Some populations of *Pan troglodytes*, *Pongo pygmaeus* and *Sapajus apella* have been observed to increase hunting (specific to *P. troglodytes*) (Rose, 1997), and tool use during the period of resource scarcity (Wrangham *et al*., 1998; Yamakoshi, 1998;

Basabose, 2002; Fox *et al*., 2004; Yamagiwa & Basabose, 2009). Even though these approaches are not exclusive to periods of resource scarcity as both hunting and tool use have been documented to also occur during the period of resource abundance (Boesch & Boesch, 1984; Basabose & Yamagiwa, 1997; Basabose, 2002; Gilby *et al*., 2006; Gilby & Wrangham, 2007; Yamagiwa & Basabose, 2009). Dietary switching can involve increasing the dietary diversity and consequently, time spent feeding, or reducing the range of foods consumed to those that are readily available, but of lower nutritional value, or those protected by hard, external shells or plant secondary metabolites (Wrangham *et al.,* 1991, 1998; van Schaik *et al*., 1993; Krishnamani, 1994; Doran, 1997; Yamakoshi, 1998; Poulsen *et al*., 2001; Fox *et al*., 2004; Doran-Sheehy *et al*., 2006; Masi *et al*., 2009; Head *et al*., 2011).

Many non-human primate species breed on a seasonal basis, wherein females give birth and lactate during the peaks of food availability (van Schaik *et al*., 1993; Di Bitetti & Janson, 2000; Nakagawa, 2000; Brockman & van Schaik, 2005; Thompson & Wrangham, 2008; Altmann, 2009; Fernandez-Duque & Heide, 2013; Foerster *et al*., 2013). In studies of apes it is well established that pregnancy and lactation places additional energetic demands on the females of a species (Clutton-Brock, 1977; Cords, 1986; Fox *et al*., 2004), while males in sexually dimorphic species may require greater caloric intake (Masi *et al*., 2009). Members of the two sexes may respond to resource scarcity in different ways, for example, females can increase diversity in the foods consumed (Galdikas, 1988; Smith *et al*., 2012), increase consumption of fruits and insects relative to males (Clutton-Brock, 1977; Rodman, 1977; Cords, 1986; Doran-Sheehy *et al*., 2009), and in some species use tools to access arils within seeds (Smith *et al*., 2012). In contrast, males can increase consumption of lipid-rich seeds (Knott, 1998; Smith *et al*., 2012), consume more leaves (Doran-Sheehy *et al*., 2009), and those in fission-fusion grouping system travel further per day to exploit other food sources, able to do so because they are not as restricted as females with offspring (Galdikas, 1988; Newton-Fisher *et al.,* 1999; Watts *et al*., 2012b). Based on the multitude of responses to resource scarcity, it is clear that there is no one universal response pattern per species, but of those responses that occur, dietary switching and range shifting are considered to be the most common behaviours that are adopted (Goodall, 1977; van Schaik *et al*., 1993; Lambert, 1999; Peres, 2000; Furuichi *et al*., 2001; Vogel *et al*., 2009; Watts *et al*., 2012b; Lambert & Rothman, 2015; Vinyard *et al*., 2016).

The foods that sustain animals during the period of resource scarcity were referred to as Keystone Resources (*sensu* Terborgh, 1983, 1986, derived from Paine, 1969).

Terborgh (1983, 1986) proposed this concept for non-human primates after studying five species of New World monkeys (*Cebus albifrons, Saguinus fuscicollis, Saguinus imperator, Saimiri sciureus and Sapajus apella*) and their responses to the period of resource scarcity. The monkeys diverged in their use of different keystone resources, and he suggested that these differences were due to their overall body size differences. According to Terborgh (1986), the larger *Sapajus* and *Cebus* species were able to use their stronger and more robust masticatory apparatus to break open palm nuts, which the smaller *Saimiri* and *Saguinus* species were unable to do, they instead had to turn to other food resources, including figs and nectar. The different morphological adaptations of the New World monkey species explain the differential resource use by them during the resource-scarce period (Terborgh, 1986; van Schaik *et al*., 1993). It was suggested that different morphologies served to enable different foods to be consumed, and as such the morphologies acted as critical functions (*sensu* Rosenberger & Kinzey, 1976; Kinzey 1978).

There are two key points to be fulfilled for a food to be defined as a keystone resource: 1) it must be available throughout the year but lower in nutritional value than foods such as fruit, or it is at the very least available consistently during the resource-scarce period (making it a reliable resource, as it shows little year-to-year variation) (Terborgh, 1986; van Schaik *et al*., 1993; Tutin *et al*., 1997; Yamakoshi, 1998; Peres, 2000; Diaz-Martin *et al*., 2014). Some keystone resources are protected by hard outer shells which are difficult to access, others contain plant secondary metabolites that are unpleasant to consume in large quantities, and others are distributed further afield, requiring more time to search for them, all factors which make them less preferred (Terborgh, 1986; van Schaik *et al*., 1993; Tutin *et al*., 1997; Yamakoshi, 1998; Peres, 2000; Diaz-Martin *et al*., 2014). 2) a keystone resource must be able to support the biomass of the forest, and should it be removed from the forest the ecosystem that depends upon it would be expected to collapse (Terborgh, 1986; Mills *et al.,* 1993; van Schaik *et al.,* 1993; Tutin *et al*., 1997; Yamakoshi, 1998; Peres, 2000).

3.2.2 Fallback Food Hypothesis

The foods that sustain non-human primates during resource scarcity are presently commonly referred to as fallback foods. The Fallback Food Hypothesis is widely used in the primatological and palaeoanthropological literature, with a special issue dedicated to the topic in the *American Journal of Physical Anthropology* in 2009. The Fallback Food Hypothesis is based on a combination of the theories behind Terborgh's (1983,

1986) Keystone Resources and Rosenberger & Kinzey's (1976) Critical Functions hypotheses. The Fallback Food Hypothesis proposes that when preferred foods are scarce animals resort to less-preferred foods (fallback foods) that may require special morphological adaptations to process them (Constantino & Wright, 2009). The key proponents of this hypothesis state that keystone resources and fallback foods are not the same, whereby fallback foods are the foods that sustain primates when preferred foods are scarce and that keystone resources are plant communities and should they be removed from the environment the community would collapse (although this is not entirely correct based on Terborgh's (1983, 1986) original application of Keystone Resources – see above) (Marshall & Wrangham, 2007; Constantino & Wright, 2009; Marshall *et al*., 2009; Harrison & Marshall, 2011). What the two approaches share is the focus on the foods that sustain primates during the preferred food scarcity and the morphological adaptations that enable these foods to be consumed (e.g., Terborgh, 1986; Tutin *et al*., 1997; Furuichi *et al*., 2001; Marshall & Wrangham, 2007; Diaz-Martin *et al*., 2014).

Fallback foods are described as highly abundant but of low nutritional quality, and consumed only when the availability of the preferred foods decreases (Marshall & Leighton, 2006; Marshall & Wrangham, 2007; Grueter *et al*., 2009; Marshall *et al*., 2009; Harrison & Marshall, 2011; Mosdossy *et al*., 2015). Fallback foods are particularly important in environments that are more affected by extremes in seasonality and consequently, more intense periods of resource scarcity (Hanya *et al*., 2006; Melin *et al*., 2014). Food quality is determined by the ease with which energy is extracted; dependent on how easy the food is processed extra-orally and then digested (Watts *et al*., 2012b; Mosdossy *et al*., 2015). Identification of the preferred and fallback foods depends on selectivity, whereby, the preferred foods will be over-selected relative to their availability, while the fallback foods will be under-selected relative to the availability of the preferred foods (Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998; Laden & Wrangham, 2005; Marshall & Leighton, 2006; Gilby & Wrangham, 2007; Marshall & Wrangham, 2007; Thompson & Wrangham, 2008; Marshall *et al*., 2009; Norconk *et al.*, 2009; Harrison & Marshall, 2011).

Preferred foods are generally those that require the greatest investment of time and energy to locate them, as they are widely distributed and only seasonally available (Lahm, 1986; Milton, 1993; Hohmann *et al*., 2006; Marshall & Leighton, 2006; Norconk *et al*., 2009). A preferred resource is thus high in quality, requiring very little effort to masticate or digest, and will yield a high nutritional return (Marshall &

Leighton, 2006; Gilby & Wrangham, 2007; Marshall *et al*., 2009; Harrison & Marshall, 2011; Watts *et al*., 2012b; Mosdossy *et al*., 2015). In defining fallback foods, a preferred resource is commonly referred to as fruit, and based on this definition Wrangham and colleagues (Laden & Wrangham, 2005; Gilby & Wrangham, 2007; Marshall & Wrangham, 2007; Constantino & Wright, 2009; Marshall *et al*., 2009; Harrison & Marshall, 2011) commonly refer to the fallback foods being consumed during fruit-scarce periods (different to a resource-scarce period). Fallback foods in contrast are lower quality, more difficult to process due to high presence in cellulose, hemicellulose and digestion-inhibiting compounds and chemicals (plant secondary metabolites). The foods, e.g., mature leaves and piths, are therefore suggested to yield low nutritional returns (Lahm, 1986; Wrangham *et al.*, 1991; Milton, 1993; Hohmann *et al*., 2006; Gilby & Wrangham, 2007; Harrison & Marshall, 2011; Chancellor *et al*., 2012; Watts *et al*., 2012b; Lambert & Rothman, 2015; Mosdossy *et al*., 2015).

Marshall & Wrangham (2007) noted that it was necessary to distinguish preference from importance when referring to fallback foods, whereby a preferred item need not be important to the diet, and an important resource need not be preferred. The preference of an animal to consume a certain food is entirely down to selection/ choice, whereas the importance of an item is defined based on the nutritional properties of the food and it being available on a seasonal basis (Marshall & Wrangham, 2007). Fallback foods can therefore be described as foods that are seasonally very important but of low preference (Marshall & Wrangham, 2007; Harrison & Marshall, 2011; Irwin *et al*., 2014).

A further addition to the definition of fallback foods was based on their frequency in the diet, whereby fallback foods were divided into staple and filler fallback foods (Marshall & Wrangham, 2007; Marshall *et al*., 2009). Staple fallback foods are resources that are present in the diet throughout the year, can seasonally make up the whole diet and are generally low in quality; while filler fallback foods are resources that are used only seasonally to ‘fill-in’ when required, thus never constitute the whole diet and are generally higher in quality (Marshall & Wrangham, 2007; Marshall *et al*., 2009). According to Marshall & Wrangham (2007) the staple fallback foods were suggested to be responsible for the morphological adaptations present in a species to increase dietary flexibility.

Lambert (2007) analysed the potential importance of fallback foods on morphology. She suggested that the potential selective stimuli acting on species would vary according to the quality of fallback foods, with those fallback foods of high quality requiring different morphological adaptations from those of lower quality fallback foods. High-quality fallback foods were suggested to result in behavioural adaptations and innovations, such as social organisation and tool use to find and access preferred resources (Lambert, 2007; Marshall *et al*., 2009; Harrison & Marshall, 2011; Rosenberger, 2013). For example, Bossou chimpanzees used tools to access foods that were high in calories, fat and sugar content, and thus ensured a high-quality diet throughout the year, reflected in a high reproductive performance (Yamakoshi, 1998).

In contrast, low-quality fallback foods are abundant, but harder to access, masticate and digest due to increased resistance to deformation and high levels of fibre and plant secondary metabolites (Lambert, 2007). Consistent with the definitions provided by Marshall & Wrangham (2007), Lambert (2007) suggested that low-quality fallback foods drive morphological adaptations to facilitate consumption of a wide variety of foods. Adaptations, pertaining especially to the masticatory apparatus and digestive system have been proposed to reflect low-quality fallback food use (Lambert *et al.*, 2004; Lambert, 2007; Marshall & Wrangham, 2007; Doran-Sheehy *et al*., 2009; Marshall *et al*., 2009). These adaptations would therefore provide a survival advantage for the species that possess them (Kinzey & Norconk, 1990; van Schaik *et al*., 1993; Marshall & Wrangham, 2007; Sauther & Cuozzo, 2009).

The proposals by Lambert (2007) and Marshall & Wrangham (2007) mostly complement each other, but they differ in their suggestions of which type of fallback food is most important for morphological adaptations. Lambert (2007) followed the more traditional outlook and suggested the foods consumed as critical resources were the stimulants (similar to Kinzey & Rosenberger, 1976; Kinzey, 1978), while Marshall & Wrangham (2007) suggested the low-quality staple fallback foods consumed throughout the year were more important. Based on the use of fallback foods by other researchers before and after the Fallback Food Hypothesis was properly defined (e.g., Newton-Fisher, 1999; Tweheyo & Lye, 2003; Lambert *et al*., 2004; Robbins *et al*., 2006; Grueter *et al*., 2009; Marshall *et al*., 2009; Vogel *et al*., 2009; Harrison & Marshall, 2011; Watts *et al*., 2012b; Rosenberger, 2013), it appears that Lambert's (2007) proposal is more commonly accepted. The definition of staple fallback foods as suggested by Marshall & Wrangham (2007) is not routinely applied in field studies, for it essentially means that all foods except for non-fig fruits are fallback foods of some sort. For example, McLennan (2013) described figs as fallbacks despite being consumed throughout the year. Instead foods consumed throughout the year are commonly referred to as staples but not staple fallback foods. Furthermore, based on dietary studies it seems fallback foods are best defined as those foods consumed during periods of resource scarcity, as opposed to those consumed during preferred food scarcity. The two terms are not the same, as preferred foods are only available for so many months of the year, but other foods that are important to maintain a balanced diet are still available, while resource-scarce periods represent the time of greatest stress, as observed by seasonal diet variation, as there is very little food available overall during this time.

Within the apes, suggested examples of high quality fallback food users are *Pan troglodytes*, and low quality fallback food users are *Gorilla* and *Pongo* (Wrangham *et al*., 1991, 1996, 1998; Conklin-Brittain *et al*., 2000; Stanford & Nkurunungi, 2003; Tweheyo & Lye, 2003; Morgan & Sanz, 2006; Taylor, 2006a; Wich *et al*., 2006b; Yamagiwa & Basabose, 2006a, b, 2009; Marshall & Wrangham, 2007; Thompson & Wrangham, 2008; Doran-Sheehy *et al*., 2009; Harrison & Marshall, 2011; Head *et al*., 2011; McLennan, 2013). In the case of *P. troglodytes,* they are suggested to fallback on fruits from oil-palm trees and figs. These fruits are heavily exploited during the resource-scarce months due to their asynchronous availability (Wrangham *et al*., 1991; Peres, 2000; Shanahan & Compton, 2001; Gilby & Wrangham, 2007; Marshall & Wrangham, 2007; Harrison & Marshall, 2011; Head *et al*., 2011; Chancellor *et al*., 2012; McLennan, 2013). In contrast, both *Gorilla* and *Pongo* exploit more THV and fruits high in fibre as fallback foods during the period of resource scarcity, although these foods are consumed during the periods of resource abundance as well (Stanford & Nkurunungi, 2003; Taylor, 2006a; Wich *et al*., 2006b; Yamagiwa & Basabose, 2006a, b, 2009; Doran-Sheehy *et al*., 2009; Morrogh-Bernard *et al*., 2009; Kanamori *et al*., 2010; Harrison & Marshall, 2011; Head *et al*., 2011; Oelze *et al*., 2014). It remains inconclusive if *Pan paniscus* fallback on any foods as their habitats are aseasonal and they consume THV (which is highly nutritious) preferentially throughout the year (Badrian *et al*., 1981; Kano, 1982; Badrian & Malenky, 1984; Kano & Mulavwa, 1984; Doran, 1997; White, 1998; Hohmann *et al*., 2006; Lambert, 2007; Harrison & Marshall, 2011; Serckx *et al*., 2015).

Due to the high competition for resources during the resource-scarce period, many researchers suggest that it is during this time of the year that the threat of mortality should be highest (van Schaik *et al*., 1993; Marshall & Wrangham, 2007; Sauther & Cuozzo, 2009; Vogel *et al*., 2009; Gogarten *et al*., 2012). Accordingly, it is not just the prolonged periods of extreme resource shortage (as suggested by Hamilton, 1985; Durham *et al*., 2008, 2010) that can increase the threat of mortality but also the annual period of resource scarcity. Adaptations that could assist with increasing the types of food available to non-human primates during resource-scarce periods could thus be the difference between survival and death of that species.

It is suggested that frugivores are more affected by the period of resource scarcity than are folivores. Frugivores have more competition for their fallback resources, while folivores have a superabundance of their fallback foods and will therefore have less competition (Marshall & Wrangham, 2007). For this reason there is increased pressure on frugivores to adapt their morphologies to enable the consumption of alternative food sources for extended periods, while a folivore that occasionally consumes fruits would not be under the same pressure to adapt its morphology (Smith, 1982).

3.3 Potential impact of fallback foods on morphology

To date, however, the Fallback Food Hypothesis has not been extensively explored with regard to its influence on morphology (Harrison & Marshall, 2011). While those studies that analysed its potential found inconclusive results. Early studies identified that aspects of the dentition may be a reflection of the consumption of critical resources, or the hardest/ toughest foods (as opposed to the most commonly consumed foods) (Rosenberger & Kinzey, 1976; Kinzey, 1978; Yamashita, 1998). Adaptations include: 1) the presence of longer molar shearing blades in the form of ectolophs and cristid obliquas to assist with the shearing of leaves, as seen in *Callithrix*, *Alouatta* and *Callicebus moloch* (Rosenberger & Kinzey, 1976; Kinzey, 1978); 2) a larger molar talonid surface area, present in *Callicebus torquatus* to break down insects (Kinzey, 1978); 3) a more robust masticatory apparatus (e.g., deeper and thicker mandibular corpora and symphyses) to consume both fauna and seeds, as seen in *Cebus nigrivittatus*, *Sapajus apella*, *Chiropotes satanas* and *Pithecia pithecia* (Cole, 1992; Anapol & Lee, 1994; Galetti & Pedroni, 1994; Altmann, 2009); 4) deep, acute basins, larger talonid than trigon areas on the molars; and 5) molar cusps that are short in height to masticate a hard-food diet, and large upper molar basins, and large trigons to masticate a strong-food diet (Yamashita, 1998).

Adaptations to the gut and dentition to enable the efficient extraction of energy from low-quality fallback foods are suggested to exist in *Pongo*, *Gorilla* and some species of Old World monkeys. These include thick dental enamel in *Gorilla*, *Pongo* (including crenulated occlusal surfaces) and *Lophocebus albigena* to protect the teeth from the potentially catastrophic effects of consuming large, hard seeds or very tough bark during resource-scarce periods (Lambert *et al*., 2004; Taylor, 2006a; Ungar, 2007; Vogel *et al*., 2008, 2009; Constantino *et al*., 2009). Other adaptations suggested to improve the processing abilities required for the consumption of tough, high-fibre fallback foods, such as mature leaves and bark, include enhanced dental topography (higher molar shearing blades and cusps), gut length (a larger and more ciliated gut), longer gut retention times that slow digestion down in order to maximise the intake of nutrients and a larger body size in *Gorilla*, and forestomach fermentation abilities in *Colobus* (Milton, 1984; Doran-Sheehy *et al*., 2009; Yamagiwa & Basabose, 2009; Cooke, 2012). All of the above linked traits are lacking in *Pan*, which instead is suggested to possess enhanced harvesting abilities (including tool use) to find and locate ripe, succulent fruits as their fallback foods (Ungar, 2004; Marshall & Wrangham, 2007; Doran-Sheehy *et al*., 2009; Yamagiwa & Basabose, 2009).

The different species and populations of *Pongo* consume different foods during the resource-scarce period. With fruit availability more constant on Sumatra than on Borneo, *P. abelii* consumes a much greater quantity of fruits and insects throughout the year compared to *P. pygmaeus*, with the latter consuming much greater quantities of bark, leaves, cambium and vegetable matter, particularly during the period of resource scarcity (MacKinnon, 1974; Taylor, 2006a, 2009; Wich *et al*., 2006a, b, 2011; Morrogh-Bernard *et al*., 2009; Russon *et al*., 2009; Knott & Kahlenberg, 2011; Smith *et al*., 2012). In particular, *P. p. morio* experiences the longest periods of resource scarcity (consistent with it being from the northeastern side of Borneo which is more affected by El Niño Southern Oscillation) and consequently, has to rely on more vegetative foods than do the other species/ subspecies (Philander, 1983; van Schaik *et al*., 1993; Taylor, 2006a; Kanamori *et al*., 2010; Knott & Kahlenberg, 2011; Wich *et al*., 2011). Observation of the mechanical properties of foods consumed by *Pongo* species reveals that the bark and vegetation that *P. pygmaeus* subspecies consume are generally more difficult to process than are those consumed by *P. abelii* (Taylor, 2006a). Indeed, the presence of deeper mandibular corpora, and deeper and wider mandibular symphyses in *P. p. morio* and *P. p. wurmbii* relative to *P. abelii*, were interpreted by Taylor (2006a, 2009) to be indications that the *P. pygmaeus* subspecies are better adapted to resisting loads relating to large foods or frequent mastication than are *P. abelii*. Taylor (2006a) suggested that it is possible that these differences can be attributed to the exploitation of critical resources or fallback foods.

The Fallback Food Hypothesis is consistent with the previously discussed Liem’s Paradox, wherein species are suggested to avoid the foods to which they are adapted when more preferred resources are available (Marshall & Wrangham, 2007). Species of cichlid fish and *Gorilla* are suggested to be examples of Liem’s Paradox (Liem, 1980;

Robinson & Wilson, 1998; Liem & Summers, 2000; Ungar *et al*., 2008; Binning *et al*., 2009; Ungar, 2011). This paradox would suggest that species are morphologically adapted to their fallback foods, rather than their main dietary regime (Liem, 1980; Robinson & Wilson, 1998; Liem & Summers, 2000; Ungar, 2011).

3.4 A critical assessment of fallback foods

There continues to be some confusion and subjectivity over how to accurately identify and apply the Fallback Food Hypothesis and how to distinguish it from Keystone Resources (Peres, 2000; Marshall & Wrangham, 2007; Constantino & Wright, 2009; Lambert, 2009; Marshall *et al*., 2009; Sauther & Cuozzo, 2009; Taylor, 2009; Cooke, 2012; McGraw & Daegling, 2012; Lambert & Rothman, 2015). For example, some researchers use keystone resources in conjunction with fallback foods, where the foods consumed throughout the year are keystone resources (alternatively called staples by other researchers), and the foods consumed during the resource-scarce period are fallback foods (e.g., Basabose, 2002; Sauther & Cuozzo, 2009; Lambert & Rothman, 2015).

Further issues have arisen because there are no clear guidelines to identify or calculate preference, which becomes a close to impossible task in short-term field studies (Cooke, 2012). This issue is particularly apparent in studies applying the fallback term to certain foods, whereby comprehensive analyses of fallback food availability and use are not included (e.g., Tweheyo *et al*., 2004; Anderson *et al*., 2006; Morgan & Sanz, 2006; Serckx *et al*., 2015; Sengupta & Radhakrishna, 2016) according to Marshall *et al*. (2009) and Watts *et al*. (2012b). To resolve this, attempts were made to clearly define what constitutes a preferred food and a fallback food (e.g., Marshall & Wrangham, 2007; Constantino & Wright, 2009; Lambert, 2009; Marshall *et al*., 2009; Harrison & Marshall, 2011). Marshall & Wrangham (2007) suggested fallback foods were negatively correlated with preferred foods. However, since many ecological and behavioural traits are co-dependent upon one another it is wrong to assume that any regression or correlation between two factors are indicative of a direct causal relationship (Clutton-Brock & Harvey, 1977).

Marshall *et al*. (2009) attempted to provide further clarity to the Fallback Food Hypothesis and clearly define what a fallback food is. Yet even within their article confusion arose with different definitions and descriptions provided. The initial definition of fallback foods provided by Marshall *et al*. (2009) was that they are the foods that are consumed when preferred resources are scarce, that are highly abundant but of low nutritional quality. This is the common operational definition of fallback foods (Altmann, 2009; Constantino & Wright, 2009; Lambert, 2009; Sauther & Cuozzo, 2009). Yet, within the same article, indeed, the same page, Marshall *et al*. (2009: 604) also define fallback foods as the foods that are consumed during a period of extreme resource scarcity, also referred to as bottlenecks or critical use times, which may not happen for a number of years, if at all within the lifetime of an individual. The two definitions are not mutually exclusive; for the first is part of an annual cycle of seasonal variation of resources, while the second is something that Marshall *et al*. (2009) acknowledge may rarely occur. Despite the lack of frequency over the latter occurrence, Marshall *et al*. (2009) suggest it is the prolonged periods of scarcity that are suggested to influence the morphology, socioecology and extinction of species. This suggestion contrasts with the suggestions that staple fallback foods (Marshall & Wrangham, 2007), or the foods consumed during the resource-scarce periods (Lambert, 2007) drive the morphological adaptations as previously proposed.

Classification of a food source as a fallback food implies that it is species-specific and fixed as a fallback resource (Gautier-Hion & Michaloud, 1989; Tutin *et al*., 1997; McGraw *et al*., 2014). Yet it is becoming increasingly apparent that fallback foods (like the rest of the available resources) are affected by temporal influences, such as seasonality, and are therefore habitat dependent, and thus population-specific. Therefore, foods that may be exploited as fallback resources during resource scarcity in one population, e.g., figs, invertebrates or bark, may be exploited throughout the year in another, or even as a preferred option in another population (Rodman, 1977, 1988; de Ruiter, 1986; Sugardjito *et al*., 1987; Galdikas, 1988; Tutin & Fernandez, 1993a; White, 1998; Yamakoshi, 1998; Newton-Fisher, 1999; Furuichi *et al*., 2001; Basabose, 2002; Lambert, 2002; Fox *et al*., 2004; Pruetz, 2006; Taylor, 2006a, 2009; Yamagiwa & Basabose, 2006a, b, 2009; Cipolletta *et al*., 2007; Marshall & Wrangham, 2007; Bogart & Pruetz, 2008, 2011; Vogel *et al*., 2008, 2009; Constantino *et al*., 2009; Harrison & Marshall, 2011; Parr *et al*., 2011; Chancellor *et al*., 2012; Watts *et al*., 2012b; Isbell *et al*., 2013; Vogel *et al*., 2014; Mosdossy *et al*., 2015).

As fallback foods are population-specific, it also appears that the description of species as high or low quality fallback food users is perhaps too generalised. For example, *Pan troglodytes* are commonly described as high-quality fallback feeders due to their reported exploitation of figs during resource scarcity (Morgan & Sanz, 2006; Yamagiwa & Basabose, 2006a, b; Marshall & Wrangham, 2007; Thompson & Wrangham, 2008; Harrison & Marshall, 2011; McLennan, 2013). Yet, despite this classification, different subspecies and populations of *P. troglodytes* are observed to fallback on different foods during the resource-scarce period. For example, *P. t. schweinfurthii* are known to exploit piths and stems at Gishwati, Rwanda (Chancellor *et al*., 2012) and at Kanyawara, Uganda (Wrangham *et al*., 1991, 1998; Potts *et al*., 2011), but not at Ngogo, Uganda (nearby Kanyawara). There they exploited young leaves (Watts *et al*., 2012b), while both young leaves and piths serve as fallbacks at Bulindi, Uganda (McLennan, 2013) and the montane site of Kahuzi-Biega (Basabose, 2002). Herbs, figs, honeybees, ants and honey (with the latter two requiring tool use) were later classified as fallback foods at the both Bulindi and Kahuzi-Biega (Yamagiwa & Basabose, 2009; McLennan, 2015). *P. t. verus* were observed to exploit bark, cambium and piths during resource scarcity (Pruetz, 2006), while *P. t. troglodytes* were observed to use tools to extract termites (Yamagiwa & Basabose, 2009). The differences at these sites for the species' use of fallbacks are likely to be a reflection of differences in vegetation available (Yamagiwa & Basabose, 2006b; Watts *et al*., 2012b). For example, Ngogo (where high quantities of young leaves are consumed) has a much higher density of saplings than Kanyawara does (Watts *et al*., 2012b). These examples highlight that each application of the hypothesis is study-specific, not repeatable and not generalizable.

Despite apparently having a common operational definition for fallback foods consistent interpretations of a species use of food is not obtained. In fact, classification of a food to be a fallback food can just be a matter of selecting one food from a list of foods consumed, one that is perceived by the authors to be less preferred, but in the process potentially ignore other foods that may also fit into this category (Mills *et al*., 1993; Peres, 2000; McGraw & Daegling, 2012).

Due to the important nutrients available in non-fruit foods it is perhaps incorrect to label them as low quality fallback foods (e.g., Conklin-Brittain *et al*., 2000; Basabose, 2002). Doing so suggests that these foods are not desired and are only consumed because there is little else to eat, when in reality these foods are highly preferred, consumed heavily when available, are vitally important as they add nutrients such as protein to the diet which is imperative in order to maintain a balanced diet, and sometimes possess medicinal and anti-parasitic properties (Nishida & Uehara, 1983; Barton *et al*., 1993; Nishihara, 1995; Tutin *et al*., 1997; Morgan & Sanz, 2006; Taylor, 2006a; Russon *et al*., 2009; Kanamori *et al*., 2010; Potts *et al*., 2011; Watts *et al*., 2012a; Hanya & Chapman, 2013; McGraw *et al*., 2014; Lambert & Rothman, 2015; Mosdossy *et al*., 2015; Vinyard *et al*., 2016). Furthermore, in at least one study piths were at their most nutritious during the period of resource scarcity (Wrangham *et al*., 1991).

Given the fact that the nutritional contents of foods are not fixed throughout the year, it would be wrong to make assumptions that underestimate the quality of diets, especially when different foods might be being consumed at their peak nutritional composition (Worman & Chapman, 2005). In fact, it is suggested that non-human primates change their diets according to the nutritional composition of foods, e.g., their lipid and protein levels, rather than availability of fruits or their plant secondary metabolites, instead they consume foods when they are at their most nutritious (Hladik, 1977; Ham, 1994; Krishnamani, 1994; Reynolds *et al*., 1998; Worman & Chapman, 2005; Boesch *et al*., 2006; Hohmann *et al*., 2006; Kunz & Linsenmair, 2010; Lambert & Rothman, 2015). For example, consumption of seeds and insects in mangabeys was negatively correlated, but as both foods provide high protein levels it was suggested that one food simply replaced the other when at its most nutritious (Ham, 1994). Based on this, the classification that piths are a low-quality fallback food for *P. troglodytes* due to them correlating negatively with fruit availability (Wrangham *et al*., 1991), could be reinterpreted as them being favoured during the wet season because they are at their most nutritious.

Currently not enough is known about the digestive physiology of many non-human primate species (although there are a few notable exceptions, such as the work by Gautier-Hion, 1980), but without this knowledge it is difficult to compare the dietary quality of different non-human primates (Boesch *et al*., 2006). Assumptions of the quality of diets consumed should therefore be avoided until the nutritional contents of the foods consumed are understood (Rothman *et al*., 2007; Lambert & Rothman, 2015). Similarly, labelling a species as a low-quality or high-quality fallback food user should be avoided, for they are probably ingesting the necessary nutrients for their diets (Lambert & Rothman, 2015). For example, in a study comparing sympatric *P. troglodytes*, *Cercopithecus ascanius* and *Lophocebus albigena* in Kibale, foods of different nutritional composition were consumed during the resource-scarce period (Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998). *P. troglodytes* maintained a highly fruit-dominated diet throughout the year, increased ripe fruit consumption when it was available, and only consumed piths as a fallback option, thereby keeping their PSM intake down. In contrast, *C. ascanius* and *L. albigena* did not increase consumption of ripe fruits, but instead consumed leaves, unripe fruits and seeds throughout the year – sometimes increasing consumption of these foods during the resource-scarce period – to maintain protein and plant secondary metabolite levels (Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998).

The consumption of protein-rich foods during the period of resource scarcity by the cercopithecines was similar to responses of *Gorilla* and *Pongo* (Doran-Sheehy *et al*., 2009; Vogel *et al*. 2014). Together, the results from the above studies have been interpreted to justify the Fallback Food Hypothesis, but perhaps they better support the fact that different species have different nutritional requirements. The cercopithecines did not increase ripe fruit consumption at a time when they could have (unlike *Pan*), but instead maintained their balanced diet, meaning that not all species need to consume large quantities of ripe fruits (Conklin-Brittain *et al*., 1998). Indeed, the high quantities of plant secondary metabolites (e.g., tannins and terpenoids) in the cercopithecines diets resulting from high consumption of leaves are probably a reflection of their greater detoxification requirements (Conklin-Brittain *et al*., 1998). While *Pan* did not consume large quantities of leaves because it has a relatively simple digestive system, meaning that it does not have the same ability to detoxify foods through fermentation (Hladik, 1977).

The nutritional contents of fallback foods were assumed to be of much poorer quality than those from non-fallback foods (Gilby & Wrangham, 2007; Doran-Sheehy *et al*., 2009). Despite this assumption, significant differences were not found in the nutrient quality or level of plant secondary metabolites in foods consumed between the period of fruit abundance and resource scarcity (Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998; Doran-Sheehy *et al*., 2009). In separate studies of *Pongo pygmaeus* Knott (1998) and Vogel *et al*. (2014) established that some populations suffered from deficiencies of calories and protein not just during the resource-scarce period, but also throughout the year. To understand more about the relative quality of diet during the periods of resource abundance and scarcity, more evidence is needed on the nutritional composition of foods, until then it remains unclear if the nutrient quality is lower during the fallback time (Irwin *et al*., 2014). This lack of evidence to support nutritional differences between preferred and fallback foods does not dispute the fact that there are fewer foods available during the resource-scarce period or that because of seasonality of resources different nutrients will be available. For example, protein increases when more leaves/ insects are consumed, but the evidence highlights that the assumption of nutritional quality decrease is yet to be categorically proven (Irwin *et al*., 2014).

It is clear that attempts to generalise about fallback foods are fraught with limitations (Gautier-Hion & Michaloud, 1989; Mills *et al.*, 1993; Tutin *et al.*, 1997; Poulsen *et al.*, 2001; Morgan & Sanz, 2006; Cooke, 2012; McGraw *et al.*, 2014). In each population, the types of food available, their nutritional contents and the behavioural and morphological responses of the non-human primates to the period of resource scarcity are context-specific (Kanazawa & Rosenberger, 1989; Mills *et al.*, 1993; van Schaik *et al.*, 1993; Tutin *et al.*, 1997; Peres, 2000; Furuichi *et al.*, 2001; Morgan & Sanz, 2006; Taylor, 2009; Gogarten *et al.*, 2012; Watts *et al.*, 2012b; Lambert & Rothman, 2015; Vinyard *et al.*, 2016).

3.4.1 Potential impact of diet and fallback foods on morphology

With regard to the notion that fallback foods can influence the masticatory morphology, it is perhaps too simplistic to view morphological adaptations as necessary to exploit fallback foods, for morphological adaptations are required to access all foods, be they preferred or less-preferred (Taylor, 2009). Without the necessary morphological adaptations to consume the more preferred foods species would struggle to survive. Therefore, not all adaptive complexes can be connected to fallback foods (Taylor, 2009).

Beyond the basic morphological adaptations of the masticatory apparatus the question of how to explain the more derived morphological characteristics of certain species rests upon whether morphology will respond to regular mastication of particular foods, or to high stress but infrequent volumes of specific foods (Yamashita, 1998; Taylor, 2009). Observations of the feeding ecologies of apes demonstrate that the various species overlap in terms of the preferred foods consumed, yet they vary in the type of foods consumed during the resource-scarce period, e.g., *Gorilla* species consume more fibrous foods than *Pan* species do (Tutin & Fernandez, 1985, 1991, 1993a; Remis, 1997; Tutin *et al.*, 1997; Remis *et al.*, 2001; Yamagiwa & Basabose, 2006a, b, 2009; Taylor, 2009; Head *et al.*, 2011; Oelze *et al.*, 2014). Thus, logically it would make sense that the shared consumption of preferred foods is unlikely to require divergent morphologies in the different species, yet the divergent diets, which can include foods consumed in larger quantities that put more strain on the morphology, such as tough foods, or infrequently consumed harder foods, could drive the different morphological adaptations (Taylor, 2009).

The idea that an animal is adapted to its fallback food is weakened by the fact that the period of resource scarcity does not consist of just one food being exploited during this time, but multiple foods, each with different mechanical properties, thus increasing the complexity (Smith, 1982; Mills *et al*., 1993; Vogel *et al*., 2014). The challenge is to identify which of those foods could potentially be having an impact on the morphology: those foods consumed frequently or those serving a critical function (fallback foods) (Taylor, 2006a, 2009). Distinguishing between frequent or infrequent consumed foods is not straightforward. Examples of this complexity are apparent in ape species. *Pongo pygmaeus* for example infrequently consumes bark (a high stress food) as a fallback food (Rodman, 1977, 1988; Galdikas, 1988; Taylor, 2009), while *P. abelii* and *Gorilla beringei beringei* consume bark throughout the year (Yamagiwa & Basabose, 2006a; Vogel *et al*., 2014). Both *P. pygmaeus* and *G. b. beringei* have more robust masticatory apparatus than *P. abelii* and together they highlight the difficulty of identifying whether frequent consumption or infrequent consumption of high-stress foods are responsible for the derived morphology present in both species (Taylor, 2009). Furthermore, the fact that different species vary in their use and preference of foods and fallback foods makes it difficult to establish common patterns.

According to the suggestion that non-human primates are morphologically adapted to their fallback foods (Lambert, 2007; Marshall & Wrangham, 2007), it is expected that these adaptations would be beneficial to the consumer. Yet analysis of the dentition of *Lemur catta* indicates that the species is poorly adapted for the consumption of its proposed fallback food, which according to Sauther & Cuozzo (2009) is tamarind fruit. The considerable antemortem tooth loss in the species is suggested to be evidence of this poor adaptation (Sauther & Cuozzo, 2009). This suggests that at least in this species fallback foods are not driving morphological adaptations, but they are in fact having a detrimental impact on the species.

Lambert *et al*. (2004) suggested that the thick dental enamel present in *Lophocebus albigena* was the result of hard-object fallback feeding. Subsequent studies also postulated that thick dental enamel in *Pongo pygmaeus* was the result of the species/ population consuming very hard (Constantino *et al*., 2009) or tough fallback foods (Harrison & Marshall, 2011). Very thick dental enamel is not always suggested to be an adaptation to fallback foods; however, as it is also suggested to be an adaptation to the regular consumption of the very hard seeds of *Sacoglottis gabonensis* in *Cercocebus atys* and *C. torquatus* (McGraw *et al*., 2011, 2014; Cooke, 2012; McGraw & Daegling, 2012). Such overlap highlights that there are multiple explanations for the same morphological expression. If the very thick dental enamel present in *Cercocebus* and *Lophocebus* – two closely related genera – is the result of different selective pressures, it indicates that thick dental enamel is a homoplastic trait. The two *Cercocebus* species highlight that morphology can respond to frequently consumed foods, not just fallback foods, and thus, invocation of the fallback argument is not necessary to explain morphological adaptations (McGraw *et al.*, 2011, 2014; Cooke, 2012; McGraw & Daegling, 2012), as Marshall & Wrangham (2007) and Lambert (2007) propose.

If using the definition of fallback foods as proposed by Marshall & Wrangham (2007) superabundant foods that require morphological adaptations to consume, such as mature seeds, fungi and herbs would be classified as low-quality fallback foods. Yet despite the superabundance and the morphological adaptations needed for consuming seeds (very thick enamel) and fungi (digestive tract specialisations to enable the nutrients from non-structural carbohydrates to be absorbed) these foods are preferentially consumed, seeds by *Cercocebus atys* and *C. torquatus*, fungi by *Callimico goeldi* and herbs by *Gorilla gorilla gorilla* as they are highly nutritious and provide high quality proteins (Nishihara, 1995; Lambert *et al.*, 2004; Porter *et al.*, 2009; McGraw *et al.*, 2011, 2014; Cooke, 2012). In fact, increased leaf consumption in *G. g. gorilla* has been suggested to compensate, not for fruit shortage, but for the low herb densities at certain sites (Head *et al.*, 2011). According to Porter *et al.* (2009); Cooke (2012) and McGraw *et al.* (2014) these examples do not accord with the definitions outlined by Marshall & Wrangham (2007).

These examples challenge how foods are classified, and highlight it is perhaps not as straightforward to classify foods as preferred, less preferred and fallbacks (Taylor, 2009). A resolution to this cannot be gained without having systematic data on the feeding ecologies between and within sites and species, the nutritional and mechanical properties of all food types, digestive capabilities of each species, and ontogenetic data on species to compare potential changes from birth and during development to determine if any patterns are the result of genetic or epigenetic changes (Hohmann *et al.*, 2006; Taylor, 2006a; Marshall & Wrangham, 2007; Rothman *et al.*, 2007; Lappan, 2009; Vinyard *et al.*, 2011; Cooke, 2012; Smith *et al.*, 2012; Hanya & Chapman, 2013; Irwin *et al.*, 2014; Oelze *et al.*, 2014; Vogel *et al.*, 2014; Lambert & Rothman, 2015). Such information is lacking for almost all non-human primates (Remis *et al.*, 2001; Taylor, 2006a; Lappan, 2009; Rothman *et al.*, 2011; Smith *et al.*, 2012; Hanya & Chapman, 2013), with the exceptions of a few studies that analyse these different points independently. For example, hardness data are available for *Cercocebus* and *Lophocebus* species (Lambert *et al.*, 2004; McGraw *et al.*, 2011, 2014; Cooke, 2012), nutritional information (including fallback foods) available for *Pan*, *Gorilla*, *Cercopithecus ascanius* and *Lophocebus albigena* (Conklin-Brittain *et al*., 1998; Wrangham *et al*., 1998; Lambert *et al*., 2004; Rothman *et al*., 2007; Doran-Sheehy *et al*., 2009; Vogel *et al*., 2014), and ontogenetic data in *Cebus* and *Homo sapiens* (Cole, 1992; Holmes & Ruff, 2011).

Of course, this is not to say that factors other than diet are influencing the morphology present, many non-human primates show some level of sexual dimorphism, ranging from extreme dimorphism in *Pongo*, *Gorilla* and *Mandrillus*, to slight in *Cebus* (Schaller, 1965; Plavcan, 2001). Such differences are known to manifest in morphological differences in the mandible (Taylor, 2006c; Martinez-Maza *et al*., 2016). Consequently, sexual dimorphism might be making attempts to identify correlations between dietary ecology and morphology more complicated (Smith *et al*., 2012).

It is also possible that the differences observed in the mandibles of closely related taxa, such as *Pongo abelii* and *P. pygmaeus*, and *Sapajus apella* and *S. libidinosus* are the result of tool use (Fox *et al*., 2004; Taylor, 2006a, 2009; Taylor & Vinyard, 2009; Wright *et al*., 2009; Smith *et al*., 2012). During periods of resource scarcity, species from the above genera have been observed to use tools to access foods that are protected by hard outer shells, foods that would otherwise remain inaccessible to them (Izawa & Mizuno, 1977; Yamakoshi, 1998; Fox *et al*., 2004; Smith *et al*., 2012; Melin *et al*., 2014).

Both *Pongo* species consume *Neesia* seeds, which are large and well protected by a tough, outer husk, yet *P. abelii* – with its more gracile morphology – are reported to access the seeds through the use of tools, while *P. pygmaeus* – with its more robust masticatory morphology – use their jaws to break open the seed (Taylor, 2006a, 2009). Similarly, *S. libidinosus* used tools to assist with the opening of extremely hard foods, harder than those consumed by the non-tool using *S. apella*, yet *S. apella* had a morphology that was seemingly better adapted to hard foods than *S. libidinosus* (Wright *et al*., 2009). In both studies, tool use appeared to mitigate the potential morphological shortcomings of a species, while not being present in the more morphologically robust species. It must be highlighted here that while *S. apella* may consume foods that are not as hard as *S. libidinosus* it still consumes foods that are very hard, indeed, up to four times harder than those consumed by *Cebus olivaceus*, and its robust morphology appears to reflect this consumption and increase the dietary repertoire available to it (Wright, 2005; Taylor & Vinyard, 2009).

3.4.2 Utility of dietary studies in palaeoanthropology

The identification of preferred resources and fallback foods is challenging enough in extant primates, but when applied to hominins different problems are encountered, primarily because their diets and behaviours cannot be observed. Due to the fact that hominin diets cannot be observed palaeoanthropologists make use of studies on the diets and ecologies of non-human primates to attempt to infer potential diets in hominins. However, studies on non-human primates were not designed with application to hominins in mind, in this respect, palaeoanthropologists and primatologists investigate different aspects of diet and the methodologies used by primatologists may not be entirely appropriate for use in palaeoanthropology.

In order to identify preferred and fallback foods in non-human primates, the length of a study is perhaps one of the most significant issues to address, because as has already been discussed an animal dependent on reproductive plant parts is subject to the annual phenological changes of the floristic composition (Nishida & Uehara, 1983; Norton *et al.*, 1987; van Schaik *et al.*, 1993; Tutin & Fernandez, 1993a; Taylor, 2009). To identify a fallback food requires the observer to have a comprehensive knowledge of the dietary requirements and preferences of the non-human primates under observation (likely to change based on sex and age differences), as well as the local flora and its phenology (van Schaik *et al.*, 1993; Hohmann *et al.*, 2006; Taylor, 2006a). While there are some studies that have been undertaken over many consecutive years that highlight the variability of non-human primate diets (e.g., Gautier-Hion, 1980; Nishida & Uehara, 1983; Norton *et al.*, 1987; Tutin *et al.*, 1997), many studies have data of their target species for one year cycles (e.g., Whitten, 1983; Isbell, 1998; Su & Lee, 2001; Chancellor *et al.*, 2012), or in some cases only for a few months of the year (e.g., Barton, 1989; Nakagawa, 1989; Krishnamani, 1994; Rogers *et al.*, 1996; Olupot *et al.*, 1997; Okecha & Newton-Fisher, 2006).

A non-human primate's diet is known to vary on a seasonal, as well as annual basis (MacKinnon, 1971; Nishida & Uehara, 1983; Norton *et al.*, 1987; Galdikas, 1988; Remis, 1997; Watts et al. 2012a; McLennan, 2013; Lambert & Rothman, 2015). Based on a short term study it is impossible to identify the full variety of foods available to animals in the forest and thus, the full dietary repertoire of many non-human primates, or indeed, recognise if a season of prolonged food shortage and the responses of the animals to that time are reflective of the norm for a particular site. Long-term studies are necessary in order to acknowledge whether a food consumed seemingly in preference one season is a commonly preferred food on a yearly basis or it is a one off, likewise a fallback food one season might not be exploited on an annual basis (Nishida & Uehara, 1983; Norton *et al*., 1987; van Schaik *et al*., 1993; Tutin *et al.*, 1997; Peres, 2000; Furuichi *et al*., 2001; Basabose, 2002; Yamagiwa *et al.,* 2005; Robbins *et al*., 2006; Vogel *et al.,* 2009; Kunz & Linsenmair, 2010; Vinyard *et al*., 2011; Watts *et al*., 2012a; Lambert & Rothman, 2015).

The value of a specific food is entirely dependent on what nutrients the other available foods available provide, or indeed, fail to provide, and these will change on an annual basis (Altmann, 1998; Lambert & Rothman, 2015). It is essential therefore that the nutritional properties of foods are obtained in long-term studies that cover many years in order to understand more about annual temporal variation in the diet and the occasional periods of extreme resource scarcity (Nishida & Uehara, 1983; Norton *et al*., 1987; van Schaik *et al*., 1993; Tutin *et al*., 1997; Furuichi *et al*., 2001; Remis *et al*., 2001; Hohmann *et al*., 2006). Only then is it possible to identify what foods are important, what foods are preferred and what foods could be considered as fallbacks (van Schaik *et al*., 1993; Furuichi *et al*., 2001; Cooke, 2012).

3.5 Chapter summary

To summarise, diet has for too long been considered in very simplistic terms by palaeoanthropologists, but it is in fact extremely complex. There are many factors, both internal and external that determine the quality of a species’ diet (Ham, 1994; Tutin *et al*., 1997; Conklin-Brittain *et al*., 1998; Hohmann *et al*., 2006; Lambert & Rothman, 2015). While both the traditional method of describing a species as for example a frugivore, or the current vogue of classifying a food as fallback and thus categorising a species by fallback quality can provide important information, they both fail to properly acknowledge the true complexity of diet (Hanya & Chapman, 2013; Lambert & Rothman, 2015; Sengupta & Radhakrishna, 2016; Vinyard *et al*., 2016). To determine quality of diet, more needs to be known about the physiology of a species, from its masticatory apparatus to its digestive anatomy, and its nutritional requirements, along with the nutritional composition of the foods consumed (Hohmann *et al*., 2006; Taylor, 2006a; Marshall & Wrangham, 2007; Rothman *et al*., 2007; Lappan, 2009; Vinyard *et al*., 2011; Cooke, 2012; Smith *et al*., 2012; Hanya & Chapman, 2013; Irwin *et al*., 2014; Oelze *et al*., 2014; Vogel *et al*., 2014; Lambert & Rothman, 2015). Studies need to look beyond labelling and assuming quality of foods and focus on obtaining very detailed information over long time periods that include many seasonal shifts. It must be remembered that every food type has a season when it is most nutritious, and they will not all overlap, fruits when available will be consumed heavily, but they alone do not provide the necessary nutrients every species needs. To achieve a balanced diet other foods high in other nutrients – such as leaves and insects (protein) and seeds (lipids) – must be consumed (Hohmann *et al*., 2006; Morgan & Sanz, 2006; Taylor, 2006a; Watts *et al*., 2012a; Hanya & Chapman, 2013; McGraw *et al*., 2014; Lambert & Rothman, 2015). They are all just as important as each other, but not necessarily in the same quantities, and potentially a shortage or indeed, excess of any nutrient could lead to ill health in the consumer (Knott, 1998; Vogel *et al*., 2014). Only once all this information has been obtained can reliable inferences of diet quality be made, and from these inferences models can be generated to theorise on hominin dietary adaptations.

Application of these models must however be treated with a degree of caution, for it must be acknowledged that foods consumed by non-human primates today (be they preferred or fallback) may not actually be what the species would have consumed in the past (Smith *et al*., 2012). Inferences of hominin adaptation made based on the combined use of dietary and morphological studies on non-human primates are therefore weakened. Within the time since museum skeletal collections were formed and the dietary studies undertaken, anthropogenically influenced factors including climate change, introduction of livestock grazing and the subsequent reduction of a species habitat will have dramatically altered what types of foods are available to be consumed (Sauther & Cuozzo, 2009; Cuozzo & Sauther, 2012; Smith *et al*., 2012; Serckx *et al*., 2015). Droughts have increased in intensity and frequency in Borneo, for example, over the last 60 years (Walsh, 1996), so it is likely that the associated inclement weather patterns will have influenced the nature of the foods available to the non-human primates present. Such factors must be taken into consideration when attempting to infer diet and how it relates to morphology (Sauther & Cuozzo, 2009).

Chapter 4 : Materials and Methods

4.1 Sample

4.1.1 Hominin sample

The sample for this project comprised extinct hominins and extant non-human primates. The data for the hominins was primarily collected from the original specimen reports, however, there were occasions when it was not possible to access the earliest reports and in those instances, the information was supplemented by the online repository the 'Human Origins Database' (available at: www.humanoriginsdatabase.org). This database uses measurements and information published by Wood (1991). The hominin specimens analysed are detailed in Table 4.1. Additional information relating to the measurements, preservation condition and reconstructed habitats are detailed in Appendix Tables 9.1-9.7.

Table 4.1: Hominin specimens used in this study

Species	Specimens			
A. afarensis	A.L. 128-23	A.L. 145.35	A.L. 176.35	A.L. 188.1
	A.L. 198.1	A. L. 198.22	A.L. 200.1b	A.L. 207.13
	A.L. 207.17	A.L. 225.8	A.L. 228.2	A.L. 241.14
	A.L. 266.1	A.L. 277.1	A.L. 288.1	A.L. 311.1
	A.L. 315.22	A.L. 330.5	A.L. 330.7	A.L. 333.44
	A.L. 333.74	A.L. 333w-1a+b	A.L. 333w-12	A.L. 333w-27
	A.L. 333w-32+60	A.L. 333w-48	A.L. 333w-57	A.L. 333w-59
	A.L. 400-1a	A.L. 411.1	A.L. 417.1a	A.L. 417.1a,b
	A.L. 418.1	A.L. 432.1	A.L. 433.1a	A.L. 436.1
	A.L. 437.1	A.L. 437.2	A.L. 438.1	A.L. 440.1
	A.L. 443.1	A.L. 444.2	A.L. 465.5	A.L. 487-1a
	A.L. 582.1l	A.L. 620.1	DIK-2-1	LH2
	LH3	LH 4	LH 14	MAK-VP1/2
	MAK-VP1/4	MAK-VP1/12		
				Total: 54
A. africanus	MLD 2	MLD 4	MLD 18	MLD 19
	MLD 24	MLD 34	MLD 40	Sts 7
	Sts 36	Sts 52	Taung	Stw 1
	Stw 3	Stw 14	Stw 47	Stw 54
	Stw 56	Stw 61	Stw 72	Stw 80
	Stw 87	Stw 90	Stw 96	Stw 106
	Stw 109	Stw 112	Stw 120	Stw 123
	Stw 131	Stw 133	Stw 134	Stw 142
	Stw 145	Stw 147	Stw 151	Stw 193
	Stw 196	Stw 212	Stw 213	Stw 220
	Stw 234	Stw 237	Stw 246	Stw 280
	Stw 285	Stw 291	Stw 295	Stw 308
	Stw 309	Stw 327	Stw 353	Stw 364
	Stw 384	Stw 385	Stw 397	Stw 404
	Stw 412	Stw 413	Stw 421	Stw 424

Species	Specimens			
	Stw 487	Stw 491	Stw 498	Stw 520
	Stw 529	Stw 537	Stw 555	Stw 560
	Stw 566	Stw 586		
				Total: 70
P. boisei	KGA 10-525	KGA 10-570	KGA 10-1720	KGA 10-2705
	KNM-ER 403	KNM-ER 404	KNM-ER 725	KNM-ER 726
	KNM-ER 727	KNM-ER 728	KNM-ER 729	KNM-ER 733
	KNM-ER 801	KNM-ER 802	KNM-ER 805	KNM-ER 810
	KNM-ER 818	KNM-ER 1171	KNM-ER 1467	KNM-ER 1468
	KNM-ER 1469	KNM-ER 1477	KNM-ER 1509	KNM-ER 1803
	KNM-ER 1806	KNM-ER 1816	KNM-ER 1819	KNM-ER 1820
	KNM-ER 3229	KNM-ER 3230	KNM-ER 3729	KNM-ER 3731
	KNM-ER 3737	KNM-ER 3885	KNM-ER 3889	KNM-ER 3890
	KNM-ER 3954	KNM-ER 5429	KNM-ER 5679	KNM-ER 5877
	KNM-ER 15930	KNM-ER 15940	KNM-ER 15950	KNM-ER 16841
	KNM-WT 17396	OH 26	OH 30	OH 38
	OMO 136-1	OMO 136-2	OMO 47-46	OMO 75-14
	OMO 84-100	OMO F203-1	OMO L427-7	OMO L628-2
	OMO L628-3	OMO L628-4	OMO L628-9	OMO L7A-125
	OMO L74A-21	Peninj 1		
				Total: 62
P. robustus	DNH 7	DNH 8	DNH 10	DNH 12
	DNH 18	DNH 19	DNH 21	DNH 26
	DNH 27	DNH 46	DNH 51	DNH 60
	DNH 67	DNH 68	DNH 75	DNH 81
	SK 6	SK12	SK 23	SK 34
	SKW 5	SKW 10	SKW 34	SKW 4767
	SKW 4769	SKX 257	SKX 258	SKX 4446
	SKX 5002	SKX 5013	SKX 5014	SKX 5015
	SKX 5023	SKX 19892	SKX 32162	TM 1517
	TM 1601b	KB 5223	TM 1536	TM 1600
				Total: 40
H. habilis	OH 7	OH 13	OH 16	OH 37
	KNM-ER 817	KNM-ER 819	KNM-ER 1462	KNM-ER 1480
	KNM-ER 1482	KNM-ER 1483	KNM-ER 1501	KNM-ER 1502
	KNM-ER 1508	KNM-ER 1590	KNM-ER 1801	KNM-ER 1802
	KNM-ER 1805	KNM-ER 3734	KNM-ER 3950	KNM-ER 60000
	KNM-ER 62003	UR 501	KNM-WT 42718	
				Total: 23
H. ergaster	KGA 10-1	KNM-BK 67	KNM-BK 8518	KNM-ER 730
	KNM-ER 731	KNM-ER 806	KNM-ER 809	KNM-ER 820
	KNM-ER 992	KNM-ER 1507	KNM-ER 1808	KNM-ER 1812
	KNM-WT 15000	OH 22	OH 23	OH 51
	SK 15			
				Total: 17

4.1.2 Comparative sample

In order to assess the impact of dietary factors and sexual dimorphism on masticatory morphology, the project focussed on the mandible from a wide selection of haplorrhine primate species, consisting of Catarrhines (both Hominoidea and

Cercopithecoidea) and Platyrrhines (Cebidae only). The use of non-human primates as comparative models has long been utilised as a way of furthering knowledge and understanding about the evolution of the early hominins (Nystrom & Ashmore, 2008; Wood & Schroer, 2012). Due to the nature of food availability and accessibility for humans today, they do not make suitable comparisons to early hominins. In contrast, extant non-human primates are still affected by seasonality of food resources; for this study, they are therefore the most suitable comparative analogues to early hominins. Each species and subspecies was selected based on their diets, habitat variation, and degree of sexual dimorphism (complete sample detailed in Table 4.2).

As this study draws upon various different adaptations of non-human primates, each species was relevant in its own way, and included to develop a broad comparative approach that allows consideration of general adaptive and evolutionary processes and patterns in the context of reconstructing extinct species' dietary ecology. The species analysed can be divided into homologous and analogous groupings, for example, as this project analysed anatomical differences, *Pan, Gorilla* and *Pongo* are the best models for these differences, as they are genetically the closest and anatomically the most similar living relatives to *Homo sapiens*, and so share homologies (Glazko & Nei, 2003; Kumar *et al*., 2005; Nystrom & Ashmore, 2008). However, non-human apes are not perfect comparisons to the hominins in question for the simple fact that they consume diets from very different isotopic pathways. The diets of *Gorilla* and *Pan* are almost entirely based on C_3 resources, which is an isotope composition similar only to *Australopithecus anamensis* and no other early hominin (Cerling *et al*., 2013). In addition, this study also analysed the adaptive responses to physical environments. For this reason, monkeys were considered to be the most appropriate models, as they provide analogous comparisons (Nystrom & Ashmore, 2008). Taking these points by Nystrom & Ashmore (2008) and Cerling *et al*. (2013) into consideration, it was important that the sample was broad enough to encompass different dietary components and to do that, the sample had to include other members of the non-human primate family, for they can contribute significantly to studies such as this. It is for this reason that genera from Cercopithecoidea and Ceboidea were explored; for they can provide further insight into how the various adaptive factors can influence the masticatory morphology. Together the use of homology and analogy to compare to the hominins, provide a more complete comparative range of diets for the analysis.

4.1.2.1 Selection criteria

In order to focus on the impact of dietary, habitat and sex differences, it was important to negate the influences of confounding variables, such as developmental issues, consequently, adult specimens were the targeted age demographic. As with other studies where age is taken into consideration (e.g., Holmes & Ruff, 2011), age was determined by the presence of the third molar (M_3) in the mandible. The presence of M_3 in the dentition is often correlated with the beginning of adulthood and thus, attaining adult morphology (Smith, 1989).

Sexual dimorphism has been observed in the mandible of extant apes, with it manifesting itself in areas such as the mandibular symphysis (Taylor, 2006c; Thayer & Dobson, 2010). By focussing on one sex only, as Fukase & Suwa (2008) do, results could lack accuracy, for they have not removed the potential for sexual dimorphism as a confounding variable. This is well summarised by Holmes & Ruff (2011: 625), who reason that “population level differences in symphyseal morphology may be greater or less within a single-sex rather than a mixed sample”. For this reason, both males and females were included in this sample; therefore the potential for sexual dimorphism to be a confounding factor in this study should have been removed. A general rule followed was that if sex was not attributed to a specimen, it was not analysed; however, there were exceptions to this. In the case of highly sexually dimorphic non-human primates, such as *Gorilla*, *Pongo* or *Mandrillus* - where males can be as much as twice the size of females (Cant, 1987; Setchell *et al.*, 2001) - a judgement was made on the sex. This was based on features that are known to be sexually dimorphic in these genera, for example, overall size relative to others of the same species and the size of canines (Plavcan, 2001).

The third premolar (P_3) was excluded from analysis due to the variable presence of sectorial morphology in some non-human primates. Sectorial morphology is a specialised adaptation in the Cercopithecoidea superfamily (Ankle-Simons, 2000), which is responsible for sharpening the maxillary canines through its elongated, single-cusped morphology (Nystrom & Ashmore, 2008). As the premolar slopes mesially, it distorts the mesiodistal length of the tooth and will thus, not provide accurate measurements of that tooth in relation to other P_3 dentition. As a result, the dentition analysed in this study included molars one to three and the fourth premolar.

Where possible, measurements were taken on the left side of the mandible, but when this was not possible, measurements were taken from the right side. The degree of asymmetry between right and left sides is disputed, for while it is recognised that the morphology present on one side is not necessarily reflected on the other, little evidence of directional asymmetry has been identified in previous studies and indicates that either side can be used for scoring (Hillson, 1996). Indeed, this lack of convention is observed in studies on hominins (left side used by Cofran (2014)) and non-human primates (right side used by Holmes & Ruff (2011)). To obtain the most reliable and comparable data it was necessary that the measurements and photographs were taken in a consistent manner throughout, and only where absolutely necessary should the side change. As with Holmes & Ruff (2011), mandibles whose appearance was in some way altered, e.g., those with extensive damage that prevented measurements being obtained, abnormalities or were edentulous, were not included in the data collection.

All specimens selected for analysis in this study were chosen based on the above factors, but a further crucial factor was where the specimens originated, i.e. whether or not they were wild-shot and if they were of known locality. These details are important, as the non-human primates might vary in their morphological adaptations if they were wild (in their natural habitats) or if they were captive (in artificial environments like zoos). While zoos and wildlife parks attempt to reconstruct species' habitats as close to what is natural, the environments are not the same (Nystrom & Ashmore, 2008), as a result, the foods consumed would not be the same, and most likely, they would not experience the impact of seasonality. In addition, by selecting specimens based on their location, it was possible to determine their species or subspecies identity based on geographical distributions of these species (for example the distributions of *Pan troglodytes* subspecies are highlighted in Figure 3.2). The museum records and the collectors' field notes determine details such as these. Generally, if a specimen's locality were unknown it would be excluded from analysis (consistent with Taylor, 2006b); however, some specimens of unknown locality would still be analysed if they were from a species or subspecies with a limited sample size. This exception is relevant for wild-shot *Gorilla beringei beringei*, as there are very few specimens of this subspecies available in museums, but the limitation of not knowing where the specimen originates is offset in the knowledge that this subspecies are only known to occupy the Bwindi Impenetrable National Park, Uganda and the Virunga Volcanoes of Rwanda, Uganda and Democratic Republic of Congo (Robbins, 2011), so in this instance it is possible to narrow down locality based on knowledge of subspecies status.

4.1.2.2 How the grouping variables were defined

4.1.2.2.1 Sexual dimorphism

Information pertaining to non-human primate species expression of sexual dimorphism was obtained primarily from Plavcan (2001), and supplemented by Jaffe & Isbell (2011), Swedell (2011) and Thierry (2011). Sexual dimorphism was defined based on differences between male and female body mass, not canine dimorphism. For the purposes of this study overall body mass dimorphism was deemed to be more important than canine dimorphism because it is a factor that corresponds with body weight and diet, along with having the potential to impact on the mandibular morphology beyond that directly surrounding the canine. Indeed, it is recognised that as body mass dimorphism increases, so too does the mandibular size dimorphism (Taylor, 2006c).

Genera and species were defined by the following expressions of dimorphism: slight, moderate, strong and extreme. These follow the definitions of Plavcan (2001). Where a genus was described as having moderate to strong (e.g., *Cercopithecus* or *Macaca*), or strong to extreme dimorphism (e.g., *Papio*), more information was sought from other sources as this clearly represented variation within the genus. While none of Jaffe & Isbell (2011), Swedell (2011) and Thierry (2011) defined sexual dimorphism as Plavcan (2001) did, they do provide indications on the variation of dimorphism within the genus. For example, using the figures from Table 14.3 in Thierry (2011), it is clear that *Macaca radiata* are among the most sexually dimorphic of the macaque species, while *M. cyclopis* and *M. sylvanus* are moderately dimorphic by comparison. Applying this knowledge to that of Plavcan (2001) it was possible to fill in gaps, so in this case, *M. cyclopis* and *M. sylvanus* represent the moderately dimorphic species, and *M. radiata* represent the strongly dimorphic species. Table 15.1 in Swedell (2011) and Table 16.6 in Jaffe & Isbell (2011) present sexual dimorphism information in a similar way (male and female body weight averages) and was once again used to complement the information from Plavcan (2001).

As discussed in Chapter 2, the degree of sexual dimorphism in hominins varied from being moderate to large. Information on estimated body mass dimorphism was obtained from the published literature and input into the hominins database.

4.1.2.2.2 Body weight

Body weight information for non-human primates comprised species averages for males and females obtained primarily from Smith & Jungers (1997). Where body weight information was an estimate only (e.g., *Mandrillus leucophaeus* and *Macaca sylvanus* in Smith & Jungers (1997)), further information was obtained from Rowe (1996). A species average body weight was generated from this information to group the monkeys and apes into small and large groups. The division of groups was achieved by dividing 130 by 4 (this was the average weight for the largest non-human primate in the sample: *Gorilla beringei beringei* into the 4 groups). All of the monkeys fell below the halfway point, and all of the apes exceeded the halfway point, making the division of the size ranges between the monkeys and apes more straightforward. The four groups therefore became small monkeys and large monkeys, and small apes and large apes. This division of body sizes was only applied to the analyses exploring tests of difference, and by analysing the data as such, it was possible to account for the size differences that were likely to manifest in the statistical analyses of the mandible and thus mask the potential morphological variation associated with diet. For the Principal Components Analysis and Multiple Regression Analysis the size variables were log transformed, so the body size groupings as described above were not used.

Body weight information for the hominin dataset was derived primarily from Grabowski *et al*. (2015) (and presented in Table 4.2). There are several other references that provide information on body mass estimates (e.g., Wolpoff, 1973; Steudel, 1980; McHenry, 1988, 1992; Antón, 2012; Holliday, 2012) in hominins, but Grabowski *et al*. (2015) incorporated all of the hominin species analysed in this project, which none of the others did. By using the data from Grabowski *et al*. (2015) it ensured that all of the estimates were made using the same method, and consequently the results were consistent.

Table 4.2: Estimated body mass of hominin species according to Grabowski *et al*. (2015)

Species	Body mass (kg)
A. afarensis	39.1
A. africanus	30.5
P. boisei	35.3
P. robustus	30.1
H. habilis	32.6
H. ergaster	51.4

4.1.2.2.3 Dietary categories

There is considerable variation in the types of foods consumed during both periods of fruit abundance and resource scarcity, as presented in detail in Chapter 3, not just by species but even subspecies, which are dependent on the nature of the environment and habitat. Long-term dietary studies help to inform on how diet can vary on a seasonal and annual basis, but uncertainty remains over the meaning and application of the Fallback Food Hypothesis. Given this uncertainty and the large variation of foods that could constitute fallbacks – even within subspecies – it was a very difficult concept to generalise and apply in this study. As a result, fallback foods were not analysed as a separate dietary variable, but instead included within the overall diet should their frequency of consumption be listed (Tables 4.4-4.6 detail diet information for each species).

4.1.2.2.3.1 Traditional dietary categories

Dietary category for a species was assigned initially using the traditional classifications of Fleagle (1999), and supplemented by other researchers where this data was unavailable. For example, *Mandrillus leucophaeus* information was provided by Owens *et al*. (2015), *Pan troglodytes schweinfurthii* by Yamagiwa & Basabose (2006a), and *Gorilla beringei graueri* by Yamagiwa & Basabose (2009). The traditional diet categories used are detailed in Table 4.3 and how they apply to each species analysed are detailed in Tables 4.4-4.6.

4.1.2.2.3.2 Specific classification coding categories

Dietary data extracted from field reports on each species analysed was compiled. Within each species, field reports were separated based on the method of observation used (focal animal sampling and faecal analysis) and the average diets for each species/ subspecies was calculated. Based on this dietary data, 10 of the most commonly occurring foods identified in field studies of non-human primates were used, but for the purposes of analysing the diets these foods were compressed into the following 5: fruit, leaves, seeds, roots and animals (Figure 4.1). Diets were then defined using combined aspects of the methods described by Plavcan & van Schaik (1992) and Muchlinski (2010), similar to Coiner-Collier *et al*. (2016). For example, a species was categorised primarily as a frugivore if more than 50% of their diet was made up of fruits (Muchlinski, 2010), then depending on the quantity of the additional foods in the diet, e.g., > 15% leaves, they would be given a mixed classification of frugivore-folivore (Plavcan & van-Shaik, 1992). Where a food item did not exceed 50% and the secondary component exceeded 25% or the second and third components were almost equal (~20% each) the species was categorised as an omnivore. The specific classification coding categories by both direct observation and faecal analysis used are detailed in Table 4.3 and how they apply to each species analysed are detailed in Tables 4.4-4.6.

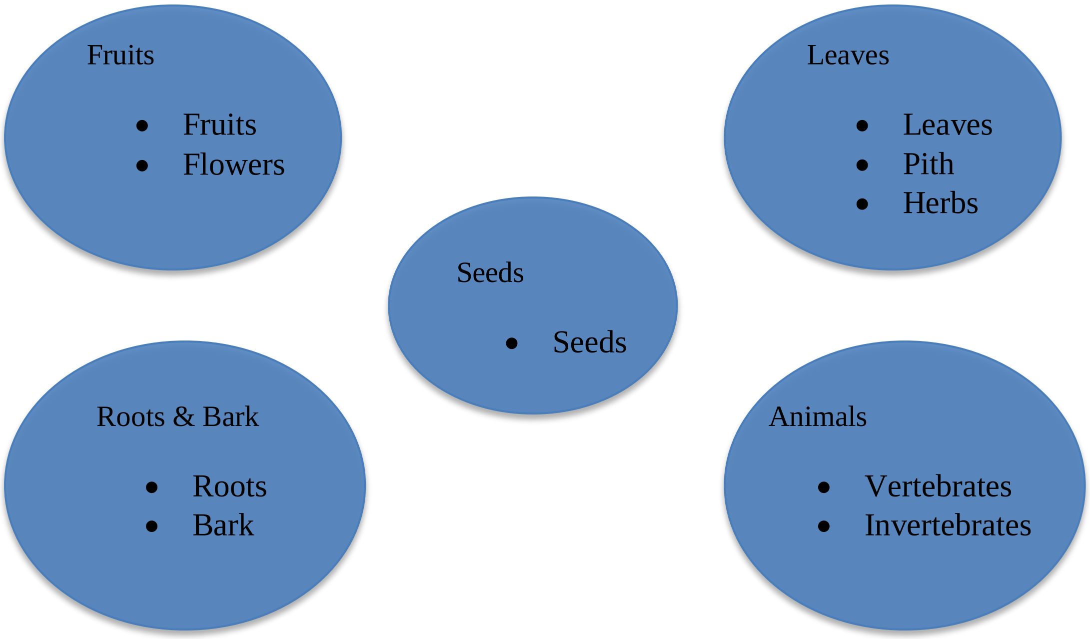

Figure 4.1: Food types used and what they were comprised of

4.1.2.2.3.3 Food Quantity Analysis

An additional dietary classification system using the same 5 food groups used previously (fruits, leaves, seeds, roots and animals) was also applied. From these 5 groups, the percentage that each contributed towards the diet was noted, for example, on average fruit contributes to 62.7% of the diet of *P. t. schweinfurthii* (when using focal animal sampling). Based on these percentages each food type was divided into ranges of high, medium and low consumption. To establish the ranges for each food group, the lowest figure was subtracted from the highest figure, and then the remaining figure was divided into three, with each segment representing low, medium or high consumption of a food. By analysing the data by quantity analysis it was anticipated that it would be possible to establish if consuming different quantities of certain foods was correlated to certain morphological patterns. The food quantity categories by both direct observation and faecal analysis used are detailed in Table 4.3 and how they apply to each species analysed are detailed in Tables 4.4-4.6.

Table 4.3: Dietary categories/ quantity categories used

Dietary categories			Food quantity categories	
Traditional	Specific classification categories by direct observation	Specific classification categories by faecal analysis	Food quantities by direct observation	Food quantities by faecal analysis
Frugivore	Folivore	Folivore-frugivore	Fruit: low, moderate, high	Fruit: low, moderate, high
Folivore	Folivore-frugivore	Frugivore-folivore	Leaves: low, moderate, high	Leaves: low, moderate, high
Omnivore	Folivore-granivore	Frugivore-granivore	Seeds: low, moderate, high	Seeds: low, moderate, high
Frugivore-insectivore	Frugivore	Frugivore-faunivore	Roots: low, moderate, high	Roots: low, moderate, high
	Frugivore-folivore	Frugivore-insectivore	Animals: low, moderate, high	Animals: low, moderate, high
	Frugivore-granivore	Omnivore		
	Frugivore-faunivore			
	Frugivore-insectivore			
	Omnivore			

Species diets and expressions of sex dimorphism presented in Tables 4.4-4.6 are based on species averages. Information relating to the individual studies that detail a particular population's location, habitat, altitude, seasonal availability of resources and overall diet is available at: https://opencontext.org/projects/a9dbf427-cff6-41b7-8462-a9ab8d9908f4.

Table 4.4: Body mass dimorphism, body weight and diet information on each species from Cercopithecoidea

Species	Body mass dimorphism	Body weight category*	Traditional diet categories	Specific classification categories by direct observation	Direct Observation					Specific classification categories by faecal analysis	Faecal Analysis				
					F	L	S	R	A		F	L	S	R	A
Cercocebus atys	Strong	Small monkey	Frugivore	Omnivore	46.3	2.5	28	0.5	19.5	No information					
Cercocebus torquatus	Strong	Small monkey	Frugivore	Frugivore/granivore	62.8	3.9	28.2	0	0	Frugivore/folivore	51.9	33.4	14.8	0	0
Cercopithecus ascanius	Moderate	Small monkey	Frugivore	Omnivore	38.2	17.5	0.2	0	40.1	Omnivore	49.8	24.5	14.9	0	11.3
Cercopithecus cephus	Moderate	Small monkey	Frugivore	Frugivore/faunivore	63.9	7.7	5.9	0	22.1	Frugivore/folivore	65.2	19.2	7.9	0	3.5
Chlorocebus aethiops	Extreme	Small monkey	Omnivore	Frugivore/folivore	68.2	18.7	0	5.7	7.4	No information					
Chlorocebus pygerythrus	Extreme	Small monkey	Omnivore	Omnivore	42.1	14.4	13.8	0.1	2.6	Omnivore	22.2	10.3	1.2	0	1.6
Chlorocebus sabaeus	Extreme	Small monkey	Omnivore	Frugivore	63.2	0	12.8	0	13.1	Omnivore	37.5	28.6	0	0	26
Chlorocebus tantalus	Extreme	Small monkey	Omnivore	No information						No information					
Erythrocebus patas	Strong	Small monkey	Omnivore	Frugivore	68.9	11.2	0.8	0	12	Omnivore	20.7	8.2	2.2	0.1	12.5
Lophocebus albigena	Strong	Small monkey	Frugivore	Frugivore/faunivore	51	8.4	11	2.5	22.5	Omnivore	39.4	20.6	24.8	0	3.3
Lophocebus aterrimus	Strong	Small monkey	Frugivore	Frugivore/granivore	60.9	3.3	30.5	0	1.6	Frugivore/granivore	60.5	10.5	28.9	0	0
Macaca cyclopis	Moderate	Small monkey	Frugivore	Frugivore/folivore	61.1	29.1	0	0	9.8	Frugivore/folivore	60.2	37.5	0	2.3	0
Macaca radiata	Strong	Small monkey	Frugivore	Frugivore	58.3	5.5	0.2	2.4	10.6	Frugivore/folivore	49.7	25.8	5.1	0.3	14.5
Macaca sylvanus	Moderate	Large monkey	Frugivore	Folivore/granivore	6.4	49.2	21.2	9.8	4.2	Omnivore	16.7	39.9	18.3	20.7	3.5
Mandrillus leucophaeus	Extreme	Large monkey	Omnivore	No information						Frugivore/faunivore	50	14.4	0.8	2.8	32.1
Mandrillus sphinx	Extreme	Large monkey	Omnivore	Omnivore	47.5	11.4	34.4	0	4.9	Omnivore	34.6	20.2	25	1.9	10.9
Papio anubis	Strong	Large monkey	Omnivore	Omnivore	39.6	29.7	9.8	6.3	3.6	Frugivore/folivore	53.9	19.5	12.9	7.4	3.9
Papio cynocephalus	Extreme	Large monkey	Omnivore	Omnivore	34.1	27.7	7.3	19.4	1.2	Omnivore	26	29.1	23.1	13.1	0

*Within the database the female and male averages of a species are tested separately. For the above table, it was necessary to group the species by the species average body weight.

F = Fruit. L = Leaves. S = Seeds. R = Roots. A = Animals. All numbers presented represent an average percentage of the diet consumed.

Table 4.5: Body mass dimorphism, body weight and diet information on each species from Hominoidea

Species	Body mass dimorphism	Body weight category*	Traditional diet categories	Specific classification categories by direct observation	Direct Observation					Specific classification categories by faecal analysis	Faecal Analysis				
					F	L	S	R	A		F	L	S	R	A
Gorilla beringei beringei	Extreme	Large ape	Folivore	Folivore	4	85.8		10.2	2	Folivore/frugivore	27.7	48	10.1	4.1	
G. b. graueri	Extreme	Large ape	Frugivore	No information						Folivore/frugivore	21.6	60.9	0.5	15.1	
G. gorilla gorilla	Extreme	Large ape	Frugivore	Folivore/frugivore	30.2	58.8	1.2		5.1	Frugivore/folivore	50.2	34.8	5.1	4.8	1.4
Pan paniscus	Moderate	Small ape	Frugivore	Frugivore/folivore	72.6	24.9			0.1	Frugivore/folivore	53.5	32.8	6.1	0.8	5.7
P. troglodytes schweinfurthii	Moderate	Small ape	Frugivore	No information						Frugivore/folivore	51.7	34.6	4.7	3.5	1.9
P. t. troglodytes	Moderate	Small ape	Frugivore	Frugivore/folivore	64.6	21.8	4.4		3.3	Frugivore/folivore	71.2	16	4.1	1	3.6
P. t. verus	Moderate	Small ape	Frugivore	Frugivore/folivore	67.2	17	2.1	2.2	11	Frugivore/folivore	60.4	29	4.2	4.5	
Pongo abelii	Extreme	Small ape	Frugivore	Frugivore/folivore	69.8	17.2		2.8	8.8	Frugivore/folivore	53.8	35.7	0	3.9	4.3
Po. pygmaeus	Extreme	Small ape	Frugivore	Frugivore	72.8	12.3		5.5	5.4	Folivore/frugivore	41.5	49.3		9.2	

*Within the database the female and male averages of a species are tested separately. For the above table, it was necessary to group the species by the species average body weight.

F = Fruit. L = Leaves. S = Seeds. R = Roots. A = Animals. All numbers presented represent an average percentage of the diet consumed.

Table 4.6: Body mass dimorphism, body weight and diet information on each species from Ceboidea

Species	Body mass dimorphism	Body weight category*	Traditional diet categories	Specific classification categories by direct observation	Direct Observation					Specific classification categories by faecal analysis	Faecal Analysis				
					F	L	S	R	A		F	L	S	R	A
Cebus albifrons	Slight	Small monkey	Frugivore	Omnivore	44.7	2.5	10.7		42	No information					
C. capucinus	Slight	Small monkey	Frugivore	Frugivore/insectivore	59.3	2.4	0.6		36.1	No information					
C. olivaceus	Slight	Small monkey	Frugivore	Frugivore/insectivore	53.8	6.6	2.9	0.5	26	No information					
Sapajus apella	Slight	Small monkey	Frugivore/ Insectivore	Omnivore	40.3	14.5	6.8	0.2	35.4	Frugivore/insectivore	57.9	12.3	3.5		21.1

*Within the database the female and male averages of a species are tested separately. For the above table, it was necessary to group the species by the species average body weight.

F = Fruit. L = Leaves. S = Seeds. R = Roots. A = Animals. All numbers presented represent an average percentage of the diet consumed.

4.1.2.3 The final sample

Once these various factors had been taken into consideration, a sample of extant non-human primates that matched the selection criteria was developed. From this sample, collection databases in museums around Europe were accessed to determine the level and nature of availability of the genera and species selected. This step was particularly important, as Excel spread sheets were created to collate individual collection sample sizes and the overall total. To ensure that the sample was representative, at least 10 females and 10 males were targeted for each group. It was decided that this minimum total would provide a large enough base sample for each group analysed to be considered reliable. If the overall total did not exceed 10 specimens in each sex, the species/ subspecies were removed from the target list. The preferred target sample was 20 specimens of each sex, but there were instances where this was not possible (for example, *Gorilla beringei beringei*); therefore, for species that were considered particularly important for this study, the data from the maximum amount of individuals were collected. The collections visited were: the Adolph Schultz Anthropology Museum and Institute (University of Zurich, Switzerland) (AIM), Royal Museum for Central Africa (Tervuren, Belgium) (RMCA), Berlin Museum of Natural History (Germany) (MFN), Powell Cotton Museum (Kent, United Kingdom) (PCM), Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany) (MPI), Bavarian State Collection of Zoology (Munich, Germany) (ZSM), Vienna Museum of Natural History (Austria) (NHMW). The final sample and the museums/ collections where the specimens were housed are presented in Table 4.7.

Table 4.7: Primate species to be analysed in this project, the sample totals and the collection locations

Hominoidea *n* = 360	M	F	?	Cercopithecoidea *n* = 633	M	F	?	Ceboidea *n* = 75	M	F	?
Gorilla beringei beringei [1,2,3]	4	5	1	*Cercocebus atys* [1,2]	20	20		*Cebus albifrons* [1,3,7]	7	8	2
Gorilla beringei graueri [2,3]	22	22	1	*Cercocebus torquatus* [1,6]	3	2		*Cebus capucinus* [3,7]	5	4	2
Gorilla gorilla gorilla [2,4]	35	24	5	*Cercocebus torquatus torquatus* [1,4]	19	6		*Cebus olivaceus* [1,3,7]	7	2	
Pan paniscus [2]	18	20	2	*Cercopithecus ascanius* [3]	4	2	1	*Sapajus apella* [1,3,7]	20	14	4
Pan troglodytes schweinfurthii [2,4]	22	21		*Cercopithecus ascanius katangue* [2]	15	15					
Pan troglodytes troglodytes [2,4]	26	34	7	*Cercopithecus ascanius schmidti* [2,3,4]	21	23					
Pan troglodytes verus [1,2,5]	17	20	7	*Cercopithecus ascanius whitesidei* [2]	20	20					
Pongo abelii [1,3,6]	6	6		*Cercopithecus cephus* [4]	31	20					
Pongo pygmaeus [1,3]	13	15	2	*Chlorocebus aethiops* [3,6,7]	20	30					
Pongo pygmaeus pygmaeus [1,6]	20	20		*Chlorocebus pygerythrus* [1,2,3,4,7]	13	12					
Pongo pygmaeus wurmbii [6]	1	3	1	*Chlorocebus sabaeus* [1,3]	10	3					
				Chlorocebus tantalus [3,7]	3	0					
				Erythrocebus patas [1,2,3,4,6,7]	13	11	3				
				Lophocebus albigena [2,4]	20	21					
				Lophocebus albigena johnstoni [2,4]	3	9	3				
				Lophocebus aterrimus [2]	20	20					
				Macaca cyclopis [1,3]	4	5	5				
				Macaca radiata [3,7]	1	1					
				Macaca sylvanus [1,3,6,7]	6	11	1				
				Mandrillus leucophaeus [1,3,4]	11	7	3				
				Mandrillus sphinx [1,2,3,6]	22	9	6				
				Papio anubis [2,3]	21	22	8				
				Papio cynocephalus [1,2,3,6,7]	17	12	5				
Totals per sex	184	190	26		317	281	35		39	28	8
[1] AIM, [2] RMCA, [3] MFN, [4] PCM, [5] MPI, [6] ZSM, [7] NHMW									**Total sample**		**1108**
M= Males. F = Females. ? = Unknown sex											

4.2 Method

4.2.1 Data collection

One of the main aims of this thesis revolved around the issue of whether there are morphological differences that correspond to differences in diet. To test this, it was important to consider what methods could best fulfil the objectives and still produce a large enough sample. The method involved collecting metric data from the mandibles and dentition of non-human primates, in order to describe and compare morphological variation among species in the study sample. This followed the method used by Wood (1991) (Table 4.8 and Figures 4.2-4.4). The measurements used were carefully selected based on three factors: 1) previous studies have shown a variable influence of diet on these areas (see for example, Taylor, 2005; Holmes & Ruff, 2011), 2) these measurements have previously been shown to be sexually dimorphic in great apes (Taylor, 2006b), and 3) the metric data can be compared directly to hominins in the fossil record. All measurements relate to features of the mandible that could be subject to changes as a result of different evolutionary stimuli. It was assumed that when focussing on an element of the anatomy that is functionally responsible for mastication, as the mandible is, diet would be one of the most important stimuli involved.

Investigation of mandibular variation in primates has focussed primarily on the functional and adaptive significance of the morphology of the mandible (Taylor, 2006c; Holmes & Ruff, 2011). Previous studies have focussed on either symphyseal morphology (e.g., Fukase & Suwa, 2008) or midcorpus morphology (e.g., Hylander, 1984, 1988; Daegling, 2001; Holmes & Ruff, 2011). However, to account for potential structural modifications to the mandible, it was considered essential that both symphyseal and corpus morphologies were analysed to generate a complete understanding of the variation present in the mandibles (Taylor, 2002; Taylor & Groves, 2003). This is because increases to the depth and width of the mandibular symphysis and corpora are considered to be important adaptations to prevent deleterious effects such as sagittal bending (countered by a deeper corpus), torsional loading (countered by a wider corpus), symphyseal bending (countered by a deeper symphysis) and wishboning (countered by a wider symphysis) during mastication and incision (Hylander, 1979a, 1979b, 1984, 1985; Daegling, 1992; Taylor, 2006c). These factors occur when there is a significant degree of loading on the mandible, which can result from eating obdurate foods (Taylor, 2006c; Norconk *et al.*, 2009).

These biomechanical factors were crucial when deciding which morphometric measurements would be utilised in this research. In addition, the same features are measured in the extinct hominin sample, so it was possible to compare the measurements from the extant non-human primates to the measurements from the extinct hominins (hominin averages for each measurement detailed in Tables 4.9-4.10).

To ascertain potential variation in tooth size in relation to mandibular symphysis and corpus size, standard dental measurements were included. The mesiodistal and buccolingual diameters were measured from the P_4 to the M_3 (measurement definitions in Table 4.8).

Table 4.8: Metric measurements as defined by Wood & Abbott (1983) and Wood (1991)

Abbreviation	Measurement	Definition
P_4 MD	Mesiodistal crown diameter (premolars)	Distance between parallel lines erected at right angles to the mesiodistal axis of the crown and arranged so as to be tangential to the most mesial and distal points on the crown; allowance is made for interstitial wear.
M_1-M_3 MD	Mesiodistal crown diameter (molars)	Maximum distance between the mesial and distal crown borders, taken parallel with the longitudinal axis of the crown, and, where relevant, making allowance for interstitial wear
P_4 BL	Buccolingual crown diameter (premolars)	Maximum distance between the buccal and lingual borders taken at right angles to the longitudinalaxis of the crown
M_1-M_3 BL	Buccolingual crown diameter (molars)	Maximum distance across the protoconid (BL1) and hypoconid (BL2) between the buccal and lingual crown borders taken at right angles to the longitudinal axis of the crown
SH	Symphyseal height	Minimum distance between the base of the symphysis and infradentale
SD	Symphyseal depth	Maximum depth, at right angles to symphyseal height at the superior transverse torus
CH	Corpus height	Minimum distance between the most inferior point on the base and the lingual alveolar margin at the midpoint of each tooth (P_4 - M_3)
CW	Corpus width	Maximum width at right angles to corpus height taken at the midpoint of each tooth (P_4 - M_3)

Table 4.9: Hominin species dental measurement averages analysed in this study

Species	P_4 MD	P_4 BL	M_1 MD	M_1 BL	M_2 MD	M_2 BL	M_3 MD	M_3 BL
A. afarensis	9.60	11.09	12.77	12.65	14.14	13.43	15.21	13.50
A. africanus	10.29	11.49	13.97	13.13	15.79	14.10	16.24	13.80
P. boisei	13.27	14.61	16.05	14.51	17.84	16.56	19.03	16.54
P. robustus	11.17	12.98	14.41	14.33	16.04	15.40	16.77	14.88
H. habilis	9.89	11.08	13.63	12.04	15.16	13.31	15.37	13.36
H. ergaster	9.03	10.20	12.90	11.58	13.40	12.12	13.66	12.03

Table 4.10: Hominin species mandibular measurement averages analysed in this study

Species	SH	SW	P_4CH	P_4CW	M_1CH	M_1CW	M_2CH	M_2CW	M_3CH	M_3CW
A. afarensis	39.00	19.52	36.70	19.48	34.14	20.38	31.91	22.29	30.22	28.30
A. africanus	31.50	18.75	36.00	21.70	33.29	21.56	33.30	25.50	33.33	29.50
P. boisei	46.83	26.45	42.26	28.45	41.56	28.65	40.63	30.91	39.65	33.53
P. robustus	41.33	22.25	36.95	24.85	36.94	25.20	34.91	27.63	35.75	30.50
H. habilis	34.41	20.67	35.36	19.94	33.24	20.69	33.40	23.48	27.90	23.00
H. ergaster	31.89	19.28	30.72	19.46	27.94	19.55	31.49	20.54	32.17	21.37

Image removed due to copyright

Figure 4.2: Mesiodistal (MD) and buccolingual (BL) crown diameters (image from Wood (1991))

Image removed due to copyright

Figure 4.3: Corpus height (M_1CDP), symphyseal height (SDP) and width (SWD) (image from Taylor, 2006b)

Image removed due to copyright

Figure 4.4: Corpus width (M_1CWD) (image from Taylor, 2006b)

Using these measurements, following the work of Taylor (2006c) and Daegling & McGraw (2007) seven shape ratios were generated to recreate the mandibular shape. These ratios were corpus and symphyseal robusticity indices, corpus and symphyseal size, dental crown area and crown shape index (definitions available in Table 4.11, and the hominin averages for each ratio are detailed in Tables 4.12-4.13).

The robusticity index[7] used for the corpus and symphyseal measurements are commonly used (Wood & Abbott, 1983; Wood, 1991; Kimbel *et al*., 2004; Taylor, 2006c). The robusticity index provides the opportunity to establish the degree of robusticity in the corpus and symphysis of each specimen and compare variation within and between non-human primate species and hominins (Kimbel *et al*., 2004).

The measure for crown area can be done in two ways according to Wood & Abbott (1983), the first using the MD and BL measurements and computing the area as MD*BL, the other method is through the use of a planimeter, which measures the exact area of a shape. Wood & Abbott (1983) compared the two methods in terms of accuracy and found that while the computed method overestimates the crown area, the results were not too dissimilar. The overall differences concealed the extensive variations that occurred between individuals (Wood & Abbott, 1983). This is likely to be a reflection of the tooth shape, where those of a more rectangular shape will be more accurate than those of an irregular shape (Wood & Abbott, 1983), and given that the measurements used are essentially for a rectangle and therefore assumes the shape being measured is a rectangle, there was always likely to be error associated with the measurement. Despite the potential error due to variation in the crown shapes, for this study, using the computed measure of crown area was most appropriate given the size of the sample and the length of time it would take to measure all four teeth per specimen using a planimeter. Crown shape index was then calculated for each tooth. This index is the expression of "the maximum buccolingual diameter as a percentage of the mesiodistal diameter" (Wood & Abbott, 1983: 202). Calculations of corpus and symphysis size using the corpus measurements obtained are functionally significant for they represent the mandible's capacity to resist shear and stress (Daegling & McGraw, 2007).

Table 4.11: Mandibular and dental shape ratios generated

Index	Equation	Reference
Corpus robusticity index (CRI)	[Corpus width / Corpus height] x 100	Wood (1991)
Corpus size (CS)	[Corpus height x Corpus width x π] / 4	Daegling & McGraw (2007)
Symphyseal robusticity index (SRI)	[Symphyseal width / Symphyseal height] x 100	Using Wood (1991) equation for corpus robusticity index
Symphysis size (SS)	[Corpus height x Corpus width x π] / 4	Daegling & McGraw (2007)
Crown area (computed) (CA)	MD x BL (maximum)	Wood (1991)
Crown shape Index (CSI)	(BL / MD x 100)	Wood & Abbott (1983)

*Using measurements taken from the photographs.

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[7] The robusticity index is a measure of the relative proportion of mandibular width to height, so mandibles that are relatively wide have a higher index value and might be described as 'more robust'. However, the term 'robust' is used in a more general context to indicate a 'big' or 'massive' mandible and such mandibles may appear larger because they have a relatively taller mandibular corpus, and thus would produce a lower robusticity index value.

Table 4.12: Hominin species dental shape ratio averages analysed in this study

Species	P_4 CA	P_4 CSI	M_1 CA	M_1 CSI	M_2 CA	M_2 CSI	M_3 CA	M_3 CSI
A. afarensis	106.46	115.52	161.54	99.06	189.90	94.98	205.34	88.76
A. africanus	118.20	111.61	183.48	94.01	222.60	89.31	224.12	84.97
P. boisei	193.86	110.06	232.91	90.45	295.40	92.80	314.86	86.90
P. robustus	144.98	116.27	206.41	99.42	246.99	96.02	249.55	88.73
H. habilis	109.55	112.02	164.11	88.29	201.84	87.83	205.40	86.93
H. ergaster	92.06	113.02	149.32	89.73	162.36	90.42	164.28	88.08

Table 4.13: Hominin species mandibular shape ratio averages analysed in this study

Species	SRI	SS	P_4CRI	P_4CS	M_1CRI	M_1CS	M_2CRI	M_2CS	M_3CRI	M_3CS
A. afarensis	50.05	597.91	53.08	561.49	59.70	546.46	69.85	558.63	93.65	671.69
A. africanus	59.52	463.88	60.28	613.55	64.78	563.70	76.58	666.92	88.50	772.31
P. boisei	56.48	972.61	67.32	944.31	68.95	935.20	76.09	986.37	84.55	1044.00
P. robustus	53.83	722.30	67.25	721.16	68.21	731.17	79.12	757.52	85.31	856.38
H. habilis	60.06	558.53	56.37	553.72	62.26	540.15	70.30	615.93	82.44	503.99
H. ergaster	60.45	482.70	63.35	469.61	69.98	429.13	65.22	507.90	66.42	539.80

Intra-observer error tests were conducted on each of the measurements taken using callipers. In total, 32 specimens were re-measured with callipers when visiting the Powell-Cotton Museum on a return visit (8 months later). Where a measurement on a specimen exceeded 2mm difference between the first and second recording, a third was taken, and from that, an average of the three recordings were used. The gap between repeat measurements was necessary in order to minimise learning effect (Markic *et al.*, 2015).

To test for the error between measurements the Technical Error of Measurement (TEM) index was used. This index represents the standard deviation between repeated measures and provides an assessment of the accuracy of the measurements taken (Knapp, 1992; Perini *et al.*, 2005; Harris & Smith, 2009). To generate the TEM index, the equations provided in the intra-evaluator TEM calculations by Perini *et al.* (2005) and Harris & Smith (2009) were followed. Each measurement recorded in the intra-observer error tests obtained a relative TEM value of less than 5% (Table 4.14 displays each variable's relative TEM value), which according to the classification parameters set out by Perini *et al.* (2005) was acceptable.

Table 4.14: Technical Error of Measurement values for repeat measurements taken

Area measured	TEM	Measurements					
Dentition		P_4MD	P_4BL	M_1MD	M_1BL1	M_1BL 2	
	Relative TEM %	1.52	1.29	2.12	4.15	2.83	
		M_2MD	M_2BL 1	M_2BL 2	M_3MD	M_3BL 1	M_3BL 2
	Relative TEM %	1.89	2.73	2.98	1.93	3.18	2.72
Corpus and symphysis		SH	SW	P_4CH	P_4CW	M_1CH	
	Relative TEM %	0.87	3.61	0.22	4.12	0.7	
		M_1CW	M_2CH	M_2CW	M_3CH	M_3CW	
	Relative TEM %	3.24	0.97	1.29	1.5	0.91	

MD = Mesiodistal. BL = Buccolingual. BL1 = measured from protoconid to metaconid. BL2 = measured from hypoconid to entoconid. SH = Symphyseal Height. SW = Symphyseal Width. CH = Corpus Height. CW = Corpus Width.

4.3 Data analysis

4.3.1 Data analysis of non-human primates

Data from metric measurements were entered into Microsoft Excel and then imported into SPSS Statistics 25. The first step of the data analysis was to determine if the data were normally distributed and to establish general patterns of variation in the dataset.

Kolmogorov-Smirnov tests for normality were used to analyse the distribution of the sample dataset. Initially this test was run on the whole dataset, and then again on different groups (family, genus, the traditional dietary categories, specific dietary classifications, food quantity analysis, body size, and sex dimorphism). The results revealed the data was a mix of normal and not normal distribution (Table 4.15).

Table 4.15: Summary of selected tests for normality that demonstrate how some variables appear to be normally distributed (non significant on the Kolmogorov-Smirnov test), while many others are not (significant on the Kolmogorov-Smirnov test).

Grouping variable	Sample	P_4-M_3 CA	M_1 CSI	M_2 CSI	M_3 CSI	SS	P_4 CS	M_1 CS	M_2 CS	M_3 CS	SRI	P_4 CRI	M_1 CRI	M_2 CRI	M_3 CRI
None	Whole sample	**0.000**	**0.03**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.003**	**0.000**	**0.000**	**0.000**	**0.004**
Family	Cercopithecoidea	**0.000**	0.051	**0.04**	0.2	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.004**	0.2
	Hominoidea	**0.000**	**0.002**	**0.003**	**0.002**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.106	0.171	**0.003**	**0.002**	0.056
	Ceboidea	**0.015**	0.2	**0.002**	0.079	0.18	0.2	0.2	**0.178**	0.063	**0.2**	0.2	0.2	0.2	0.2
Genus	*Cercocebus*	0.2	0.2	0.2	0.2	**0.000**	**0.000**	**0.000**	**0.001**	**0.005**	0.071	**0.018**	0.2	0.2	0.2
	Lophocebus	0.062	**0.023**	0.2	**0.006**	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	Papio	0.2	0.2	0.2	0.2	**0.001**	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	Mandrillus	0.2	**0.013**	0.2	0.2	**0.018**	0.2	0.2	0.2	0.2	0.2	0.19	0.2	0.18	0.2
	Cercopithecus	**0.013**	0.2	0.2	0.082	**0.045**	0.2	0.2	0.2	0.2	0.2	**0.004**	0.086	0.2	0.2
	Chlorocebus	0.2	**0.009**	0.2	0.2	0.2	0.2	0.2	**0.03**	0.2	0.099	0.2	0.2	0.2	0.2
	Erythrocebus	0.125	0.2	0.2	0.2	0.133	0.171	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	Macaca	0.2	0.2	0.198	0.2	0.2	0.076	0.2	**0.035**	0.191	**0.03**	0.2	0.2	**0.025**	0.2
	Gorilla	0.167	**0.011**	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.073	**0.000**	**0.044**
	Pan	0.2	**0.000**	0.2	0.2	0.059	0.2	**0.002**	**0.002**	0.081	**0.003**	**0.038**	**0.005**	0.2	0.2
	Pongo	**0.05**	**0.019**	0.2	0.2	**0.027**	0.2	0.2	0.125	0.167	0.2	0.2	0.2	0.2	0.2
	Cebus	0.2	0.2	**0.011**	0.2	0.061	0.2	0.156	0.2	0.2	**0.017**	0.2	0.2	0.2	0.2
	Sapajus	0.2	0.093	0.2	0.091	0.118	0.181	**0.032**	0.2	**0.015**	0.2	0.2	0.2	0.2	0.2
Sex dimorphism	Slight	**0.015**	0.2	**0.002**	0.079	**0.018**	0.2	0.2	0.178	0.063	0.2	0.2	0.2	0.2	0.2
	Moderate	**0.000**	**0.000**	0.099	0.2	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.032**	**0.001**	**0.000**	**0.001**	0.168
	Strong	**0.000**	0.2	0.2	**0.025**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.2	0.098	**0.043**	0.2	0.2
	Extreme	**0.000**	**0.000**	0.2	**0.003**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.2	**0.000**	**0.002**	0.2	0.2
Traditional diet categories	Folivore	**0.000**	0.2	0.2	0.2	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.2	0.132	0.111	0.082	0.2
	Frugivore	**0.000**	**0.001**	**0.001**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.2	**0.000**	**0.000**	**0.000**	**0.018**
	Omnivore	**0.000**	0.2	**0.042**	0.2	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.2	0.2	**0.001**	0.098	0.2
	Frugivore-Insectivore	0.2	0.093	0.2	0.091	0.118	0.181	**0.032**	0.2	**0.015**	0.2	0.2	0.2	0.2	0.2

4.3.2 Univariate and exploratory statistics

General descriptive statistics were run to provide an insight into the distribution of the morphological data. These tests were run on the whole sample, as well as by genus and diet. Scatterplots provided a visual representation of what to expect from the data.

Research question 1 was split in two parts and required a series of steps to be taken in order to answer it. The first part was to establish that morphological differences were present in consumers of different diets, and the second part was to establish which diets varied and how.

To identify whether morphological differences were present in consumers of different diets, exploratory analyses were run using significance tests. As the data were both normally and not normally distributed, parametric and non-parametric tests were used. *T*-tests and Mann-Whitney U, and ANOVA and Kruskal Wallis tests were run to test for differences within the sample. For the vast majority of the tests run the parametric and non-parametric results were consistent. As a result, where the tests of difference results are displayed (Tables 5.11-5.22, and Appendix Tables 9.9-9.24), only the parametric results are given, but where they differed from the non-parametric results they were highlighted.

The tests were run to investigate whether different morphologies were present in consumers of different diets and between species of different body sizes. To establish whether different morphologies were present, several steps had to be taken and these were broken down as detailed in Table 4.16.

Table 4.16: Tests of difference used and the steps taken for each test

Tests run	Steps taken
• *T*-tests/ Mann-Whitney U	To establish differences in morphologies of consumers of the same diets but with different body sizes: 1. Select taxon: monkey or ape 2. Select diet category (from traditional, specific classification coding and quantity analyses), e.g., frugivores. 3. Run *t*-test/ Mann-Whitney U using the raw data (crown area, crown shape index, corpus/ symphysis size, corpus/ symphysis robusticity index) as the test variables and body size as the grouping variables.
• *T*-tests/ Mann-Whitney U • ANOVA/ Kruskal-Wallis	To establish differences in morphologies of consumers of different diets but with the same body size: 1. Select taxon: monkey or ape 2. Select body size (small or large) 3. Run *t*-test/ Mann-Whitney U or ANOVA/ Kruskal-Wallis* using the raw metric data (crown area, crown shape index, corpus/ symphysis size, corpus/ symphysis robusticity index) as the test variables and the diet categories as the grouping variables.

Usage of either the *t*-test or ANOVA depended on the number of dietary categories present, if only 2 dietary categories/ quantity categories were available in a given body size range a *t*-test was used, but if 3 or more dietary categories/ quantity categories were available an ANOVA was used.

Body size differences and their effects upon masticatory morphology were not a primary focus of this thesis, mainly because the hominins this research was inspired by are not reconstructed to present very different body sizes (Grabowski *et al*., 2015). Nevertheless, body size is potentially an important factor and must not be overlooked when exploring morphological variables in non-human primates.

These tests of difference were run on the raw data, this is despite the fact other researchers have been known to log transform their datasets (e.g., Plavcan & Daegling, 2006; Taylor, 2006c), and run subsequent tests of difference, including non-parametric tests, on the log transformed data. This approach was not followed here because it is considered by some researchers that by transforming data it makes interpretation of results more complicated, due to the fact the relationship between variables that have been transformed and those that have not is no longer the same (Osborne, 2002; Wilson, 2007; Zuur *et al*., 2010). An influence over the relationship of the variables as described above would be detrimental to this project, which aimed to establish patterns of correlation between variables. Furthermore, some variables (size variables) of this dataset were log-transformed for analyses that followed later and the explorative output from the Kolmogorov-Smirnov test for normality of distribution still resulted in data that were not normally distributed. It was decided therefore that it was not necessary to run the tests of difference on the log-transformed data, as the raw data would provide the confidence that any differences observed when using both parametric and non-parametric tests were or were not significant. Analysis on the raw data thus enabled identification of basic patterns of variability in the data with respect to the different kinds of grouping variables used.

4.3.3 Multivariate analyses

Multivariate analyses were run to address the second step of research question 1 (to explore which diets varied and how), along with research questions 2 (whether consumers of different quantities of foods vary morphologically) and 3 (how much diet contributes to morphological variation). The analyses used to answer these questions were Principal Components Analysis (PCA) and Multiple Regression. The steps taken to run the PCA and Multiple Regression analyses are detailed in Table 4.17.

Table 4.17: Multivariate analyses run to answer research questions 1-3 and the steps taken for each analysis

Research question	Tests run	Steps taken
1 (part 2): *Are there morphological differences present between consumers of different diets? How do they manifest?*	PCA and bivariate graphs	1. Log-transform size variables 2. Enter dental and mandibular variables with orthogonal rotation (varimax) 3. Bivariate scatter plots were generated using each of the PCA components on the x and y axes by the dietary categories
2: *Are there morphological differences between consumers of low quantities of particular foods to consumers of higher quantities of the same foods?*	Bivariate scatter plots using PCA components	1. Bivariate scatter plots were generated using each of the PCA components on the x and y axes by the quantity categories
3: *How much does diet contribute towards morphological variation?*	Multiple regression analysis using PCA components	1. PCA components used as dependent variables 2. Body size, sex and dietary categories used as independent variables 3. Method of data entry: Enter

4.3.3.1 Principal Component Analysis

A PCA is generally run with two intentions, the first to reduce the data into smaller, more manageable grouping of variables (as described below), and the second, by using the components instead of individual variables, patterns can be identified in the data that would not be seen otherwise (Quinn & Keogh, 2002; Field, 2018). Prior to the PCA being run it was necessary to log-transform all of the size variables. Had the raw data been used there would have been too much residual variation from the heteroscedasticity present in the data. The heteroscedasticity present corresponded to the lack of normality identified previously in the Kolmogorov-Smirnov tests of normality, but unlike in the tests of differences where both parametric and non-parametric tests could be used, it was necessary to log-transform the raw data. Using the natural logarithm all measurements of size were transformed, this included the following: corpus size, symphysis size, tooth crown area and body size. The indices were not log-transformed as their residuals appeared to be reasonably distributed around the regression line and as a result, did not display heteroscedasticity (McKillup, 2012).

A PCA determines which variables account for most of the variance present. The identification of those variables that account for the majority of variance makes the PCA a statistical analysis that is particularly important to studies attempting to identify morphological variation, and therefore commonly used in palaeoanthropology (e.g., Norconk *et al.*, 2009). The PCA uses the coefficients and eigenvectors from a variable to determine its contribution to a component, whereby the further the coefficient is from zero (i.e. the closer it is to one) the greater its contribution is to that component (Quinn & Keogh, 2002; Field, 2018). A grouping of variables with similar coefficients will then form a component that can then be analysed (Quinn & Keogh, 2002; Field, 2018). Identification of which variables contribute most towards a particular component can be obtained through the rotated components matrix in the PCA output. Bivariate scatter plots were then generated using each of the components on the x and y axes by the various dietary categories used in this thesis. The bivariate graphs were useful in determining potential patterns in the data, particularly with regard to whether consumers of a particular diet varied from consumers of another diet (part 2 of research question 1), or if species that consumed large quantities of, for example seeds, plotted differently to species that consumed very small quantities of seeds (research question 2).

4.3.3.2 Multiple Regression Analysis

To answer research question 3, a multiple regression analysis was run using the PCA components as the dependent (y) variable. The multiple regression enabled analysis of the dependent variable (each principal component) by several independent variables at once, to try to establish which was the best predictor of the morphology present and how much each independent variable contributed to the variation (Madrigal, 1998; Quinn & Keogh, 2002; Field, 2018). The use of the principal components in a regression analysis is preferential to the use of each individual variable (e.g., P_4, M_1, M_2 and M_3 crown shape indices) because the components are orthogonal, which meant that the potential problem of multicollinearity was overcome (Quinn & Keogh, 2002; Field, 2018). For each component the independent variables of log body size and sex were entered along with one of traditional diet, specific classification coding categories (DO and FA) and the food quantity analyses (DO and FA). As the traditional diet and the specific classification coding systems both used categorical data it was necessary to convert them into dummy variables in order for them to be included in the multiple regression analysis (Field, 2018). The dummy variables meant that each category within for example traditional diet became their own variable and were assigned a value of 1 or 0. So for example, when a species was described as being a folivore they would have a 1 in their folivore column, but a 0 in their frugivore, omnivore and frugivore-insectivore columns. By necessity, when a 1 was present in one variable (dietary category) a 0 would be present for the rest (Field, 2018). The diet grouping with the highest n was excluded from the regression as a baseline group for all the other groups to be compared against as advised by Field (2018). For the traditional diet group frugivores were excluded, while in the specific classification coding by direct observation (DO) frugivores were excluded, and in the specific classification coding by faecal analysis (FA) frugivore-folivores were excluded.

When the multiple regression analysis was run on the food quantity analysis percentages (FQA 1) problems were encountered with regard to missing dietary information. Not many non-human primate species have complete information about their diets, at least not complete in terms of the categories used in this thesis, so where the amount of fruits consumed would always be available, leaf, seed, root and animal consumption could vary between presence and absence in the different species. For example, *Cercocebus torquatus* are recorded as consuming 62.8% fruits, 3.9% leaves and 28.2% seeds, but no roots or animals (species average) (study-specific field reports are available at: https://opencontext.org/projects/a9dbf427-cff6-41b7-8462-a9ab8d9908f4). This missing data meant that when the multiple regression analysis was run with the food quantity analysis category (FQA 1) any species with missing data, such as *C. torquatus*, would be excluded from the analysis, which in turn reduced the number of species analysed to 235 (DO) and 307 (FA) out of 772 (DO) and 797 (FA), respectively. The missing data could potentially miss any patterns associated with particular diet types and morphologies. Two approaches were used to overcome this issue: 1) all missing data were entered as 0 in the database (labelled as FQA 2) so that information available from other variables were included in the observations, and 2) when the multiple regressions were run the foods were entered in one by one with fruit as the constant, e.g., Fruits & Leaves, Fruit & Seeds, Fruits & Roots, and Fruits & Animals, etc. While neither approach was ideal – the presence of zeros meant that the average consumption for each food type was brought down considerably, and entering each diet one at a time potentially ignored the importance of a combination of foods – these approaches enabled a more thorough exploration of the data than simply using FQA 1.

The method selected to enter the data into the regression was Enter, this was because it enters all of the predictor variables in at once and their potential value to the *y* variable assessed. Enter is regarded by some researchers as the most appropriate method of variable entry for theory testing (Studenmund & Cassidy, 1987; Field, 2018). Other methods that could have been used are forms of stepwise, which include forward, backward and stepwise (combines forward and backward), but these methods are not recommended by statisticians for exploratory model building (Field, 2018). When the variables were entered into the regression body size and sex were input first and then in the next column the dietary variables were entered. By entering the data this way it meant that the variance explained by size and sex were identified first followed by the variance explained by diet. This was considered to be more informative than simply entering all of the data in at the same time, which if done so would give the overall percentage of variance explained by everything together, not their individual contributions. The Enter method does not make any assumptions about the order of the variables entered, so separating size and sex from diet as described should not impact on the effectiveness of the model (Field, 2018).

4.3.4 Data analysis of hominins compared to non-human primates

The focus on the second part of the data analysis was on research questions 4-5, exploring how the hominins compared to the non-human primates. To do this, the hominins dataset was combined with the non-human primate dataset. Within the hominins data were the genera, species, estimated species body size, estimated degree of sexual dimorphism, dietary information (which required new labels to be created which were called ‘unknown’), and their metric information. Species average body size and all of the size variables were log-transformed again. As there are few hominins that have complete information from the mandible and dentition – as collected for the non-human primates – a PCA using the whole dataset would contain too much missing data. It was decided therefore to reduce the whole dataset to an average for each species. By reducing the dataset in such a way meant that each species had an average measure for each variable. A PCA was therefore run on non-human primate and hominin averages. Bivariate scatter plots were once again created using each of the PCA components on the *x* and *y* axes to answer research questions 4-5 (Table 4.18). These scatter plots compared how the hominins scored in relation to extant non-human primates of known taxonomy and diet. From these bivariate graphs it was possible to make basic inferences about the hominins and their potential diet adaptations (research question 6, which is addressed in the Discussion chapter).

Table 4.18: Multivariate analyses run to answer research questions 4-5 and the steps taken for each analysis

Research question	Tests run	Steps taken
4: *Is the hominin morphology comparable to that present in non-human primates?*	PCA and bivariate graphs	1. Log transform size variables 2. Use averages of each species 3. Enter dental and mandibular variables with orthogonal rotation (varimax) 4. Bivariate scatter plots were generated using each of the PCA components on the *x* and *y* axes by genera.
5: *Is it possible to associate the morphological features of the hominins with dietary categories analogous to non-human primates?*	Bivariate scatter plots using PCA components	1. Bivariate scatter plots were generated using each of the PCA components on the *x* and *y* axes by the dietary and quantity categories.

Chapter 5 : Statistical analysis of non-human primates and hominins

This chapter presents the results produced from the exploratory and multivariate analyses undertaken on the non-human primates (section 1) and hominins (section 2). The results presented answer the research questions introduced in Section 1.1-1.2.

5.1. Section 1: Statistical analyses on non-human primate database (research questions 1-3)

This section is divided into three parts to address the research questions. Research question one (*Are there morphological differences present between consumers of different diets?*) is addressed in part one to confirm if differences are present, and part two to establish where differences occur. Research question two (*Are there morphological differences between consumers of low quantities of particular foods to consumers of higher quantities of the same foods?*) is also addressed in part two. Research question three (*How much does diet contribute towards morphological variation?*) is explored in part three.

Basic descriptive statistics were run to establish how the data were distributed taxonomically and by diet. The means, standard deviations and numbers present for each measurement taken by genus are detailed in tables 5.1-5.4. How the different genera compare to each other are displayed in scatterplots (Figures 5.1-5.7).

Table 5.1: Genus means, standard deviations and numbers present for P_4 – M_1 dental measurements

	P_4 Mesiodistal length			P_4 Buccolingual length			M_1 Mesiodistal length			M_1 Buccolingual length		
Genus	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Cebus	3.24	0.2324	34	4.42	0.5349	34	4.16	0.2982	36	4.35	0.279	36
Sapajus	3.52	0.3802	37	4.79	0.443	37	4.52	0.291	38	4.67	0.3343	38
Cercocebus	5.87	0.4131	69	5.71	0.5719	68	7.15	0.4435	69	6.37	0.4299	68
Lophocebus	4.69	0.4026	96	4.61	0.4091	96	6.1	0.321	96	5.34	0.3347	96
Chlorocebus	4.32	0.5007	89	3.43	0.2815	89	5.33	0.4142	90	4.28	0.3024	90
Erythrocebus	5.26	0.4871	26	4.15	0.5738	26	6.27	0.473	27	4.98	0.3679	27
Cercopithecus	3.88	0.3751	169	3.07	0.3298	169	4.79	0.3596	172	3.79	0.2995	172
Macaca	5.3	0.6589	34	5.07	0.5457	34	6.88	0.6359	33	5.62	0.4721	33
Mandrillus	8.82	0.8797	57	7.08	0.8985	57	9.47	0.7538	57	7.62	0.602	57
Papio	7.97	1.1454	85	7.13	0.9224	85	10.06	1.3131	85	8.5	1.0557	85
Gorilla	11.13	0.8321	120	13.26	1.0379	120	15.29	0.9219	120	13.72	1.0613	120
Pan	7.17	0.8393	185	8.35	0.8946	185	9.99	0.7868	184	9.38	0.8166	184
Pongo	10.25	0.8583	87	11.22	1.1654	87	12.49	0.8682	87	11.73	0.9002	87

Table 5.2: Genus means, standard deviations and numbers present for M_2 – M_3 dental measurements

	M_2 Mesiodistal length			M_2 Buccolingual length			M_3 Mesiodistal length			M_3 Buccolingual length		
Genus	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Cebus	3.9	0.2865	35	4.1	0.2438	35	3.38	0.4489	30	3.54	0.2737	30
Sapajus	4.22	0.3442	37	4.48	0.2956	37	3.49	0.2963	27	3.755	0.3013	27
Cercocebus	8.07	0.5243	68	7.63	0.6694	66	9.02	0.7954	69	7.4	0.7606	68
Lophocebus	6.8	0.3592	96	6.37	0.327	96	7.59	0.6256	94	6.11	0.3915	95
Chlorocebus	5.94	0.4308	90	5.18	0.3663	90	5.94	0.5168	86	5.09	0.4249	86
Erythrocebus	7.29	0.4102	27	5.93	0.4034	27	7.15	0.5713	22	5.74	0.375	22
Cercopithecus	5.22	0.4204	172	4.53	0.3477	172	5.08	0.3823	170	4.27	0.3205	170
Macaca	8.33	0.841	34	6.95	0.663	34	10.62	1.2937	33	7.4	0.9858	33
Mandrillus	11.53	0.9292	57	9.88	0.9881	57	13.85	1.4285	55	10.51	1.059	55
Papio	11.98	1.4503	85	10.54	1.3546	85	15.03	1.9194	85	11.29	1.4747	85
Gorilla	17.2	1.3179	120	15.45	1.0438	120	17.14	1.497	118	14.86	1.1362	118
Pan	10.44	1.124	186	9.97	0.9196	185	9.84	0.9289	179	9.45	0.9468	180
Pongo	13.284	1.2232	87	12.49	1.0688	87	13.25	1.3403	86	11.91	1.2199	86

Figures 5.1-5.4 highlight that while there is overlap between genera, there are morphological differences present in the dataset relating to phylogeny. These differences were best highlighted on the dentition at the P_4 and M_3, while similar patterns were present on the M_1-M_2 but with less distinction between genera. For this reason, the scatterplots of the dentition at the P_4 and M_3 are the graphs presented here (Figures 5.1-5.2).

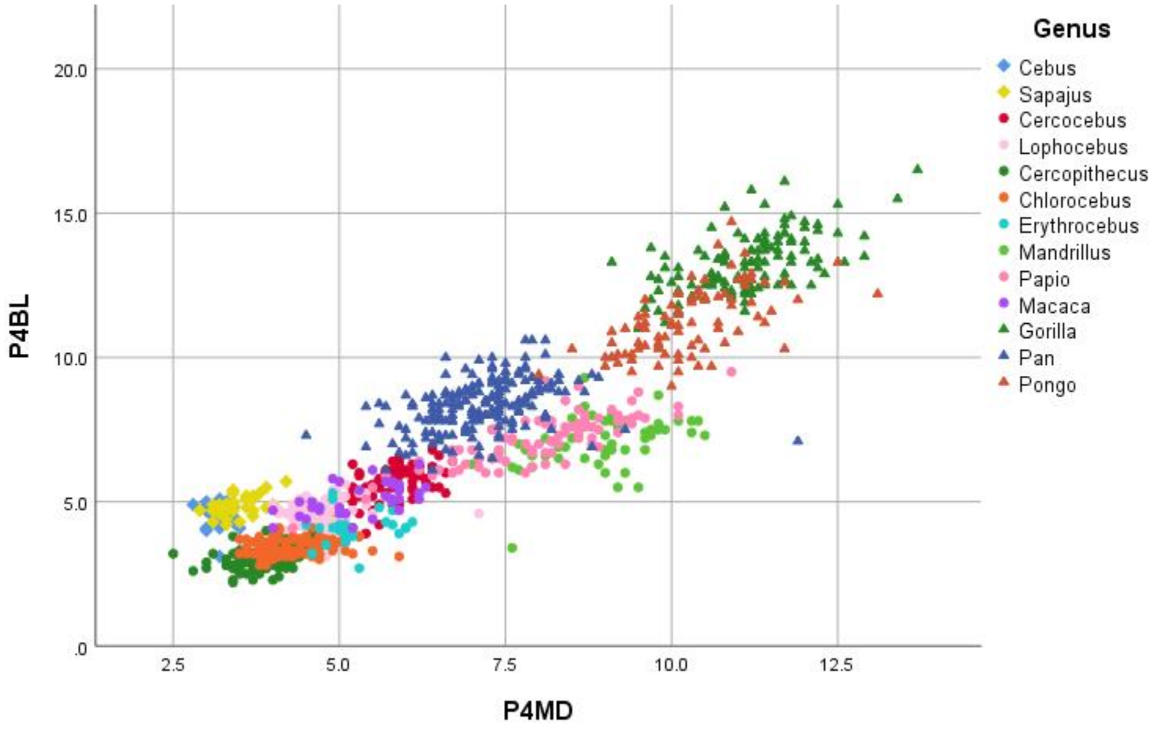

Figure 5.1: Distribution of genera by P_4 buccolingual and mesiodistal dimensions

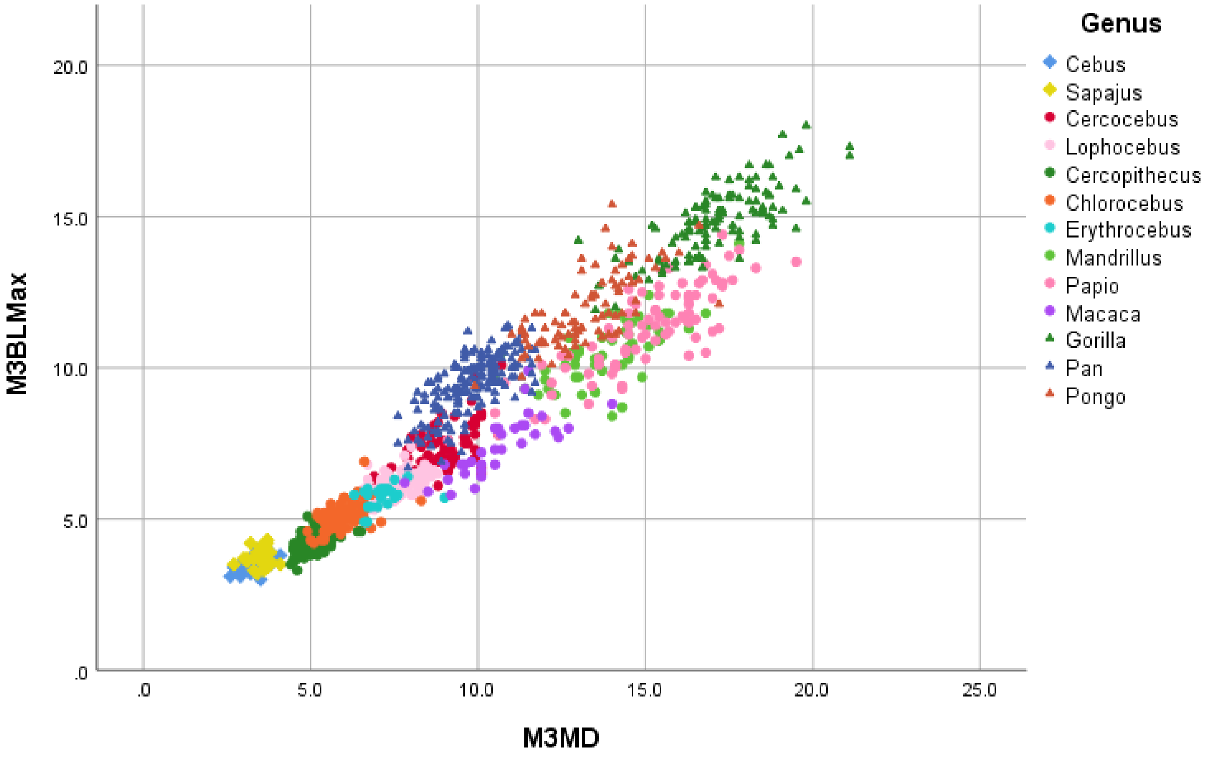

Figure 5.2: Distribution of genera by M_3 buccolingual and mesiodistal dimensions

Table 5.3: Genus means, standard deviations and numbers present for symphyseal and P_4 corpus dimensions

	Symphyseal Height			Symphyseal Width			P_4 Corpus Height			P_4 Corpus Width		
Genus	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Cebus	18.7	1.9527	36	7.53	0.7855	36	11.99	1.12218	36	5.88	0.6252	36
Sapajus	21.14	2.2221	38	9.08	1.0063	38	14.16	1.4164	38	7.29	0.7196	38
Cercocebus	29.32	5.8169	70	13.08	2.8055	70	22.18	3.273	70	8.95	1.249	70
Lophocebus	28	3.0007	95	11.84	1.2127	95	21.61	1.9162	96	8.08	0.8118	96
Chlorocebus	21.08	3.1242	89	8.91	1.3607	89	14.71	1.9362	91	5.63	0.675	91
Erythrocebus	27.1	6.1092	27	11.06	2.0588	27	18.14	3.3194	27	6.69	0.8655	27
Cercopithecus	16.95	2.3497	172	6.72	0.8679	172	13.54	1.4373	172	5.33	0.6361	172
Macaca	28.4	4.3354	34	12.28	1.8003	34	20.59	2.9548	34	8.71	1.2543	34
Mandrillus	52.45	11.1082	58	25.89	7.8947	58	32.89	5.8926	58	12.88	2.1039	58
Papio	44.41	9.4691	84	22.06	5.6917	84	31.52	5.4101	85	11.85	1.8699	85
Gorilla	63.66	7.7375	120	26.52	3.3396	120	38.81	5.0579	120	20.19	2.1663	120
Pan	4.76	5.6711	194	15.3	2.073	194	27.49	3.7253	192	14.18	1.9872	192
Pongo	56.66	7.8014	87	19.01	3.2668	87	36.61	5.1209	87	16.76	2.2566	87

Phylogenetic differences are present in the corpus and symphyseal dimensions, however more overlap exists here than in the dentition between the genera, particularly the monkeys. Differences between the genera are best displayed at the corpus at the P_4 and M_2 and the symphysis (Figures 5.3-5.7). The distributions of the data at the M_1 and M_3 are less distinct and are therefore not presented here.

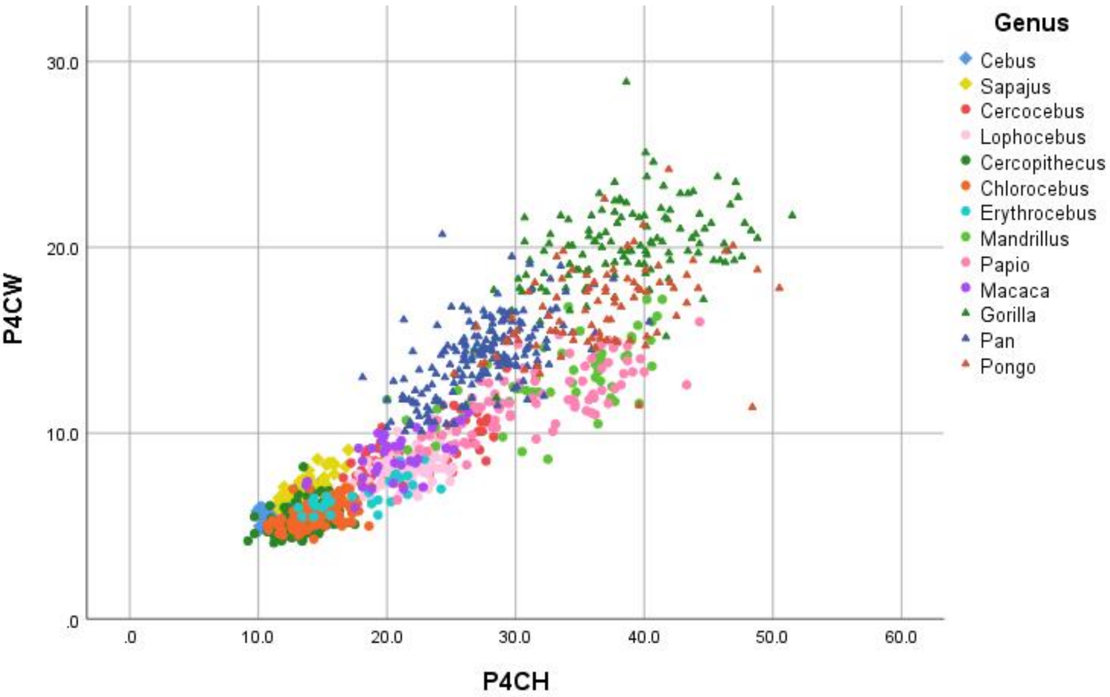

Figure 5.3: Distribution of genera by P$_4$ corpus height and width dimensions

Table 5.4: Genus means, standard deviations and numbers present for M_1-M_3 corpus dimensions

	M_1 Corpus Height			M_1 Corpus Width			M_2 Corpus Height			M_2 Corpus Width			M_3 Corpus Height			M_3 Corpus Width		
Genus	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Cebus	12.37	1.3268	36	5.78	0.6448	36	12.49	1.3423	36	5.93	0.6798	36	13.14	1.3183	36	6.25	0.8768	36
Sapajus	14.684	1.6426	38	7.27	0.772	38	14.93	1.6769	38	7.58	0.7836	38	15.93	1.5767	35	8.02	0.9623	35
Cercocebus	22.59	3.5848	70	9.17	1.0692	70	21.66	3.4527	70	10.32	1.3057	70	20.81	3.4525	70	11.55	1.4645	70
Lophocebus	21.92	1.9947	96	8.15	0.7913	96	21.51	2.0565	96	8.6	0.8206	96	21.45	2.021	95	9.8	0.9919	95
Chlorocebus	14.03	1.8668	91	5.84	0.5962	91	12.86	1.6371	91	6.69	0.6891	91	13.24	1.3891	89	7.46	0.7808	89
Erythrocebus	17.67	3.1723	27	6.52	0.7261	27	16.34	2.7488	27	7.26	0.6669	27	16.44	2.6907	25	7.94	0.6884	25
Cercopithecus	13.57	1.3891	172	5.29	0.544	172	13.21	1.3347	172	5.7	0.565	172	13.36	1.4163	171	6.47	0.6511	171
Macaca	21.56	2.9629	34	8.89	1.2474	34	20.91	2.9218	34	10.03	1.4651	34	20.35	2.6996	34	11.59	1.7613	34
Mandrillus	33.43	5.6783	58	12.16	1.7453	58	30.58	5.2807	58	13.2	1.6762	58	27.95	4.278	57	15.03	1.7413	57
Papio	31.84	5.2419	85	11.8	1.6588	85	28.64	4.5295	85	13.05	1.8733	85	26.47	3.9901	85	14.96	2.1888	85
Gorilla	38.54	4.7764	120	19.76	1.8541	120	36.69	4.621	119	22.51	2.0376	120	38.76	4.7328	119	24.86	2.1479	119
Pan	26.3	3.485	192	13.72	1.865	193	25.36	3.0441	194	14.76	1.9128	194	26.11	2.8366	189	16.34	1.9442	189
Pongo	36.41	4.9761	87	17.04	2.0092	87	35.52	4.8873	87	19.16	2.5688	87	36.02	4.7292	87	22.11	2.9856	87

More distinctions appeared to be present in the ape genera at the M_2 corpus than at other points along the corpus (Figure 5.4). It was not apparent if the divergent distribution of the *Gorilla*, *Pan* and *Pongo* genera reflected species differences, so for this reason, a further scatterplot focussing only on the apes at the species level was generated (Figure 5.5). With the exception of *Pan paniscus* and *Pan troglodytes*, there appeared to be overlap present between both *Gorilla* species and *Pongo* species.

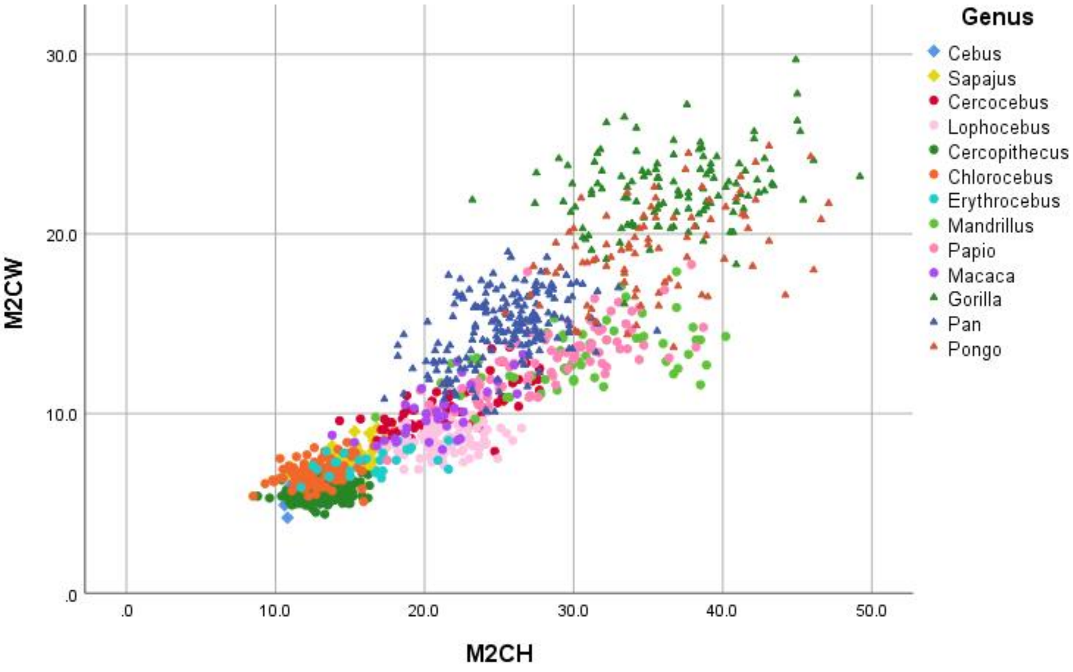

Figure 5.4: Distribution of genera by M_2 corpus height and width dimensions

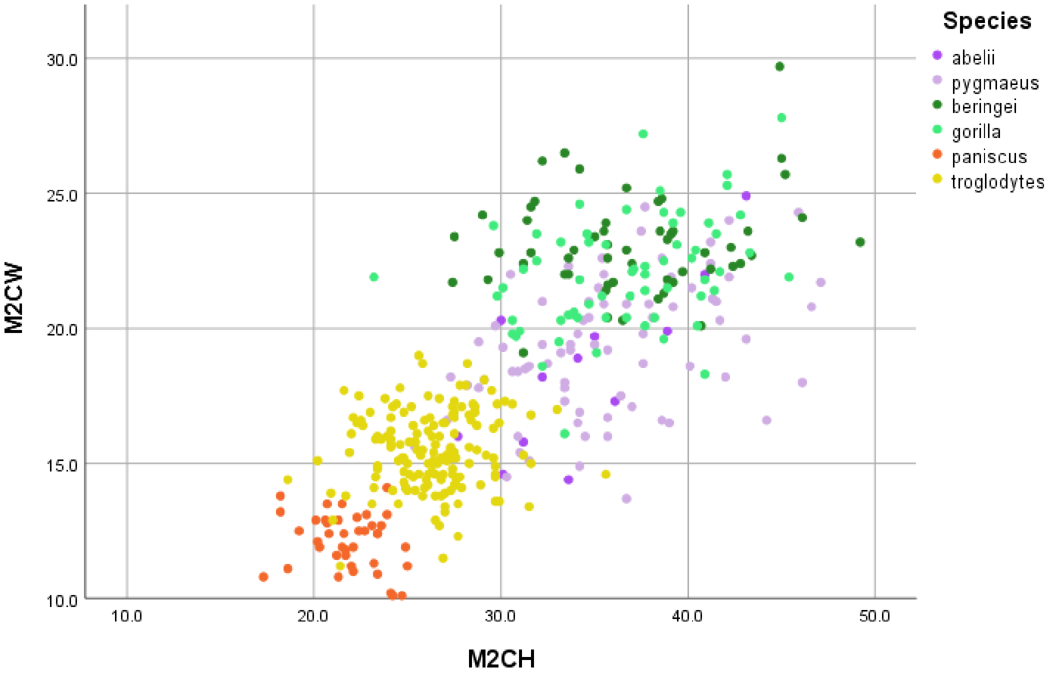

Figure 5.5: Distribution of ape species by M_2 corpus height and width dimensions

As with M_2 corpus dimensions, more distinctions were present between the ape genera at the symphysis (Figure 5.6). Once again, it was not apparent if the divergent distribution of the ape genera reflected species differences, and so, a further scatterplot focussing only on the apes at the species level was generated (Figure 5.7). *Pan paniscus* and *Pan troglodytes* were again distinguished from each other, and potentially differences maybe present between the two *Pongo* species but it is not very clear based on Figure 5.7. There appeared to be overlap present between both *Gorilla* species again. The symphyseal breadth dimensions appear to be reversals of the corpus width dimensions for all genera.

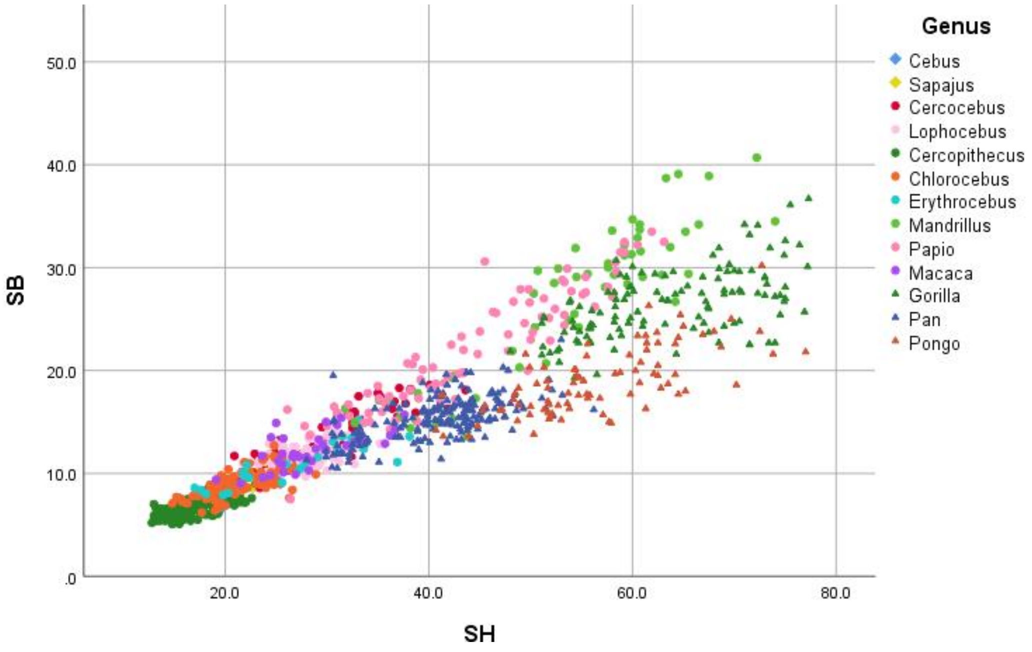

Figure 5.6: Distribution of genera by symphyseal height and width dimensions

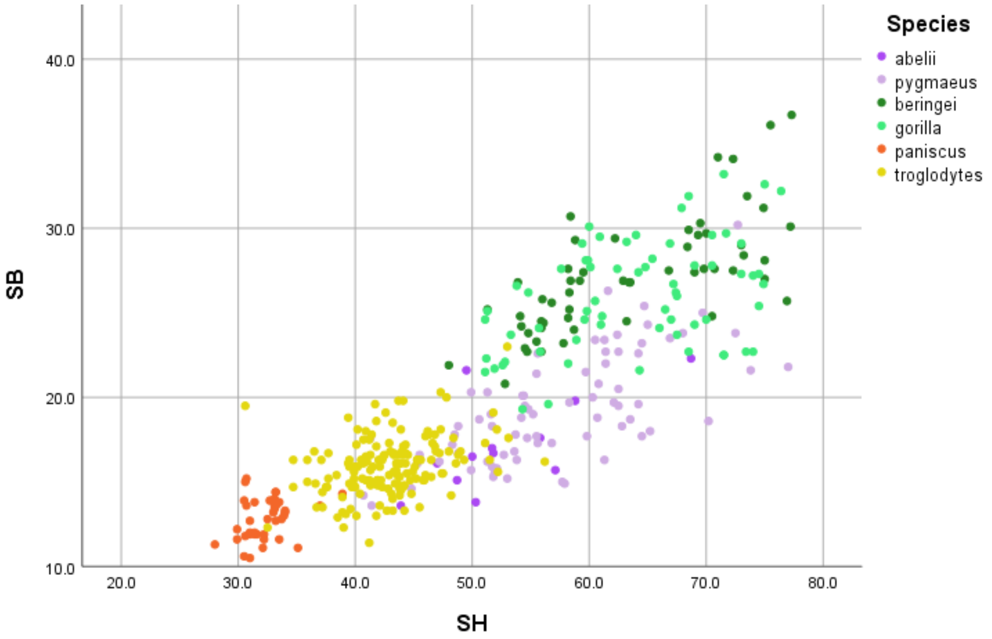

Figure 5.7: Distribution of ape species by symphyseal height and width dimensions

The means, standard deviations and numbers present for each measurement taken distinguished by the traditional diet categories are detailed in tables 5.5-5.8. How the different diet categories compare to each other are displayed in scatterplots (Figures 5.8-5.12). Different diet categories were analysed in this study, but for the purposes of analysing the descriptive statistics the traditional diet categories were the only ones selected to be presented here.

Table 5.5: Diet means, standard deviations and numbers present for P_4 - M_1 dental measurements

	P_4 Mesiodistal			P_4 Buccolingual			M_1 Mesiodistal			M_1 Buccolingual		
Traditional Diet Categories	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Folivores	7.12	3.1025	36	6.88	4.5341	36	8.78	4.2166	37	7.44	4.134	37
Frugivores	6.67	2.7199	783	7.2	3.5999	782	8.74	3.7234	786	7.87	3.5738	785
Omnivores	6.78	2.1575	231	5.69	1.9358	231	8.08	2.3891	232	6.65	2.0495	232
Frugivore-insectivores	3.52	0.3802	37	4.79	0.443	37	4.52	0.291	38	4.67	0.3343	38

Table 5.6: Diet means, standard deviations and numbers present for M_2 - M_3 dental measurements

	M_2 Mesiodistal			M_2 Buccolingual			M_3 Mesiodistal			M_3 Buccolingual		
Traditional Diet Categories	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Folivores	10.16	4.8479	37	8.67	4.608	37	10.43	5.0288	32	8.69	4.4975	32
Frugivores	9.51	4.1531	787	8.78	3.8033	784	9.61	4.1099	768	8.42	3.6851	769
Omnivores	9.53	3.0413	232	8.3	2.684	232	11.29	4.449	226	8.74	3.0749	226
Frugivore-insectivores	4.22	0.3442	37	4.48	0.2956	37	3.49	0.2963	27	3.76	0.3013	27

Figures 5.8-5.12 highlight that while there is overlap between diet categories, there are morphological differences present in the dataset relating to diet. These differences were best highlighted on the dentition at the P_4 and M_3, while similar patterns were present on the M_1-M_2 but with less distinction between diets. For this reason, the scatterplots of the dentition at the P_4 and M_3 are the graphs presented here (Figures 5.8-5.9).

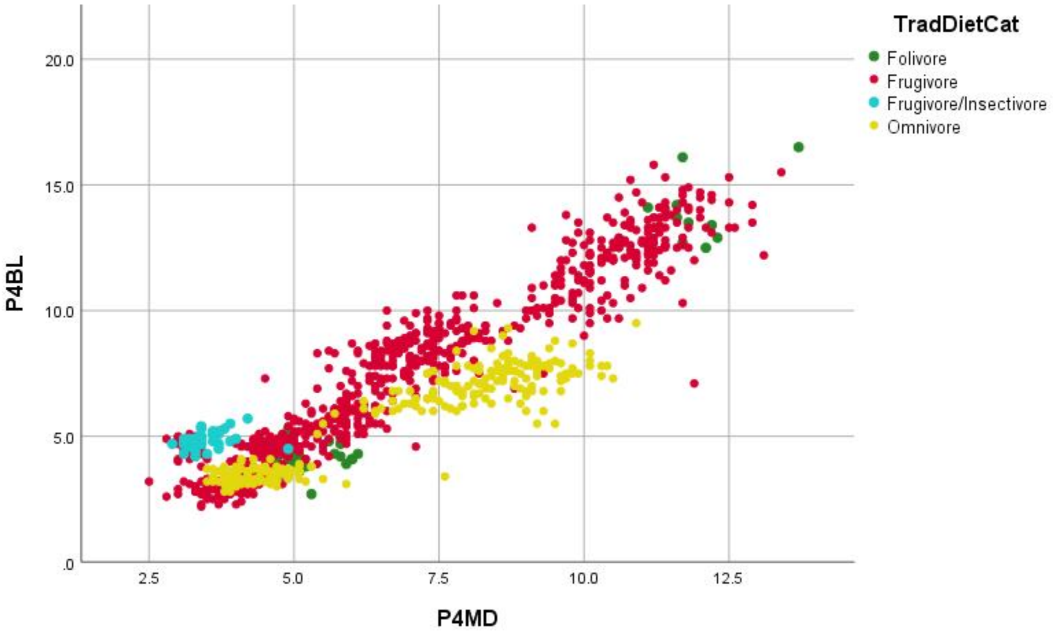

Figure 5.8: Distribution of diet categories by P_4 buccolingual and mesiodistal dimensions

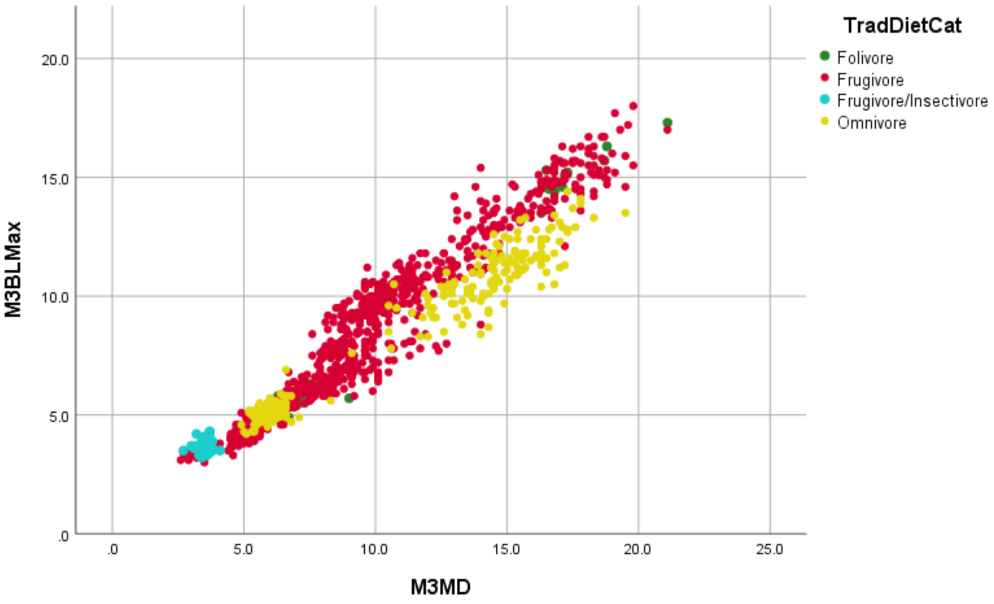

Figure 5.9: Distribution of diet categories by M_3 buccolingual and mesiodistal dimensions

Table 5.7: Diet means, standard deviations and numbers present for symphyseal and P_4 corpus dimensions

	Symphyseal Height			Symphyseal Breadth			P_4 Corpus Height			P_4 Corpus Width		
Traditional Diet Categories	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Folivores	37.27	18.1549	37	15.69	7.9713	37	24.28	10.9141	37	10.71	6.7686	37
Frugivores	36.43	17.0616	797	14.28	6.5696	797	24.83	9.6219	796	11.55	5.4158	796
Omnivores	37.44	15.6434	231	17.95	9.0287	231	25.32	9.6304	234	9.69	3.6299	234
Frugivore-insectivores	21.14	2.2221	38	9.08	1.0063	38	14.16	1.4164	38	7.29	0.7196	38

Table 5.8: Diet means, standard deviations and numbers present for M_1-M_2 corpus dimensions

	M_1 Corpus Height			M_1 Corpus Width			M_2 Corpus Height			M_2 Corpus Width		
Traditional Diet Categories	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*
Folivores	23.78	10.7934	37	10.62	6.8787	37	22.48	10.6895	37	12.03	8.0324	37
Frugivores	24.62	9.3749	796	11.43	5.2439	797	23.8	8.8833	797	12.59	6.0136	798
Omnivores	25.31	10.0398	234	9.57	3.2846	234	22.99	9.0173	234	10.61	3.4619	234
Frugivore-insectivores	14.68	1.6426	38	7.27	0.772	38	14.93	1.6769	38	7.58	0.7836	38

Table 5.9: Diet means, standard deviations and numbers present for M_3 corpus dimensions

	M_3 Corpus Height			M_3 Corpus Width		
Traditional Diet Categories	Mean	S.D.	*N*	Mean	S.D.	*N*
Folivores	23.82	12.401	35	13.19	8.5034	35
Frugivores	24.26	9.3331	790	14.11	6.7317	790
Omnivores	21.74	7.5352	231	12.09	4.0255	231
Frugivore-insectivores	15.93	1.5767	35	8.02	0.9623	35

Dietary differences are present in the corpus and symphyseal dimensions, and are best displayed at the corpus at the P_4 – M_2 and the symphysis (Figures 5.10-5.11). In contrast, the distributions of the data at the M_3 display considerably more overlap (Figure 5.12).

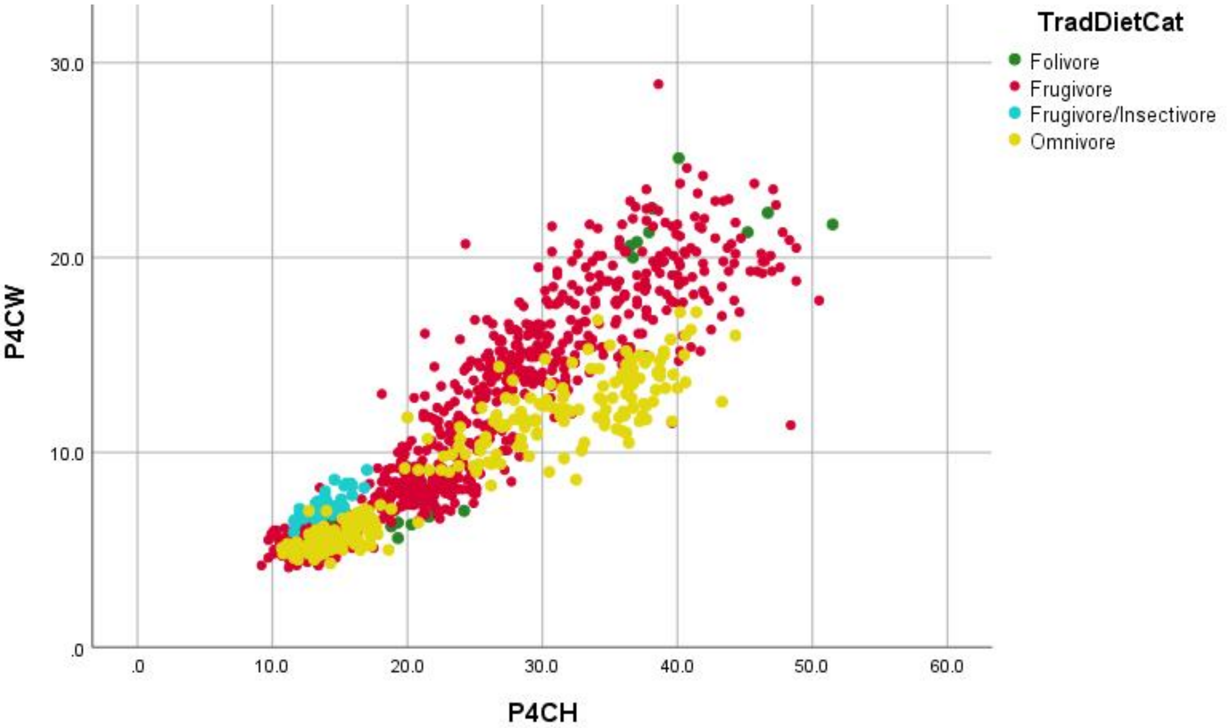

Figure 5.10: Distribution of diet categories by P_4 corpus height and width dimensions. The distribution of the data in this figure is also reflective of the distributions at the corpus of M_1 and M_2.

As with Figures 5.4 and 5.6 the distribution of the corpus width data appears to be reversed in symphyseal breadth (Figure 5.10 compared to 5.11).

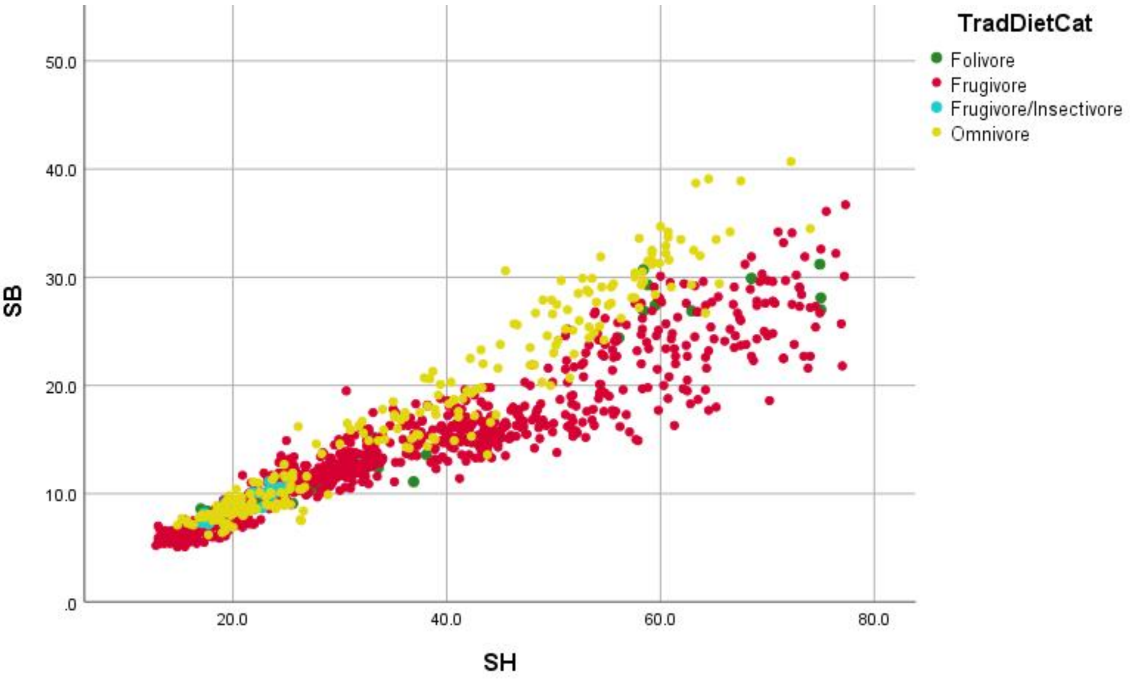

Figure 5.11: Distribution of diet categories by symphyseal dimensions

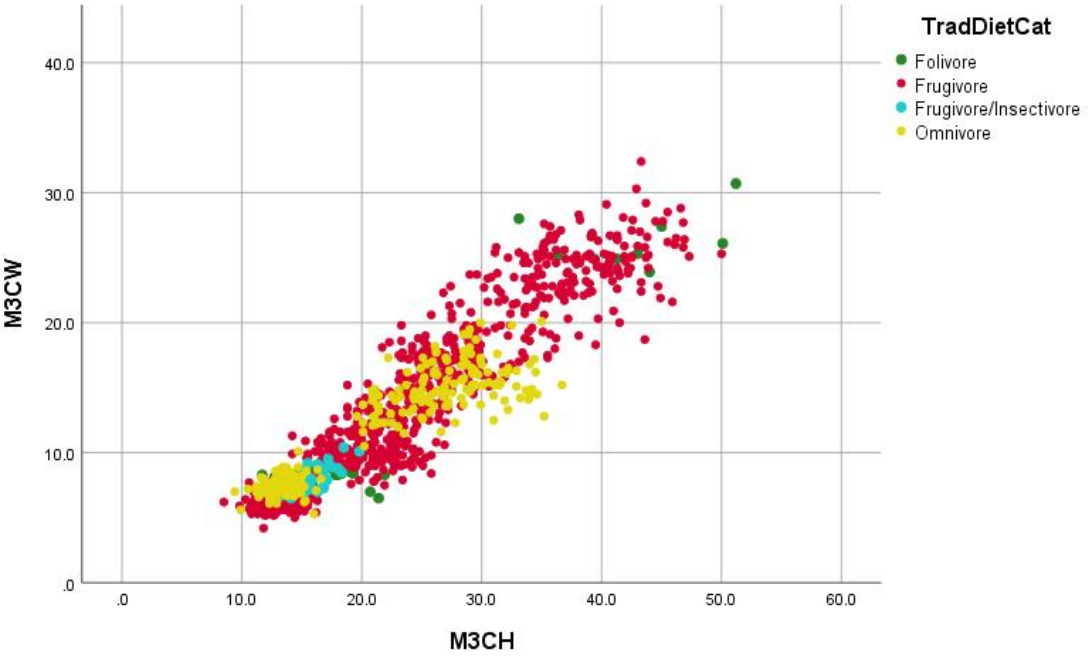

Figure 5.12: Distribution of diet categories by M3 corpus height and width dimensions

5.1.1 Morphological differences between species of different body sizes and consumers of different diets (first part of research question 1)

The results analysing morphological differences between the different body sizes and consumers of different diets are presented in this section. Significant values (p = <0.05) were obtained between the large and small monkeys consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for all of the crown area and corpus/ symphysis size variables. Almost all of the tests run failed the Levene's tests for the Equality of Variances. These results indicate that there are significant differences between the large and small body sizes within each dietary grouping. M_1 crown area and M_1 corpus size are documented in Table 5.10, and are representative of the rest of the size-related variables.

Table 5.10: *T*-test results on monkeys and diet categories, grouped by body size using M_1 Crown Area (CA) and M_1 Corpus Size (CS)

Diet category	M_1 CA				M_1 CS			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	31.154	**0.000**	-19.214	**0.000**	12.318	**0.000**	-9.557	**0.000**
Traditional Diet: Omnivore	108.137	**0.000**	-36.01	**0.000**	136.905	**0.000**	-32.569	**0.000**
Fruit DO: moderate	79.832	**0.000**	-31.67	**0.000**	136.418	**0.000**	-29.103	**0.000**
Leaves DO: low	1.296	0.255	-36.902	**0.000**	61.821	**0.000**	-20.325	**0.000**
Leaves DO: moderate	42.857	**0.000**	-13.167	**0.000**	22.17	**0.000**	-11.502	**0.000**
Seeds DO: low	247.408	**0.000**	-27.485	**0.000**	137.357	**0.000**	-23.46	**0.000**
Seeds DO: moderate	0.07	0.793	-25.837	**0.000**	20.614	**0.000**	-14.649	**0.000**
Seeds DO: high	0.117	0.733	-20.001	**0.000**	32.51	**0.000**	-12.972	**0.000**
Roots DO: low	80.922	**0.000**	-21.353	**0.000**	70.365	**0.000**	-17.51	**0.000**
Animals DO: low	157.866	**0.000**	-26.126	**0.000**	129.201	**0.000**	-24.572	**0.000**
Specific Classification FA: Frugivore/ Folivore	28.447	**0.000**	-21.269	**0.000**	11.779	**0.001**	-17.043	**0.000**
Specific Classification FA: Omnivore	54.918	**0.000**	-24.001	**0.000**	89.121	**0.000**	-18.205	**0.000**
Fruit FA: low	13.525	**0.000**	-16.967	**0.000**	2.543	0.115	-14.342	**0.000**
Fruit FA: moderate	37.578	**0.000**	-28.39	**0.000**	35.581	**0.000**	-15.484	**0.000**
Fruit FA: high	125.851	**0.000**	-23.855	**0.000**	62.259	**0.000**	-20.296	**0.000**
Leaves FA: low	154.882	**0.000**	-29.618	**0.000**	128.486	**0.000**	-26.578	**0.000**
Leaves FA: moderate	38.978	**0.000**	-14.11	**0.000**	6.273	**0.013**	-12.046	**0.000**
Seeds FA: low	18.799	**0.000**	-23.11	**0.000**	257.974	**0.000**	-10.537	**0.000**
Seeds FA: moderate	67.402	**0.000**	-14.731	**0.000**	12.851	**0.000**	-13.453	**0.000**
Seeds FA: high	74.192	**0.000**	-29.297	**0.000**	86.319	**0.000**	-15.656	**0.000**
Roots FA: low	19.23	**0.000**	-28.528	**0.000**	31.457	**0.000**	-17.165	**0.000**
Animals FA: low	255.175	**0.000**	-15.551	**0.000**	76.968	**0.000**	-14.748	**0.000**
Animals FA: moderate	22.147	**0.000**	-32.539	**0.000**	119.039	**0.000**	-19.457	**0.000**
Animals FA: high	11.725	**0.002**	-20.962	**0.000**	33.4	**0.000**	-10.252	**0.000**
Sig (*n* = 24)				**24**				**24**
% Significant				**100%**				**100%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis
Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Tables 5.11-5.12 indicate that significant values were obtained on most of the variables between the large and small monkeys consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for the crown shape indices. The frequency with which these variables obtain significant differences increases more posteriorly along the tooth row, with M_3 CSI obtaining significant differences approximately 95% of the time on both the *t*-tests and Mann-Whitney U. Many of the tests run failed the Levene's tests for Equality of Variances. These results indicate that there are significant crown shape index differences between the large and small body sizes within many of the dietary groupings.

Table 5.11: *T*-test results on monkeys and diet categories, grouped by body size using P_4 – M_1 Crown Shape Indices (CSI)

Diet category	P_4 CSI				M_1 CSI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	3.106	0.079	-0.051	0.959	4.711	**0.031**	3.356	**0.003**
Traditional Diet: Omnivore	0.685	0.409	-4.295	**0.000**	2.792	0.096	-2.738	**0.007**
Fruit DO: moderate	79.478	**0.000**	-4.34	**0.000***	52.856	**0.000**	2.769	**0.006***
Leaves DO: low	24.625	**0.000**	-6.075	**0.000**	11.303	**0.001**	2.685	**0.008***
Leaves DO: moderate	1.391	0.242	2.882	**0.005**	0	0.996	-0.618	0.538
Seeds DO: low	74.458	**0.000**	3.487	**0.001***	44.548	**0.000**	1.779	0.076
Seeds DO: moderate	0.467	0.497	-5.073	**0.000**	1.313	0.257	-0.734	0.466
Seeds DO: high	1.923	0.168	8.935	**0.000**	6.116	**0.015**	5.208	**0.000**
Roots DO: low	31.4	**0.000**	5.034	**0.000**	20.375	**0.000**	4.76	**0.002**
Animals DO: low	21.699	**0.000**	-1.054	0.293	7.316	**0.007**	-1.117	0.265
Specific Classification FA: Frugivore/ Folivore	12.945	**0.000**	-2.94	**0.004**	4.264	**0.040**	-2.661	**0.009**
Specific Classification FA: Omnivore	8.305	**0.004**	-1.185	0.237	0.059	0.809	-1.616	0.107
Fruit FA: low	0.027	0.87	-4.599	**0.000**	0.278	0.6	-1.545	0.127
Fruit FA: moderate	2.219	0.139	5.104	**0.000**	5.358	**0.022**	2.724	**0.007**
Fruit FA: high	31.775	**0.000**	2.859	**0.005***	20.757	**0.000**	2.381	**0.018***
Leaves FA: low	61.887	**0.000**	4.818	**0.000***	30.554	**0.000**	3.933	**0.000**
Leaves FA: moderate	17.641	**0.000**	-1.631	0.106	5.599	**0.019**	-1.689	0.095
Seeds FA: low	11.999	**0.001**	3.81	**0.000***	7.772	**0.006**	3.163	**0.003***
Seeds FA: moderate	13.044	**0.000**	-4.229	**0.000**	9.512	**0.002**	-1.357	0.177
Seeds FA: high	0.258	0.612	9.093	**0.000**	12.028	**0.001**	4.469	**0.000**
Roots FA: low	8.034	**0.006**	2.335	**0.022**	0.602	0.44	-0.095	0.924
Animals FA: low	14.467	**0.000**	-2.448	**0.015**	4.701	**0.031**	-1.123	0.263
Animals FA: moderate	16.923	**0.000**	4.017	**0.000***	5.723	**0.018**	1.793	0.078
Animals FA: high	0.034	0.854	-0.935	0.357	2.3	0.139	1.358	0.184
Sig (*n* = 24) **% Significant**				**18** **75%**				**11** **45.83%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis
Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the independent *t*-test and Mann-Whitney U.

Table 5.12: *T*-test results on monkeys and diet categories, grouped by body size using $M_2 – M_3$ Crown Shape Indices (CSI)

Diet category	M_2 CSI				M_3 CSI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	6.082	**0.014**	7.487	**0.000**	0.983	0.322	7.336	**0.000**
Traditional Diet: Omnivore	0.912	0.34	0.322	0.748	0.466	0.496	12.132	**0.000**
Fruit DO: moderate	40.565	**0.000**	6.345	**0.000**	24.751	**0.000**	12.4	**0.000**
Leaves DO: low	16.203	**0.000**	5.779	**0.000**	7.745	**0.006**	11.05	**0.000**
Leaves DO: moderate	0.235	0.629	-2.913	**0.005**	3.092	0.082	-4.132	**0.000**
Seeds DO: low	42.867	**0.000**	5.11	**0.000**	21.213	**0.000**	13.709	**0.000**
Seeds DO: moderate	1.284	0.262	3.187	**0.002**	0	0.998	-7.175	**0.000**
Seeds DO: high	0.533	0.467	7.815	**0.000**	2.202	0.14	2.7	**0.008**
Roots DO: low	17.472	**0.000**	6.755	**0.000**	19.376	**0.000**	9.491	**0.000**
Animals DO: low	8.857	**0.003**	0.856	0.393	10.478	**0.001**	8.092	**0.000**
Specific Classification FA: Frugivore/ Folivore	15.962	**0.000**	0.045	0.964	6.466	**0.012**	6.264	**0.000**
Specific Classification FA: Omnivore	6.058	**0.014**	3.215	**0.002**	0.65	0.421	10.346	**0.000**
Fruit FA: low	1.602	0.21	0.439	0.662	0.054	0.817	6.089	**0.000**
Fruit FA: moderate	0.283	0.595	6.321	**0.000**	0.16	0.69	5.666	**0.000**
Fruit FA: high	25.595	**0.000**	5.496	**0.000**	11.486	**0.001**	10.919	**0.000**
Leaves FA: low	45.334	**0.000**	5	**0.000**	28.682	**0.000**	9.152	**0.000**
Leaves FA: moderate	6.775	**0.01**	4.297	**0.000**	0.625	0.43	10.151	**0.000**
Seeds FA: low	10.005	**0.002**	3.978	**0.000***	3.735	0.055	5.154	**0.000**
Seeds FA: moderate	11.025	**0.001**	4.476	**0.000**	0.284	0.595	12.513	**0.000**
Seeds FA: high	1.001	0.319	8.276	**0.000**	0.252	0.617	4.997	**0.000**
Roots FA: low	1.076	0.302	-3.424	**0.001**	5.27	**0.024**	-0.415	0.679
Animals FA: low	12.727	**0.000**	3.426	**0.001**	0.9	0.344	8.126	**0.000**
Animals FA: moderate	9.416	**0.002**	3.102	**0.003**	5.709	**0.018**	7.106	**0.000**
Animals FA: high	0.298	0.589	2.649	**0.013**	0.016	0.899	5.866	**0.000**
Sig (*n* = 24)				**20**				**23**
% Significant				**83.33%**				**95.83%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis
Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the independent *t*-test and Mann-Whitney U.

Tables 5.13-5.14 indicate that significant values were obtained on most of the variables between the large and small monkeys consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for the symphyseal and corpus robusticity indices. The frequency with which these variables obtain significant differences increases more posteriorly along the corpus. Equality of Variance were assumed for most of the Levene's tests, except the SRIs. These results indicate that there are significant robusticity index differences between the large and small body sizes within many of the dietary groupings.

Table 5.13: ***T*-test results on monkeys and diet categories, grouped by body size using Symphyseal Robusticity Index (SRI), and $P_4 – M_1$ Corpus Robusticity Indices (CRI)**

Diet category	SRI				P_4 CRI				M_1 CRI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	0.038	0.846	-0.582	0.561	0.848	0.358	-2.207	**0.028**	0.256	0.613	-1.27	0.205
Traditional Diet: Omnivore	3.973	**0.047**	-9.139	**0.000**	0.579	0.448	-0.047	0.963	11.801	**0.001**	7.619	**0.000**
Fruit DO: moderate	21.281	**0.000**	-13.54	**0.000**	19.696	**0.000**	6.06	**0.000**	32.096	**0.000**	10.168	**0.000**
Leaves DO: low	21.829	**0.000**	-8.588	**0.000**	3.702	0.055	4.055	**0.000**	12.532	**0.000**	8.292	**0.000**
Leaves DO: moderate	0.317	0.575	-1.884	0.063	2.393	0.126	0.363	0.718	0.046	0.83	1.365	0.176
Seeds DO: low	5.044	**0.025**	-13.433	**0.000**	18.374	**0.000**	6.242	**0.000**	25.794	**0.000**	7.08	**0.000**
Seeds DO: moderate	0.01	0.922	0.014	0.988	0	0.989	-4.278	**0.000**	1.224	0.274	0.048	0.962
Seeds DO: high	16.165	**0.000**	-4.347	**0.000**	0.697	0.405	0.727	0.468	0.696	0.406	4.261	**0.000**
Roots DO: low	0.781	0.378	-10.686	**0.000**	13.808	**0.000**	3.705	**0.000**	17.569	**0.000**	7.824	**0.000**
Animals DO: low	11.093	**0.001**	-9.356	**0.000**	0.418	0.518	-0.873	0.384	9.475	**0.002**	4.647	**0.000**
Specific Classification FA: Frugivore/ Folivore	1.352	0.246	-10.078	**0.000**	1.503	0.222	2.844	**0.005**	1.211	0.272	3.612	**0.000**
Specific Classification FA: Omnivore	27.065	**0.000**	-7.285	**0.000**	9.119	**0.003**	-1.595	0.113	0.029	0.866	2.079	**0.039**
Fruit FA: low	0.043	0.837	-0.618	0.539	0.001	0.973	-4.738	**0.000**	1.822	0.182	-1.288	0.202
Fruit FA: moderate	9.067	**0.003**	-6.088	**0.000**	2.469	0.118	0.696	0.488	0.088	0.768	3.332	**0.001**
Fruit FA: high	2.538	0.112	-12.208	**0.000**	9.011	**0.003**	1.844	0.067	14.134	**0.000**	4.227	**0.000**
Leaves FA: low	13.085	**0.000**	-12.166	**0.000**	13.967	**0.000**	2.509	**0.013***	26.423	**0.000**	5.886	**0.000**
Leaves FA: moderate	13.336	**0.000**	-4.173	**0.000**	2.138	0.145	0.391	0.696	0.001	0.979	0.665	0.506
Seeds FA: low	16.985	**0.000**	-4.281	**0.001**	2.813	0.095	0.301	0.764	11.726	**0.001**	3.383	**0.002***
Seeds FA: moderate	1.727	0.191	-6.931	**0.000**	0.096	0.757	-2.091	**0.038**	0.225	0.636	-0.323	0.747
Seeds FA: high	11.429	**0.001**	-6.878	**0.000**	5.233	**0.023**	-0.073	0.942	0.327	0.568	1.738	0.084*
Roots FA: low	7.572	**0.007**	-4.846	**0.000**	0.298	0.586	-0.548	0.585	3.461	0.066	2.161	**0.033***
Animals FA: low	0.778	**0.04**	-1.769	**0.000**	0.778	0.379	-1.769	0.078	0.042	0.837	0.654	0.514
Animals FA: moderate	29.312	**0.000**	-6.784	**0.000**	4.856	**0.029**	2.78	**0.007**	8.962	**0.003**	6.418	**0.000**
Animals FA: high	3.394	0.075	-1.889	0.068*	0.019	0.89	-1.712	0.097	4.77	**0.036**	1.464	0.162
Sig (*n* = 24)				**19**				**11**				**15**
% Significant				**79.17%**				**45.83%**				**62.50%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis

Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the independent *t*-test and Mann-Whitney U.

Table 5.14: *T*-test results on monkeys and diet categories, grouped by body size using M_2 – M_3 Corpus Robusticity Indices (CRI)

Diet category	M_2 CRI				M_3 CRI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	1.262	0.262	-3.275	**0.001**	4.944	**0.027**	-6.665	**0.000**
Traditional Diet: Omnivore	4.705	**0.031**	-8.395	**0.000**	0.745	0.389	0.696	0.487
Fruit DO: moderate	5.131	**0.024**	4.026	**0.000**	0	0.992	-3.745	**0.000**
Leaves DO: low	4.579	**0.033**	3.384	**0.001**	0.333	0.564	-2.78	**0.006**
Leaves DO: moderate	0.111	0.74	-0.494	0.622	0.467	0.496	-1.665	0.100
Seeds DO: low	9.839	**0.002**	-2.407	**0.017**	0.739	0.39	-10.275	**0.000**
Seeds DO: moderate	3.338	0.073	1.973	0.054*	2.905	0.094	-1.123	0.266
Seeds DO: high	0.643	0.424	3.822	**0.000**	1.01	0.317	1.496	0.137
Roots DO: low	15.878	**0.000**	2.426	**0.017**	4.029	**0.046**	-4.523	**0.000**
Animals DO: low	17.289	**0.000**	4.224	**0.000**	2.897	0.09	-2.304	**0.022**
Specific Classification FA: Frugivore/ Folivore	2.623	0.107	-1.174	0.242	0.228	0.633	-5.437	**0.000**
Specific Classification FA: Omnivore	1.966	0.162	-0.474	0.636	0.968	0.326	-5.425	**0.000**
Fruit FA: low	4.724	**0.033**	0.103	0.918	8.335	**0.005**	-3.241	**0.002**
Fruit FA: moderate	2.206	0.14	-1.266	0.208	0.147	0.702	-5.13	**0.000**
Fruit FA: high	4.323	**0.038**	-3.503	**0.001**	0.601	0.439	-9.51	**0.000**
Leaves FA: low	4.621	**0.032**	1.165	0.245	1.369	0.243	-7.137	**0.000**
Leaves FA: moderate	1.701	0.193	-3.171	**0.002**	1.85	0.175	-6.037	**0.000**
Seeds FA: low	2.353	0.127	-1.208	0.228	0.58	0.447	-6.012	**0.000**
Seeds FA: moderate	0.465	0.496	-4.159	**0.000**	0.057	0.812	-7.354	**0.000**
Seeds FA: high	1.494	0.223	-3.728	**0.000**	1.513	0.22	-6.873	**0.000**
Roots FA: low	0.108	0.743	1.576	0.118	0.1	0.752	-1.629	0.107
Animals FA: low	8.123	**0.005**	-4.072	**0.000**	2.986	0.086	-9.761	**0.000**
Animals FA: moderate	1.521	0.219	3.9	**0.000**	0.111	0.739	-0.768	0.443
Animals FA: high	0.156	0.696	1.47	0.151	0.05	0.825	-1.976	0.059
Sig (*n* = 24)				**14**				**17**
% Significant				**58.33%**				**70.83%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Significant values were obtained between the large and small apes consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for all of the crown area and corpus/ symphysis size variables. Equality of Variance were assumed for the majority of the Levene’s tests. These results indicate that there are significant differences between the large and small body sizes within each dietary grouping. M_1 crown area and M_1 corpus size are documented in Table 5.15, and are representative of the rest of the size-related variables.

Table 5.15: *T*-test results on apes and diet categories, grouped by body size using M_1 Crown Area (CA) and M_1 Corpus Size (CS)

Diet category	M_1 CA				M_1 CS			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	3.026	0.083	-29.893	**0.000**	0.798	0.372	-17.585	**0.000**
Seeds DO: low	27.65	**0.003**	-30.095	**0.000**	32.111	**0.000**	-19.146	**0.000**
Animals DO: low	1.946	0.164	-32.362	**0.000**	2.583	0.109	-21.615	**0.000**
Specific Classification FA: Folivore/ Frugivore	0.166	0.684	-15.303	**0.000**	0.729	0.395	-5.516	**0.000**
Specific Classification FA: Frugivore/ Folivore	4.674	**0.032**	-29.92	**0.000**	6.657	**0.010**	-19.505	**0.000**
Fruit FA: moderate	0.24	0.627	-10.404	**0.000**	0.067	0.798	-5.53	**0.000**
Fruit FA: high	4.674	**0.032**	-29.92	**0.000**	6.657	**0.010**	-19.505	**0.000**
Leaves FA: moderate	0.317	0.574	-28.107	**0.000**	1.938	0.165	-19.548	**0.000**
Leaves FA: high	0.166	0.684	-15.303	**0.000**	0.729	0.395	-5.516	**0.000**
Seeds FA: low	33.591	**0.000**	-40.758	**0.000**	33.183	**0.000**	-26.166	**0.000**
Roots FA: low	8.438	**0.004**	-33.3	**0.000**	10.424	**0.001**	-21.677	**0.000**
Animals FA: low	3.011	0.084	-32.257	**0.000**	3.098	**0.08**	-20.473	**0.000**
Sig (*n* = 12)				**12**				**12**
% Significant				**100%**				**100%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Tables 5.16-5.17 indicate that significant values were obtained on most of the variables between the large and small apes consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for the crown shape indices. The molar teeth obtained significant differences on almost all tests, whereas P_4 CSI obtained significant differences on less than half of the tests. Most of the tests failed the Levene's tests for the Equality of Variance. These results indicate that there are significant differences between the large and small body sizes within many of the dietary groupings.

Table 5.16: *T*-test results on apes and diet categories, grouped by body size using P_4 – M_1 Crown Shape Index (CSI)

Diet category	P_4 CSI				M_1 CSI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	17.352	**0.000**	-3.629	**0**	4.136	**0.043**	7.632	**0.000**
Seeds DO: low	15.92	**0.000**	-0.896	0.371	5.645	**0.019**	7.436	**0.000**
Animals DO: low	17.056	**0.000**	-5.059	**0.041***	4.812	**0.029**	7.127	**0.000**
Specific Classification FA: Folivore/ Frugivore	0.041	0.839	-5.647	**0.000**	0.312	0.578	3.497	**0.001**
Specific Classification FA: Frugivore/ Folivore	16.021	**0.000**	-1.646	0.101	6.836	**0.009**	8.231	**0.000**
Fruit FA: moderate	1.195	0.28	-2.071	**0.044**	0.18	0.673	2.41	**0.020**
Fruit FA: high	16.021	**0.000**	-1.646	0.101	6.836	**0.009**	8.231	**0.000**
Leaves FA: moderate	13.596	**0.000**	-1.648	0.101	5.908	**0.016**	7.957	**0.000**
Leaves FA: high	0.041	0.839	-5.647	**0.000**	0.312	0.578	3.497	**0.001**
Seeds FA: low	20.97	**0.000**	-1.818	0.07	6.297	**0.013**	6.948	**0.000**
Roots FA: low	16.28	**0.000**	-1.372	0.172	7.339	**0.007**	7.988	**0.000**
Animals FA: low	16.392	**0.000**	-1.808	0.072	6.551	**0.011**	6.754	**0.000**
Sig (*n* = 12)				**5**				**12**
% Significant				**41.67%**				**100%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 5.17: *T*-test results on apes and diet categories, grouped by body size using M_2 – M_3 Crown Shape Index (CSI)

Diet category	M_2 CSI				M_3 CSI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	18.253	**0.000**	9.238	**0.000**	20.903	**0.000**	10.571	**0.000**
Seeds DO: low	11.343	**0.001**	9.199	**0.000**	7.017	**0.009**	10.571	**0.000**
Animals DO: low	12.178	**0.001**	7.702	**0.000**	24.484	**0.000**	8.495	**0.000**
Specific Classification FA: Folivore/ Frugivore	1.458	0.23	5.586	**0.000**	2.078	0.153	4.974	**0.000**
Specific Classification FA: Frugivore/ Folivore	10.987	**0.001**	7.494	**0.000**	19.805	**0.000**	8.147	**0.000**
Fruit FA: moderate	0.029	0.866	2.858	**0.006**	2.896	0.095	1.915	0.062
Fruit FA: high	10.987	**0.001**	7.494	**0.000**	19.805	**0.000**	8.147	**0.000**
Leaves FA: moderate	14.299	**0.000**	6.543	**0.000**	22.815	**0.000**	6.741	**0.000**
Leaves FA: high	1.458	0.23	5.586	**0.000**	2.078	0.153	4.974	**0.000**
Seeds FA: low	21.944	**0.000**	8.571	**0.000**	12.824	**0.000**	12.523	**0.000**
Roots FA: low	12.294	**0.001**	7.673	**0.000**	22.034	**0.000**	9.153	**0.000**
Animals FA: low	5.327	**0.022**	4.985	**0.000**	18.791	**0.000**	6.158	**0.000**
Sig (*n* = 12)				**12**				**11**
% Significant				**100%**				**91.67%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Tables 5.18-5.19 indicate that significant values were not obtained on many of the variables between the large and small apes consuming similar diets using both the parametric (*t*-tests) and non-parametric (Mann-Whitney U) tests of difference for the robusticity indices. M_2 CRI and SRI were the only variables that regularly obtained significant differences. Equality of Variance were assumed for the majority of the Levene's tests. These results indicate that there are significant differences between the large and small body sizes within many of the dietary groupings for M_2 CRI and SRI, but rarely for the other corpus robusticity indices.

Table 5.18: *T*-test results on apes and diet categories, grouped by body size using Symphyseal Robusticity Indices (SRI) and P_4 – M_1 Corpus Robusticity Indices (CRI)

Diet category	SRI				P_4 CRI				M_1 CRI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	0.015	0.903	-9.654	**0.000**	0.295	0.587	-3.065	**0.002**	0.766	0.382	-1.053	0.293
Seeds DO: low	2.019	0.157	-4.256	**0.000**	0.956	0.33	-0.21	0.834	2.03	0.156	2.243	**0.026**
Animals DO: low	1.861	0.174	-5.37	**0.000**	0.377	0.54	-1.508	0.133	2.929	0.088	0.211	0.833
Specific Classification FA: Folivore/ Frugivore	0.14	0.709	-11.032	**0.000**	0.157	0.693	-3.763	**0.000**	2.216	0.14	-2.779	**0.007**
Specific Classification FA: Frugivore/ Folivore	2.301	0.13	-5.232	**0.000**	0.77	0.381	-1.416	0.158	2.228	0.137	0.576	0.565
Fruit FA: moderate	0.413	0.524	-6.728	**0.006**	0.001	0.97	-2.546	**0.014**	0.071	0.791	-3.085	**0.003**
Fruit FA: high	2.301	0.13	-5.232	**0.000**	0.77	0.381	-1.416	0.158	2.228	0.137	0.576	0.565
Leaves FA: moderate	0.736	0.392	-3.973	**0.000**	0.731	0.393	-1.596	0.112	1.721	0.191	0.153	0.878
Leaves FA: high	0.14	0.709	-11.032	**0.000**	0.157	0.693	-3.763	**0.000**	2.216	0.14	-2.779	**0.007**
Seeds FA: low	0.628	0.429	-7.146	**0.000**	1.677	0.196	-0.844	0.4	0.502	0.479	1.243	0.215
Roots FA: low	2.598	0.108	-5.92	**0.000**	1.135	0.288	-1.321	0.188	1.469	0.227	0.387	0.699
Animals FA: low	6.229	0.013	-6.042	**0.000**	0.978	0.324	-2.079	**0.039**	0.63	0.428	-0.472	0.637
Sig (*n* = 12)				**12**				**6**				**4**
% Significant				**100%**				**50%**				**33.33%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis

Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Table 5.19: *T*-test results on apes and diet categories, grouped by body size using M_2 – M_3 Corpus Robusticity Indices (CRI)

Diet category	M_2 CRI				M_3 CRI			
	F	EoV (sig)*	t	*t*-test (sig)	F	EoV (sig)	t	*t*-test (sig)
Traditional Diet: Frugivore	1.618	0.204	-5.003	**0.000**	0	0.99	-2.732	**0.007**
Seeds DO: low	0.026	0.873	-0.767	0.444	0.066	0.798	0.163	0.871
Animals DO: low	0.003	0.957	-2.712	**0.007**	0.066	0.798	-1.084	0.279
Specific Classification FA: Folivore/ Frugivore	4.216	0.043	-3.935	**0.000**	0.205	0.652	-0.659	0.512
Specific Classification FA: Frugivore/ Folivore	0.062	0.803	-2.321	**0.021**	0.019	0.891	-1.525	0.128
Fruit FA: moderate	0.213	0.647	-2.849	**0.006**	0.235	0.63	0.382	0.704
Fruit FA: high	0.062	0.803	-2.321	**0.021**	0.019	0.891	-1.525	0.128
Leaves FA: moderate	0.178	0.674	-2.564	**0.011**	0.01	0.921	-1.949	0.053
Leaves FA: high	4.216	**0.043**	-3.935	**0.000**	0.205	0.652	-0.659	0.512
Seeds FA: low	1.67	0.197	-3.377	**0.001**	0.046	0.83	-2.151	**0.032**
Roots FA: low	0	0.986	-2.763	**0.006**	0.053	0.818	-1.365	0.173
Animals FA: low	0.008	0.931	-2.97	**0.003**	0.046	0.83	-2.124	**0.035**
Sig (*n* = 12)				**11**				**3**
% Significant				**91.67%**				**25%**

* EoV = Levene's test of the Equality of Variances. DO = Direct Observation. FA = Faecal Analysis
Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

These results indicate that dental and mandibular variables related to size consistently differ significantly in both small and large monkeys and small and large apes when diet category is held constant. In contrast, greater variation is present in the results from the shape variables (crown shape index, corpus robusticity index). For the monkey species these differences manifest more in the M_3 crown shape index and corpus robusticity index (Tables 5.12-5.14), while in apes the differences manifest throughout the molar tooth row (M_1-M_3 crown shape indices) and predominantly at the symphysis and M_2 corpus robusticity index (Tables 5.16-5.19). While the dental and mandibular shape variables differ significantly in both the small and large monkeys and apes from the same diet categories, the location of these differences vary in the two primate groups.

When keeping the diet categories constant, there are morphological differences present between small and large monkeys and small and large apes (Tables 5.10-5.19). These results are important as they show that primate size does influence morphological expression. It is therefore an important aspect to consider when analysing morphological form. However, while this is true, the effects of body size do not comprise the core focus of this research (the reasons are explained in the Discussion chapter). Instead the primary focus was on exploring whether morphological differences were present in consumers of different diets.

The results from the *t*-tests and ANOVA (and the Mann-Whitney U and Kruskal-Wallis) comparing consumers of different diet categories within the different body sizes of apes and monkeys are presented in the following tables. These results analysing the traditional diet categories are reflective of the results obtained from specific classification coding and the quantity analyses, whereby significant differences were identified between the consumers of different diets, therefore only the results from the traditional diet categories are presented here (the other results are presented in Appendix tables 9.9-9.24).

The *t*-tests and ANOVAs often violated the equality/ homogeneity of variances tests (both the Levene's and Welch's robust tests). A point that perhaps reinforces the fact that the data was not normally distributed and that non-parametric tests were most appropriate. Comparison of the results from the parametric tests to those of the non-parametric tests revealed that the results were the same on almost all of the tests run. As a result, where possible (i.e., when more than two groups were analysed in a test) the ANOVA data were analysed in order to explore the post-hoc data, so as to understand where differences between groups occurred.

The following ANOVA analysed the differences between consumers of different diets from the small monkeys. All variables failed the Welch's robust tests for the equality of means except M_1 and M_2 corpus robusticity indices (CRI). According to the ANOVA results in Table 5.20 there are significant differences between the consumers of the different dietary categories at each variable.

Table 5.20: Descriptive statistics and ANOVA results from One-Way ANOVA on small monkeys with diets categorised using the Traditional Diet categories

		Descriptives				ANOVA*	
		N	Mean	Std. Deviation	Std. Error	Statistic^a	Sig.
P_4CA	Folivore	26	21.876	3.8176	0.7487		
	Frugivore	383	18.927	8.5931	0.4391		
	Omnivore	89	14.872	2.2591	0.2395		
	Frugivore-Insectivore	37	16.892	2.5037	0.4116		
	Total	535	18.255	7.6004	0.3286	42.269	**0.000**
M_1CA	Folivore	27	31.304	4.1046	0.7899		
	Frugivore	388	27.239	11.1317	0.5651		
	Omnivore	90	22.885	2.8197	0.2972		
	Frugivore-Insectivore	38	21.208	2.5440	0.4127		
	Total	543	26.297	9.8319	0.4219	57.812	**0.000**
M_2CA	Folivore	27	43.274	4.7968	0.9232		
	Frugivore	385	35.463	16.1516	0.8232		
	Omnivore	90	30.897	4.0074	0.4224		
	Frugivore-Insectivore	37	18.979	2.4398	0.4011		
	Total	539	33.960	14.6063	0.6291	296.424	**0.000**
M_3CA	Folivore	22	41.091	4.8668	1.0376		

		Descriptives				ANOVA*	
		N	Mean	Std. Deviation	Std. Error	Statistic^a	Sig.
	Frugivore	379	37.060	20.1473	1.0349		
	Omnivore	86	30.378	4.5690	0.4927		
	Frugivore-Insectivore	27	13.101	1.6283	0.3134		
	Total	514	34.856	18.3626	0.8099	528.491	**0.000**
P_4CSI	Folivore	26	79.5173	12.61984	2.47495		
	Frugivore	383	93.5425	19.67788	1.00549		
	Omnivore	89	80.3184	10.21596	1.08289		
	Frugivore-Insectivore	37	137.4327	17.12701	2.81566		
	Total	535	93.6964	22.21718	0.96053	129.134	**0.000**
M_1CSI	Folivore	27	79.596	5.8110	1.1183		
	Frugivore	388	85.559	9.1413	0.4641		
	Omnivore	90	80.738	6.7509	0.7116		
	Frugivore-Insectivore	38	103.422	6.7622	1.0970		
	Total	543	85.714	9.9935	0.4289	111.363	**0.000**
M_2CSI	Folivore	27	81.392	4.3703	0.8411		
	Frugivore	385	91.580	8.0805	0.4118		
	Omnivore	90	87.334	5.3279	0.5616		
	Frugivore-Insectivore	37	106.522	8.5540	1.4063		
	Total	539	91.387	8.9812	0.3868	91.604	**0.000**
M_3CSI	Folivore	22	80.654	6.3714	1.3584		
	Frugivore	379	84.131	9.6029	0.4933		
	Omnivore	86	85.989	6.5982	0.7115		
	Frugivore-Insectivore	27	108.441	11.7570	2.2626		
	Total	514	85.570	10.6749	0.4709	39.963	**0.000**
SS	Folivore	27	243.763	92.9308	17.8845		
	Frugivore	389	181.084	114.3764	5.7991		
	Omnivore	89	149.866	41.4445	4.3931		
	Frugivore-Insectivore	38	152.268	31.2572	5.0706		
	Total	543	177.067	102.5797	4.4021	14.052	**0.000**
P_4CS	Folivore	27	96.967	28.1439	5.4163		
	Frugivore	390	97.269	49.8124	2.5223		
	Omnivore	91	65.640	14.5264	1.5228		
	Frugivore-Insectivore	38	81.629	15.1083	2.4509		
	Total	546	90.894	44.7499	1.9151	45.092	**0.000**
M_1CS	Folivore	27	91.623	24.1676	4.6511		
	Frugivore	390	99.527	52.1666	2.6416		
	Omnivore	91	64.792	13.0054	1.3633		
	Frugivore-Insectivore	38	84.488	17.2282	2.7948		
	Total	546	92.300	46.7583	2.0011	54.689	**0.000**
M_2CS	Folivore	27	93.971	21.4570	4.1294		
	Frugivore	390	104.921	56.0188	2.8366		
	Omnivore	91	67.815	12.8729	1.3494		
	Frugivore-Insectivore	38	89.555	17.3613	2.8164		
	Total	546	97.126	50.0108	2.1403	58.718	**0.000**
M_3CS	Folivore	25	102.483	18.8812	3.7762		
	Frugivore	388	117.146	60.0434	3.0482		
	Omnivore	89	77.784	12.8550	1.3626		
	Frugivore-Insectivore	35	101.299	21.0743	3.5622		
	Total	537	108.907	53.7583	2.3198	57.771	**0.000**
SRI	Folivore	27	41.423	4.4365	0.8538		
	Frugivore	388	41.639	4.5665	0.2318		
	Omnivore	89	42.504	4.7556	0.5041		
	Frugivore-Insectivore	38	42.969	2.5747	0.4177		

		Descriptives				ANOVA*	
		N	Mean	Std. Deviation	Std. Error	Statistic[a]	Sig.
	Total	542	41.864	4.4938	0.1930	3.035	**0.034**
P_4CRI	Folivore	27	37.500	4.7522	0.9146		
	Frugivore	390	40.291	5.7152	0.2894		
	Omnivore	91	38.624	4.7247	0.4953		
	Frugivore-Insectivore	38	51.639	3.8803	0.6295		
	Total	546	40.665	6.2281	0.2665	107.666	**0.000**
M_1CRI	Folivore	27	37.651	5.5094	1.0603		
	Frugivore	389	39.874	5.0412	0.2556		
	Omnivore	91	42.139	5.4050	0.5666		
	Frugivore-Insectivore	38	49.693	4.2749	0.6935		
	Total	545	40.827	5.7080	0.2445	62.388	**0.000**
M_2CRI	Folivore	27	45.297	6.5270	1.2561		
	Frugivore	390	44.074	6.0071	0.3042		
	Omnivore	91	52.632	7.1792	0.7526		
	Frugivore-Insectivore	38	51.067	4.9769	0.8074		
	Total	546	46.047	7.0564	0.3020	51.511	**0.000**
M_3CRI	Folivore	25	49.502	8.9201	1.7840		
	Frugivore	388	49.739	7.7653	0.3942		
	Omnivore	89	56.818	7.1447	0.7573		
	Frugivore-Insectivore	35	50.438	4.1907	0.7084		
	Total	537	50.947	7.9680	0.3438	23.111	**0.000**

*ANOVA using Welch Robust Tests of Equality of Means

a. Asymptotically F distributed.

The post-hoc results indicate that significant differences were present between all diets on each of the crown area variables. Significant differences were also present between most of the diets consumed and the rest of the morphological variables analysed. Where significant differences were not present between diets there did not appear to be many identifiable patterns present, meaning that the morphologies present in the consumers of the different diets appeared to be very different. However, two sets of diets did present a morphology that was not significantly different on a number of variables, these were: folivores and omnivores, and folivores and frugivores. Folivores and omnivores were not significantly different on P_4 – M_1 CSI, and P_4 CRI. Folivores and frugivores were not significantly different on M_3 CSI, M_1 CRI – M_2 CRI, and P_4 CS – M_2 CS.

The following *t*-test analysed the differences between frugivores and omnivores in the large monkeys. All of the size-related variables (crown area and corpus size) failed the Equality of Variances tests, while most of the shape variables passed them (except M_3 corpus robusticity index (CRI)) (Table 5.21). According to the *t*-test results there are significant differences between frugivores and omnivores on every variable, except M_1 crown shape index (CSI) and M_3 CRI.

Table 5.21: Descriptive statistics and *T*-test results from Independent Samples *T*-test comparing frugivorous and omnivorous large monkeys

Group Statistics						**Independent Samples Test**					
							Levene's Test for Equality of Variances		*t*-test for Equality of Means		
Traditional Diet Categories		*N*	Mean	Std. Deviation	Std. Error Mean		F	Sig.	t	df	Sig. (2-tailed)
P_4CA	Frugivore	18	30.642	3.8745	0.9132	Equal variances assumed	17.529	**0.000**	-9.044	158	0.000
	Omnivore	142	59.700	13.5265	1.1351	Equal variances not assumed			-19.945	85.501	**0.000**
M_1CA	Frugivore	17	43.951	2.5545	0.6196	Equal variances assumed	20.618	**0.000**	-8.053	157	0.000
	Omnivore	142	81.036	18.9144	1.5873	Equal variances not assumed			-21.765	155.440	**0.000**
M_2CA	Frugivore	18	67.309	5.4187	1.2772	Equal variances assumed	15.885	**0.000**	-8.711	158	0.000
	Omnivore	142	122.680	26.8269	2.2513	Equal variances not assumed			-21.392	132.514	**0.000**
M_3CA	Frugivore	17	94.629	12.2003	2.9590	Equal variances assumed	15.774	**0.000**	-7.196	155	0.000
	Omnivore	140	162.134	38.3469	3.2409	Equal variances not assumed			-15.382	66.412	**0.000**
P_4CSI	Frugivore	18	93.7820	10.84614	2.55646	Equal variances assumed	0.688	0.408	2.973	158	**0.003**
	Omnivore	142	86.2084	10.09948	0.84753	Equal variances not assumed			2.812	20.912	0.010
M_1CSI	Frugivore	17	81.412	4.2708	1.0358	Equal variances assumed	1.355	0.246	-1.093	157	0.276
	Omnivore	142	83.114	6.2381	0.5235	Equal variances not assumed			-1.467	25.032	0.155
M_2CSI	Frugivore	18	83.660	3.8877	0.9163	Equal variances assumed	0.976	0.325	-2.719	158	**0.007**
	Omnivore	142	87.106	5.1897	0.4355	Equal variances not assumed			-3.396	25.391	0.002
M_3CSI	Frugivore	17	71.061	6.5960	1.5998	Equal variances assumed	0.080	0.778	-2.953	155	**0.004**
	Omnivore	140	75.647	5.9801	0.5054	Equal variances not assumed			-2.734	19.331	0.013
SS	Frugivore	18	298.954	72.4971	17.0877	Equal variances assumed	36.296	**0.000**	-5.849	158	0.000
	Omnivore	142	939.460	462.6388	38.8238	Equal variances not assumed			-15.100	153.227	**0.000**

Group Statistics						**Independent Samples Test**					
							Levene's Test for Equality of Variances		*t*-test for Equality of Means		
Traditional Diet Categories		*N*	Mean	Std. Deviation	Std. Error Mean		F	Sig.	t	df	Sig. (2-tailed)
P_4CS	Frugivore	18	166.600	29.2450	6.8931	Equal variances assumed	18.163	**0.000**	-6.445	159	0.000
	Omnivore	143	315.528	97.2437	8.1319	Equal variances not assumed			-13.970	78.941	**0.000**
M_1CS	Frugivore	18	177.760	30.7227	7.2414	Equal variances assumed	16.140	**0.000**	-6.286	159	0.000
	Omnivore	143	310.574	88.7586	7.4224	Equal variances not assumed			-12.808	63.141	**0.000**
M_2CS	Frugivore	18	195.425	38.4511	9.0630	Equal variances assumed	8.238	**0.005**	-5.690	159	0.000
	Omnivore	143	307.481	82.2484	6.8780	Equal variances not assumed			-9.849	40.608	**0.000**
M_3CS	Frugivore	18	221.400	40.1020	9.4521	Equal variances assumed	7.930	**0.005**	-5.420	158	0.000
	Omnivore	142	322.045	77.3235	6.4888	Equal variances not assumed			-8.778	35.839	**0.000**
SRI	Frugivore	17	42.381	5.5025	1.3345	Equal variances assumed	1.522	0.219	-4.316	157	**0.000**
	Omnivore	142	49.065	6.0908	0.5111	Equal variances not assumed			-4.677	20.987	0.000
P_4CRI	Frugivore	18	43.521	4.4104	1.0395	Equal variances assumed	0.197	0.657	3.820	159	**0.000**
	Omnivore	143	38.655	5.1689	0.4322	Equal variances not assumed			4.322	23.303	0.000
M_1CRI	Frugivore	18	41.751	4.3260	1.0196	Equal variances assumed	0.847	0.359	4.654	159	**0.000**
	Omnivore	143	37.159	3.8973	0.3259	Equal variances not assumed			4.290	20.625	0.000
M_2CRI	Frugivore	18	49.011	5.0724	1.1956	Equal variances assumed	0.804	0.371	2.725	159	**0.007**
	Omnivore	143	45.128	5.7685	0.4824	Equal variances not assumed			3.012	22.913	0.006
M_3CRI	Frugivore	18	58.741	5.3679	1.2652	Equal variances assumed	6.043	**0.015**	1.387	158	0.167
	Omnivore	142	56.106	7.8195	0.6562	Equal variances not assumed			1.849	27.139	0.075

The following *t*-test analysed the differences between folivores and frugivores in the large apes. All of the variables passed the Equality of Variances tests (Table 5.22). According to the *t*-test results there are significant differences between folivores and frugivores on all of the corpus size variables and the P_4 crown area, however, significant differences are not present on the rest of the data.

Table 5.22: Descriptive statistics and T-test results from Independent Samples T-test comparing folivorous and frugivorous large apes

Group Statistics						Independent Samples Test					
							Levene's Test for Equality of Variances		t-test for Equality of Means		
Traditional Diet Categories		*N*	Mean	Std. Deviation	Std. Error Mean		F	Sig.	t	df	Sig. (2-tailed)
P_4CA	Folivore	10	167.586	23.2109	7.3399	Equal variances assumed	0.004	0.951	3.263	117	**0.001**
	Frugivore	109	146.507	19.2153	1.8405	Equal variances not assumed			2.786	10.164	0.019
M_1CA	Folivore	10	219.749	18.2909	5.7841	Equal variances assumed	1.515	0.221	1.118	117	0.266
	Frugivore	109	209.799	27.5342	2.6373	Equal variances not assumed			1.565	13.084	0.141
M_2CA	Folivore	10	289.523	39.2391	12.4085	Equal variances assumed	0.571	0.451	1.974	117	0.051
	Frugivore	109	265.816	36.0855	3.4564	Equal variances not assumed			1.840	10.446	0.094
M_3CA	Folivore	10	269.905	42.4905	13.4367	Equal variances assumed	0.023	0.879	1.127	115	0.262
	Frugivore	107	255.249	39.0545	3.7755	Equal variances not assumed			1.050	10.472	0.317
P_4CSI	Folivore	10	116.6563	10.69954	3.38349	Equal variances assumed	1.627	0.205	-1.110	117	0.269
	Frugivore	109	119.7462	8.20499	0.78590	Equal variances not assumed			-0.890	9.995	0.395
M_1CSI	Folivore	10	90.654	4.5343	1.4339	Equal variances assumed	0.194	0.661	0.636	117	0.526
	Frugivore	109	89.659	4.7514	0.4551	Equal variances not assumed			0.662	10.895	0.522
M_2CSI	Folivore	10	89.711	4.9468	1.5643	Equal variances assumed	0.463	0.498	-0.169	117	0.866
	Frugivore	109	89.935	3.9269	0.3761	Equal variances not assumed			-0.139	10.068	0.892
M_3CSI	Folivore	10	86.130	3.0712	0.9712	Equal variances assumed	2.823	0.096	-0.495	115	0.622
	Frugivore	107	86.956	5.1827	0.5010	Equal variances not assumed			-0.756	14.342	0.462
SS	Folivore	10	1437.126	230.0501	72.7482	Equal variances assumed	0.793	0.375	1.096	117	0.275
	Frugivore	109	1330.566	299.0119	28.6401	Equal variances not assumed			1.363	11.982	0.198
P_4CS	Folivore	10	692.771	108.8877	34.4333	Equal variances assumed	0.014	0.905	2.051	117	**0.042**
	Frugivore	109	612.776	118.7511	11.3743	Equal variances not assumed			2.206	11.060	0.049
M_1CS	Folivore	10	687.472	99.1728	31.3612	Equal variances assumed	0.256	0.614	2.519	117	**0.013**
	Frugivore	109	594.536	112.6303	10.7880	Equal variances not assumed			2.802	11.243	0.017
M_2CS	Folivore	10	764.556	114.4916	36.2054	Equal variances assumed	0.109	0.742	3.367	116	**0.001**
	Frugivore	108	641.208	110.5134	10.6342	Equal variances not assumed			3.269	10.613	0.008
M_3CS	Folivore	10	875.884	159.0545	50.2975	Equal variances assumed	0.386	0.536	2.850	116	**0.005**
	Frugivore	108	750.576	130.5908	12.5661	Equal variances not assumed			2.417	10.155	0.036

Group Statistics						**Independent Samples Test**					
							Levene's Test for Equality of Variances		t-test for Equality of Means		
Traditional Diet Categories		*N*	Mean	Std. Deviation	Std. Error Mean		F	Sig.	t	df	Sig. (2-tailed)
SRI	Folivore	10	43.949	5.0628	1.6010	Equal variances assumed	0.002	0.961	1.444	117	0.151
	Frugivore	109	41.720	4.6400	0.4444	Equal variances not assumed			1.342	10.435	0.208
P_4CRI	Folivore	10	53.328	6.1736	1.9523	Equal variances assumed	0.205	0.652	0.334	117	0.739
	Frugivore	109	52.564	6.9711	0.6677	Equal variances not assumed			0.370	11.216	0.718
M_1CRI	Folivore	10	54.327	5.8404	1.8469	Equal variances assumed	0.037	0.848	1.399	117	0.164
	Frugivore	109	51.588	5.9345	0.5684	Equal variances not assumed			1.418	10.778	0.185
M_2CRI	Folivore	10	64.425	8.4718	2.6790	Equal variances assumed	0.095	0.758	0.826	116	0.411
	Frugivore	108	62.002	8.9114	0.8575	Equal variances not assumed			0.861	10.929	0.408
M_3CRI	Folivore	10	63.152	9.2112	2.9129	Equal variances assumed	0.124	0.725	-0.739	116	0.461
	Frugivore	108	64.997	7.3884	0.7109	Equal variances not assumed			-0.615	10.101	0.552

For the small and large monkeys there were many significant shape variables. In fact, more shape variables obtained significant values between diet categories from monkey species with the same body size than they did when exploring the body size differences within dietary categories (compare Tables 9.11-9.12, 9.15-9.16 and Tables 5.11-5.14). This suggests that there is more morphological variation in crown shape indices and mandibular robusticity among consumers of different diets than between the different body sizes in monkeys. In contrast, the frequency with which the shape indices obtain significant values in apes are much reduced with a number of variables not obtaining any significant values (e.g., P_4 CSI and M_2 CSI in large apes, and M_1 and M_2 CSI in small apes) (Tables 9.19-9.20). These results indicate that dental and mandibular shape variables sometimes differ significantly in apes that consume different diets from the same body size category, with more significant differences occurring in the smaller species.

The results demonstrate that there are significant differences between the morphologies present in consumers of different diets, particularly in the monkeys. Based on these results it was necessary to explore the data using more comprehensive multivariate analyses.

5.1.2 Location of morphological differences between consumers of different diets (second part of research question 1 and research question 2)

This subsection is divided into two parts. Part one displays the results from a Principal Components Analysis (PCA), and part two analyses where morphological differences occur between consumers of different diets.

The PCA on the non-human primates database passed the KMO and Bartlett's Test requirements. The results indicated that the total variance explained by the four components accounted for almost 89% of the cumulative variance (Table 5.23). Where the variables load on the different components is detailed in Table 5.24. The key components of this dataset are highlighted, with component 1 dominated by size variables (crown area and corpus size), component 2 dominated by corpus robusticity indices, component 3 dominated by crown shape indices, and component 4 dominated by symphyseal robusticity indices.

Table 5.23: Total variance explained by each component in the PCA

Component	Initial Eigenvalues		
	Total	Percent of variance	Cumulative percent
1	7.461	49.739	49.739
2	3.183	21.220	70.960
3	1.678	11.186	82.146
4	0.961	6.409	88.554

Table 5.24: Variables that contribute to each component in the Rotated Component Matrix. Variable clusters are highlighted.

	Component			
Variable	1	2	3	4
LogP4M3CA	0.950	0.273	0.014	0.002
LogSS	0.971	0.111	0.050	0.102
LogP4CS	0.970	0.182	0.109	-0.016
LogM1CS	0.975	0.174	0.106	-0.010
LogM2CS	0.970	0.197	0.106	-0.022
LogM3CS	0.961	0.225	0.106	-0.040
P4CSI	0.295	0.281	0.754	-0.070
M1CSI	0.212	0.107	0.85	-0.018
M2CSI	-0.020	0.017	0.881	0.016
M3CSI	-0.119	0.257	0.755	-0.243
SRI	0.009	-0.055	-0.154	0.978
P4CRI	0.183	0.759	0.414	0.052
M1CRI	0.151	0.870	0.359	-0.054
M2CRI	0.235	0.919	0.113	-0.061
M3CRI	0.347	0.809	-0.066	-0.043
Cumulative % variance explained	49.7%	71%	82.1%	88.6%

Rotation Method: Varimax with Kaiser Normalization

Rotation converged in 5 iterations.

The component clusters identified in the rotated components matrix of the PCA (Table 5.24) were used in bivariate graphs to analyse dietary differences. The following diets were included in these graphs: 1) traditional diet categories, 2) specific classification coding categories by both direct observation and faecal analysis, and 3) quantity categories by both direct observation and faecal analysis. The graphs that best displayed the differences between taxa were used in this section.

There was little to separate out the traditional diet categories using component 1 (loading factors dominated by size variables) and component 2 (loading factors dominated by corpus robusticity indices) on the *x* and *y* axes, yet when component 3 (loading factors dominated by crown shape indices) was used on the *y*-axis differences emerged. Frugivore-insectivores were small in size (plot lower on component 1) and had wide crowns (plot higher on component 3), yet there was a lot of overlap in size for the rest of the groups (Figure 5.21). The omnivores and folivores had the longest crowns (plotting lowest on component 3), while there was a lot of overlap within the frugivore category ranging from both ends of the crown shape index spectrum (long – wide) (Figure 5.21). There were morphological differences present relating to component 2 (corpus robusticity indices) and component 3 (crown shape indices) in the species characterised by different dietary categories, even when component 1 (size variables) was removed from the graph (Figure 5.22).

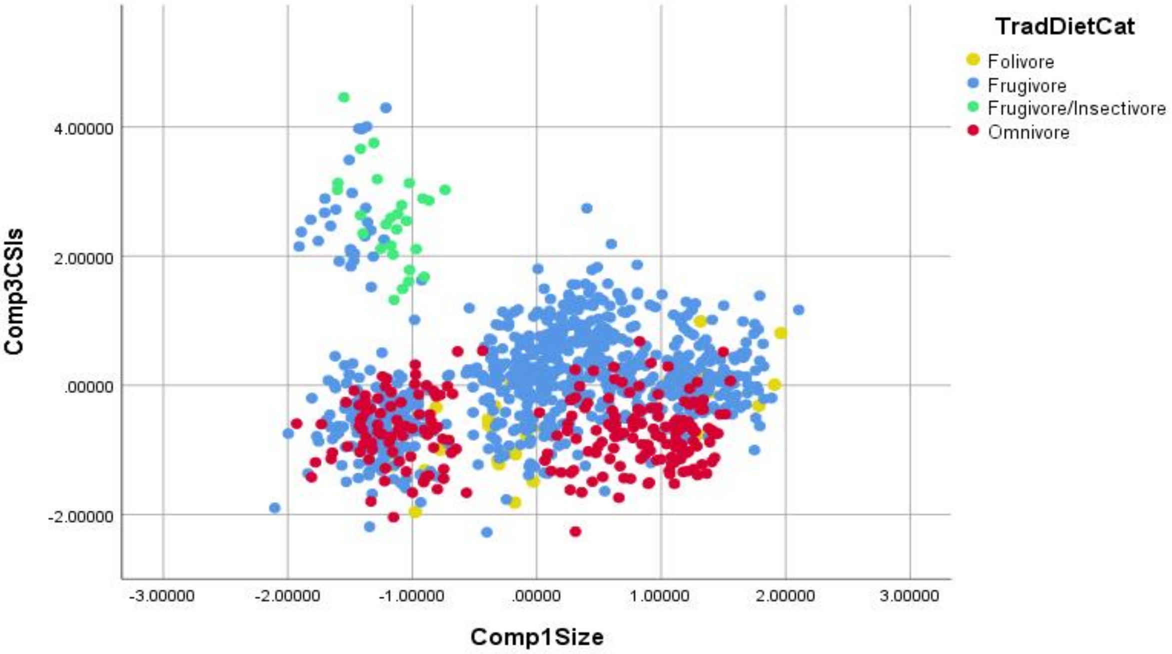

Figure 5.13: Traditional dietary categories by components 1 (size variables) and 3 (crown shape indices (CSI))

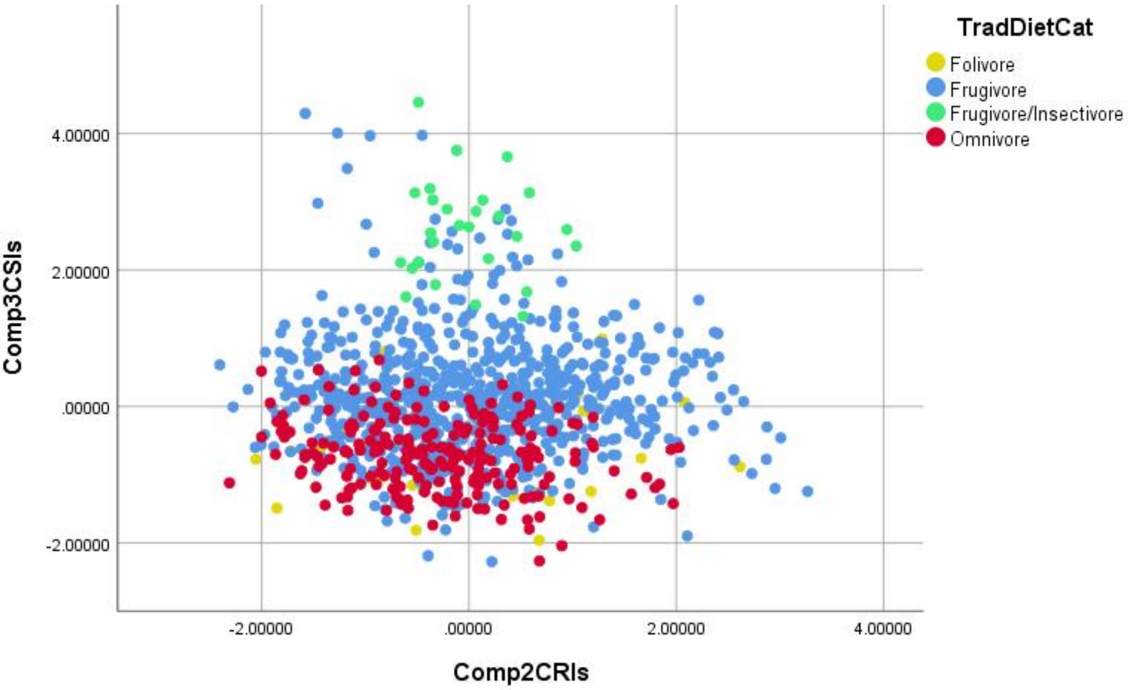

Figure 5.14: Traditional dietary categories by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI))

When the specific classification coding categories were used, the output was very different between those using direct observation (Figures 5.23-5.24) and faecal analysis (Figures 5.25-5.27). The number of categories used largely determined the clarity of the graphs. For the graphs using data obtained through direct observation, the folivore-based categories clustered together, as did frugivore-based categories, while omnivores were more dispersed (Figure 5.23). There appear to be size-related patterns in the graphs; folivore-based species were generally larger (plot higher on component 1 (size variables)), while frugivore-insectivores were smaller (plot lower on component 1 (size variables)) than the other categories. Furthermore, the two groups that have seeds as a secondary food item (folivore-granivore, frugivore-granivore) clustered closer together on both axes, indicating that consumption of seeds occurs in similarly sized non-human primates, with slightly different corpus robusticity indices (the folivore-based group has a wider corpus and the frugivore-based group a taller corpus) (Figure 5.23).

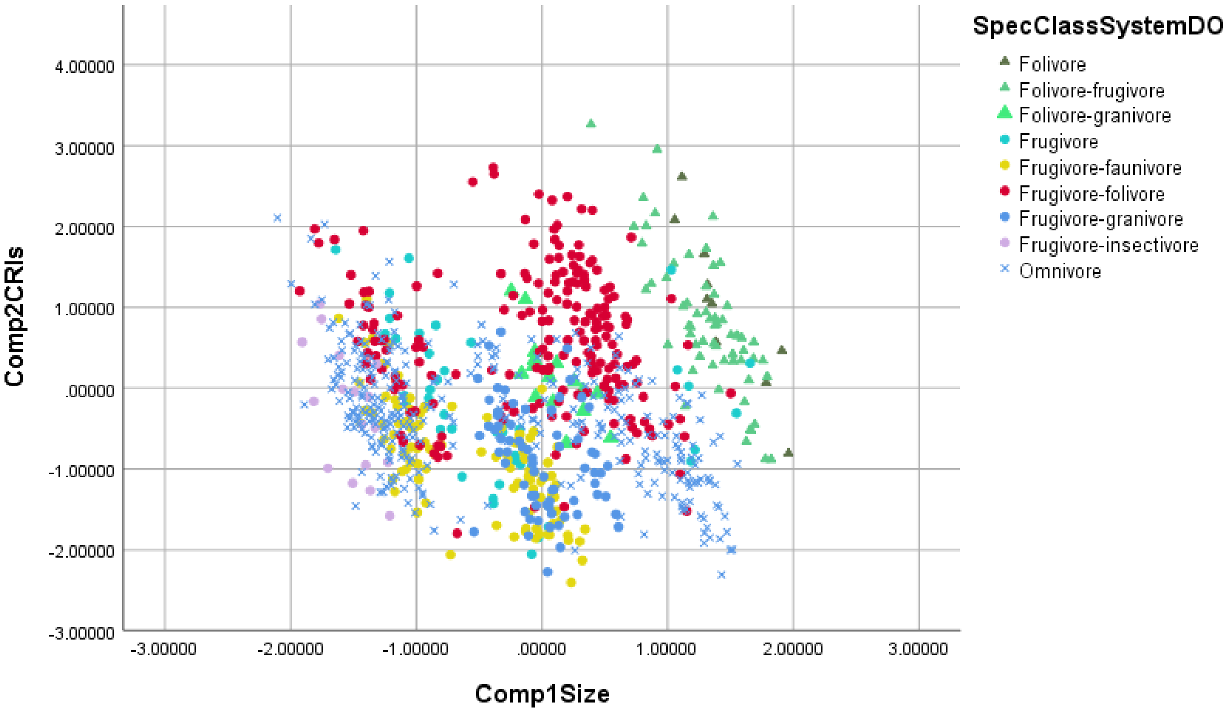

Figure 5.15: Specific classification coding categories by direct observation (DO) for components 1 (size variables) and 2 (corpus robusticity indices (CRI))

When the shapes (component 2 (corpus robusticity indices) and component 3 (crown shape indices)) were plotted against each other the patterns were less clear. Despite this, folivore-based diets plot higher on component 2 (corpus robusticity indices), while frugivore-based diets and omnivores plot lower on component 2 (corpus robusticity indices), indicating that consumers of a folivorous-based diet present relatively wider mandibular corpora to consumers of frugivorous-based foods and omnivores (Figure 5.24).

The exception to this pattern is the frugivore-folivores who appear to overlap more with folivorous-based diets. Patterns are not quite as defined across component 3 (crown shape indices) with plenty of overlap present, but frugivore-insectivores plot highest on component 3 (crown shape indices), while frugivores and folivore-based diets plot lowest on component 3 (crown shape indices), and omnivores overlap both ranges (Figure 5.24). These plots indicate frugivore-insectivores present relatively wider tooth crowns while frugivores and folivore-based diets present relatively longer tooth crowns, and omnivores present both long and wide tooth crowns, and the rest of the dietary categories plot midway between these groups.

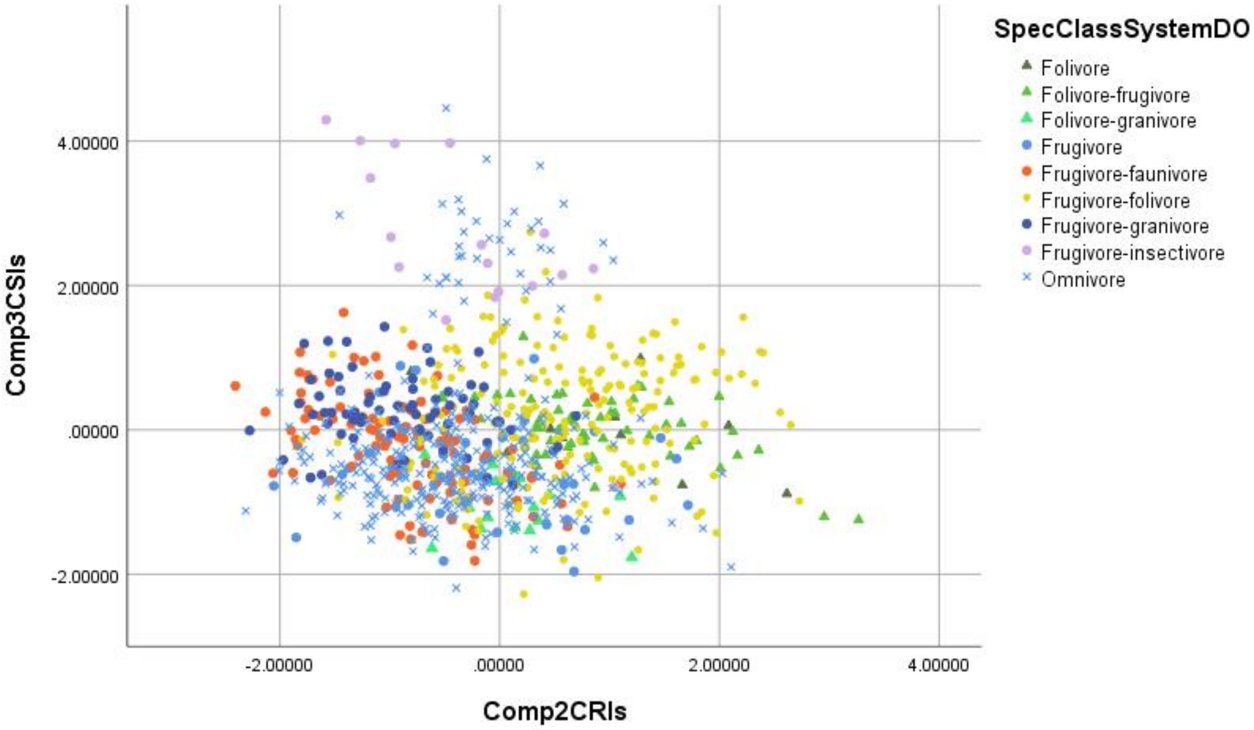

Figure 5.16: Specific classification coding categories by direct observation (DO) for components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI))

There were fewer dietary categories for specific classification coding using faecal analysis than direct observation. As a result, clearer patterns emerged in the way the groups clustered. Most of the dietary groups clustered in a way that reflected size. Frugivore-insectivores were the smallest (plot lowest on component 1 (size variables)); then frugivore-granivores; then frugivore-faunivores; and finally folivore-frugivores were the largest in size (plot highest on component 1 (size variables)), overlapping all of these diet categories were frugivore-folivores and omnivores (Figure 5.25).

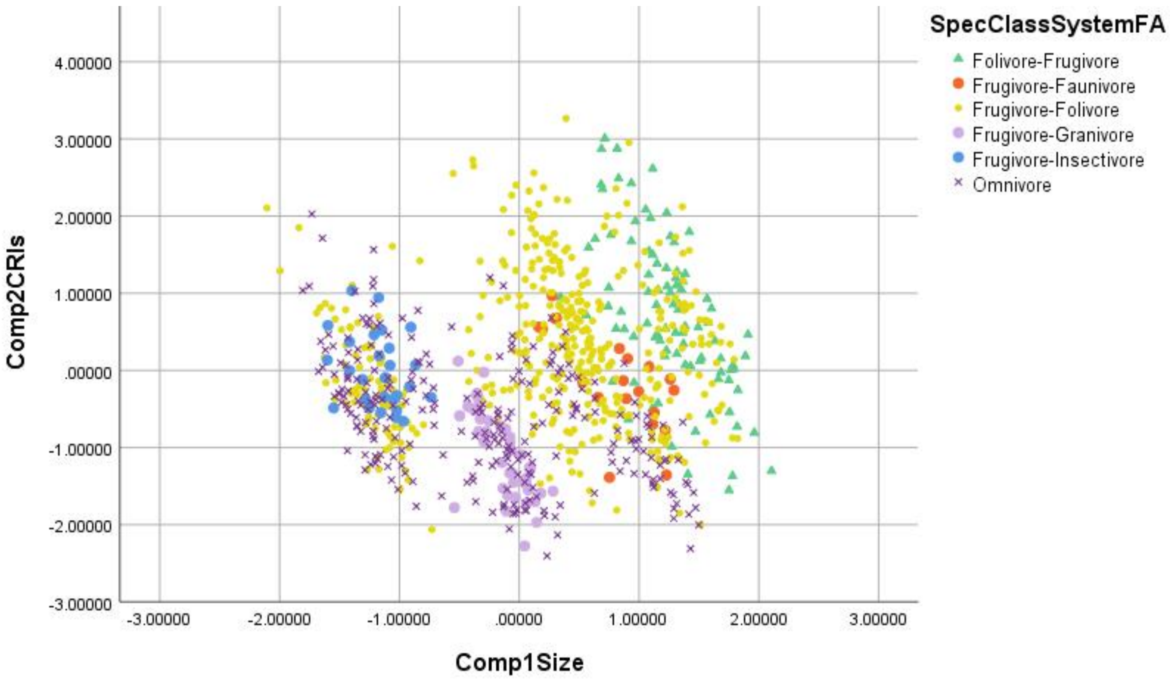

Figure 5.17: Specific classification coding categories by faecal analysis (FA) for components 1 (size variables) and 2 (corpus robusticity index (CRI))

When only shape-based variables were included there was considerably more overlap between the dietary categories, but still clustering of the groups remained (Figures 5.26-5.27). Frugivore-insectivores had wider tooth crowns (plot higher on component 3 (crown shape indices)) and frugivore-faunivores had longer tooth crowns (plot lower on component 3 (crown shape indices)) relative to the other dietary categories, with the rest displaying extensive overlap (Figures 5.26-5.27). Omnivores, frugivore-granivores and frugivore-faunivores had relatively taller corpora (plot lower on component 2 (corpus robusticity indices)), while folivore-frugivores had wider corpora (plot higher on component 2 (corpus robusticity indices)). Frugivore-folivores overlapped the rest of the diet categories and presented both tall and wide corpora relative to the other dietary categories (ranging from low – high on component 2 (corpus robusticity indices)), while frugivore-insectivores plotted at the midpoint of component 2 (corpus robusticity indices), indicating they were neither tall nor wide at the corpus (Figure 5.26).

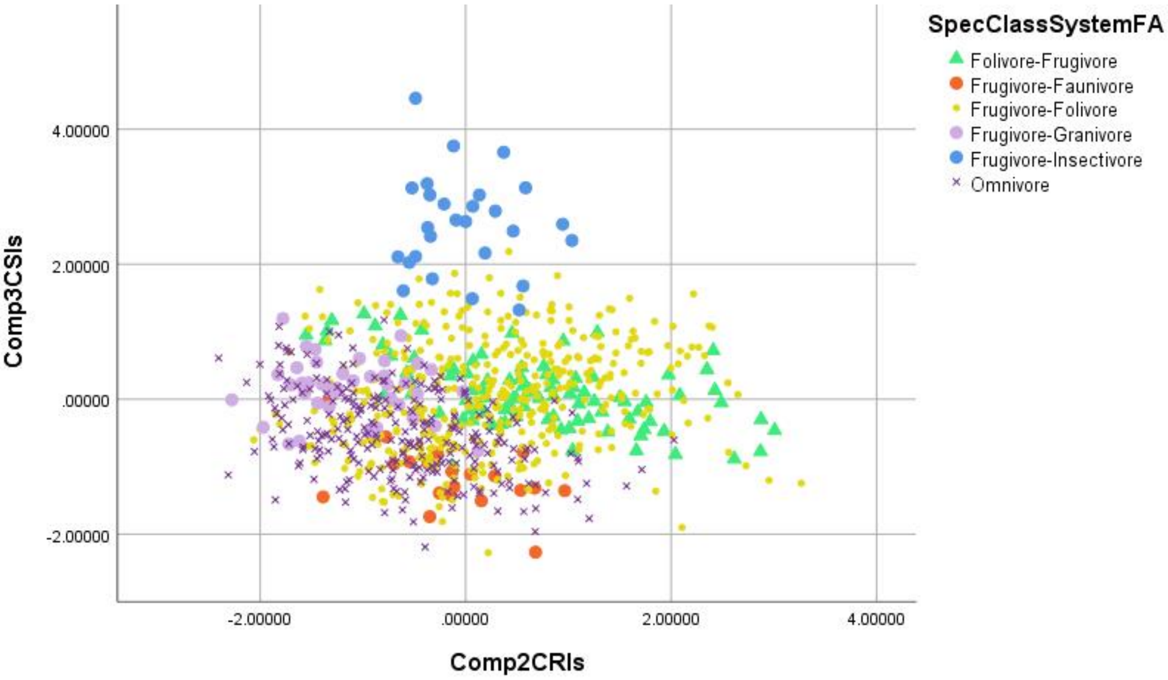

Figure 5.18: Specific classification coding categories by faecal analysis (FA) for components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI))

Frugivore-faunivores, frugivore-insectivores, frugivore-granivores and omnivores plot higher on component 4 (loading factors dominated by symphyseal robusticity indices), indicating they have relatively wider mandibular symphyses, while folivore-frugivores had taller mandibular symphyses (plot lower on component 4 (symphyseal robusticity indices)) (Figure 5.27). Frugivore-folivores overlapped the rest of the diet categories and presented both tall and wide symphyses relative to the other dietary categories (ranging from low – high on component 4 (symphyseal robusticity indices) (Figure 5.27).

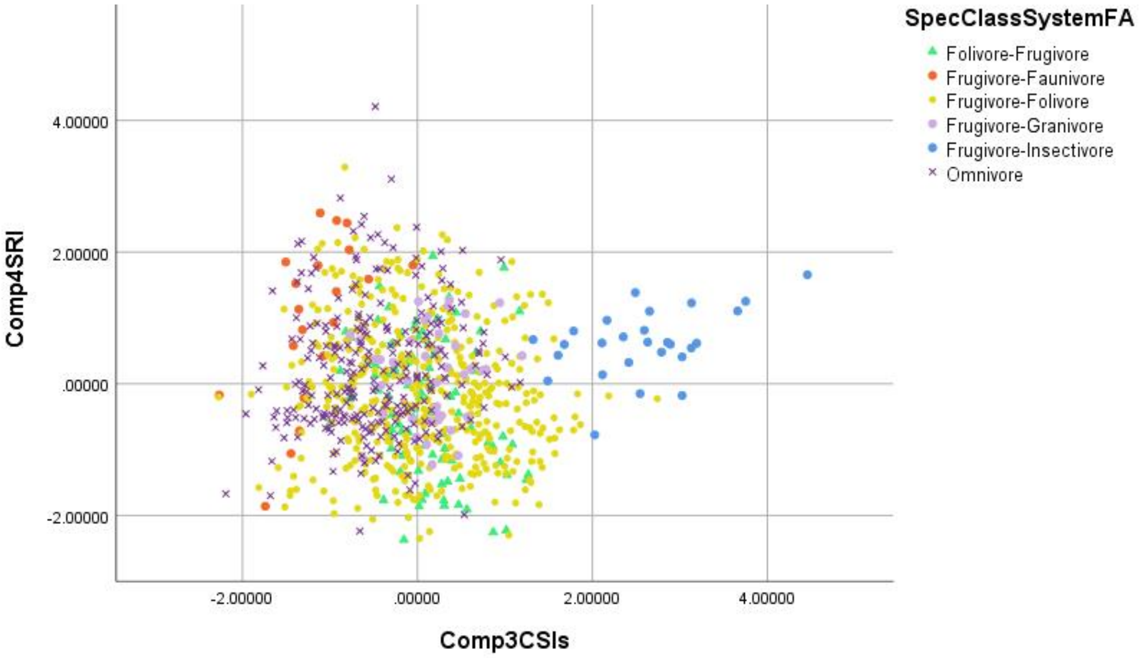

Figure 5.19: Specific classification coding categories by faecal analysis for components 3 (crown shape indices (CSI)) and 4 (symphyseal robusticity indices (SRI)

When the quantity categories (low, moderate and high consumption groups) of different foods (fruits, leaves, seeds, roots and animals) were included the most distinction in the groupings consistently arose with component 1 (size variables), but there were instances where that was not the case. Due to the fact that size differences do dominate the graphs so heavily, it was decided to focus on the graphs where component 1 (size variables) was not included to determine how differences in quantities of certain foods might correspond to the shape variables.

Fruit consumption

Differences between groups consuming different quantities of fruits were best illustrated by component 2 (corpus robusticity indices), when comparing component 2 and 3 (crown shape indices) by faecal analysis (Figure 5.28), as displayed below. High (3) consumption of fruits is very widely distributed, overlapping with the other two groups but with no particular pattern (Figure 5.28). In contrast, low (1) and moderate (2) consumers are more distinct. Low consumers of fruits plot relatively higher on component 2 (corpus robusticity indices) than do moderate consumers, indicating that low consumers have relatively wider mandibular corpora and moderate consumers have relatively taller corpora. There does not appear to be a pattern between low, moderate and high consumers of fruits on component 3 (crown shape indices).

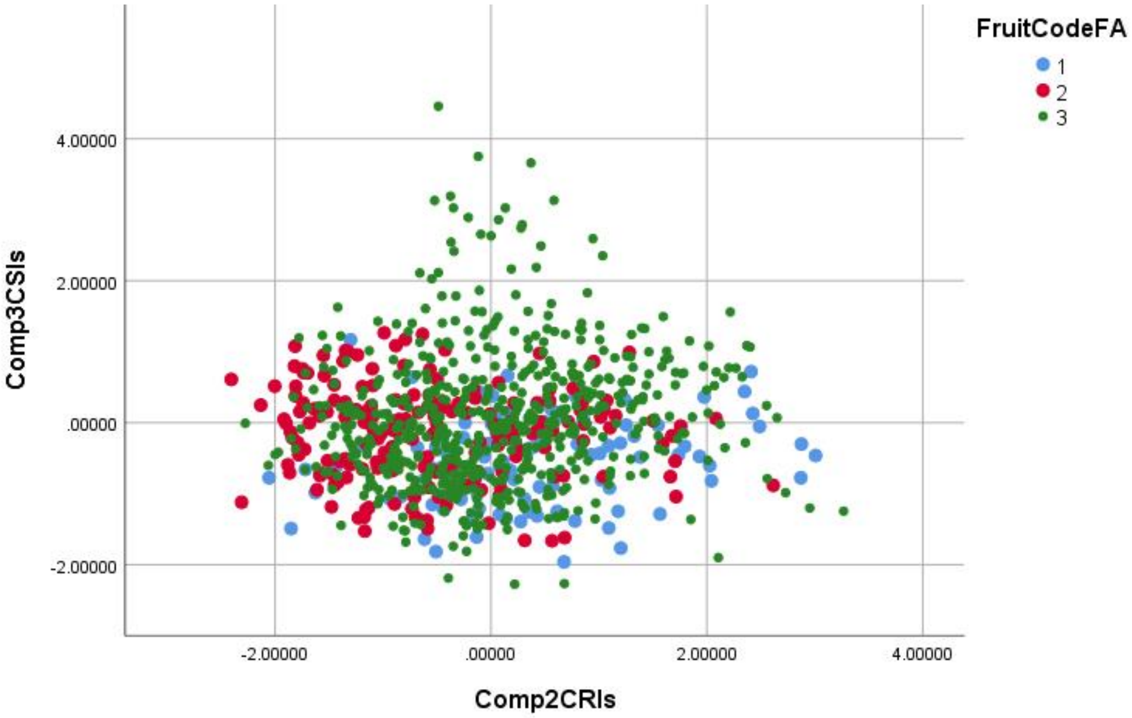

Figure 5.20: Fruit consumption using faecal analysis (FA) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

Overall, consuming a high quantity of fruit does not appear to correspond to a particularly defined morphology; in contrast, consumption of lower quantities of fruits appears to be associated with a more distinct morphological pattern. It is possible that the latter point is a reflection of the variation in the food mechanical properties of the other foods making up the rest of the diet.

Leaf consumption

Differences between groups consuming different quantities of leaves were best illustrated by graph using direct observation and components 2 (corpus robusticity indices) and 3 (crown shape indices), while trends are displayed using components 3 (crown shape indices) and 4 (symphyseal robusticity indices) (Figures 5.29-5.30). Low consumers of leaves are scattered across all components, and extend higher on component 3 (crown shape indices) and lower on component 4 (symphyseal robusticity indices) than do moderate and high consumers of leaves (Figures 5.29-5.30). This pattern of distribution for low consumers of leaves indicates they can be characterised by tall and wider corpus and symphyses, and long and wide tooth crowns. High consumers of leaves plot higher on component 2 (corpus robusticity indices) and component 3 (crown shape indices) than do moderate consumers, indicating that high consumers have relatively wider mandibular corpora and tooth crowns, while moderate consumers have relatively taller corpora and longer tooth crowns (Figures 5.29-5.30). On component 4 (symphyseal robusticity indices), high consumers plot somewhat lower than do moderate consumers, indicating that high consumers of leaves have somewhat taller mandibular symphyses and moderate consumers of leaves have relatively wider symphyses (Figure 5.30).

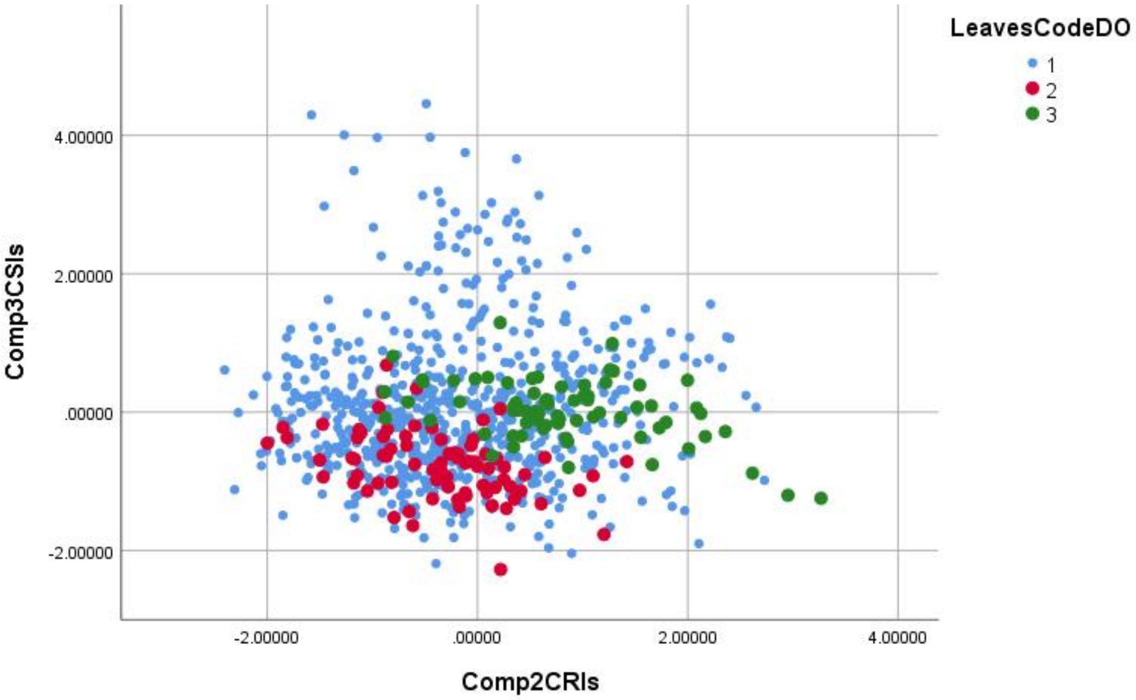

Figure 5.21: Leaves consumption using direct observation (DO) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI)). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

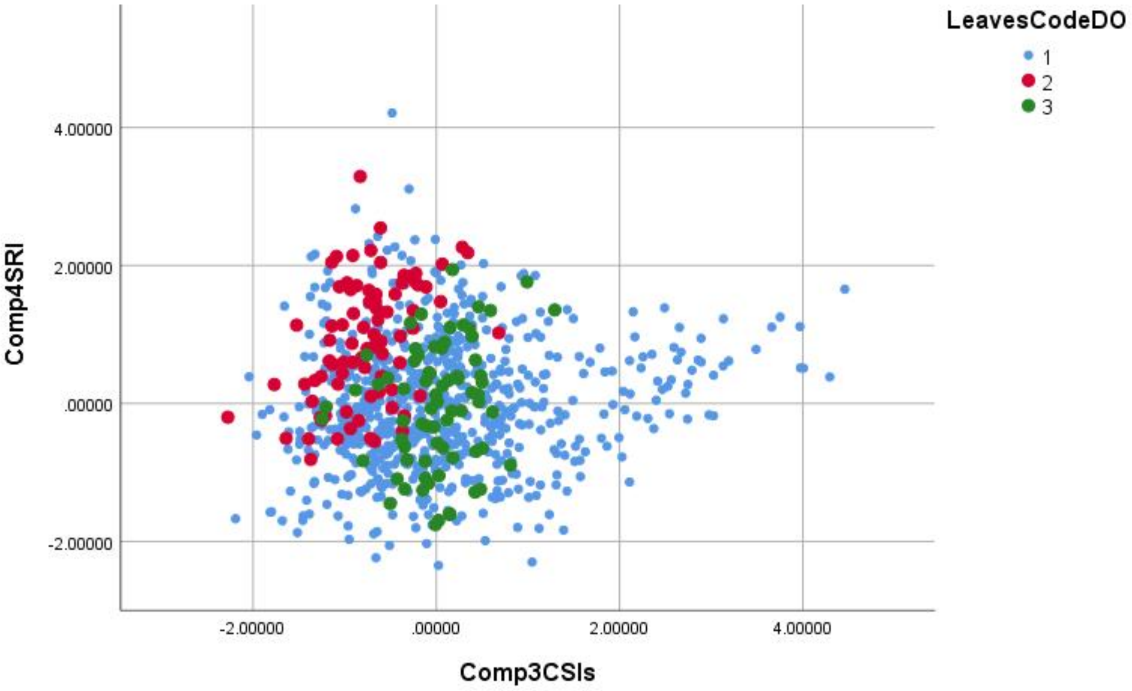

Figure 5.22: Leaves consumption using direct observation (DO) by components 3 (crown shape indices (CSI)) and 4 (SRI). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

Consuming a low quantity of leaves does not appear to correspond to a particularly defined morphology, with variation present in both the corpus and crown morphology, as evinced by the scattered distribution of low consumers across the various components. In contrast, consumption of moderate and high quantities of leaves appears to be associated with more limited and distinct ranges of variation, and thus a more distinct morphological pattern.

Seed consumption

Trends between groups consuming different quantities of seeds were best illustrated by components 2 (corpus robusticity indices) and 3 (crown shape indices) by direct observation (Figure 5.31). Low consumers of seeds are scattered across all components, extending higher on components 2 (corpus robusticity indices) and 3 (crown shape indices) than do moderate and high consumers of seeds (Figure 5.19). These patterns of distribution for low consumers of seeds indicate they can be characterised by tall and wider corpora, and long and wide tooth crowns. High consumers of seeds plot lower on component 2 (corpus robusticity indices) and slightly higher on component 3 (crown shape indices) than do moderate consumers, indicating that high consumers have relatively taller mandibular corpora and wider tooth crowns, while moderate consumers have relatively wider mandibular corpora and longer tooth crowns (Figure 5.31).

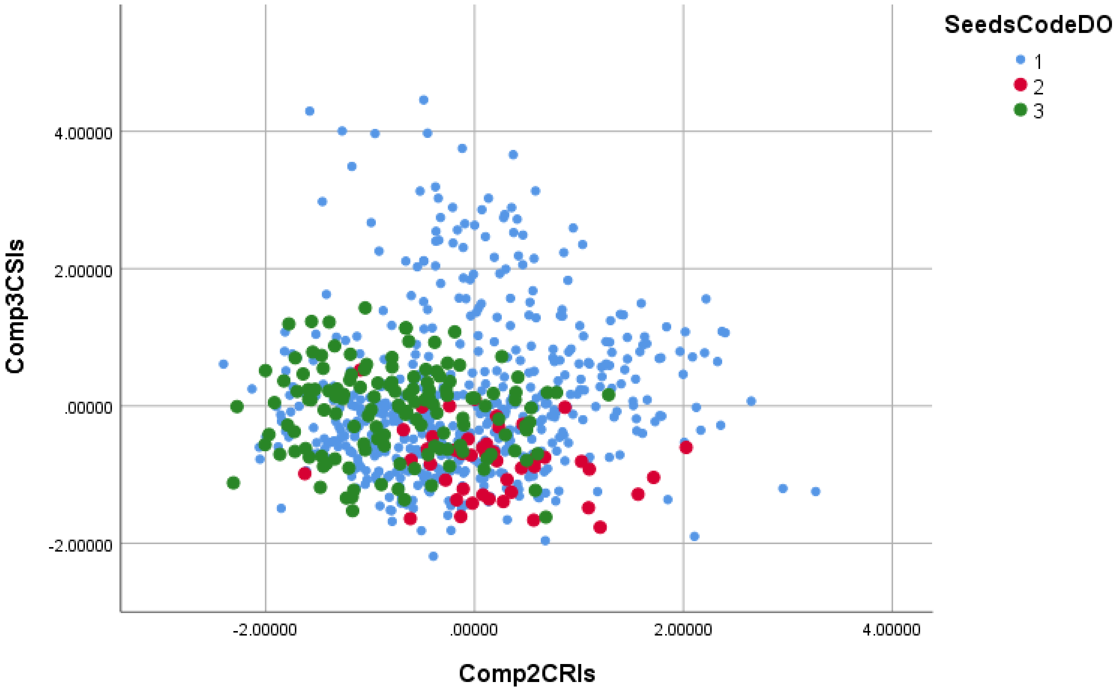

Figure 5.23: Seeds consumption using direct observation (DO) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI)). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

Consuming a low quantity of seeds does not appear to correspond to a particularly defined morphology, with variation present in both the corpus and crown morphology, as evinced by the scattered distribution of low consumers across the various components. In contrast, consumption of moderate and high quantities of seeds appears to be associated with more limited and distinct ranges of variation, and thus a more distinct morphological pattern.

Root consumption

The bivariate graphs using components 1-4 are somewhat different depending on whether root consumption by direct observation or faecal analysis is used. Low consumption of roots is very widely distributed in graphs using both direct observation and faecal analysis, overlapping with both moderate and high consumers but with no particular pattern (Figures 5.32-5.33). Low consumers are characterised by having both wider and taller, and thus more varied mandibular corpora.

The trends present in graphs using direct observation and faecal analysis were reversals of each other, with those by direct observation indicating high consumers of roots plot lower on component 2 (corpus robusticity indices) than do moderate consumers, while the graphs using faecal analysis indicate high consumers of roots plot higher on component 2 (corpus robusticity indices) than do moderate consumers. So depending on whether direct observation or faecal analysis is used, a high root consumer will either display a relatively taller mandibular corpus (direct observation) or relatively wider mandibular corpus (faecal analysis), while moderate consumers will either display a relatively wider mandibular corpus or taller mandibular corpus (Figures 5.32-5.33). There does not appear to be a pattern between low, moderate and high consumers of roots on component 3 (crown shape indices) by either direct observation or faecal analysis.

Consuming a low quantity of roots does not appear to correspond to a particularly defined morphology, with variation present in both the corpus and crown morphology, as evinced by the scattered distribution of low consumers across the various components. In contrast, consumption of moderate and high quantities of roots appears to be associated with more limited and distinct ranges of variation, and thus a more distinct morphological pattern, particularly on component 2 (corpus robusticity indices).

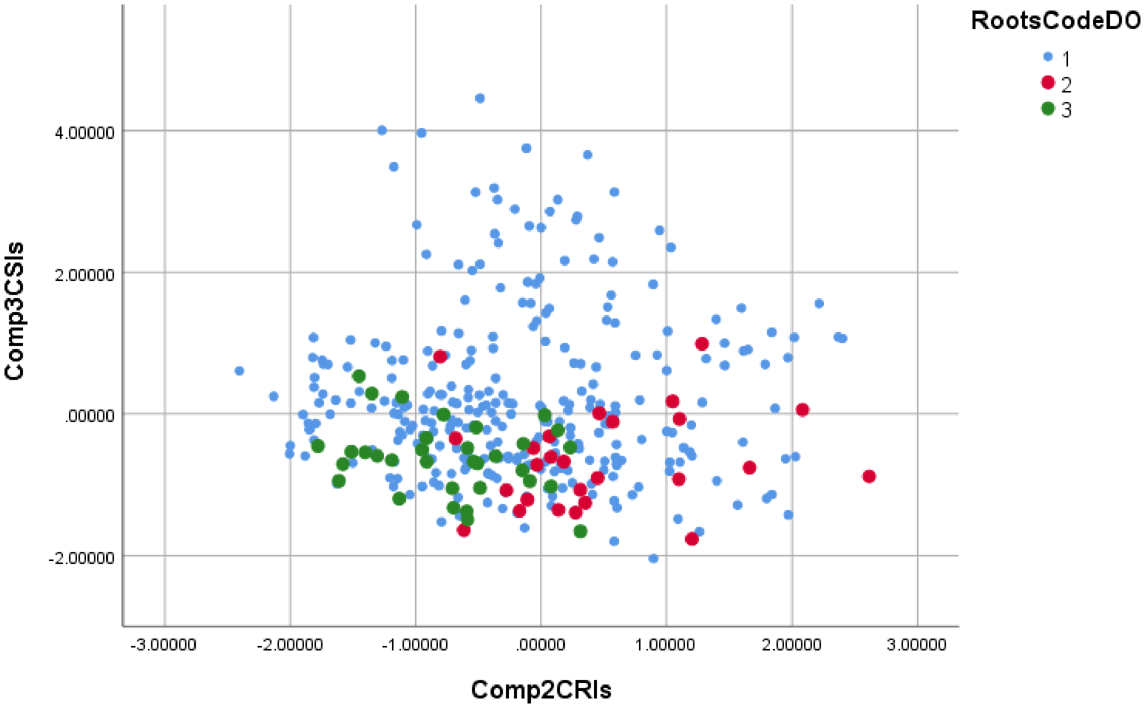

Figure 5.24: Roots consumption using direct observation (DO) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI)). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

Sample size was reduced for the graphs on roots by direct observation (Figure 5.32), because not many of the species analysed are recorded to be consumers of roots. In contrast, more species are present for those analysed by faecal analysis (Figure 5.33).

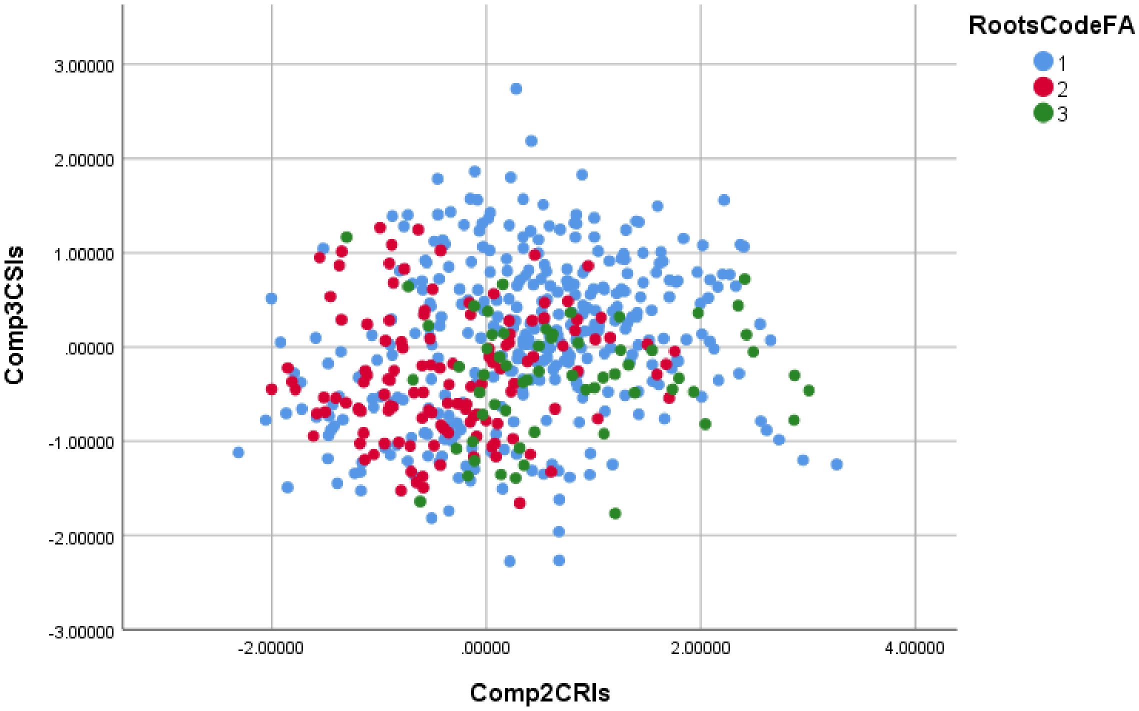

Figure 5.25: Roots consumption using faecal analysis (FA) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI)). 1 = low consumption, 2 = moderate consumption, 3 = high consumption.

These graphs for root consumption highlight the different patterns that can emerge depending on the data collection method used (direct observation or faecal analysis). They highlight the importance of analysing the data obtained by the two methods separately.

Animal consumption

Differences between groups consuming different quantities of animals were best illustrated by component 3 (crown shape indices) when using components 2 (corpus robusticity indices) and 3 (crown shape indices) by faecal analysis as shown in Figure 5.34. Moderate and high consumption groups cluster in distinct patterns on component 3 (crown shape indices), although the pattern for moderate consumers is unique. Moderate consumers are clustered in groups at both ends of component 3 (crown shape indices) axis, while high consumers are clustered at the low range of the same axis. These patterns indicate species consuming moderate quantities of animals can be characterised by both long and wide tooth crowns, while high consumers have relatively longer crowns. Low consumers appear to be distributed all over the place on component 2 (corpus robusticity indices) and around the midline of component 3 (crown shape indices), indicating low consumers have a varied corpus morphology, neither long nor wide tooth crowns (Figure 5.34).

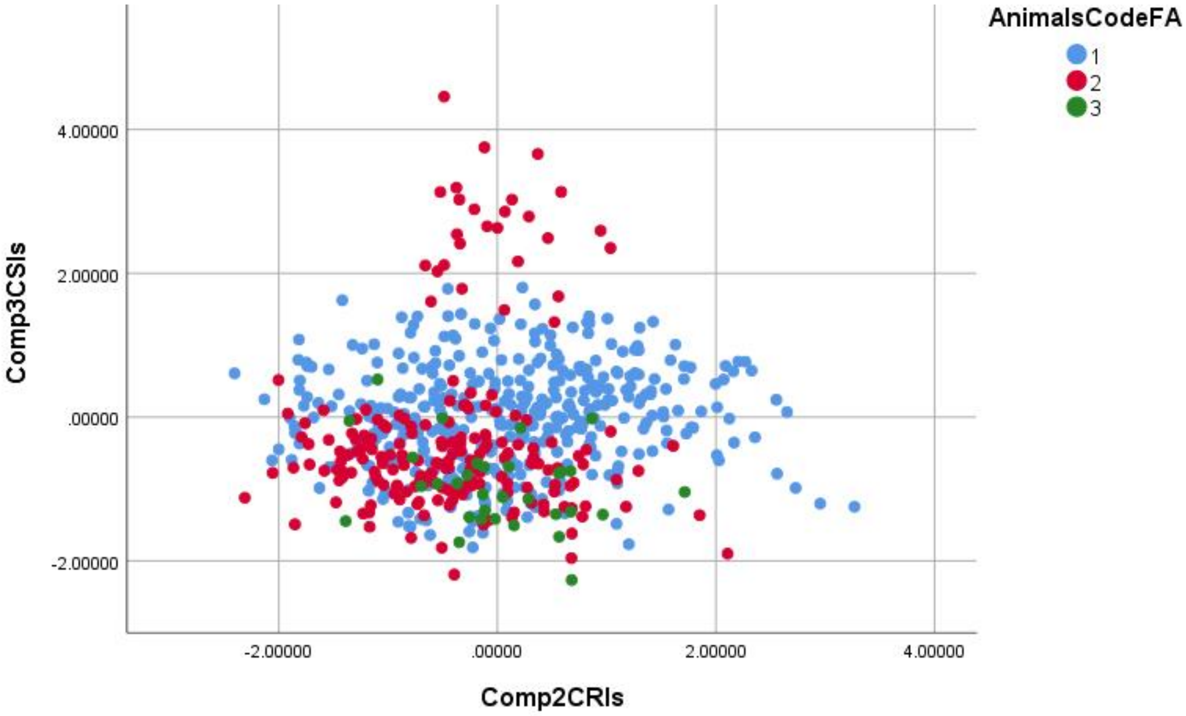

Figure 5.26: Animals consumption using faecal analysis (FA) by components 2 (corpus robusticity indices (CRI)) and 3 (crown shape indices (CSI)). 1 = low consumption, 2 = moderate consumption, 3 = high consumption. The more isolated cluster of moderate consumers that plot higher up on component 3 (crown shape indices) is the capuchin genera (*Cebus* and *Sapajus*).

5.1.3 Contribution of diet to morphological variation (research question 3)

There was a reasonably consistent pattern across each of the multiple regression analyses using each of the components (1-4) in terms of which dietary categories/ food quantities best explained the morphological variance present. As explained in the Methods, for each component analysed different models were run for the different types of diet categories (traditional diet, specific classification categories and quantity categories using both direct observation and faecal analysis) and of those, the regression models that best explained the morphological variance are presented here. The model summaries/ ANOVA results are detailed in Table 5.25, and their coefficient values detailed in Table 5.26.

All of the Adjusted R^2 model summaries and ANOVAs for component 1 (loadings dominated by dental and mandibular size variables) were consistent and significant, with all dietary categories accounting for approximately 10% of the variance. The model that best explained the morphological variance present included log body size, sex, fruits & seeds by direct observation, which according to the Adjusted R^2 in the model summaries accounted for as much as 86.8% of variance for component 1 (Table 5.25). The inclusion of fruits & seeds direct observation increased the percentage of variance accounted for from 77.8% to 86.8%.

All of the Adjusted R^2 model summaries and ANOVAs for component 2 (loadings dominated by corpus robusticity indices) were consistent and significant. The model that best explained the morphological variance present included log body size, sex, fruits, leaves & seeds (FA), which according to the Adjusted R^2 in the model summaries accounted for 51.7% of variance for component 2 (Table 5.25). The inclusion of fruits, leaves & seeds (FA) increased the percentage of variance from 31% to 51.7%.

The Adjusted R^2 model summaries and ANOVAs for component 3 (loadings dominated by crown shape indices) were consistent and significant. The model that best explained the morphological variance present in component 3 was that which included log body size, sex, fruits, roots & leaves (FA), which according to the Adjusted R^2 in the model summaries accounted for as much as 40.4% of the variance (Table 5.25). The inclusion of fruits, roots & leaves (FA) increased the percentage of variance accounted for from 22.8% to 40.4%.

All of the Adjusted R^2 model summaries and ANOVAs for component 4 (loadings dominated by symphyseal robusticity indices) were consistent and significant. The dietary category that best explained the morphological variance was log body size, sex, fruits, leaves & roots (FA), which according to the Adjusted R^2 in the model summaries accounted for 20.7% of the variance for component 4 (Table 5.25). The inclusion of these different food types increased the variance explained from 0.012% (just sex and body weight) to 20.7%.

Each of the model summaries from components 1-4 show that diet is an important variable to explain morphological variation in the mandible and dentition, particularly in the shape variables. For components 1 and 2 the diets that incorporate fruits and seeds in them appear to be the ones that best explain the variance (on top of body size and sex), but for components 3 and 4 the diets that included fruits, leaves and roots appear to best explain the variance present (on top of body size and sex).

Table 5.25: Percentage of variance explained (Adjusted R^2) and ANOVA results for the final model of each multiple regression analysis for Components 1-4.

Model summaries				ANOVA			
Comp.	Diet contents	Model	Model Summary (Adjusted R^2)	Model	df	*F*	Sig
1	Fruits & seeds using direct observation (*n* = 661)	1: Log body weight, sex	0.778				
		2: Log body weight, sex, fruits & seeds	0.868	Regression	4	1090.629	**0.000**
				Residual	656		
2	Fruit, leaves & seeds using faecal analysis (*n* = 721)	1: Log body weight, sex	0.31				
		2: Log body weight, sex, fruits, leaves & seeds	0.517	Regression	5	154.89	**0.000**
				Residual	715		
3	Fruit, leaves & roots using faecal analysis (*n* = 482)	1: Log body weight, sex	0.228				
		2: Log body weight, sex, fruits, leaves & roots	0.404	Regression	5	66.296	**0.000**
				Residual	476		
4	Fruit, leaves & roots using faecal analysis (*n* = 482)	1: Log body weight, sex					
		2: Log body weight, sex, fruits, leaves & roots	0.012	Regression	5	26.037	**0.000**
			0.207	Residual	476		

The unstandardised coefficients for components 1-4 by the different dietary categories present largely consistent results throughout each component (Table 5.26). Overall, the two highest coefficients outside of the constant were log body size (highest for components 1 and 3, and joint highest with sex for component 4) and sex (highest coefficient for component 2 and joint highest with body size for component 4). For each component, within each dietary category there was minimal variation between the coefficients for the different foods, with the exception of some foods reporting negative and positive values.

The food type that best explained the variance present for component 1 (highest loading factors = dental and mandibular size variables) was fruits & seeds using direct observation and is largely reflective of the rest of the dietary categories analysed for this component. The multiple regression analysis for component 1 predicts that log body size (*B* = 0.713, *p* = 0.000) and seed (*B* = 0.026, *p* = 0.000) consumption significantly increased as component 1 increased, but fruit (*B* = -0.007, *p* = 0.000) consumption significantly decreased as component 1 increased. Sex differences (*B* = 0.042, *p* = 0.127) did not obtain a significant *p*-value on the *t*-statistic, indicating it did not increase or decrease with component 1 (Table 5.26).

The food type that best explained the variance present for component 2 (highest loading factors = corpus robusticity indices) was fruits, leaves & seeds using faecal analysis and is reflective of the rest of the dietary categories analysed for this component. The multiple regression analysis for component 2 predicts that log body size (*B* = 0.221, *p* = 0.000), and fruit (*B* = 0.011, *p* = 0.000) and leaf (*B* = 0.016, *p* = 0.000) consumption significantly increased as the component 2 increased, but sex differences (*B* = -0.624, *p* = 0.000) and seed consumption (*B* = -0.046, *p* = 0.000) significantly decreased as component 2 increased (Table 5.26).

The food type that best explained the variance present for component 3 (highest loading factors = crown shape indices) was fruits, leaves & roots using faecal analysis and is largely reflective of the rest of the dietary categories analysed for this component. The multiple regression analysis for component 3 predicts that log body size (*B* = 0.261, *p* = 0.000), and fruit (*B* = 0.025, *p* = 0.000) and leaf (*B* = 0.017, *p* = 0.000) consumption significantly increased as component 3 increased, but sex differences significantly decreased as the component 3 increased (*B* = -0.131, *p* = 0.041). Root consumption (*B* = -0.015, *p* = 0.081) did not obtain a significant *p*-value on the *t*-statistic, indicating it did not increase or decrease with component 3 (Table 5.26).

The food type that best explained the variance present for component 4 (highest loading factors = symphyseal robusticity indices) was fruits, leaves & roots using faecal analysis and is largely reflective of the rest of the dietary categories analysed for this component. The multiple regression analysis for component 4 predicts that sex differences (*B* = 0.325, *p* = 0.002) and root consumption (*B* = 0.057, *p* = 0.000) significantly increased as component 4 increased, but log body size (*B* = 0.261, *p* = 0.007), and fruit (*B* = -0.015, *p* = 0.000) and leaf (*B* = -0.028, *p* = 0.000) consumption significantly decreased as component 4 increased (Table 5.26).

Despite these dietary categories clearly contributing towards the morphological variance as indicated by the increased Adjusted R^2 values, the coefficients Table (5.26) does not reveal any of the diets present high *B* coefficients. This finding indicates that none of the diets contribute much towards the morphological variance in any of components 1-4. Instead, for components 2 and 4, sex presented the highest *B* coefficient, and for components 1 and 3 log body size presented the highest *B* coefficient (outside of the constant). The high loadings on the coefficients for log body size and sex, and the low loadings for the foods do not correspond to the Adjusted R^2 for components 2-4 in the model summary from Table 5.25.

Table 5.26: Coefficients of components 1-4 by the models that best explained the morphological variance

Components	Dietary categories	Model	Unstandardised coefficients		Standardised Coefficients	
			B	Std. Error	*t*	Sig.
1	Fruit & seeds using direct observation (*n* = 661)	Constant	-1.826	0.068	-26.822	**0.000**
		Log body weight	0.713	0.012	61.828	**0.000**
		Sex	0.042	0.028	1.528	0.127
		Fruit	-0.007	0.001	-7.697	**0.000**
		Seeds	0.026	0.001	20.711	**0.000**
2	Fruit, leaves & seeds using faecal analysis (*n* = 721)	Constant	-0.199	0.219	-0.911	0.363
		Log body weight	0.221	0.026	8.454	**0.000**
		Sex	-0.624	0.055	-11.43	**0.000**
		Fruit	0.011	0.002	4.547	**0.000**
		Leaves	0.016	0.003	4.823	**0.000**
		Seeds	-0.046	0.004	-12.892	**0.000**
3	Fruit, leaves & roots using faecal analysis (*n* = 482)	Constant	-2.377	0.189	-12.55	**0.000**
		Log body weight	0.261	0.049	5.298	**0.000**
		Sex	-0.131	0.064	-2.048	**0.041**
		Fruit	0.025	0.003	9.598	**0.000**
		Leaves	0.017	0.004	4.739	**0.000**
		Roots	-0.015	0.009	-1.747	0.081
4	Fruit, leaves & roots using faecal analysis (*n* = 482)	Constant	1.531	0.31	4.944	**0.000**
		Log body weight	-0.219	0.081	-2.711	**0.007**
		Sex	0.325	0.104	3.118	**0.002**
		Fruit	-0.015	0.004	-3.612	**0.000**
		Leaves	-0.028	0.006	-4.629	**0.000**
		Roots	0.057	0.014	4.031	**0.000**

Multiple regression analyses were run to predict components 1 (dental and mandibular size variables), 2 (corpus robusticity indices), 3 (crown shape indices), and 4 (symphyseal robusticity indices) from log body size, sex and the various dietary categories. In each multiple regression, log body size and sex were entered for step 1, and the dietary categories were entered for step 2. Log body size and sex explained almost 80% of the variance for component 1, 31% of the variance for component 2, almost 23% of the variance for component 3, and approximately 1% of the variance for component 4.

For component 1, after entering fruits and seeds by direct observation for step 2 the total variance explained by the model increased to 86.8%, F (4, 656) = 1090.629, $p <$ .000. The dietary categories explained an additional 9% of the variance in component 1.

For component 2, after entering fruits, leaves and seeds by faecal analysis for step 2 the total variance explained by the model increased to 51.7%, F (5, 715) = 154.89, $p <$ 0.000. The dietary categories explained an additional 20.7% of the variance in component 2.

For component 3, after entering fruits, leaves and roots by faecal analysis for step 2 the total variance explained by the model increased to 40.4%, F (5, 476) = 66.296, $p <$ 0.000. The dietary categories explained an additional 17.6% of the variance in component 3.

For component 4, after entering fruits, leaves and roots by faecal analysis for step 2 the total variance explained by the model increased to 20.7%, F (5, 476) = 26.037, $p <$ 0.000. The dietary categories explained an additional 19.5% of the variance in component 4.

5.2 Section 2: Morphological analysis on non-human primates and hominins

This section is divided into two parts to address the research questions. Research question four (*Is the hominin morphology comparable to that present in non-human primates?*) is addressed in part one, and research question five (*Is it possible to associate the morphological features of the hominins with dietary categories analogous to non-human primates?*) is addressed in part two.

The Principal Components Analysis on the non-human primates and hominins database passed the KMO and Bartlett's Test requirements, meaning it was possible to proceed with analysis. Three components had eigenvalues greater than 1, and in combination explained 92.8% of the variance (Table 5.27). Where the variables load on the different components is detailed in Table 5.28. The key components of this dataset are highlighted, with component 1 dominated by size variables (crown area and corpus size), component 2 dominated by crown shape indices and component 3 dominated by corpus robusticity indices.

Table 5.27: Total variance explained by each component in the PCA on non-human primates and hominins

Component	Initial Eigenvalues		
	Total	Percent of variance	Cumulative percent
1	8.668	57.785	57.785
2	3.596	23.975	81.760
3	1.661	11.076	92.836

Table 5.28: Variables that contribute to each component in the Rotated Component Matrix. Clustered variables highlighted.

	Component		
Variable	1	2	3
LogP4M3CA	0.943	-0.008	0.325
LogSS	0.977	0.000	0.038
LogP4CS	0.940	0.087	0.320
LogM1CS	0.945	0.084	0.307
LogM2CS	0.941	0.086	0.319
LogM3CS	0.940	0.093	0.314
P4CSI	0.224	0.897	0.192
M1CSI	0.175	0.948	0.093
M2CSI	-0.023	0.936	0.016
M3CSI	-0.173	0.905	0.054
SRI	0.097	-0.193	0.832
P4CRI	0.329	0.476	0.765
M1CRI	0.343	0.399	0.822
M2CRI	0.457	0.229	0.817
M3CRI	0.541	0.042	0.778
Cumulative % variance explained	57.76	81.76	92.84

Rotation Method: Varimax with Kaiser Normalization

Rotation converged in 5 iterations.

5.2.1 Comparable morphological variation between hominins and non-human primates (research question 4).

In this section, bivariate graphs using the components extracted from the PCA were used to analyse morphological differences between different hominin and non-human primate taxa. When components 1 (size variables) and 2 (crown shape indices) were used the hominins plotted within the range of extant non-human primates, particularly the apes and the hard-object feeding mangabeys (*Cercocebus* and *Lophocebus* species) (Figures 5.35 and 5.36). When component 3 (corpus robusticity indices) was analysed, the patterns changed completely. The hominins score very high on component 3 (corpus robusticity indices) and as a result, completely separate from the non-human primates. This indicates that they have wider mandibular corpora and symphyses than any primate (*Macaca radiata* is the closest) (Figures 5.36-5.37).

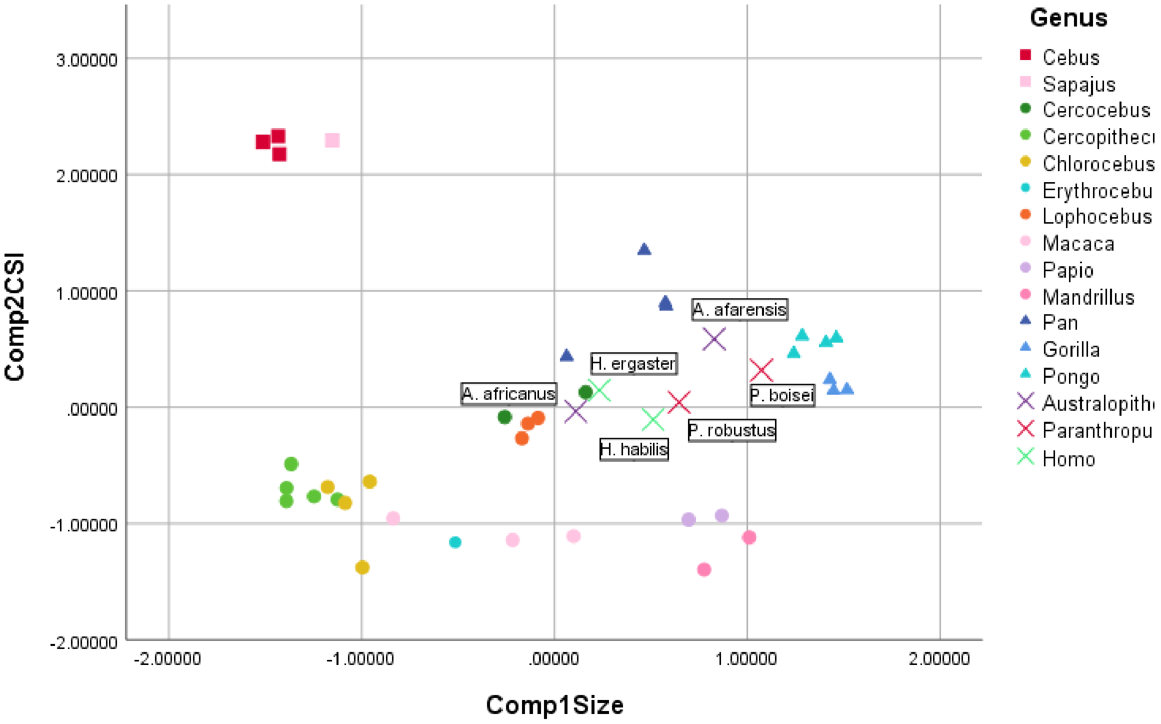

Figure 5.27: All non-human primate and hominin genera by components 1 (size variables) and 2 (crown shape indices (CSI)). *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other genera on component 2 (crown shape indices).

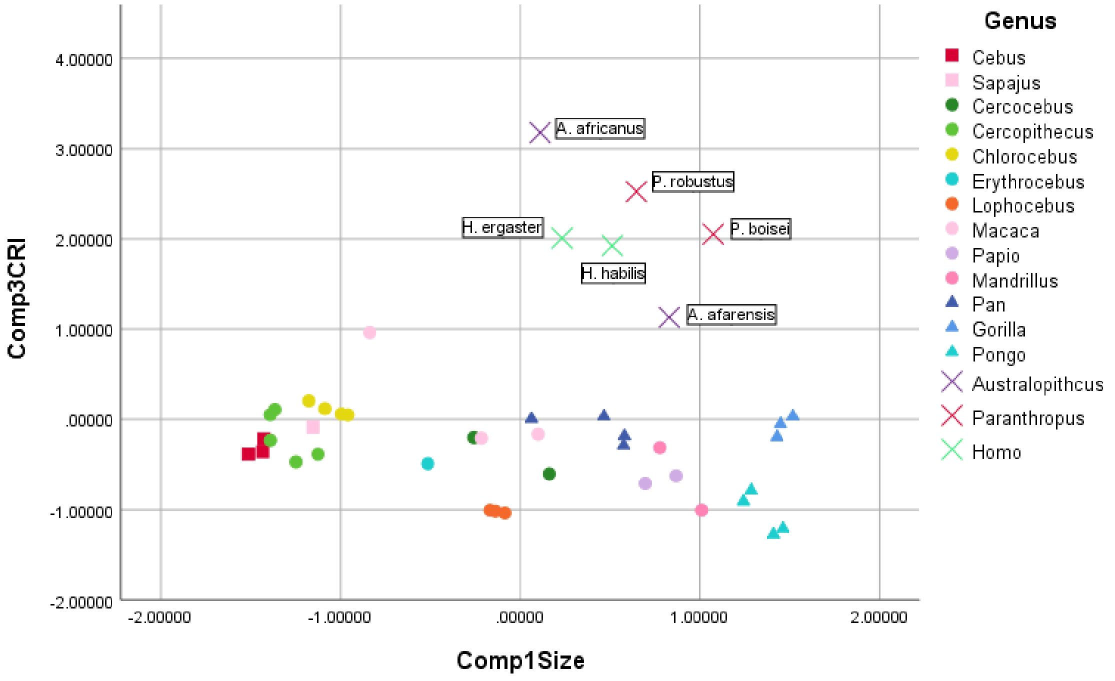

Figure 5.28: All non-human primate and hominin genera by components 1 (size variables) and 3 (corpus robusticity indices (CRI))

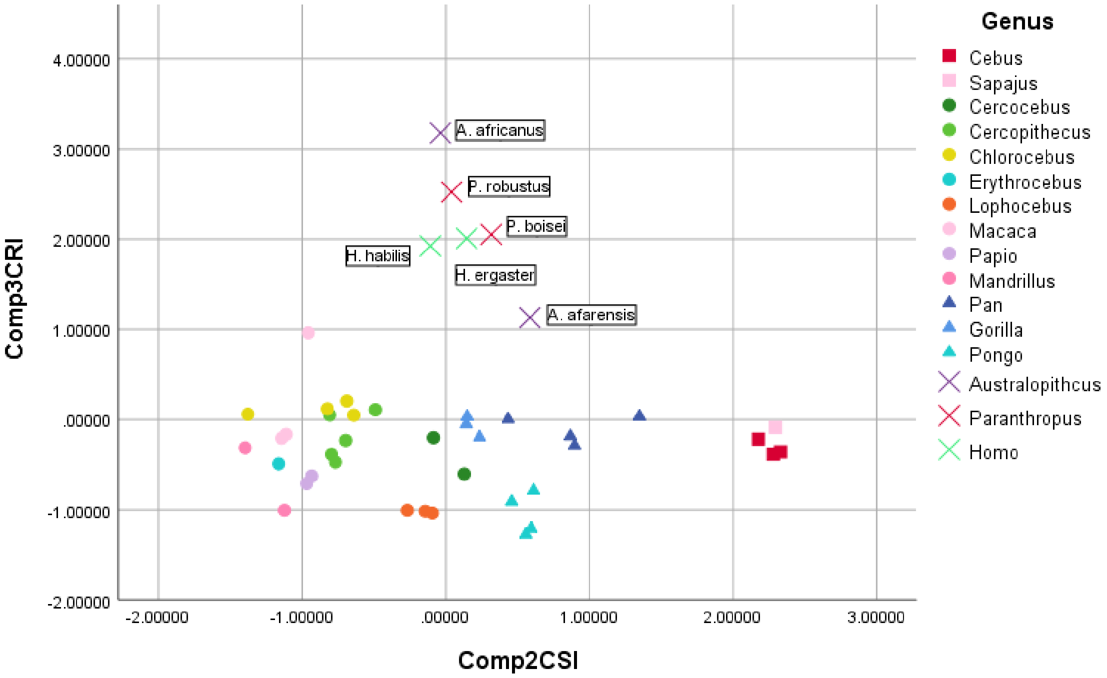

Figure 5.29: All non-human primate and hominin genera by components 2 (crown shape indices (CSI) and 3 (corpus robusticity indices (CRI))

As the hominins plot closest to the extant apes for components 1 (size variables) and components 2 (crown shape indices) (Figure 5.35), it was decided to narrow down the comparisons to the species level for the apes and hominin species. *Gorilla* and *Pongo* display similar patterns while *Pan* deviates from them, which means there are two groupings for extant apes. In contrast, the hominins are more dispersed. *P. boisei* was closer in size to *Gorilla* and *Pongo*, while the other hominins were closer in size to *Pan* for component 1 (size variables) (Figure 5.38). For component 2 (crown shape indices) *Pan* appears to be more of an outlier, while *Gorilla* and *Pongo* largely scored with hominins. Overall, the hominins appear to have crown shapes similar to the *Gorilla* and *Pongo* species/ subspecies, being slightly wider than they are long, with the exceptions of *Australopithecus africanus*, *Paranthropus robustus* and the early *Homo* species, who all plot around 0 meaning they have crown shapes that are as wide as they are long.

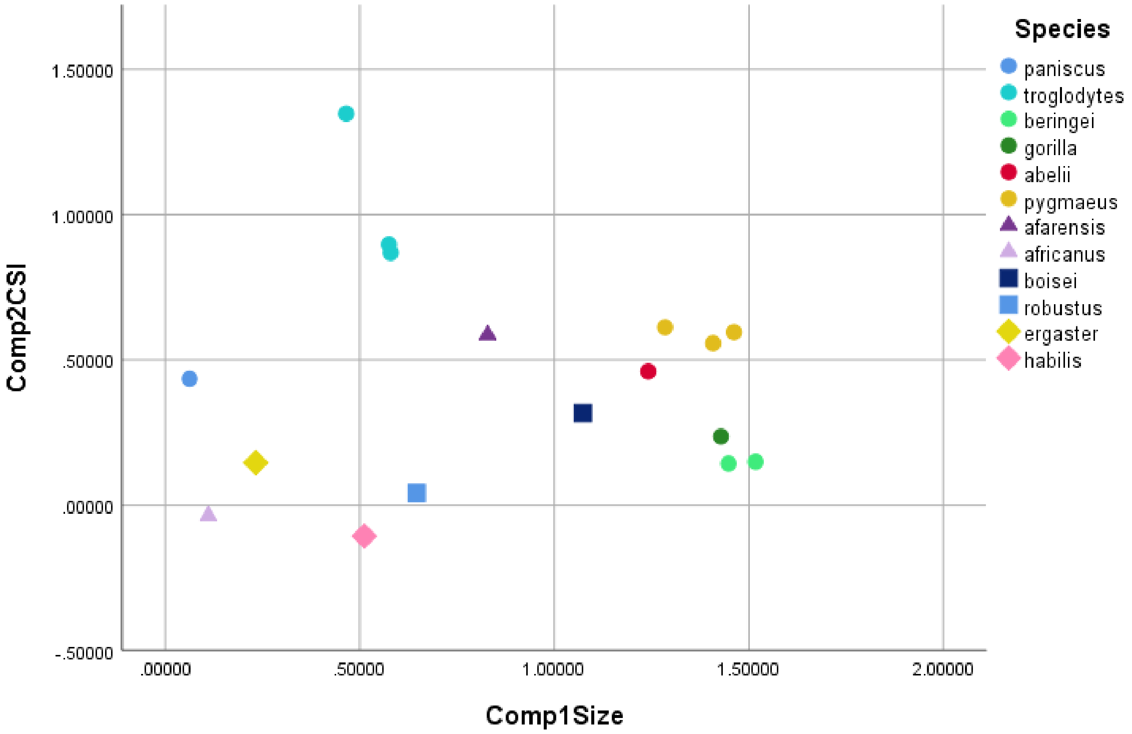

Figure 5.30: Ape and hominin species by components 1 (size variables) and 2 (crown shape indices (CSI))

When the shape components were compared (components 2 (crown shape indices) and 3 (corpus robusticity indices)) on the graphs the way the hominins plot changed completely. Whereas before with the graph using components 1 (size variables) and 2 (crown shape indices) the hominins plotted within the range of non-human primates, the usage of component 3 (corpus robusticity indices) sees them plot completely independent of any extant non-human primate (Figures 5.39-5.40). All hominins have wider symphyses and corpora than any extant ape.

Figures 5.39-5.40 also highlight how distinct the congeners *Australopithecus afarensis* and *A. africanus* are on components 2 (crown shape indices) and 3 (corpus robusticity indices). Of the hominins present *A. afarensis* has the widest crown shape (buccolingually) and the tallest mandible, while *A. africanus* has the widest mandible and among the longest tooth crowns (mesiodistally).

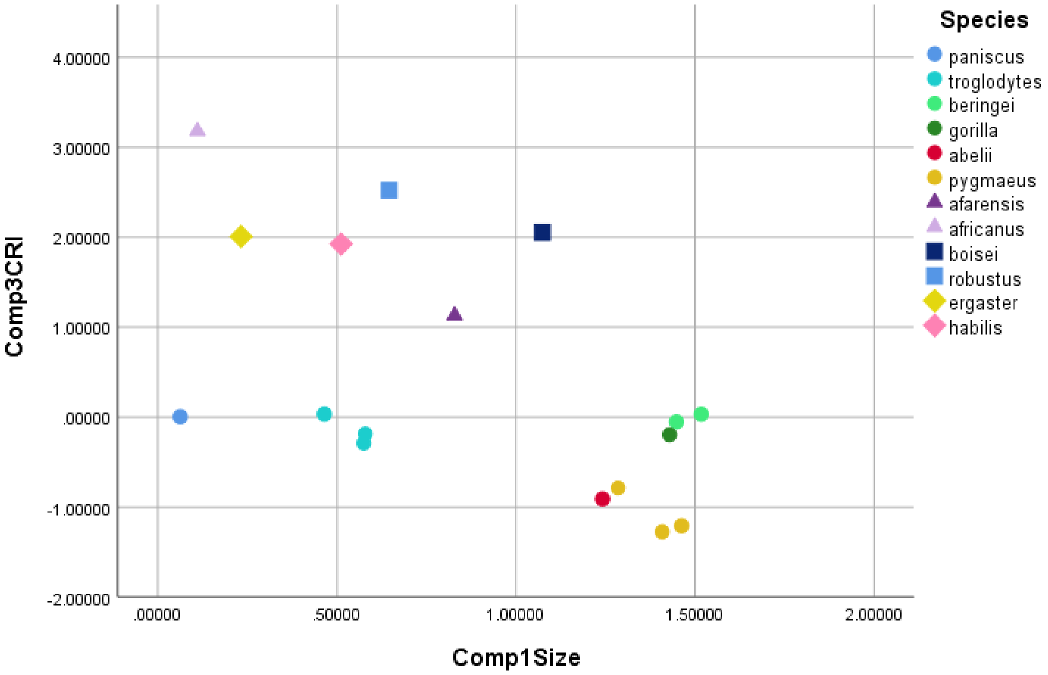

Figure 5.31: Ape and hominin species by components 1 (size variables) and 3 (corpus robusticity indices (CRI))

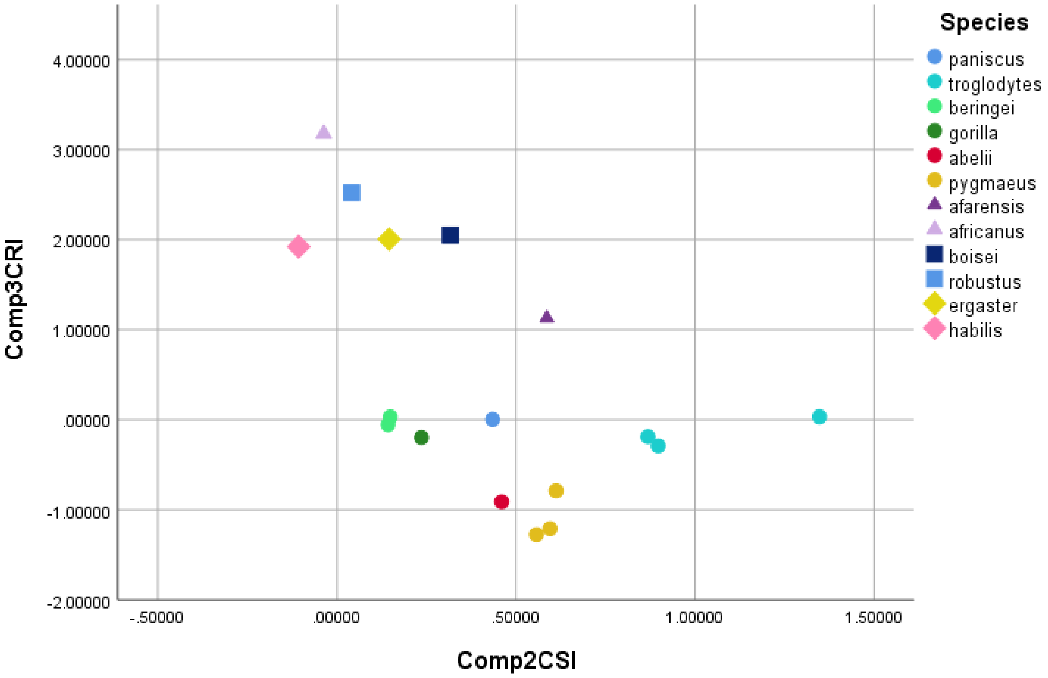

Figure 5.32: Ape and hominin species by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). *Pan troglodytes* plots distinct from its congener, *Pan paniscus*, and *Gorilla* and *Pongo*

5.2.2 Association of hominin morphological features to non-human primate diet categories (research question 5)

In this section, bivariate graphs using the components extracted from the PCA were used to analyse morphological differences between hominins and non-human primates of known diet. Diets analysed include: 1) traditional diet categories, 2) specific classification coding categories by both direct observation and faecal analysis, and 3) the quantity categories (low, moderate and high consumption) of foods (fruits, leaves, seeds, roots and animals) by both direct observation and faecal analysis.

For component 1 (size variables) using the traditional dietary categories, the categories appear to be widely dispersed along the size ranges, with both frugivore and omnivore species appearing at both ends of the size spectrum. Only frugivore-insectivores (small) and folivores (large) are distinct. The hominins (unknown diet category) plot alongside the upper right cluster of frugivores, some omnivores, and the folivore (Figure 5.41). For component 2 (crown shape indices), there are three distinct groupings. Omnivores plot at the lower end of the component and frugivore insectivores at the higher end of the graph. The hominins plot in a distinct cluster, which includes some frugivores and the folivore. Some frugivores are present in all three clusters suggesting some distinction exist within this diet category. When component 3 (corpus robusticity indices) was introduced the hominins were completely distinct from the other diet groups, with the exception *A. afarensis* in relation to the frugivorous *M. radiata* (circled) (Figure 5.42).

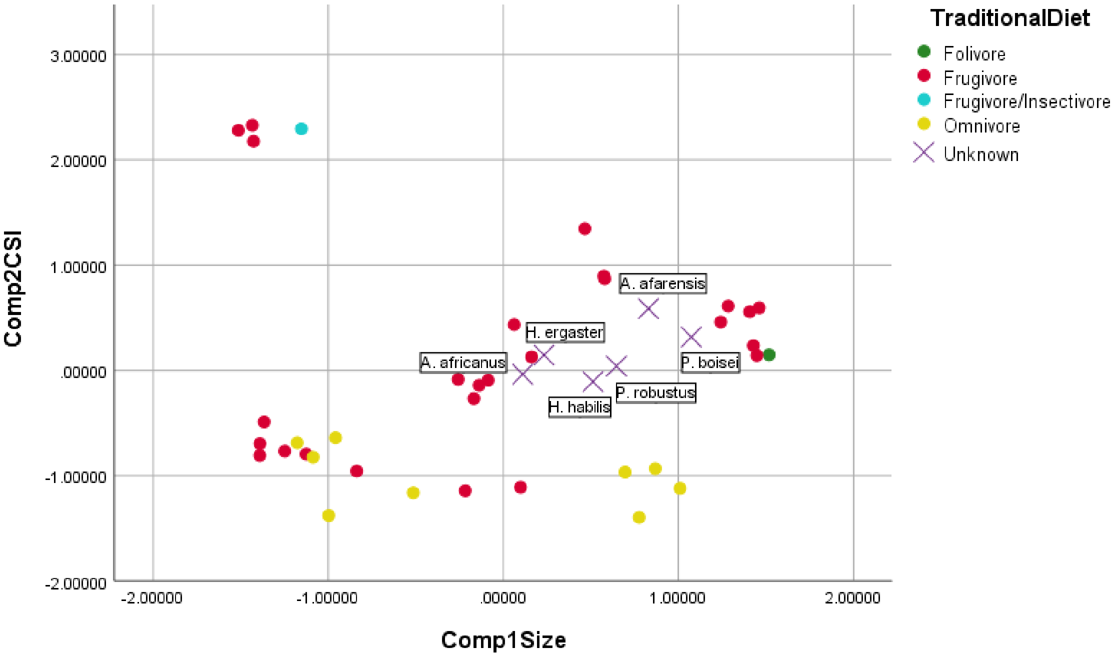

Figure 5.33: Traditional diet categories with non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI))

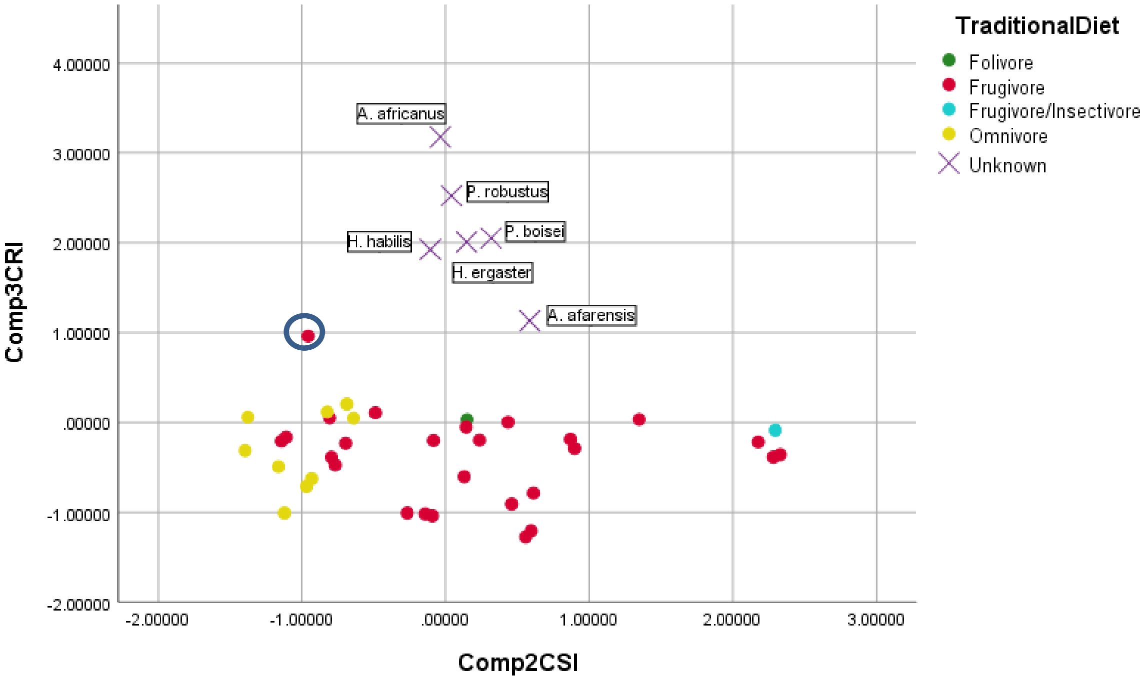

Figure 5.34: Traditional diet categories with non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). *Macaca radiata* (circled) is the only extant non-human primate species to plot near a hominin species (*A. afarensis*) on component 3 (corpus robusticity indices (CRI)).

For component 1 (size variables) using the specific classification coding categories by direct observation, the categories appear to be widely dispersed along the size ranges, with frugivores, frugivore-folivores and omnivores appearing at both ends of the size spectrum. Frugivore-insectivores (small), folivores and folivore-frugivores (large), and frugivore-granivores, folivore-granivores and frugivore-faunivores (medium-sized) are distinct. The hominins (unknown diet category) plot alongside a number of different dietary groupings (Figure 5.43). *P. boisei* plot alongside the furthest cluster, which includes some of the following dietary categories: folivores, folivore-frugivores, frugivores and frugivore-folivores and omnivores, while *A. afarensis*, *P. robustus* and *H. habilis* plot in line with some of the omnivores and frugivore-folivores, and *H. ergaster* and *A. africanus* plot in line with some of the frugivore-folivores, frugivore-granivores, frugivore-faunivores and folivore-granivores (Figure 5.43).

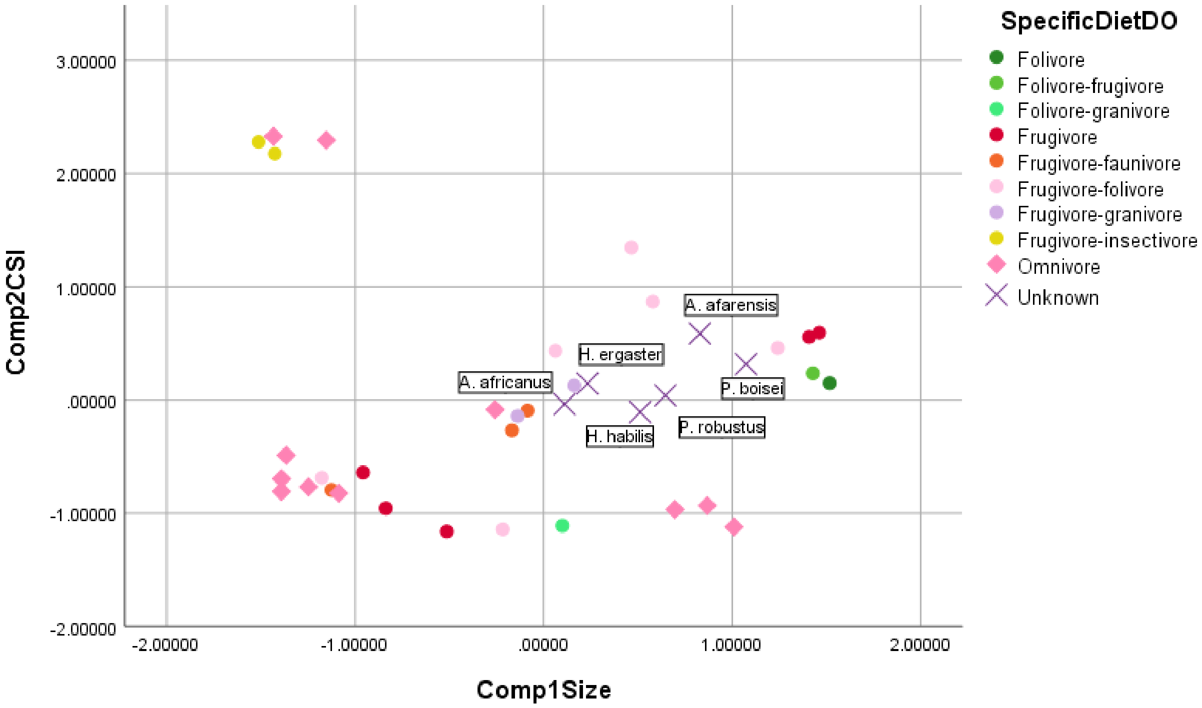

Figure 5.35: Specific classification coding categories by direct observation (DO) with non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, but overlap exists between the dietary categories present. Folivore-granivore (longest crown shape), frugivore-faunivore, frugivore-granivore, folivore-frugivore, and folivores (tooth crowns as long as they are wide), and frugivore-insectivores (widest crown shapes) plot distinctly. Some omnivores are present in all three clusters, while frugivore-folivores are present in two clusters suggesting some distinction exist within these diet categories. The hominins plot in a distinct cluster, with *A. afarensis* plotting in line with some frugivores and frugivore-folivores, while *P. boisei* and *H. ergaster* plot in line with some folivores, folivore-frugivores, frugivore-folivores, frugivores and frugivore-granivores, and *P. robustus*, *A. africanus* and *H. habilis* all plot in line with some frugivore-granivores, frugivore-faunivores and omnivores (Figures 5.43-5.44). When component 3 (corpus robusticity indices) was introduced the hominins were completely distinct from the other diet groups, with the exception *A. afarensis* in relation to the frugivorous *M. radiata* (Figure 5.44).

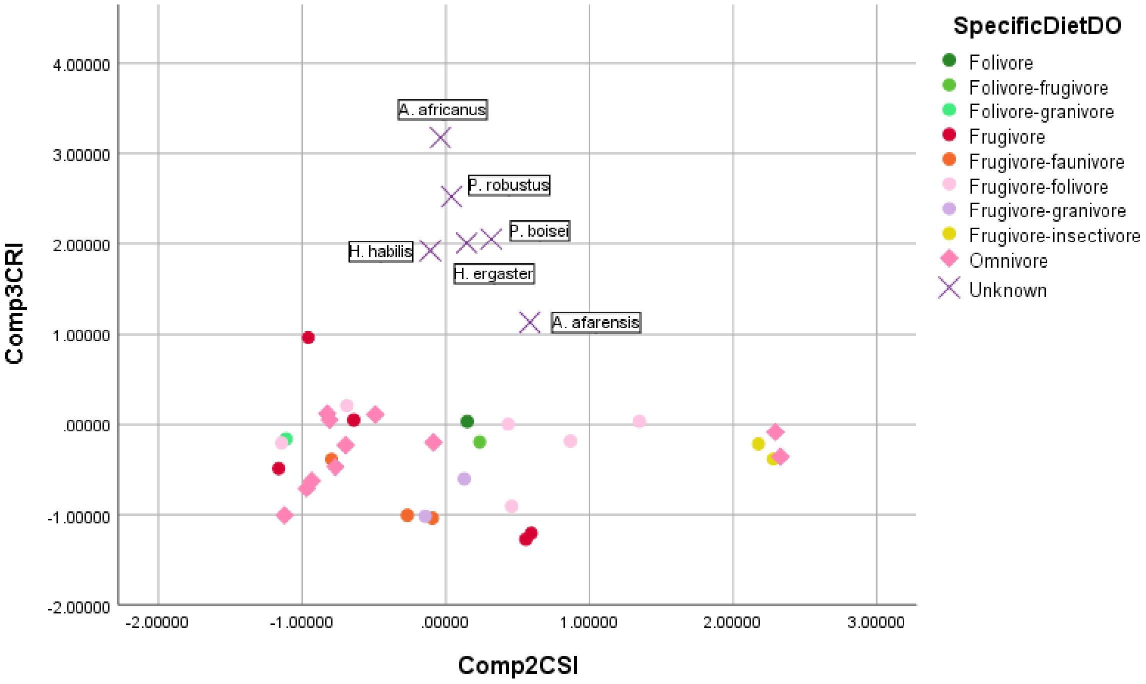

Figure 5.36: Specific classification coding categories by direct observation (DO) with non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 1 (size variables) using the specific classification coding categories by faecal analysis, the categories appear to be widely dispersed along the size ranges, with frugivore-folivores and omnivores appearing at both ends of the size spectrum. Frugivore-insectivores (small), folivore-frugivores and frugivore-faunivores (large), and frugivore-granivores (medium-sized) are distinct. The hominins (unknown diet category) plot alongside a number of different dietary groupings (Figure 5.45). *A. afarensis*, *P. boisei*, *P. robustus* and *H. habilis* plot within a cluster of some folivore-frugivores, frugivore-folivores, omnivores and frugivore-faunivore, while *H. ergaster* and *A. africanus* plot more in line with some of the frugivore-folivores, frugivore-granivores and omnivores (Figure 5.45).

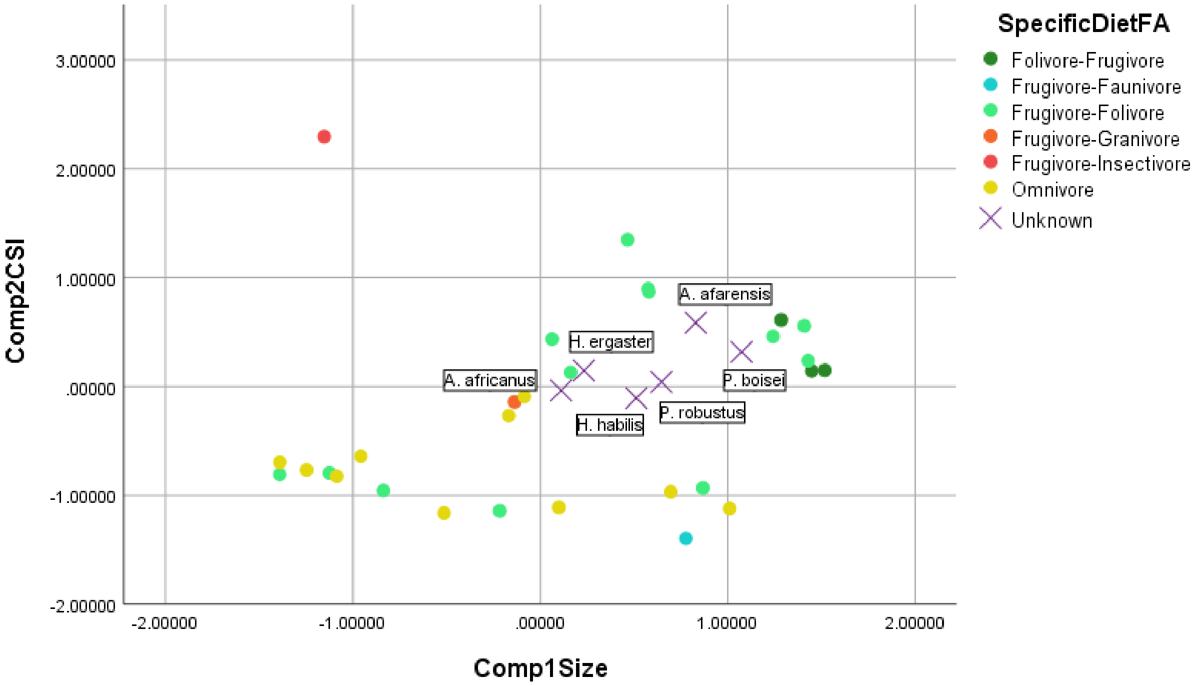

Figure 5.37: Specific classification coding categories using faecal analysis (FA) with non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). *Sapajus* plots at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings. Frugivore-faunivores (longest crown shape), folivore-frugivores and frugivore-granivores (tooth crowns as long as they are wide), and frugivore-insectivores (widest crown shapes) plot distinctly. Some omnivores and frugivore-folivores are present in two of the three clusters suggesting some distinction exist within these diet categories. The hominins plot in a distinct cluster, with *A. afarensis, P. boisei* and *H. ergaster* plotting in line with some of the frugivore-folivores and folivore-frugivores, *A. africanus* and *H. habilis* plot in line with some of the frugivore-granivores and omnivores, while *P. robustus* plots between all of the above categories (Figures 5.45-5.46). As before, when component 3 (corpus robusticity indices) was introduced the hominins were completely distinct from the other diet groups, with the exception *A. afarensis* in relation to one species of frugivore-folivore (Figure 5.46).

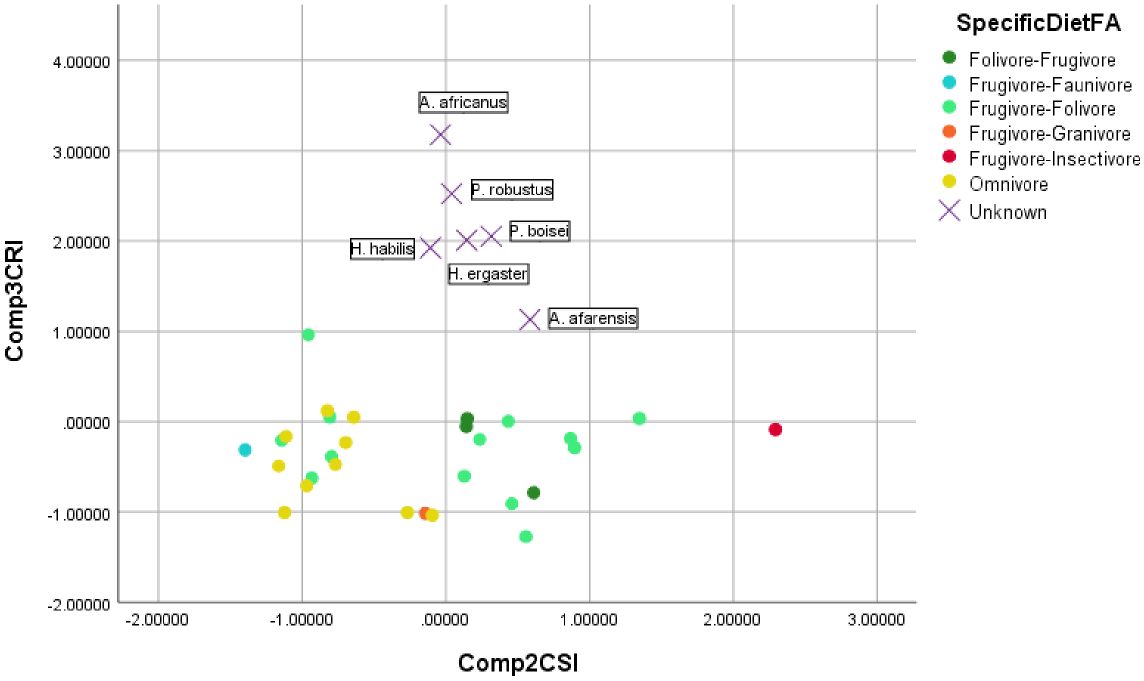

Figure 5.38: Specific classification coding categories using faecal analysis (FA) with non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

When the quantity categories were entered into the graphs the hominins appeared to align themselves differently according to the components used. The food quantity (low, moderate and high consumption) categories used were 1) fruits, 2) leaves, 3) seeds, 4) roots, and 5) animals.

Fruit consumption

The graphs produced comparing hominins to non-human primates for fruit consumption by direct observation and faecal analysis were very similar, so results using direct observation are presented. For component 1 (size variables), the quantity categories appear to be widely dispersed along the size ranges, with moderate and high consumers appearing at both ends of the size spectrum, while low consumers appear both midway and high up on the graph (Figure 5.47). The hominins (unknown diet category) plot predominantly surrounded by some of the high consumers of fruits (Figures 5.47-5.48), although *A. afarensis*, *A. africanus*, *P. robustus* and *P. boisei* also plot in line and near some of the low and moderate consumers of fruits.

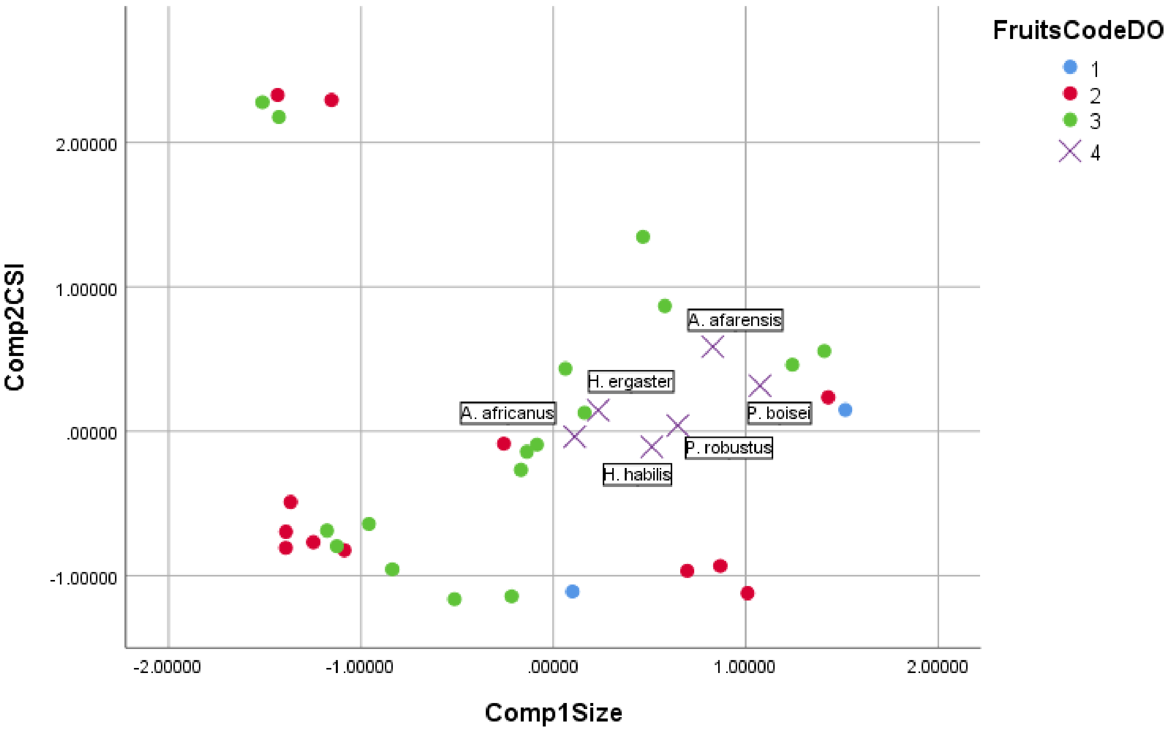

Figure 5.39: Fruit consumption using direct observation (DO) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, but overlap exists with the quantity categories present in each. Consumers of moderate and high quantities of fruits are present in each of the clusters, and low quantities are present in two of the three clusters suggesting some distinction exist within these quantity categories. The hominins plot in a distinct cluster, with *A. afarensis* plotting in line with some of the high consumers, *P. boisei* and *H. ergaster* plotting in line with some of the low, moderate and high consumers, *A. africanus* and *H. habilis* in line with moderate and high consumers, while *P. robustus* plots between some of the low, moderate and high consumers (Figures 5.47-5.48). As before, when component 3 (corpus robusticity indices) was introduced the hominins were distinct from the non-human primates, with the exception of *A. afarensis*, which plotted in line with one of the high fruit consumers (Figure 5.48).

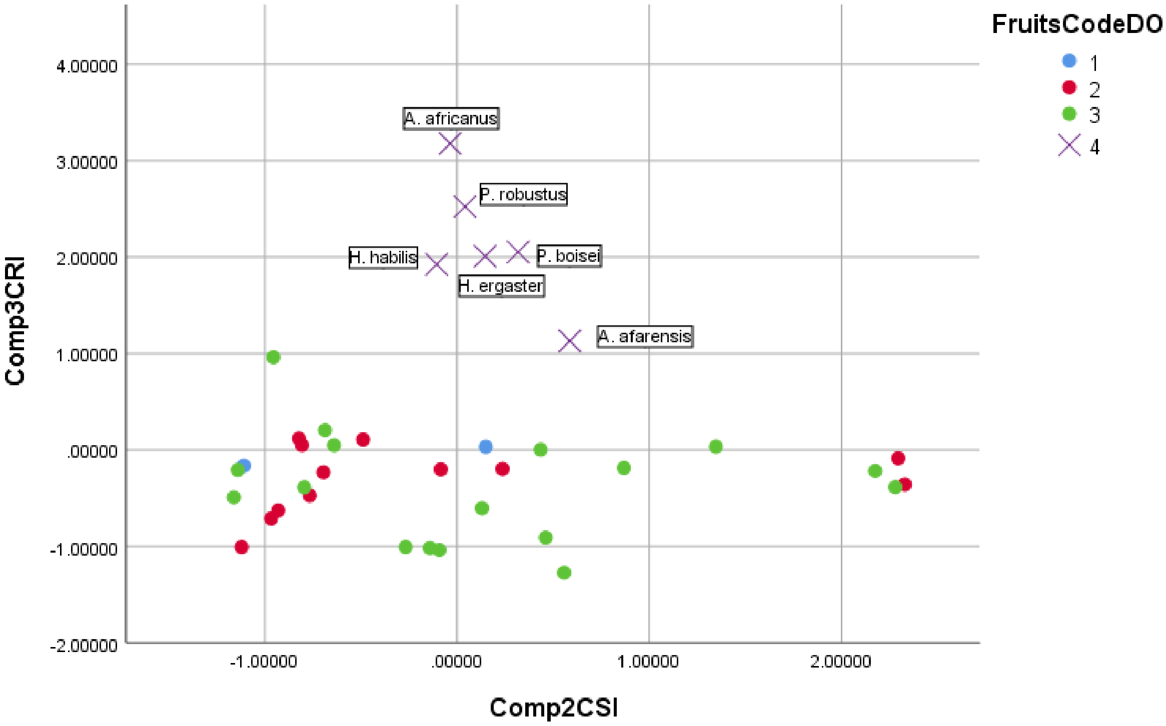

Figure 5.40: Fruit consumption using direct observation (DO) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

Leaf consumption

The graphs produced to compare the hominins to non-human primates for leaf consumption were very different depending upon whether the diet information was using direct observation or faecal analysis, hence data for both are presented. For component 1 (size variables) using direct observation, the low quantity category appears to be widely dispersed along the size ranges, while moderate consumers plot closer to the midline, and high consumers plot at the high end of the range (Figure 5.49). The hominins (unknown diet category) plot predominantly surrounded by some of the low consumers of leaves, although *A. afarensis* and *A. africanus*, also plot in line with some of the moderate consumers, and *P. boisei* plots near the high consumers of leaves (Figures 5.49-5.50).

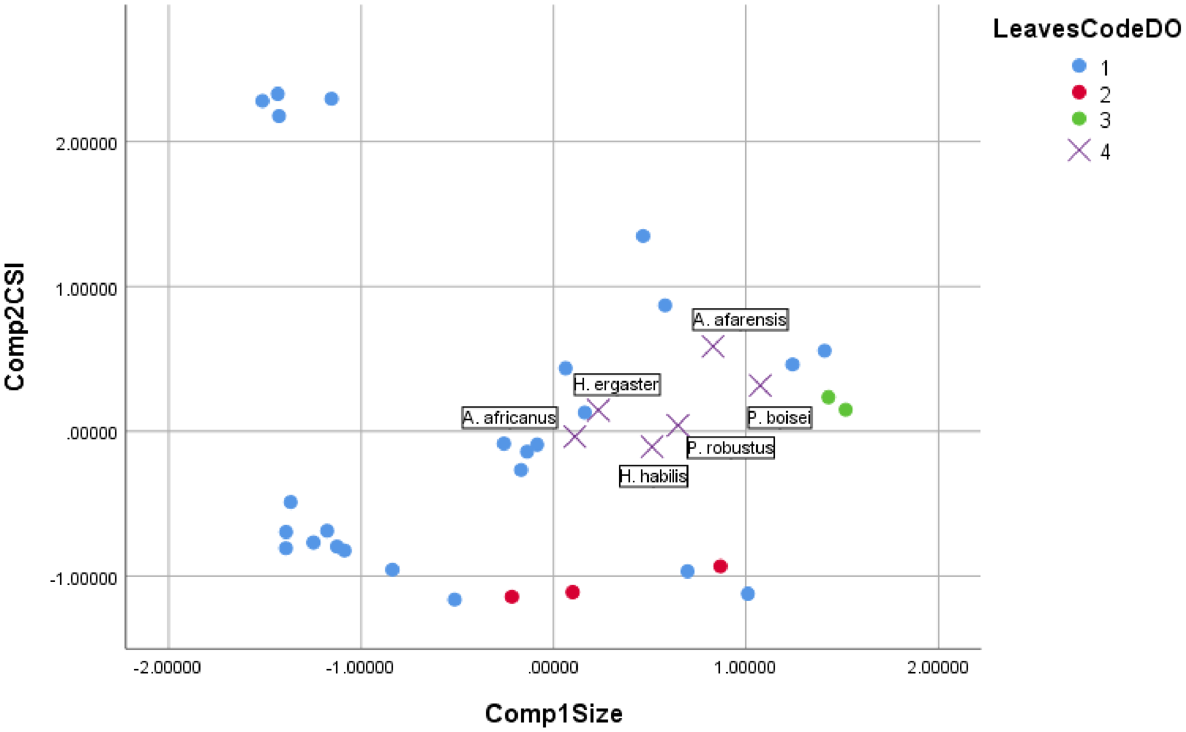

Figure 5.41: Leaf consumption using direct observation (DO) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, with some overlap in the quantity categories present. Consumers of low quantities of leaves are present in each of the clusters suggesting some distinction exist within this quantity category. In contrast, moderate consumers are present in one cluster (those with longer tooth crowns) and high consumers are present in another (the cluster closest to the midline). The hominins plot in a distinct cluster, in line mostly with low consumers of leaves, with the exception of *H. ergaster* and *P. boisei* who also plot in line with the high consumers (Figures 5.49-5.50). As before, when component 3 (corpus robusticity indices) was introduced the hominins were distinct from the non-human primates, with the exception of *A. afarensis*, which plotted in line with a low leaf consumer (Figure 5.50).

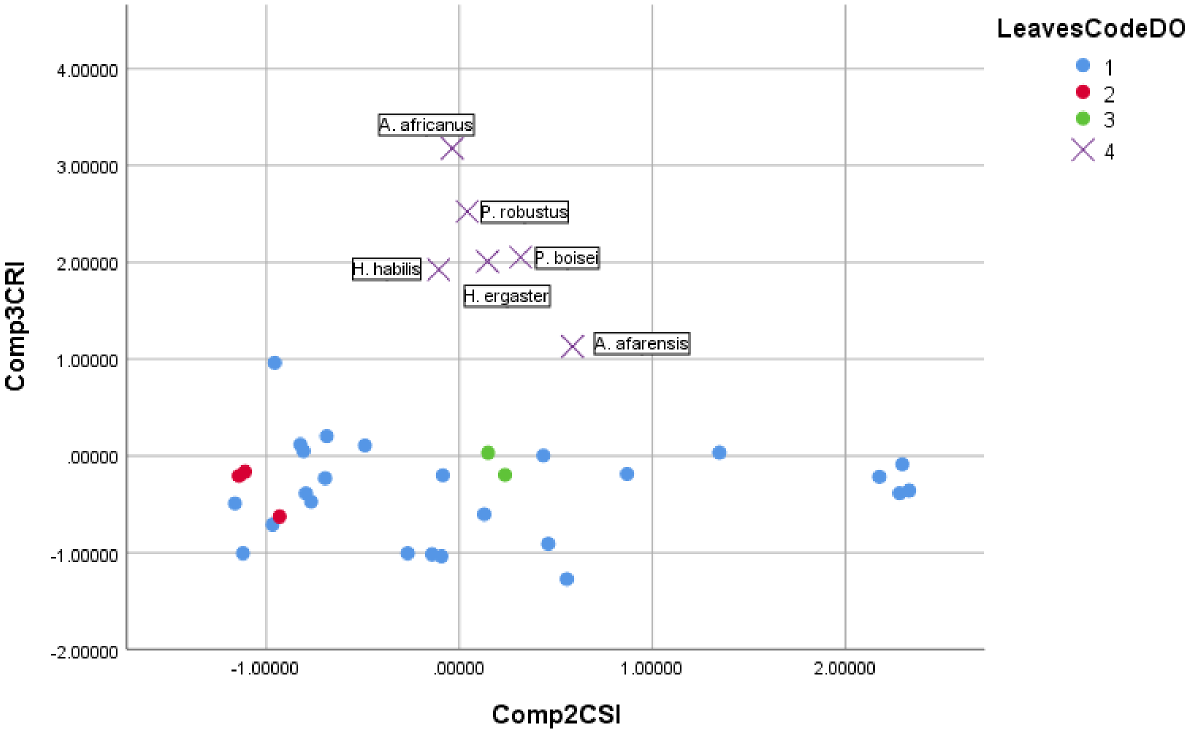

Figure 5.42: Leaves consumption using direct observation (DO) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 1 (size variables) using faecal analysis, the low and moderate quantity categories appear to be widely dispersed along the size ranges, while high consumers plot at the high end of the range (Figure 5.51). The hominins (unknown diet category) plot predominantly surrounded by some of the moderate consumers of leaves, although *A. afarensis*, *A. africanus*, *P. robustus* and *P. boisei* also plot in line with some of the low consumers, with the latter also nearest to the high consumers of leaves (Figures 5.51-5.52).

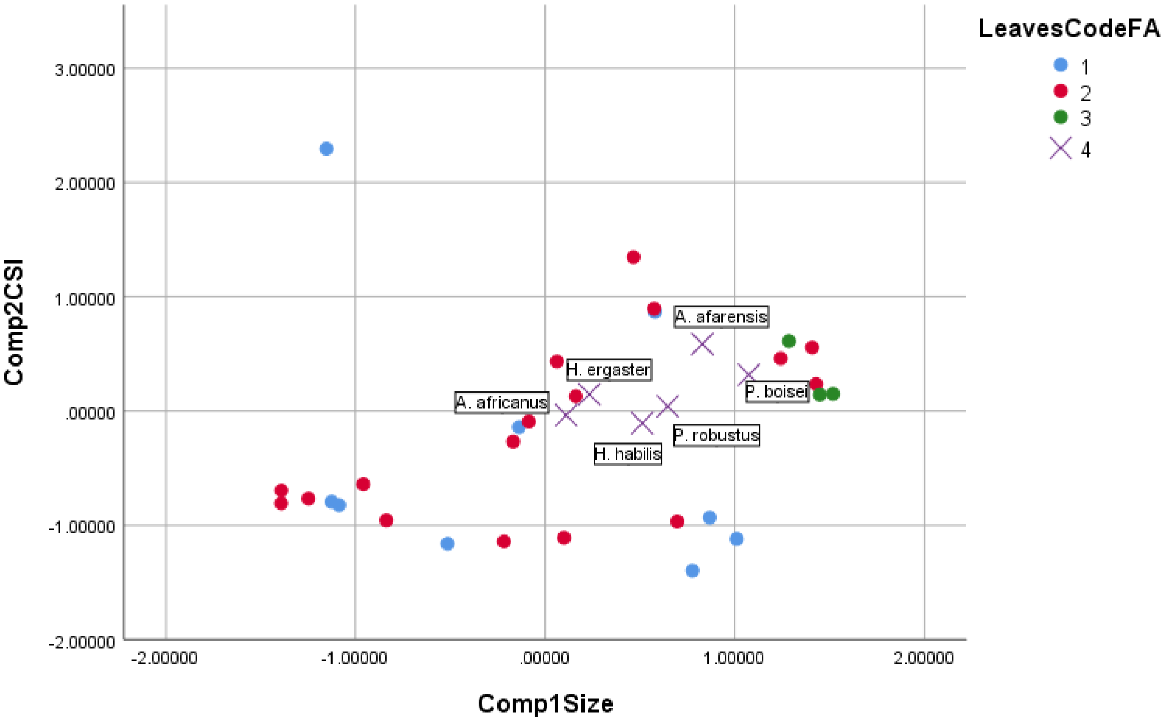

Figure 5.43: Leaves consumption using faecal analysis (FA) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, with some overlap in the quantity categories present. Consumers of low quantities of leaves are present in each of the clusters and consumers of moderate quantities of leaves are present in two of the three clusters, suggesting some distinction exist within these quantity categories. In contrast, high consumers are present in one cluster (the cluster closest to the midline). The hominins plot in a distinct cluster, in line mostly with some of the moderate and high consumers of leaves, with the exception of *A. africanus* and *H. habilis* who also plot in line with some of the low consumers (Figures 5.51-5.52). As before, when component 3 (corpus robusticity indices) was introduced the hominins were distinct from the non-human primates, with the exception of *A. afarensis*, which plotted in line with one of the moderate leaf consumers (Figure 5.52).

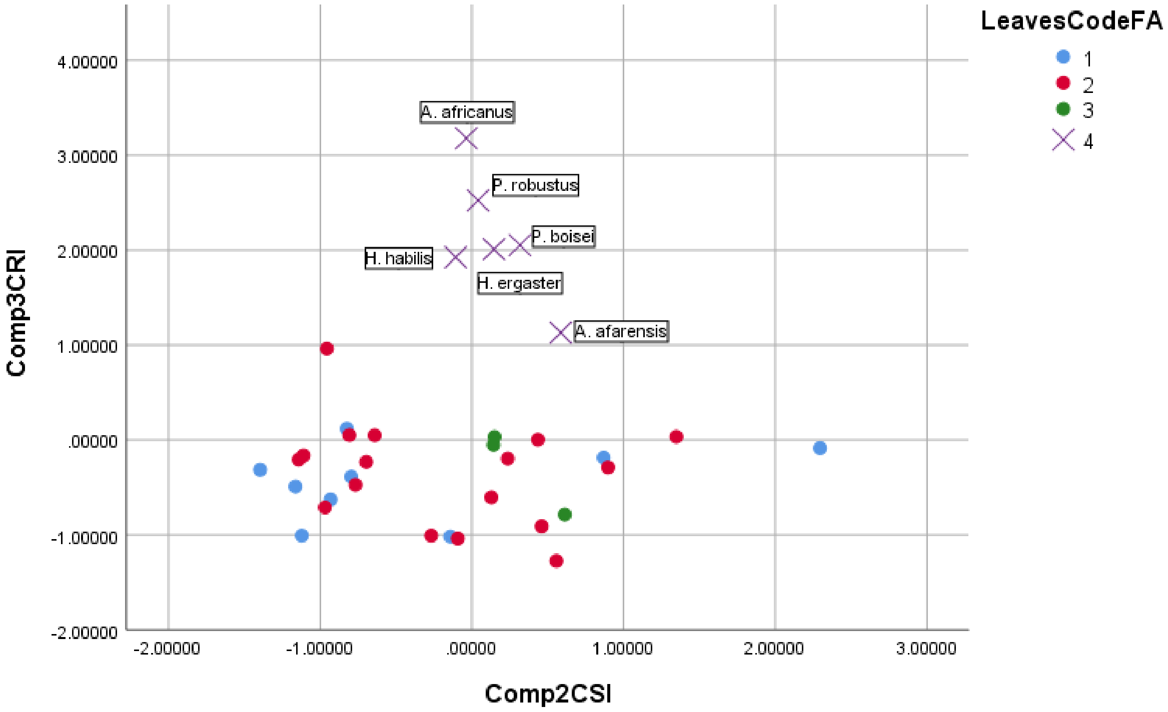

Figure 5.44: Leaves consumption using faecal analysis (FA) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

Seed consumption

The graphs produced to compare the hominins to non-human primates for seed consumption were similar when using direct observation and faecal analysis, and as such the graphs by direct observation are displayed below. For component 1 (size variables), the low quantity category appears to be widely dispersed along the size ranges, while moderate consumers plot from lower towards the midline on the graph, and high consumers plot around the midline to the high end of the graph (Figure 5.53). The hominins (unknown diet category) plot predominantly surrounded by some of the low consumers of seeds, although, *P. boisei*, *H. ergaster* and *A. africanus* all plot in line with some of the moderate and high consumers of seeds (Figures 5.53-5.54).

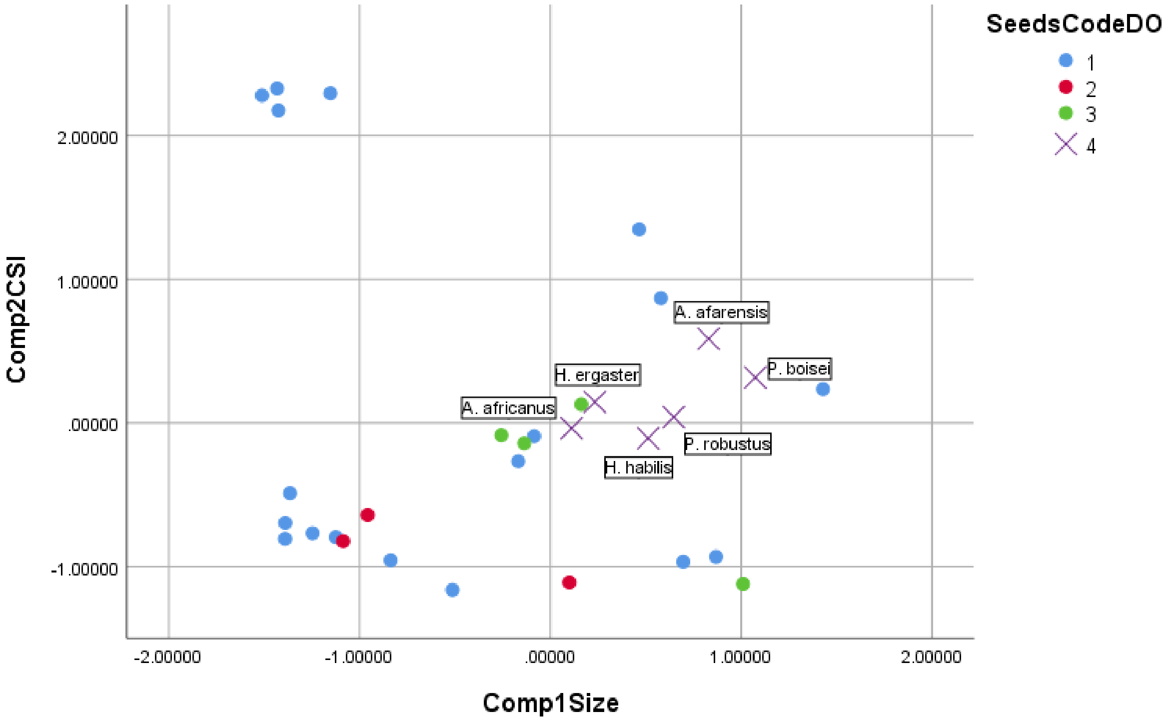

Figure 5.45: Seeds consumption using direct observation (DO) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, with some overlap in the quantity categories present. Consumers of low quantities of seeds are present in each of the clusters and consumers of high quantities of seeds are present in two of the three clusters, suggesting some distinction exist within these quantity categories. In contrast, moderate consumers are present in one cluster (the lowest cluster, indicating they are associated with long tooth crowns). The hominins plot in a distinct cluster, in line mostly with some of the low and high consumers of seeds. *A. africanus, P. robustus, H. ergaster and H. habilis* all plot in line with some of the high consumers of seeds, while *A. afarensis* and *P. boisei* plot in line with some low consumers of seeds (Figures 5.54). *A. afarensis* plotted in line with a low seed consumer on component 3 (corpus robusticity indices) (Figure 5.54).

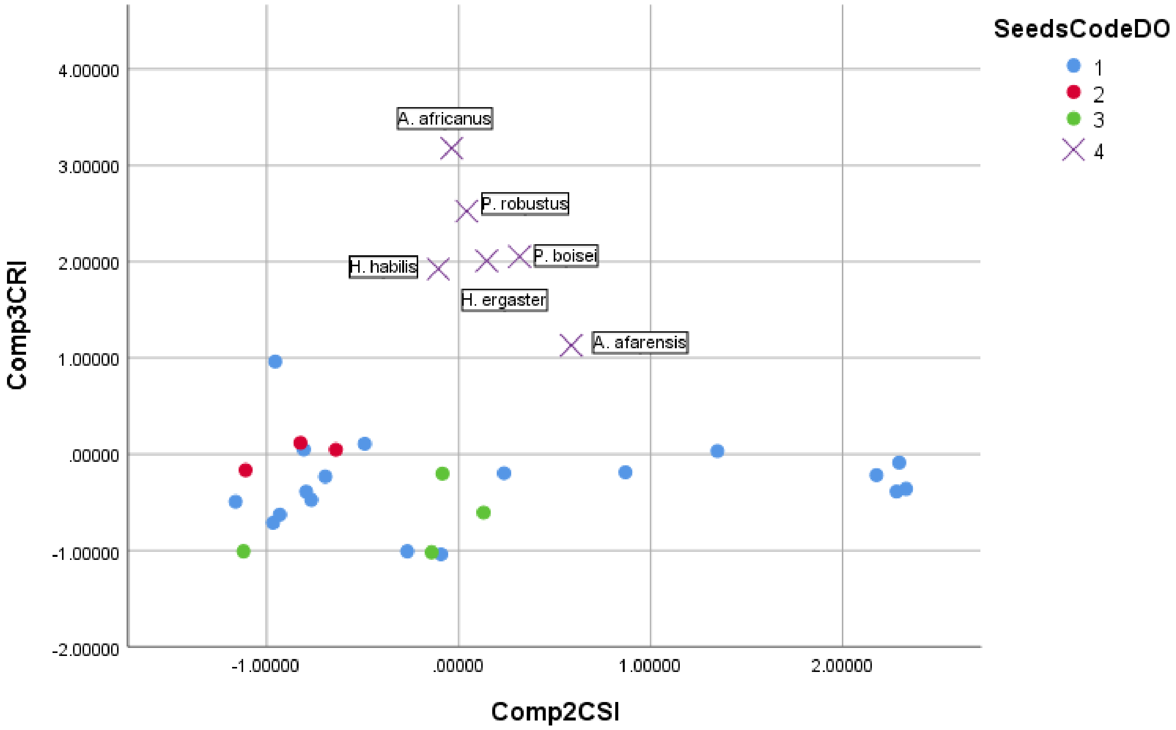

Figure 5.46: Seeds consumption using direct observation (DO) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

Root consumption

The graphs produced to compare the hominins to non-human primates for root consumption were similar when using direct observation and faecal analysis, and as such the graphs by direct observation are displayed below. For component 1 (size variables), the low quantity category appears to be widely dispersed along the size ranges, while moderate consumers plot around the midline to the high end of the graph, and high consumers plot towards the high end of the graph (Figure 5.55). The hominins (unknown diet category) plot predominantly surrounded by some of the low consumers of roots, although, *A. africanus* plots in line with one of the moderate consumers, and *H. habilis* and *P. robustus* plot in line with the high consumer of roots (Figures 5.55-5.56).

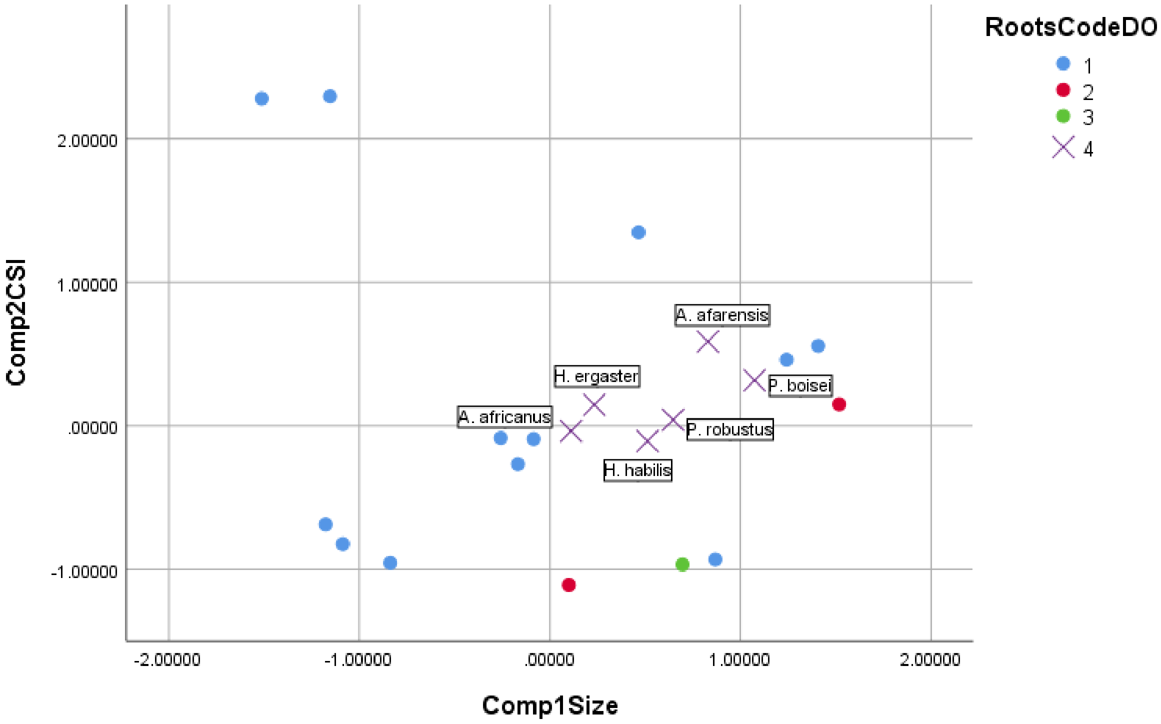

Figure 5.47: Roots consumption using direct observation (DO) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, with some overlap in the quantity categories present. Consumers of low quantities of roots are present in each of the clusters and consumers of high quantities of roots are present in all three of the clusters, while consumers of moderate quantities of roots are present in two of the three clusters, suggesting some distinction exist within these quantity categories. In contrast, high consumers are present in one cluster (the lowest cluster, indicating they are associated with long tooth crowns). The hominins plot in a distinct cluster, mostly in line with some of the low consumers of roots. The only exception to this pattern is *H. ergaster*, which plots in line with one of the moderate consumers of roots (Figures 5.55-5.56). *A. afarensis* plotted in line with a low root consumer on component 3 (corpus robusticity indices) (Figure 5.56).

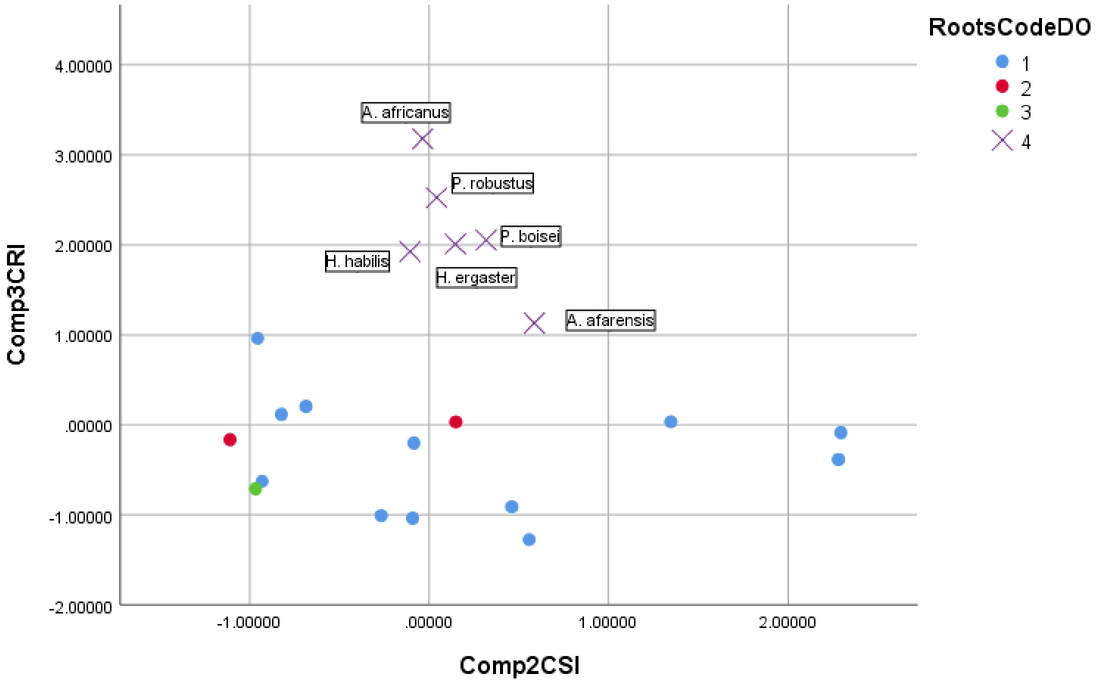

Figure 5.48: Roots consumption using direct observation (DO) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

Animal consumption

The graphs produced to compare the hominins to non-human primates for animal consumption were similar when using direct observation and faecal analysis, and as such the graphs by direct observation are displayed below. For component 1 (size variables), the low quantity category appears to be widely dispersed along the size ranges, while moderate consumers plot from the low end of the graph to the midline, and high consumers plot at the lowest end of the graph (Figure 5.57). The hominins (unknown diet category) plot predominantly surrounded by some of the low consumers of animals, although, *A. africanus* plots near some of the moderate consumers (Figures 5.57-5.58).

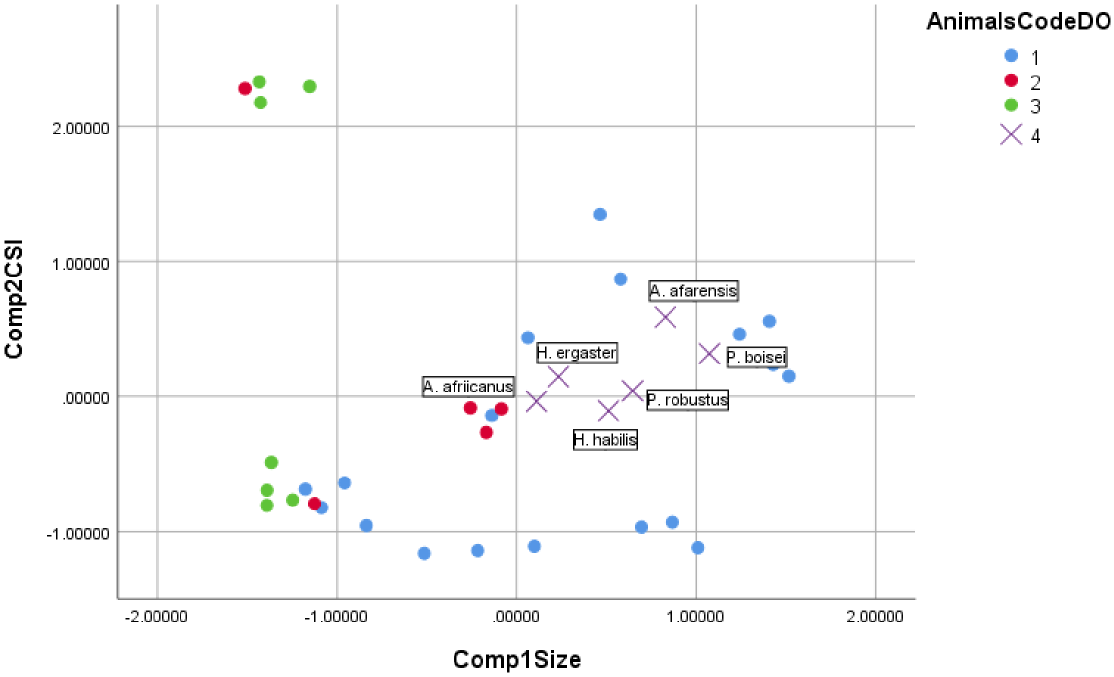

Figure 5.49: Animal consumption using direct observation (DO) by non-human primates and hominins by components 1 (size variables) and 2 (crown shape indices (CSI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* plot at the lowest end of the scale for component 1 (size variables) and cluster distinctly from all other taxa on component 2 (crown shape indices).

For component 2 (crown shape indices), there are three distinct groupings, with some overlap in the quantity categories present. Consumers of low, moderate and high quantities of animals are each present in two of the three clusters, with low and moderate both present in the groups at the lowest end of the graph and the midpoint, while high consumers are present in the groups at the lowest and the highest end of the graph, suggesting some distinction exist within these quantity categories. The hominins plot in a distinct cluster, mostly in line with some of the low consumers of animals, although *A. africanus* and *H. habilis* also plots in line with some of the moderate consumers of animals (Figures 5.57-5.58). *A. afarensis* plotted in line with a low animal consumer on component 3 (corpus robusticity indices) (Figure 5.58).

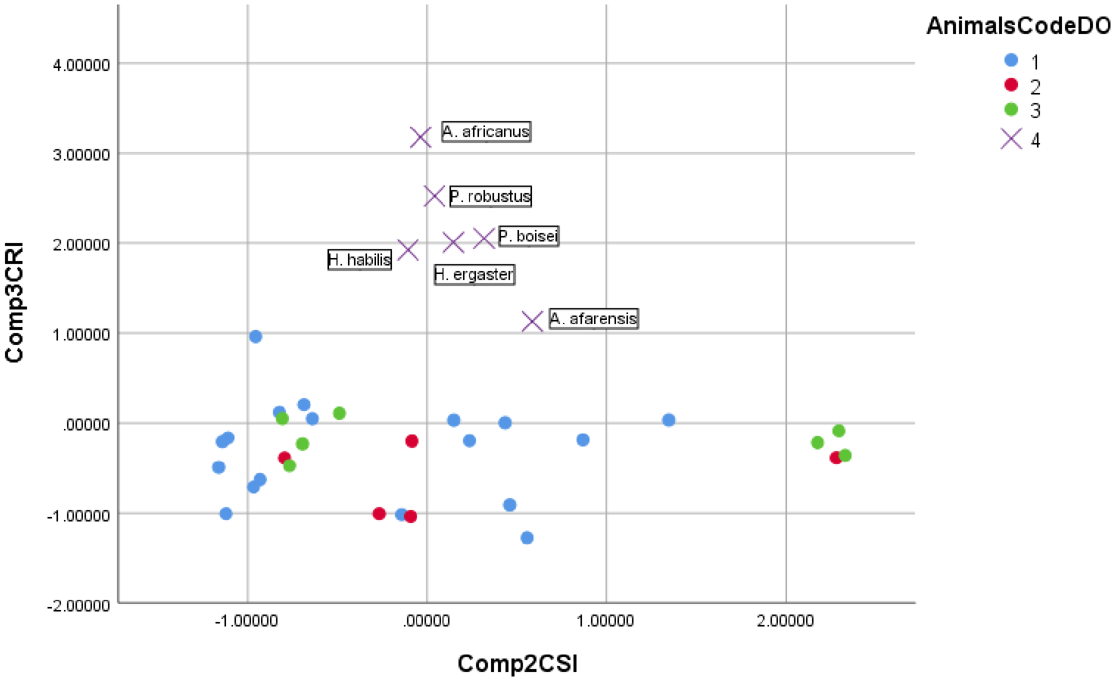

Figure 5.50: Animal consumption using direct observation (DO) by non-human primates and hominins by components 2 (crown shape indices (CSI)) and 3 (corpus robusticity indices (CRI)). 1= low consumption, 2 = moderate consumption, 3 = high consumption, 4 = unknown consumption. *Cebus* and *Sapajus* cluster distinctly from all other taxa on component 2 (crown shape indices).

Chapter 6 : Discussion

This thesis aimed to explore the potential association between diet and masticatory morphology in non-human primates, as a basis from which to compare extinct hominins to extant non-human primates of known-diet. Based on this information, it was possible to hypothesise about the types of diets the hominins could have consumed. The potential implications of these results and how they compare to current interpretations are discussed in this chapter.

6.1 Discussion of the results obtained in relation to the research questions and other existing research

An important aspect of morphological variation in extant non-human primates is associated with body size differences. Indeed, the effects of body size differences are apparent throughout the analyses run (Tables 5.10-5.19), a fact also consistent with another study on non-human primates (Veneziano *et al.*, 2019) and a study on African antelopes (Louys *et al*., 2015a). The patterns observed also appear to conform to the Jarman-Bell principle, whereby the larger species consumed greater quantities of leaf-based foods (foliage), while the smaller species consumed greater quantities of insect-based foods (Figures 5.21, 5.23, 5.25). Clearly when analysing morphology and diet, the impact of body size is considerable and cannot be overlooked.

The overall morphological differences between *Paranthropus* and *Australopithecus* cannot, however, be explained by body size differences. While *Paranthropus* does present a masticatory apparatus that is larger relative to that of *Australopithecus* (Robinson, 1954a, b, 1963), the reconstructions of body mass based on various morphological traits taken from the femur and tibia indicate that there is very little estimated body mass difference between the two genera (information available in Table 4.3). The range of body size variation present in the two hominin genera would be similar to that of large bodied primates, and thus would not show the same level of distinction that is present in the non-human primate dataset. Furthermore, it has been demonstrated the tooth size differences between *Australopithecus* and *Paranthropus* are not the consequence of body size differences (Kay, 1975b; Wood & Stack, 1980; Daegling & Grine, 1991). It would therefore appear that the clear morphological differences present in the masticatory apparatus of *Paranthropus* and *Australopithecus* are not the result of body size differences. Other factors must therefore be considered.

6.1.1 Examination of the association between diet and morphology in non-human primates

Previous research identified that there is an association between foods that initiate high stress and strain and the masticatory morphology (Hylander, 1979a, 1979b, 1984, 1985, 1988; Hylander & Johnson, 1994; Taylor, 2002, 2006a; Vinyard *et al*., 2006). Refining the relationship further between form and function/ diet has however proven difficult. The association between dentition and diet is suggested to be somewhat more straightforward, whereby inferences can be made regarding the general dietary adaptation of a species based on the size and shape of their dentition (Kay, 1975; Kinzey, 1978; Happel, 1988; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Lucas *et al*., 2008b; Lee *et al*., 2010; Ungar 2011, 2015). Yet research shows that while the dentition is historically more informative than the mandibular morphology with regard to diet adaptation, it is not without its limitations.

To this end, the first research topics considered here pertain to: 1) whether it is possible to identify morphological differences in consumers of different diets, 2) whether consumers of large quantities of particular foods vary morphologically from consumers of low quantities of the same foods, and 3) how much of the morphological variation can be explained by diet. To address these questions a range of non-human primate species with different dietary preferences, occupying various habitats and subject to seasonal shortage and abundance of foods were analysed using a series of commonly used metric measurements to test the role of different independent variables, such as size and diet in relation to the morphology of non-human primates. Initially, it was intended to explore the potential impact of fallback foods on the masticatory morphology, but despite collecting a very large dataset attempts to classify foods as fallback were unsuccessful (the reasons for this are discussed later in this chapter). As a result, diet had to be tested as a whole, and not separated into preferred and fallback.

6.1.1.1 Morphological differences between consumers of different diets

There were significant ($p = <0.05$) morphological differences between consumers of different diets, especially evident within the monkey group (includes both New World and Old World monkeys) (Table 6.1). Morphological differences between dietary groups manifest more clearly when using the indices, particularly as pertaining to the mandibular corpus and dentition in monkeys rather than between the different body size groupings (compare percentages in Table 6.2). In contrast, while significant morphological differences between consumers of different diets were present in the apes, particularly the smaller species, they did not occur as frequently as morphological differences between the small and large apes (compare percentages in Table 6.3). The greater amount of differences among the small-bodied species of apes could be a result of differences in sample size, as reported by Meloro *et al*. (2015), who found that when larger samples were analysed greater morphological distinctions associated with feeding adaptations were identified in the mandibles than when smaller samples were analysed. This is likely because in larger samples there is a greater diversity of morphologies present. Differences identified here could therefore represent phylogenetic differences as much as body size differences. In contrast, in smaller samples there is less morphological diversity, and consequently fewer significant differences between morphologies.

Table 6.1: Comparison of the number of times (by percentage) consumers of different diets presented significantly different morphology in monkeys and apes

	Crown area				Crown shape index				Corpus size					Corpus robusticity index				
	P_4	M_1	M_2	M_3	P_4	M_1	M_2	M_3	SS	P_4	M_1	M_2	M_3	SRI	P_4	M_1	M_2	M_3
Monkeys	86.96	100	86.90	86.96	86.96	65.22	73.91	86.96	91.30	86.96	86.96	86.96	86.96	65.22	86.96	86.96	91.30	69.57
Apes	92.31	84.62	92.31	69.23	30.77	23.08	0	69.23	38.46	69.23	76.92	76.92	76.92	61.54	38.46	38.46	0	0

Dietary categories analysed by small monkeys = 11. Dietary categories analysed by large monkeys = 12.

Dietary categories analysed by small apes = 5. Dietary categories analysed by large apes = 8.

Table 6.2: Comparison of the number of times (by percentage) different body sizes and consumers of different diets presented significantly different shape morphology in monkeys

	Crown shape index				Corpus robusticity index				
	P_4	M_1	M_2	M_3	SRI	P_4	M_1	M_2	M_3
Percentage of variables significantly different between body sizes	75.00	45.83	**83.33**	**95.83**	**79.17**	45.83	62.50	58.33	70.83
Percentage of variables significantly different between consumers of different diets	**86.96**	**65.22**	73.91	86.96	65.22	**86.96**	**86.96**	**91.30**	**69.57**

Numbers in bold denote the higher frequency of significant variables

Table 6.3: Comparison of the number of times (by percentage) different body sizes and consumers of different diets presented significantly different shape morphology in apes

	Crown shape index				Corpus robusticity index				
	P_4	M_1	M_2	M_3	SRI	P_4	M_1	M_2	M_3
Percentage of variables significantly different between body sizes	**41.67**	**100**	**100**	**97.67**	**100**	**50**	33.33	**91.67**	**25**
Percentage of variables significantly different between consumers of different diets	30.77	23.08	0	69.23	61.54	38.46	**38.46**	0	0

Numbers in bold denote the higher frequency of significant variables

Different morphological patterns were present in consumers of different diets across the variables analysed. Tooth crown differences emerged between the different diets, with frugivore-insectivores presenting relatively wider tooth crowns than folivores and omnivores who present relatively longer tooth crowns (Figures 5.21-5.22). In contrast, frugivores appeared to overlap with all of the categories, with no distinct pattern present. This last point indicates that a derived morphology is not required to consume a high fruit diet and that a frugivores' morphology reflects more of a 'jack of all trades', generalist morphology.

Corpus and symphysis differences were also present between consumers of different diets. Frugivore-granivores, frugivore-faunivores, frugivore-insectivores and omnivores all consistently displayed taller mandibular corpora and wider symphyses. In contrast, folivores, folivore-frugivores and frugivore-folivores (although there is also extensive overlap with this group to the other frugivore-based groups), all displayed relatively wider mandibular corpora and taller symphyses (Figures 5.24, 5.26-5.27). These results largely appear to contrast with much of the work done by Hylander (1979b) and Bouvier (1986a, b) that suggested a deeper mandibular corpus was associated with folivory as a way of resisting parasagittal bending loads. Instead, a diet consisting of harder foods is here associated with a deeper mandible, which is consistent with the findings for the hard-object feeding *Lophocebus albigena* (Hylander, 1979b) and *Pongo pygmaeus* (Taylor, 2006a), and a diet consisting of tougher foods is here associated with a wider mandible. In this instance, it may be that the deeper mandibular corpus and wider symphyses associated with hard-object feeding is an adaptation to resist parasagittal bending loads and wishboning, and the wider mandibular corpus and taller symphysis associated with tough-object feeding may be an adaptation to resist axial torsion and vertical bending (Hylander, 1979a, 1985).

These results potentially differ to those of previous research for two reasons: 1) the sample used was different, and 2) some of the variables used were different. In the present study, focus was on frugivores with folivores, such as colobines (commonly used as the folivore reference species) not included. Future research using more folivorous species would confirm or challenge the above findings. Additionally, it is possible the use of different variables has had an effect on how the results from this study compare to others. Bouvier (1986a, b) and Ravosa (1991) both analysed jaw form by scaling M_2 corpus height and M_2 corpus width to body size and jaw length, whereas corpus robusticity indices as used here directly compare corpus height to corpus width from P_4-M_3.

A pattern that emerged from the dietary data based on field reports (direct observation) was the close clustering of frugivore-granivores and folivore-granivores on component 1 (size variables) but the slight differences on component 2 (corpus robusticity indices) (Figure 5.23). Folivore-granivores appear to have relatively wider mandibular corpora than do frugivore-granivores, which have relatively taller mandibular corpora. These two categories (frugivore-granivores and folivore-granivores) indicate that seed consumption (a secondary food) is associated with variation in size variables, while fruits or leaves (primary foods) are associated with variation in corpus robusticity indices. Overall, the bivariate graphs using traditional diet categories demonstrate that that there are some differences present in the masticatory morphology associated with dietary differences. However, the usage of the specific classification coding categories is preferred as it identifies the more subtle morphological differences between dietary categories.

In the food quantity analyses, different quantities of each of the foods did appear to correspond to different morphological patterns. High fruit consumption does not appear to have much bearing on morphology, but low and moderate consumption does, with low consumers characterised by relatively wider corpus robusticity indices and longer tooth crowns, and moderate consumers characterised by relatively taller corpus robusticity indices (Figure 5.28). Differences in fruit consumption could be a result of the varied foods that make up the rest of the diet when fruit consumption is low.

High consumers of leaves present wider mandibular corpora, taller symphyses, and wider tooth crowns relative to low and moderate consumers of leaves (Figures 5.29-5.30). High consumption of seeds is associated with a relatively taller mandibular corpus and wider crown shapes compared to low and moderate consumers of seeds (Figure 5.31). Once again, these results contrast with those of Hylander (1979b) and Bouvier (1986a, b). For the species analysed here it appears that tough-object feeders may be adapted to resist the axial torsion from the working side of the mandible in the corpus and vertical bending of the symphysis, while hard-object feeders may present adaptations to resist parasagittal bending in the corpus (Hylander, 1979a).

Depending on whether faecal analysis or direct observation is used, high consumption of roots can correspond to relatively taller (by direct observation) or wider mandibular corpora (by faecal analysis), and little difference to the crown shape indices (both by direct observation), compared to low and moderate consumers (Figures 5.32-5.33). This could mean that resistance to either parasagittal bending or axial torsion in the corpus are possible biomechanical adaptations associated with root consumption

(Hylander, 1979a, 1985). Different proportions of animal consumption are not reflected by different morphologies by direct observation, but they are by faecal analysis on the crown shape indices. Low consumers of low quantities of animal matter present relatively wider crowns and high consumers present relatively longer crowns (Figure 5.34).

The results of the food quantity analyses, therefore indicate that consumers of high quantities of more obdurate foods, e.g., seeds and leaves appeared to cluster in more distinct groupings, while consumers of lower quantities of the same foods appeared more dispersed. In contrast, high consumers of fruits (assumed here to be a soft food) do not cluster in defined patterns, presenting a more scattered appearance on the morphospace, while the low and moderate consumers of fruits cluster in more distinct groupings, indicating the other foods consumed had an important effect.

The finding that the more obdurate foods, such as seeds and leaves, that generally involve higher stress and strains on the bone than softer foods, such as fruits, appear to be more important determinants of the mandibular corpus robusticity indices than are those of low strain is consistent with extensive literature on the subject (Hylander, 1979b, 1984, 1985; Bouvier, 1986a, b; Ravosa, 1991, 1996; Daegling, 1992; Yamashita, 1996, 1998; Bouvier & Ravosa, 1998; Lambert *et al*., 2004; Foster *et al*., 2006; Dominy *et al*., 2008; Norconk *et al*., 2009; Daegling *et al*., 2011; McGraw *et al*., 2016; Ross *et al*., 2016). In fact, if leaves and seeds can be taken as proxies for representing tough and hard foods, respectively – which is cautioned against, but in this case necessary (Yamashita, 1998; Grine *et al*., 2006b, 2012; Taylor, 2006b; Vogel *et al*., 2014; Smith *et al*., 2015; Coiner-Collier *et al*., 2016; Talebi *et al*., 2016), there are different morphologies present in tough food eaters compared to hard food eaters (Figures 5.29-5.31). In this study, hard food consumers display relatively taller mandibular corpora, whereas, tough food consumers display relatively wider (more robust, i.e. a higher corpus robusticity index) mandibular corpora, along with taller symphyses. Previous researchers had suggested that it might not be possible to distinguish between morphologies of hard or tough food eaters (Hylander, 1979b; Smith, 1983; Daegling & Grine, 1991; Ravosa, 1996; Daegling & McGraw, 2001; Hogue, 2008; McGraw & Daegling, 2012; Daegling *et al*., 2013; Grine & Daegling, 2017). Yet the results from this study and Veneziano *et al*. (2019) suggest that some subtle distinctions may be possible.

The potential reasons that this research and that of Veneziano *et al*. (2019) identified a different relationship between hard and tough foods include, 1) sample size, 2) classification of diet categories, and 3) morphological variables examined. Firstly, the samples used in the present study were much larger than in many other studies and as a result the dietary proclivities of the non-human primates were more diverse. For example Hylander's (1979a) study was based on very limited species diversity as it focussed on *Macaca fascicularis* and *Galago crassicaudatus*.

Second, diet was analysed differently, for example, Smith (1983) used a binary diet categorisation (frugivory or folivory) and while those categories were used in this study, so too were more detailed categories, e.g., frugivore-folivore, as well as more quantity categories, which included seeds to represent harder foods. The additional diet categories used revealed some consistency among morphological patterns and diet, e.g., folivores when using specific classification coding categories by both direct observation and faecal analysis, and high leaf consumers both score in similar ways on the bivariate graphs (Figures 5.24, 5.26, 5.29-5.30). The diet categories also revealed some differences, e.g., folivory in the traditional diet categories (Figure 5.22) does not cluster in a defined way on the corpus robusticity indices as it does in all of the other dietary classification systems (Figures 5.24, 5.26, 5.29-5.30). This indicates that the traditional diet classification system is perhaps not refined enough to identify distinct associated patterns of morphological variation. In addition, root consumption results vary depending on whether they were obtained through direct observation or faecal analysis (Figures 5.32-5.33). The use of more extensive diet categories is therefore recommended so as to obtain a more accurate reflection of the association between diet and morphology.

Finally, this study used different variables and or variations of different variables to previous studies. For example, Daegling (1992) analysed the cross-sectional area of the corpus at the M_2. Where the variables used overlapped with other studies, this study used more. For example, here the corpus robusticity indices were analysed from P_4-M_3, whereas other studies e.g., Smith (1983) used just the M_1 corpus robusticity indices, Daegling & McGraw (2001) used M_2 corpus robusticity indices, and Pitirri & Begun (2019) used M_1-M_2 corpus robusticity indices. Which corpus variables are used is potentially important, because slightly different patterns were present in monkeys and apes for those variables that were significantly different between consumers of different diets (Table 6.1). For monkeys, the major differences arose on P_4-M_2 corpus robusticity indices (>80%), with significant differences also found on symphyseal robusticity indices and M_3 corpus robusticity indices (>60%). For apes, the major differences arose on symphyseal, P_4-M_1 corpus robusticity indices (100%), but rarely on M_2 corpus robusticity indices (20%) and never on M_3 corpus robusticity indices. It is likely therefore that because more corpus variables were analysed in this study than in others (e.g., Pitirri & Begun 2019) different morphological patterns associated with different diets were identified. Pitirri & Begun (2019) focussed their study on apes, and used M_1-M_2 corpus robusticity indices as defining variables. However, as shown here the best variables to identify variation associated with diet in apes are symphyseal robusticity indices, and P_4-M_1 corpus robusticity indices. Thus, Pitirri & Begun (2019) potentially missed identifying a stronger relationship between the corpus robusticity indices and diet because they did not use a greater number of variables, and particularly those that best identified the morphological differences. If both monkeys and apes are used in studies assessing the potential association between diet and corpus robusticity indices then all corpus robusticity indices from P_4-M_3 should be included to maximise the potential for identifying morphological variability associated with different diets. The use of only 1 or 2 variables potentially misses out on important patterns of association.

An additional pattern to emerge from this study is that the most robust non-human primates (those with the widest mandibular corpora, as defined by the robusticity index) were the consumers of folivorous diets. That folivory corresponds to a more robust mandible is consistent with some published research (Hylander, 1979b; Bouvier, 1986a, b; Ravosa, 1991), but not all, as other researchers have found that a robust mandibular corpus is associated with a harder food diet (Daegling, 1992; Veneziano *et al.*, 2019). It is possible that the present study and that of Veneziano *et al*. (2019) did not report similar findings in terms of which food type corresponds best to mandibular robusticity because the two studies use different ways of assessing dietary hardness/ toughness. It is assumed here that high quantities of seeds in the diet equals high quantities of hard foods, and equally that high quantities of leaves in the diet equals high quantities of tough foods. In contrast, Veneziano *et al*. (2019) use dental microwear patterns to assess hardness/ toughness, so they are using the traces of the mechanical properties of foods for comparison. The approach of Veneziano *et al*. (2019) is perhaps one of the best ways to determine the dietary hardness/ toughness, and is an approach that should probably be used in future studies. However, such data were not available for the wide range of primate species included in this study sample, and so could not be used in this research.

It is also possible that the results from the present study reported differences on the diets best associated with robusticity due to the fact that the term used in previous research might reflect slightly different morphology than robusticity reported in this study (what the robusticity index measures is addressed in Section 4.2.2). Generally, *P. boisei* are commonly regarded as the most robust hominin (Broom, 1938; Dean, 1988; Grine & Martin, 1988; Wood & Strait, 2004; Wood & Constantino, 2007), yet in the present study *P. boisei* did not exhibit greater robusticity than other hominins. In fact, *A. africanus* actually scored the highest value on component 3 (corpus robusticity indices) (Figure 5.40). As a result, further research is necessary in order to confirm this trend, perhaps using a different definition of robusticity.

In contrast to the patterns present on the corpus, there appears to be very little to separate seed consumption (hard foods) from leaf consumption (tough foods) using dental traits. This finding is in contrast to extensive literature which suggests that the relationship between eating hard or tough food is more correlated with the dentition than that of the mandibular corpus (Kay, 1975; Rosenberger & Kinzey, 1976; Kinzey, 1978; Happel, 1988; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Lucas *et al*., 2008b; Lee *et al*., 2010; Ungar 2011, 2015; Vinyard *et al*., 2011). In terms of the dentition, it is likely that the lack of correlation present between the nature of the food consumed and the dentition is again a reflection of the variables analysed. Crown area and crown shape indices were the variables analysed for this study, but in many other studies where morphological differences between diets have been reported, cusp size and shape (e.g., whether cusps were low and blunt), the degree of shear on the shearing blade and dental enamel thickness were all found to be more informative than the size and shape of the crown area (Kay, 1975; Kinzey, 1978; Happel, 1988; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Lucas *et al*., 2008b; Lee *et al*., 2010; Ungar 2011, 2015). It appears therefore that morphological differences between consumers of different diets are not readily identified using crown area and crown shape indices. As a result, further analyses on more detailed morphological features of the dentition should be undertaken in order to either confirm or challenge the results obtained so far.

6.1.1.2 Assessing the contribution of diet towards morphological form

In the regression models analysing the contribution of diet towards the dental and mandibular variation, diet explained between 10 and 20% of the variance present (Table 5.25). In the regression models using component 1 (size variables), log body weight and sex explained the majority of the variance present (77%), with diet contributing a further 9% of the variance. This result concurs with Louys *et al.* (2015a) and Veneziano *et al*. (2019) who also found that dental size was mainly influenced by body size.

The amount of variance explained by log body weight and sex was reduced in the regression models run on components 2 (corpus robusticity indices = 31%), 3 (crown shape indices = 23%), and 4 (symphyseal robusticity indices = 1%), compared to component 1 (size variables = 77%). Meanwhile, when diet was included in the models, the amount of variance on the dependent variable explained increased by 21% for component 2 (corpus robusticity indices), by 19% for component 3 (crown shape indices), and 20% for component 4 (symphyseal robusticity indices), compared to the 9% for component 1 (size variables) (Table 5.25). The increased association between component 2 (corpus robusticity indices) and diet was again similar to that of Veneziano *et al*. (2019), who found that mandibular corpus robusticity indices were linked to food mechanical properties. In contrast, the association between component 4 (symphyseal robusticity indices) and diet in this study differs from that of Vaneziano *et al*. (2019), who did not find any association between diet and symphyseal robusticity indices, instead finding that this variable correlated best with log body size and phylogeny. These results and those of Vaneziano *et al*. (2019) highlight that diet, while not predicted to be the most important variable to explain variance, is consistently an important factor in explaining morphological variance, and is important to consider when analysing the various aspects of mandibular morphology.

The diets that appear to result in higher variance explained for each component also appear to show a pattern. Components 1 (size variables) and 2 (corpus robusticity indices) are best explained by diets that contained fruits and seeds, while components 3 (crown shape indices) and 4 (symphyseal robusticity indices) are best explained by diets that contained fruits, leaves and roots. This could indicate that different components of the morphology respond in different ways to different diets. In this case, size and the corpus have a stronger association with harder foods, while the dentition and the symphysis have a stronger association with tough foods. If different types of diets have a greater association with different components of the morphology as suggested by the multiple regression analyses, then it is potentially very interesting as regards to *Paranthropus*. It has been suggested by some (Wood & Schroer, 2012; Strait *et al*., 2013; Smith *et al*., 2015) that it is inconceivable that as one aspect of morphology becomes better adapted to hard foods, another simultaneously becomes better adapted to tough foods. These multiple regression results indicate that this might be possible in non-human primates. It would be useful for future work to elucidate the subtle mandibular morphological differences in *Paranthropus* and other hominins in relation to proposed dietary variation.

6.1.1.3 Other factors that contribute to morphological form

The results from this research in combination with those of other studies (e.g., Hylander, 1979b, 1984, 1985; Bouvier, 1986; Ravosa, 1991, 1996; Yamashita, 1996, 1998; Bouvier & Ravosa, 1998; Lambert *et al*., 2004; Norconk *et al*., 2009; Daegling *et al*., 2011; McGraw *et al*., 2016; Ross *et al*., 2016) indicate that there is an association between the nature of the foods consumed (food mechanical properties) and the morphology of species. The results from this study also highlight that there are other factors besides diet associated with morphological form. Throughout the analyses, size was clearly an important factor in explaining variation, while biological sex (Table 5.25) and taxonomy contributed to variation (Figures 5.1-5.7). They demonstrate differences associated with species characterised by different degrees of sex dimorphism and the different family groupings. There may be other important contributing factors, but they have not been explored here. The fact that log body weight, sex and dietary categories did not account for all of the variance present supports this conclusion.

It must be remembered that the mandible is a component of the masticatory apparatus, which also comprises the muscles of mastication, both the internal and external aspects of the mandible, the temporomandibular joint, the tongue and the cheek, among other hard and soft tissues (Bock & von Wahlert, 1965; Grine *et al*., 2010; Ungar, 2015). All of which means that the mandible is not a singular feature, but rather part of a character complex (Bock & von Wahlert, 1965). With this in mind, a robust masticatory morphology is not necessarily a functional adaptation to resist stress because the craniofacial apparatus does not function only to masticate foods (Smith, 1983; Hylander, 1984; Daegling, 1993b; Daegling & McGraw, 2001; Taylor, 2002, 2006a, b, 2009; Koyabu & Endo, 2009; Larson *et al*., 2018). The craniofacial apparatus, along with the rest of the skeleton, is governed also by several non-dietary factors. These include: allometry, phylogeny, genetic drift, ontogenetic changes, sexual dimorphism, the relationship with other tissues, spatial demands for the growth of the dentition, respiration, digestion, display behaviours and communication (with the latter factors particularly relevant for the masticatory apparatus) (Bock & von Wahlert 1965; Smith, 1983; Kanazawa & Rosenberger, 1989; Cole, 1992; Daegling, 1992, 1996; Yamashita, 1996; Daegling & McGraw, 2001; Taylor, 2006c, 2009; Cardini & Elton, 2008b; Grine *et al*., 2012; Daegling *et al*., 2013; Elton *et al*., 2016; Ross *et al*., 2016; Grine & Daegling, 2017; Larson *et al*., 2018; Veneziano *et al*., 2019). Thus, feeding behaviour and diet are not the only selective forces acting on the mandible, and since all of these factors are likely to vary by species, so too may the mandibular form (Bock & von Wahlert 1965; Koyabu & Endo 2009; Veneziano *et al*., 2019). In fact, the effect of phylogeny, for example means that there are many apparently novel shapes and adaptations that are likely to reflect developmental factors, and not selective pressures (Bock, 1980; Vinyard & Ravosa, 1998; Lucas *et al*., 2008a; McGraw *et al*., 2012; Ungar, 2015; Gailer *et al.*, 2016; Ungar & Hlusko, 2016; Grine & Daegling, 2017; Zanolli *et al*., 2017; Veneziano *et al*., 2019). In the case of *Paranthropus*, it appears that factors such as phylogeny, allometry or tooth size are not responsible for the derived masticatory apparatus, as discussed in Section 2.2.1. As a result, other factors, such as diet need to be explored further.

Another potential explanation for the difference in morphology is that the morphological differences (robusticity) between *Australopithecus* and *Paranthropus* were reflective of difference in tool use. It has been proposed as an explanation for differences in the mandibular robusticity in the more gracile *Pongo abelii* and the more robust *P. pygmaeus*. *P. abelii* use tools to break large and tough *Neesia* seeds, while *P. pygmaeus* use their jaws to break such seeds open (Taylor, 2006a, 2009). In this case, it is suggested tool use has reduced the selective demands on the morphology of *P. abelii* (Taylor, 2006a; Vogel *et al*., 2014).

There are potentially many contributing factors to masticatory morphological form, which is to be expected given it forms part of a character complex (Bock & von Wahlert, 1965; Bock, 1980). Acknowledgement of these other factors is crucial in gaining a more comprehensive understanding of how dietary and non-dietary factors interact to produce the varying mandibular structures analysed (Daegling & McGraw, 2011; Vogel *et al*., 2014). Ultimately, however, these other factors were not within the scope of this thesis to explore. Furthermore, it is important to stress that the results from this research reinforce the association between diet and morphology.

6.1.2 Morphological variation in hominins and non-human primates

With an association between diet and morphology being identified, the second part of the thesis focussed on comparing the morphology of the hominins to the non-human primates. On the basis of stable carbon isotopes and dental microwear texture analysis much of what was assumed regarding hominin dietary adaptation has been revised (Berthaume *et al*., 2010; Grine *et al*., 2012; Wood & Shroer, 2012; Scott *et al*., 2014). Both techniques challenged earlier assumptions (*sensu* Robinson, 1954a, 1963) about the diets of hominins and further questioned whether morphology can act as an indicator of dietary adaptation. The last point was the focus of the thesis overall, focussing first on the association between diet and morphology in non-human primates, and then extrapolating that information further to hypothesise about whether the morphology of non-human primates of known-diet could provide some indications of potential dietary adaptation in the hominins.

6.1.2.1 Comparing the morphological variation present in hominins to non-human primates

The research questions for this section examined how morphologically comparable the hominins are to the non-human primates analysed, and whether by using non-human primates as models the morphological features of hominins can be associated with the dietary categories of extant species. Components extracted from a new PCA were used to compare hominins to non-human primates. The hominins fall within the range of non-human primates, especially the apes when component 1 (size variables) is compared with component 2 (crown shape indices) (Figure 5.35). In contrast, the hominins have greater scores on component 3 (corpus robusticity indices) than any non-human primate species. Only *A. afarensis* and *Macaca radiata* scored at the same level (Figures 5.36-5.37).

Across each of the components, there existed a large amount of variation between the hominin species, greater than that present within *Gorilla* and *Pongo*, but more similar to that present between *Pan paniscus* and *P. troglodytes*, and within *P. troglodytes* (Figures 5.38-5.40). The exception to this pattern was between the two *Australopithecus* species, who present a range greater than any single extant species analysed here (Figures 5.38-5.40).

6.1.2.2 Associating hominin morphological features to non-human primate diet categories

The hominins analysed in this study align with various diets based on how their morphologies compare to non-human primates of known diet (Figures 5.41-5.58). The results from the hominins have been summarised and compared to stable carbon isotope and dental microwear results in Tables 6.4-6.5. The results that are of particular interest are those from the non-*Homo* species: *A. afarensis, A. africanus, P. boisei* and *P. robustus.* These are the same species that yielded the stable carbon isotope and microwear results that have focussed attention upon the form-function relationship in hominins (Sponheimer & Lee-Thorp, 1999; Scott *et al*., 2005; Sponheimer *et al*., 2005a, 2006a, 2013; Ungar *et al*., 2008).

Based on how the hominins score compared to non-human primates (based only on the recordings from components 1 (size variables) and 2 (crown shape indices), it is likely that there were dietary differences between all of the hominins, including *P. robustus* and *P. boisei* (Tables 6.4-6.5). Many of the dietary differences suggested for the hominins are reflective of omnivorous diets, with each hominin species appearing to overlap with a number of different diet categories and food types, but not in the same way. The suggested diets that the hominins align with are based only on the recordings from components 1 (size variables) and 2 (crown shape indices), as the hominins did not align with any non-human primate for component 3 (corpus robusticity indices), with the exception of *A. afarensis* in relation to *M. radiata.*

Given how distinct the hominins score on component 3 (corpus robusticity indices) in relation to the non-human primates, it would appear the hominins were somewhat overdesigned relative to the extant species. The notion of the mandible being overdesigned has been discussed before (see Ward, 1991) and dismissed (Daegling & Hylander, 1997), but that was not in the same context as this. Future work could assess corpus morphology in different ways, e.g., analysing the mandible with Finite Element Analysis to assess the loading and strain capabilities (Toro-Ibacache *et al*., 2016; Stansfield *et al*., 2018a, b), which would help to clarify the possibility of the hominins appearing to be overdesigned.

Table 6.4: Hominin dietary interpretations based on how they plot to known-diet non-human primate dietary categories compared to stable carbon isotope and dental microwear results

Species	Stable Carbon Isotope Analysis	Dental Microwear Texture Analysis	Components	Traditional Diet	Specific Classification Coding DO	Specific Classification Coding FA
A. afarensis	C_3 - C_4/ CAM consumer. [1, 2, 3]	Lacking both complexity and anisotropy signals = softer food diet [4, 5]	1: Size	Omnivore	Omnivore	Frugivore-folivore, frugivore-faunivore
			2: CSI	Frugivore	Frugivore	Frugivore-folivore, folivore-frugivore
			3: CRI	Frugivore	Frugivore	Folivore-frugivore
A. africanus	C_3 - C_4 consumer (60/40). [1, 6, 7, 8, 9]	Slightly more anisotropy than complexity present = varied diet but more tough foods present [10, 11, 12, 13]	1: Size	Frugivore	Folivore-granivore, frugivore-folivore	Frugivore-folivore, frugivore-granivore, omnivore
			2: CSI	Frugivore	Omnivore, frugivore-faunivore	Omnivore, frugivore-granivore
P. boisei	Predominantly a C_4 consumer (C_3 = 25% / C_4 = 75%), with an increase in C_4 consumption over time (20/80). [1, 8, 14]	Low complexity and low-to-moderate anisotropy = softer/ slightly tough food diet. [8, 11, 15]	1: Size	Omnivore	Omnivore	Omnivore (near to frugivore-folivore, folivore-frugivore)
			2: CSI	Frugivore	Frugivore-folivore, folivore-frugivore	Frugivore-folivore
P. robustus	C_3 - C_4 consumer (65/35). [1, 6, 8, 16, 17]	Highly varied diet, with high complexity and low anisotropy = harder food diet. [9, 10, 18, 19, 20]	1: Size	Omnivore	Omnivore, frugivore-folivore	Omnivore, frugivore-folivore
			2: CSI	Frugivore	Frugivore-granivore, frugivore-faunivore, omnivore	Omnivore, frugivore-granivore, frugivore-folivore, folivore-frugivore
H. habilis	C_3 - C_4 consumer (65/ 35) in early years, changing to an increase in C_4 consumption later (45/55). [1, 21, 22]	Varied diets, lacking both complexity and anisotropy signals = softer food diet. [23]	1: Size	Frugivore	Frugivore-folivore	Frugivore-folivore
			2: CSI	Frugivore	Omnivore, frugivore-faunivore, frugivore-granivore	Omnivore, frugivore-granivore
H. ergaster	C_3 - C_4 consumer (75/25). [9, 24]	Highly varied diet, with high complexity and low anisotropy = harder food diet. [9, 23]	1: Size	Frugivore	Frugivore-granivore	Frugivore-folivore, frugivore-granivore, omnivore
			2: CSI	Folivore	Folivore, folivore-frugivore, frugivore-granivore	Frugivore-folivore, folivore-frugivore

[1] Sponheimer *et al*., 2013; [2] Wynn *et al*., 2013; [3] Levin *et al*., 2015; [4] Ungar *et al*., 2010; [5] Grine *et al*., 2006b; [6] Sponheimer & Lee-Thorp, 1999; [7] van der Merwe *et al*., 2003; [8] Sponheimer *et al*., 2005a; [9] Ungar & Sponheimer, 2011; [10] Scott *et al*., 2005; [11] Ungar, 2011; [12] Grine *et al*., 2012; [13] Peterson *et al*., 2018; [14] Cerling *et al*., 2011; [15] Ungar *et al*., 2008; [16] Lee-Thorp *et al*., 1994; [17] Sponheimer *et al*., 2006a; [18] Grine, 1981; [19] Grine, 1986; [20] Kay & Grine, 1988; [21] Cerling *et al*., 2013; [22] van der Merwe *et al*., 2008; [23] Ungar *et al*., 2006; [24] Lee-Thorp *et al*., 2000

Table 6.5: Hominin dietary interpretations based on how they plot to known-diet non-human primate quantity categories compared to stable carbon isotope and dental microwear results

Species	Stable Carbon Isotope Analysis	Dental Microwear Texture Analysis	Comp.	Direct observation					Faecal analysis				
				Fruit	Leaves	Seeds	Roots	Animals	Fruit	Leaves	Seeds	Roots	Animals
A. afarensis	C_3 - C_4/ CAM consumer.[1, 2, 3]	Lacking both complexity and anisotropy signals = softer food diet[4, 5]	1: Size	Mod.	Low/ Mod.	Low	Low/ High	Low	High	Low	Low/ Mod.	Mod.	Low
			2: CSI	High	Low	Low	Low	Low	Mod./ High	Mod./ High	Low	Mod.	Low
			3: CRI	High	Low	Low	Low	Low	High	Mod.	Low	Low	Mod.
A. africanus	C_3 - C_4 consumer (60/40).[1, 6, 7, 8, 9]	Slightly more anisotropy than complexity present = varied diet but more tough foods present[10, 11, 12, 13]	1: Size	Low/ High	Low/ Mod.	Mod./ High	Mod.	Low (near Mod.)	Low/ High	Mod.	Low/ Mod.	Low/ Mod.	Low
			2: CSI	Mod./ High	Low	Mod./ High	Low	Mod.	Mod./ High	Low/ Mod.	High	-	Low
P. boisei	Predominantly a C_4 consumer (C_3 = 25% / C_4 = 75%), with an increase in C_4 consumption over time (20/80).[1, 8, 14]	Low complexity and low-to-moderate anisotropy = softer/ slightly tough food diet.[8, 11, 15]	1: Size	Mod.	Low	High	Low	Low	Mod. (near low/ high)	Low	High	Low	Mod.
			2: CSI	Mod./ High	Low/ High	Low	Low	Low	High	Mod.	Low	Low	Low
P. robustus	C_3 - C_4 consumer (65/35).[1, 6, 8, 16, 17]	Highly varied diet, with high complexity and low anisotropy = harder food diet.[9, 10, 18, 19, 20]	1: Size	Mod./ High	Low	Low	High	Low	Mod./ High	Mod.	Low/ High	Low/ Mod.	Low
			2: CSI	Low/ High	Low/ High	High	Low	Low	Low, Mod., High	Mod./ High	Low/ Mod.	Low/ High	Low
H. habilis	C_3 - C_4 consumer (65/ 35) in early years, changing to an increase in C_4 consumption later (45/55).[1, 21, 22]	Varied diets, lacking both complexity and anisotropy signals = softer food diet.[23]	1: Size	High	Low	Low	Low	Low	High	Low/ Mod.	Low	Low	Low
			2: CSI	Mod./ High	Low	Low/ High	Low	Low/ Mod.	Mod./ High	Low/ Mod.	High	-	Low
H. ergaster	C_3 - C_4 consumer (75/25).[9, 24]	Highly varied diet, with high complexity and low anisotropy = harder food diet.[9, 23]	1: Size	High	Low	Mod./ High	Mod.	Low	High	Mod.	Mod.	Low	Low
			2: CSI	Low, Mod., High	Low/ High	High	Mod.	Low	Low, Mod., High	Mod/ High	Low/ Mod.	Low/ High	Low

[1] Sponheimer *et al*., 2013; [2] Wynn *et al*., 2013; [3] Levin *et al*., 2015; [4] Ungar *et al*., 2010; [5] Grine *et al*., 2006b; [6] Sponheimer & Lee-Thorp, 1999; [7] van der Merwe *et al*., 2003; [8] Sponheimer *et al*., 2005a; [9] Ungar & Sponheimer, 2011; [10] Scott *et al*., 2005; [11] Ungar, 2011; [12] Grine *et al*., 2012; [13] Peterson *et al*., 2018; [14] Cerling *et al*., 2011; [15] Ungar *et al*., 2008; [16] Lee-Thorp *et al*., 1994; [17] Sponheimer *et al*., 2006a; [18] Grine, 1981; [19] Grine, 1986; [20] Kay & Grine, 1988; [21] Cerling *et al*., 2013; [22] van der Merwe *et al*., 2008; [23] Ungar *et al*., 2006; [24] Lee-Thorp *et al*., 2000

Stable carbon isotope analyses indicate that *A. afarensis* consumed diets that were from C_3, C_4 and CAM isotopic pathways (Wynn *et al*., 2013; Levin *et al*., 2015), and the dental microwear texture analyses indicated that the diet consumed was predominantly one comprising softer foods (Grine *et al*., 2006b; Ungar *et al*., 2010). Hypothetically, these isotopic reconstructions are supported by the way in which *A. afarensis* score in relation to some of the extant non-human primates. *A. afarensis* could have consumed an omnivorous diet dominated by fruits, and supplemented by leaves and some seeds, roots and animals (Tables 6.4-6.5). These are foods that could correspond to the reconstructions based on the microwear and stable carbon isotopes. Fruits and seeds could come from the C_3 resources and the leaves[8] and roots from the C_4 resources, while the animal matter could be reflective of either photosynthetic pathway, depending on what pathway the foods they consumed came from (Sponheimer *et al*., 2005a, 2006a; Cerling *et al*., 2013). The mechanical properties associated with fruits, leaves, seeds and animal matter could also correspond to those of softer foods, as the fruits could be soft and fleshy, and the leaves could be consumed in relatively low quantities. Seeds and roots might not have featured prominently in the diets based on a lack of correspondence to microwear. Depending on whether the animals were vertebrates or invertebrates determines their resistance to fracture. A vertebrate may be tough and fleshy, while an invertebrate could be soft-bodied, e.g., caterpillars and termites, or hard if they had hard exoskeletons, e.g., beetles (Smith, 1983; Melin *et al.*, 2014; Mossdossy *et al*., 2015). Neither hard nor extensively tough features have been identified on microwear studies of *A. afarensis* to date, meaning animal consumption (should it have occurred) could reflect consumption of the softer-bodied invertebrates. Termite fishing as observed in *Pan* has been proposed as a potential dietary activity the hominins could have undertaken to obtain the necessary protein requirements (Bogart & Pruetz, 2008, 2011). While the earliest occurrence of *A. afarensis* from approximately 3.9 million years ago (Wynn *et al*., 2006; Reed, 2008)) precedes the earliest known date of stone tools currently (Lomekwi stone tools are dated to 3.3 million years old (Harmand *et al*., 2015)), it is possible the hominins could have used perishable tools, such as twigs, to procure social insects, such as termites (McGrew, 1992; Ungar & Teaford, 2002; Bogart & Pruetz, 2011).

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[8] Leaves as used in this section do not simply refer to leaves that are found on trees, but also include grass leaves, piths, stems, and herbs. Essentially, they are the foliage off of a plant/ tree. This is a potential limitation as the description is vague, however, it would be extremely difficult to obtain meaningful results when analysing many different dietary categories. Information on what foods were included in each of the following categories fruits, leaves, seeds, roots and animals is available in Appendix C, Table C.2.

Stable carbon isotope analyses and dental microwear texture analysis indicate that *A. africanus* consumed highly varied diets that were from a mix of C_3 and C_4 resources that consisted of some hard and tough foods (Sponheimer & Lee-Thorp, 1999; van der Merwe *et al*., 2003; Scott *et al*., 2005; Sponheimer *et al*., 2005a; Peterson *et al*., 2018). These reconstructions are supported by the way in which *A. africanus* score in relation to some of the extant non-human primates. *A. africanus* could have consumed a mixed diet dominated by fruits and seeds, and supplemented by leaves, roots and animals (Tables 6.4-6.5). Once again, these are all foods that could correspond to the reconstructions based on the microwear and stable carbon isotopes, as the fruits and seeds could come from the C_3 resources and the leaves and roots from the C_4 resources, while the animals could be reflective of either photosynthetic pathway. The mechanical properties associated with fruits, seeds, leaves, roots and animals could also correspond to those of tougher and harder foods. Depending on the part of the food item consumed, its maturity and seasonality, along with other factors, the fruits could be soft or tough, the leaves and roots could be tough, the seeds hard, and again, the animals could be a mixture of both hard and tough, or soft and or leave no trace behind if they were consuming termites.

It is likely that the hominins, such as *A. afarensis* and *A. africanus* both consumed leaf-based foods to some extent, based not just on the results from this study, but also an understanding of the need to achieve a balanced diet. However, why their microwear patterns differed is unclear. It is possible that because dental microwear reflects the mechanical properties of food items consumed shortly before death (Grine, 1986; Teaford & Oyen, 1989), *A. africanus* and *A. afarensis* consumed foods of a different nature. Perhaps *A. africanus* specimens perished when leaves were more mature and thus left more of a microwear signal, while *A. afarensis* perished when leaves were younger and consequently, did not leave defined microwear signals. This scenario is very unlikely. So too is the implication that all specimens would have died under one environmental condition. The differences could also reflect environmental differences between East and South Africa, where maybe in South Africa there were tougher foods, fewer trees flushing, or more dusts present compared to East Africa. As highlighted by Geissler *et al*. (2018) where on the forest floor foods were picked up would determine how much grit covered the foods, with those collected from above the leaf litter coated in significantly less grit than the foods from beneath the leaf litter. Perhaps *A. africanus* consumed seeds regularly found beneath the leaf litter, and *A. afarensis* consumed seeds from above the leaf litter, or higher in the canopy. It is possible therefore that the environmental differences between East and South Africa could explain the differences in dietary signals between *A. africanus* and *A. afarensis.* However, it is not possible to make precise inferences about the microwear differences because there is no evidence to either confirm or deny the suggestions.

The stable carbon isotope and dental microwear texture analysis results from *P. boisei* indicate this species continued the trend of the East African hominins (from *A. afarensis* to *P. aethiopicus*) of consuming a diet dominated by tough, C_4 foods (Ungar & Sponheimer, 2011; Cerling *et al*., 2011, 2013; Sponheimer *et al*., 2013; Levin *et al*., 2015). The C_4 isotopic pathway accords with the environmental reconstructions associated with *P. boisei* specimens (open woodlands, edaphic grasslands, savannah, and bushland habitats) (Reed, 1997; Dominguez-Rodrigo *et al*., 2001; Schwartz & Tattersall, 2005; Plummer *et al*., 2015; Linder, 2017). The dental microwear patterns indicate *P. boisei* consumed a diet with softer and tougher foods, characterised by striations across the occlusal surfaces (Ungar *et al.*, 2008, 2012). Due to these reconstructions, it was suggested that the morphology could reflect the repetitive chewing of tough, fibrous foods, rather than the infrequent consumption of hard foods (Grine *et al.*, 2012; Ungar *et al*., 2012; Pampush *et al*., 2013; Macho, 2014; Scott *et al*., 2014; Alemseged, 2015; Berthaume *et al*., 2018). Research has been undertaken to explore foods that are from C_4 isotopic pathways and tough to masticate. Foods could have included grass leaves (Cerling *et al*., 2011; Lee-Thorp, 2011; Ungar & Sponheimer, 2011; Sponheimer *et al*., 2013; Paine *et al*., 2018), grass seeds (Jolly, 1970), and sedges (Sponheimer *et al*., 2005a, 2013; Dominy *et al*., 2008; Cerling *et al*., 2011; Lee-Thorp, 2011; Ungar & Sponheimer, 2011; Macho, 2014; Levin *et al*., 2015).

These reconstructions are supported by the way *P. boisei* score compared with some of the non-human primates. *P. boisei* could have consumed a diet consisting of high quantities of leaves and fruits, with a low quantity of seeds, roots and animals (Tables 6.4-6.5). It is not possible based on the present results to support or reject suggestions mentioned above, as foods were not analysed at the level of grass leaves, seeds and sedges (leaves here essentially include all things folivorous). Consumption of leaves and fruits, with low quantities of seeds, roots and animals could correspond to the reconstructions based on the microwear and stable carbon isotopes. This is because the leaves and roots could come from the C_4 resources, the fruits and seeds from the C_3 resources (these make up approximately 23% of the diet according to Cerling *et al.* (2013)), and the animals from either pathway. The mechanical properties associated with these foods could also correspond to those of softer/ tougher foods, as the fruits could be soft and the leaves and roots somewhat tougher. A further support to the idea that *P. boisei* frequently consumed tough foods is that the most robust non-human primates (those with the widest mandibular corpora) also had a diet that was either dominated by or supplemented by foliage (folivores, folivore-frugivores and frugivore-folivores), supporting the findings of Hylander (1979b), Bouvier (1986a, b) and Ravosa (1991). Thus, the folivorous diets of non-human primates appear to be associated with more robust mandibular corpora (as defined by component 2) and could represent a directional trend that the hominins continue (Figures 5.24, 5.26, 5.29-5.30). Of course, the same caveat discussed before regarding the robusticity indices applies here. The folivores analysed in this study display the widest mandibular corpora, and thus the highest robusticity index, other studies using different ways of analysing robusticity might obtain different results. Further clarity on robusticity and how it is best measured is vital.

The idea that the morphology of *P. boisei* could reflect the repetitive chewing of tough foods, rather than the infrequent consumption of hard foods was argued against because a low-cusped dentition appeared to be poorly adapted to such a diet (Hylander, 1988; Wood & Strait, 2004; Wood & Schroer, 2012; Strait *et al*., 2013; Smith *et al*., 2015). However, it is possible that with the exception of the low-cusped dentition, the rest of the masticatory morphology could have been well adapted to tough foods. The morphology would still be able to generate and transmit the high, repetitive loads required when grinding tough foods. In so doing, it would compensate for the apparent sub-optimal dental adaptation (Daegling & McGraw, 2007; Ungar & Sponheimer, 2011; Scott *et al*., 2014; Ungar & Hlusko, 2016). Indeed, consensus has shifted away from the idea that the derived masticatory morphology of *Paranthropus* was an optimally designed morphological solution to a hard-food diet (Ungar & Hlusko, 2016; Grine & Daegling, 2017). Despite the fact that the dentition was not ideally suited to masticating tough foods it does not mean that it could not perform the job efficiently (Daegling *et al*., 2013; Scott *et al*., 2014; Gailer *et al*., 2016). *Cercocebus atys* and the bovid, *Kobus ellipsiprymnus* provide evidence of extant animals consuming foods not expected to be consumed based on their morphologies. *Cercocebus atys* frequently consume extremely hard seeds, and grazing bovids frequently consume tough plant materials, yet the morphology in both appears to be sub-optimally suited to those foods (Daegling *et al*., 2011, 2013; McGraw & Daegling, 2012; Gailer *et al*., 2016).

Alternatively, if the C_4 foods consumed by *P. boisei* were leaves of grasses and sedges in their membranous state they would not require the dentition to be reflective of a typical folivore, with high shearing cusps (Talebi *et al*., 2016). Indeed the low-cusped molars could have been suitable adaptations to crushing the tough foods in a milling and grinding action (Macho, 2014; Scott *et al*., 2014).

Stable carbon isotope analyses indicate that *P. robustus* consumed a mixed diet of C_3 and C_4 resources (Lee-Thorp *et al*., 1994; Sponheimer & Lee-Thorp, 1999; Sponheimer *et al*., 2005a, 2006a). This is an observation that could be consistent with the results of the dental microwear texture analyses, which indicated that the diet was highly varied, and included hard, brittle foods (Grine, 1981, 1986; Kay & Grine, 1988; Scott *et al*., 2005; Peterson *et al*., 2018). These reconstructions are supported by the way in which *P. robustus* score in relation to some of the non-human primates. *P. robustus* could have consumed a mixed diet, which consisted of high quantities of fruits, leaves and seeds, and supplemented by roots and animals (Tables 6.4-6.5). These are all foods that could correspond to the reconstructions based on the microwear and stable carbon isotopes, as the fruits and seeds could come from the C_3 resources and the leaves and roots from the C_4 resources, while the animals could be reflective of either photosynthetic pathway. The mechanical properties associated with these foods could also correspond to those of tougher and harder foods, as the fruits could be soft, leaves and roots could be tough, the seeds hard, and the animals could be hard, tough or soft depending on the type of animal consumed (vertebrate or invertebrate).

The results from this study support the stable carbon isotopes and dental microwear texture analysis results that suggest *P. robustus* and *P. boisei* probably consumed different foods. It is likely that both species consumed varied diets, and were thus dietary generalists, but perhaps they concentrated on different combinations of foods. The diet of *P. robustus* appears to overlap with a diverse range of diet types, whereas *P. boisei* appears to be more restricted with the diet types it overlaps with, falling more in the range of some of the frugivores and some of the folivores (Tables 6.4-6.5).

Stable carbon isotope analyses indicate that *H. habilis* consumed a largely C_3 diet, with consumption of C_4 resources increasing over time (van der Merwe *et al*., 2008; Cerling *et al*., 2013). This is an observation that could be consistent with the results of the dental microwear texture analyses, which indicated that the diet was mostly dominated by soft foods due to a lack of either anisotropy or complexity signals (Ungar *et al*., 2006). Such reconstructions are partially supported by the way in which *H. habilis* score in relation to some of the non-human primates. *H. habilis* could have consumed a mixed diet, which consisted of high quantities of fruits, and potentially moderate-high quantities of leaves and seeds, with a presence of animal and root consumption too (Tables 6.4-6.5). These are all foods that could correspond to the reconstructions based on the microwear and stable carbon isotopes, as the fruits and seeds could come from the C_3 resources and the leaves and roots from the C_4 resources, while the animals could be reflective of either photosynthetic pathway. Aside from the fact that fruits could be soft, the rest of the assumed mechanical properties associated with these foods do not completely correspond to the microwear signals. There are two potential reasons for this lack of association: 1) the maturity of the foods consumed and 2) the proposed use of tools by early *Homo*. The hominins could have been consuming young leaves and ripe seeds, both of which could potentially have been at their softest and lacking the plant defences that mature leaves and unripe seeds would possess (Kinzey, 1978; Kinzey & Norconk, 1990; Milton, 1993; Krishnamani, 1994; Reynolds *et al*., 1998; Norconk *et al*., 2009; Rosenberger, 2013; Lambert & Rothman, 2015). Alternatively, tools could have been used for the butchering of animals or the breaking down of the hard outer shell of seeds, as seen in non-human primates, e.g., in *Pan troglodytes*, *Pongo abelii* and *Sapajus apella* (Yamakoshi, 1998; Fox *et al*., 2004; Taylor, 2006a, 2009; Taylor & Vinyard, 2009; Wright *et al*., 2009; Yamagiwa & Basabose, 2009; Smith *et al*., 2012; McLennan, 2015; Pante *et al*., 2018). As neither hard nor tough features have been identified on the microwear of *H. habilis* specimens to date, they were unlikely to consume hard or tough animals, instead they could have consumed soft-bodied invertebrates with or without the use of tools.

Stable carbon isotope analyses indicate that *H. ergaster* consumed a highly varied diet with a mix of C_3 and C_4 resources (Lee-Thorp *et al*., 2000), an observation that is consistent with the results of the dental microwear texture analyses, which also indicated that the diet was highly varied, with both anisotropy and complexity signals present (Ungar *et al*., 2006). In fact, there are more complexity signals present on *H. ergaster* than any hominin, except *P. robustus* (Ungar *et al*., 2006). These reconstructions are supported by the way in which *H. ergaster* score in relation to some of the non-human primates. *H. ergaster* could have consumed a mixed diet, which consisted of high quantities of fruits, leaves and seeds, and supplemented by roots and animals (Tables 6.4-6.5). These are all foods that could correspond to the reconstructions based on the microwear and stable carbon isotopes, as the fruits and seeds could come from the C_3 resources and the leaves and roots from the C_4 resources, while the animals could be reflective of either photosynthetic pathway, depending on what pathway the foods they consumed came from. The mechanical properties associated with these foods could also correspond to those of tougher and harder foods, as the fruits could be soft, leaves and roots could be tough, the seeds hard, and the animals could be hard, tough or soft depending on the type of animal consumed (vertebrate or invertebrate).

These results highlight the importance of future studies extensively exploring food mechanical properties. It is clear that there is variation in food mechanical properties and while the variation has been acknowledged here, many assumptions have had to be made as well. In combination with the stable carbon isotope and dental microwear texture analysis results, interpretations of the bivariate graphs from the Principal Component Analyses (PCA) potentially provides more context for how and where the hominin diets varied. Furthermore, the results could provide a useful context in which to develop questions and approaches for future research in this area. The results from this study continue to challenge the early assumption of *Paranthropus* being a dietary specialist. With the exception of *H. habilis* (reasons for this have been discussed), the potential diets the hominins align with support each species microwear and stable carbon isotope signals. Particularly of interest from these graphs is that they also support the conclusion made on other grounds that *P. boisei* and *P. robustus* consumed different diets from each other.

6.2 General discussion

6.2.1 How this study can inform on **Paranthropus** *mandibular and dental morphology*.

One of the most important aspects of the stable carbon isotopes and dental microwear texture analysis results on *P. robustus* and *P. boisei* was the fact that reconstructions indicated the two species consumed foods from different isotopic pathways and from different mechanical properties. As a result, *P. robustus* may no longer be considered a dietary specialist, while *P. boisei* could still have been but not on hard foods (Lucas *et al*., 2008a; Constantino *et al*., 2010, 2011; Pampush *et al*., 2013; Strait *et al*., 2013; Smith *et al*., 2015). This led to suggestions that *P. boisei* and *P. robustus* were not adapted to the same dietary regime (Cerling *et al*., 2011; Ungar & Sponheimer, 2011; Sponheimer *et al*., 2013). While it is true that *P. boisei* does display the most derived morphological features of the hominins and a C_4 dominated diet could indicate a dietary specialism, other interpretations have been presented. Wood & Strait (2004) argued that the derived morphology could have had the effect of broadening the nature of the foods available rather than restricting it, and Macho (2014) demonstrated a diet dominated by C_4 resources need not be considered a specialist one. In fact, as with extant animals, it would have been essential for the hominins to balance their diets, and a diet dominated by C_4 resources could still achieve a nutritional balance (Macho, 2014). Indeed, the bivariate graphs (as broken down in Tables 6.4-6.5) support the idea that *P. boisei* consumed a broad diet and as a result was adaptively a generalist.

The stable carbon isotopes and dental microwear texture analysis results have been suggested to indicate that *P. boisei* and *P. robustus* were not consuming the same types of foods or those from the same pathway (Sponheimer *et al*., 2006a, 2013; Ungar *et al*., 2008), but it is still not possible to rule out the possibility they were adapted to a similar dietary regime. Ultimately, morphology and behaviour evolve at different rates, whereby feeding behaviour can change within the lifetime of an individual but it takes many generations for the adaptive modifications to come into effect (Bock & von Wahlert 1965; Gailer *et al*., 2016). Morphology is a legacy of the ancestor and is the direct indication of what a species was capable of eating, but not necessarily what it did eat. Instead, what a species actually consumes is dependent on the environment and what is available to them (Daegling & Grine, 1991; Ungar *et al.*, 2008, 2012; Grine *et al*., 2012; Louys *et al*., 2012; Sponheimer *et al*., 2013; Macho, 2014; Grine & Daegling, 2017).

Environmental reconstructions for the *P. boisei* and *P. robustus* sites in East and South Africa are somewhat similar (site information available in Appendix Tables 9.2-9.3). Yet the nature of foods available to them would likely differ, along with the weather patterns and seasonality of resources, as observed in non-human primates, with diet known to differ between populations as a result of environmental differences, relating to the type of local fauna and flora, seasonality of resources and climatic differences (Yamagiwa & Basabose, 2006b; Potts *et al*., 2011; Watts *et al*., 2012b; Macho, 2014; Veneziano *et al*., 2019). Considering that differences have been identified in the microwear patterns of *Gorilla gorilla* and *Gorilla beringei* (Tables 6.6-6.9), it is not that remarkable they have been identified in *P. robustus* and *P. boisei*. *P. boisei* and *P. robustus* could therefore represent generalist dietary consumers eating regionally different foods (Cerling *et al*., 2011), with *P. robustus* consuming harder foods on an infrequent basis and *P. boisei* consuming tougher foods more regularly (Ungar & Sponheimer, 2011). The two *Paranthropus* species would therefore represent examples of adaptive divergence (Cerling *et al*., 2011).

The dominance of C_4 resources in the diet of *P. boisei* could be used as evidence the species was a dietary specialist, particularly as sympatric early *Homo* species were consuming a mixed C_3/C_4 diet (Cerling *et al*., 2011, 2013; Sponheimer *et al*., 2013).

However, a change in percentages of C_3/C_4 in the diets of early *Homo* occurred, and specimens analysed from later in the early *Homo* presence shows the diet shifted to one dominated slightly by C_4 resources (ratio of C_3/C_4-based resources of 45/55) (Cerling *et al*., 2013). These differences between the C_3/C_4 ratios in the diets of *P. boisei* and early *Homo* need not reflect dietary specialisms, but they could simply be a reflection of different species adapting to the environment at a different rate, as seen with the gradual shift towards a C_4-based diet in many animals from 9.9 million years ago in East Africa (Uno *et al*., 2011; Linder, 2017). For example, equids and rhinocerotids diets were dominated by C_4 foods from 9.9 and 9.6 mya, respectively, yet suid diets were not dominated by C_4 foods until between 6.5 and 4.2 mya (Uno *et al*., 2011).

The second key point to be discussed based on the results from stable carbon isotopes and dental microwear texture analyses was that overlap existed using both techniques between *P. robustus* and *A. africanus*. The stable carbon isotope results showed that both species consumed foods from C_3 and C_4 isotopic pathways (Lee-Thorp *et al.,* 1994; Sponheimer & Lee-Thorp, 1999; van der Merwe *et al*., 2003; Sponheimer *et al*., 2005a, 2006a), while the microwear analyses show that although both species overlapped in certain aspects of food type consumed (both consumed softer foods), they differed in other areas. *P. robustus* is characterised by complex features indicative of the occasional consumption of a harder food diet, and *A. africanus* is characterised by anisotropic features indicative of the occasional consumption of a tougher food diet (Grine, 1981, 1986; Kay & Grine, 1988; Scott *et al*., 2005; Strait *et al*., 2013; Peterson *et al*., 2018). Scott *et al*. (2005) suggested that where the dental microwear texture analyses differed between the species was reflective of them consuming fallback foods of different mechanical properties. The presence of hard foods as fallback foods were proposed to explain the more derived morphology of *P. robustus* in relation to that of *A. africanus* (Scott *et al*., 2005). Equally, fallback foods were also used to explain the derived morphology of *P. boisei* too (Ungar *et al*., 2008). Such an adaptation would therefore accord with the dominant perceptions and understanding of the highly derived morphology of *Paranthropus* being an adaptation for a hard-food diet.

To invoke the Fallback Food Hypothesis to explain morphological differences between hominins as many researchers do (e.g., Ungar, 2004, 2011; Laden & Wrangham, 2005; Scott *et al*., 2005, 2014; Grine *et al*., 2006a, 2006b, 2012; Ungar *et al*., 2008) is problematic. As highlighted in Section 3.4 there are fundamental problems and inconsistencies in the hypothesis and its application to dietary interpretations. These same problems were identified in this research when attempting to test the Fallback Food Hypothesis.

Problems with the Fallback Food Hypothesis were encountered often when attempting to classify foods as fallback foods, some of these problems are listed below in the context of *Pan troglodytes*. The Fallback Food Hypothesis was proposed in the 1990s but was not commonly used until after 2005 (following the application of it to hominins by Laden & Wrangham (2005) and Scott *et al.* (2005)), yet many of the studies detailing the dietary ecology of *Pan troglodytes* occur before this time. This means that these studies do not list what they consider to be fallback foods, a decision therefore had to be made when creating the non-human primate diet database: is a food assigned fallback on the basis of assumed quality and seeming lack of preference, or was that study left blank? As it would have been highly subjective for an individual who was not present when the study was undertaken to make the decision on fallback foods and likely using a different operating strategy as other studies and therefore being inconsistently applied, the fallback food column was left empty. A further issue to that above is the fact that there is no clear consensus in how to define and apply the hypothesis in primatology (e.g., Lambert, 2007; Marshall & Wrangham, 2007; Marshall *et al*., 2009; Harrison & Marshall, 2011), which means that for those studies that did record fallback foods in *P. troglodytes* (e.g., Morgan & Sanz, 2006; Yamagiwa & Basabose, 2006a, b; Marshall & Wrangham, 2007; Thompson & Wrangham, 2008; Harrison & Marshall, 2011; McLennan, 2013), they might have done so in an approach different to each other. Once again indicating that the hypothesis can be inconsistently applied. These issues correspond to problems identified by other researchers, whereby the Fallback Food Hypothesis was found to be extremely subjective despite the fact that many researchers have previously attempted to define it (e.g., Marshall & Wrangham, 2007; Constantino & Wright, 2009; Lambert, 2009; Marshall *et al*., 2009; Sauther & Cuozzo, 2009; Taylor, 2009; Cooke, 2012; McGraw & Daegling, 2012; Lambert & Rothman, 2015).

On the occasions that a fallback food was assigned further problems were encountered. In the case of *P. troglodytes,* it is routinely described as being a high-quality fallback feeder due to their consumption of figs (Morgan & Sanz, 2006; Yamagiwa & Basabose, 2006a, b; Marshall & Wrangham, 2007; Thompson & Wrangham, 2008; Harrison & Marshall, 2011; McLennan, 2013), yet upon closer inspection this description does not hold up. Fallback foods in *P. troglodytes* range from piths and stems (Wrangham *et al*., 1991, 1998; Potts *et al*., 2011; Chancellor *et al*., 2012), young leaves (Watts *et al*., 2012b), herbs, figs, honeybees, ants and honey (Yamagiwa & Basabose, 2009; McLennan, 2015), bark and cambium (Pruetz, 2006), and termites (Yamagiwa & Basabose, 2009). Based on this diversity of foods consumed and defined as fallbacks it soon became apparent that there was not one food that could be generalised for species, or even subspecies as a fallback. This is because a food important to one species or population may not be for another, so it is impossible to generalise beyond population-specific studies (Clutton-Brock, 1977; Barton *et al*., 1993; Krishnamani, 1994; Conklin-Brittain *et al*., 1998; Remis *et al*., 2001; Worman & Chapman, 2005; Hohmann *et al*., 2006; Watts *et al*., 2012b; Lambert & Rothman, 2015). Not to mention the fact that based on those foods highlighted above, it could be questioned whether *P. troglodytes* could routinely be described as a high-quality fallback feeder. A consequence of the fact that there is such diversity of foods labelled fallback foods in *P. troglodytes* (as an example) meant that foods could not be generalised and as a result, could not be tested against the morphological data collected in this study.

Additional problems that were identified in other studies are detailed below. To properly understand what foods could constitute a fallback food would require years of extensive field observation to monitor the seasonal and annual diet variation of populations, not the one or two year field studies that are most commonly available (Nishida & Uehara, 1983; Norton *et al*., 1987; van Schaik *et al*., 1993; Tutin *et al.*, 1997; Peres, 2000; Vogel *et al.,* 2009; Vinyard *et al*., 2011; Watts *et al*., 2012a; Lambert & Rothman, 2015). Even after such extensive field studies, there is no guarantee a food that might act as a fallback food one season would do so again another season (Norton *et al*., 1987; Mills *et al*., 1993; van Schaik *et al*., 1993; Tutin *et al.*, 1997; Peres, 2000; Yamagiwa *et al.,* 2005; Vogel *et al.,* 2009; Kunz & Linsenmair, 2010; Vinyard *et al*., 2011; Watts *et al*., 2012a; Lambert & Rothman, 2015). Until more is known about the dietary, nutritional and digestive requirements of various non-human primate species it remains a very subjective approach, and attempts to invoke it may in fact be holding researchers back (Mills *et al.,* 1993; Hohmann *et al*., 2006; Taylor, 2006a; Rothman *et al*., 2007; Lappan, 2009; Vinyard *et al*., 2011; Cooke, 2012; McGraw & Daegling, 2012; Irwin *et al*., 2014; Vogel *et al*., 2014; Lambert & Rothman, 2015).

The question then of whether or not a fallback food has the capacity to influence the morphology of an animal depends on how one defines fallback foods. Too often it is used as an easy term to explain seasonality of resources (McGraw & Daegling, 2012;

Grine & Daegling, 2017). Here, it is argued that the foods that are consumed during the annual period of resource scarcity are not fallbacks, but instead they are foods that are available at different times of the year and consequently, consumed on a seasonal basis, like fruits. An animal has to maintain a balanced diet, and while it is logical that they would prefer fruit they cannot survive on fruit alone, other foods high in different nutrients are essential, e.g., seeds for lipids, leaves for proteins (Hladik, 1977; Milton, 1993; Tutin *et al*., 1997; Conklin-Brittain *et al*., 1998; Rothman *et al*., 2007; Felton *et al*., 2009a, b, c; Norconk *et al*., 2009; McGraw *et al*., 2014; Lambert & Rothman, 2015; Vinyard *et al*., 2016). These other foods are all equally important in maintaining the balanced diet, but not necessarily required in the same quantities (Knott, 1998; Vogel *et al*., 2014). This adds to the suggestion that these other foods are simply part of seasonal diet variation, and do not constitute fallback foods. Instead, a fallback food should be that which is consumed in times of famine and peak stress. This after all will be the critical time that determines whether an animal will live or die. However, given the fact that periods of famine may not occur on a frequent basis, or at all within the lifetime of an individual, it is not considered here that fallback foods are responsible or invoke a selective pressure on the adaptive morphology. In fact, the idea that an animal may be adapted to a food that they may or may not consume on an infrequent basis is illogical. There would be no selective pressure acting upon a species if the food was not regularly (in this case annually) consumed. Nor would it be efficient to develop a derived morphological adaptation that would only occasionally serve a function (Daegling, 2007). Instead, a derived morphological adaptation can be explained through the consumption of high stress foods on a cyclical basis or infrequently throughout the year that are part of the seasonal diet variation, such as tough or hard foods.

When observing the masticatory morphologies of for example, *Pan* and *Gorilla*, they are distinct, but as many field studies have shown their diets overlap during the periods of fruit abundance but diverge during scarcity (Tutin *et al*., 1991, 1997; Tutin & Fernandez, 1993; Tutin, 1999; Head *et al*., 2011). It does therefore make sense that the shared consumption of preferred foods is unlikely to require different morphologies in the different species, yet the divergent diets, which can include foods consumed in larger quantities that put more strain on the morphology, such as tough foods, or infrequently consumed harder foods, could drive the different morphological adaptations (Daegling & McGraw, 2007; Taylor, 2009). There are numerous examples within the literature of an association between morphology and high stress foods (e.g., Hylander, 1979b, 1984, 1985; Bouvier, 1986; Ravosa, 1991, 1996; Yamashita, 1996, 1998; Bouvier & Ravosa, 1998; Lambert *et al*., 2004; Foster *et al*., 2006; Dominy *et al*., 2008; Norconk *et al*., 2009; Daegling *et al*., 2011; McGraw *et al*., 2016; Ross *et al*., 2016). This is further supported by the results from this research, looking at quantity of foods consumed. High consumption of fruits (assuming they are soft and fleshy) does not appear to result in distinct morphologies according to Figure 5.28, yet those species characterised by low consumption of fruits did present more distinct morphologies, which could be considered a reflection of the morphological response to other foods in the diet. In addition, those species recorded to consume high quantities of obdurate foods such as leaves or seeds, cluster in distinct ways on the bivariate graphs (Figures 5.29-5.31).

The Fallback Food Hypothesis as an explanation for the derived morphology present in *Paranthropus* compared to *Australopithecus* as suggested by Laden & Wrangham (2005) and Scott *et al*. (2005) is on first consideration a plausible and convincing argument. Upon further examination of the hypothesis and unsuccessful attempts at testing, it was found to be fundamentally flawed, insomuch that it could not be tested, a point also highlighted by other researchers (e.g., McGraw & Daegling, 2012; Wood & Schroer, 2012; Daegling *et al*., 2013; Lambert & Rothman, 2015; Grine & Daegling, 2017). The reality is that it is hard enough to identify diet in a broad sense in hominins (Ungar, 2011; Macho, 2014; Alemseged, 2015), because "individuals have different food preferences and access to different resources in different places and at different times" (Ungar, 2011: 54). It is therefore, harder still to identify fallback foods and their effects on morphology in the fossil record (Berthaume *et al*., 2018). For this very reason the Fallback Food Hypothesis as an explanation for the derived morphology present in *P. boisei* was dismissed because no evidence of hard-object feeding has been found on any *P. boisei* specimen (Ungar, 2011). The suggestions that microwear traces have not identified evidence of fallback foods because specimens did not perish during that time, as Strait *et al*. (2013) and Scott *et al*. (2014) suggest, is farfetched (McGraw & Daegling, 2012). Many researchers have suggested that it is during the periods of resource-scarcity, defined by some (van Schaik *et al*., 1993; Marshall & Wrangham, 2007; Constantino & Wright, 2009; Sauther & Cuozzo, 2009; Vogel *et al*., 2009) as the fallback period, that competition for resources is greatest, and thus the threat of mortality is greatest (although see Grine *et al.*, (2012) and Gogarten & Grine (2013) for alternative interpretations). It would be expected that traces of fallback foods would therefore be identified, or indeed overrepresented in the microwear signals (Gogarten *et al*., 2012), to then not find a single example of a fallback signal on a specimen perishing during this time is inconceivable (Kimbel & Delezene, 2009). The Fallback Food Hypothesis, at least in its current state, is not a viable theory to explain the morphological differences between *Paranthropus* and *Australopithecus*.

Furthermore, to use stable carbon isotopes and dental microwear texture analyses to refute Robinson's Dietary Hypothesis (1954a, b, 1963) and instead justify the Fallback Food Hypothesis as Scott *et al*. (2005); Ungar *et al*. (2008); Marshall *et al*. (2009), among others do is a leap, particularly as there appears to have been a misunderstanding about what Robinson (1963) meant by *Paranthropus* being a dietary specialist. Robinson (1963) did not specifically state that *Paranthropus* ***only*** consumed the food to which it was adapted, but that the morphology reflected an adaptation to crushing and grinding tough vegetation. Foods that were likely to be included in their diets were roots and bulbs, however, the nature of the vegetation available to them would depend on seasonality of food resources (Robinson, 1963). The evidence from stable carbon isotopes and dental microwear texture analyses does not contradict this, as *P. robustus* could have crushed its food, and *P. boisei* could have ground down its food. It still stands to reason that the derived morphology is a beneficial adaptation to the break down and mastication of obdurate foods. All evidence from biomechanical studies, stable carbon isotopes, dental microwear texture analyses, and even this study indicate more obdurate foods were likely to have been available to hominins. Crucially, evidence also indicates that there is an association between obdurate foods and morphology.

It is also important to note here that while overlap existed in the microwear and stable carbon isotope results of *P. robustus* and *A. africanus* (Lee-Thorp *et al.,* 1994; Sponheimer & Lee-Thorp, 1999; van der Merwe *et al*., 2003; Scott *et al*., 2005; Sponheimer *et al*., 2005a, 2006a; Peterson *et al*., 2018), it does not mean that the two species consumed the same diets; rather they consumed some foods with similar material properties and from similar isotopic pathways. The Dietary Hypothesis of Robinson (1954a, 1963) is not therefore undermined. Equally, it does not appear necessary to invoke the Fallback Food Hypothesis to explain the morphological differences between the species.

Of course, it would be remiss to discuss the results obtained from stable carbon isotope and dental microwear texture analyses without also a discussion where improvements or further information would be beneficial. The contributions that studies using stable carbon isotopes and dental microwear texture analysis have made to palaeoanthropology cannot be underestimated, for they, in combination, have helped to refine the understanding of the dietary ecologies of hominins. The two methods do not, however, tell the whole story of diet adaptation in hominins. The two methods provide indications of the photosynthetic pathways of food consumed at the start of life (stable carbon isotope analysis) and the mechanical properties of the foods consumed towards the end of life (dental microwear texture analysis), but they do not inform on what a species was capable of consuming, which is why analysing morphology remains particularly important.

Between consumers of C_3 foods there is much morphological variation (as shown by the M_1 crown area and M_1 corpus robusticity index) and dietary variation within this isotopic range, as highlighted by Tables 6.6-6.9. Future research could explore this further, by investigating how much variation exists in a similar isotope value range. Indeed, this could involve conducting Principal Components Analyses (PCA) and using the isotope value categories to interpret the PCA plots.

There are also different microwear patterns within genera, e.g., *Gorilla*, meaning different types of foods are consumed, e.g., harder foods by *Gorilla gorilla* and tougher foods by *Gorilla beringei* (Scott *et al*., 2012), similar to *P. boisei* and *P. robustus* (Scott *et al*., 2005; Ungar *et al*., 2008). These results may therefore prompt the question, is too much being made of the stable carbon isotope and dental microwear texture analysis results from the hominins? Given the results from the two techniques and this study complement each other it suggests that they are accurate. Equally, given there can exist large morphological variation within isotopic pathways it also highlights the continued value of comparative morphology studies.

Table 6.6: Stable carbon isotopes, microwear patterns, habitat information, diet, M_1 Crown Area (averages) and M_1 Corpus Robusticity Indices (averages) (data taken from averages obtained in this study) for apes.

Genus	δ_{13}C	Microwear	Diet	Habitat	M_1 crown area	M_1 corpus robusticity index
Pan	C_3.[1, 2, 3, 4, 5, 6, 7, 8, 9, 10]	Varied diet. Some studies report greater complexity than anisotropy, while other studies report greater anisotropy than complexity.[11, 12, 13]	Consume mostly fruits, and supplement with leaves, piths, flowers, seeds, roots and animals. Variation present between subspecies and even populations.[14, 15, 16, 17]	Ranges from savannah to rainforest, and low to high altitude.[18, 19, 20, 21, 22]	• *P. paniscus*: 76.65. • *P. troglodytes schweinfurhtii*: 94.55. • *P. troglodytes troglodytes*: 95.26. *P. troglodytes verus*: 107.71.	• *P. paniscus*: 49.51. • *P. troglodytes schweinfurthii*: 54.91. • *P. troglodytes troglodytes*: 52.76. *P. troglodytes verus*: 55.04.
Gorilla	C_3.[23, 24]	Different patterns are present on *G. gorilla* (higher complexity consistent with harder foods) compared with *G. beringei* (higher anisotropy consistent with tougher foods), indicating different diets are consumed.[11, 12, 13]	Large variation between species and even subspecies. *Gorilla gorilla gorilla* consumes a diet dominated by fruits and supplement with leaves, piths, seeds, flowers, bark and insects. *Gorilla beringei beringei* and *Gorilla beringei graueri* both consume diets dominated by leaves, although *Gorilla beringei beringei* consumes considerably more leaves and *Gorilla beringei graueri* supplements their diet with more fruits.[25, 26, 27, 28, 29, 30, 31, 32]	Ranges from savannah to evergreen to montane forests, and from low to very high altitude.[25, 27, 30, 33, 34]	• *G. gorilla gorilla*: 200.62. • *G. beringei beringei:* 219.76. • *G. beringei graueri*: 222.56	• *G. gorilla gorilla*: 51.60. • *G. beringei beringei:* 54.33. • *G. beringei graueri*: 51.49
Pongo	C_3.[35]	Varied diet. Some studies report complexity present, while others report low levels of complexity and anisotropy.[11, 12, 13]	Fruits and leaves dominate all diets, but variation exists between species and even within subspecies.[36, 37, 38, 39, 40, 41, 42]	Ranges from coastal peat swamps to primary tropical rainforest, and low to high altitude.[39, 40, 42]	• *P. abelii*: 140.80. • *P. pygmaeus pygmaeus*: 147.69. • *P. pygmaeus wurmbii*: 145.80	• *P. abelii*: 49.47. • *P. pygmaeus pygmaeus*: 46.84. • *P. pygmaeus wurmbii*: 44.66

[1] Schoeninger *et al*., (1999); [2] Schoeninger *et al*., (2016); [3] Sponheimer *et al*., 2006b; [4] Oelze *et al*., (2011); [5] Oelze *et al*., (2014); [6] Loudon *et al*., (2016); [7] Cerling *et al*., (2004); [8] Smith *et al*., (2010); [9] Carter & Bradbury (2016); [10] Carlson & Crowley (2016); [11] Teaford & Walker (1984); [12] King *et al*., (1999); [13] Scott *et al*., (2012); [14] Badrian & Malenky (1984); [15] Head *et al*., (2011); [16] Watts *et al*., (2012a); [17] Bessa *et al*., (2015); [18] White (1998); [19] Myers-Thompson (2002); [20] Chapman *et al*., (1994); [21] Hunt & McGrew (2002); [22] McGraw & Zuberbuhler (2007); [23] Oelze *et al*., (2014); [24] Blumenthal *et al*., (2012); [25] Williamson *et al*., (1990); [26] Tutin *et al*., (1991); [27] Tutin *et al*., (1997); [28] Nishihara, (1995); [29] Doran *et al*., (2002); [30] Head *et al*., (2011); [31] Remis (1997); [32] Yamagiwa *et al*., (2005); [33] Rothman *et al*., (2007); [34] Fossey & Harcourt (1977); [35] Pushkina *et al*., (2010); [36] MacKinnon (1974); [37] Rodman (1977); [38] Galdikas (1988); [39] Wich *et al*., (2006b); [40] Russon *et al*., (2009); [41] Fox *et al*., (2004); [42] Morrogh-Bernard *et al*., (2009).

Table 6.7: Stable carbon isotopes, microwear patterns, habitat information, diet, M_1 Crown Area (averages) and M_1 Corpus Robusticity Indices (averages) (data taken from averages obtained in this study) for Old World monkeys.

Genus	$\delta_{13}C$	Microwear	Diet	Habitat	M_1 crown area	M_1 corpus robusticity index
Cercocebus	$C_{3.}$ [1,2]	High microwear complexity and low anisotropy, indicative of a hard-food diet. [3]	Consume mostly fruits and seeds, and supplement with invertebrates, piths, stems. Leaves, flowers and roots make up the rest of the diet. [4, 5, 6, 7, 8]	Tropical evergreen forests at low altitude. [4, 7, 9]	- *C. atys*: 43.97. - *C. torquatus*: 47.96	- *C. atys*: 43.47. - *C. torquatus*: 39.64
Lophocebus	$C_{3.}$ [10]	Varied diet. Some studies report high complexity patterns, while others report high complexity and high anisotropy, indicating that hard and tough foods were consumed. [3, 11, 12, 13, 14, 15]	Consume mostly fruits and seeds, and supplement with leaves and invertebrates. Flowers, piths, stems and bark make up the rest of the diet. [16 17, 18, 19, 20, 21, 22]	Ranges from savannah to primary evergreen forest, and from low to high altitude. [21, 22, 23, 24, 25]	- *L. albigena*: 33.78. - *L. aterrimus*: 31.21.	- *L. albigena*: 38.09. - *L. aterrimus*: 36.47
Cercopithecus	$C_{3.}$ [2, 10]	Anisotropy present, indicative of a tough food diet. [26, 27]	Diet dominated by fruits, and supplement with leaves and invertebrates. Flowers, seeds, pith and stems make up the rest of the diet. [19, 21, 28, 29, 30, 31]	Ranges from savannah to evergreen forest, and from low to high altitude. [19, 28,30, 32]	- *C. ascanius*: 17.59. - *C. cephus*: 19.92	- *C. ascanius*: 39.94. - *C. cephus*: 38.93
Chlorocebus	$C_{4.}$ [33, 34]	Anisotropy present, indicative of a tough food diet. [26, 27]	Variation between species. Highly varied diets, with high consumption of fruits, leaves, flowers and invertebrates. [35, 36. 37. 38, 39, 40, 41]	Ranges from thorn bush - riverine forest. Mostly high altitude. [35, 36, 39]	- *Ch. aethiops*: 22.06. - *Ch. pygerythrus* 23.49. - *Ch. sabaeus*: 24.99	- *Ch. aethiops*: 41.92. - *Ch. pygerythrus* 41.64. - *Ch. sabaeus*: 39.83
Erythrocebus			Varied diets, dominated by gums, thorns and flowers. [38, 42, 43]	Semiarid, open woodlands and high altitude. [38, 42]	- *E. patas*: 31.31	- *E. patas*: 37.65

[1] Krigbaum *et al*., (2013); [2] Cerling *et al*., (2004); [3] Scott *et al*., (2012); [4] Mitani (1989); [5] Bergmüller (1998); [6] McGraw *et al*., (2011); [7] Cooke (2012); [8] Daegling *et al*., (2011); [9] Range & Noe (2002); [10] Carter & Bradbury (2016); [11] Teaford & Walker (1984); [12] El-Zaatari *et al*., (2005); [13] Scott *et al*., (2006); [14] Ungar *et al*., (2006); [15] Ungar *et al*., (2008); [16] Freeland (1979); [17] Horn (1987); [18] Ham (1994); [19] Tutin *et al*., (1997); [20] Poulsen *et al*., (2002); [21] Tutin (1999); [22] Poulsen *et al*., (2001); [23] Freeland (1980); [24] Doran-Sheehy *et al*., (2009); [25] Waser (1977); [26] Galbany & Perez-Perez (2004); [27] Galbany *et al*., (2005); [28] Struhsaker (1978); [29] Cords (1986); [30] Chapman *et al*., (2002); [31] Bryer *et al*., (2013); [32] McGrew *et al*., 1996; [33] Sponheimer & Lee-Thorp (2001); [34] Loudon *et al*., (2014); [35] Dunbar & Dunbar (1974); [36] Galat & Galat-Luong (1978); [37] Harrison (1983); [38] Isbell *et al*., (1998); [39] Whitten (1983); [40] Wrangham & Waterman (1981); [41] Lee & Hauser (1998); [42] Isbell (1998); [43] Nakagawa (1989).

Table 6.8: Stable carbon isotopes, microwear patterns, habitat information, diet, M_1 Crown Area (averages) and M_1 Corpus Robusticity Indices (averages) (data taken from averages obtained in this study) for Old World monkeys (continued).

Genus	δ13C	Microwear	Diet	Habitat	M_1 crown area	M_1 corpus robusticity index
Mandrillus			Highly varied diets. High consumption of fruits, leaves, seeds, flowers, roots and invertebrates. [1, 2, 3, 4, 5, 6, 7]	Ranges from savannah zone to mature forest, and low to high altitude. [1, 2, 7]	• *M. leucophaeus*: 70.25. • *M. sphinx*: 73.71	• *M. leucophaeus*: 39.18. • *M. sphinx*: 35.5
Papio	C_3/ C_4. [8, 9, 10]	High anisotropy and high complexity, indicative of tough and hard foods being present. [11, 12, 13, 14, 15, 16, 17, 18]	Highly varied diets. [19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33]	Predominantly savannah-type environments. Low to high altitude. [19, 22, 24, 26]	• *P. anubis*: 95.16. • *P. cynocephalus*: 74.3	• *P. anubis*: 37.54. • *P. cynocephalus*: 37.13
Macaca		Higher complexity than anisotropy, indicative of a harder food diet. [16]	Large variation between species. *M. cyclopis* and *M. radiata* have fruit dominated diets, and supplement with flowers, piths and invertebrates. *M. sylvanus* consumes a diet dominated by leaves, seeds, roots and herbs. [34, 35, 36, 37, 38, 39, 40, 41]	Predominantly evergreen forest, ranging from low to high altitude. [34, 36, 38]	• *M. cyclopis*: 34.36. • *M. radiata*: 26.75. • *M. sylvanus*: 43.96	• *M. cyclopis*: 40.34. • *M. radiata*: 47.5. • *M. sylvanus*: 41.77

[1] Owens *et al*., (2015); [2] Hoshino (1985); [3] Lahm (1986); [4] Norris (1988); [5] Rogers *et al*., (1996); [6] Tutin *et al*., (1997); [7] Tutin (1999); [8] Carter & Bradbury (2016); [9] Cerling *et al*., (2004); [10] Codron *et al*., (2008); [11] Ryan (1981); [12] Daegling & Grine (1999); [13] Nystrom *et al*., (2004); [14] El Zaatari *et al*., (2005); [15] Ungar *et al*., (2006); [16] Scott *et al*., (2012); [17] Galbany & Perez-Perez (2004); [18] Galbany *et al*., (2005); [19] Post, *et al*., (1980); [20] Barton (1989); [21] Pochron (2000); [22] Harding (1976); [23] Stacey (1986); [24] Kunz & Linsenmair (2008); [25] Norton *et al.*, (1987); [26] Okecha & Newton-Fisher (2006); [27] Dunbar & Dunbar (1974); [28] Barton *et al*., (1993); [29] Post (1982); [30] Bentley-Condit (2009); [31] Kay (1981); [32] Swindler (2002); [33] Plavcan (2001); [34] Ali (1986); [35] Krishnamani (1994); [36] Su & Lee (2001); [37] Ménard (1985); [38] Ménard & Vallet (1986); [39] Mehlman (1988); [40] El Alami *et al*., (2012); [41] Ménard *et al*., (2014)

Table 6.9: Stable carbon isotopes, microwear patterns, habitat information, diet, M_1 Crown Area (averages) and M_1 Corpus Robusticity Indices (averages) (data taken from averages obtained in this study) for New World monkeys.

Genus	δ13C	Microwear	Diet	Habitat	M_1 crown area	M_1 corpus robusticity index
Cebus	C_3. [1]	Variation between species, with some presenting higher levels of anisotropy and others with higher levels of complexity. Indicating diets range from hard and tough between species. [2, 3, 4, 5]	Fruits and invertebrates dominate the diets. Leaves, flowers, seeds, pith and stems, roots, vertebrates, and other foods make up the rest of the diet. [6, 7, 8, 9, 10, 11, 12, 13, 14]	Mostly tropical, dry forests. [13, 14]	• *C. albifrons*: 18.24. • *C. capucinus*: 18.28. • *C. olivaceus*: 17.71	• *C. albifrons*: 46.62. • *C. capucinus*: 47.81. • *C. olivaceus*: 46.14
Sapajus		High complexity present, indicative of a hard-food diet. [3, 15, 16, 17, 18, 19]	Fruits and invertebrates dominate the diets. Leaves, flowers, seeds, pith and stems, roots, vertebrates, and other foods make up the rest of the diet. [13, 20, 21, 22, 23, 24, 25, 26]	Ranges from tropical rainforest to mountain savannah forest, and from mid to high altitude. [21, 22, 25]	• *S. apella*: 21.22	• *S. apella*: 49.69

[1] Schoeninger *et al*., (1997); [2] Scott *et al*., (2012); [3] Teaford (1985); [4] Teaford & Runestad (1992); [5] Teaford & Robinson (1989); [6] Defler (1979); [7] Robinson (1986); [8] Chapman (1987); [9] Chapman & Fedigan (1990); [10] Fragaszy & Boinski (1995); [11] Williams & Vaughan (2001); [12] McKinney (2011); [13] Terborgh (1983); [14] Tomblin & Cranford (1994); [15] Teaford & Walker (1984); [16] Scott *et al*., (2005); [17] Scott *et al*., (2006); [18] Ungar *et al*., (2006); [19] Ungar *et al*., (2008); [20] Izawa (1979); [21] Mittermeier & van Roosmalen (1981); [22] Brown & Zunino (1990); [23] Galetti & Pedroni (1994); [24] Peres (1994); [25] Stevenson *et al*., (2000); [26] Gomez-Posada (2012).

There are still areas where more information would be beneficial and could further improve understanding of the dietary ecologies of hominins. A potential weakness of the inferences made from stable carbon isotope analyses is not based on the method of analysis, but rather the nature of the data collected. Stable carbon isotopes have been extracted on each of the hominin species included in this study, but the isotopes are predominantly taken from specimens from the same localities. Within those localities specimens are taken from different members or stratigraphic layers, which means that they can represent changes in the nature of the environments, but it is likely that environmental differences are greater between sites than within sites (Appendix Table 9.8 details the exact specimens used in stable carbon isotope analysis and their isotopic value, locations, reconstructed environments and dates of presence). It is possible therefore, that there is some environmental variation and thus isotopic variation in many of the species that has not been identified. For example, despite the fact that *A. africanus* has been found in 4 sites, stable carbon isotopes have only been extracted in specimens from 2 of those sites, and of those from 4 specimens from Makapansgat and 18 from Sterkfontein (Table 6.10). The environmental reconstructions from Sterkfontein and Makapansgat are quite similar throughout the different formations (ranging from open to closed habitats), but the environmental reconstructions for Gladysvale and Taung are slightly different (closed habitats) (Appendix Tables 9.2-9.3). Based on these environmental reconstructions, it is expected that the Sterkfontein and Makapansgat specimens would range from C_3/ C_4 resources, yet Gladysvale and Taung could be predominantly C_3.

A similar pattern is present with *P. robustus*, identified at 5 different South African sites, but specimens are only tested from Swartkrans (n = 21) and Kromdraai (n = 1) (Table 6.10). The particular members the specimens tested are associated with are reconstructed to have been mixed environments with open habitats and woodland nearby (Reed, 1997; Pickering *et al*., 2011; Herries & Adams, 2013). In contrast, the sites/ members associated with *P. robustus* remains at Coopers, Drimolen and Sterkfontein are all reconstructed to have been more open and grassland environments (Appendix Tables 9.2-9.3). Based on these environmental reconstructions, it is expected that the Swartkrans and Kromdraai specimens would range from C_3/ C_4 resources, yet Coopers, Drimolen and Sterkfontein could be slightly more C_4 dominated (similar to *P. boisei*). Extraction of the stable carbon isotopes from the other sites would therefore be highly beneficial and further enhance the understanding of each species' dietary ecology.

Table 6.10: Hominin species, their associated locations, dates of presence, locations and ages of specimens where stable carbon isotopes have been extracted (information summarised from Appendix Table A.10.

Species	Date of presence (MYA)	Locations	Locations from where isotopes have been taken	Specimen ages (MYA)
A. anamensis	4.2 - 3.8	**Ethiopia:** Asa Issie; Aramis; Galili; Woranso-Mille. **Kenya:** Allia Bay; Kanapoi	Allia Bay (*n* = 4), Kanapoi (*n* = 13)	Kanapoi = 4.12 - 4.06. Allia Bay = 4
A. afarensis	3.9 - 2.8	**Ethiopia:** Belohdelie; Dikika; Fejej; Galili; Hadar; Laetoli; Ledi-Gararu; Maka; Omo; Woranso-Mille. **Kenya:** Koobi Fora and West Turkana; Lothagam	Hadar (*n* = 20)	Hadar = 3.8 - 2.94
A. africanus	3.5 - 2.0	**South Africa**: Gladysvale; Makapansgat; Sterkfontein; Taung.	Makapansgat (*n* = 4), Sterkfontein (*n* = 18)	Makapansgat = 2.9 - 2.6. Sterkfontein = 2.65 - 2
P. aethiopicus	2.7 - 2.3	**Ethiopia:** Omo. **Kenya:** West Turkana	Turkana (*n* = *5*)	Turkana = 2.52 - 2.3
P. boisei	2.3 - 1.2	**Ethiopia:** Omo Shungura and Konso-Gardula. **Kenya:** Chesowanja; Koobi Fora, West Turkana. **Tanzania:** Olduvai; Peninj	Koobi Fora (*n* = 24), West Turkana (*n* = 3), Olduvai (*n* = 1), Peninj (*n* = 1), Baringo (*n* = 1)	Koobi Fora = 1.82 - 1.46. West Turkana = 1.77. Olduvai = 1.82. Peninj = 1.62. Baringo = 1.42
P. robustus	2.31 - 0.6	**South Africa:** Coopers; Drimolen; Gondolin; Kromdraai; Swartkrans	Swartkrans (*n* = 21), Kromdraai (*n* = 1)	Swartkrans = 2.31 - 0.6. Kromdraai = 1.8-1.6
H. habilis sensu stricto	2.3 - 1.4	**Kenya:** Koobi Fora; **Tanzania:** Olduvai; **Malawi**: Uraha; **South Africa:** Sterkfontein	Koobi Fora (*n* = 4), Olduvai (*n* = 3)	Koobi Fora = 1.97 - 1.76. Olduvai = 1.8 - 1.75
H. ergaster	1.8 - 1.3	**Kenya:** Koobi Fora; **South Africa**: Swartkrans	Koobi Fora (*n* = 4)	Koobi Fora = 1.59 - 1.46

As far as dental microwear texture analysis is concerned, increased sample sizes would be beneficial. For example, the dental microwear texture analyses taken from *P. boisei* might not be reflective of the species, given that they are only taken on 9 specimens (Ungar *et al.,* 2008, 2012). So perhaps it is not a large enough sample size to be making large generalisations about the diets of this species. However, the specimens do come from a number of sites and time periods, so Ungar *et al*. (2008, 2012) suggest that the results should be reasonably reliable. Furthermore, Scott *et al.* (2005) analysed 19 specimens of *P. robustus* and *A. africanus*, and concluded that the two species overlapped in certain aspects of their diets, but diverged in other areas. These conclusions were later supported by a study on a much greater number of specimens ($n = 110$) from the same species (Peterson *et al.*, 2008), indicating that at least in these cases the smaller subsample analysed previously was accurate. Nonetheless, more information is always beneficial when reconstructing diets of hominins.

Stable carbon isotopes, dental microwear texture analysis and comparative morphological analysis should all be used in conjunction to further elucidate the dietary ecologies of hominins and non-human primates. There is no doubting how valuable stable carbon isotope and dental microwear texture analyses are, but using them without field studies on non-human primates could lack context. For example, *Pan* and *Pongo* overlap in their isotopes and microwear (Teaford & Walker, 1984; King *et al*., 1999; Schoeninger *et al*., 1999, 2016; Sponheimer *et al*., 2006b; Pushkina *et al*., 2010; Scott *et al*., 2012), yet the field studies provide the necessary context and highlight the diets were not the same (Rodman, 1977; Galdikas, 1988; Fox *et al*., 2004; Wich *et al*., 2006b; Head *et al*., 2011; Watts *et al*., 2012a; Bessa *et al*., 2015). It is possible the same could be said for the hominins and the comparative morphological analysis is needed to understand what the hominins were capable of consuming. There does appear to be an association between diet and morphology, so the value comparative morphological analysis should not be overlooked.

6.3 Potential limitations of this research

Of course, as with any research study there are potential limitations to the approach taken in this study. The potential challenges of the research undertaken include those faced by many other researchers. A key challenge is highlighted by McGraw & Daegling (2012), whereby the specimens that were measured were not the same as those observed in the wild in field studies, therefore the dietary information could be unreliable when applied to the morphology. It is also possible that the foods consumed by non-human primates at the time of the observations were not actually what the species would have consumed at the time the skeletal samples were collected (Smith *et al*., 2012). Within the time since museum skeletal collections were formed and the dietary studies undertaken, anthropogenically influenced factors including climate change, introduction of livestock grazing and the subsequent reduction of a species habitat will have dramatically altered the seasons and environments and as a result the types of foods available (Sauther & Cuozzo, 2009; Cuozzo & Sauther, 2012; Smith *et al*., 2012; Serckx *et al*., 2015). To then attempt to take this a step further and apply this information to hominins is problematic for several reasons. One such reason is the fact that the aims and objectives of primatologists undertaking field research are different to those of the palaeoanthropologists who use their data, potentially leading to important data being missed or factors that are not important being overemphasised. Ultimately, the dietary data collected for research projects such as the present one are dependent on other researchers and the methods they use, and inferences of hominin adaptation made based on the combined use of dietary and morphological studies on non-human primates are therefore potentially weakened. These are fundamental issues with all studies, so inferences have to be made with caution.

Despite these inherent issues with the use of non-human primate dietary data and morphological analysis as they are used here, it was the best approach available, as none of the hominins analysed in this study are alive today to observe in the wild, meaning that non-human primates are the best comparisons available. It was intended that limitations would be further offset by trying to include as many dietary studies of the different species as possible, to create a more accurate description of the overall dietary ecologies of the various species.

The usage of generic dietary classifications, such as folivore or frugivore have been suggested to be of little relevance for studies aiming to investigate a possible correlation between diet and morphology, for within each category there is much variation of consistency and texture of the food items of the food items (Smith, 1983; Yamashita, 1996, 1998; Ankel-Simons, 2007; McGraw & Daegling, 2012; McGraw *et al*., 2016). Indeed, the mechanical properties of foods can overlap from one dietary classification to another, meaning that these dietary groupings are not biomechanically informative but are vague and coarse-grained (Kinzey & Norconk, 1993; Yamashita, 1996, 1998; Taylor *et al*., 2008; McGraw & Daegling, 2012; Vogel *et al*., 2014; Coiner-Collier *et al*., 2016; McGraw *et al*., 2016). Similarly, it is wrong to assume that all fruits are soft, all leaves are tough, and all seeds are hard, for there is much variation in the mechanical properties of each food type (as discussed in chapter 3) (Yamashita, 1998; Grine *et al.*, 2006b, 2012; Taylor, 2006b; Vogel *et al.*, 2014; Smith *et al.*, 2015; Coiner-Collier *et al.*, 2016; Talebi *et al.*, 2016). However, when analysing the morphology of the non-human primates and hominins in this thesis the dietary categories and assumptions of food mechanical properties were used to provide some context and comparison. These assumptions were made despite knowing that they are problematic because information on the mechanical properties of foods for almost all of the species analysed in this thesis is currently unavailable, thus assumptions were necessary. By including multiple ways of assessing diet, from the traditional dietary categories, the specific classification coding categories, and the food quantity analyses, it was intended that a more comprehensive overview of diet would be taken and the potential pitfalls of any one of these approaches would be mitigated. Indeed, patterns were identified with some dietary factors that were consistent regardless of the dietary category used, while patterns were sometimes found to differ depending on the diet classification used. Future research on mechanical properties of foods for the various non-human primates analysed in this study would help to elucidate patterns further.

The above were factors that required consideration when designing the research project. Given the time and funding available for this research the approaches taken were the most appropriate. From these potential limitations and experiences from the study, the following section discusses the recommendations for future research.

6.4 Future avenues of research

Based on the results from this project there are three aspects recommended for further exploration. The first considers further research and any suggested amendments to the research method, the second covers suggested aspects to explore in field studies of non-human primates, and the third covers suggested aspects to explore in studies of the hominins.

6.4.1 Further research opportunities and amendments

When preparing this research project, preliminary studies assisted in refining the approach and improving the methodology. Initial plans included 3D scanning of mandibles and dentition using a Structured Light 3D Scanner (by 3D3 Solutions). However, a pilot study showed that this was not a feasible inclusion in data collection. In brief, some of the major obstacles faced were due to the time taken per scan and its suitability to travel. A future study focussing entirely on imaging different species and subspecies could have great value. With attention only on imaging, and with the advancements that have already been made in scanning equipment, it should be possible to develop a vast dataset of non-human primates in virtual space. The high-resolution scans that are developed can then be used in combination with geometric morphometrics and Finite Element Analysis. The potential benefits of these techniques to palaeoanthropology are substantial. For example, a Finite Element Analysis would enable the researcher to simulate different loading scenarios on the mandible and assess its performance under strain (Toro-Ibacache *et al.*, 2016; Stansfield *et al.*, 2018a, b). Given that an association has been identified between mandibular morphology and diets that involve high stress and strain, explorative studies using Finite Element Analysis to analyse the mandibular morphology of the hominins under varying strains would be extremely useful.

A further aspect of the method that was developed but not addressed in this study was the observation of non-metric traits. Non-metric data were recorded on all of the specimens analysed, but time did not permit complete analysis of the non-metric traits. Non-metric traits, such as a *Tuberculum sextum* and *Tuberculum intermedium* are regularly observed on hominins, and have even been used to distinguish *Paranthropus* from *Australopithecus* and early *Homo*, (e.g., Wood & Abbott, 1983, Prat *et al*., 2005, Irish *et al*., 2018). To date, with the exception of Swindler (2002), knowledge on presence and variation in non-metric traits in non-human primates remains mainly unexplored. The large sample analysed in this project provides an opportunity to further develop knowledge on the appearance of these traits, and it will be analysed and published following the submission of this PhD.

During the initial formulation of this study, the focus was on frugivorous non-human primates since it was considered that they were most affected by seasonality of resources. However, recent research on responses to periods of resource scarcity highlights how folivorous species are also affected by seasonality of resources (Snaith & Chapman, 2005, 2007; Gogarten *et al*., 2012). It would therefore be useful for future studies to include the feeding ecologies, digestive capabilities and morphology of non-human primates that consume foliage preferentially, and indeed other foods. Comparisons can then be made to the non-human primates and hominins used in this study to more accurately ascertain morphological variation in relation to dietary differences. By including more species characterised by different diet categories, such as a greater sample of folivores, it would provide further comparisons to the patterns observed on the corpus robusticity indices and determine whether the patterns identified in this study continue in a wider sample.

Cebus and *Sapajus* were included in the sample because they were suggested to be essential species to include to analyse the effects of fallback foods (Wright, 2005). However, throughout the PCA graphs comparing the morphologies of extant non-human primates to hominins, *Cebus* and *Sapajus* consistently clustered in distinct ways to the rest of the species in the morphospace (Figures 5.35-5.58). These species may not therefore represent the most appropriate comparisons to Old World monkeys, apes and hominins, as they have probably solved the challenges they have faced in their own ways, unique to the species of the Old World.

The corpus robusticity indices present in the hominins are unlike any of the extant species analysed, which does impact on the ability to interpret the extinct species morphology compared to extant species. Examination of Miocene hominoids, such as *Gigantopithecus* – which is said to have presented similarly robust and derived masticatory morphology to *Paranthropus* – would be valuable (Frayer, 1973; Miller *et al*., 2008; Olejniczak *et al*., 2008; Dickson, 2011). In particular, it would be worthwhile exploring how the Miocene hominoids compare to each other, to the rest of the hominins and extinct and extant non-human primates.

The use of corpus robusticity indices in the present study (and also Veneziano *et al*. 2019) was successful in distinguishing between a leaf-based diet (used as a proxy for toughness) and a seed-based diet (used as a proxy for hardness). Yet many studies reported an inability to distinguish these diets (Hylander, 1979b; Smith, 1983; Daegling & Grine, 1991; Ravosa, 1996; Daegling & McGraw, 2001; Hogue, 2008; McGraw & Daegling, 2012; Daegling *et al*., 2013; Grine & Daegling, 2017). It would be useful therefore, for more research to explore the potential morphological differences between a hard and tough-food diet, and between those foods that are frequently consumed to those that are infrequently consumed (Sponheimer *et al*., 2013). To identify the differences between hard and tough foods microwear studies can be used in conjunction with the morphological analyses, as Veneziano *et al.* (2019) do. Furthermore, the inclusion of stable carbon isotopes in these analyses would further clarify morphological variation present within each isotopic pathway. Exploration of other aspects of the morphology, e.g., cortical bone thickness and distribution (Daegling, 2007) would further elucidate morphological variation associated with diet.

Based on the present study, the more detailed dietary classification techniques were more successful in identifying patterns of association between diet and the corpus morphology than the traditional dietary classification categories. Future studies are therefore advised to explore diet using more refined approaches, such as the quantity categories and the specific classification coding systems.

The dental variables analysed in the present study were unable to identify clear morphological differences between diets, regardless of the dietary classification system used. As previous research (e.g., Kay, 1975; Kinzey, 1978; Happel, 1988; Yamashita, 1998; Teaford & Ungar, 2000; Lucas, 2004; Lucas *et al*., 2008b; Lee *et al*., 2010; Ungar 2011, 2015) established that diets can be distinguished based on the dentition, it is advised that those dental variables be used again to confirm or challenge the patterns observed on the corpus robusticity indices.

There appears to be a discontinuity between what is generally observed to be a robust morphology, e.g., that present in *P. boisei*, to the results obtained in the corpus robusticity indices. Future research should concentrate on defining robusticity and refining how best to measure it.

6.4.2 Suggested next steps for field studies of non-human primates

When palaeoanthropologists are addressing adaptations in hominins, especially pertaining to diet, they are reliant on comparative data collected by primatologists. However, the research approaches of the two disciplines are not always congruent. One such aspect is how foods are classified and assessing the potential quality of those foods. To determine the quality of the foods consumed and the potential effects of those foods upon morphology, it is important to understand: 1) the nutritional and 2) mechanical properties of the foods, 3) the digestive capabilities of the consumers, 4) their feeding behaviours, and 5) to recognise how requirements change throughout life (Rothman *et al*., 2007; Lappan, 2009; Norconk *et al*., 2009; Vinyard *et al*., 2011; Ross *et al*., 2012; Hanya & Chapman, 2013; Irwin *et al*., 2014; Oelze *et al*., 2014; Vogel *et al*., 2014; Lambert & Rothman, 2015).

To properly understand seasonal diet variation and what foods could accurately be described as preferred foods and fallback foods long-term observation of species dietary habits are essential. There are many field schools observing and recording the dietary ecologies of non-human primates and it would be useful if the data were made freely available, perhaps through online databases.

Future studies on dental microwear texture analysis should follow the methods of Nystrom *et al*. (2004), Yamashita *et al*. (2016) and Percher *et al*. (2018), in observing the non-human primates in their natural habitats and what they consume to compare to their dental microwear signatures. Such an approach would be highly beneficial to understanding the microwear patterns observed in non-human primates, and for subsequent use on the hominins.

6.4.3 Suggested next steps for research on hominins

Conclusions drawn from the results from the present study indicate there remain further avenues to explore with regard to hominin dietary ecology. One aspect is that of the suggested changes to the microwear analyses on non-human primates as highlighted above. The inclusion of as many corpus measurements as possible would also be beneficial. Corpus robusticity indices at the M_1 has been the focus in many studies on hominin mandibles (e.g., Brown & Walker, 1993; White *et al*., 2000; Kimbel *et al*., 2004; de Ruiter *et al.*, 2008; Leakey *et al*., 2012). Poor perseveration of mandibles has led to very limited measurements; for some species (*A. anamensis* and *P. aethiopicus*) only M_1 corpus robusticity indices were recorded (Leakey & Walker, 1988; Ward *et al*., 2001, 2013). Based on the analyses run it is clear that variation exists in the corpus morphology from P_4-M_3 in non-human primates (Tables 6.1-6.3), and there is no reason to suggest that will not be the case in hominins. Future research on hominins should therefore include comprehensive information on the corpus measurements, e.g., robusticity indices all along the molar tooth row (if available) to ascertain potential variation in the corpus.

The importance of stable carbon isotopes to the study of hominin diets is undisputed, but there are areas where more information would be beneficial. It is clear that C_4 foods formed an important component of the diets of hominins (Elton, 2008), particularly in East Africa, but currently not enough is known about C_4 plants (Ungar & Sponheimer, 2011; Sponheimer *et al*., 2013). Since C_4 plants includes a wide variety species, more information is needed about their distribution and abundance in habitats, their nutritional properties, and the potential variation in their mechanical properties before any valuable inferences can be made about hominin diets and adaptations (Sponheimer *et al*., 2013).

To date, stable carbon isotope analysis data are available for each of the hominin species analysed in this study, but the inclusion of specimens at their earliest and latest dates of presence and from different locations would be useful. Given that the various hominin species are found at a number of different sites across a large timescale (detailed information on hominin localities available in Appendix Tables 9.2-9.3), it is possible that isotopic pathways recorded on specimens from one locality will differ from another, especially if their location in time differ. To have information on potential isotopic stability or change in a species would be highly beneficial for understanding the dietary pathways of hominin species over time.

In order to understand more about the hominins it is necessary to integrate the different approaches of collecting information, as the use of a single approach may provide a very biased or incomplete picture (Daegling & McGraw, 2007; Ungar & Sponheimer, 2011; Grine *et al.*, 2012; Alemseged, 2015). Different information can be derived from the different approaches, and when used together can complement each other, helping to build an idea of what the hominins were both capable of consuming and what types of foods they consumed at the start and end of their lives (Ungar *et al.*, 2008, 2012; Ungar & Sponheimer, 2011; Sponheimer *et al.*, 2013).

Chapter 7 : Conclusion

7.1 General conclusions

Attempts to understand the potential stimuli behind the highly derived morphology observed in *Paranthropus* occupied the attentions of palaeoanthropologists for many years, with the consensus of many being that *Paranthropus* and *Australopithecus* diverged due to very different diet adaptations (*sensu* Robinson, 1954a, 1963). Interest in these hominins and their morphology was renewed with the application of stable carbon isotopes and dental microwear texture analyses to the hominins. These analyses challenged the conventional understandings of the adaptive morphologies of both *Paranthropus* and *Australopithecus*, whereby they suggest that *Paranthropus* and *Australopithecus* were not divided by clear dietary differences as Robinson (1954, 1963) proposed. Instead, overlap existed in the diets of *P. robustus* and *A. africanus* (Scott *et al*., 2005), while the diets of *P. boisei* and *P. robustus* diverged (Cerling *et al*., 2011). In order to reconcile the morphological differences between *Paranthropus* and *Australopithecus*, it was proposed that they were morphologically adapted to their fallback foods (Laden & Wrangham, 2005; Scott *et al*., 2005; Ungar *et al*., 2008).

In light of the confusion surrounding the possible explanations for *Paranthropus* morphology in relation to that of *Australopithecus*, this study set out to explore if it was possible to identify morphological differences in non-human primates that correspond to differences in diet. Dental and mandibular morphology was assessed in a broad sample of haplorhine primate species (n = 37) that reflect different dietary preferences, habitats and body sizes. Age (juvenile or adult), sex, specimen provenance (wild shot or from captivity) and health condition (e.g., whether the specimen was edentulous or not) were all factors taken into account when selecting specimens to be analysed. An additional sample of 6 species of hominins was also collected to compare the morphology to that of known-diet non-human primates.

The aims, objectives and research questions as set out in the Introduction have been met and answered (as detailed below). As a result, new evidence in support of an association between diet, and in particular, the food mechanical properties of diet and morphology has been gathered. This finding supports extensive literature on the subject.

1. *Are there morphological differences present between consumers of different diets?*

Morphological differences were present in consumers of different diets. These differences manifested themselves in different areas of the mandibular and dental morphologies. Dietary differences also corresponded to body size differences. According to the Jarman-Bell principle, folivores are generally recognised as being larger species, while insectivores are generally recognised as being smaller species, and indeed this is acknowledged in the results of this study. The largest species analysed in this study, *Gorilla*, are observed to consume large quantities of foliage (although exact quantities of foliage depends on the subspecies and populations analysed), while the smallest species in this study, *Cebus/ Sapajus*, consume large quantities of insects in their diets. The size-related variables (crown area and corpus size) reflect these dietary and body size differences in these species.

When the dietary categories were analysed by the other morphological variables different patterns emerged, indicating that there is an association between diet and morphology, outside of body size. Diets cluster in particular patterns on each of the following variables: corpus robusticity indices, crown shape indices and symphyseal robusticity indices.

Different corpus and symphysis shapes emerged in the different dietary categories. Consumers of diets dominated primarily by fruits and supplemented by other foods, e.g., frugivore-insectivores, presented taller mandibular corpora and wider symphyses relative to consumers of diets dominated by foliage and supplemented by other foods, e.g., folivore-frugivores, who presented wider mandibular corpora and taller symphyses.

Different crown shapes also emerged in the different dietary categories. Frugivore-insectivores consistently displayed the widest tooth crowns, while folivores and omnivores presented the longest tooth crowns relative to the other categories.

2. *Are there morphological differences between consumers of low quantities of particular foods relative to consumers of higher quantities of the same foods?*

Morphological differences were present in consumers of different quantities of the same foods. Depending on the foods consumed, low quantities of certain foods, e.g., fruits, resulted in more defined clusters, while in other foods, e.g., seeds and leaves, low quantities resulted in a more varied and scattered appearance. Equally, depending on the foods consumed, high quantities of certain foods, e.g., seeds and leaves, resulted in more defined clusters, while in other foods, e.g., fruits, high quantities resulted in a more varied and dispersed appearance. Relative to low consumers of the following foods, high consumption of leaves corresponds to a wider mandibular corpus, taller symphysis and wider tooth crowns; high consumption of seeds corresponds to a taller mandibular corpus and wider crown shape; high consumption of roots corresponds to both a wider and taller corpus and a wider symphysis; high consumption of roots corresponds to longer tooth crowns. In contrast, low consumers of fruits present wider mandibular corpora and longer tooth crowns, while moderate consumers of fruits present taller mandibular corpora.

These differences appear to reflect an association between the mechanical properties of foods and morphology. Indeed, it is possible that the more defined clustering of the low consumers of fruits reflects the mechanical properties of the foods that make up the rest of the diet.

In this study a folivorous diet (as shown by research question 1) and one that contains higher quantities of leaves (as shown by research question 2) is associated with a wider mandibular corpus, a result that differs from research by Hylander (1979b) and Bouvier (1986a, b), which found folivory was associated with a taller mandibular corpus. In the present study, differences were also identified between consumers of seeds (used as a proxy for hard foods) and consumers of leaves (used as a proxy for tough foods), which previous researchers had suggested might not be possible (Hylander, 1979b; Daegling & Grine, 1991). Based on the trends present in the results, the most robust non-human primates (those with the widest mandibular corpora) were the consumers of folivorous diets. This result is consistent with some work (Hylander, 1979b; Bouvier, 1986a, b) but not all (Daegling, 1992; Veneziano *et al.*, 2019). The potential reasons for these differences could include: 1) sample size: a larger dataset was used here than in many other studies (both in terms of the different species used and the number of specimens from each species analysed), although it was lacking some of the focus species used in the other studies. 2) diet was classified using a variety of different approaches. 3) more morphological variables were analysed from across the molar tooth row, and 4) the potential vagaries that surround assessing robusticity and the appropriateness of the robusticity index.

3. How much does diet contribute towards morphological variation?

Depending on the variable analysed diet explains between 10 and 20% of the morphological variation. For size variables diet is predicted to explain a small proportion (~9%) of the variance in comparison to log body size and sex, which are predicted to explain considerably more of the variance (~77%). The association between the variables represented by size variables and log body size is also consistent with other research. For corpus robusticity indices diet is predicted to explain approximately 21% of the variance and log body size and sex 31%. The increased association between diet and corpus robusticity indices is also consistent with other research. For crown shape indices diet is predicted to explain approximately 18% of the variance and log body size and sex 23%. For symphyseal robusticity indices diet is predicted to explain 19.5% of the variance and log body size and sex 1.2%. For the shape variables (indices) diet is predicted to explain a greater percentage of the variance than it is for size variables. In fact, the predicted contribution of diet to the shape variables remains consistent throughout the models, while the predicted influence of size decreases in the shape variables from that present in the size variables. Diet, while not being the most important factor based on the regression analyses is clearly an important variable when analysing morphological variance.

4. Is there comparable morphological variation within hominins to non-human primates?

Depending on the variables analysed there is some comparable morphological variation within hominins to non-human primates. When analysing corpus sizes, crown areas and crown shape indices hominins score within the range of extant non-human primates, but when analysing the corpus robusticity indices hominins are completely distinct from non-human primates.

5. Is it possible to associate the morphological features of the hominins with dietary categories analogous to non-human primates?

Using size variables and crown shape indices it is possible to associate morphological features with dietary categories analogous to non-human primates. In contrast, because the corpus robusticity indices of the hominins were so distinct, their morphological features could not be associated with specific dietary categories in non-human primates.

6. *Can the way hominins compare with known-diet non-human primates be used to frame hypotheses about diet variation in relation to morphological patterns in early hominins?*

Based on the various diets and food types entered it is likely that there were dietary differences between the hominins. Each of the hominins aligned with various diet types, indicating they could each have consumed an omnivorous/ generalist diet, even *P. boisei*. While each species is consistent with an omnivorous diet, it appears that variation in diet would have existed between species. The dietary variation is consistent with suggestions based on the stable carbon isotopes and dental microwear texture analyses. The results of this research therefore support the following revisions: 1) *P. robustus* and *P. boisei* both represent generalist diet consumers/ adaptations, with a capacity to consume tough/ hard foods depending on what is available. 2) The differences in quantities of C_4 in their diets could reflect adaptations to their environments. It is possible they were similarly constrained by nutritional requirements, but as discussed previously, diets in non-human primates vary from species to species, and indeed, within species, between populations. This variation in diet consumed is a reflection of a species' need to achieve a nutritionally balanced diet with the resources available to them. 3) Overlap in stable carbon isotopes and partial overlap in dental microwear texture analyses in *A. africanus* and *P. robustus* does not mean they were consuming the same diets. It is still entirely possible that their diets were very different.

The fact that the hominins exceed the limit of the non-human primates on the corpus robusticity indices makes it difficult to hypothesise what type of diet was consumed based on this variable alone. However, should the hominins follow the trend present in the non-human primates that indicates a more folivorous diet corresponds to a wider mandibular corpus (i.e. a more robust mandibular morphology as defined by the higher score on the robusticity index), it is possible to speculate that the robust mandibles present in the hominins represent an adaptation to regular consumption of tough foods. Further research is needed to confirm or challenge this suggestion, particularly with regards to refining how robusticity is best defined and measured.

- ***Sub-aim:* To assess the potential viability of the Fallback Food Hypothesis as an explanation for the morphological differences present in *Paranthropus* and *Australopithecus*.**

The Fallback Food Hypothesis could not be tested in this research because it lacked a clear operational definition. This research relied upon field reports of the feeding ecologies of non-human primates and without a clear consensus of fallback foods in those reports to then label a food a fallback food was a problem. An inability to test the hypothesis is a fundamental flaw and it appears to be a convenient explanation for the results obtained in the dental microwear texture and stable carbon isotope analyses in *Paranthropus* and *Australopithecus*. Before invoking the Fallback Food Hypothesis to explain the morphological differences observed in *Paranthropus* and *Australopithecus* more work is needed to understand food mechanical properties, and specifically the relationship between infrequently consumed high-impact foods and morphology, and regularly consumed, tough foods and morphology.

The results indicate that answers have been obtained to the research questions established at the start. While this is true, there were limitations present in the study and there still remains plenty of scope for further research.

7.2 Limitations of study and recommended areas for future research

There are limitations associated with this research, and while attempts were made to overcome them it is important to acknowledge what they were. Limitations include the following: 1) the specimens analysed morphologically are not the same as those for which dietary data is available, and as a result 2) assumptions were made regarding the quality and food mechanical properties of diets. While these limitations are all clearly important, by analysing a broad sample of non-human primates, and collecting as much dietary information and analysing it in different ways for each species/ subspecies as is done here, it was considered that the limitations were mitigated somewhat. In fact, what was once a potential limitation of the study is now a potential strength, as the diverse diet categories (specific classification coding systems and quantity analyses) identified morphological patterns that the traditional diet categories missed. They also identified differences in consumers of tough and hard foods, which had previously not been considered possible. These limitations are commonly encountered in this discipline and these approaches are widely used in research such as this.

There remain plenty of avenues for further research to understand more about the association between diet and morphology and beyond that to further understand the palaeobiology of *Paranthropus*. In addition there still remains further work that can be done with the existing dataset. As such, the following recommendations for future research are suggested:

- Using the data available from this research explore the potential importance of non-metric traits and their association with diet and phylogeny. It is intended that these data will be analysed and published following PhD submission.
- Increasing the sample further to include more dietary categories, including more folivorous species and the Miocene hominoids.
- Based on the analyses from this research, it is advised that when morphological variables are recorded on specimens they include a more exhaustive number of variables for analysis than is the norm. For example, if analysing corpus robusticity indices, it is recommended they are recorded from P_4-M_3, instead of just M_1 or M_2. This is because variation exists between both monkeys and apes, and by focussing only on M_1 or M_2 morphological variation corresponding to dietary differences is potentially lost.
- Using alternative approaches to analysing morphology, including 3D geometric morphometrics/ Finite Element Analysis. These approaches can help inform on potential loading capabilities.
- Combining comparative morphological analysis with stable carbon isotope and dental microwear texture analyses. This would involve using the morphometric data in relation to the microwear surface patterns to determine food hardness/ toughness from each specimen, as Veneziano *et al*. (2019) do, and the isotopic pathways of each specimen. That way a more accurate way of assessing dietary hardness/ toughness is utilised, along with identifying morphological variation within isotopic pathways. Both factors that would be very useful to understand more in relation to the hominins.
- More work is needed to understand the relationship between infrequently consumed high-impact foods and morphology, and regularly consumed, tough foods and morphology.
- It would also be useful if more work were undertaken to understand more about C_4 foods. Specifically, about what C_4 foods include, their mechanical properties and their nutritional properties.
- Use multiple ways of analysing diet. Traditional techniques do appear to miss morphological variation when compared with the more detailed classification techniques.
- Refine how robusticity is measured.

The current study elaborates on analyses already conducted that assess the association between diet and morphology, this time with a more complete and taxonomically diverse data set, a more refined dietary classification, and the acknowledgement of other factors, such as sexual dimorphism and body size differences. Ultimately, there is no one particular driver of morphology, as there are a number of different factors that could potentially contribute to morphological form (Larson *et al*., 2018). However, evidence suggests that it is possible to distinguish between general dietary adaptations and consumers of greater or lesser quantities of foods on the mandibular morphology. Thus, there appears to be an association between the mechanical properties of foods and the mandibular and dental morphology of non-human primates. Despite this, it remains unclear which factor is more important for determining masticatory form out of repetitive/ cyclical loads (average forces) or peak masticatory forces (Happel, 1988; Yamashita, 1998; Taylor *et al*., 2008; McGraw & Daegling, 2012). If the way in which morphology in non-human primates responds to the mechanical properties of foods can be considered an accurate proxy for hominin morphology, then it appears likely that the mechanical properties of foods consumed by the early hominins would have also contributed to the morphology observed. Whether diet was the most important component is unclear (Berthaume *et al*., 2010), but further analysis of the hominins through stable carbon isotopes, dental microwear texture analysis, comparative morphology and 3D scanning and its associated technologies can only help to further the understanding of the dietary ecologies of the hominins.

Chapter 8 : Bibliography

Adams, J. W., Herries, A. I. R., Kuykendall, K. L. and Conroy, G. C. (2007). Taphonomy of a South African cave: geological and hydrological influence on the GD1 fossil assemblage at Gondolin, a Plio-Pleistocene paleocave system in the Northwest Province, South Africa. *Quaternary Science Reviews*, 26: 2526-2543.

Agrawal, A. A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science*, 294: 321-326.

Aguirre, L., Castillo, D., Solarte, D. and Moreno, F. (2006). Frequency and variability of five non-metric dental crown traits in the primary and permanent dentitions of a racially mixed population from Cali, Columbia. *Dental Anthropology*, 19 (2): 39-48.

El Alami, A., van Lavieren, E., Rachida, A. and Chait, A. (2012). Differences in activity budgets and diet between semi-provisioned and wild-feeding groups of the endangered Barbary Macaque (*Macaca sylvanus*) in the Central High Atlas Mountains, Morocco. *American Journal of Primatology*, 74: 210-216.

Alemseged, Z. (2015). Stable isotopes serving as a checkpoint. *Proceedings of the National Academy of Sciences*, 112 (40): 12232-12233.

Alemseged, Z., Wynn, J. G., Kimbel, W. H., Reed, D., Geraads, D. and Bobe, R. (2005). A new hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia, and its geological context. *Journal of Human Evolution*, 49: 499-514.

Ali, R. (1986). Feeding ecology of the bonnet macaque at the Mundanthurai sanctuary, Tamilnadu. *Journal of the Bombay Natural History Society*, 83: 98-110.

Altmann, S. A. (1998). *Foraging for survival: yearling baboons in Africa.* Chicago, Chicago University Press.

Altmann, S. A. (2009). Fallback foods, eclectic omnivores, and the packaging problem. *American Journal of Physical Anthropology*, 140: 615-629.

Anapol, F. and Lee, S. (1994). Morphological adaptation to diet in platyrrhine primates. *American Journal of Physical Anthropology*, 94: 239-261.

Anderson, D., Nordheim, E. V., Boesch, C. and Moermond, T. C. (2006). Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. *In* C. Boesch, G. Hohmann, and L. Marchant (eds), *Behavioural diversity in chimpanzees and bonobos.* Cambridge, Cambridge University Press. Pages: 90-101.

Anderson, P. C. and Pendleton, A. E. (2001). *The Dental Assistant*. 7th edition. New York, Delmar Cengage Learning.

Andrews, P. J, (1981). Species diversity and diet in monkeys and apes during the Miocene. *In*: C. B. Stringer (eds) *Aspects of Human Evolution*. London, Taylor and Francis. Pages: 25-61.

Andrews, P. J. (1989). Palaeoecology of Laetoli. *Journal of Human Evolution*, 18: 173-181.

Ankle-Simons, F. (2007). *Primate Anatomy: An Introduction*. London, Academic Press.

Arambourg, C. & Coppens, Y. (1968). Découverte d'un Australopithecien nouveau dans les gisements de l'Omo (Ethiopia). *South African Journal of Science*, 64: 58-59.

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. and Suwa, G. (1999). *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science*, 284: 629-635.

Ashley, G. M., Bunn, H. T., Delaney, J. S., Barboni, D., Dominguez-Rodrigo, M., Mabulla, A. Z. P., Gurtov, A. N., Bulayot, R., Beverly, E. J. and Baquedano, E. (2014). Paleoclimatic and paleoenvironmental framework of FLK North archaeological site, Olduvai Gorge, Tanzania. *Quaternary International*, 322-323: 54-65.

Ashley, G. M., Dominguez-Rodrigo, M., Bunn, H. T., Mabulla, A. Z. P. and Baquedano, E. (2010). Sedimentary geology and human origins: a fresh look at Olduvai Gorge, Tanzania. *Journal of Sedimentary Research*, 80: 703-309.

Ashley, G. M., Tactikos, J. C. and Owen, R. B. (2009). Hominin use of springs and wetlands: Paleoclimate and archaeological records from Olduvai Gorge (~1.79-1.74). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272: 1-16.

Ashton, P. S., Givnish, T. J. and Appanah, S. (1988). Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist*, 132 (1): 44-66.

Astaras, C., Muhlenberg, M. and Waltert, M. (2008). Note on Drill (*Mandrillus leucophaeus*) ecology and conservation status in Korup National Park, Southwest Cameroon. *American Journal of Primatology*, 70: 306-310.

Badrian, N. and Malenky, R. K. (1984). Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. *In*: R. Susman (eds) *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. London, Plenum Press. Pages: 275-298.

Badrian, N., Badrian, A. and Susman, R.L. (1981). Preliminary observations on the feeding behavior of *Pan paniscus* in the Lomako forest of central Zaire. *Primates*, 22: 173-181.

Báez-Molgado, S., Hart, K., Najarro, E., Sholts, S. and Gilbert, H. (2013). Cranium and mandible imaging protocol: a guide for publication-quality digital photography of the skull. Available at: http://forensicosteology.org/im.php?language=en. (Accessed on 23.10.14).

Balasse, M., Obein, G., Ughetto-Monfrin, J. and Mainland, I. (2012). Investigating seasonality and season of birth in past herds: a reference set of sheep enamel stable oxygen isotope ratios. *Archaeometry*, 54 (2): 349-368.

Barr, W. A. (2015). Paleoenvironments of the Shungura Formation (Plio-Pleistocene: Ethiopia) based on ecomorphology of the bovid astragalus. *Journal of Human Evolution*, 88: 97-107.

Barton, Robert. (1989). *Foraging strategies, diet and competition in olive baboons*. PhD thesis, University of St Andrews.

Barton, R.A. and Whiten, A. (1993) Feeding competition among female olive baboons. *Animal Behaviour*, 46: 777-789.

Barton, R. A., Whiten, A., Byrne, R. W. and English, M. (1993). Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatologica*, 61: 1-20.

Basabose, A.K. (2002). Diet composition of chimpanzees inhabiting the Montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology*, 58: 1-21.

Basabose, A. K. and Yamagiwa, J. (1997). Predation on mammals by chimpanzees in the montane forest of Kahuzi, Zaire. *Primates*, 36: 45-55.

Beecher, R. M. (1983). Evolution of the mandibular symphysis in Notharctinae (Adapidae, Primates). *International Journal of Primatology*, 4 (1): 99-112.

Behrensmeyer, A. K. (2006). Climate change and human evolution. *Science*, 311: 476-478.

Behrensmeyer, A. K. and Reed, K. E. (2013). Reconstructing the habitats of *Australopithecus:* Paleoenvironments, site taphonomy, and faunas. *In* K. E. Reed, J. G. Fleagle, and R. Leakey (eds) *The Paleobiology of Australopithecus*. Vertebrate Paleobiology and Paleoanthropology Series. Dordrecht, Springer. Pages: 41-60.

Bentley-Condit, V. K. (2009). Food choices and habitat use by the Tana River yellow baboons (*Papio cynocephalus*): a preliminary report on five years of data. *American Journal of Primatology*, 71: 432-436.

Berger, L. R., de Ruiter, D. J., Steininger, C. M. and Hancox, J. (2003). Preliminary results of excavations at the newly investigated Coopers D deposit, Gauteng, South Africa. *South African Journal of Science*, 99: 276-278.

Bergmuller. R. (1998). *Nahrungsokologie der Rauschgraven Mangabe (Cercocebus torquatus atys) Ein Schlussel zur sozialen organisation?* Diplomarbeit. Universitat Erlangen-Nurnberg. Cited in: McGraw, W. S. (1998). Posture and support use of Old World Monkeys (Cercopithecidae): The influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items. *American Journal of Primatology*, 46: 229-250.

Berthaume, M. (2016). Food mechanical properties and dietary ecology. *American Journal of Physical Anthropology*, 159: S79-S104.

Berthaume, M. A., Delezene, L. K. and Kupczik, K. (2018). Dental topography and the diet of *Homo naledi*. *Journal of Human Evolution*, 118: 14-26.

Berthaume, M., Grosse, I. R., Patel, N. D., Strait, D. S., Wood, S. and Richmond, B. G. (2010). The effect of early hominin occlusal morphology on the fracturing of hard food items. *The Anatomical Record*, 293: 594-606.

Bessa, J., Sousa, C. and Hockings, K. J. (2015). Feeding ecology of chimpanzees (*Pan troglodytes verus*) inhabiting a forest-mangrove-savanna-agricultural matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau: Chimpanzee Feeding Behavior. *American Journal of Primatology*, 77: 651-665.

Biggerstaff, R. H. (1968). On the Cope-Osborn nomenclature for molar cusps. *Journal of Dental Research*, 47 (3): 508.

Binning, S. A., Chapman, L. J. and Cosandey-Godin, A. (2009). Specialized morphology for a generalist diet: evidence for Liem's Paradox in a cichlid fish. *Journal of Fish Biology*, 75: 1683-1699.

Bishop, W., Hill, A. and Pickford, M. (1978). Chesowanja: A revised geological interpretation. *Geological Society London Specieal Publications,* 6 (1): 309-327.

Blumenthal, S. A., Chritz, K. L., Rothman, J. M. and Cerling, T. E. (2012). Detecting intraannual dietary variability in wild mountain gorillas by stable isotope analysis of feces. *Proceedings of the National Academy of Sciences*, 109 (52): 21277-21282.

Bobe, R. (2006). The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments*, 66: 564-584.

Bobe, R. (2011). Fossil mammals and paleoenvironments in the Omo-Turkana Basin. *Evolutionary Anthropology,* 20: 254-263.

Bobe, R. and Behrensmeyer, A. K. (2004). Expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 207: 399-420.

Bobe, R., Behrensmeyer, A. K. and Chapman, R. E. (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution*, 42: 475-497.

Bobe, R., Behrensmeyer, A. K., Eck, G. G. and Harris, J. M. (2007). Patterns of abundance and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya and Ethiopia. *In* R. Bobe, Z. Alemseged, and A. K. Behrensmeyer (eds.) *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Vertebrate Paleobiology and Paleoanthropology Series. Dordrecht, Springer. Pages: 129-157.

Bock, W. J. (1980). The definition and recognition of biological adaptation. *American Zoologist,* 20 (1): 217-227.

Bock, W. J. and von Wahlert, G. (1965). Adaptation and the form-function complex. *Evolution*, 19 (3): 269-299.

Boesch, C. and Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, 13: 415-440.

Boesch, C., Bi, Z. B. G., Anderson, D. and Stahl, D. (2006). Food choice in Tai chimpanzees: are cultural differences present? *In* G. Hohmann, M. M. Robbins, and Boesch, C. (eds), *Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects.* Cambridge, Cambridge University Press. Pages: 183-202.

Bogart, S. L. and Pruetz, J. D. (2008). Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology*, 70: 605-612.

Bogart, S. L. and Pruetz, J. D. (2011). Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology*, 145: 11-20.

Bonnefille, R. and Riollet, G. (1987). Palynological spectra from the Upper Laetolil Beds. *In* M. D. Leakey, and J. M. Harris (eds) *Laetoli: A Pliocene site in Northern Tanzania.* Oxford, Clarendon Press. Pages: 52-61

Borries, C., Larney, E., Lu, A., Ossi, K. and Koenig, A. (2008). Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. *Behavioural Ecology*, 19: 1186-1194.

Bouvier, M. (1986a). A biomechanical analysis of mandibular scaling in Old World monkeys. *American Journal of Physical Anthropology*, 69: 473-482.

Bouvier, M. (1986b). Biomechanical scaling of mandibular dimensions in New World monkeys. *International Journal of Primatology*, 7: 551-567.

Bouvier, M. and Hylander, W. L. (1981). Effect of bone strain on cortical bone structure in macaques (*Macaca mulatta*). *Journal of Morphology*, 167: 1-12.

Brace, C.L, Smith, B. H. and Hunt, K. D. (1991). What big teeth you had grandma! Human tooth size, past and present. *In*: M. A. Kelley and C. S. Larson (eds), *Advances in dental anthropology*. New York: Wiley-Liss. Pages: 33-57.

Braun, D. R., Harris, J. W. K., Levin, N. E., McCoy, J. T., Herries, A. I. R., Bamford, M. K., Bishop, L. C., Richmond, B. G. and Kibunjia, M. (2010). Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National Academy of Sciences*, 107 (22): 10002-10007.

Brockman, D. K. and van Schaik, C. P. (2005). *Seasonality in primates: studies of living and extinct human and non-human primates.* Cambridge, Cambridge University Press.

Bromage, T. G., Schrenk, F. and Zonneveld, F. W. (1995). Palaeoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *Journal of Human Evolution*, 28: 71-108.

Broom, R. (1938). The Pleistocene anthropoid apes of South Africa. *Nature*, 142**:** 377-379.

Brown, A. D. and Zunino, G. E. (1990). Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica*, 54: 187-195.

Brown, B. (1997). Miocene hominoid mandibles: Functional and phylogenetic perspectives. *In* D. R. Begun, C. V. Ward, and M. D. Rose. (eds), *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*. New York, Plenum. Pages: 153-171.

Brown, B. and Walker, A. (1993). The Dentition. *In* A. Walker, and R. Leakey (eds), *The Nariokotome* Homo erectus *skeleton*. London, Springer-Verlag. Pages: 161-194.

Brown, F. H. (1994). Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites. *In* R. S. Corruccini, and R. I. Ciochon (Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honor of E Clark Howell.* Englewood Cliffs, Prentice Hall. Pages: 285-312.

Brown, F H., Harris, J., Leakey, R. and Walker, A. (1985). Early *Homo erectus* skeleton from West Lake Turkana, Kenya. *Nature*, 316 (6031): 788-792.

Bryer, M. A. H., Chapman, C.A. and Rothman, J. M. (2013). Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour*, 150: 277-293.

Cadman, A. and Rayner, R. J. (1989). Climate change and the appearance of *Australopithecus africanus* in the Makapansgat sediments. *Journal of Human Evolution*, 18: 107-113.

Campbell, C. J., Fuentes, A., Mackinnon, K. C., Bearder, S. K. and Stumpf, R. M. (eds) (2011). *Primates in Perspective*. Oxford, Oxford University Press.

Cant, J. G. H. (1987). Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (*Pongo pygmaeus*). *American Journal of Physical Anthropology*, 74 (2): 143–148.

Cardini, A. and Elton, S. (2008a). Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. *Biological Journal of the Linnean Society*, 93: 813-834.

Cardini, A. and Elton, S. (2008b). Variation in guenon skulls (II): sexual dimorphism. *Journal of Human Evolution*, 54: 638-647.

Carney, J., Hill, A., Miller, J. A. and Walker, A. (1971). Late Australopithecine from Baringo District, Kenya. *Nature*, 230: 509-514.

Carlson, B. A. and Crowley, B. E. (2016). Variation in carbon isotope values among chimpanzee foods at Ngogo, Kibale National Park and Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology*, 78: 1031-1040.

Carter, M. L. and Bradbury, M. W. (2016). Oxygen isotope ratios in primate bone carbonate reflect amount of leaves and vertical stratification in the diet. *American Journal of Primatology*, 78: 1086-1097.

Cerling, T. E., Hart, J. A., Hart, T. B. (2004). Stable isotope ecology in the Ituri Forest. *Oecologia*, 138: 5-12.

Cerling, T. E., Mbua, E., Kirera, F. M., Manthi, F. K., Grine, F. E., Leakey, M. G., Sponheimer, M. and Uno, K. T. (2011). Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences*, 108 (23): 9337-9341.

Cerling, T. E., Manthi, F. K., Mbua, E. N., Leakey, L. N., Leakey, M. G., Leakey, R. E., Brown, F. H., Grine, F. E., Hart, J. A., Kaleme, P. Roche, H., Ubo, K. T. and Wood, B. A. (2013). Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proceedings of the National Academy of Sciences*, 110 (26): 10501-10506.

Cerny, C. A. and Kaiser, H. F. (1977). A study of a measure of sampling adequacy for factor-analytic correlation matrices. *Multivariate Behavioral Research*, 12 (1): 43-47.

Chalk-Wilayto, J., Ossi-Lupo, K. and Raguet-Schofield, M. (2016). Growing up tough: comparing the effects of food toughness on juvenile feeding in *Sapajus libidinosus* and *Trachypithecus phayrei crepusculus*. *Journal of Human Evolution*, 98: 76-89.

Chamberlain, A. T. and Wood, B. A. (1985). A reappraisal of variation in hominid mandibular corpus dimensions. *American Journal of Physical Anthropology*, 66: 399-405.

Chancellor, R. L., Rundus, A. S. and Nyandwi, S. (2012). The influence of seasonal variation on Chimpanzee (*Pan troglodytes schweinfurthii*) fallback food consumption, nest group size, and habitat use in Gishwati, a montane rain forest fragment in Rwanda. *International Journal of Primatology*, 33: 115-133.

Chapman, C. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica*, 49: 90-105.

Chapman, C. A., Chapman, L. J., Cord, M., Gathua J. M., Gautier-Hion, A., Lambert, J. E., Rode, K., Tutin, E. G. and White, L. J. T. (2002). Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. *In*: M. E. Glenn and M. Cords (eds) *The Guenons: Diversity and adaptation in African Monkeys*. London, Kluwer Academic/ Plenum Publishers. Pages: 325-350.

Chapman, C. A. and Fedigan, L. M. (1990). Dietary differences between neighbouring *Cebus capucinus* groups: local traditions, food availability or responses to food profitability? *Folia Primatologica*, 54: 177-186.

Chapman, C. A., White, F. J. and Wrangham, R. W. (1994). Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. *In* R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. Heltne (eds) *Chimpanzee Cultures*. London, Harvard University Press. Pages: 41-57.

Cipolletta, C., Spagnoletti, N., Todd, A., Robbins, M. M., Cohen, H. and Pacyna, S. (2007). Termite feeding by *Gorilla gorilla gorilla* at Bai Hokou, Central African Republic. *International Journal of Primatology*, 28: 457-476.

Clarke, R. J. (2006). A deeper understanding of the stratigraphy of Sterkfontein fossil hominid site. *Transactions of the Royal. Society of South Africa*, 61 (2), 111-120.

Clarke, R. J. (2012). A *Homo habilis* maxilla and other newly-discovered hominid fossils from Olduvai Gorge, Tanzania. *Journal of Human Evolution*, 63: 418-428.

Clutton-Brock, T. H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. *In* T. H. Clutton-Brock (ed), *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes.* London, Academic Press. Pages: 539-556.

Clutton-Brock, T. H. and Harvey, P. H. (1977). Species differences in feeding and ranging behaviour in primates. *In* T. H. Clutton-Brock (ed), *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes.* London, Academic Press. Pages: 557-579.

Codron, D., Lee-Thorp, J., Sponheimer, M., de Ruiter, D. and Codron, J. (2008). What insights can baboon feeding ecology provide for early hominin niche differentiation? *International Journal of Primatology*, 29 (3): 757-772.

Cofran, Z. (2014). Mandibular development in *Australopithecus robustus*. *American Journal of Physical Anthropology*, 154 (3): 436-446.

Coffing, K., Feibel, C., Leakey, M. and Walker, A. (1994). Four-million-year-old hominids from East Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 93: 55-65.

Coiner-Collier, S., Scott, R. S., Chalk-Wilayto, J., Cheyne, S. M., Constantino, P., Dominy, N. J., Elgart, A. A., Glowacka, H., Loyola, L. C., Ossi-Lupo, K., Raguet-Schofield, M., Talebi, M. G., Sala, E. A., Sieradzy, P., Taylor, A. B., Vinyard, C. J., Wright, B. W., Yamashita, N., Lucas, P. W. and Vogel, E. R. (2016). Primate dietary ecology in the context of food mechanical properties. *Journal of Human Evolution*, 98: 103-118.

Cole, T. M. (1992). Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. *Journal of Human Evolution*, 23: 253-282.

Conklin, N. L. and Wrangham, R. W. (1994). The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. *Biochemical Systematics and Ecology*, 22 (2): 137-151.

Conklin-Brittain, N. L., Knott, C. D. and Wrangham, R. W. (2000). The feeding ecology of apes. In: Chicago Zoological Society. *The Apes: Challenges for the 21st Century held at Brookfield Zoo.* Chicago. Pages: 167-174.

Conklin-Brittain, N. L., Wrangham, R. W. and Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, 19 (6): 971-998.

Constantino, P. J., Lee, J. J.-W., Chai, H., Zipfel, B., Ziscovici, C., Lawn, B. R. and Lucas, P. W. (2010). Tooth chipping can reveal the diet and bite forces of fossil hominins. *Biology. Letters*, 6: 826-829.

Constantino, P. J., Lee, J. J.-W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, B. R. and Lucas, P. W. (2012). The role of tooth enamel mechanical properties in primate dietary adaptation. *American Journal of Physical Anthropology*, 148: 171-177.

Constantino, P. J., Lee, J. J.-W., Morris, D., Lucas, P. W., Hartstone-Rose, A., Lee, W-K., Dominy, N. J., Cunningham, A., Wagner, M. and Lawn, B. R. (2011). Adaptation to hard-object feeding in seas otters and hominins. *Journal of Human Evolution*, 61: 89-96.

Constantino, P. J., Lucas, P. W., Lee, J. J.-W. and Lawn, B. R. (2009). The influence of Fallback Foods on great ape tooth enamel. *American Journal of Physical Anthropology*, 140: 653-660.

Constantino, P. J. and Wright, B. W. (2009). The importance of fallback foods in primate ecology and evolution. *American Journal of Physical Anthropology*, 140: 599-602.

Cooke, Catherine. (2012). The Feeding, ranging, and positional behaviors of *Cercocebus torquatus*, the Red-Capped Mangabey, in Sette Cama Gabon: A Phylogenetic Perspective. PhD Thesis. Ohio State University.

Cope, E. D. (1883a). Note on the trituberculate type of superior molar and the origin of the quadrituberculate. *American Naturalist*, 17: 407-408.

Cope, E. D. (1883b). On the trituberculate type of molar tooth in the Mammalia. *Proceedings of the American Philosophical Society*, 21: 324-326.

Cope, E. D. (1888). On the tritubercular molar in the human dentition. *Journal of Morphology,* 2: 7-23.

Copeland, S. R., Spoheimer, M., de Ruiter, D. J., Lee-Thorp, J., Codron, D., le Roux, P. J., Grimes, V. and Richards, M. P. (2011). Strontium isotope evidence for landscape use by early hominins. *Nature*, 474: 76-79.

Coppens, Y. (1970). Les restes d'Hominidés des séries inférieures et moyennes des formations plio-villafranchiénnes de L'Omo en Ethiopie. *Comptes Rendus de l'Académie des Sciences Paris*, 271: 2286-2289. Cited in Wood, B. A. (1991). *Koobi Fora Research Project. Volume 4: Hominid Cranial Remains.* Oxford: Clarendon Press.

Coppens, Y. (1971). Les restes d'Hominidés des séries supérieures des formations plio-villafranchiénnes de L'Omo en Ethiopie. *Comptes Rendus de l'Académie des Sciences Paris*, 272: 36-39. Cited in Wood, B. A. (1991). *Koobi Fora Research Project. Volume 4: Hominid Cranial Remains.* Oxford: Clarendon Press.

Coppens, Y. (1973a). Les restes d'Hominidés des séries inférieures et moyennes des formations plio-villafranchiénnes de L'Omo en Ethiopie (récoltes 1970, 1971 et 1972). *Comptes Rendus de l'Académie des Sciences Paris*, 276: 1823-1826. Cited in Wood, B. A. (1991). *Koobi Fora Research Project. Volume 4: Hominid Cranial Remains.* Oxford: Clarendon Press.

Coppens, Y. (1973b). Les restes d'Hominidés des séries supérieures des formations plio-villafranchiénnes de L'Omo en Ethiopie (récoltes 1970, 1971 et 1972). *Comptes Rendus de l'Académie des Sciences Paris*, 276: 1981-1984. Cited in Wood, B. A. (1991). *Koobi Fora Research Project. Volume 4: Hominid Cranial Remains.* Oxford: Clarendon Press.

Cords, M. (1986). Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *Cercopithecus mitis*. *Journal of Animal Ecology*, 55 (3): 811-827.

Cosandey-Godin, A., Binning, S. A. and Chapman, L. J. (2008). Specialised morphology for a non-specialised diet: Liem's paradox in an African cichlid fish. *McGill Science Undergraduate Research Journal*, 3: 19-23.

Crowley, B. E., Carter, M. L., Karpanty, S. M., Zihlman, A. L., Koch, P. L. and Dominy, N. J. (2010). Stable carbon and nitrogen isotope enrichment in primate tissues. *Oecologia*, 164: 611-626.

Cuozzo, F. P. and Sauther, M. L. (2012). What is dental ecology? *American Journal of Physical Anthropology*, 148: 163-170.

Curnoe & Tobias (2006). Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein StW 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution*, 50 (1): 36-77.

Daegling, D. J. (1989). Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. *American Journal of Physical Anthropology*, 80: 91-106.

Daegling, D. J. (1992). Mandibular morphology and diet in the genus *Cebus*. *International Journal of Primatology*, 13 (5): 545-570.

Daegling, D. J. (1993a). Shape variation in the mandibular symphysis of apes: an application of a median axis method. *American Journal of Physical Anthropology*, 91: 505-516.

Daegling, D. J. (1993b). The relationship of *in vivo* bone strain to mandibular corpus morphology in *Macaca fascicularis*. *Journal of Human Evolution*, 25: 247-269.

Daegling, D. J. (1996). Growth in the mandibles of African apes. *Journal of Human Evolution*, 30: 315-341.

Daegling, D. J. (2001). Biomechanical scaling of the hominoid mandibular symphysis. *Journal of Morphology*, 250 (1): 12-23.

Daegling, D. J. (2007). Relationship of bone utilization and biomechanical competence in hominoid mandibles. *Archives of Oral Biology*, 52: 51-63.

Daegling, D. J. and Grine, F. E. (1991). Compact bone distribution and biomechanics of early hominid mandibles. *American Journal of Physical Anthropology*, 86: 321-339.

Daegling, D. J. and Grine, F. E. (1999). Terrestrial foraging and dental microwear in *Papio ursinus*. *Primates*, 40 (4): 559-572.

Daegling, D. J. and Grine, F. E. (2007). Mandibular biomechanics and the paleontological evidence for the evolution of human diet. *In*: P. S. Ungar (ed). *The evolution of human diet: the known, the unknown, and the unknowable*. Oxford, Oxford University Press. Pages: 77-105.

Daegling, D. J. and Grine, F. E. (2017). Feeding behaviour and diet in *Paranthropus boisei*: the limits of functional inference from the mandible. *In*: A. Marom and E. Hovers (eds.). *Human Paleontology and Prehistory: Contributions in Honor of Yoel Rak*. Dordrecht, Springer. Pages: 109-125.

Daegling, D. J. and Hylander, W. L. (1997). Occlusal forces and mandibular bone strain: is the primate jaw “overdesigned”? *Journal of Human Evolution*, 33: 705-717.

Daegling, D. J. and McGraw, W. S. (2001). Feeding, diet, and jaw form in West African *Colobus* and *Procolobus*. *International Journal of Primatology*, 22 (6): 1033-1055.

Daegling, D. J. and McGraw, S. W. (2007). Functional morphology of the mangabey mandibular corpus: relationship to dental specializations and feeding behavior. *American Journal of Physical Anthropology*, 134 (1): 50-62.

Daegling, D. J., Judex, S., Ozcivici, E., Ravosa, M. J., Taylor, A. B., Grine, F. E., Teaford, M. F. and Ungar, P. S. (2013). Viewpoints: Feeding mechanics, diet, and dietary adaptations in early hominins. *American Journal of Physical Anthropology*, 151: 356-371.

Daegling, D. J., McGraw, S. W., Ungar, P. S., Pampush, J. D., Vick, A. E. and Bitty, A. (2011). Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PLoS ONE*, 6 (8): e23095.

Dahlberg, A. A. (1963). Analysis of the American Indian Dentition. *In* D. R. Brothwell. *Symposia of the Society for the Study of Human Biology: Volume V: Dental Anthropology*. Basel, S. Karger. Pages: 149-178.

Dart, R. A. (1925). *Australopithecus africanus:* the Man-Ape of South Africa. *Nature*, 115 (2884): 195-199.

Dart, R. A. (1948). The adolescent mandible of *Australopithecus prometheus*. *American Journal of Physical Anthropology*, 6: 391-409.

Day, M. H. and Leakey, R. E. F. (1973). New evidence of the Genus *Homo* from East Rudolf, Kenya. (I). *American Journal of Physical Anthropology*, 39: 341-354.

Day, M. H., Leakey, R. E. F., Walker, A. C. and Wood, B. A. (1976). New hominids from East Turkana, Kenya. *American Journal of Physical Anthropology*, 45: 369-436.

Day, M. H. and Wickens, E. H. (1980). Laetoli Pliocene hominid footprints and bipedalism. *Nature*, 286: 385-387.

Dean, M. C. (1988). Growth of teeth and development of the dentition in *Paranthropus*. *In*: F. E. Grine (ed), *Evolutionary History of the Robust Australopithecines.* New York, Aldine de Gruyter. Pages: 43-53.

Defler, T. R. (1979). On the ecology and behavior of *Cebus albifrons* in eastern Colombia: I. Ecology. *Primates*, 20 (4): 475-490.

DeGusta, D., Everett, M. A. and Milton, K. (2003). Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). *Proceedings of the Royal Society B: Biological Sciences*, S270: S15-S17.

deMenocal, P. B. (2004). African climate change and faunal evolution during the Plio-Pleistocene. *Earth and Planetary Science Letters*, 220: 3-24.

Demes, B. and Creel, N. (1988). Bite force, diet, and cranial morphology of fossil hominids. *Journal of Human Evolution*, 17: 657-670.

Denny, E. G., Gerst, K. L., Miller-Rushing, A. J., Tierney, G. L., Crimmins, T. M., Enquist, C. A. F., Guertin, P., Rosemartin, A. H., Schwartz, M. D., Thomas, K. A. and Weltzin, J. F. (2014). Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology*, 58 (4): 591-601.

de Oliveira, F. T., Soares, M. Q., Sarmento, V. A., Rubira, C. M., Lauris, J. R. and Rubira-Bullen, I. R. (2015). Mandibular ramus length as an indicator of chronological age and sex. *International Journal of Legal Medicine*, 129 (1): 195-201.

Depew, L. A. (1983). Ecology and behaviour of baboons (*Papio anubis*) in the Shai Hills Game Production Reserve, Ghana. MSc Dissertation, Cape Coast University. Cited in: Kunz, B. K. and Linsenmair, K. E. (2008). Diet and behavioural ecology of Olive Baboons in the Comoé National Park. *Folia Primatologica*, 79: 31-51.

de Ruiter, D. J., Pickering, R., Steininger, C. M., Kramers, J. D., Hancox, P. J., Churchill, S. E., Berger, L. R. and Backwell, L. (2009). New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa). *Journal of Human Evolution*, 56: 497-513.

de Ruiter, J. R. (1986). The influence of group size of predator scanning and foraging behaviour of wedge-capped capuchin monkeys (*Cebus olivaceus*). *Behaviour*, 77: 240-258.

DeSilva, J. M., Proctor, D. J. and Zipfel, B. (2012). A complete second metatarsal (StW 89) from Sterkfontein Member 4, South Africa. *Journal of Human Evolution*, 63: 487-496.

Devreese, L. and Gilbert, C. C. (2015). Phylogenetic relationships within the *Cercocebus-Mandrillus* clade as indicated by craniodental morphology: Implications for evolutionary biogeography. *American Journal of Physical Anthropology*, 158: 227-241.

deVries, M. S., Stock, B. C., Christy, J. H., Goldsmith, G. R. and Dawson, T. E. (2016). Specialised morphology corresponds to a generalist diet: linking form and function in smashing mantis shrimp crustaceans. *Oecologia*, 182: 429-442.

Diaz-Martin, Z., Swarmy, V., Terborgh, J., Alvarez-Loayza, P. and Cornejo, F. (2014). Identifying keystone plant resources in an Amazonian forest using a long-term fruit-fall record. *Journal of Tropical Ecology*, 30: 291-301.

Di Bitetti, M. S. and Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*, 50: 109-130.

Dickson, P. (2011). *Gigantopithecus*: a reappraisal of dietary habits. *Totem: the University of Western Ontario Journal of Anthropology*, 11 (1): 28-35.

Dominguez-Rodrigo, M., Lopez-Saez, J. A., Vincens, A., Alcala, L., Luque, L. and Serallonga, J. (2001). Fossil pollen from the Upper Humbu Formation of Peninj (Tanzania): hominid adaptation to a dry open Plio-Pleistocene savanna environment. *Journal of Human Evolution*, 40: 151-157.

Dominy, N. J., Lucas, P. W., Osorio, D. and Yamashita, N. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology*, 10: 171-186.

Dominy, N. J., Vogel, E. R., Yeakel, J. D., Constantino, P. and Lucas, P. W. (2008). Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology*, 35: 159-175.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. *International Journal of Primatology*, 18 (2): 183-206.

Doran, D. M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. and Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology*, 58: 91-116.

Doran-Sheehy, D. M., Mongo, P., Lodwick, J., Conklin-Brittain, N. L. (2009). Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus Old World Monkey foraging strategies. *American Journal of Physical Anthropology*, 140: 727-738.

Doran-Sheehy, D. M., Shah, N. F. and Heimbauer, L. A. (2006). Sympatric western gorilla and mangabey diet: re-examination of ape and monkey foraging strategies. *In*: G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 25-47

Drapeau, M. S. M. and Harmon, E. H. (2013). Metatarsal torsion in monkeys, apes, humans and australopiths. *Journal of Human Evolution*, 64: 93-108.

Drapeau, M. S. M., Ward, C. V., Kimbel, W. H., Johanson, D. C. and Rak, Y. (2005). Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *Journal of Human Evolution*, 48: 593-642.

Du Brul, E. L. (1977). Early hominid feeding mechanisms. *American Journal of Physical Anthropology*, 47: 305-320.

Dunbar, R. I. M. (1988). *Primate Social Systems*. New York, Cornell University Press.

Dunbar, R. I. M. and Dunbar, E. P. (1974). Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatologica*, 21: 36-60.

Durham, A. E., Erhart, E. M., Overdorff, D. J. and Wright, P. C. (2008). Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. *Biological Conservation*, 141 (1): 287-297.

Durham, A. E., Erhart, E. M., and Wright, P. C. (2010). Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, 17 (1): 219-222.

Eldredge, N. (1979). Alternative approaches to evolutionary theory. *Bulletin of the Cambridge Museum of Natural History*, 13: 7-19.

Elton, S. (2001). Locomotor and habitat classifications of Cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa. *Palaeontologia africana*, 37: 115-126.

Elton, S. (2008). The environmental context of human evolutionary history in Eurasia and Africa. *Journal of Anatomy*, 212: 377-393.

Elton, S., Jansson, A-U., Meloro, C., Louys, J., Plummer, T. and Bishop, L. C. (2016). Exploring morphological generality in the Old World monkey postcranium using an ecomorphological framework. *Journal of Anatomy,* 228: 534-560.

El-Zaatari, S., Grine, F. E., Teaford, M. F. and Smith, H. F. (2005). Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. *Journal of Human Evolution*, 49: 180-205.

Fahy, G. E., Boesch, C., Hublin, J.-J. and Richards, M. P. (2015). The effectiveness of using carbonate isotope measurements of body tissues to infer diet in human evolution: Evidence from wild western chimpanzees (*Pan troglodytes verus*). *Journal of Human Evolution*, 88: 70-78.

Fawcett, Kathryn. (2000). *Female relationships and food availability in a forest community of chimpanzees*. PhD thesis, University of Edinburgh.

Feibel, C. S. (2011). A geological history of the Turkana Basin. *Evolutionary Anthropology*, 20: 206-216.

Feibel, C. S. and Brown, F. H. (1993). Microstratigraphy and Paleoenvironments. *In* A. Walker, and R. Leakey (eds), *The Nariokotome* Homo erectus *skeleton*. London, Springer Verlag. Pages: 21-39.

Felton, A. M., Felton, A., Lindenmayer, D. B. and Foley, W. J. (2009c). Nutritional goals of wild primates. *Functional Ecology,* 23: 70-78.

Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., Wallis, I R. and Lindenmayer, D. B. (2009a). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioural Ecology,* 20 (4): 685-690.

Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., Wallis, I R. and Lindenmayer, D. B. (2009b). Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choice. *International Journal of Primatology*, 30: 675-696.

Fernández, P. J., Holowka, N. B., Demes, B. and Jungers, W. L. (2016). Form and function of the human and chimpanzee forefoot: implications for early hominin bipedalism. *Scientific Reports*, 6: 30532.

Fernandez-Duque, E. and van der Heide, G. (2013). Dry season resources and their relationship with Owl Monkey (*Aotus azarae*) feeding behaviour, demography, and life history. *International Journal of Primatology*, 34: 752-769.

Ferreira, T. and Rasband, W. (2012). ImageJ user guide. Available at: http://imagej.nih.gov/ij/docs/index.html. (Accessed on 30.12.14).

Ferriss, S., Robbins, M. M. and Williamson, E. A. (2005). Eastern gorilla (*Gorilla beringei*). *In*: J. Caldecott, and L. Miles (eds), *The World Atlas of Great Apes and their Conservation.* California, University California Press. Pages: 129-152.

Field, A. (2018). *Discovering statistics using IBM SPSS statistics.* 5th Edition. London, Sage.

Fleagle, J. G. (1999). *Primate adaptation and evolution.* 1st Edition. London, Academic Press.

Fleagle, J. G. (2013). *Primate adaptation and evolution.* 3rd Edition. London, Academic Press.

Fleagle, J. G. and McGraw, W. S. (2002). Skeletal and dental morphology of African papionins: unmasking a cryptic clade. *Journal of Human Evolution*, 42: 267-292.

Fooden, J. and Wu, H. Y. 2001. Systematic review of the Taiwanese macaque, *Macaca cyclopis* Swinhoe,1863. *Fieldiana: Zoology*, 98: 1-70.

Fossey, D. and Harcourt, H. (1977). Feeding ecology of free-ranging Mountain Gorilla (*Gorilla beringei beringei*). *In*: T. H. Clutton-Brock (eds) *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press Inc. Pages: 415-447.

Foster, K. D., Woda, A. and Peyron, M. A. (2006). Effect of texture of plastic and elastic model foods on the parameters of mastication. *Journal of Neurophysiology*, 95: 3469-3479.

Fox, E. A., van Schaik, C. P., Sitompul, A. and Wright, D. N. (2004). Intra-and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: Implications for the invention of tool use. *American Journal of Physical Anthropology*, 125: 162-174.

Fragaszy, D. M. and Boinski, S. (1995). Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology*, 109 (4): 339- 348.

Frayer, D. W. (1973). *Gigantopithecus* and its relationship to *Australopithecus*. *American Journal of Physical Anthropology*, 39: 413-426.

Freeland, W. J. (1979) Mangabey (*Cercocebus albigena*): social organization and population density in relation to food use and availability. *Folia Primatologica*, 32: 108-124.

Freeland, W. J. (1980). Mangabey (*Cerocebus albigena*) movement patterns in relation to food availability and fecal contamination. *Ecology*, 61 (6): 1297-1303.

Freeman, P. W. (1988). Frugivorous and animalivorous bats (Microchiroptera): Dental and cranial adaptations. *Biological Journal of the Linnean Society*, 33: 249-272.

Fukase, H. and Suwa, G. (2008). Growth related changes in prehistoric Jomon and modern Japanese mandibles with emphasis on cortical bone distribution. *American Journal of Physical Anthropology*, 136: 441-454.

Furuichi, T., Hashimoto, C. and Tashiro, Y. (2001). Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. *International Journal of Primatology*, 22 (6): 929-945.

Gailer, J. P., Calandra, I., Schulz-Kornas, E. and Kaiser, T. M. (2016). Morphology is not destiny: discrepancy between form, function and dietary adaptation in bovid cheek teeth. *Journal of Mammalian Evolution*, 23: 369-383.

Galbany, J., Moyà-Solà, S. and Pérez-Pérez, A. (2006). Dental microwear variability on buccal tooth enamel surfaces of extant Catarrhini and the Miocene fossil *Dryopithecus laietanus* (Hominoidea). *Folia Primatologica*, 76: 325-341.

Galbany, J. and Pérez-Pérez, A. (2004). Buccal enamel microwear variability in Cercopithecoidea primates as a reflection of dietary habits in forested and open savanna environments. *Anthropologie*, 42, 13-19.

Galat, G. and Galat-Luong, A. (1978). Diet of green monkeys in Senegal. *In*: D. J. Chivers and J. Herbert (eds) *Recent Advances in Primatology: Behaviour*. London, Academic Press. Pages 257-258.

Galdikas, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, 9 (1): 1-35.

Galetti, M., Laps, R. and Pizo, M. A. (2000). Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic forest of Brazil. *Biotropica*, 32: 842-850.

Galetti, M. & Pedroni, F. (1994). Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in south-east Brazil. *Journal of Tropical Ecology*, 10 (1): 27-39.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A. and McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, 25: 1043-1072.

Gathua, M. (2000). *Intraspecific variation in foraging patterns of Redtail monkeys* (Cercopithecus ascanius) *in the Kakamega Forest, Kenya*. PhD Thesis, Colombia University, New York.

Gaulin, S. J. C. (1979). A Jarman/ Bell model of primate feeding niches. *Human Ecology*, 7 (1): 1-20.

Gautier-Hion, A. (1978). Food niches and coexistence in sympatric primates in Gabon. *In*: D. J. Chivers and J. Herbert (eds) *Recent Advances in Primatology: Behaviour*. London, Academic Press. Pages 269-286.

Gautier-Hion, A (1980). Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology*, 49 (1): 237-269.

Gautier-Hion, A. and Michaloud, G. (1989). Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, 70 (6): 1826-1833.

Geissler, E., Daegling, D. J. and McGraw, W. S. (2018). Forest floor leaf cover as a barrier for dust accumulation in Tai National Park: implications for primate dental wear studies. *International Journal of Primatology*, 39: 633-645.

Geraads, D., Bobe, R. and Reed, K. E. (2012). Pliocene Bovidae (Mammalia) from the Hadar Formation of Hadar and Ledi-Geraru, Lower Awash, Ethiopia. *Journal of Vertebrate Paleontology*, 32 (1): 180-197.

Gilby, I. C., Eberly, L. E., Pintea, L. and Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan trologlodytes schweinfurthii*. *Animal Behaviour*, 72: 169-180.

Gilby, I. C. and Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioural Ecology and Sociobiology*, 61: 1771-1779.

Glazko, G. V. and Nei, M. (2003). Estimation of divergence times for major lineages of primate species. *Molecular Biology and Evolution*, 20 (3): 424-434.

Gogarten, J. F., Brown, L. M., Chapman, C. A., Cords, M., Doran-Sheehy, D., Fedigan, L. M., Grine, F. E., Perry, S., Pusey, A. E., Sterck, E. H. M., Wich, S. W. and Wright, P. C. (2012). Seasonal mortality patterns in non-human primates: implications for variation in selection pressures across environments. *Evolution*, 66 (10): 3252-3266.

Gogarten, J. F. and Grine, F. E. (2013). Seasonal mortality patterns in primates: implications for the interpretation of dental microwear. *Evolutionary Anthropology*, 22: 9-19.

Gómez-Posada, C. (2012). Dieta y comportamiento alimentario de un grupo de mico maicero *Cebus apella* de acuerdo a la variación en la oferta de frutos y artrópodos, en la Amazonía colombiana. *Acta Amazonica*, 42 (3): 363-372.

Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. *In*: I. deVore (eds) *Primate Behavior: Field studies of monkeys and apes*. London, Holt, Rinehart and Winston. Pages: 425-473.

Goodall, A. (1977). Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla beringei*) in the Tshibinda-Kahuzi Region (Zaire). *In* T. H. Clutton-Brock (ed), *Primate Ecology: studies of* *feeding and ranging behaviour in lemurs, monkeys and apes.* London, Academic Press. Pages: 450-479.

Gordon, A. D., Green, D. J. and Richmond, B. G. (2008). Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. *American Journal of Physical Anthropology*, 135: 311-328

Gordon, K. (1982). A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology*, 59: 195-215.

Gould, S. J. (1975). Allometry in primates, with emphasis on scaling and the evolution of the brain. *In* F. Szalay (eds). *Approaches to Primate Paleobiology (Contributions to Primatology)*. Basel, John Wiley & Sons. Pages: 244-292.

Goulson, D. and Darvill, B. (2004). Niche overlap and diet breadth in bumblebees; are rare species more specialised in their choice of flowers? *Apidologie*, 35: 55-63.

Goussard, B., Collet, J. Y., Garin, Y., Tutin, C. E. and Fernandez, M. (1983). The intestinal entodiniomorph ciliates of wild lowland gorllas (*Gorilla gorilla gorilla*) in Gabon, West Africa. *Journal of Medical Primatology*, 12 (5): 239-249.

Grabowski, M., Hatala, K. G., Jungers, W. L. and Richmond, B. G. (2015). Body mass estimates of hominin fossils and the evolution of human body size. *Journal of Human Evolution*, 85: 75-93.

Granger, D. E., Gibbon, R. J., Kuman, K., Clarke, R. J., Bruxelles, L. and Caffee, M. W. (2015). New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature*, 522: 85-88.

Greaves, W. S. (1988). Functional consequence of an ossified mandibular symphysis. *American Journal of Physical Anthropology*, 77: 53-56.

Grine, F. E. (1981). Trophic differences between "gracile" and "robust" australopithecines: a scanning electron microscope analysis of occlusal events. *South African Journal of Science*, 77: 203-230.

Grine, F. E. (1986). Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution*, 15: 783-822.

Grine, F. E. (1988). New craniodental fossils of *Paranthropus* from the Swartkrans Formation and their significance in "Robust" australopithecine evolution. *In* F. E. Grine (eds) *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter. Pages: 223-243.

Grine, F. E. (1989). New hominid fossils from the Swartkrans Formation (1979-1986 Excavations): Craniodental specimens. *American Journal of Physical Anthropology*, 79: 409-449.

Grine, F. E. (1993). Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans Formation. *In* C. K. Brain, *Swartkrans: A cave's chronicle of early man.* Pretoria, Transvaal Museum. Pages: 75-116.

Grine, F. E. and Daegling, D. J. (1993). New mandible of *Paranthropus robustus* from Member 1, Swartkrans Formation, South Africa. *Journal of Human Evolution*, 24: 319-333.

Grine, F. E. and Daegling, D. J. (2017). Functional morphology, biomechanics and the retrodiction of early hominin diets. *Comptes Rendus Palevol*, 16 (5-6): 613-631.

Grine, F. E., Judex, S., Daegling, D. J., Ozcivici, E., Ungar, P. S., Teaford, M. F., Sponheimer, M., Scott, J., Scott, R. S. and Walker, A. (2010). Craniofacial biomechanics and functional and dietary inferences in hominin paleontology. *Journal of Human Evolution*, 58: 293-308.

Grine, F. E. and Martin, L. B. (1988). Enamel thickness and development in *Australopithecus* and *Paranthropus*. *In*: F. E. Grine (eds), *Evolutionary History of the Robust Australopithecines.* New York, Aldine de Gruyter. Pages: 3-42.

Grine, F. E., Sponheimer, M., Ungar, P. S., Lee-Thorp, J. and Teaford, M. F. (2012). Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *American Journal of Physical Anthropology*, 148: 285-317.

Grine, F. E. and Strait, D. S. (1994). New hominid fossils from Member 1 “Hanging Remnant”, Swartkrans Formation, South Africa. *Journal of Human Evolution*, 26: 57-75.

Grine, F. E., Ungar, P. S. and Teaford, M. F. (2006a). Was the Early Pliocene hominin *Australopithecus anamensis* a hard object feeder? *South African Journal of Science*, 102 (7-8): 301-310.

Grine, F. E., Ungar, P. S., Teaford, M. F. and El-Zaatari, S. (2006b). Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *Journal of Human Evolution*, 51: 297-319.

Groves, C. P. and Mazák, V. (1975). An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Casopis pro mineralogii a geologii*, 20: 225-247.

Gruber, T., Clay, Z. and Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. *Animal Behaviour*, 80 (6): 1023-1033.

Grueter, C. C., Li, D., Ren, B., Wei, F., Xiang, Z. and van Schaik, C. P. (2009). Fallback Foods of temperate-living primates: a case study on Snub-Nosed monkeys. *American Journal of Physical Anthropology*, 140: 700-715.

Hafner, H., Pineau, O. and Kayser, Y. (1994). Ecological determinants of annual fluctuations in numbers of breeding little egrets (*Egretta garzetta* L.) in the Camargue, S. France. *Revue d’Ecologie (La Terre et la Vie)*, 49: 53-62.

Haile-Selassie, Y., Latimer, B. M., Alene, M., Deino, A. L, Gilbert, L., Melillo, S. M., Saylor, B. Z., Scott, G. R. and Lovejoy, O. C. (2010a). An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences*, 107 (27): 12121-12126.

Haile-Selassie, Y., Saylor, B. Z., Deino, A., Alene, M. and Latimer, B. M. (2010b). New hominid fossils from Woranso-Mille (Central Afar, Ethiopia) and Taxonomy of Early *Australopithecus*. *American Journal of Physical Anthropology*, 141: 406-417.

Ham, R. (1994). *Behaviour and ecology of grey-cheeked mangabeys (*Cercocebus albigena*) in the Lope Reserve, Gabon*. PhD thesis, University of Sterling.

Hamilton, W. J. (1985). Demographic consequences of a food and water shortage to desert chacma baboons, *Papio ursinus*. *International Journal of Primatology*, 6: 451-462.

Hanya, G. and Chapman, C. A. (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecological Research,* 28: 183-190.

Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y. and Chijiiwa, A. (2006). Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates*, 47: 275-278.

Hanya, G., Tsuji, Y. and Grueter, C. C. (2013). Fruiting and flushing phenology in Asian tropical and temperate forests: implications for primate ecology. *Primates*, 54: 101-110.

Happel, R. (1988). Seed-eating by West African Cercopithecines, with reference to possible evolution of bilophodont molars. *American Journal of Physical Anthropology*, 75: 303-327.

Harding, R. S. O. (1976). Ranging patterns of a troop of baboon (*Papio anubis*) in Kenya. *Folia Primatologica*, 25: 143-185.

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boës, X., Quinn, R. L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J-P., Leakey, L., Mortlock, R. A., Wright, J. D., Lokorodi, S., Kirwa, C., Kent, D. V. and Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, 521: 310-315.

Harris, E. F. and Smith, R. N. (2009). Accounting for measurement error: a critical but often overlooked process. *Archives of Oral Biology*, 54: 107-117.

Harris, J. M., Brown, F. H. and Leakey, M. G. (1988). *Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya.* Contributions in Science, 399, Natural History Museum of Los Angeles County.

Harris, T. R., Chapman, C. A. and Monfort, S. L. (2010). Small folivorous primate groups exhibit behavioural and physiological effects of food scarcity. *Behavioural Ecology*, 21: 46-56.

Harrison, M. J. S. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. *Animal Behaviour*, 31: 969-977.

Harrison, M. E. and Marshall, A. J. (2011). Strategies for the use of fallback foods in apes. *International Journal of Primatology*, 32: 531-565.

Harvey, P. H. and Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hay, R. L. (1987). Geology of the Laetoli area. *In* M. D. Leakey and J. M. Harris (eds) *Laetoli: A Pliocene site in Northern Tanzania*. Oxford, Clarendon Press. Pages: 23-47.

Head, J. S., Boesch, C., Makaga, L. and Robbins, M. M. (2011). Sympatric Chimpanzees (*Pan troglodytes troglodytes*) and Gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology*, 32: 755-775.

Herries, A. I. R. and Adams, J. W. (2013). Clarifying the context, dating and age range of the Gondolin hominins and *Paranthropus* in South Africa. *Journal of Human Evolution*, 65: 676-681.

Herries, A. I. R., Adams, J. W., Kuykendall, K. L. and Shaw, J. (2006). Speleology and magnetobiostratigraphic chronology of the GD2 locality of the Gondolin hominin-bearing paleocave deposits, North West Province, South Africa. *Journal of Human Evolution*, 51: 617-631.

Herries, A. I. R., Curnoe, D. and Adams, J. W. (2009). A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quaternary International*, 202: 14-28.

Herries, A. I. R., Pickering, R., Adams, J. W., Curnoe, D., Warr, G., Latham, A. G. and Shaw, J. (2013). A multi-disciplinary perspective on the age of *Australopithecus* in Southern Africa. *In* K. E. Reed, J. G. Fleagle and R. E. Leakey (eds.). *The Paleobiology of Australopithecus.* Dordrecht, Springer. Pages: 21-40.

Herries, A. I. R. and Shaw, J. (2011). Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: Implications for the age of the hominin fossils and stone tool industries. *Journal of Human Evolution*, 60: 523-539.

Hicks, T. C., Fouts, R. S. and Fouts, D. H. (2005). Chimpanzee (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *American Journal of Primatology*, 65 (3): 221-237.

Hill, R. A. and Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*, 16: 579-593.

Hillson, S. (1996). *Dental Anthropology.* Cambridge, Cambridge University Press.

Hladik, C. M. (1973). Alimentation et activité d’un groupe de Chimpanzés réintroduits en foret Gabonaise. *La Terre et la Vie*, 27: 343-413.

Hladik, C. M. (1977). Chimpanzees of Gabon and Chimpanzees of Gombe: some comparative data on the diet. *In*: T. H. Clutton-Brock (eds) *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press Inc. Pages: 481-501.

Hogue, A. S. (2008). Mandibular corpus form and its functional significance: Evidence from marsupials. *In*: C. Vinyard, M. J. Ravosa and C. E. Wall (eds.) *Primate craniofacial function and biology*. New York, Springer. Pages: 329-356.

Hohmann, G., Fowler, A., Sommer, V. and Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. *In* G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 123-160.

Holmes, M. A. and Ruff, C. B. (2011). Dietary effects on development of the human mandibular corpus. *American Journal of Physical Anthropology*, 145: 615-628.

Horn, A. D. (1987). The socioecology of the Black Mangabey (*Cercocebus aterrimus*) Near Lake Tumba, Zaire. *American Journal of Primatology*, 12: 165-180.

Hoshino, J. (1985). Feeding ecology of mandrills (*Mandrillus sphinx*) in campo animal reserve, Cameroon. *Primates*, 26 (3): 248-273.

Howell (1969). Remains of Hominidae from Pliocene/Pleistocene Formations in the Lower Omo Basin, Ethiopia. *Nature*, 223: 1234-1239.

Howell, F. C. and Coppens, Y. (1974). Inventory of remains of Hominidae from Pliocene/Pleistocene Formations of the Lower Omo Basin, Ethiopia (1967-1972). *American Journal of Physical Anthropology*, 40: 1-16.

Hunt, K. D. (1994). The evolution of human bipedality: ecology and functional morphology. *Journal of Human Evolution*, 26: 183-202.

Hunt, K. D. (1998). Ecological morphology of *Australopithecus afarensis*. *In*: E. Strasser, J. G., Fleagle, A. L. Rosenberger and H. M. McHenry. (eds) *Primate Locomotion*. Boston, Springer. Pages: 397-418.

Hunt, K. D. and McGrew, W. C. (2002). Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. *In*: C. Boesch, G. Hohmann and L. F. Marchant. (eds) *Behavioural diversity in Chimpanzees and Bonobos*. Cambridge, Cambridge University Press. Pages: 35-51.

Hylander, W. L. (1979a). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: an in vivo approach to stress analysis in the mandible. *Journal of Morphology,* 159: 253-296.

Hylander, W. L. (1979b). The functional significance of primate mandibular form. *Journal of Morphology*, 160: 223-240.

Hylander, W. L. (1984). Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. *American Journal of Physical Anthropology*, 64: 1-46.

Hylander, W. L. (1985). Mandibular function and biomechanical stress and scaling. *American Zoologist*, 25: 315-330.

Hylander W. L. (1988). Implications of *in-vivo* experiments for interpreting the functional significance of "robust" australopithecine jaws. *In* F. E. Grine (eds). *Evolutionary History of the "Robust" Australopithecines.* New York, Aldine de Gruyter. Pages: 55-83.

Hylander, W. L. and Johnson, K. R. (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *American Journal of Physical Anthropology*, 94 (4): 523-547.

Hylander, W. L., Johnson, K. R. and Crompton, A. W. (1987). Loading patterns and jaw movements during mastication in *Macaca fascicularis*: a bone-strain, electromyographic, and cineradiographic analysis. *American Journal of Physical Anthropology*, 72: 287-314.

Irish, J. D., Bailey, S. E., Guatelli-Steinberg, D., Delezene, L. K. and Berger, L. R. (2018). Ancient teeth, phonetic affinities, and African hominins: another look at where *Homo naledi* fits in. *Journal of Human Evolution*, 122: 108-123.

Irwin, M. T., Raharison, J-L., Raubenheimer, D., Chapman, C. A. and Rothman, J. M. (2014). Nutritional correlates of the "lean season": effects of seasonality and frugivory on the nutritional ecology of Diademed Sifakas. *American Journal of Physical Anthropology*, 153: 78-91.

Isbell, L. A. (1998). Diet for a small primate: Insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). *American Journal of Primatology*, 45: 381-398.

Isbell, L. A., Pruetz, J. D. and Young, T. P. (1998). Movements of Vervets (*Cercopithecus aethiops*) and Patas Monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology*, 42 (2): 123-133.

Isbell, L. A., Rothman, J. M., Young, P. J. and Rudolph, K. (2013). Nutritional benefits of *Crematogaster mimosa* ants and *Acacia drepanolobium* gum for patas monkeys and vervets in Laikipia, Kenya. *American Journal of Physical Anthropology*, 150: 286-300.

Izawa, K. (1979). Foods and feeding behavior of wild black-capped capuchin (*Cebus apella*). *Primates*, 20: 57-76.

Izawa, K. and Mizuno, A. (1977). Palm-fruit cracking behaviour of wild Black-capped capuchin (*Cebus apella*). *Primates*, 18 (4): 773-792.

Jack, K. M. (2011). The Cebines: toward an explanation of variable social structure. *In*, C. Campbell, A. Fuentes, K. MacKinnon, S, Bearder and R. Stumpf (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 108-121.

Jaffe, K. E. and Isbell, L. A. (2011).The Guenons: polyspecific associations in socioecological perspective. *In*, C. Campbell, A. Fuentes, K. MacKinnon, S, Bearder and R. Stumpf (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 277-299.

Johanson, D. C., Lovejoy, O. C., Kimbel, W. H., White, T. D., Ward, C., Bush, M. E., Latimer, B. M. and Coppens, Y. (1982c). Morphology of the Pliocene Partial Hominid Skeleton (A.L. 288.1) from the Hadar Formation, Ethiopia. *American Journal of Physical Anthropology*, 57: 403-451.

Johanson, D. C., Taieb, M. and Coppens, Y. (1982a). Pliocene hominids from the Hadar Formation: Ethiopia (173-1977): Stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *American Journal of Physical Anthropology*, 57: 373-402.

Johanson, D. C., White, T. D. and Coppens, Y. (1978). A new species of the genus *Australopithecus* (Primates; Hominidae) from the Pliocene of Eastern Africa. *Kirtlandia*, 28: 1-14.

Johanson, D. C., White, T. D. and Coppens, Y. (1982b). Dental remains from the Hadar Formation, Ethiopia: 1974 - 1977 Collections. *American Journal of Physical Anthropology*, 57: 545-603.

Jolly, C. J. (1970). The Seed-Eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, 5 (1): 5-26.

Jones, C., Jones, C. A., Jones, J. K. Jr. and Wilson, D. E. (1996). *Pan troglodytes*. *American Society of Mammologists*, 529: 1-9.

Kaiser, H. (1974). An index of factor simplicity. *Psychometrika*, 39: 31-36.

Kamilar, J. M. and Cooper, N. (2013). Phylogenetic signal in primate behavior, ecology, and life history. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368, 20120341.

Kanamori, T., Kuze, N., Bernard, H., Malim, T. P. and Kohshima, S. (2010). Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malaysia: a 3-year record including two mast fruitings. *American Journal of Primatology*, 72: 820-840.

Kanazawa, E. and Rosenberger, A. L. (1989). Interspecific allometry of the mandible, dental arch, and molar area in anthropoid primates: functional morphology of masticatory components. *Primates*, 30 (4): 543-560.

Kano, T. (1982). An ecological study of the Pygmy Chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology*, 4 (1): 1-31.

Kano, T. and Mulavwa, M. (1984). Feeding ecology of the Pygmy Chimpanzee (*Pan paniscus*) of Wamba. *In*: R. Susman (eds) *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. London, Plenum Press. Pages: 233-273.

Kay, R. F. (1975). The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology*, 43: 195-216.

Kay, R. (1981). The Nut-Crackers – a new theory of the adaptations of the Ramapithecinae. *American Journal of Physical Anthropology*, 55: 141-151.

Kay, R. F. and Grine, F. E. (1988). Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from southern Africa. *In* F. E. Grine (Ed), *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter. Pages: 427-447.

Keyser, A. W. (2000). The Drimolen Skull: the most complete australopithecine cranium and mandible to date. *South African Journal of Science*, 96: 189-193.

Keyser, A. W., Menter, C. G., Moggi-Cecchi, J., Pickering, T. R. and Berger, L. R. (2000). Drimolen: a new hominid-bearing site in Gauteng, South Africa. *South African Journal of Science*, 96: 193-197.

Kimbel, W. H. and Delezene, L. K. (2009). "Lucy" redux: A review of research on *Australopithecus afarensis*. *Yearbook of Physical Anthropology*, 52: 2–48.

Kimbel, W. H., Johanson, D. C. and Rak, Y. (1994). The first skull and other new discoveries of *Australopithecus afarensis* in Hadar, Ethiopia. *Nature*, 368: 449-451.

Kimbel, W. H., Johanson, D. C. and Rak, Y. (1997). Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *American Journal of Physical Anthropology*, 103: 235-262.

Kimbel, W. H., Rak, Y. and Johanson, D. C. (2004). Elements of the Disarticulated Skull. *In*: W. H. Kimbel, Y. Rak, D. C. Johanson, R. L. Holloway and M. S. Yuan (eds), *The Skull of Australopithecus afarensis*. New York, Oxford University Press. Pages: 136-209.

Kimbel, W. and White, T. (1988). Variation, sexual dimorphism and the taxonomy of *Australopithecus*. *In* F. E. Grine (Ed), *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter. Pages: 175-192.

King, S. J., Arrigo-Nelson, S. J., Pochron, S. T., Semprebon, G. M., Godfrey, L. R., Wright, P. C. and Jernvall, J. (2005). Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences*, 102: 16579-16583.

King, T., Aiello, L. C. and Andrews, P. (1999). Dental microwear of *Griphopithecus alpani*. *Journal of Human Evolution*, 36: 3-31.

Kinzey, W. G. (1978). Feeding behaviour and molar features in two species of Titi monkey. *In* D. J. Chivers and J. Herbert (eds) *Recent Advances in Primatology: Behaviour*. London, Academic Press. Pages: 373-385.

Kinzey, W. G. (1992). Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology*, 88: 499-514.

Kinzey, W. G. (1997). *New World Primates: Ecology, evolution, and behaviour*. Aldine de Gruyter, New York.

Kinzey, W. G. and Norconk, M. A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, 81: 5-15.

Kinzey, W. G. and Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology*, 14 (2): 207-227.

Kissel, M. and Hawks, J. (2015). What are the Lothagam and Tabarin Mandibles? *PaleoAnthropology*, 2015: 37-43.

Klien, R. G. (2013). Stable carbon isotopes and human evolution. *Proceedings of the National Academy of Sciences*, 110 (26): 10470-10472.

Knapp, T. R. (1992). Technical Error of Measurement: A methodological critique. *American Journal of Anthropology*, 87: 235-236.

Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*, 19 (6): 1061-1079.

Knott, C. D. and Kahlenberg, S. M. (2011). Orangutans: understanding forced copulations. *In*, C. Campbell, A. Fuentes, K. MacKinnon, S, Bearder and R. Stumpf (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 313-325.

Kovarovic, K. and Andrews, P. (2007). Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *Journal of Human Evolution*, 52: 663-680.

Kovarovic, K., Andrews, P. and Aiello, L. (2002). The palaeoecology of the Upper Ndolanya Beds at Laetoli, Tanzania. *Journal of Human Evolution*, 43: 395-418.

Koyabu, D. B. and Endo, H. (2009). Craniofacial variation and dietary adaptations of African colobines. *Journal of Human Evolution*, 56: 525-536.

Kramer, A. (1986). Hominid-Pongid distinctiveness in the Miocene-Pliocene fossil record: the Lothagam mandible. *American Journal of Physical Anthropology*, 70: 457-473.

Krigbaum, J., Berger, M. H., Daegling, D. J. and McGraw, W. S. (2013). Stable isotope canopy effects for sympatric monkeys at Taï Forest, Côte d'Ivoire. *Biology Letters*, 9: 20130466.

Krishnamani, R. (1994). Diet composition of the Bonnet Macaque (*Macaca radiata*) in a tropical dry evergreen forest of Southern India. *Tropical Biodiversity*. 2 (2): 285-302.

Kullmer, O., Sandrock, O., Abel, R., Schrenk, F., Bromage, T. G. and Juwayeyi, Y. M. (1999). The first *Paranthropus* from the Malawi Rift. *Journal of Human Evolution*, 37: 121-127.

Kullmer, O., Sandrock, O., Viola, T. B., Hujer, W., Said, H. and Seidler, H. (2008). Suids, elephantoids, paleochronology, and paleoecology of the Pliocene hominid site Galili, Somali Region, Ethiopia. *PALAIOS*, 23: (7/8): 452-464.

Kumar, S., Filipski, A., Swarna, V., Walker, A. and Hedges, S. B. (2005). Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proceedings of the National Academy of Sciences*, 102 (52): 18842-18847.

Kunz, B. K. and Linsenmair, K. E. (2008). Diet and behavioural ecology of Olive Baboons in the Comoé National Park. *Folia Primatologica*, 79: 31-51.

Kunz, B. K. and Linsenmair, K. E. (2010). Fruit traits in baboon diet: A comparison with plant species West Africa. *Biotropica*, 42 (3): 363-371.

Kuroda, S., Nishihara, T., Suzuki, S. and Oko, R. A. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. *In*: W. C. McGrew, L. F. Marchant and T. Nishida (eds), *Great Ape Societies*. Cambridge, Cambridge University Press. Pages; 71-81.

Kuykendall, K. L. and Conroy, G. C. (1999). Description of the Gondolin teeth: Hyper-robust hominids in South Africa? *American Journal of Physical Anthropology*, 108: 176.

Laden, G. and Wrangham, R. (2005). The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution*, 49: 482-498.

Lahm, S. A. (1986). Diet and habitat preference of *Mandrillus sphinx* in Gabon: Implications of foraging strategy. *American Journal of Primatology*, 11: 9-26.

Lambert, J. E. (1999). Seeding handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, 109: 365-386.

Lambert, J. E. (2002). Resource switching and species coexistence in Guenons: a community analysis of dietary flexibility. *In*: M. E. Glenn and M. Cords (eds) *The Guenons: Diversity and adaptation in African Monkeys*. London, Kluwer Academic/ Plenum Publishers. Pages: 309-324.

Lambert, J. E. (2007). Seasonality, fallback strategies, and natural selection: a chimpanzee and Cercopithecoid model for interpreting the evolution of the hominin diet. *In* P. S. Ungar (ed). *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford, Oxford University Press. Pages: 324-343.

Lambert, J. E. (2009). Summary to the symposium issue: primate fallback strategies as adaptive phenotypic plasticity – scale, pattern, and process. *American Journal of Physical Anthropology*, 140: 759-766.

Lambert, J. E., Chapman, C. A., Wrangham, R. W. and Conklin-Brittain, N. L. (2004). Hardness of Cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, 125: 363-368.

Lambert, J. E. and Rothman, J. M. (2015). Fallback Foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. *Annual Reviews of Anthropology*, 44: 493-512.

Langergraber, K. E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Muruyama, M., Mitani, J. C., Muller, M. N., Robbins, M. M., Schubert, G., Stoinski, T. S., Viola, B., Watts, D., Wittig, R. M., Wrangham, R. W., Zuberbühler, K., Pääbo, S. and Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences*, 109 (39): 15716-15721.

Lappan, S. (2009). Flowers are an important food for small apes in southern Sumatra. *American Journal of Primatology*, 71: 624-635.

Larson, J. R., Manyama, M. F., Cole, J. B., Gonzalez, P. N., Percival, C. J., Liberton, D. K., Ferrera, T. M., Riccardi, S. L., Kinwaga, E. A., Mathayo, J., Spitzmacher, J. A., Rolian, C., Jamniczky, H. A., Weinberg, S. M., Roseman, C. C., Klein, O., Lukowiak, K., Spritz, R. A. and Hallgrimsson, B. (2018). Body size and allometric variation in facial shape in children. *American Journal of Physical Anthropology,* 165: 327-342.

Leakey, L. S. B. (1959). A new fossil skull from Olduvai. *Nature*, 184 (4685): 491-493.

Leakey, L. S. B., Tobias, P. V. and Napier, J. R. (1964). A new species of the genus *Homo* from Olduvai Gorge. *Nature,* 202: 7-9.

Leakey, M. D. (1971). *Olduvai Gorge*. *Volume 3: Excavations in Beds I and II, 1960-1963.* London, Cambridge University Press.

Leakey, M. D. and Hay, R. L. (1979). Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. *Nature*, 278: 317-323.

Leakey, M. G., Feibel, C. S., Bernor, R. L., Harris, J. M., Cerling, T. E., Stewart, K. M., Storrs, G. W., Walker, A., Werdelin, L. and Winkler, A. J. (1996). Lothagam: a record of faunal change in the late Miocene of East Africa. *Journal of Vertebrate Paleontology*, 16 (3): 556-570.

Leakey, M. G., Feibel, C. S., McDougall, I. and Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376: 565-571.

Leakey, M. G., Feibel, C. S., McDougall, I., Ward, C. and Walker, A. (1998). New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature*, 393, 62-66.

Leakey, M. G., Spoor, F., Brown, F. H., Gathogo, P. N., Kiarie, C., Leakey, L. N. McDougall, I. (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature*, 410: 433-440.

Leakey, M. G., Spoor, F., Dean, M. C., Feibel, C. S., Antón, S. C., Kiarie, C. and Leakey, L. N. (2012). New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature*, 488: 201-204.

Leakey, M. G. and Walker, A. C. (2003). The Lothagam hominids. *In* M. G. Leakey and J. M. Harris (eds.), *Lothagam: The dawn of humanity in Eastern Africa.* New York, Columbia University Press. Pages: 249–257.

Leakey, R. E. F. and Walker, A. C. (1985). Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *American Journal of Physical Anthropology*, 67: 135-163.

Leakey, R. E. F. and Walker, A. C. (1988). New *Australopithecus boisei* specimens from East and West Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 76: 1-24.

Leakey, R. E. F. and Wood, B. A. (1973). New evidence of the Genus *Homo* from East Rudolf, Kenya. (II). *American Journal of Physical Anthropology*, 39: 355-368.

Leakey, R. E. F. and Wood, B. A. (1974). New evidence of the Genus *Homo* from East Rudolf, Kenya. (IV). *American Journal of Physical Anthropology*, 41: 237-244.

Lee, J. J.-W., Morris, D., Constantino, P. J., Lucas, P. W., Smith, T. M. and Lawn, B. R. (2010). Properties of tooth enamel in great apes. *Acta Biomaterialia*, 6: 4560-4565.

Lee, P. C. and Hauser, M. D. (1998). Long-term consequences of changes in territory quality on feeding and reproductive strategies of Vervet Monkeys. *Journal of Animal Ecology*, 67 (3): 347-358.

Lee-Thorp, J. (2011). The demise of ‘The Nutcracker Man’. *Proceedings of the National Academy of Sciences*, 108 (23): 9319-9320.

Lee-Thorp, J., Sealy, J. C. and van der Merwe, N. J. (1989). Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*, 16 (6): 585-599.

Lee-Thorp, J. A., Sponheimer, M., Passey, B. H., de Ruiter, D. J. and Cerling, T. E. (2010). Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365: 3389–3396.

Lee-Thorp, J., Thackeray, J. F. and van der Merwe, N. J. (2000). The hunters and the hunters revisited. *Journal of Human Evolution*, 39: 565-576.

Lee-Thorp, J., van der Merwe, N. J. and Brain, C. K. (1994). Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *Journal of Human Evolution*, 27: 361-372.

Leigh, S. R. (1995). Socioecology and the ontogeny of sexual size dimorphism in Anthropoid Primates. *American Journal of Physical Anthropology*, 97: 339-356.

Leuteneger, W. (1982). Scaling of sexual dimorphism in body weight and canine size in primates. *Folia Primatologica*, 37: 163-176.

Levin, N. E., Haile-Selassie, Y., Frost, S. R. and Saylor, B. Z. (2015). Dietary change among hominins and cercopithecids in Ethiopia during the early Pliocene. *Proceedings of the National Academy of Science*, 112 (40): 12304-12309.

Lieberman, D. E., Krovitz, G. E., Yates, F. W., Devlin, M. and Claire, M. (2004). Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *Journal of Human Evolution*, 46: 655-677.

Liem , K. F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of Cichlid fishes. *American Zoologist*, 20 (1): 295-314.

Liem, K. F. and Summers, A. P. (2000). Integration of versatile functional design, population ecology, ontogeny and phylogeny. *Netherlands Journal of Zoology*, 50 (2): 245-259.

Lin, Y. S., Lu, J. F. and Lee, L. L. (1988). *The study on the population and habitat use of Formosan macaques in Nanshi Logging Road in Yushan National Park*. Yushan Naitonal Park Publications, Nantou, Taiwan. Cited in: Su, H-H. and Lee, L-L. (2001). Food habits of Formosan Rock Macaques (*Macaca cyclopis*) in Jentse, Northeastern Taiwan, assessed by fecal analysis and behavioral observation. *International Journal of Primatology*, 22 (3): 359-377.

Linder, H. P. (2017). East African Cenozioc vegetation history. *Evolutionary Anthropology*, 26: 300-312.

Lockwood, C. A. (1999). Sexual dimorphism in the face of *Australopithecus africanus. American Journal of Physical Anthropology*, 108:97–127.

Lockwood, C. A., Menter, C. G., Moggi-Cecchi, J. and Keyser, A. W. (2007). Extended male growth in a fossil hominin species. *Science*, 318: 1443-1446.

Loudon, J. E., Grobler, J. P., Sponheimer, M., Moyer, K., Lorenz, J. G. and Turner, T. R. (2014). Using the stable carbon and nitrogen isotope compositions of Vervet Monkeys (*Chlorocebus pygerythrus*) to examine questions in ethnoprimatology. *PLoS ONE*, 9 (7): e100758.

Loudon, J. E., Sandberg, P. A., Wrangham, R. W., Fahey, B. and Sponheimer, M. (2016). The stable isotope ecology of *Pan* in Uganda and beyond. *American Journal of Primatology*, 78: 1070-1085.

Louys, J., Ditchfield, P., Meloro, C., Elton, S. and Bishop, L. (2012). Stable isotopes provide independent support for the use of mesowear variables for inferring diets in African antelopes. *Proceedings of the Royal Society, B*, 279: 4441-4446.

Louys, J., Meloro, C., Elton, S., Ditchfield, P. and Bishop, L. (2011). Mesowear as a mean of determining diets in African antelopes. *Journal of Archaeological Science*, 38: 1485-1495.

Louys, J., Meloro, C., Elton, S., Ditchfield, P. and Bishop, L. (2015a). The potential and pitfalls of using simple dental metrics to infer the diets of African antelopes (Mammalia: Bovidae). *Palaeontologia africana*, 49: 8-24.

Louys, J., Meloro, C., Elton, S., Ditchfield, P. and Bishop, L. (2015b). Analytical framework for reconstructing heterogeneous environmental variables from mammal community structure. *Journal of Human Evolution*, 78: 1-11.

Lucas, P. W. (1979). The dental-dietary adaptations of mammals. *Neues Jahrbuch für Geologie und Paläontologie*, 8: 486-512.

Lucas, P. W. (2004). *Dental Functional Morphology: How Teeth Work*. Cambridge, Cambridge University Press.

Lucas, P. W., Constantino, P. J. and Wood, B. A. (2008b). Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade. *Journal of Anatomy*, 212: 486-500.

Lucas, P. W., Constantino, P., Wood, B. and Lawn, B. (2008a). Dental enamel as a dietary indicator in mammals. *BioEssays*, 30: 374-385.

Lucas, P. W., Copes, L., Constantino, P. L., Vogel, E. R. Chalk, J., Talebi, M., Landis, M. and Wagner, M. (2012). Measuring the toughness of primate foods and its ecological value. *International Journal of Primatology*, 33 (3): 598-610.

Lucas, P. W. and Luke, D. A. (1984). Chewing it over – basic principles of food breakdown. *In*: D. J. Chivers, B. A. Wood and A. Bilsborough (eds), *Food Acquisition and Processing in Primates*, New York, Plenum Press. Pages 283-302.

Lucas, P. W. and Teaford, M. (1994). Functional morphology of colobine teeth. *In*: A. G. Davies and J. F. Oates (eds), *Colobine monkeys: Their Ecology, Behaviour and Evolution*. Cambridge, Cambridge University Press. Pages 173-203.

Macho, G. (2004). On the scaling relationship between enamel prism length and enamel thickness in primate molars: a comment. *Annals of Anatomy*, 186: 413-416.

Macho, G. (2014). Baboon feeding ecology informs the dietary niche of *Paranthropus boisei*. *PLOS One*, 9 (1): e84942.

Macho, G. A. and Shimizu, D. (2009). Dietary adaptations of South African australopiths: inference from enamel prism attitude. *Journal of Human Evolution*, 57: 241-247.

Macho, G. A. and Spears, I. R. (1999). Effects of loading on the biomechanical behaviour of molars of *Homo, Pan,* and *Pongo*. *American Journal of Physical Anthropology*, 109: 211-227.

Macho, G. A., Leakey, M. G., Williamson, D. K. and Jiang, Y. (2003). Palaeoenvironmental reconstruction: evidence for seasonality at Allia Bay, Kenya, at 3.9 million years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199: 17-30.

MacKinnon, J. (1971). The Orangutan in Sabah today. *Oryx*, XI (2): 234-242.

MacKinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour*, 22: 3-74.

Madrigal, L. (1998). *Statistics for anthropology*. Cambridge, Cambridge University Press.

Makkar, H. P. S., Siddhuraju, P. and Becker, K. (2007). *Plant Secondary Metabolites*. New Jersey, Humana Press.

Markic, G., Müller, L., Patcas, R., Roos, M., Lochbühler, N., Peltomäki, T., Karlo, C. A., Ullrich, O. and Kellenberger, C. J. (2015). Assessing the length of the mandibular ramus and the condylar process:

a comparison of OPG, CBCT, CT, MRI, and lateral cephalometric measurements. *European Journal of Orthodontics*, 37 (1): 13-21

Marshall, A. J., Boyko, C. M. Feilen, K. L., Boyko, R. H. and Leighton, M. (2009). Defining Fallback Foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, 140: 603-614.

Marshall, A. and Leighton, M. (2006). How does food availability limit the population density of white-bearded gibbons? *In* G. Hohmann, M. M. Robbins and C. Boesch (eds), *Feeding Ecology in Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 313-335.

Marshall, A. J. and Wrangham, R. W. (2007). Evolutionary consequences of Fallback Foods. *International Journal of Primatology*, 28: 1219-1235.

Martinez-Maza, C., Freidline, S. E., Strauss, A. and Nieto-Diaz, M. (2016). Bone growth dynamics of the facial skeleton and mandible in *Gorilla gorilla* and *Pan troglodytes*. *Evolutionary Biology*. 43: 60-80.

Masi, S., Cipolletta, C. and Robbins, M. M. (2009). Western Lowland Gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology*, 71: 91-100.

Matsumoto-Oda, A. and Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica*, 70: 154-162.

Matthews, L. J. (2009). Activity patterns, home range size, and intergroup encounters in *Cebus albifrons* support existing models of Capuchins socioecology. *International Journal of Primatology*, 30: 709-728.

Mbua, E., Kusaka, s., Kunimatsu, Y., Geraads, D., Sawada, Y., Brown, F. H., Sakai, T., Boisserie, J-R., Saneyoshi, M., Omuombo, C., Muteti, S., Hirata, T., Hayashida, A., Iwano, H., Danhara, T., Bobe, R., Jicha, B. and Nakatsukasa, M. (2016). Kantis: A new *Australopithecus* site on the shoulders of the Rift Valley near Nairobi, Kenya. *Journal of Human Evolution*, 94: 28-44.

McGraw, W. S. (1998). Posture and support use of Old World Monkeys (Cercopithecidae): The influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items. *American Journal of Primatology*, 46: 229-250.

McGraw, W. S. and Daegling, D. J. (2012). Primate feeding and foraging: integrating studies of behavior and morphology. *Annual Review of Anthropology*, 41: 203-219.

McGraw, W. S., van Casteren, A., Kane, E., Geissler, E., Burrows, B. and Daegling, D. J. (2016). Feeding and oral processing behaviours of two colobine monkeys in Tai Forest, Ivory Coast. *Journal of Human Evolution*, 98: 90-102.

McGraw, W. S. and Fleagle, J. G. (2006). Biogeography and evolution of the *Cercocebus-Mandrillus* clade: evidence from the face. *In* S. M. Lehman and J. G. Fleagle (eds) *Primate Biogeography: Progress and Prospects.* New York, Springer Verlag. Pages: 201-204.

McGraw, S. W., Pampush, J. D. and Daegling, D. J. (2012). Brief communication: enamel thickness and durophagy in mangabeys revisited. *American Journal of Physical Anthropology*, 147 (2): 326-333.

McGraw, W. S., Vick, A. E. and Daegling, D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, 144: 140-153.

McGraw, W. S., Vick, A. E. and Daegling, D. J. (2014). Dietary variation and food hardness in Sooty Mangabeys (*Cercocebus atys*): implications for foods and dental adaptation. *American Journal of Physical Anthropology*, 154 (3): 413-423.

McGraw, W. S. and Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. *In*: W. S. McGraw, K. Zuberbühler and R. Noe (eds), *Monkeys of the Tai Forest: An African Primate Community*. Cambridge, Cambridge University Press. Pages: 1-48.

McGrew, W. C., Baldwin, P. J. and Tutin, C. E. G. (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: 1 Composition. *American Journal of Primatology*, 16 (3): 213-226.

McGrew, W. C. (1992). *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.

McGrew, W. C., Marchant, L. F. and Nishida, T. (1996). Appendix: great ape study sites. *In*: W. C. McGrew, L. F. Marchant, and T. Nishida (eds), *Great Ape Societies*. Cambridge, Cambridge University Press. Pages: 309-320.

McHenry, H. M. (1988). New estimates of body weight in early hominids and their significance to encephalisation and megadontia in robust Australopithecines. *In* F. E. Grine (ed), *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter. Pages: 133-148.

McHenry, H. M. (1991a). Sexual dimorphism in *Australopithecus afarensis*. *Journal of Human Evolution*, 20: 21-32.

McHenry, H. M. (1991b). The petite bodies of the "robust" australopithecines. *American Journal of Physical Anthropology*, 86: 445-454.

McHenry, H. M. (1992). Body size and proportions in early hominids. *American Journal of Physical Anthropology*, 87: 407-431.

McHenry, H. M. and Berger, L. R. (1998). Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *Journal of Human Evolution*, 35: 1-22.

McHenry, H. M. and Coffing, K. (2000). *Australopithecus* to *Homo*: transformations in body and mind. *Annual Reviews of Anthropology*, 29: 125-146.

McHenry, L. J. (2012). A revised stratigraphic framework for Olduvai Gorge Bed I based on tuff geochemistry. *Journal of Human Evolution*, 63: 284-299.

McKillup, S. (2012). *Statistics Explained: an introductory guide for life scientists*. Cambridge, Cambridge University Press.

McKinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (*Cebus capucinus*). *American Journal of Primatology*, 73: 439-448.

McLennan, M. (2011). Tool-use to obtain honey by chimpanzees at Bulindi: new record from Uganda. *Primates*, 52 (4): 315-322.

McLennan, M. R. (2013). Diet and feeding ecology of Chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging strategies at the forest–farm interface. *International Journal of Primatology*, 34: 585-614.

Mehlman, P. T. (1988). Food resources of the wild Barbary Macaque (*Macaca sylvanus*) in high-altitude fir forest, Ghomaran Rif, Morocco. *Journal of Zoology*, 214: 469-490.

Melin, A. D., Young, H. C., Mosdossy, K. N. and Fedigan, L. M. (2014). Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. *Journal of Human Evolution*, 71: 77-86.

Meloro, C., Cáceres, N. C., Carotenuto, F., Sponchiado, J., Melo, G. L., Passaro, F. and Raia, P. (2015). Chewing on the trees: constraints and adaptation in the evolution of the primate mandible. *Evolution*, 69: 1690-1700.

Ménard, N. (1985). Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: I. – Régime en chênaie décidue. *Reviews of Ecology (Terre Vie)*, 40: 451-466.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., Vallet, D., Qarro, M., Tattou, M. I. and Pierre, J-S. (2014). Effect of habitat quality on diet flexibility in Barbary Macaques. *American Journal of Primatology*, 76: 679-693.

Ménard, N. and Vallet, D. (1986). Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: II. – Régime en forêt sempervirente et sur les sommes rocheux. *Reviews of Ecology (Terre Vie)*, 41: 173-192.

Millet, S. F., White, J. L. and Ciochon, R. L. (2008). Assessing mandibular shape variation within *Gigantopithecus* using a geometric morphometric approach. *American Journal of Physical Anthropology*, 137: 201-212.

Mills, L. S., Soulé, M. E. and Doak, D. F. (1993). The Keystone-Species concept in ecology and conservation. *American Institute of Biological Sciences*, 43 (4): 219-224.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, 114 (3): 362-378.

Milton, K. (1984). The role of food-processing factors in primate food choice. *In* P. S. Rodman, and J. G. H. Cant (eds), *Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys, and apes*. New York, Colombia University Press. Pages: 249-279.

Milton, K. (1993). Diet and Primate Evolution. *Scientific American*, 269 (2): 86-93.

Mitani, M. (1989). *Cercocebus torquatus:* adaptive feeding and ranging behaviours related to seasonal fluctuations of food resources in the tropical rain forest of South-western Cameroon. *Primates*, 30 (3): 307-323.

Mittermeier, R. A. and van Roosmalen, M. G. M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatologica*, 36: 1-39.

Mitteroecker, P., Gunz, P., Bernhard, M., Schaefer, K. and Bookstein, F. L. (2004). Comparison of cranial ontogenetic trajectories among great apes and humans, *Journal of Human Evolution*, 46: 679-698.

Moggi-Cecchi, J., Grine, F. E. and Tobias, P. V. (2006). Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966-1996 excavations): Catalogue, individual associations, morphological descriptions and initial metrical analysis. *Journal of Human Evolution*, 50: 239-328.

Moggi-Cecchi, J., Menter, C., Boccone, S. and Keyser, A. (2010). Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa. *Journal of Human Evolution*, 58: 374-405.

Moggi-Cecchi, J., Tobias, P. V. and Beynon, A. D. (1998). The mixed dentition and associated skull fragments of a juvenile fossil hominid from Sterkfontein, South Africa. *American Journal of Physical Anthropology*, 106: 425-465.

Montaña, C. G. and Winemiller, K. O. (2013). Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. *Biological Journal of the Linnean Society*, 109: 146-164.

Morgan, D. and Sanz, C. (2006). Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. *In*: G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 97-122.

Morrogh-Bernard, H. C., Husson, S. K., Knott, C. D., Wich, S. A., van Schaik, C. P., van Noordwijk, M. A., Lackman-Ancrenaz, I., Marshall, A. J., Kanamori, T., Kuze, N. and bin Sakong R. (2009). Orangutan activity budgets and diet. *In*: S. A. Wich, S. S. U. Atmoko, T. M. Setia and C. P. van Schaik (eds), *Geographic variation in behavioral ecology and conservation.* Oxford, Oxford University Press. Pages: 119-134.

Mosdossy, K. N., Melin, A. D. and Fedigan, L. M. (2015). Quantifying seasonal fallback on invertebrates, pith, and bromeliad leaves by White-Faced Capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. *American Journal of Physical Anthropology*, 158: 67-77.

Muchlinski, M. N. (2010). Ecological correlates of infraorbital foramen area in primates. *American Journal of Physical Anthropology*, 141: 131-141.

Muri, H. (1999). Weather situation, aspects of reproduction and population density in roe deer (*Capreolus capreolus* L.). *Zeitschrift für Jagdwissenschaft*, 45: 88-95.

Musiba, C., Magori, C., Stoller, M., Stein, T., Branting, S., Vogt, M., Tuttle, R., Hallgrimsson, B., Killindo, S., Mizambwa, F., Ndunguru, F. and Mabulla, A. (2007). Taphonomy and paleoecological context of the Upper Laetoli Beds (Localities 8 and 9), Laetoli in northern Tanzania. *In* R. Bobé, Z. Alemseged, and A. K. Behrensmeyer (eds), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence.* Netherlands, Springer. Pages: 257-278.

Myers-Thompson, J. A. (2002). Bonobos of the Lukuru wildlife research project. *In*: C. Boesch, G. Hohmann and L. F. Marchant (eds), *Behavioural diversity in Chimpanzees and Bonobos*. Cambridge, Cambridge University Press. Pages: 61-70.

Nakagawa, N. (1989). Activity budget and diet of Patas Monkeys in Kala Maloue National Park, Cameroon: a preliminary report. *Primates.* 30 (1): 27-34.

Nakagawa, N. (2000). Foraging energetics in patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*): implications for reproductive seasonality. *American Journal of Primatology*, 52: 169-185.

Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology,* 37: 344-354.

Nishida, T. (1976). The bark-eating habits in Primates, with special reference to their status in the diet of wild chimpanzees. *Folia Primatologica*, 25: 277-287.

Nishida, T. and Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *African Study Monographs,* 3: 109-130.

Nishida, T., Wrangham, R. W., Goodall, J. and Uehara, S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution*, 12: 467-480.

Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabalé-Ndoki National Park, Congo. *Primates*, 36 (2): 151-168.

Norconk, M. A. and Veres, M. (2011). Physical properties of fruit and seeds ingested by primate seed predators with emphasis on Sakis and Bearded Sakis. *The Anatomical Record*, 294: 2092-2111.

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L. and Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in Platyrrhine dietary adaptations. *In*: P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, and K. B. (eds.), *South American Primates:*

comparative perspectives in the study of behavior, ecology, and conservation. New York, Springer. Pages: 279-319.

Norris, J. (1988). Diet and feeding behavior of semi-free ranging mandrills in an enclosed Gabonais forest. *Primates*, 29 (4): 449-463.

Norton, G. W., Rhine, R. J., Wynn, G. W. and Wynn, R. D. (1987). Baboon diet: a five-year study of stability and variability in the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Folia Primatologica*, 48 (1-2): 78-120.

Nystrom, P. and Ashmore, P. (2008). *The life of primates*. Pearson Prentice Hall, New Jersey.

Nystrom, P., Phillips-Conroy, J. E. and Jolly, C. J. (2004). Dental microwear in anubis and hybrid baboons (*Papio hamadryas*, sensu lato) living in Awash National Park, Ethiopia. *American Journal of Physical Anthropology*, 125: 279-291.

Oakley, K. P., Campbell, B. G. and Molleson, T. I. (1977). *Catalogue of Fossil Hominids: Africa*. London, British Museum (Natural History).

Oelze, V. M. (2016). Reconstructing temporal variation in great ape and other primate diets: A methodological framework for isotope analyses in hair. *American Journal of Primatology*, 78: 1004–1016.

Oelze, V. M., Fuller, B. T., Richards, M. P., Fruth, B., Surbeck, M., Hublin, J.-J. and Hohmann, G. (2011). Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. *Proceedings of the National Academy of Sciences*, 108 (24): 9792–9797.

Oelze, V. M., Head, J. S., Robbins, M. M., Richards, M. and Boesch, C. (2014). Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. *Journal of Human Evolution*, 66: 95-106.

Okecha, A. A. and Newton-Fisher, N. E. (2006). The diet of Olive Baboons (*Papio anubis*) in the Budongo Forest Reserve, Uganda. *In*: N. E. Newton-Fisher, H. Notman, J. D. Paterson, and V. Reynolds (eds), *Primates of Western Uganda*. New York, Springer. Pages: 61-73.

Olejniczak, A. J., Smith, T. M., Wang, W., Potts, R., Ciochon, R., Kullmer, O., Schrenk, F. and Hublin, J.-J. (2008) Molar enamel thickness and dentine horn height in *Gigantopithecus blacki*. *American Journal of Physical Anthropology*, 135: 85-91.

Olupot, W., Chapman, C. A., Waser, P. M. and Isabirye–Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, 43: 65-78.

O'Malley, R. C. and Power, M. L. (2014). The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution*, 71: 46-58.

Osborn, H. F. (1888). The evolution of the mammalian molars to and from the tritubercular type. *American Naturalist*, 22: 1067-1079.

Osborne, J. W. (2002). The effects of minimum values on data transformations. *Annual Meeting of the American Educational Research Association, held in New Orleans.*

Owens, J. R., Honarvar, S., Nessel, M. and Hearn, G. W. (2015). From frugivore to folivore: Altitudinal variations in the diet and feeding ecology of the Bioko Island Drill (*Mandrillus leucophaeus poensis*). *American Journal of Primatology*, 77: 1263-1275.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103 (929): 91-93.

Paine, O. C. C., Koppa, A., Henry, A. G., Leichliter, J. N., Codron, D., Codron, J., Lambert, J. E. and Sponheimer, M. (2018). Grass leaves as potential hominin dietary resources. *Journal of Human Evolution*, 117: 44-52.

Pampush, J. D., Duque, A. C., Burrows, B. R., Daegling, D. J., Kenney, W. F. and McGraw, W. S. (2013). Homoplasy and thick enamel in primates. *Journal of Human Evolution*, 64: 216-224.

Pante, M. C., Njau. J. K., Hensley-Marschand, B., Keevil, T. L., Martín-Ramos, C., Peters, R. F. and de la Torre, I. (2018). The carnivorous feeding behaviour of early *Homo* at HWK EE, Bed II, Olduvai Gorge, Tanzania. *Journal of Human Evolution*, 120: 215-235.

Parker, S. T. (2004). The life history and development of great apes in comparative perspective. *In* S. T. Parker, R. W. Mitchell, and H. L. Miles (eds). *The Mentalities of Gorillas and Orangutans: Comparative Perspectives.* Cambridge, Cambridge University Press. Pages: 43-69.

Parr, N. A., Melin, A. D. and Fedigan, L. M. (2011). Figs are more than fallback foods: the relationship between *Ficus* and *Cebus* in a tropical dry forest. *International Journal of Zoology*, 967274: 1-10.

Patterson, B. and Howells, W. W. (1967). Hominid humeral fragment from early Pleistocene of Northwestern Kenya. *Science*, 156: 64-66.

Pellegrini, M. and Snoeck, C. (2016). Comparing bioapatite carbonate pre-treatments for isotopic measurements: Part 2 - Impact on carbon and oxygen isotope compositions. *Chemical Geology*, 420: 88–96.

Percher, A. M., Merceron, G., Akoue, G. N., Galbany, J., Romero, A. and Charpentier, M. J. E. (2018). *American Journal of Physical Anthropology*, 165: 123-138.

Peres, C. A. (1994). Primate responses to phenological changes in an Amazonian Terra Firme Forest. *Biotropica*, 26 (1): 98-112.

Peres, C. A. (2000). Identifying keystone plant resources in tropical forest: the case of gums from *Parkia* pods. *Journal of Tropical Ecology*, 16: 287-317.

Perini, T. A., de Oliveira, G. L., dos Santos Ornellas, J. and de Oliveira, F. P. (2005). Technical error of measurement in anthropometry. *Revista Brasileira de Medicina do Esporte*, 11 (1): 86-90.

Peters, C. R. (1987). Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably Ape-men. *American Journal of Physical Anthropology*, 73: 333-363.

Peters, C. R., O'Brien, E. M., Boaz, N. T., Conroy, G. C., Godfrey, L. R., Kawanaka, K., Kortlandt, A., Nishida, T., Poirier, F. E. and Smith, E. O. (1981). The early hominid plant-food niche: Insights from an analysis of plant exploitation by *Homo*, *Pan*, and *Papio* in Eastern and Southern Africa [and Comments and Reply]. *Current Anthropology*, 22 (2): 127-140.

Peterson, A., Abella, E. F., Grine, F. E., Teaford, M. F. and Ungar, P. S. (2018). Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *Journal of Human Evolution*, 119: 42-63.

Philander, S. G. H. (1983). El Niño Southern Oscillation phenomena. *Nature*, 302: 295-301.

Pickering, R. and Kramers, J. D. (2010). Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *Journal of Human Evolution*, 59: 70-86.

Pickering, R., Kramers, J. D., Hancox, P. J., de Ruiter, D. J. and Woodhead, J. D. (2011). Contemporary flowstone development links early hominin bearing cave deposits in South Africa. *Earth Planetary Science Letters*, 306: 23-32.

Pilbeam, D. (1972). *The Ascent of Man: an Introduction to Human Evolution*. The Macmillan Company, New York

Pilbeam, D. and Gould, S. J. (1974). Size and scaling in human evolution. *Science*, 186 (4167): 892-901.

Pitirri, M. K. and Begun, D. (2019). A new method to quantify mandibular corpus shape in extant great apes and its potential application to the hominoid fossil record. *American Journal of Physical Anthropology*, 168: 318-328.

Plavcan, M. J. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology*, 44: 25-53.

Plavcan, J. M. and Daegling, D. J. (2006). Interspecific and intraspecific relationships between tooth size and jaw size in primates. *Journal of Human Evolution,* 51: 171-184.

Plavcan, J. M., Lockwood, C. A., Kimbel, W. H., Lague, M. R. and Harmon, E. H. (2005). Sexual dimorphism in *Australopithecus afarensis* revisited: how strong is the case for a human-like pattern of dimorphism? *Journal of Human Evolution*, 48: 313-330.

Plavcan, J. M. and van Schaik, C. P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 87: 461-477.

Plavcan, J. M. and van Schaik, C. P. (1997). Interpreting hominid behaviour on the basis of sexual dimorphism. *Journal of Human Evolution*, 28: 245-276.

Plummer, T. W., Ferraro, J. V., Louys, J., Hertel, F., Alemseged, Z., Bobe, R. and Bishop, L. C. (2015). Bovid ecomorphology and hominin paleoenvironments of the Shungura Formation, lower Omo River Valley, Ethiopia. *Journal of Human Evolution*, 88: 108-126.

Pochron, S. T. (2000). The core dry-season diet of Yellow Baboons (*Papio hamadryas cynocephalus*) in Ruaha National Park, Tanzania. *Folia Primatologica*, 71: 346–349.

Pontzer, H., Raichlen, D. A. and Sockol, M. D. (2009). The metabolic cost of walking in humans, chimpanzees, and early hominins. *Journal of Human Evolution*, 56: 43-54.

Porter, L. M., Garber, P. A. and Nacimento, E. (2009). Exudates as a fallback food for *Callimico goeldi*. *American Journal of Primatology*, 71: 120-129.

Porter, L. M., Gilbert, C. C. and Fleagle, J. G. (2014). Diet and Phylogeny in Primate Communities. *International Journal of Primatology*. 35: 1144-1163.

Post, D. G. (1978). *Feeding and ranging behaviour of the yellow baboon* (Papio cynocephalus). PhD Thesis, Yale University.

Post, D. G. (1982). Feeding behavior of Yellow Baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *International Journal of Primatology*, 3 (4): 403-430.

Post, D. G., Hausfater, G. and McCuskey, S. A. (1980). Feeding behavior of Yellow Baboons (*Papio cynocephalus*): Relationship to age, gender and dominance rank. *Folia Primatologica*, 34: 170-195.

Potts, K. B., Watts, D. P. and Wrangham, R. W. (2011). Comparative feeding ecology of two communities of Chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology*, 32: 669-690.

Potts, R. (1998). Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology*, 41: 93-136.

Poulsen, J. R., Clark, C. J., Connor, E. F. and Smith, T. B. (2002). Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, 83 (1): 228-240.

Poulsen, J. R., Clark, C. J. and Smith, T. B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, 54: 91-105.

Prang, T. C. (2015). Calcaneal robusticity in Plio-Pleistocene hominins: implications for locomotor diversity and phylogeny. *Journal of Human Evolution*, 80: 135-146.

Prat, S., Brugal, J-P., Tiercelin, J-J., Barrat, J-A., Bohn, M., Delagnes, A., Harmand, S., Kimeu, K., Kibunjia, M., Texier, P-J. and Roche, H. (2005). First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3-2.4 Myr. *Journal of Human Evolution*, 49: 230-240.

Pruetz, J. D. (2006). Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *In*: G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 161-182.

Preutz, J. D. (2009). *The socioecology of adult female patas monkeys and vervets in Kenya*. Pearson Prentice Hall, New Jersey.

Pigliucci, M., Murren, C. J. and Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, 209: 2362-2367.

Pushkina, D., Bocherens, H., Chaimanee, Y. and Jaeger, J.-J. (2010). Stable carbon isotope reconstructions of diet and paleoenvironment from the late Middle Pleistocene Snake Cave in Northeastern Thailand. *Naturwissenschaften*, 97: 299–309.

Quinn, G. P. and Keogh, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge, Cambridge University Press.

Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D. and Randall Haas, Jr. W. (2010). Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLOS ONE*, 5 (3): 9769

Ramos-Elorduy, J., Moreno, J. M. P., Prado, E. E., Perez, M. A., Otero, J. L. and de Guevara, O. L. (1997). Nutritional value of edible insects from the state of Oaxaca, Mexico. *Journal of Food Composition and Analysis*, 10: 142-157.

Range, F. and Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*: 56: 137-153.

Ravosa, M. J. (1991). Structural allometry of the prosimian mandibular corpus and symphysis. *Journal of Human Evolutio*n, 20 (1): 3-20.

Ravosa, M. J. (1996). Jaw morphology and function in living and fossil Old World Monkeys. *International Journal of Primatology*, 17 (6): 909-932.

Ravosa, M. J., Ross, C. F., Williams, S. H. and Costley, D. B. (2010). Allometry of masticatory loading parameters in mammals. *The Anatomical Record*, 293: 557-571.

Ray, T. J., McGraw, W. S., Sun, Z., Jeon, M., Johnson, T., Cheffins, K., Daegling, D. J. and Kim, D.-G. (2015). Mandibular bone mineral density variation in three West African Cercopithecoid monkey species: Associations with diet and feeding behavior. *Archives of Oral Biology*, 60: 1714-1720.

Reed, D. A. and Ross, C. F. (2010). The influence of food material properties on jaw kinematics in the primate, *Cebus*. *Archives of Oral Biology*, 55: 946-962.Reed, D. N. (2007). Serengeti micromammals and Olduvai paleoenvironments. *In* R. Bobé, Z. Alemseged, and A. K. Behrensmeyer (eds), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence.* Netherlands, Springer. Pages: 217-255.

Reed, K. E. (1997). Early hominin evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution*, 32: 289-322.

Reed, K. E. (2008). Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. *Journal of Human Evolution*, 54: 743-768.

Remis, M. J. (1997). Western Lowland Gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology*, 43: 87-109.

Remis, M. J., Dierenfeld, E. S., Mowry, C. B. and Carroll, R. W. (2001). Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *International Journal of Primatology*, 22 (5): 807-836.

Reno, P. L., McCollum, M. A., Meindl, R. S. and Lovejoy, O. C. (2010). An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. *Philosophical Transactions of the Royal Society: Biological Sciences*, 365 (1556): 3355-3363.

Reno, P. L., Meindl, R. S., McCollom, M. A. and Lovejoy, O. C. (2003). Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proceedings of the National Academy of Sciences*, 100 (16): 9404-9409.

Reynolds, S. C. and Kibii, J. M. (2011). Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa. *Palaeontologica africana*, 46: 59-88.

Reynolds, V., Plumptre, A. J., Greenham, J. and Harborne, J. (1998). Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Oecologia*, 115: 331-336.

Reynolds, V. and Reynolds, F. (1965). Chimpanzees of the Budongo Forest. *In*: I. deVore (ed) *Primate Behavior: Field studies of monkeys and apes*. London, Holt, Rinehart and Winston. Pages: 368-424.

Rightmire, P. G. (1990). *The evolution of* Homo erectus: *comparative anatomical studies of an extinct human species.* Cambridge, Cambridge University Press.

Robbins, M. M. (2011). Gorillas: diversity in ecology and behaviour. *In*, C. Campbell, A. Fuentes, K. MacKinnon, S, Bearder and R. Stumpf (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 326-339.

Robbins, M. M. and Hohmann, G. (2006). Primate feeding ecology: An integrative approach. *In* G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology in Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 1-13.

Robbins, M. M., Nkurunungi, J. B. and McNeilage, A. (2006). Variability of the feeding ecology of eastern gorillas. *In*: G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 25-47.

Robinson, B. W. and Wilson, D. S. (1998). Optimal foraging, specialization, and a solution to Liem’s Paradox. *The American Naturalist*, 151 (3): 223–235.

Robinson, J. T. (1954a). Prehominid dentition and hominid evolution. *Evolution*, 8 (4): 324-334.

Robinson, J. T (1954b). The genera and species of the Australopithecinae. *American Journal of Physical Anthropology*, 12: 181-200.

Robinson, J. T. (1963). Adaptive radiation in the Australopithecines and the origin of man. *In*: F. C. Howell, and F. Bourliere (eds), *African Ecology and Human Evolution*. Chicago, Aldine Publishing Company. Pages: 385-416.

Robinson, J. G. (1986). Seasonal variation in use of time and space by the Wedge-capped Capuchin monkey, *Cebus olivaceus*: Implications for Foraging Theory. *Smithsonian Contributions to Zoology*, 431: 1-56.

Rodman, P. S. (1977). Feeding behaviour of Orang-utans of the Kutai Nature Reserve, East Kalimantan. *In*: T. H. Clutton-Brock (eds) *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press Inc. Pages: 384-413.

Rodman, P. (1988). Diversity and consistency in ecology and behavior. *In*: J. H. Schwartz (eds) *Orang-utan Biology*. Oxford, Oxford University Press. Pages: 31-51.

Rogers, M. E., Maisels, F., Williamson, E. A., Tutin, C. E. G. and Fernandez, M. (1990). The diet of the gorillas in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia*, 84: 326-339.

Rogers, M. E., Abernethy, K. A., Fontaine, B., Wickings, E. J., White, L. J. T. and Tutin, C. E. G. (1996). Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. *American Journal of Primatology*, 40: 297-313.

Rose, M. D. (1984). A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 63 (4): 371-378.

Rosenberger, A. L. (2013). Fallback foods, preferred foods, adaptive zones, and primate origins. *American Journal of Physical Anthropology*, 75: 883-890.

Rosenberger, A. L. and Kinzey, W. G. (1976). Functional patterns of molar occlusion in Platyrrhine primates. *American Journal of Physical Anthropology*, 45: 281-298.

Ross, C.F. and Iriarte-Diaz, J. (2014). What does feeding system morphology tell us about feeding? *Evolutionary Anthropology*, 23: 105-120.

Ross, C. F., Iriarte-Diaz, J. and Nunn, C. L. (2012). Innovative approaches to the relationship between diet and mandibular morphology in primates. *International Journal of Primatology*, 33: 632-660.

Ross, C. F., Iriarte-Diaz, J., Reed, D. A., Stewart, T. A. and Taylor, A. B. (2016). *In vivo* bone strain in the mandibular corpus of *Sapajus* during a range of oral food processing behaviours. *Journal of Human Evolution*, 98: 36-65.

Rothman, J. M., Plumptre, A. J., Dierenfeld, E. S. and Pell, A. N. (2007). Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. *Journal of Tropical Ecology*, 23: 673-682.

Rothman, J. M., Raubenheimer, D. and Chapman, C. A. (2011). Nutritional geometry: Gorillas prioritise non-protein energy while consuming surplus protein. *Biology Letter*, 7: 847-849.

Rowe, N. (1996). *The pictorial guide to the living primates*. Rhode Island, Pogonias Press.

Ruff, C. B. (2018). Functional morphology in the pages of the *AJPA*. *American Journal Physical Anthropology*, 165: 688-704.

Russon, A. E., Wich, S. A., Ancrenaz, M., Kanamori, T., Knott, C. D., Kuze, N., Morrogh-Bernard, H. C., Pratje, P., Ramlee, H., Rodman, P., Sawang, A., Sidiyasa, K., Singleton, I. and van Schaik, C. P. (2009). Geographic variation in orangutan diets. *In*: S. A. Wich, S. S. U. Atmoko, T. M. Setia, and C. P. van Schaik (eds) *Geographic variation in behavioral ecology and conservation.* Oxford, Oxford University Press. Pages: 135-156.

Ryan, A. S. (1981). Anterior dental microwear and its relationship to diet and feeding behavior in three African primates (*Pan troglodytes troglodytes, Gorilla gorilla gorilla and Papio hamadryas*). *Primates*, 22 (4): 533-550.

Sabater Pí, J. (1977). Contribution to the study of alimentation of Lowland Gorillas in the natural state, in Río Muni, Republic of Equatorial Guinea (West Africa). *Primates*, 18 (1): 183-204.

Sabater-Pí, J. (1979). Feeding behaviour and diet of Chimpanzees (*Pan troglodytes troglodytes*) in the Okorobikó Mountains of Rio Muni (West Africa). *Ethology*, 50 (3): 265-281.

Sakura, O. (1994). Factors affecting party size and composition of Chimpanzees (*Pan troglodytes verus*) Bossou, Guinea. *International Journal of Primatology*, 15 (2): 167-183.

Saldaña-Vázquez, R. A., Ruiz-Sanchez, E., Herrera-Alsina, L. and Schondube, J. E. (2015). Digestive capacity predicts diet diversity in Neotropical frugivorous bats. *Journal of Animal Ecology*, 84: 1396-1404.

Sandrock, O., Kullmer, O., Schrenk, F., Juwayeyi, Y. M. and Bromage, T. G. (2007). Fauna, taphonomy, and ecology of the Plio-Pleistocene Chiwondo Beds, Northern Malawi. *In* R. Bobé, Z. Alemseged, and A. K. Behrensmeyer (eds), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence.* Netherlands, Springer. Pages: 315-332.

Sauther, M. L. and Cuozzo, F. P. (2009). The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology*, 140: 671-686.

Schaller, G. B. (1963). *The mountain gorilla: Ecology and Behavior*. Chicago, University of Chicago Press.

Schaller, G. B. (1965). Behavioural comparisons of the apes. *In* I. deVore (ed) *Primate Behaviour: field studies of monkeys and apes.* London, Holt, Rinehard and Winston. Pages: 474-481.

Schoeninger, M. J., Iwaniec, U. T. and Glander, K. E. (1997). Stable isotope ratios indicate diet and habitat use in New World Monkeys. *American Journal of Physical Anthropology*, 103: 69-83.

Schoeninger, M. J., Moore, J. and Sept, J. M. (1999). Subsistence strategies of two "savanna" chimpanzee populations: the stable isotope evidence. *American Journal of Primatology,* 49: 297-314.

Schoeninger, M. J., Most, C. A., Moore, J. J. and Somerville, A. D. (2016). Environmental variables across *Pan troglodytes* study sites correspond with the carbon, but not the nitrogen, stable isotope ratios of chimpanzee hair. *American Journal of Primatology,* 78: 1055-1069.

Schoeninger, M. J., Reeser, H. and Hallin, K. (2003). Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. *Journal of Anthropological Archaeology*, 22: 200-207.

Schwartz, J. H and Tattersall, I. (2005). *The Human Fossil Record, Volume Four: Craniodental Morphology of Early Hominids (Genera* Australopithecus, Paranthropus, Orrorin) *and Overview.* New Jersey, Wiley-Liss.

Scott, J. E. (2012). Molar size and diet in the Strepsirrhini: implications for size-adjustment in studies of primate dental adaptation. *Journal of Human Evolution,* 63: 796-804.

Scott, J. E., McAbee, K. R., Eastman, M. M. and Ravosa, M. J. (2014). Experimental perspective on fallback foods and dietary adaptations in early hominins. *Biology Letters*, 10: 20130789-20130789.

Scott, J. R., Godfrey, L. R., Junger, W. L., Scott, R. S., Simons, E. L., Teaford, M. F., Ungar, P. S. and Walker, A. (2009). Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. *Journal of Human Evolution*, 56: 405-416.

Scott, R. S., Teaford, M. F. and Ungar, P. S. (2012). Dental microwear texture and anthropoid diets. *American Journal of Physical Anthropology*, 147: 551-579.

Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Childs, B. E., Teaford, M. F. and Walker, A. (2006). Dental microwear texture analysis: technical considerations. *Journal of Human Evolution*, 51: 339-349.

Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Grine, F. E., Teaford, M. F. and Walker, A. (2005). Microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*, 436: 693-695.

Schrenk, F., Bromage, T. G., Betzler, C. G., Ring, U. and Juwayeyi, Y. M. (1993). Oldest *Homo* and Pliocene biogeography of the Malawi Rift. *Nature,* 365: 833-836.

Sengupta, A. and Radhakrishna, S. (2016). Influence of fruit availability on fruit consumption in a generalist primate, the Rhesus Macaque *Macaca mulatta*. *International Journal of Primatology*, 37: 703-717.

Serckx, A., Kühl, H., Beudels-Jamar, R. C., Poncin, P., Bastin, J-F. and Huynen, M-C. (2015). Feeding ecology of bonobos living in forest-savannah mosaics: diet seasonal variation and importance of fallback foods. *American Journal of Primatology*, 77: 948-962.

Setchell, J. M., Lee. P. C., Wickings, E. J. and Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 115 (4): 349-360.

Setchell, J. M. and Wickings, E. J. (2004). Sequences and timing of dental eruption in semi-free-ranging Mandrills (*Mandrillus sphinx*). *Folia Primatologica*, 75 (3): 121-132.

Setchell, J. M., Wickings, E. J. and Knapp, L. A. (2006). Life history in male Mandrills (*Mandrillus sphinx*): Physical development, dominance rank, and group association. *American Journal of Physical Anthropology,* 131: 498-510.

Shanahan, M. and Compton, S. G. (2001). Vertical stratification of figs and fig-eaters in a Bornean lowland rain forest: how is the canopy different? *Plant Ecology*, 153: 121-132.

Shea, B. T. (1983). Allometry and heterochrony in the African Apes. *American Journal of Physical Anthropology*, 62: 275-289.

Shellis, R. P., Beynon, A. D., Reid, D. J. and Hiiemae, K.M. (1998). Variations in molar enamel thickness among primates. *Journal of Human Evolution*, 35: 507-522.

Sheppard, D. J. (2000). *Ecology of the Budongo Forest Redtail: Patterns of habitat use and population density in primary and regenerating forest sites.* MSc thesis, University of Calgary, Calgary, Alberta, Canada.

Shipman, P. and Harris, J. M. (1988). Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. *In* F. E. Grine (eds) *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter. Pages: 343-381.

Singleton, M. (2004). Geometric morphometric analysis of functional divergence in mangabey facial form. *Journal of Anthropological Sciences*, 82: 27-44.

Silcox, M. T. and Teaford, M. F. (2002). The diet of worms: an analysis of mole dental microwear. *Journal of Mammology*, 83 (3): 804-814.

Sillen, A. (1992). Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans. *Journal of Human Evolution*, 23 (6): 495-516

Sillen, A., Hall, G. and Armstrong, R. (1995). Strontium calcium ratios (Sr/Ca) and strontium isotopic ratios (87Sr/86Sr) of *Australopithecus robustus* and *Homo* sp. from Swartkrans. *Journal of Human Evolution*, 28:277-285.

Smith, A. L., Benazzi, S., Ledogar, J. A., Tamvada, K., Pryor Smith, L. C., Weber, G. W., Spencer, M. A., Lucas, P. W., Michael, S., Shekeban, A., Al-Fadhalah, K., Almusallam, A. S., Dechow, P. C., Grosse, I. R., Ross, C. F., Madden, R. H., Richmond, B. G., Wright, B. W., Wang, Q., Byron, C., Slice, D. E., Wood, S., Dzialo, C., Berthaume, M. A., van Casteren, A. and Strait, D. S. (2015). The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *The Anatomical Record*, 298: 145–167.

Smith, C. C., Morgan, M. E. and Pilbeam, D. (2010). Isotopic ecology and dietary profiles of Liberian chimpanzees. *Journal of Human Evolution*, 58: 43-55.

Smith, H. (1989). Dental development as a measure of life history in primates. *Evolution*, 43 (3): 683-688.

Smith, H. (1992). Life history and the evolution of human maturation. *Evolutionary Anthropology*, 1 (4): 134-142.

Smith, R. J. (1982). On the mechanical reduction of functional morphology. *Journal of Theoretical Biology*, 96: 99-106.

Smith, R. J. (1983). The mandibular corpus of female primates: taxonomic, dietary, and allometric correlates of interspecific variations in size and shape. *American Journal of Physical Anthropology*, 61: 315-330.

Smith, R. J. and Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution*, 32: 523-559.

Smith, T. M., Kupczik, K., Machanda, Z., Skinner, M. M. and Zermeno, J. P. (2012). Enamel thickness in Bornean and Sumatran orangutan dentitions. *American Journal of Physical Anthropology*, 147: 417-426.

Snaith, T. V. and Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. *Behavioural Ecology and Sociobiology*, 59: 185-190.

Snaith, T. V. and Chapman, C. A. (2007). Primate group size and socioecological models: do folivores really play by different rules? *Evolutionary Anthropology*, 16: 94-106.

Sponheimer, M., Alemseged, Z., Cerling, T. E., Grine, F. E., Kimbel, W. H., Leakey, M. G., Lee-Thorp, J., Manthi, F. K., Reed, K. E., Wood, B. A. and Wynn, J. G. (2013). Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences*, 110 (26): 10513-10518.

Sponheimer, M., Codron, D., Passey, B. H., de Ruiter, D. J., Cerling, T. E. and Lee-Thorp, J. A. (2009). Using carbon isotopes to track dietary change in modern, historical, and ancient primates. *American Journal of Physical Anthropology*, 140: 661-670.

Sponheimer, M. and Lee-Thorp, J. A. (1999). Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science*, 283: 368-370.

Sponheimer, M. and Lee-Thorp, J. A. (2001). The oxygen isotope composition of mammalian enamel carbonate from Morea Estate, South Africa. *Oecologia*, 126 (2): 153-157.

Sponheimer, M. and Lee-Thorp, J. A. (2003). Differential resource utilization by extant great apes and australopithecines: towards solving the C_4 conundrum. *Comparative Biochemistry and Physiology Part A*, 136: 27-34.

Sponheimer, M., Lee-Thorp, J., de Ruiter, D., Codron, D., Codron, J., Baugh, A. T. and Thackeray, F. (2005a). Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *Journal of Human Evolution*, 48: 301-312.

Sponheimer, M., Loudon, J. E., Codron, D., Howells, M. E., Pruetz, J. D., Codron, J., de Ruiter, D. J., Lee-Thorp, J. A. (2006b). Do "savanna" chimpanzees consume C_4 resources? *Journal of Human Evolution*, 51: 128-133.

Sponheimer, M., Passey, B. H., de Ruiter, D. J., Guatelli-Steinberg, D., Cerling, T. E. and Lee-Thorp, J. A. (2006a). Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus. Science*, 314: 980-982.

Sponheimer, M., de Ruiter, D., Lee-Thorp, J. and Späth, A. (2005b). Sr/Ca and early hominin diets revisited: new data from modern and fossil tooth enamel. *Journal of Human Evolution*, 48: 147-156.

Stacey, P. B. (1986). Group size and foraging efficiency in yellow baboons. *Behavioral Ecology and Sociobiology*, 18: 175-187.

Stanford, C., Allen, J. S. and Antón, S. C. (2009). *Biological Anthropology*. (2^{nd} Eds.) Pearson Prentice Hall, London.

Stanford, C. B. and Nkurunungi, J. B. (2003). Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: Diet. *International Journal of Primatology*, 24 (4): 901-918.

Stanistreet, I. G. (2012). Fine resolution of early hominin time, Beds I and II, Olduvai Gorge, Tanzania. *Journal of Human Evolution*, 63: 300-308.

Stansfield, E., Parker, J. and O'Higgins, P. (2018). A sensitivity study of human mandibular biting simulations using finite element analysis. *Journal of Archaeological Science: Reports*, 22: 420-432.

Stansfield, E., Evteev, A. and O'Higgins, P. (2018). Can diet be inferred from the biomechanical response to simulated biting in modern and pre-history human mandibles? *Journal of Archaeological Science: Reports*, 22: 433-443.

Steininger, C., Berger, L. R. and Kuhn, B. F. (2008). A partial skull of *Paranthropus robustus* from Cooper's Cave, South Africa. *South African Journal of Science*, 104: 143-146.

Stern, J. T. and Susman, R. L. (1983). The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 60: 279-317.

Stevenson, P. R., Quinones, M. J. and Ahumada, J. A. (2000). Influence of fruit availability on ecological overlap among four Neotropical Primates at Tinigua National Park, Colombia. *Biotropica*, 32 (3): 533-544.

Strait, D. S., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Ross, C.F., Grosse, I. R., Wright, B. W., Wood, B. A., Weber, G. W., Wang, Q., Byron, C., Slice, D. E., Chalk, J., Smith, A. L., Smith, L. C., Wood, S., Berthaume, M., Benazzi, S., Dzialo, C., Tamvada, K. and Ledogar, J. A. (2013). Viewpoints: Diet and dietary adaptations in early hominins: the hard food perspective. *American Journal of Physical Anthropology*, 151: 339-355.

Strait, D. S., Weber, G. W., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., Ross, C. F., Grosse, I. R., Wright, B. W., Wood, B. A., Wang, Q., Byron, C. and Slice, D. E. (2012). Microwear, mechanics and the feeding adaptations of *Australopithecus africanus*. *Journal of Human Evolution*, 62: 165-168.

Strait, D. S., Weber, G. W., Neubauer, S., Chalk, J., Richmond, B. G., Lucas, P. W., Spencer, M. A., Schrein, C., Dechow, P. C., Ross, C. F. Gross, I. R., Wright, B. W., Constantino, P., Wood, B. A., Lawn, B., Hylander, W. L., Wang, Q., Byron, C., Slice, D. E. and Smith, A. L. (2009). The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proceedings of the National Academy of Sciences*, 106 (7): 2124-2129.

Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale forest, Uganda. *In*: D. J. Chivers and J. Herbert (eds) *Recent Advances in Primatology: Behaviour*. London, Academic Press. Pages 225-248.

Studenmund, A. H. and Cassidy, H. J. (1987). *Using econometrics: A practical guide.* Boston, Little Brown.

Stumpf, R. (2011). Chimpanzees and Bonobos: inter- and intraspecies diversity. *In*, C. Campbell *et al*. (eds). *Primates in Perspective.* Oxford, Oxford University Press. Pages: 340-357.

Su, D. F. and Harrison, T. (2007). The paleoecology of the Upper Laetoli Beds at Laetoli. *In* R. Bobé, Z. Alemseged, and A. K. Behrensmeyer (eds), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence.* Netherlands, Springer. Pages: 279-313.

Su, D. F and Harrison, T. (2008). Ecological implications of the relative rarity of fossil hominins at Laetoli. *Journal of Human Evolution*, 55: 672-681.

Su, H-H. and Lee, L-L. (2001). Food habits of Formosan Rock Macaques (*Macaca cyclopis*) in Jentse, Northeastern Taiwan, assessed by fecal analysis and behavioral observation. *International Journal of Primatology*, 22 (3): 359-377.

Sugardjito, J., te Boekhorst, I. J. A. and van Hooff, J. A. R. A. M. (1987). Ecological constraints on the grouping of wild orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *International Journal of Primatology*, 8 (1): 17-41.

Sugiyama, Y. (1994). Tool use by wild chimpanzees. *Nature*, 367 (6461): 327.

Sugiyama, Y. and Koman, J. (1987). A preliminary list of chimpanzees' alimentation at Bossou, Guinea. *Primates*, 28 (1): 133-147.

Sutton, M. B., Pickering, T. R., Pickering, R., Brain, C. K., Clarke, R. J., Heaton, J. L. and Kuman, K. (2009). Newly discovered fossil- and artifact-bearing deposits, uranium-series ages, and Plio-Pleistocene hominids at Swartkrans Cave, South Africa. *Journal of Human Evolution*, 57 (6): 688-696.

Suwa, G. (1988). Evolution of the "robust" australopithecines in the Omo Succession: evidence from mandibular premolar morphology. *In*: F. E. Grine (eds), *Evolutionary History of the Robust Australopithecines.* New York, Aldine de Gruyter. Pages: 199-222.

Suwa, G., Asfaw, B., Beyene, Y., White, T. D., Katoh, S., Nagaoka, S., Nakaya, H., Uzawa, K., Renne, P. and Woldegabriel, G. (1997). The first skull of *Australopithecus boisei. Nature*, 389: 489-492.

Suwa, G., Asfaw, B., Haile-Selassie, Y., White, T., Katoh, S., Woldegabriel, G., Hart, W. K., Nakaya, H. and Beyene, Y. (2007). *Anthropological Science*, 115: 133-151.

Swedell, L. (2011). African Papionins: diversity of social organisation and ecological flexibility. *In*, C. Campbell *et al*. (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 241-276.

Swindler, D. R. (2002). *Primate Dentition: An introduction to the teeth of non-human primates*. Cambridge, Cambridge University Press.

Szalay, F. S. (1975). Hunting-scavenging protohominids: a model for human origins. *Man*, 1: 420-429.

Talebi, M. G., Sala, E. A., Carvalho, B., Villani, G. M., Lucas, P. W. and van Casteren, A. (2016). Membrane-plate transition in leaves as an influence on dietary selectivity and tooth form. *Journal of Human Evolution*, 98: 18-26.

Taylor, A. B. (2002). Masticatory form and function in the African apes. *American Journal of Physical Anthropology*, 117:133-156.

Taylor, A. B. (2005). A comparative analysis of temporomandibular joint morphology in the African apes. *Journal of Human Evolution*, 48: 555-574.

Taylor, A. B. (2006a). Feeding behaviour, diet, and the functional consequences of jaw form in orang-utans, with implications for the evolution of *Pongo*. *Journal of Human Evolution*, 50: 377-393.

Taylor, A. B. (2006b). Diet and mandibular morphology in African apes. *International Journal of Primatology*, 27 (1): 181-201.

Taylor, A. B. (2006c). Size and shape dimorphism in Great Ape mandibles and implications for fossil species recognition. *American Journal of Physical Anthropology*, 129: 82-98.

Taylor, A. B. (2009). The functional significance of variation in jaw form in orang-utans. *In* S. A. Wich, S. S. U. Atmoko, T. M. Setia, and C. P. van Schaik (eds) *Orangutans: Geographic variation in behavioural ecology and conservation*. Oxford, Oxford University Press. Pages 15-31.

Taylor, A. B. and Groves, C. P. (2003). Patterns of mandibular variation in *Pan* and *Gorilla* and implications for African ape taxonomy. *Journal of Human Evolution*, 44: 529-561.

Taylor, A. B. and Vinyard, C. J. (2009). Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. *Journal of Human Evolution*, 57: 710-720.

Taylor, A. B., Vogel, E. R. and Dominy, N. J. (2008). Food material properties and mandibular load resistance abilities in large-bodied hominoids. *Journal of Human Evolution*, 55: 604-616.

Teaford, M. F. (1985). Molar microwear and diet in the genus *Cebus*. *American Journal of Physical Anthropology*, 66 (4): 363-370.

Teaford, M. F. and Oyen, O. J. (1989). Differences in the rate of molar wear between monkeys raised on different diets. *Journal of Dental Research*, 68 (11): 1513-1518.

Teaford, M. F. and Robinson, J. G. (1989). Seasonal or ecological differences in diet and molar microwear in *Cebus nigrivittatus*. *American Journal of Physical Anthropology*, 80: 391-401.

Teaford, M. F. and Runestad, J. A. (1992). Dental microwear and diet in Venezuelan primates. *American Journal of Physical Anthropology*, 88: 347-364.

Teaford, M. F. and Ungar, P. S. (2000). Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences*, 97 (25): 13506-13511.

Teaford, M. F. and Walker, A. (1984). Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. *American Journal of Physical Anthropology*, 64: 191-200.

Terborgh, J. (1983). *Five New World Primates*. Surrey, Princeton University Press.

Terborgh, J. (1986). Keystone plant resources in the tropical forest. *In* M. Soule (ed), *Conservation biology: The science of scarcity and diversity*. Massachusetts, Sinauer Associates. Pages 330-344.

Terhune, C. E. (2011). Dietary correlates of temporomandibular joint morphology in New World primates. *Journal of Human Evolution*, 61: 583-596.

Thackeray, J. F., de Ruiter, D. J., Berger, L. R. and van der Merve, N. J. (2001). Hominid fossils from Kromdraai: a revised list of specimens discovered since 1938. *Annals of the Transvaal Museum*, 38: 43-56.

Thayer, Z. M. and Dobson, S. D. (2010). Sexual dimorphism in chin shape: implications for adaptive hypotheses. *American Journal of Physical Anthropology*, 143:417-425.

Thierry, B. (2011). The Macaques: a double-layered social organisation. *In*, C. Campbell, A. Fuentes, K. MacKinnon, S, Bearder and R. Stumpf (eds). *Primates in perspective.* Oxford, Oxford University Press. Pages: 229-240.

Thompson, C. L. Valença-Montenegro, M. M., Melo, L. C. d. O., Valle, Y. B. M., Oliveira, M. A. B. d., Lucas, P. W. and Vinyard, C. J. (2014). Accessing foods can exert multiple distinct, and potentially competing, selective pressures on feeding in common marmoset monkeys. *Journal of Zoology*, 294: 161-169.

Thompson, M. E. and Wrangham, R. W. (2008). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park. *American Journal of Physical Anthropology*, 135: 171-181.

Tiercelin, J-J., Schuster, M., Roche, H., Brugal J-P., Thuo, P., Prat, S., Harmand, S., Davitan, G., Barrat, J-A. and Bohn, M. (2010). New considerations on the stratigraphy and the environmental *Journal of African Earth Sciences*, 58: 157-184.

Tobias, P. V. (1967). *Olduvai Gorge. Volume 2: The cranium and maxillary dentition of* Australopithecus (Zinjanthropus) boisei. New York, Cambridge University Press.

Tobias, P. V. (1976). White African: an appreciation and some personal memories of Louis Leakey. *In*: G. L. Isaac and E. R. McCown (eds): *Human Origins: Louis Leakey and the East African Evidence*. Menlo Park, California: A. Staples Press, W. A. Benjamin Inc. Pages: 54-74.

Tomblin, D. C. and Cranford, J. A. (1994). Ecological niche differences between *Alouatta palliata* and *Cebus capucinus* comparing feeding modes, branch use, and diet. *Primates*, 35 (3): 265-274.

Toro-Ibacache, V., Fitton, L. C., Fagan, M. J. and O'Higgins, P. (2015). Validity and sensitivity of a human cranial finite element model: implications for comparative studies of biting performance. *Journal of Anatomy*, 228 (1): 70-84.

Tutin, C. E. G. (1999). Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates*, 40 (1): 249- 265.

Tutin, C. E. G. and Fernandez, M. (1985). Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: Some preliminary data. *International Journal of Primatology*, 6 (1): 27-43.

Tutin, C. E. G. and Fernandez, M. (1993a). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology*, 30 (3): 195-211.

Tutin, C. E. G. and Fernandez, M. (1993b). Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. *Journal of Tropical Ecology*, 9: 241-248.

Tutin, C. E. G., Fernandez, M., Rogers, M. E., Williamson, E. A., McGrew, W. C., Altmann, S. A., Southgate, D. A. T., Crowe, I., Tutin, C. E. G., Whiten, A., Conklin, N. L. and Barrett, L. (1991). Foraging profiles of sympatric Lowland Gorillas and Chimpanzees in the Lope Reserve, Gabon [and discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 334 (1270): 179-186.

Tutin, C. E. G., Ham, R. M., White, L. J. and Harrison, M. J. (1997). The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology*, 42: 1-24.

Tweheyo, M. and Lye, K. A. (2003). Phenology of figs in Budongo Forest Uganda and its importance of the chimpanzee diet. *African Journal of Ecology*, 41: 306-316.

Tweheyo, M., Lye, K. A. and Weladji, R. B. (2004). Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management*, 188: 267-278.

UNEP-WCMC and IUCN (International Union for Conservation of Nature) 2008. *Pan troglodytes. The IUCN Red List of Threatened Species. Version 2014.2.* Available at: http://maps.iucnredlist.org/map.html?id=15933. (Accessed on 14.10.14).

Ungar, P. S. (2004). Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *Journal of Human Evolution*, 46: 605-622.

Ungar, P. S. (2007). Dental functional morphology: the known, the unknown, and the unknowable. *In* P. S. Ungar (ed), *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford, Oxford University Press. Pages: 39-55.

Ungar, P. S. (2010). *Mammal Teeth: Origin, Evolution, and Diversity*. Baltimore, The Johns Hopkins University Press.

Ungar, P. S. (2011). Dental evidence for the diets of Plio-Pleistocene hominins. *Yearbook of Physical Anthropology*, 54: 47-62.

Ungar, P. S. (2015). Mammalian dental function and wear: a review. *Biosurface and Biotribology*, 1: 25-41.

Ungar, P. S., Grine, F. E. and Teaford, M. F. (2008). Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE*, 3 (4): e2044.

Ungar, P. S., Grine, F. E., Teaford, M. F. and El Zaatari, S. (2006). Dental microwear and diets of African early *Homo*. *Journal of Human Evolution*, 50: 78-95.

Ungar, P. S. and Hlusko, L. J. (2016). The evolutionary path of least resistance. *Science*, 353 (6294): 29-30.

Ungar, P. S., Krueger, K. L., Blumenschine, R. J., Njau, J. and Scott, R. S. (2012). Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Palaeoanthropology Project, 1995-2007. *Journal of Human Evolution*, 63: 429-437.

Ungar, P. S., Merceron, G. and Scott, R. S. (2007). Dental mircrowear texture analysis of Varswater Bovids and early Pliocene palaeoenvironments of Langebaanweg, Western Cape Province, South Africa. *Journal of Mammal Evolution*, 14: 163-181.

Ungar, P. S., Scott, R. S., Grine, F. E. and Teaford, M. F. (2010). Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philosophical Transactions of the Royal Society London B*, 365: 3345-3354.

Ungar, P. S. and Sponheimer, M. (2011). The diets of early hominins. *Science*, 334: 190-193.

Ungar, P. S. and Teaford, M. F. (2002). *Human diet: its origin and evolution*. Westport, Bergin & Garvey.

Uno, K. T., Cerling, T. E., Harris, J. M., Kunimatsu, Y., Leakey, M. G., Nakatsukasa, M. and Nakaya, H. (2011). Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences*, 108 (16): 6509-6514.

Uribelarrea, D., Dominguez-Rodrigo, M., Perez-Gonzalez, A., Salamanca, J. V., Baquedano E., Mabulla, A., Musiba, C., Barboni, D. and Cobo-Sanchez, L. (2014). Geo-archaeological and geometrically corrected reconstruction of the 1.84 Ma FLK Zinj paleolandscape at Olduvai Gorge, Tanzania. *Quaternary International*, 322-323: 7-31.

van Casteren, A., Venkataraman, V., Ennos, A. R. and Lucas, P. W. (2016). Novel developments in field mechanics. *Journal of Human Evolution*, 98: 5-17.

van der Merwe, N. J., Masao, F. T. and Bamford, M. K. (2008). Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science*, 104:153-155.

van der Merwe, N. J., Thackeray, J. F., Lee-Thorp, J. and Luyt, J. (2003). The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *Journal of Human Evolution*, 44: 581-597.

van Doorn, A. C., O'Riain, M. J. and Swedell, L. (2010). The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal Chacma baboons (*Papio ursinus*) in the Cape Peninsula of South Africa. *American Journal of Primatology*, 72: 104-112.

van Lawick-Goodall, J., Lawick, H. van. and Packer, C. (1973). Tool-use in free-living baboons in the Gombe National Park, Tanzania. *Nature*, 241 (5386): 212.

van Schaik, C. P. and Knott, C. D. (2001). Geographic variation in tool use on *Neesia* fruits in orangutans. *American Journal of Physical Anthropology*, 114: 331-342.

van Schaik, C. P., Terborgh, J. W. and Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24: 353-377.

Veneziano, A., Irish, J. D., Meloro, C., Stringer, C. and de Groote, I. (2019). The functional significance of dental and mandibular reduction in *Homo*: a catarrhine perspective. *American Journal of Primatology*, 81: 1-10.

Vinyard, C. J. and Ravosa, M. J. (1998). Ontogeny, function, and scaling of the mandibular symphysis in papionin primates. *Journal of Morphology*, 235: 157-175.

Vinyard, C. J., Taylor, A. B., Teaford, M. F., Glander, K. E., Ravosa, M. J., Rossie, J. B., Ryan, T. M. and Williams, S. H. (2011). Are we looking for loads in all the right places? New research directions for studying the masticatory apparatus of New World monkeys. *The Anatomical Record*, 294: 2140-2157.

Vinyard, C. J., Thompson, C. L., Doherty, A. and Robl, N. (2016). Preference and consequences: a preliminary look at whether preference impacts oral processing in non-human primates. *Journal of Human Evolution*, 98: 27-35.

Vinyard, C. J., Wall, C. E., Williams, S. H., Johnson, K. R. and Hylander, W. L. (2006). Masseter electromyography during chewing in ring-tailed Lemurs (*Lemur catta*). *American Journal of Physical Anthropology*, 130: 85-95.

Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P. and Dominy, N. J. (2009). Foraging and ranging behaviour during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology*, 140: 716-726.

Vogel, E. R., van Woerden, J. T., Lucas, P. W., Utami Atmoko, S. S., van Schaik, C. and Dominy, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution*, 55: 60-74.

Vogel, E. R., Zulfa, A., Hardus, M., Wich, S. A., Dominy, N. J. and Taylor, A. B. (2014). Food mechanical properties, feeding ecology, and the mandibular morphology of wild orangutans. *Journal of Human Evolution*. 75: 110-124.

Vrba, E. S. (1980). Evolution, species and fossils: how does life evolve? *South African Journal of Science*, 76: 61-84.

Walker, A. (1981). Dietary hypotheses and human evolution. *Philosophical Transactions of the Royal Society, B*, 292: 57-66.

Walker, A., Leakey, R. E., Harris, J. M. and Brown, F. H. (1986). 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, 322: 517-522.

Walsh, R. P. D. (1996). Drought frequency changes in Sabah and adjacent parts of Northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology*, 12: 385-407.

Ward, C. V., Kimbel, W. H., Harmon, E. H. and Johanson, D. C. (2012). New postcranial fossils of *Australopithecus afarensis* from Hadar, Ethiopia (1990-2007). *Journal of Human Evolution*, 63: 1-51.

Ward, C. V., Leakey, M. G. and Walker, A. C. (1999). The new hominid species, *Australopithecus anamensis*. *Evolutionary Anthropology*, 7: 197-205.

Ward, C. V., Leakey, M. G. and Walker, A. C. (2001). Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human of Evolution*, 41: 255-368.

Ward, C. V., Manthi, F. K. and Plavcan, J. M. (2013). New fossils of *Australopithecus anamensis* from Kanapoi, West Turkana, Kenya (2003-2008). *Journal of Human Evolution*, 65: 501-524.

Ward, S. C. (1991). Taxonomy, palaeobiology and adaptations of the “robust” australopithecines. *Journal of Human Evolution*, 21: 469-483.

Warren, Y. (2003). *Olive baboons* (Papio cynocephalus anubis): *behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria*. PhD Thesis, Roehampton University.

Waser, P. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *African Journal of Ecology*, 13: 249-263.

Waser, P. (1977). Feeding, ranging and group size in the Mangabey *Cercocebus albigena*. *In*: T. H. Clutton-Brock (ed) *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press Inc. Pages: 183-222.

Watts, D. P. (1984). Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology,* 7: 323-356.

Watts, D. P., Potts, K. B., Lwanga, J. S. and Mitani, J. C. (2012a). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American Journal of Primatology*, 74: 114-129.

Watts, D. P., Potts, K. B., Lwanga, J. S. and Mitani, J. C., (2012b). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology*, 74: 130-144.

Webster, T. H., McGrew, W. C., Marchant, L. F., Payne, C. L. R. and Hunt, K. D. (2014). Selective insectivory at Toro-Semliki, Uganda: Comparative analyses suggest no ‘savanna’ chimpanzee pattern. *Journal of Human Evolution*, 71: 20-27.

Weidenreich, F. (1937). *The dentition of* Sinanthropus pekinensis*: a comparative odontology of the hominids*. China, Palaeontologia sinica.

West-Eberhard, M. J. (2005). Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences*, USA, 102: 6543-6549.

White, F. J. (1992). Activity budgets, feeding behavior, and habitat use of Pygmy Chimpanzees at Lomako, Zaire. *American Journal of Primatology*, 26: 215-223.

White, F. J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to Bonobo sociality. *International Journal of Primatology*, 19 (6): 1013-1027.

White, T. D. (1977). New fossil hominids from Laetolil, Tanzania. *American Journal of Physical Anthropology*, 46: 197-230.

White, T. D. and Johanson, D. C. (1982). Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974-1977 collections. *American Journal of Physical Anthropology*, 57: 501-544.

White, T. D., Johanson, D. C. and Kimbel, W. H. (1981). *Australopithecus africanus*: its phylogenetic position reconsidered. *South African Journal of Science*, 77: 445-470.

White, T. D., Moore, R. V. and Suwa, G. (1984). Hadar biostratigraphy and hominid evolution. *Journal of Vertebrate Paleontology*, 4 (4): 575-583.

White, T. D., Suwa, G., Hart, W. K., Walter, R. C., Woldegabriel, G., de Heinzelin, J, Clark, J. D., Asfaw, B. and Vrba, E. (1993). New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature*, 366: 261-265.

White, T. D., Suwa. G., Simpson, S. and Asfaw, B. (2000). Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *American Journal of Physical Anthropology*, 111: 45-68.

White, T. D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R. L., Boisserie, J-R., Currie, B., Gilbert, H., Haile-Selassie, Y., Hart, W. K., Hlusko, L. J., Howell, F. C., Kono, R. T., Lehmann, T., Louchart, A., Lovejoy, C. O., Renne, P. R., Saegusa, H., Vrba, E. S., Wesselman, H. and Suwa, G. (2006). Asa Issie, Aramis and the origin of *Australopithecus*. *Nature*, 440: 883-889.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G., Henzi, S. P., Hawkes, K., Widdowson, E. M., Altmann, S. A., Milton, K. and Dunbar, R. I. M. (1991). Dietary and foraging strategies of baboons [and discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 334 (1270): 187-197.

Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, 5: 139-159.

Wich, S. A., Atmoko, S. S. U., Setia, T. M. and van Schaik, C. P. (2009). *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford, Oxford University Press.

Wich, S. A., Guerts, M. L., Setia, T. M. and Utami-Atmoko, S. S. (2006a). Influence of fruit availability on Sumatran orang-utan sociality and reproduction. *In* G. Hohmann, M. M., Robbins, and C. Boesch (eds.) *Feeding ecology in apes and other primates.* Cambridge, Cambridge University Press. Pages: 337-358.

Wich, S. A., Utami-Atmoko, S. S., Mitra Setia, T., Djoyosudharmo, S. and Geurts, M. L. (2006b). Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *International Journal of Primatology*, 27 (6): 1535-1550.

Wich S. A. and van Schaik C. P. (2000). The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malaysia. *Journal of Tropical Ecology*, 16: 563-577.

Wich, S. A., Vogel, E. R., Larsen, M. D., Fredriksson, G., Leighton, M., Yeager, C. P., Brearley, F. Q., van Schaik, C. P. and Marshall, A. J. (2011). Forest fruit production is higher on Sumatra than on Borneo. *PLOS ONE*, 6 (6): e21278.

Wickings, E. J, and Dixson, A. F. (1992). Development from birth to sexual maturity in a semi-free ranging colony of mandrills (*Mandrillus sphinx*) in Gabon. *Journal of Reproductive Fertility*, 95:129-138.

Williams, H. E. and Vaughan, C. (2001). White-faced monkey (*Cebus capucinus*) ecology and management in neotropical agricultural landscapes during the dry season. *Revista de Biología Tropical*, 49 (3-4): 1199-1206.

Williams, S. H., Stover, K. K., Davis, J. S. and Montuelle, S. J. (2011). Mandibular corpus bone strains during mastication in goats (*Capra hircus*): a comparison of ingestive and rumination chewing. *Archives of Oral Biology*, 56: 960-971.

Williamson, E. A., Tutin, C. E. G., Rogers, M. E. and Fernandez, M. (1990). Composition of the diet of Lowland Gorillas at Lopé in Gabon. *American Journal of Primatology*, 21: 265-277.

Wilson, J. B. (2007). Priorities in statistics, the sensitive feet of elephants, and don't transform data. *Folia Geobotanica*, 42: 161-167.

Woldegabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W. K. and Heiken, G. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, 371: 330-333.

Wolpoff, M. H. (1975). Some aspects of human mandibular evolution. *In* J. A. McNamara Jr. (eds) *Determinants of mandibular form and growth. Craniofacial Growth Series*, *No. 4*. Ann Arbor, University of Michigan Press. Pages: 1-64.

Wood, B. A. (1991). *Koobi Fora Research Project*. *Volume 4: Hominid Cranial Remains.* Oxford: Clarendon Press.

Wood, B. A and Abbott, S. A. (1983). Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. *Journal of Anatomy*, 136: 197-219.

Wood, B. A. and Collard, M. (1999). The human genus. *Science*, 284: 65-71.

Wood, B. A. and Constantino, P. (2007). *Paranthropus boisei*: fifty years of evidence and analysis. *Yearbook of Physical Anthropology*, 50: 106-132.

Wood, B. A. and Leakey, M. (2011). The Omo-Turkana basin fossil hominins and their contribution to our understanding of human evolution in Africa. *Evolutionary Anthropology*, 20 (6): 264-292.

Wood, B. A. and Richmond, B. G. (2000). Human evolution: taxonomy and palaeobiology. *Journal of Anatomy*, 196: 19-60.

Wood, B. A. and Schroer, K. (2012). Reconstructing the diet of an extinct hominin taxon: the role of extant primate models. *International Journal of Primatology*, 33: 716–742.

Wood, B. A. and Stack, C. G. (1980). Does allometry explain the differences between “gracile” and “robust” australopithecines? *American Journal of Physical Anthropology*, 52: 55-62.

Wood, B. A. and Strait, D. (2004). Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution*, 46: 119-162.

Worman, C. O’D. and Chapman, C. A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology*, 21: 689-697.

Wrangham, R. W. (1977). Feeding behaviour of Chimpanzees in Gombe National Park, Tanzania. *In*: T. H. Clutton-Brock (ed) *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press Inc. Pages: 504-538.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P. and Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. *In*: W. C. McGrew, L. F. Marchant and T. Nishida (eds) *Great Ape Societies*. Cambridge, Cambridge University Press. Pages; 45-57.

Wrangham, R. W., Conklin-Brittain, N. L. and Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19 (6): 949-970

Wrangham, R. W., Conklin, N. L., Chapman, C. A., Hunt, K. D., Milton, K., Rogers, E., Whiten, A. and Barton, R. A. (1991). The significance of fibrous foods for Kibale Forest chimpanzees [and discussion].*Philosophical Transactions: Biological Sciences*, 334 (1270): 171-178.

Wrangham, R. W. and Waterman, P. G. (1981). Feeding behaviour of Vervet Monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *Journal of Animal Ecology*, 50 (3): 715-731.

Wright, B. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution*, 48: 473-492.

Wright, B. W., Wright, K. A., Chalk, J., Verderane, M. P., Fragaszy, D., Visalberghi, E., Izar, P., Ottoni, E. B., Constantino, P. and Vinyard, C. (2009). Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among Capuchins and implications for interpreting morphological variation. *American Journal of Physical Anthropology*, 140: 687-699.

Wynn, J. G. (2000). Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *Journal of Human Evolution*, 39: 411-432.

Wynn, J. G., Alemseged, Z., Bobe, R., Geraads, D., Reed, D. and Roman, D. C. (2006). Geological and palaeontological context of a Pliocene juvenile hominin at Dikika, Ethiopia. *Nature*, 443: 332-336.

Wynn, J. G., Sponheimer, M., Kimbel, W. H., Alemseged, Z., Reed, K., Bedaso, Z. K. and Wilson, J. N. (2013). Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation, Ethiopia. *Proceedings of the National Academy of Sciences*, 110 (26): 10495-10500.

Yamagiwa, J. and Basabose, A. K. (2006a). Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi–Biega National Park. *Primates*, 47: 74-90.

Yamagiwa, J. and Basabose, A. K. (2006b). Effects of fruit scarcity on foraging strategies of sympatric gorillas and chimpanzees. *In*: G. Hohmann, M. M. Robbins, and C. Boesch (eds), *Feeding Ecology of Apes and other Primates*. Cambridge, Cambridge University Press. Pages: 73-96.

Yamagiwa, J. and Basabose, A K. (2009). Fallback foods and dietary partitioning among Pan and Gorilla. *American Journal of Physical Anthropology*, 140: 739-750.

Yamagiwa, J., Basabose, A. K., Kaleme, K. and Yumoto, T. (2005). Diet of Grauer’s gorillas in the montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, 26 (6): 1345-1373.

Yamagiwa, J., Maruhashi, T., Yumoto, T. and Mwanza N. (1996). Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. *In*: W. C. McGrew, L. F. Marchant and T. Nishida (eds) *Great Ape Societies*. Cambridge, Cambridge University Press. Pages; 82-98.

Yamagiwa, J., Yumoto, T. and Maruhashi, T. (1994). Seasonal change in the composition of the diet of Eastern Lowland Gorillas. *Primates*, 35 (1): 1-14.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, 106: 283-295.

Yamashita, N. (1996). Seasonality and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). *International Journal of Primatology*, 17 (3): 355-387.

Yamashita, N. (1998). Functional dental correlates of food properties in five Malagasy Lemur species. *American Journal of Physical Anthropology*, 106: 169-188.

Yamashita, N., Cuozzo, F. P., Sauther, M. L., Fitzgerald, E., Riemenschneider, A. and Ungar, P. S. (2016). Mechanical food properties and dental topography differentiate three populations of *Lemur catta* in southwest Madagascar. *Journal of Human Evolution*, 98: 66-75.

Zanolli, C., Bayle, P., Bondioli. L., Dean, C. M., Luyer, M. L., Mazurier, A., Morita, W. and Macchiarelli, R. (2017). Is the deciduous/ permanent molar enamel thickness ratio a taxon-specific indicator in extant and extinct hominids? *Comptes Rendus Palevol*, 16: 702-714.

Zavada, M. S. and Cadman, A. (1993). Palynological investigations at the Makapansgat Limeworks: an australopithecine site. *Journal of Human Evolution*, 25: 337-350.

Zihlman, A. L., Stahl, D. and Boesch, C. (2008). Morphological variation in adult chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. *American Journal of Physical Anthropology*, 135: 34-41.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, 1: 3-14.

Chapter 9 : Appendix

Appendix A: Hominins information

Appendix A details the condition and state of preservation of the hominins, the palaeoenvironments they are associated with, their dental and mandibular measurements, their reconstructed body sizes, and their stable carbon isotope results. Table 9.1 presents information on the specimens analysed and their state of preservation/ condition.

Table 9.1: Hominin specimens used, their condition and comments from Tables 9.4 – 9.8

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
Australopithecus afarensis		
AL 128-23	Right mandibular fragment with C - M_2	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on M_1 and M_2 corpus breadth measurements.
AL 145.35	Left mandibular corpus with broken P_3, P_4; intact M_1 and M_2	Measurements and description from Johanson *et al*. (1982b). All accessory cusps from this author are listed as present/ absent. Kimbel *et al*. (2004) differ on P_4, M_1 and M_2 corpus breadth measurements.
AL 176.35	P_4	Kimbel *et al*. (2004) do not specify the side from which the measurements were taken, or the condition of the specimens represented, element identified is deduced by measurements available.
AL 188.1	Right mandible fragment with distal root of P_3, P_4, and M_1 roots, and intact M_2, M_3	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on M_2 corpus height measurements.
AL 198.1	Left mandibular corpus with I_1 socket, I_2 root, C to M_3	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4, M_1 and M_2 corpus breadth. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.
AL 198.22	M_1	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_1 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 200.1b	RM_1	Measurements and description from Johanson *et al*. (1982b).
AL 207.13	Fragmentary left mandible with intact P_3, P_4, M_2, and broken M_3	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4 (corpus breadth), M_1 and M_2 (corpus breadth and height) measurements. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.
AL 207.17	M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_3 based on measurements.
AL 225.8	M_2 and M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_2 and M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 228.2	P_4 and M_1	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4 and M_1 based on measurements.

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
		Side used for corpus measurements unknown (left side assumed).
AL 241.14	LM_2	Measurements and description from Johanson *et al*. (1982b).
AL 266.1	Mandible with incisor and canine alveoli, LP_3 to M_1, and RP_3 to M_3	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ in corpus breadth measurements at P_4, M_1 (and height) and M_2. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.
AL 277.1	Left mandible fragment with C to M_2	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4, M_1 and M_2 corpus breadth measurements. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.
AL 288.1	Mandible almost complete. The left P_3 and M3 are isolated. Left M_2, P_3, and C as well as right I_2 and C are represented by empty alveoli. The left M_1, P_4, I_2, I_1, and right I_1 are represented by broken roots.	Measurements from Johanson *et al*. (1982b), accessory cusps information and condition of specimen from Johanson *et al*. (1982c). Kimbel *et al*. (2004) differ on P_4, M_1 and M_2 corpus breadth measurements. Wood (1991); Kimbel *et al*. (2004) report same robusticity index.
AL 311.1	Left mandibular corpus with C - M_3	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4 corpus breadth.
AL 315.22	M_1	Measurements from Kimbel *et al.* (2004), no description of specimen condition available, assumed to be an M_1 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 330.5	P_4-M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4-M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 330.7	P_4 and M_1	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4 and M_1 based on measurements.
AL 333.44	LP_4	Measurements and description from Johanson *et al.* (1982b).
AL 333.74	Left mandible fragment with M_1 - M_3	Measurements and description from Johanson *et al*. (1982b).
AL 333w-1a+b	Left mandible fragment with P_3 to M_2, and right mandible fragment with P_3 to M_2, and RM_3 fragment	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4 corpus breadth, and both height and breadth at M_1 and M_2. Wood (1991); Kimbel *et al*. (2004) report average of this robusticity index.
AL 333w-12	Right mandible fragment with RM_1	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4 and M_1 corpus breadth measurements. Wood (1991); Kimbel *et al.* (2004) report different M_1 robusticity index.
AL 333w-27	Left mandible fragment with LM_2	Measurements and description from Johanson *et al.* (1982b).
AL 333w-32+60	Fragmentary mandible with most of the left corpus with RC, RI_2, LP_3 - M_3. Small fragment of right corpus with M_3.	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on P_4, M_1 and M_2 corpus breadth measurements. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
AL 333w-48	RM_2	Measurements and description from Johanson *et al*. (1982b).
AL 333w-57	Left mandible fragment with M_2 - M_3	Measurements and description from Johanson *et al*. (1982b).
AL 333w-59	Left mandible fragment with M_2 - M_3	Measurements and description from Johanson *et al*. (1982b).
AL 400-1a	Mandible with full dentition (except RI_1).	Measurements and description from Johanson *et al*. (1982b). Kimbel *et al*. (2004) differ on M_1 corpus breadth measurements. Wood (1991); Kimbel *et al*. (2004) report different M_1 robusticity index.
AL 411.1	Right mandible fragment with broken M_1 - M_3	Measurements and description from Johanson *et al*. (1982c).
AL 417.1a	P_4 - M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4- M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 417.1a,b	M_2 and M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_2 - M_3 based on measurements. Measurements are averages.
AL 418.1	M_2	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_2 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 432.1	Condition unknown	Measurements from Kimbel *et al*. (2004), no description of specimen condition available. Side used for corpus measurements unknown (left side assumed).
AL 433.1a	P_4	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4- M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 436.1	Condition unknown	Measurements from Kimbel *et al*. (2004), no description of specimen condition available. Side used for corpus measurements unknown (left side assumed).
AL 437.1	M_2 and M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4- M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 437.2	M_2	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4- M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 438.1	Right mandibular corpus and ramus	Measurements from Kimbel *et al*. (2004), description from Drapaeu *et al*., (2005).
AL 440.1	M_1 and M_2	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_1 - M_2 based on measurements.
AL 443.1	P_4 and M_2	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4 and M_2 based on measurements.
AL 444.2	P_4 and M_1	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4- M_1 based on measurements. Side used for corpus measurements unknown (left side assumed).
AL 465.5	M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_3 based on measurements.
AL 487-1a	M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_3 based on measurements.
AL 582.1l	P_4	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be a P_4 based on measurements. Measurements are averages. Side used for corpus measurements unknown (left side assumed).
AL 620.1	M_3	Measurements from Kimbel *et al*. (2004), no description of specimen condition available, assumed to be an M_3 based on measurements. Side used for corpus measurements unknown (left side assumed).
DIK-2-1	Left mandibular corpus and a	Measurements and description from Alemseged *et al*. (2005).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
	portion of the symphysis. The P_3, M_1, M_3, and part of M_2 crown were recovered.	
LH2	Mandible with intact crowns R + L dm_2; unerupted crowns R + L I_1, C, P_3; damaged crowns R + L dC, dm_1, M_1; broken roots R + L dI_1, dI_2.	Measurements and description from White (1977).
LH3	Isolated permanent and deciduous teeth from both the mandible and maxilla. Mandibular dentition: RdC, Rdm_1, I, R + L C, RP_3, R + L P_4, R + LM_1.	Measurements and description from White (1977). All accessory cusps identified by this author are listed as present/ absent.
LH 4	Mandibular corpus with broken RC, RM_1, RM_2; intact R & L P_4; RP_3, M_3; LM_1, LM_2	Measurements and description from White (1977). Kimbel *et al*. (2004) provide averages of these measurements.
LH 14	Isolated teeth: LI_1 - LC, LP_4; RI_1 - RC, RM_1 or $_2$.	Measurements and description from White (1977).
MAK-VP1/2	Right side of mandible, with condyle, M_1 - M_3.	Measurements and description from White *et al*. (2000). Kimbel *et al*. (2004) provide the same measurements.
MAK-VP1/4	RM_2	Measurements and description from White *et al*. (1993)
MAK-VP1/12	Mandible with LI_2 - LM_3. RP_3 - RM_3.	Measurements and description from White *et al*. (2000). Kimbel *et al*. (2004) provide averages of these measurements.
Australopithecus africanus		
MLD 2	Subadult mandible with LP_4 - LM_2, RI_1 - RP_3, RM_1 – RM_2	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_2s changed to reflect principle cusps present.
MLD 4	RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
MLD 18	Mandible with LI_1-LP_4, RI_1-RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
MLD 19	LM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_3s changed to reflect principle cusps present.
MLD 24	LM_2	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
MLD 34	Mandible with RM_2 and RM_3 roots	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
MLD 40	Left mandibular corpus with C-root of M_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).

Species/ Specimen	**Condition**	**Comments on measurements from Tables 9.4 – 9.8**
Sts 7	Mandible with M_2 and M_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
Sts 36	Adult mandible	Measurements and description from de Ruiter *et al*. (2013).
Sts 52	Mandible with full dentition	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_2s and LM_3 changed to reflect principle cusps present.
Taung	Juvenile cranium and mandible with M_1	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_1s changed to reflect principle cusps present.
Stw 1	LM_1	Measurements and description from Moggi-Cecchi *et al*. (2006). All accessory cusps identified by this author are listed as present/ absent.
Stw 3	LM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 14	Mandible with teeth: RP_3, RM_1 - RM_3, LP_4, LM_1 (in pieces) -LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 47	RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 54	LM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 56	LP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 61	RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006). Inconsistent use of term postmetaconulid (described by Swindler (2002) as a synonym for a protostylid), but here referred to as a feature present on the distal ridge of the metaconid, similar to location of the C7.
Stw 72	LM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 80	Mandible with teeth: Complete, except no RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 87	RP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 90	RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006). Postmetaconulid referred to as a separate trait from the C6 and C7.
Stw 96	LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 106	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 109	Right mandibular fragment M_2-M_3	Measurements and description from Moggi-Cecchi *et al*. (2006). An incipient C7 occurs in the form of a postmetaconulid.
Stw 112	LP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 120	LM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 123	LM_1 and RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006). An incipient postmetaconulid is present.
Stw 131	Right mandibular fragment with P_4 - M_1 and LP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 133	LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 134	LM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 142	Right mandibular fragment with C, P_3, P_4, M_1 and LM_1 - LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
Stw 145	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 147	RP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 151	Associated lower teeth	Measurements and description from Moggi-Cecchi *et al*. (2006). Additional measurements and accessory cusp information (listed as present/ absent) from Moggi-Cecchi *et al*., (1998).
Stw 193	Isolated mandibular teeth: LP_4, LM_1, LM_2, RP_3, RP_4	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 196	LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006). Uncertainty about whether a feature is a postmetaconulid or a C7, a C7 has been included in the spreadsheet.
Stw 212	Isolated mandibular teeth: LP_3 - LM_3, RP_4, RM_2 - RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 213	Isolated mandibular teeth: LC-LM_2, RC-RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 220	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 234	RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 237	LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 246	LM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 280	Maxillary and mandibular teeth: RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006). Incipient development of a postmetaconulid.
Stw 285	LM_2 and RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 291	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 295	Isolated mandibular teeth: RM_1-RM_3, LM_1 - LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 308	RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 309	LM_1 and RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 327	Left mandibular corpus: LP_4 - LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 353	RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006). Possible postmetaconulid present.
Stw 364	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 384	Right mandibular corpus: RP_4 - RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 385	Left mandibular fragment with M_2 - M_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 397	RM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 404	Right mandibular corpus: RC - RM_3, and LM_3	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 412	LM_2 and RM_2	Measurements and description from Moggi-Cecchi *et al*. (2006). A large but incipiently developed postmetaconulid, but no C7.

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
Stw 413	LP$_4$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 421	LM$_1$ and RM$_1$	Measurements and description from Moggi-Cecchi *et al*. (2006). An incipient postmetaconulid.
Stw 424	LM$_2$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 487	Isolated mandibular teeth: LP$_4$, RM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 491	Isolated mandibular teeth: RI$_1$, RC, RP$_4$, LC, LM$_1$ - LM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 498	Left and right mandible	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 520	RM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 529	Maxillary and mandibular teeth: RM$_2$ -RM$_3$, LM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 537	Isolated mandibular teeth: LI$_2$, LC, LP$_4$-LM$_3$, RI$_2$, RC, RM$_2$, RM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 555	LM$_2$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Stw 560	Isolated mandibular teeth: LP$_4$ - LM$_3$, RM$_2$ - RM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006). A well-developed postmetaconulid (c.f. C7).
Stw 566	RM$_1$	Measurements and description from Moggi-Cecchi *et al*. (2006). A small C7 and a postmetaconulid are present.
Stw 586	LM$_3$	Measurements and description from Moggi-Cecchi *et al*. (2006).
Paranthropus boisei		
KGA 10-525	Partial skull	Measurements and description from Suwa *et al*. (1997).
KGA 10-570	Juvenile mandible	Measurements and description from Suwa *et al*. (1997).
KGA 10-1720	LM$_3$	Measurements and description from Suwa *et al*. (1997).
KGA 10-2705	RM$_2$	Measurements and description from Suwa *et al*. (1997).
KNM-ER 403	Right mandibular fragment	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 404	Right mandibular fragment	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 725	Left mandibular body	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 726	Left mandibular body	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 727	Right mandibular fragment	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 728	Right mandibular body	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 729	Mandible	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007). Cusp numbers from RM$_2$ and both M$_3$s changed to reflect principle cusps present.
KNM-ER 733	Skull fragments	Measurements and cusp numbers on RM$_3$ from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 801	Right mandibular body, plus LM$_3$ crown	Measurements from Wood (1991), condition of specimen from Oakley *et al.* (1977). Cusp numbers from RM$_2$ and both M$_3$s changed to reflect principle cusps present.

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
KNM-ER 802	Mandible RP_4-RM_1, RM_3, LP_4 - LM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from RM_1, LM_2 and both M_3s changed to reflect principle cusps present.
KNM-ER 805	Mandible fragment	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 810	Left mandibular body with LM_3	Measurements and condition of specimen from Wood (1991).
KNM-ER 818	Left adult mandible	Measurements and condition of specimen from Wood (1991).
KNM-ER 1171	LP_4, LM_2, RM_1 - RM_2	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from RM_1 and both M_2s changed to reflect principle cusps present.
KNM-ER 1467	RM_3	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991).
KNM-ER 1468	Right mandibular body	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991). Wood (1991) differs from all M_1 and M_2 measurements (except M_2 corpus height).
KNM-ER 1469	Left mandibular body	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991). Wood (1991) differs from all M_1 and M_2 measurements.
KNM-ER 1477	Juvenile mandible	Measurements and description from Day *et al*. (1976). Wood (1991) differs on symphyseal height.
KNM-ER 1509	LM_1 and LM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al.*, (1977). Cusp numbers from LM_3 changed to reflect principle cusps present.
KNM-ER 1803	Right mandibular body	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991). Wood (1991) concurs with corpus measurements at M_1.
KNM-ER 1806	Edentulous adult mandible	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991). Wood (1991) differs on symphyseal measurements.
KNM-ER 1816	Fragmentary juvenile mandible	Measurements and description from Day *et al*. (1976), additional measurements from Wood (1991). Wood (1991) differs on measurements for P_4, M_1 and M_2 (MD). Cusp numbers from LM_2 changed to reflect principle cusps present.
KNM-ER 1819	LM_3	Measurements and condition from Wood (1991). Cusp numbers from LM_3 changed to reflect principle cusps present.
KNM-ER 1820	Left juvenile mandible	Dental measurements from Wood (1991), symphyseal measurements and description from Day *et al*. (1976). Wood (1991) differs on symphyseal measurements. Cusp numbers from LM_1 changed to reflect principle cusps present.
KNM-ER 3229	LP_4 and RP_4	Measurements from Wood (1991) and description from Leakey & Walker (1985).
KNM-ER 3230	Adult mandible with complete dentition	Measurements and condition from Wood (1991), non-metric trait information from Leakey & Walker (1985). Cusp numbers from RM_2 and RM_3 changed to reflect principle cusps present.
KNM-ER 3729	Eroded left mandibular fragment	Measurements and condition from Wood (1991).
KNM-ER 3731	Left mandibular body	Measurements and condition from Wood (1991).
KNM-ER 3737	Associated dentition including: RM_1 and RM_3	Measurements from Wood (1991), condition of specimen from Grine (1988). Cusp numbers from RM_3 changed to reflect principle cusps present.
KNM-ER	RP_4: unworn crown	Measurements from Wood (1991), condition of specimen from Leakey & Walker (1985).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
3885		
KNM-ER 3889	Mandible fragment	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
KNM-ER 3890	Left lower molar	Measurements from Wood (1991), condition of specimen from Leakey & Walker (1985). Cusp numbers from LM_1 changed to reflect principle cusps present.
KNM-ER 3954	Weathered edentulous adult mandible.	Measurements and condition from Wood (1991),
KNM-ER 5429	Fragmentary adult mandible	Measurements and condition from Wood (1991).
KNM-ER 5679	Isolated tooth: LM_2	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007). Cusp numbers from LM_2 changed to reflect principle cusps present.
KNM-ER 5877	Right side of mandible with RM_3	Measurements and description from Leakey & Walker (1985). Non-metric data from Wood (1991).
KNM-ER 15930	Left mandibular body	Measurements and description from Leakey & Walker (1988). Wood (1991) differs on all measurements, except M_2 corpus height.
KNM-ER 15940	LM_3 and RM_3	Measurements and description from Leakey & Walker (1988).
KNM-ER 15950	LM_3: heavily weathered	Measurements and description from Leakey & Walker (1988).
KNM-ER 16841	Edentulous mandible	Measurements and description from Leakey & Walker (1988). Wood (1991) differs on all measurements, except P_4 and M_3 corpus width.
KNM-WT 17396	LM_3	Measurements and description from Leakey & Walker (1988).
OH 26	RM_3 mesial crown. Although Wood & Constantino (2007) describe this as a maxillary molar.	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
OH 30	Deciduous and permanent dentition: LM_1	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007). Cusp numbers from LM_1 changed to reflect principle cusps present.
OH 38	RM_2 and two incisors	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007).
OMO 136-1	LM_3	Measurements from Coppens (1973b*), condition of specimen from Howell & Coppens (1974).
OMO 136-2	LM_3 crown	Measurements from Coppens (1973a*), condition of specimen from Howell & Coppens (1974).
OMO 47-46	RM_2: worn	Measurements from Coppens (1971*), condition of specimen from Howell & Coppens (1974).
OMO 75-14	Associated teeth: LP_3-LM_3, RP_3-RM_3	Measurements from Coppens (1971*), condition of specimen from Howell & Coppens (1974).
OMO 84-100	RM_3	Measurements from Coppens (1973a*), condition of specimen from Howell & Coppens (1974).
OMO F203-1	RM_3	Measurements from Coppens (1973b*), condition of specimen from Howell & Coppens (1974).
OMO L427-7	Right hemi-mandible with M_2	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
OMO L628-2	LM_3	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
OMO L628-3	LM_3	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
OMO L628-4	LP_4	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
OMO L628-9	LM_2	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
OMO L7A-125	Mandible with complete dentition, except incisors	Measurements from Howell (1969), with additional measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
OMO L74A-21	Right hemi-mandible with P_4	Measurements from Wood (1991), condition of specimen from Howell & Coppens (1974).
Peninj 1	Mandible	Measurements from Wood (1991), condition of specimen from Wood & Constantino (2007). Cusp numbers from LM_1 and both M_3s changed to reflect principle cusps present.
Paranthropus robustus		
DNH 7	Cranium and mandible, both complete with dentition	Measurements and description from Keyser (2000).
DNH 8	Mandible with complete dentition	Measurements and description from Keyser (2000). All non-metric data for the Drimolen material is from Moggi-Cecchi *et al*. (2010).
DNH 10	Right mandibular fragment with M_3	Measurements and description from Keyser *et al*. (2000).
DNH 12	RM_3	Data and description from Moggi-Cecchi *et al*. (2010).
DNH 18	RM_3	Measurements and description from Keyser *et al*. (2000).
DNH 19	Left mandibular body with P_3, P_4, M_1, M_2 and M_3	Measurements and description from Keyser *et al*. (2000).
DNH 21	Left mandibular body with M_2, M_3	Measurements and description from Keyser *et al*. (2000).
DNH 26	RP_4	Measurements and description from Keyser *et al*. (2000).
DNH 27	LP_4	Measurements and description from Keyser *et al*. (2000).
DNH 46	RM_1	Measurements from Keyser *et al*., (2000). Non-metric data and condition from Moggi-Cecchi *et al*., (2010).
DNH 51	Right mandibular fragment with P_3, P_4, M_1, M_2, M_3	Measurements and description from Keyser *et al*., (2000).
DNH 60	Cranial fragments and associated teeth (Rdm_1, Rdm_2, RM_1, RM_2)	Measurements from Keyser *et al*. (2000). Non-metric data and condition from Moggi-Cecchi *et al*. (2010).
DNH 67	RM_1	Measurements and description from Moggi-Cecchi *et al*. (2010).
DNH 68	Right mandibular body (fragments) with C (fragment), P_3, P_4, M_1, M_2, M_3	Measurements and description from Keyser *et al*. (2000).
DNH 75	RM_3	Measurements and description from Keyser *et al*. (2000).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
DNH 81	RM_1	Measurements from Keyser *et al*. (2000). Non-metric data and condition from Moggi-Cecchi *et al*. (2010).
SK 6	Mandible with LP_3 - LM_3 and RP_4 - RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_1s and M_2s changed to reflect principle cusps present.
SK12	Mandible with LP_3 - LM_3 and RP_3 - RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al.* (1977). Cusp numbers from LM_3 changed to reflect principle cusps present.
SK 23	Mandible with complete dentition	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from LM_2 and RM_3 changed to reflect principle cusps present.
SK 34	Mandible with LP_4 - LM_3, RI_1 - RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al.* (1977). Cusp numbers from both M_2s and M_3s changed to reflect principle cusps present.
SKW 5	Mandible	Measurements and description from Grine & Daegling (1993). Grine (1993) also reports the same measurements for the teeth dimensions, but reports different measurements for all corpus height and breadth.
SKW 10	RM_1: buccal and distal portions of crown	Measurements and description from Grine & Strait (1994). Grine (1993) reports the same measurements for the teeth dimensions.
SKW 34	Right mandibular corpus	Measurements and description from Grine & Strait (1994). Grine (1993) reports the same measurements for the teeth dimensions.
SKW 4767	RM_1: complete crown with damaged roots	Measurements and description from Grine & Strait (1994). Grine (1993) reports the same measurements for the teeth dimensions.
SKW 4769	LM_2: distal portions of cracked crown	Measurements and description from Grine & Strait (1994). Grine (1993) reports the same measurements for the teeth dimensions.
SKX 257	RM_1	Measurements and description from Grine (1989). Grine (1993) reports the same measurements for the teeth dimensions.
SKX 258	LM_1	Measurements and description from Grine (1989). Grine (1993) reports the same measurements for the teeth dimensions.
SKX 4446	Subadult mandible with RP_4, RM_1 and RM_2	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements, except for the symphyseal width (reports 26.7mm).
SKX 5002	LM_3: complete crown	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements.
SKX 5013	Partial left mandibular corpus with distal root of P_4, intact M_1, M_2 root neck and incomplete M_3 root socket	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements.
SKX 5014	RM_3	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements.
SKX 5015	LM_3: distal crown portion	Data and condition from Grine (1989)
SKX 5023	RM_1: complete and worn crown	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements.
SKX 19892	LM_2: incomplete and worn crown	Measurements from Grine (1988), condition of specimen from Grine (1989). Grine (1993) reports the same measurements.
SKX 32162	RP_4: incomplete and unworn crown	Measurements from Grine (1988), condition of specimen from Grine (1989).
TM 1517	Mandible with RP_3 - M_3 and associated LP_3 and LP_4	Measurements and description from Thackeray *et al*. (2001). Non-metric trait information from Wood (1991).
TM 1536	Right mandible with RI_1,	Measurements and description from Thackeray *et al*. (2001).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
	Rdi$_2$, Rdc$_1$, Rdm$_1$-$_2$, RM$_1$, Ldc, Ldm$_1$	
TM 1600	Left mandible fragment with P$_3$, M$_2$-M$_3$	Measurements and description from Thackeray *et al*. (2001).
TM 1601b	LP$_4$	Measurements and description from Thackeray *et al*. (2001).
KB 5223	Isolated permanent and deciduous mandibular teeth: Ldc, Ldm$_1$, Ldm$_2$, LI$_1$, LI$_2$, Lc, LM$_1$, Rdm$_2$, RI$_1$, RI$_2$, RM$_1$	Measurements and description from Thackeray *et al*. (2001).
Homo habilis		
OH 7	Mandible with LI$_1$ - LM$_2$, RI$_1$ - RM$_1$	Measurements from Wood (1991), condition of specimen from Oakley *et al.* (1977). Cusp numbers from LM$_2$ changed to reflect principle cusps present.
OH 13	Mandible with complete dentition	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M$_3$s changed to reflect principle cusps present.
OH 16	Mandible RI$_2$ - RM$_3$, LI$_1$ - LM$_3$	Measurements from Wood (1991), condition of specimen from Oakley *et al.* (1977). Cusp numbers from RM$_2$ and both M$_3$s changed to reflect principle cusps present.
OH 37	Left mandibular corpus with M$_1$ - M$_2$, roots of I$_2$, C, P$_4$ and M$_3$	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
KNM-ER 817	Left mandibular body	Measurements and description from Leakey & Wood (1973).
KNM-ER 819	Cracked and eroded left mandibular body.	Measurements and description from Wood (1991). Assigned to *H. habilis* by Brown & Walker (1993).
KNM-ER 1462	LM$_3$ crown	Measurements and description from Leakey & Wood (1974).
KNM-ER 1480	RM$_3$ crown	Measurements and description from Leakey & Wood (1974).
KNM-ER 1482	Mandible with RP$_4$, LP$_4$ - LM$_3$, roots of RI$_2$ - RM$_1$, LI$_2$, C, LM$_1$	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from LM$_3$ changed to reflect principle cusps present.
KNM-ER 1483	Fragmentary adult mandible	Measurements from Wood (1991), condition of specimen from Leakey & Wood (1974).
KNM-ER 1501	Right mandibular corpus with roots of C-M$_3$	Measurements from Leakey & Wood (1974), Wood (1991), and description from Oakley *et al*. (1977).
KNM-ER 1502	Right mandibular body	Measurements and description from Leakey & Wood (1974). Additional measurements and non-metric information from Wood (1991). Cusp numbers from RM$_1$ changed to reflect principle cusps present. Brown & Walker (1993) report the same dental measurements, but assign it to *H. ergaster*.
KNM-ER 1508	RM$_1$ or $_2$	Measurements and description from Leakey & Wood (1974).

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
KNM-ER 1590	Cranium and mandibular LM_2	Measurements and description from Day *et al*. (1976).
KNM-ER 1801	Left mandibular body	Measurements and description from Day *et al*. (1976). Wood (1991) differs on dental measurements for P_4 and M_1, and measurements for M_1 corpus thickness.
KNM-ER 1802	Well-preserved mandibular body	Measurements and description from Day *et al*. (1976). Wood (1991) differs on dental measurements for P_4, M_1 and M_2, and symphyseal thickness. Cusp numbers from both M_1s and M_2s changed to reflect principle cusps present. Brown & Walker (1993) report the same dental measurements.
KNM-ER 1805	Cranium and mandible	Measurements and description from Day *et al*. (1976). Wood (1991) differs on dental measurements for M_2 and M_3 (MD), but concurs with M_1 corpus height.
KNM-ER 3734	Left mandibular body	Measurements and description from Wood (1991). Assigned to *H. habilis* by Brown & Walker (1993).
KNM-ER 3950	Adult mandibular symphysis	Measurements and description from Wood (1991). Assigned to *H. habilis* by Brown & Walker (1993).
KNM-ER 60000	Nearly complete mandible	Measurements and description from Leakey *et al*. (2012) (S.I.). Coronoid height: [96]; Condyle height: 89.
KNM-ER 62003	Right mandibular fragment	Measurements and description from Leakey *et al*. (2012) (S.I.).
UR 501	Mandibular corpus broken in half	Measurements and description from Bromage *et al*. (1995). Shrenk *et al*. (1993) also provide measurements for mandibular and dental metrics. But the measurements from Bromage *et al*. (1995) were used because they followed the method of Wood (1991). Cusp numbers from RM_2 changed to reflect principle cusps present.
KNM-WT 42718	RM_1	Measurements and description from Prat *et al*. (2005).
Homo ergaster		
KGA 10-1	Left mandibular body	Measurements and description from Suwa *et al*. (2007). Accessory cusps defined as present/absent.
KNM-BK 67	Young adult mandible LM_2 - LM_3, roots of LP_3-LM_1, RP_3-RM_3, alveoli of Left and Right I_1-C	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from LM_3 changed to reflect principle cusps present.
KNM-BK 8518	Mandible	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
KNM-ER 730	Mandible	Measurements and condition from Day & Leakey (1973), additional measurements and LM_3 cusp numbers from Wood (1991). Brown & Walker (1993) report the same dental measurements.
KNM-ER 731	Left mandibular fragment	Measurements and condition from Day & Leakey (1973), additional measurements from Wood (1991).
KNM-ER 806	LM_1 - LM_3, RM_3	Measurements and condition from Leakey & Wood (1973), additional measurements from Wood (1991). Cusp numbers from all left mandibular molars changed to reflect principle cusps present.
KNM-ER 809	LM_1	Measurements and condition from Leakey & Wood (1973).
KNM-ER 820	Juvenile mandible	Measurements and condition from Leakey & Wood (1973), additional measurements from Wood (1991). Brown & Walker (1993) report the same dental measurements.

Species/ Specimen	Condition	Comments on measurements from Tables 9.4 – 9.8
KNM-ER 992	Adult mandible	Measurements and condition from Leakey & Wood (1973), additional measurements from Wood (1991). Brown & Walker (1993) report the same dental measurements.
KNM-ER 1507	Juvenile left mandibular body	Measurements and condition from Leakey & Wood (1974), additional measurements from Wood (1991). Cusp numbers from LM_1 changed to reflect principle cusps present. Brown & Walker (1993) report the same dental measurements.
KNM-ER 1808	Fragmentary mandible RM_2 - RM_3	Measurements from Wood (1991) and Brown & Walker (1993), condition of specimen from Oakley *et al*., (1977). But Brown & Walker (1993) list this as left sided dentition, and the measurements from RM_2 as LM_3.
KNM-ER 1812	Fragmentary right mandible	Measurements from Wood (1991), additional observation and condition of specimen from Day *et al*. (1976). Both differ on reports of symphyseal thickness.
KNM-WT 15000	Mandible with right and left dentition from C - M_2.	Measurements and description from Brown *et al*. (1985). Additional measurements from Brown & Walker (1993) and Wood (1991). Measurements from Brown & Walker (1993) differ from those of Brown *et al*. (1985) on LP_4 (BL), RM_1 (MD), LM_1 (MD and BL), both M_2s (MD and BL).
OH 22	Right mandibular corpus with P_3 - M_2, and roots of I_1- C, M_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
OH 23	Left mandibular corpus P_4-M_2 (abraded) and roots of P_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977).
OH 51	LM_1	Measurements from Wood (1991), no description of specimen condition available, assumed to be LM_1 based on measurements.
SK 15	Mandible LM_1 - LM_3, RM_2 - RM_3	Measurements from Wood (1991), condition of specimen from Oakley *et al*. (1977). Cusp numbers from both M_3s changed to reflect principle cusps present.

* cited in Wood (1991). It was not possible to obtain access to the original specimen reports from Coppens.

See Oakley *et al*., (1977), along with the original specimen reports cited above for further information about each specimen, including the exact unit in which each were found.

Table 9.2 provides the reconstructed environments for each site and stratigraphic layer associated with hominin fossils. Table 9.3 provides the same information for those hominins of questionable/ unknown taxonomic attribution.

Table 9.2: Hominin sites of occupation, dates of presence and reconstructed palaeoenvironments

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
*A. afarensis****	Hadar Formation	Basal member	3.8 - 3.42	Mosaic of woodland and shrubland, near water	Johanson *et al*. (1982a); Alemseged *et al*. (2005); Wynn *et al*. (2006); Reed (2008)	Dikika specimen comes from this Member (Alemseged *et al*., 2005)
		Sidi Hakoma Member	3.42 - 3.26	Medium - open density woodland, grassland, shrubland	Johanson *et al*. (1982a); Reed (1997, 2008)	Most hominins come from the Sidi Hakoma and Denen Dora Members (Johanson *et al*., 1982a)
		Denen Dora Member	3.26 - 3.2	Mixed habitats, woodland, bushlands, edaphic grasslands, wetlands	Johanson *et al*. (1982a); Reed (1997, 2008)	
		Kada Hadar	3.2 - 3.12	KH-1: Open woodland with some edaphic grassland	Reed (2008)	A.L. 288-1 near the base of this Member (White *et al*., 1984)
			3.12 - 2.94	KH-2: Open woodland/ shrubland	Reed (2008)	A.L. 438 and A L. 444 found in this horizon (Kimbel *et al*., 1997)
	Koobi Fora: Turkana Basin	Tulu Bor	3.36 - 3	Scrub woodland and flooding river.	Reed (1997)	
	Omo: Usno Formation	U-10	3.6 - 2.7	Wooded riverine habitat with some edaphic grasslands	Reed (1997); Brown (1994)	
	West Turkana: Nachukui Formation	Kataboi and Lomekwi Members	3.6 - 3.3	Mosaic habitats of woodland and forest, but becoming increasingly dry and open	Harris *et al*. (1988); Leakey *et al*. (2001); Bobe (2011)	
	Kantis	Kantis Fossil Site	3.45 - 2.77	Open landscape with secondary closed landscapes	Mbua *et al*. (2016)	
	Laetoli	Upper Unit Laetolil Beds	3.76 - 3.46	Heavy woodland-bushland cover	Andrews (1989); Leakey *et al*. (1995); Reed (1997, 2008); Kovarovic & Andrews (2007)	Andrews (1989) provides the chronology for this site.
		Upper Unit Laetolil Beds	3.76 - 3.46	Lightly wooded to open habitats. Grassland savannah with seasonal aridity. Areas of thicker vegetation nearby.	Hay (1987); Bonnefille & Riollet (1987); Leakey *et al*. (1995); Louys *et al*. (2015b)	Musiba *et al*. (2007) and Su and Harrison (2007, 2008) describe Laetoli as a mosaic of woodland, shrubland, bushland and grassland, which follows the transition of environments through the two members.
		Ndolanya Beds	2.6	Open grassland and light woodland/ bushland cover	Kovarovic *et al*. (2002); Kovarovic & Andrews (2007)	
	Maka	SHT/ Tulu Bor Tuff	3.85 - 3.4	Intermediate between open, dry and closed, mesic environments	White *et al*. (1993)	

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
A. africanus	Sterkfontein	Member 4	2.65 - 2.0	Open woodland, riparian forest, bushland and grassland	Reed (1997); Reynolds & Kibii (2011); Pickering & Kramers (2010); Herries *et al*. (2013)	Pickering & Kramers (2010) and Herries *et al*. (2013) report on the chronology of this site. Although see Pickering *et al*. (2011) for a slightly broader time frame, and Wood & Strait (2004) for a narrower time frame.
		Silberberg Grotto	3.67 - 2.2	Riverine gallery forest, with grassland nearby	Reynolds & Kibii (2011); Herries & Shaw (2011); Granger *et al.*, (2015)	Herries & Shaw (2011) provide the lower limits; and Granger *et al*. (2015) provide the upper limits for this site.
		Jacovec Cavern	< 2.4	Mosaic of open and closed habitats, riverine gallery forest and bushland	Reynolds & Kibii (2011); Herries *et al*. (2013)	Herries *et al*. (2013) provide chronology for this site.
	Makapansgat	Member 3	2.9 - 2.6	Mosaic habitat, riparian woodland, bushland, and edaphic grassland. Dramatic vegetation shift occurred during this time.	Cadman & Rayner (1989); Reed (1997); Behrensmeyer & Reed (2013); Herries *et al*. (2013)	Different interpretations have been given for Makapansgat, but this is likely a reflection of material being extracted from different times of deposition (Cadman and Rayner, 1989). Herries *et al.* (2013) provide chronology for these sites.
		Member 4	2.7 - 2.5	Diversity of habitats, ranging from woodland (riparian habitats) - bushland (dryer habitats)	Zavada & Cadman (1993); Reed (1997); Herries *et al.* (2013)	
	Gladsyvale	Gladysvale Breccia Dumps	2.4 - 2.0	Closed vegetation	Behrensmeyer & Reed (2013); Herries *et al*. (2013)	Herries *et al*. (2013) provide chronology for this site.
	Taung	Taung Dart Deposits	3.0 - 2.6	Dense woodland	Behrensmeyer & Reed (2013); Herries *et al*. (2013)	Herries *et al*. (2013) provide chronology for this site.
P. boisei	Koobi Fora: Turkana Basin	Burgi	3.0 - 2.0	Open woodland, edaphic grasslands and riparian woodland	Reed (1997)	
		KBS Member	1.88 - 1.6	Grassland/ shrubland environment	Reed (1997)	
		Okote Member	1.6 - 1.39	Wetlands and edaphic grasslands	Reed (1997)	
	Omo: Shungura Formation	Member G	2.33 - 1.8	Open woodland, edaphic grasslands, river nearby	Reed (1997); Plummer *et al*. (2015)	
	Olduvai Gorge	Bed I: FLKN	1.85 - 1.84	Freshwater spring	Clarke (2012); McHenry (2012); Ashley *et al*. (2014)	Presence here according to Clarke (2012). Site description from Ashley *et al*. (2014). Dates are estimations based

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
						on Figure 3 in McHenry (2012)
		Bed I: FLKNN	1.85 - 1.84	Closed/ freshwater spring surrounded by wetlands	Shipman & Harris (1988); Ashley *et al*. (2010); McHenry (2012); Uribelarrea *et al*, (2014)	Dates are estimations based on Figure 3 in McHenry (2012)
		Bed I: FLK-Zinj	1.84 - 1.79	Closed/ wet habitat. Palm and *Acacia* woodland. Alternatively reconstructed as being grassland, woodland and bushland.	Shipman & Harris (1988); Ashley *et al*. (2010); McHenry (2012); Uribelarrea *et al*, (2014)	Lower limits of dates are based on estimations from Figure 3 in McHenry (2012). For alternative reconstruction see Reed (2008).
		Bed II: BK Locality	1.79 - 1.15	Closed/ wet habitat	Shipman & Harris (1988); Ashley *et al*. (2010); Stanistreet (2012)	Exact locality dates not available so dates of Bed II obtained from Stanistreet (2012)
		Bed II: HWK Locality	1.79 - 1.15	Open/ arid. Alternatively reconstructed with abundant springs and wetlands	Shipman & Harris (1988); Ashley *et al*. (2010); Stanistreet (2012)	See Ashley *et al*. (2010) for alternative environmental reconstruction. Exact locality dates not available so dates of Bed II obtained from Stanistreet (2012)
	Peninj Humbu Formation	Lake Natron	1.7 - 1.3	Savannah grassland	Dominguez-Rodrigo *et al*. (2001); Schwartz & Tattersall (2005)	Schwartz & Tattersall (2005) provide chronology of this site.
	Konso		1.4	Dry grassland	Suwa *et al*. (1997)	
	Lake Malawi	Chiwondo Beds 3A: Malema	~2.5 - 2.3	Open environment: grass-bushland habitats	Kullmer *et al*. (1999); Sandrock *et al*. (2007)	
	Chesowanja	Chemoigut	1.4 - 1.1	Bushed grassland habitat, with riverine and lacustrine elements	Carney *et al*. (1971); Bishop *et al*. (1978); Wood & Strait (2004)	Carney *et al*. (1971) provide lower limits of site date; Bishop *et al*. (1978) provide description but information obtained from Wood & Strait (2004), who also provide upper limits of the site.
	West Turkana	Lokalalei Member: Kokiselei: I	1.86 - 1.53	Mosaic habitat ranging from closed/wet and closed/dry to open edaphic grasslands, or wet grasslands	Leakey & Walker (1988); Shipman & Harris (1988); Bobe *et al*. (2007); Bobe (2011)	Leakey & Walker (1988) describe position of locality. Bobe *et al*. (2007) provide dates for Tuffs. Shipman & Harris (1988) and Bobe (2011) give time- and region-specific environmental descriptions, they are not site specific.
		Lokalelei member: Kaito	1.86 - 1.6	Closed, wet woodland habitat	Harris *et al*. (1988); Shipman & Harris (1988); Wood & Strait (2004)	Presence here according to Wood & Strait (2004). Position of Unit according to Harris *et al*. (1988).

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
P. robustus	Coopers: Monte Cristo Formation	Cooper's Cave D	1.62 - 1.4	Grassland with woodlands and water source nearby.	de Ruiter *et al*. (2009); Pickering *et al*. (2011); Herries & Adams (2013)	Chronology from Pickering *et al*. (2011) and Herries & Adams (2013), which has updated the earlier estimations from Berger *et al*. (2003); Steininger *et al*. (2008) and de Ruiter *et al*. (2009). N.B. Hominin remains were also identified from Cooper's A and B, but it has not been possible to obtain information regarding the two site's deposition chronology or their reconstructed environments.
	Drimolen		2 - 1.5	Mixed environment with grassland	Keyser (2000)	Herries *et al*. (2009) provide a narrower time frame of 1.9 - 1.6mya, alternatively Herries & Adams (2013) report an age of 2.0 - 1.4mya. Given that the time range has not changed too much since the original specimen report, it was decided to maintain the original dating estimates.
	Kromdraai B	Member 3	1.8 - 1.6	Open grassland with riparian woodland	Reed (1997)	Chronology from Herries & Adams (2013), who provide a narrower time frame than does Reed (1997), but slightly greater time-frame than the earlier work by Herries *et al*. (2009).
	Sterkfontein	Member 5b	1.4 - 1.1	Open or wooded grassland/ plains region	Reed (1997); Herries *et al*. (2009); Pickering & Kramers (2010); Herries & Adams (2013)	Chronology from Herries *et al*. (2009) and Herries & Adams (2013). Member position from Pickering & Kramers (2010). Reed does not distinguish between Members 5A-C in the description of the site.
	Swartkrans	Member 1	2.31 - 1.64	Open habitat with a riverine woodland nearby	Reed (1997); Elton, 2001; Pickering *et al*. (2011); Herries & Adams (2013)	This member includes Lower Bank and Hanging Remnant, dates from Pickering *et al*. (2011) and Herries & Adams (2013) (more refined than those earlier provided by Herries *et al*. (2009). Reed does not distinguish between the two levels in the description of the site.
		Member 2	1.7 - 1.1	Wooded grassland with wetlands. Alternatively:	Reed (1997); Herries *et al*. (2009); Herries & Adams (2013)	Chronology from Herries *et al*. (2009) and Herries & Adams (2013). Open

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
				open habitat.		habitat according to Elton (2001).
		Member 3	1.3 - 0.6	Open edaphic grasslands with a river/ stream	Reed (1997); Herries & Adams (2013)	Chronology from Herries & Adams (2013), which partially overlaps Herries *et al*. (2009)
H. habilis	Koobi Fora: Turkana Basin	Burgi	3.0 - 2.0	Open woodland, edaphic grasslands and riparian woodland	Reed (1997)	
		KBS Member	1.88 - 1.6	Grassland/ shrubland environment	Reed (1997)	Presence here according to Kimbel *et al*. (1997)
		Okote Member	1.6 - 1.39	Wetlands and edaphic grasslands	Reed (1997)	Presence here according to Wood & Strait (2004)
	Omo: Shungura Formation	Member G	2.33 - 1.8	Open woodland, edaphic grasslands, river nearby	Reed (1997); Plummer *et al*. (2015)	
	West Turkana: Nachukui Formation	Kalochoro Member: Lokalalei 1α	2.4 - 2.3	Mosaic habitat, wet grassland, marsh or lagoon conditions associated with this site	Harris *et al*. (1988); Prat *et al*. (2005); Tiercelin *et al*. (2010)	Site and date information from Prat *et al*., (2005). Habitat description is from Tiercelin *et al*. (2010)
	Hadar Formation	Kada Hadar	2.92 - 2.33	Dry, open habitat	Kimbel *et al*. (1997)	A.L. 666 found between BKT-2 and BKT-3 tephras (Kimbel *et al*., 1997)
	Hadar Busidima Formation	Makaamitalu Basin	~2.35	Wooded grasslands	Reed (2008)	
		Danauli Basin	~2	Open wet grasslands and floodplains	Reed (2008)	
	Olduvai Gorge	Bed I: FLKNN	1.85 - 1.84	Closed/ freshwater spring surrounded by wetlands	Leakey *et al*. (1964); Shipman & Harris (1988); Ashley *et al*. (2010); McHenry (2012); Uribelarrea *et al*. (2014).	For site location see Leakey *et al*. (1964). Dates are approximations based on Figure 3 in McHenry (2012). Habitat descriptions are from Shipman & Harris (1988); Ashley *et al*. (2010); Uribelarrea *et al*. (2014).
		Bed II: HWK W Locality	1.79 - 1.15	Freshwater spring	Ashley *et al*. (2009); Clarke (2012); Stanistreet (2012)	Presence here according to Clarke (2012); site description from Ashley *et al*. (2009); exact locality dates not available so dates of Bed II obtained from Stanistreet (2012)
		Bed II: MCK Locality	1.79 - 1.15	Freshwater spring	Ashley *et al*., (2009); Clarke (2012); Stanistreet (2012)	Presence here according to Clarke (2012); site description from Ashley *et al*. (2009); exact locality dates not

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
						available so dates of Bed II obtained from Stanistreet (2012)
	Lake Malawi	Chiwondo Beds 3A: Uraha Locality	2.5 - 2.3	Closed/ dry habitats: variable density woodlands and grasslands	Bromage *et al*. (1995); Sandrock *et al*. (2007)	
	Sterkfontein	Member 5a	1.8 - 1.4	Open or wooded grassland/ plains region	Reed (1997); Herries *et al*. (2009); Herries & Shaw (2011)	Chronology from Herries *et al*. (2009). Member position from Herries & Shaw (2011). Reed does not distinguish between Members 5A-C in the description of the site. This is the site of Stw 53, attributed to *Homo habilis* by Curnoe & Tobias (2006), but see Clarke (2007) for alternative attribution to *Australopithecus africanus*.
H. ergaster	Koobi Fora: Turkana Basin	Burgi	3.0 - 2.0	Open woodland, edaphic grasslands and riparian woodland	Reed (1997)	Presence here according to Wood & Strait (2004)
		KBS Member	1.88 - 1.6	Grassland/ shrubland environment	Reed (1997)	
		Okote Member	1.6 - 1.39	Wetlands and edaphic grasslands	Reed (1997)	Presence here according to Wood & Strait (2004)
	West Turkana: Nachukui Formation	Natoo Member	1.64 - 1.33	Mosaic habitat: limited development of forest, narrow riparian woodland, open grassland, and seasonal marshes.	Feibel & Brown (1993); Reed (1997)	Alternatively, Harris *et al*. (1988) describe this Member as being arid grassland.
	Olduvai Gorge	Bed II	1.79 - 1.15	Open, arid and closed, wet habitats	Shipman & Harris (1988); Wood & Strait (2004)	Presence here according to Wood & Strait (2004). Exact locality not given by Wood & Strait (2004), so general Bed II habitat description by Harris & Shipman (1988) used.
	Sterkfontein	Member 5c	1.3 - 0.8	Open or wooded grassland/ plains region	Reed (1997); Herries *et al*. (2009); Pickering & Kramers (2010)	Chronology from Herries *et al*. (2009). Member position from Pickering & Kramers (2010). Reed does not distinguish between Members 5A-C in the description of the site.
	Swartkrans	Member 1	2.31 - 1.64	Open habitat with a	Reed (1997); Pickering *et al*. (2011);	This member includes Lower Bank

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
				riverine woodland nearby	Herries & Adams (2013)	and Hanging Remnant, dates from Pickering *et al*. (2011) and Herries & Adams (2013) (more refined than those earlier provided by Herries *et al*. (2009). Reed does not distinguish between the two levels in the description of the site.
		Member 2	1.7 - 1.1	Wooded grassland with wetlands	Reed (1997); Herries & Adams (2013)	Chronology from Herries *et al*. (2009) and Herries & Adams (2013)

**N.B*. MYA: million years ago. **No universal definition for savannah available, so it is assumed that all references that describe a savannah environment are similar to that described by Wynn (2000: 414), where a savannah is somewhere "between tropical rainforests and mid-latitude deserts, with seasonally dry vegetation which is characterized by a herbaceous stratum, with or without woody vegetation of variable height and spacing". ***No information could be obtained regarding the palaeoenvironments of Belohdelie or Fejej.

For additional information on palaeoenvironmental reconstructions see Reed (1997); Potts (1998); Wood & Strait (2004) and Behrensmeyer & Reed (2013)

Table 9.3: Locations of questionable species attributions

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
cf. A. afarensis	Galili	Shabeley Laag Member	~ 3.8 - 3.5	Open woodland, bushland-woodland and shrubland	Kullmer *et al.* (2008)	Member chronology estimated based on Figure 7 in Kullmer *et al*., (2008)
	Hadar Formation	Ledi-Gararu**	3.45 - 3.18	Woodland, grasslands - open woodland	Geraads *et al.* (2012)	According to Behrensmeyer & Reed (2013) this is an *A. afarensis* site, although Geraads *et al*., (2012) discuss only bovids identified at this site. This could be a site where hominin remains are likely but not yet published as Behrensmeyer & Reed (2013) make reference to in Table 4.1.
cf. A. africanus	Olduvai Gorge	Bed II: MCK Locality:	1.79 - 1.15	Freshwater spring	Ashley *et al*. (2009); Clarke (2012); Stanistreet (2012)	Presence here according to Clarke (2012); site description from Ashley *et al*. (2009); exact locality dates not available so dates of Bed II obtained from Stanistreet (2012)
		Bed II: VEK Locality:	1.79 - 1.15	Freshwater spring	Ashley *et al*. (2009); Clarke (2012); Stanistreet (2012)	Presence here according to Clarke (2012); site description from Ashley *et al*. (2009); exact locality dates not available so dates of Bed II obtained from Stanistreet (2012)

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
Australopithecus sp.	Galili	Lasdanan Member	~ 4.5 - 4.2	Open woodland, bushland-woodland and shrubland	Kullmer *et al*, (2008)	Member chronology estimated based on Figure 7 in Kullmer *et al*. (2008)
		Dhidinley Member	~ 4.2 - 4.1	Open woodland, bushland-woodland and shrubland	Kullmer *et al*. (2008)	Member chronology estimated based on Figure 7 in Kullmer *et al*. (2008)
		Shabeley Laag Member	~ 3.8 - 3.5	Open woodland, bushland-woodland and shrubland	Kullmer *et al*. (2008)	Member chronology estimated based on Figure 7 in Kullmer *et al.* (2008)
	Lothagam: Nawata Formation		7.5 - 5.5	Mix of gallery forest, open woodlands, grassland, close to a large river and ponds. Becoming more open towards the latter stages of this Formation	Leakey *et al*. (1996); Bobe (2011); Behrensmeyer & Reed (2013)	Kissel & Hawks (2015) attribute the mandible KNM-LT 329 to *Australopithecus* sp. But see Kramer (1986) for attribution to cf. *Australopithecus afarensis*.
	Lothagam: Nachukui Formation	Apak Member	4.9 - 4.2	Woodland, grassland and river nearby	Su & Harrison (2007)	
		Kaiyumung Member	<3.9	Open habitat: grasslands, bushlands and lake nearby	Su & Harrison (2007)	
	Omo: Shungura Formation	Member B	3.36 - 2.85	Closed woodland, riverine forest and edaphic grasslands	Reed (1997); Plummer *et al*. (2015)	Shipman & Harris (1988) describe the Shungura Formation as one that is closed but of varying degrees of wetness, which is reflected throughout the reconstructed Members. Wood & Strait (2004) do not list Australopithecus sp. as present in Member D, but Reed (1997) does.
		Member C	2.85 - 2.52	Bushland - woodland, riverine forest and edaphic grasslands	Reed (1997); Barr (2015); Plummer *et al*. (2015)	
		Member D	2.52 - 2.4	Riverine forests, woodland - bushland and edaphic grasslands	Reed (1997); Plummer *et al*. (2015)	
	Woranso-Mille		3.8 - 3.57	Mosaic habitats: riverine gallery forest, closed and open woodland, grassland	Haile-Selassie *et al*. (2010b)	
Paranthropus sp.	Gondolin	GD 1	1.8 - 1.7	Outside the cave mesic conditions with	Adams *et al*. (2007);	

Species	Site	Unit	Age (MYA)*	Reconstructed palaeoenvironments	Reference	Notes
				extensive vegetative cover. Carnivores could have used this area as a feeding retreat/ den, and the remains were then washed inside the cave by a water source.	Herries & Adams (2013)	
		GD2	1.95 - 1.78	Cave with water source nearby, but likely a primary carnivore den	Herries *et al*. (2006); Herries & Adams (2013)	
Homo habilis (sensu lato)?	Omo: Shungura Formation	Member E	2.4 - 2.36	Well-watered woodland-bushland, riparian woodland or forest	Reed (1997); Plummer *et al*. (2015)	Taxonomic attribution queried by Wood & Strait (2004)
		Member F	2.36 - 2.33	Edaphic grasslands, open woodland and bushland	Reed (1997); Barr (2015); Plummer *et al*. (2015)	Taxonomic attribution queried by Wood & Strait (2004)

*MYA: million years ago. **Information originally extracted from Behrensmeyer & Reed (2013)

For additional information on palaeoenvironmental reconstructions see Reed (1997); Potts (1998), Wood & Strait (2004) and Behrensmeyer and Reed (2013).

The following Tables (9.4-9.7) detail the measurements taken from each hominin specimen analysed in this study. Tables 9.4-9.5 detail the hominin specimens with measurements from the mandibular corpus and symphysis. This information had to be broken up into two tables: Table 9.4 includes measurements on the symphysis, and corpus measurements at the P_4-M_1, and Table 9.5 includes measurements on the corpus at M_2-M_3. Tables 9.6-9.7 detail the dental measurements from the P_4-M_1 (Table 9.6), and M_2-M_3 (Table 9.7).

Table 9.4: Hominin specimens and their symphyseal and P$_4$ and M$_1$ corpus measurements. References for each measurement numbered, but where no references are provided (e.g., on the Robusticity Indices) these have been worked out using the formula from Wood (1991).

Species/ specimen	Symphysis			P$_4$ Corpus						M$_1$ Corpus					
	H	W	R.I.*	H		W		R.I.		H		W		R.I.	
				L	R	L	R	L	R	L	R	L	R	L	R
Australopithecus afarensis															
AL 128-23							16.6^{1**}						18.6^{1}		
AL 145.35				28^{1}		19.3^{1}		68.9		27.8^{1}		22.4^{31}		75^{2}	
AL 188.1															
AL 198.1				32.2^{1}		15.7^{1}		48.8		31.1^{1}		17.3^{1}		52^{2}	
AL 198.22												21.7^{3}			
AL 207.13						17.7^{1}				30.4^{1}		18.4^{1}		59^{2}	
AL 225.8										31.1^{3}					
AL 228.2				36^{3}		16^{3}		44.4		31.8^{3}		16.3^{3}		51.3^{3}	
AL 266.1		20^{2}			39.8^{1***}		20.6^{1}		51.8		30.5^{31}		22^{1}		70^{2}
AL 277.1				39.2^{1}		18.2^{1}		46.4		37^{1}		18^{1}		49^{2}	
AL 288.1	32.5^{2}	17.5^{2}	53.9		29.3^{1}		16.8^{1}		57.3	30^{1}	29.4^{31}		19.1^{1}		57^{2}
AL 311.1						24.8^{1}						24.2^{1}			
AL 315.22				33^{3}		17.3^{3}		52.4		29.7^{3}		19.2^{3}		64.6^{3}	
AL 330.5				31.4^{3}		18.5^{3}		58.9		31.1^{3}		20.9^{3}		67.2^{3}	
AL 333w-1a+b					37.5^{1}		18.7^{1}		49.9	35.5^{1}	35.1^{1}	20^{1}	20.3^{1}	56^{2}	54^{2}
AL 333w-12					31.1^{1}		17.4^{1}		55.9		30.6^{1}		19.3^{1}		57^{2}
AL 333w-32+60	45^{2}	22^{2}	48.9	40.1^{1}		22.2^{1}		55.4		38.4^{1}		23.4^{1}		61^{2}	
AL 400-1a	39.5^{2}	19^{2}	48.1		35.6^{1}		18.5^{1}**		51.9		35.4^{1}		19.1^{1}		52^{2}
AL 417.1a				37.2^{3}		18.4^{3}		49.5		36^{3}		18^{3}		50^{2}	
AL 418.1															
AL 432.1															
AL 433.1a,b						20.3^{3}				35^{3}		20.2^{3}		57.7^{3}	
AL 436.1															
AL 437.1				44^{3}		21.2^{3}		48.2		40^{3}		20^{3}		50^{3}	
AL 437.2				43.4^{3}		22.2^{3}		51.2		38.5^{3}		22.2^{3}		57.7^{3}	
AL 438.1					42^{3}		25^{53}		59.5		41.3^{3}		24.7^{53}		59.9^{3}
AL 444.2				43.9^{3}		21.1^{3}		48.1		41.2^{3}		23^{3}		55.8^{3}	
AL 582.1				40.5^{3}		22.6^{3}		55.8				21.4^{3}			

AL 620.1				38[3]		19.5[3]		51.3		36.2[3]		20.5[3]		56.6[3]	
LH 4	39[4]	19.1[4]	48.9	35.3[4]	34[4]	17.4[4]	17.6[4]	49.3	51.8	31.4[4]		19.2[4]	19.6[4]	60[4]	
MAK-VP1/2													19.6[5]		
MAK-VP1/12				33.6[5]	31.3[5]	17.2[5]	18.2[5]	51.2	58.2	31.3[5]	29.7[5]	18.6[5]	18.8[5]	59.4	63.3
Australopithecus africanus															
MLD 2	20[2]	21.5[2]	107.5							25[2]	24[2]		23[2]		95.8
MLD 18		21[2]					20.5[42]				34[2]		20.5[2]		60[2]
MLD 34											32[2]		19.5[2]		61[2]
MLD 40				37[2]		23.5[2]		63.5		36[2]		23.5[2]		65[2]	
Sts 7	46[2]				41[2]		24[6]		58.5		41.5[2]		24[6]		57.8
Sts 36					37[6]		19[6]		51.4		36[6]		20[6]		55.7
Sts 52	35[2]	18[2]	51.4	31.5[2]	29[2]		21.5[2]		74.1		29.5[2]		24.5[2]		84[2]
Taung	25[2]	14.5[2]	58									18[2]	17.5[2]		
Paranthropus boisei															
KNM-ER 403											47[2]		30.5[42]		65[42]
KNM-ER 404															
KNM-ER 725		30[2]		38.5[2]		27.5[2]		71.4		41[2]		29.5[2]		72[2]	
KNM-ER 726				44[2]		30.5[2]		69.3		46[2]		30[2]		65[2]	
KNM-ER 727											35[2]		24[2]		69[2]
KNM-ER 728											37[2]		26[2]		70[2]
KNM-ER 729	50[2]	32.5[2]	65	45[2]	46[42]	29[2]	28[2]	64.4	60.9	43.5[2]	44.5[2]	29[2]	27.5[2]	62[2]	67[2]
KNM-ER 733		20.5[2]			39[42]		26[2]		66.7		39.5[2]		27[2]		68[2]
KNM-ER 801	45[2]										43.5[2]		29.5[2]		68[2]
KNM-ER 805										41[2]		29[2]		71[2]	
KNM-ER 810		26[2]		40.5[2]		24.5[2]		60.5		40[2]		26[2]		65[2]	
KNM-ER 818	57[2]	30[2]	52.6	52[2]		39[2]		75		50[2]		36[2]		72[2]	
KNM-ER 1468	50[2]	26[2]	52		50[42]		33[2]		66		48.1[8]		36.9[8]		75[2]
KNM-ER 1469		27[2]		46.5[2]		32[2]		68.8		[42][8]		33[8]		80[2]	
KNM-ER 1477	23.1[8]	13[8]	56.3												
KNM-ER 1803											42[8]		25[8]		60[2]
KNM-ER 1806	48[8]	23[8]	47.9	47[2]	47[8]	28[8]	27[8]	59.6	57.4	44[2]	45[8]	29[8]	27.5[8]	61[8]	66[2]
KNM-ER 1820	29.5[8]	21[2]	71.2									24[2]			
KNM-ER 3229	50[2]				41[2]		25[2]		61		39[2]		[28][2]		72[2]
KNM-ER 3230	52[2]	25[2]	48.1	42[2]	41[2]	26[2]	29[2]	70.7	61.9	42[2]	42[2]	28[2]	30[2]	66.7[2]	71.4[2]

KNM-ER 3729				37[2]		26[2]		70.3		38[2]		28[2]		74[2]	
KNM-ER 3731				32[2]						30[2]		18[2]		60[2]	
KNM-ER 3889	45[2]	28[2]	62.2												
KNM-ER 3954				33[42]		25[42]		75.8		34[42]		26[42]		<76[2]	
KNM-ER 5429	50[42]				44[42]						44[42]		>30[2]		> 68[2]
KNM-ER 5877											44[2]		29[2]		66[2]
KNM-ER 15930		23[7]		34.9[7]		23.2[7]		66.5		34.2[7]		25.2[7]		71[2]	
KNM-ER 16841	39.8[7]	29.7[7]	74.6		42.8[7]		26[7]		60.8		42.6[7]		26.9[7]		64[2]
OMO L7A-125	57[2]	35[2]	61.4	48[2]	47[2]	37[2]		77.1		48[2]	49[2]	36[2]	33[2]	75[2]	67.4[2]
OMO L74A-21	47[2]	26[2]	55.3		46[2]		24[2]		52.8		43.5[2]		25[2]		57[2]
Peninj 1	50[2]	24[2]	48	41.5[2]	40.5[2]	26.5[2]	25.5[2]	63.9	63	40.5[2]	39[2]	30[2]	28[2]	74[2]	72[2]
Paranthropus robustus															
SK 6										37.5[2]		24[2]		64[2]	
SK 12				43[2]	41[2]	31[2]	32[2]	72.1	78.1	44[2]	42[2]	33[2]	31[2]	75[2]	74[2]
SK 23	50[2]			40[2]	40[2]	23.5[2]	23.5[2]	58.8	58.8	37[2]	39[2]	24.5[2]	24.5[2]	66[2]	63[2]
SK 34				41[2]	41[2]	21[2]	25[2]	51.2	61	40[2]	41[2]	22[2]	23[2]	55[2]	56[2]
SKW 5	37[9]	20[9]	54.1		34[9]		23[9]		67.7	34[9]	33[9]	25[9]	26[9]	73.5	78.8
SKW 34													26[10]		
SKX 4446	37[11]	24.5[11]	66.2		34[11]		22.9[11]		67.4		32.8[11]		24[11]		73.1
SKX 5013				31.7[11]		22.7[11]		71.6		32.3[11]		24.1[11]		74.6	
Homo habilis															
KNM-ER 817				30[12]		18[12]		60		29[12]		18[12]		62.1	
KNM-ER 819				40[2]		26[2]		65		38[2]		27[2]		71[2]	
KNM-ER 1482	36[2]	22[2]	61.1	32.5[2]	31[2]	20[2]	21[2]	61.5	67.7	31[2]		20[2]	20[2]	65[2]	
KNM-ER 1483	40[2]	25[2]	62.5	40[2]		20[2]		50		39.5[2]		26.5[2]		67[2]	
KNM-ER 1501					32[13]		16[13]		50		30[13]		16[13]		59[2]
KNM-ER 1502											28[13]		17[13]		63[2]
KNM-ER 1801	32[2]			36[8]		19[8]		52.8		34[8]		19.3[8]		59[2]	
KNM-ER 1802	36[8]	24.3[8]	67.5		40[8]	20[8]	20[8]		50		38[8]	23[8]	23[8]		61[2]
KNM-ER 1805	22[8]	26[8]	118.2	47[2]		23[2]		48.9		30[2]		21[2]		70[2]	
KNM-ER 3734				35[2]		19[2]		54.3		33[2]		19.5[2]		59[2]	
KNM-ER 3950	31[2]	18.5[2]	59.7												
KNM-ER 60000	43[14]	21[14]	48.8	39[14]		21[14]		53.9		38[14]		20[14]		53[14]	
KNM-ER 62003	36[14]	20[14]	55.6		33[14]		20[14]		60.6		32[14]		[19] [14]		[59][14]

OH 7						23.5[2]						25[2]			
OH 13	25[2]	18[2]	72		26[2]		16.5[2]		63.5		26.5[2]		18[2]		68[2]
OH 37	29[2]	19[2]	65.5	31[2]		20[2]		64.5		32[2]		19.5[2]		61[2]	
UR 501	36.1[15]	20.3[15]	56.2	35.1[15]	35.8[15]	19.6[15]	20[15]	55.8	55.9	34.3[15]	35[15]	22.4[15]	21.3[15]	65.3	60.9
Homo ergaster															
KGA 10-1				[33.5][16]		20.7[16]		61.8[16]		[32.5][16]		21.3[16]		66[16]	
KNM-BK 67	31[2]	19.5[2]	62.9	35[2]	33[2]		17.5[2]		53	35[2]	33[2]		17[2]		52[2]
KNM-BK 8518	30[2]	21.5[2]	71.7	29[2]	27.5[2]	18.5[2]	19[2]	63.8	69.1	30[2]	30.5[2]	21[2]	20.5[2]	70[2]	66[2]
KNM-ER 730	32.7[17]	17.7[17]	54.1	32.5[2]		19[2]		58.5		32.3[17]		19[17]		60[2]	
KNM-ER 731		20[2]								25[17]		19.3[17]		70[2]	
KNM-ER 820	27[12]	16.5[12]	61.1							18[12]	19[12]	17[12]	17[12]	94.4	89.5
KNM-ER 992	37[2]	21[2]	56.8	31[12]	32[12]	20[12]	21[12]	64.5	65.6	31[12]	32[12]	20[12]	20[12]	65[2]	63[2]
KNM-ER 1507										19[13]		19[13]		100	
KNM-ER 1808					[30][18]						29[18]				
KNM-ER 1812	32[8]	17[8]	53.1												
KNM-WT 15000				27.2[19]	25.3[19]	18.1[19]	19[19]	66.5	75.1	24.4[19]	23.2[19]	19.5[19]	20.5[19]	79.9	88.4
OH 22	33.5[2]	20[2]	59.7		29[2]		20.5[2]		70.7		28.5[2]		21[2]		74[2]
OH 23				32[2]		20[2]		62.5		33[2]		21[2]		64[2]	
SK 15 (Brain 1993)				[28][20]		17[20]		60.7		[27.5] [20]		18.5[20]		67.3	

*Height **(H);** Width **(W);** Robusticity Index **(R.I.).** Robusticity Index - ([corpus width]/[corpus height]) x 100 (adults)

Measurements from Minimum Corpus Breadth, instead of Perpendicular Corpus Breadth. * Measurements from Minimum Corpus Height: Base to occlusal Rim, instead of Base to the midpoint of the alveolar margin of the tooth.

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[1] White & Johanson, 1982; [2] Wood, 1991; [3] Kimbel *et al*., 2004; [4] White *et al*., 1977; [5] White *et al*., 2000; [6] de Ruiter *et al*., 2013; [7] Leakey & Walker, 1988; [8] Day *et al*., 1976; [9] Grine & Daegling, 1993; [10] Grine & Strait, 1994; [11] Grine, 1989; [12] Leakey & Wood, 1973; [13] Leakey & Wood, 1974; [14] Leakey *et al*., 2012; [15] Bromage *et al*., 1995; [16] Suwa *et al*., 2007; [17] Day & Leakey, 1973; [18] Leakey & Walker, 1985; [19] Brown & Walker, 1993; [20] Rightmire, 1990.

Table 9.5: Hominin specimens and their M_2 and M_3 corpus measurements. References for each measurement numbered, but where no references are provided (e.g., on the Robusticity Indices) these have been worked out using the formula from Wood (1991).

Species/ specimen	M_2 Corpus						M_3 Corpus					
	H		W		R.I.		H		W		R.I.	
	L	R	L	R	L	R	L	R	L	R	L	R
Australopithecus afarensis												
AL 128-23				23^{1}								
AL 145.35			25.6^{1}									
AL 188.1		33.3^{1}		22.3^{1}		66.9						
AL 198.1	30.8^{1}		17.7^{1}		57.5		31.3^{1}					
AL 198.22	34^{3}		20.9^{3}		61.5							
AL 207.13	27.3^{1}		20.4^{1}**		74.7		26.5^{1}					
AL 225.8	28.1^{3}		21.4^{3}		76.2							
AL 228.2												
AL 266.1		27.6^{1}		24.2^{1**}		87.7						
AL 277.1			21.2^{1}									
AL 288.1		27.6^{1}						26^{1}				
AL 311.1												
AL 315.22	28^{3}		20^{3}		71.4							
AL 330.5	28.3^{3}		19.5^{3}		68.9							
AL 333w-1a+b	32.4^{1}		24.3^{1}	24.4^{1}	75							
AL 333w-12												
AL 333w-32+60	35.4^{1}		26^{1}		73.5							
AL 400-1a												
AL 417.1a	32.8^{3}		18.4^{3}		56.1							
AL 418.1	36^{3}											
AL 432.1			20.3^{3}									
AL 433.1a,b			20.8^{6}									
AL 436.1	26^{3}		19.6^{3}		75.4							
AL 437.1			19.6^{3}									
AL 437.2	37^{3}		24.2^{3}		65.4							
AL 438.1		37.1^{3}		28.1^{3}		75.7						
AL 444.2	37.6^{3}		30.5^{3}		81.1							
AL 582.1												

Species/ specimen	M_2 Corpus						M_3 Corpus					
	H		W		R.I.		H		W		R.I.	
	L	R	L	R	L	R	L	R	L	R	L	R
AL 620.1	34.5[3]		22.6[3]		65.5							
LH 4	29.5[4]		22.4[4]		75.9							
MAK-VP1/2		32.6[5]		21.4[5]		65.6		30.7[5]				
MAK-VP1/12	31.1[5]	[27.7][5]	20.3[5]	20.8[5]	65.3	77	33.9[5]	[28.2][5]				
Australopithecus africanus												
MLD 2												
MLD 18		31.5[2]		25[2]		79.4		32[2]		29[2]		90.6
MLD 34		33[2]		22[2]		66.7						
MLD 40	36[2]		27[2]		75		35[2]		30[2]		85.7	
Sts 7		37[2]						33[2]				
Sts 36												
Sts 52		29[2]		28[2]		96.6						
Taung												
Paranthropus boisei												
KNM-ER 403		45.5[2]		32.5[2]		71.4		45[2]		34[2]		75.6
KNM-ER 404		45.5[2]		35[2]		76.9						
KNM-ER 725	41.5[2]		32.5[2]		78.3		37.5[2]		36[2]		96	
KNM-ER 726	45[2]		31[2]		68.9		41[2]		33[2]		80.5	
KNM-ER 727		33[2]		26[2]		78.8						
KNM-ER 728		37.5[2]		27[2]		72						
KNM-ER 729	41[2]	43[2]	31.5[2]	29[2]	67.4	76.8		43[2]		36[2]		83.7
KNM-ER 733		36[2]		29[2]		80.6						
KNM-ER 801		42.5[2]		32[2]		75.3		40[2]				
KNM-ER 805	39[2]		33.5[2]		85.9							
KNM-ER 810	41[2]		33.5[2]		81.7		41[2]		33[2]		80.5	
KNM-ER 818	48[2]		36[2]		75							
KNM-ER 1468		47[8]		33.8[8]		71.9		47[2]		35[2]		74.5
KNM-ER 1469	40[8]		33.5[8]		83.8		45[2]		41[2]		91.1	
KNM-ER 1477												
KNM-ER 1803												
KNM-ER 1806	41[2]	41[8]	30[8]	28.5[8]	73.2[8]	69.5						

Species/ specimen	M_2 Corpus						M_3 Corpus					
	H		W		R.I.		H		W		R.I.	
	L	R	L	R	L	R	L	R	L	R	L	R
KNM-ER 1820												
KNM-ER 3229	41[2]		33[2]		80.5		40[2]		34[2]		85	
KNM-ER 3230	42[2]	41[2]		35[2]		85.4				[36][2]		
KNM-ER 3729	36[2]		28.5[2]		79.2		33[2]		28[2]		84.9	
KNM-ER 3731	28[2]		21[2]		75							
KNM-ER 3889												
KNM-ER 3954			28[2]				29[2]					
KNM-ER 5429				>34[2]								
KNM-ER 5877		43.5[2]		35.5[2]		81.6						
KNM-ER 15930	32[7]		29.7[7]		92.8		32.3[7]		27.3[7]		84.5	
KNM-ER 16841		43.8[7]		27.4[7]		62.6		39.8[7]		[32][7]		80.4
OMO L7A-125	48[2]	48[2]	32[2]	35[2]	66.7	72.9	47.5[2]	48[2]	34.5[2]	35[2]	72.6	72.9
OMO L74A-21												
Peninj 1	39[2]	37[2]	30.5[2]	31.5[2]	78.2	85.1	34.5[2]	33.5[2]	36[2]	32[2]	104.3	95.5
Paranthropus robustus												
SK 6	33[2]		27.5[2]		83.3							
SK 12	41[2]	40[2]	33[2]	31[2]	80.5	77.5	41[2]	37[2]	35[2]		85.4	
SK 23	34.5[2]	36[2]	27.5[2]	26[2]	79.7	72.2	34[2]	35[2]	28[2]	27[2]	82.4	77.1
SK 34	37[2]	41[2]	25[2]	23[2]	67.6	56.1	35[2]	38[2]	31[2]		85.6	
SKW 5	32[9]	32[9]	29[9]	31[9]	90.6	96.9	33[9]	34[9]	29[9]	32[9]	87.9	94.1
SKW 34				31[10]								
SKX 4446		31.2[11]		27.2[11]		87.2						
SKX 5013	31.2[11]		26.3[11]		84.3							
Homo habilis												
KNM-ER 817												
KNM-ER 819	40[2]		29[2]		72.5							
KNM-ER 1482	30[2]		22[2]		73.3		30[2]		24[2]		80	
KNM-ER 1483												
KNM-ER 1501		30[13]		19.5[13]		65		26[13]		21[13]		80.8
KNM-ER 1502												
KNM-ER 1801												

Species/ specimen	**M_2 Corpus**						**M_3 Corpus**					
	H		**W**		**R.I.**		**H**		**W**		**R.I.**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
KNM-ER 1802		[38][8]		27[8]		71.1						
KNM-ER 1805	30[2]		24[2]		80		26[2]					
KNM-ER 3734	32[2]		20[2]		62.5		29[2]		17[2]		58.6	
KNM-ER 3950												
KNM-ER 60000	35[14]		21[14]		60							
KNM-ER 62003												
OH 7			25[2]									
OH 13		28.5[2]		22.5[2]		79		26.5[2]		23[2]		86.8
OH 37	34.5[2]		23.5[2]		68.1		31[2]		24[2]		77.4	
UR 501		36[15]	26.3[15]	26.5[15]		73.6						
Homo ergaster												
KGA 10-1	[31.5][16]		22.1[16]		70[16]							
KNM-BK 67	34.5[2]	34[2]		18.5[2]		54.4	35[2]	34[2]	22.5[2]	20.5[2]	64.3	60.3
KNM-BK 8518	31.5[2]	31[2]	23[2]	22[2]	73	71	32.5[2]	30.5[2]	22[2]	21.5[2]	67.7	70.5
KNM-ER 730	31.4[17]		18.7[17]		59.6		30.5[17]		19.2[17]		63	
KNM-ER 731												
KNM-ER 820												
KNM-ER 992	33[12]	35[12]	22[1412]	24[12]	66.7	68.6	35[12]	37[12]	24[12]	25[12]	68.6	67.6
KNM-ER 1507												
KNM-ER 1808		30.5[18]		20[18]		65.6		30[18]		21[18]		70
KNM-ER 1812												
KNM-WT 15000	24.8[19]	23.5[19]	21[19]	21.3[19]	84.7	90.6						
OH 22		28.5[2]		21[2]		73.7		33[2]		22[2]		66.7
OH 23	32[2]		20[2]		62.5							
SK 15	[24][20]		[23.5][20]		97.9		[24.5][20]		[23.5][20]		95.9	

*Height **(H);** Width **(W);** Robusticity Index **(R.I.).** Robusticity Index - ([corpus width]/[corpus height]) x 100 (adults)
**Measurements from Minimum Corpus Breadth, instead of Perpendicular Corpus Breadth.

[1] White & Johanson, 1982; [2] Wood, 1991; [3] Kimbel *et al*., 2004; [4] White *et al*., 1977; [5] White *et al*., 2000; [6] de Ruiter *et al*., 2013; [7] Leakey & Walker, 1988; [8] Day *et al*., 1976; [9] Grine & Daegling, 1993; [10] Grine & Strait, 1994; [11] Grine, 1989; [12] Leakey & Wood, 1973; [13] Leakey & Wood, 1974; [14] Leakey *et al*., 2012; [15] Bromage *et al*., 1995; [16] Suwa *et al*., 2007; [17] Day & Leakey, 1973; [18] Leakey & Walker, 1985; [19] Brown & Walker, 1993; [20] Rightmire, 1990.

Table 9.6: Hominin specimens and their P_4 and M_1 dental measurements. References for each measurement numbered.

Species/	P_4 MD		P_4 BL		M_1 MD		M_1 BL Max		M_1 BL1		M_1 BL2	
	L	R	L	R	L	R	L	R	L	R	L	R
Australopithecus afarensis												
A.L. 128-23	7.7[1]		10[1]		11.2[1]		11.1[1]					
A.L. 145.35	9.5[1]				13[1]		13.4[1]					
A.L. 176.35	10.7[2]		10.6[2]									
A.L. 188.1												
A.L. 198.1	8.5[1]		9.8[1]		8.8[1]							
A. L. 198.22					12.8[2]							
A.L. 200.1b						12.8[1]		12.5[1]				
A.L. 207.13	8.7[1]		10[1]									
A.L. 207.17												
A.L. 225.8												
A.L. 228.2	9.6[2]		10.9[2]		12.8[2]		12[2]					
A.L. 241.14												
A.L. 266.1	9[1]	9[1]	11[1]	10.4[1]	12[1]	12[1]	11.9[1]	11.9[1]				
A.L. 277.1	9.5[1]		11.8[1]		12[1]							
A.L. 288.1		7.4[1]		10.5[1]		11.7[1]		11[1]				
A. L. 315.22					13.4[2]							
A.L. 330.5	8.7[2]		10.4[2]		12.4[2]		12.1[2]					
A.L. 330.7	10.5[2]		12.1[2]		13.7[2]		13.4[2]					
A.L. 333.44	10[1]		11.2[1]									
A.L. 333.74					12.6[1]		13.5[1]					
A.L. 333w-1a+b	9.4[1]	9.5[1]	10.5[1]	10.5[1]	12.7[1]	12.7[1]	12.1[1]	12.2[1]				
A.L. 333w-12						12.4[1]		12.7[1]				
A.L. 333w-27												
A.L. 333w-	9.5[1]		12.8[1]		12.8[1]		13.2[1]					
A.L. 333w-48												
A.L. 333w-57												
A.L. 333w-59												
A.L. 400-1a	9.1[1]	9.1[1]	11.1[1]	11.3[1]	12.2[1]	12.4[1]	12.4[1]	12.7[1]				
A.L. 411.1						12.5[1]						

Species/	P_4 MD		P_4 BL		M_1 MD		M_1 BL Max		M_1 BL1		M_1 BL2	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
A.L. 417.1a	8.6[3]		11.2[3]		12.4[3]		11.9[3]					
A.L. 417.1a,b												
A.L. 418.1												
A.L. 433.1a	9.5[2]											
A.L. 437.1												
A.L. 437.2												
A.L. 438.1												
A.L. 440.1					14.8[2]		13.1[2]					
A.L. 443.1	10.8[2]		11.7[2]									
A.L. 444.2	11.4[2]				14.6[2]							
A.L. 465.5												
A.L. 487-1a												
A.L. 582.1l	11.4[2]		11.8[2]									
A.L. 620.1												
DIK-2-1					14.7[4]		14[4]					
LH2					[13.7][5]	[14][5]		[13.9][5]				
LH3	11.1[5]	10.9[5]	11.7[5]	11.9[5]	13.4[5]		13.3[5]					
LH 4	9.5[5]	9.4[5]	11[5]	10.7[5]	11.9[5]	11.8[5]		12.6[5]				
LH 14	10.6[5]		11.5[5]									
MAK-VP1/2						13.1[6]		12.4[6]				
MAK-VP1/4												
MAK-VP1/12	8.8[6]	9.5[6]	9.9[6]	10.8[6]	12.8[6]	12.6[6]	12.2[6]	12.1[6]				
Australopithecus africanus												
MLD 2					14.8[8]	14.7[8]	14.1[8]	13.9[8]	14.1[8]	13.9[8]	13.7[8]	13.8[8]
MLD 4												
MLD 18		8.9[8]		11.8[8]		12.6[8]		13.1[8]				
MLD 19												
MLD 24												
MLD 40	9.7[8]		11.3[8]		13.1[8]		12.4[8]		12.2[8]		12.3[8]	
Sts 7												
Sts 52		9.8[8]		12.1[8]		13.8[8]		13.2[8]		13.1[8]		12.8[8]
Taung					13.3[8]	13.4[8]	13.3[8]	13[8]				

Species/	P$_4$ MD		P$_4$ BL		M$_1$ MD		M$_1$ BL Max		M$_1$ BL1		M$_1$ BL2	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Stw 1					13.4[9]		12.6[9]					
Stw 3												
Stw 14	10[9]		12[9]									
Stw 47												
Stw 54												
Stw 56	11.1[9]		12.4[9]									
Stw 61												
Stw 72												
Stw 80	9.5[9]		10[9]									
Stw 87		9.3[9]		12.1[9]								
Stw 90												
Stw 96												
Stw 106						12.4[9]		11.5[9]				
Stw 109												
Stw 112	8.7[9]		9.3[9]									
Stw 120												
Stw 123					13.4[9]	13.3[9]	12.1[9]	11.8[9]				
Stw 131	10.7[9]	10.1[9]	11.9[9]	11.7[9]		14.4[9]		12.6[9]				
Stw 133												
Stw 134												
Stw 142		9.8[9]		11.1[9]	14.7[9]		14.1[9]					
Stw 145						13.7[9]		12.6[9]				
Stw 147		10.1[9]		10[9]								
Stw 151	9.6[9]		10.3[9]	[9.4][10]	13.8[9]	14[9]	11.7[9]	11.8[9]				
Stw 193	9.5[9]	10.4[9]	12.4[9]	11.8[9]			12.8[9]					
Stw 196												
Stw 212		10.5[9]		12.2[9]								
Stw 213	9.9[9]	9.7[9]	10.5[9]	10.3[9]								
Stw 220								13.2[9]				
Stw 234												
Stw 237												
Stw 246					15.8[9]		12.9[9]					

Species/	**P_4 MD**		**P_4 BL**		**M_1 MD**		**M_1 BL Max**		**M_1 BL1**		**M_1 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Stw 280												
Stw 285												
Stw 291						14.4[9]		13.4[9]				
Stw 295							14[9]					
Stw 308												
Stw 309					14.8[9]	14.8[9]	13.7[9]	13.9[9]				
Stw 327	11.6[9]		11.5[9]		13.8[9]		12.8[9]					
Stw 353												
Stw 364						13.8[9]		12.7[9]				
Stw 384		11.5[9]		13.2[9]		15.5[9]		15.1[9]				
Stw 385												
Stw 397												
Stw 404		10.2[9]		10.6[9]		12.6[9]		12.5[9]				
Stw 412												
Stw 413	10[9]		10.9[9]									
Stw 421					15.3[9]	15.3[9]	13.8[9]	13.7[9]				
Stw 424												
Stw 487	12.3[9]											
Stw 491					13.3[9]		12.7[9]					
Stw 498	11.4[9]		12.9[9]		14.6[9]		14.1[9]					
Stw 520												
Stw 529												
Stw 537	11.2[9]		12.7[9]		15[9]		13.5[9]					
Stw 555												
Stw 560	11.4[9]											
Stw 566						13[9]		12.2[9]				
Stw 586												
Paranthropus boisei												
KGA 10-525												
KGA 10-570						16.2[16]		14.9[16]				
KGA 10-1720												
KGA 10-2705												

Species/	**P$_4$ MD**		**P$_4$ BL**		**M$_1$ MD**		**M$_1$ BL Max**		**M$_1$ BL1**		**M$_1$ BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
KNM-ER 403						15^{8}						
KNM-ER 404												
KNM-ER 729	15^{8}	14.3^{8}	14.6^{8}	16.3^{8}		16.4^{8}		16^{8}				
KNM-ER 733												
KNM-ER 801												
KNM-ER 802	13.7^{8}	13.6^{8}	14.5^{8}	14.9^{8}		16.5^{8}		15.8^{8}				
KNM-ER 810												
KNM-ER 818	15.1^{8}		15.9^{8}	10.5^{8}	17.8^{8}							
KNM-ER 1171	15.7^{8}		15.3^{8}									
KNM-ER 1467												
KNM-ER 1477					[15]^{17}	[15]^{17}	[12]^{17}	[12]^{17}				
KNM-ER 1509					15.3^{8}		14.4^{8}		14.2^{8}		14.4^{8}	
KNM-ER 1816	14^{17}	13^{17}	15.6^{17}	14.4^{17}	16.6^{17}		13.8^{17}		13.4^{8}		13.7^{8}	
KNM-ER 1819												
KNM-ER 1820					15.3^{8}		14.4^{8}		13.4^{8}		14.3^{8}	
KNM-ER 3229	13^{8}	12.8^{8}	13.2^{8}	14.1^{8}								
KNM-ER 3230	13.7^{8}	14.5^{8}		16.5^{8}		17^{8}		15.4^{8}		14.8^{8}		15.4^{8}
KNM-ER 3737						15.5^{8}						
KNM-ER 3885		12.2^{8}		14.1^{8}								
KNM-ER 3890					15.6^{8}		14^{8}		13.3^{8}		14^{8}	
KNM-ER 5679												
KNM-ER 5877												
KNM-ER 15930	12^{12}		14^{12}		14.6^{12}		12.8^{12}					
KNM-ER 15940												
KNM-ER 15950												
KNM-WT 17396												
OH 26												
OH 30					17^{8}		14.5^{8}		13.5^{8}		14.4^{8}	
OH 38												
OMO 136-1												
OMO 136-2												
OMO 47-46												

Species/	**P_4 MD**		**P_4 BL**		**M_1 MD**		**M_1 BL Max**		**M_1 BL1**		**M_1 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
OMO 75-14		11.4^{14}		12.7^{14}		15.6^{14}		14.1^{14}				
OMO 84-100												
OMO F203-1												
OMO L427-7												
OMO L628-2												
OMO L628-3												
OMO L628-4	10.3^{8}		11.5^{8}									
OMO L628-9												
OMO L7A-125	11.7^{19}		18.9^{19}		16.8^{19}		18.7^{19}					
OMO L74A-21		13.4^{8}		12.7^{8}								
Peninj 1	14.6^{8}	13.2^{8}	15^{8}	14.9^{8}	16.6^{8}	16.4^{8}	15.4^{8}	15.5^{8}	14.7^{8}	14.9^{8}	15.4^{8}	15.4^{8}
Paranthropus robustus												
DNH 7	$[10.3]^{20}$	$[10.1]^{20}$	12.6^{20}	11.9^{20}	$[13.4]^{20}$		12.6^{20}	$[12.7]^{20}$				
DNH 8	11.3^{20}	11.4^{20}	13.6^{20}	13.4^{20}	$[15.7]^{20}$	$[15.2]^{20}$	14.5^{20}	14.7^{20}				
DNH 10												
DNH 12												
DNH 18												
DNH 19	$[12.3]^{22}$		$[13.2]^{22}$									
DNH 21												
DNH 26		$[10.9]^{22}$										
DNH 27	$[11.2]^{22}$		$[12.9]^{22}$									
DNH 46						$[14.7]^{22}$		$[13.5]^{22}$				
DNH 51		$[11]^{22}$		$[12.5]^{22}$		$[14.3]^{22}$						
DNH 60						13.6^{22}		11.9^{22}				
DNH 67						14.6^{21}		12.2^{21}				
DNH 68		9.9^{22}				$[14.5]^{22}$						
DNH 75												
DNH 81						$[14.6]^{22}$		13^{22}				
SK 6	11^{8}		12.3^{8}		16.7^{8}	16.7^{8}	15.5^{8}	14.8^{8}	14.9^{8}	14.2^{8}	15.5^{8}	14.7^{8}
SK12												
SK 23	11.1^{8}	11.1^{8}	14.4^{8}	13.7^{8}	15.2^{8}	15^{8}	14.8^{8}	14.7^{8}	14.1^{8}	14.4^{8}	14.7^{8}	14.7^{8}
SK 34	12.3^{8}		13.8^{8}		15^{8}	15.1^{8}	13.8^{8}	14.8^{8}	13.7^{8}	14^{8}	13.8^{8}	14.5^{8}

Species/	**P_4 MD**		**P_4 BL**		**M_1 MD**		**M_1 BL Max**		**M_1 BL1**		**M_1 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
SKW 5	11.2[23]	10.8[23]	12.7[23]	12.5[23]		13.3[23]	13.3[23]	13.2[23]		12.6[23]	13.3[23]	13.2[23]
SKW 10						15.3[24]						
SKW 4767						16.1[24]		14.4[24]				
SKW 4769												
SKX 257						13.3[25]		11.6[25]				
SKX 258					13.6[25]		11.8[25]					
SKX 4446		11.7[26]		12.5[26]		15.1[26]		14.3[26]				
SKX 5002												
SKX 5013					13.2[26]		12[26]					
SKX 5014												
SKX 5015												
SKX 5023						13.2[26]		12.8[26]				
SKX 19892												
SKX 32162		10.8[26]										
TM 1517	11.7[27]	11.6[27]	13.2[27]	13.1[27]		14.5[27]		13[27]				
TM 1601b	10.8[27]		12.1[27]									
KB 5223					14.3[27]	14[27]	12.5[27]	12.6[27]				
TM 1536						[12.8][27]		11.8[27]				
TM 1600												
Homo habilis												
OH 7	10.4[8]	10.6[8]	10.7[8]	10.7[8]	14.1[8]	14.3[8]	12.5[8]	12.6[8]	12.4[8]	12.4[8]	12.3[8]	12.3[8]
OH 13	9[8]	9[8]	9.8[8]	9.9[8]		13[8]		11.6[8]		11.5[8]		11.4[8]
OH 16	10.1[8]	10.2[8]	11[8]	10.9[8]		14.6[8]		12.8[8]		12.6[8]		12.8[8]
OH 37					13[8]		10.9[8]		10.9[8]		10.5[8]	
KNM-ER 1462												
KNM-ER 1480												
KNM-ER 1482	9.7[8]		12.2[8]	12.6[8]	13.2[8]		13.3[8]					
KNM-ER 1483												
KNM-ER 1502						13.4[27]		11.4[27]		11.4[8]		11.5[8]
KNM-ER 1508						13.6[27]		12.2[27]				
KNM-ER 1590												
KNM-ER 1801	9.3[17]		11[17]		12.4[17]		13.3[17]		13.1[8]		13.1[8]	

Species/	P_4 MD		P_4 BL		M_1 MD		M_1 BL Max		M_1 BL1		M_1 BL2	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
KNM-ER 1802	11.4[17]	11.3[17]	12[17]	12.1[17]	14.7[17]	14.6[17]	13.3[17]	13.2[17]	13[8]	13[8]	13.1[8]	13[8]
KNM-ER 1805												
KNM-ER 3734	9.1[8]		8.1[8]		13.6[8]		10.6[8]		10.1[8]		10.6[8]	
KNM-ER 60000	8.8[28]	8.7[28]	9.8[28]	9.8[28]	12.8[28]	[13][28]	11.4[28]	11.4[28]				
KNM-ER 62003		[10][28]		[11.7][28]								
UR 501	10.3[29]	10.4[29]	11.5[29]	11.8[29]	15.1[29]	15.2[29]	12.6[29]	12.8[29]				
KNM-WT 42718						13.7[3]		11.6[3]		11.3[3]		11.6[3]
Homo ergaster												
KGA 10-1	9.7[31]		[10.2][31]		[13.5][31]		[12.8][31]					
KNM-BK 67												
KNM-ER 730					11.7[32]		11.7[32]				11.5[8]	
KNM-ER 806					13.7[33]		12.6[33]		12.5[8]		12.5[8]	
KNM-ER 809					12.5[33]		12.7[33]					
KNM-ER 820					12.3[33]	12.2[33]	10.7[33]	10.8[33]	10.6[8]	10.7[8]		10.4[8]
KNM-ER 992	8.4[33]	8.6[33]	11.1[33]	11.1[33]	12[33]	11.9[33]	10.9[33]	10.7[33]	10.8[8]	10.7[8]	10.8[8]	10.7[8]
KNM-ER 1507					13.3[27]		11.1[27]		10.9[8]		11.1[8]	
KNM-ER 1808												
KNM-ER 1812												
KNM-WT 15000	9[35]	9[34]	9.5[35]	10.2[34]	12.2[35]	11.9[35]	10.9[35]	11.1[35]				
OH 22		9[8]		10[8]		13.4[8]		12[8]		12[8]		11.6[8]
OH 51					14[8]		12.9[8]		12.7[8]		12.9[8]	
SK 15					13.3[8]		11.9[8]		11.1[8]		11.8[8]	

MD = Mesiodistal Crown Diameter. **BLMax** = Buccolingual Crown Diameter maximum distance, **BL1** = Buccolingual Crown Diameter from Protoconid - Metaconid, **BL2** = Buccolingual Crown Diameter from Hypoconid - Entoconid.

[1] Johanson *et al*., 1982b. [2] Kimbel *et al*., 2004. [3] Kimbel *et al*., 1994. [4] Alemseged *et al*., 2005. [5] White 1977. [6] White *et al*., 2000. [7] White *et al*., 1993. [8] Wood 1991. [9] Moggi-Cecchi *et al*., 2006. [10] Moggi-Cecchi *et al*., 1998. [11] Kuykendall & Conroy 1999. [12] Leakey & Walker 1988. [13] Coppens 1973a. [14] Coppens 1971. [15] Coppens 1973b. [16] Suwa *et al*., 1997. [17] Day *et al*., 1976. [18] Leakey & Walker 1985. [19] Howell 1969. [20] Keyser 2000. [21] Moggi-Cecchi *et al*., 2010. [22] Keyser *et al*., 2000. [23] Grine & Daegling 1993. [24] Grine & Strait 1994. [25] Grine 1988. [26] Thackeray *et al*., 2001. [27] Leakey & Wood 1974. [28] Leakey *et al*., 2012. [29] Bromage *et al*., 1995. [30] Prat *et al*., 2005. [31] Suwa *et al*., 2007. [32] Day & Leakey 1973. [33] Leakey & Wood 1973. [34] Brown & Walker 1993. [35] Brown *et al*., 1985.

Table 9.7: Hominin specimens and their M_2 and M_3 dental measurements. References for each measurement numbered.

Species/	M_2 MD		M_2 BL Max		M_2 BL1		M_2 BL2		M_3 MD		M_3 BL Max		M_3 BL1		M_3 BL2	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Australopithecus afarensis																
A.L. 128-23	12.1[1]		12.5[1]													
A.L. 145.35	15.4[1]		14.2[1]													
A.L. 176.35																
A.L. 188.1		14.8[1]		15.2[1]								14.9[1]				
A.L. 198.1	11.2[1]		12.4[1]						14.1[1]		12.1[1]					
A. L. 198.22																
A.L. 200.1b																
A.L. 207.13	13[1]		12.5[1]													
A.L. 207.17									13.4[2]		11.3[2]					
A.L. 225.8	13.4[2]		11.1[2]						15[2]		13.8[2]					
A.L. 228.2																
A.L. 241.14	14.6[1]		[13.5][1]													
A.L. 266.1		13[1]		14[1]						15[1]		13.8[1]				
A.L. 277.1	14.3[1]		14.5[1]													
A.L. 288.1		13[1]		12.2[1]					14[1]	14.1[1]	12.2[1]	12.2[1]				
A. L. 315.22																
A.L. 330.5	12.7[2]		12.8[2]						13.7[2]		12.7[2]					
A.L. 330.7																
A.L. 333.44																
A.L. 333.74	13.3[1]								13.9[1]		13.8[1]					
A.L. 333w-1a+b	13.2[1]	13.7[1]	12.5[1]	13[1]												
A.L. 333w-12																
A.L. 333w-27	15[1]		[14.1][1]													
A.L. 333w-	14.2[1]		14.6[1]						14.2[1]	14.1[1]	[14.4][1]	14.2[1]				
A.L. 333w-48		12.6[1]		[12.1][1]												
A.L. 333w-57	13.5[1]		12.1[1]						14.4[1]		12.5[1]					
A.L. 333w-59	13.2[1]		14.4[1]						14[1]		[13.1][1]					
A.L. 400-1a	14.8[1]	14.3[1]	14.6[1]	14.5[1]					14.8[1]	15.2[1]	13.5[1]	13.8[1]				
A.L. 411.1										[15][1]						

Species/	**M_2 MD**		**M_2 BL Max**		**M_2 BL1**		**M_2 BL2**		**M_3 MD**		**M_3 BL Max**		**M_3 BL1**		**M_3 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
A.L. 417.1a	13^{3}		13.1^{3}							14.9^{3}		13.3^{3}				
A.L. 417.1a,b	13.2^{2}		13.1^{2}						15.4^{2}		13.3^{2}					
A.L. 418.1	16.5^{2}															
A.L. 433.1a																
A.L. 437.1	16.1^{2}		13.9^{2}						16.5^{2}		13.6^{2}					
A.L. 437.2	15.6^{2}															
A.L. 438.1		16^{2}								16.5^{2}						
A.L. 440.1	15.8^{2}		13.8^{2}													
A.L. 443.1	15.2^{2}		14.2^{2}													
A.L. 444.2																
A.L. 465.5									14^{2}							
A.L. 487-1a									17.2^{2}							
A.L. 582.1l																
A.L. 620.1									17.4^{2}		15.3^{2}					
DIK-2-1									18.1^{4}		14.7^{4}					
LH2																
LH3																
LH 4	13.7^{5}	13.9^{5}	13.6^{5}							15.9^{5}		14.2_{5}				
LH 14																
MAK-VP1/2		14.7^{6}		13^{6}						15.6^{6}		13^{6}				
MAK-VP1/4		16.2^{7}		13.8^{7}												
MAK-VP1/12	13.6^{6}	13.8^{6}	13.3^{6}	13.3^{6}					14.8^{6}	14.9^{6}	13.4_{6}	13.4_{6}				
Australopithecus africanus																
MLD 2	16.8^{8}	16.2^{8}	15.3^{8}		15^{8}	15.3^{8}	15.2^{8}									
MLD 4											14.2^{8}		14.2^{8}		13.7^{8}	
MLD 18		14.2^{8}		14.7^{8}				14.3^{8}		14.2^{8}		13.9^{8}		13.8^{8}		13.5^{8}
MLD 19									15.1^{8}		13.6^{8}		13.7^{8}		13.3^{8}	
MLD 24	15.1^{8}		13.8^{8}		13.6^{8}		13.8^{8}									
MLD 40	15.3^{8}		14.1^{8}		13.7^{8}		14^{8}									
Sts 7	15.8^{8}	15.3^{8}	14.6^{8}	15.3^{8}	14.4^{8}	14.9^{8}	14.6^{8}	15.2^{8}	16.4^{8}		14.4^{8}		14.4^{8}			
Sts 52	15.2^{8}	14.4^{8}	13.5^{8}	13.4^{8}	13.5^{8}	13.3^{8}	12.9^{8}	12.7^{8}	13.7^{8}	13.7^{8}	13^{8}	12.8^{8}	12.9^{8}	12.8^{8}	12.3^{8}	11.7^{8}
Taung																

Species/	**M_2 MD**		**M_2 BL Max**		**M_2 BL1**		**M_2 BL2**		**M_3 MD**		**M_3 BL Max**		**M_3 BL1**		**M_3 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Stw 1																
Stw 3	15.9[9]		13.8[9]													
Stw 14		15.8[9]		14.2[9]						17.8[9]		14.6[9]				
Stw 47										15.8[9]		14.2[9]				
Stw 54			14.9[9]													
Stw 56																
Stw 61		15.9[9]		14.3[9]												
Stw 72	16.7[9]		15.1[9]													
Stw 80										15.2[9]						
Stw 87																
Stw 90										16.8[9]		14.3[9]				
Stw 96											15.8[9]					
Stw 106																
Stw 109		16.7[9]		15.6[9]						17.4[9]		15.6[9]				
Stw 112																
Stw 120	16.1[9]		15.4[9]													
Stw 123																
Stw 131																
Stw 133									16.5[9]		15[9]					
Stw 134	16.4[9]		14.9[9]													
Stw 142									16.4[9]		15.4[9]					
Stw 145																
Stw 147																
Stw 151																
Stw 193			14.3[9]													
Stw 196											12.9[9]					
Stw 212		16[9]		14.8[9]					16.7[9]		13.9[9]					
Stw 213	14.4[9]	14.4[9]	12.8[9]	12.7[9]												
Stw 220																
Stw 234		14.4[9]		13.3[9]												
Stw 237									18[9]		15.9[9]					
Stw 246																

Species/	**M_2 MD**		**M_2 BL Max**		**M_2 BL1**		**M_2 BL2**		**M_3 MD**		**M_3 BL Max**		**M_3 BL1**		**M_3 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Stw 280										16.8[9]		16.4[9]				
Stw 285	14.2[9]		13.5[9]													
Stw 291																
Stw 295	15.5[9]		14.5[9]						15.4[9]	15.1[9]	14.2[9]	14.4[9]				
Stw 308		17[9]		14.3[9]												
Stw 309																
Stw 327	16.6[9]		14.3[9]													
Stw 353										13.5[9]		12.2[9]				
Stw 364																
Stw 384		17[9]		16.8[9]						18.2[9]		16.8[9]				
Stw 385	15.5[9]		14.9[9]						16[9]		14.8[9]					
Stw 397										16.7[9]						
Stw 404		14.4[9]		13.7[9]						14.8[9]		14.1[9]				
Stw 412	14.6[9]	14.6[9]	13[9]	13[9]												
Stw 413																
Stw 421																
Stw 424	17.7[9]		16[9]													
Stw 487										17.9[9]		14.7[9]				
Stw 491	14.7[9]		13.9[9]						15.8[9]		14[9]					
Stw 498	17.6[9]		15.8[9]						18.5[9]		16.1[9]					
Stw 520										16.2[9]		14.3[9]				
Stw 529		15.1[9]		14.4[9]					15.2[9]	15.2[9]	14.6[9]	14[9]				
Stw 537	16.6[9]	16.6[9]	15.5[9]	15.3[9]					16.1[9]		16.1[9]					
Stw 555	15.2[9]		13.4[9]													
Stw 560	179	16.99	15.99	16.59					17.4[9]	17[9]	15.9[9]	16.1[9]				
Stw 566																
Stw 586																
Paranthropus boisei																
KGA 10-525			[16.8][16]						21[16]		17.7[16]					
KGA 10-570																
KGA 10-1720									18.7[16]		14.9[16]					
KGA 10-2705				[17.5][16]												

Species/	M_2 MD		M_2 BL Max		M_2 BL1		M_2 BL2		M_3 MD		M_3 BL Max		M_3 BL1		M_3 BL2	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
KNM-ER 403		15[8]														
KNM-ER 404		19[8]		17[8]												
KNM-ER 729	20.5[8]	19.8[8]	18[8]	18.1[8]	17.3[8]	17.9[8]	18[8]	17.9[8]	21.28	22.2[8]	19[8]	19[8]	19[8]	18.5[8]	17.8[8]	18.6[8]
KNM-ER 733										19[8]						
KNM-ER 801		19.2[8]		16.7[8]						19.2[8]		16[8]		15.5[8]		
KNM-ER 802			15[8]							18.7[8]		16.4[8]		16.2[8]		16.3[8]
KNM-ER 810									17.7[8]		15.7[8]		15.5[8]		15.6[8]	
KNM-ER 818	20.3[8]		18.4[8]						21.9[8]		18.2[8]		18.2[8]			
KNM-ER 1171	19[8]	19.3[8]	17[8]	16.8[8]	17[8]		16.6[8]	16.4[8]								
KNM-ER 1467										18.8[16]		15.5[16]		15.4[8]		15.1[8]
KNM-ER 1477																
KNM-ER 1509									19.8[8]		15.9[8]		15.9[8]		15[8]	
KNM-ER 1816	17.3[17]		16.2[17]				15.8[8]									
KNM-ER 1819									22.2[8]							
KNM-ER 1820																
KNM-ER 3229																
KNM-ER 3230	20.2[8]	20.8[8]	19[8]	18.6[8]	18[8]	17.9[8]	18.9[8]	18.6[8]	20.5[8]	21.3[8]	16.5[8]	16.9[8]	16.4[8]	16.7[8]	16.3[8]	16.9[8]
KNM-ER 3737																
KNM-ER 3885																
KNM-ER 3890																
KNM-ER 5679	19[8]						16.3[8]									
KNM-ER 5877										23.5[18]		[20] [18]				
KNM-ER	16[12]		14.5[12]						18.2[12]		15[12]					
KNM-ER									18[12]	18.5[12]	15.5[12]	15.9[12]				
KNM-ER									20[12]		17[12]					
KNM-WT									[19][12]		[17][12]					
OH 26														16.7[8]		
OH 30																
OH 38		18.5[8]		17.6[8]		17.6[8]		17.1[8]								
OMO 136-1									17.9[15]		15.6[15]					
OMO 136-2									16.7[13]		14.6[13]					
OMO 47-46		16.8[14]		16.4[14]												

Species/	M_2 MD		M_2 BL Max		M_2 BL1		M_2 BL2		M_3 MD		M_3 BL Max		M_3 BL1		M_3 BL2	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
OMO 75-14	16.7[14]	17.5[14]	15.4[14]	15.4[14]					15.1[14]		14.1[14]					
OMO 84-100										16.5[13]						
OMO F203-1										17.2[15]		15.9[15]				
OMO L427-7		16.4[8]		15.2[8]		14.7[8]		15.2[8]								
OMO L628-2									19[8]		17.8[8]		17.8[8]		15.4[8]	
OMO L628-3									18.7[8]		16.2[8]		16.1[8]		16.2[8]	
OMO L628-4																
OMO L628-9	15.4[8]		14.2[8]		14.2[8]		14[8]									
OMO L7A-125	16.2[8]		18[8]							18.2[19]		14.8[19]				
OMO L74A-21																
Peninj 1	17.8[8]	17.6[8]	16.2[8]	16.2[8]	16[8]	15.9[8]		16.1[8]	18.2[8]	18.8[8]	16.1[8]	15.7[8]	15.8[8]	15.3[8]	16.1[8]	15.7[8]
Paranthropus robustus																
DNH 7	[13.4][20]	[14.2][20]	13.5[20]	13.5[20]					[15.2][20]	[15.4][20]	13.6[20]	13.4[20]				
DNH 8	[15.9][20]	[15.5][20]	15[20]	[14.8][20]					19.1[20]	18.8[20]	16.2[20]	15.5[20]				
DNH 10										[15.7][22]		[14.7][22]				
DNH 12																
DNH 18										[17.2][22]		[15.7][22]				
DNH 19	[16.6][22]		[15.2][22]													
DNH 21	[15.3][22]		[13.9][22]						[14.3][22]		[13.7][22]					
DNH 26																
DNH 27																
DNH 46																
DNH 51		[16.8][22]		13.9[22]						[17][22]		13.9[22]				
DNH 60		14.522		13[22]												
DNH 67																
DNH 68		[17.2][22]		[14.3][22]						[14.7][22]						
DNH 75										[17.3][22]		13.4[22]				
DNH 81																
SK 6	17.9[8]	18[8]	16.2[8]	16.4[8]	16[8]	15.8[8]	16.1[8]	16.3[8]	18.7[8]	18.4[8]	15.5[8]	16.2[8]		16.2[8]		16.1[8]
SK12									17.3[8]		15.3[8]		15.3[8]		15.2[8]	
SK 23	16[8]	15.6[8]	14.9[8]	14.9[8]	14.8[8]	14.7[8]	14.8[8]	14.9[8]	16.8[8]	17.5[8]	13.1[8]	14.4[8]	13[8]	14.4[8]	12.9[8]	13.9[8]
SK 34	17.1[8]	17[8]	16.5[8]	16.4[8]	16.4[8]	15.9[8]	16.4[8]	16.2[8]	18.1[8]	18.2[8]	16[8]	17[8]	15.6[8]	16.7[8]	15.8[8]	16.3[8]

Species/	**M$_2$ MD**		**M$_2$ BL Max**		**M$_2$ BL1**		**M$_2$ BL2**		**M$_3$ MD**		**M$_3$ BL Max**		**M$_3$ BL1**		**M$_3$ BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
SKW 5	15.9[23]	16[23]	14.4[23]	14.4[23]	14[23]	14[23]	14.3[23]	14.4[23]		16.7[23]	[14.3][23]	14[23]	[14.3][23]	14[23]		13.2[23]
SKW 10																
SKW 4767																
SKW 4769			16.5[24]													
SKX 257																
SKX 258																
SKX 4446		17.1[25]		15.8[25]												
SKX 5002									17.6[25]		13.9[25]					
SKX 5013																
SKX 5014										17.2[25]		15[25]				
SKX 5015																
SKX 5023																
SKX 19892			14.8[25]													
SKX 32162																
TM 1517				14.1[26]						16.2[26]		13.9[26]				
TM 1601b																
KB 5223																
TM 1536																
TM 1600	14.8[26]		14.7[26]						16[26]		14.7[26]					
Homo habilis																
OH 7	15.7[8]		13.7[8]		13.5[8]		13.5[8]									
OH 13		14.2[8]		12[8]		11.8[8]		11.9[8]	14.8[8]	14.8[8]	12.3[8]	12.4[8]	12.1[8]	12.2[8]	12.2[8]	12.4[8]
OH 16		15.4[8]		15.1[8]		14.9[8]		14.5[8]	15.9[8]	15.9[8]	14.3[8]	14.4[8]	14.3[8]	14.4[8]	14[8]	13.8[8]
OH 37	14.7[8]		13.3[8]		13.2[8]		13[8]									
KNM-ER 1462									14.5[27]		13.6[27]					
KNM-ER 1480										15.3[27]		12.5[27]				
KNM-ER 1482	15[8]		14[8]								14.6[8]				14.3[8]	
KNM-ER 1483			12.9[8]		12.9[8]		12.6[8]									
KNM-ER 1502																
KNM-ER 1508																
KNM-ER 1590	13.9[17]		16.8[17]													
KNM-ER 1801									17[8]		14.6[8]		14.5[8]		14.3[8]	

Species/	**M_2 MD**		**M_2 BL Max**		**M_2 BL1**		**M_2 BL2**		**M_3 MD**		**M_3 BL Max**		**M_3 BL1**		**M_3 BL2**	
	L	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
KNM-ER 1802	16.6[17]	16.5[17]	14.1[17]	14.3[17]	14.1[8]	13.9[8]	14.2[8]	14[8]								
KNM-ER 1805		13.8[17]		12.8[17]		12.8[8]		12.8[8]		14.4[17]		12.2[17]		12.2[8]		12[8]
KNM-ER 3734	14.1[8]		11.7[8]		10.5[8]		11.6[8]									
KNM-ER	14[28]	13.9[28]	12.8[28]	12.6[28]					15.7[28]	15.4[28]	12.9[28]	13.3[28]				
KNM-ER																
UR 501		18.3[29]		14.9[29]												
KNM-WT																
Homo ergaster																
KGA 10-1	14.4[31]		13[31]						[13][31]		11.8[31]					
KNM-BK 67	13.5[8]	13[8]	11.2[8]	10.9[8]	11.1[8]	10.9[8]	11.1[8]	10.9[8]	12.9[8]	12.8[8]	11.4[8]	11.2[8]	11.4[8]	11.2[8]	10.8[8]	10.7[8]
KNM-ER 730	12[32]		11.6[32]						13[32]		11.5[32]		11.4[8]		11.4[8]	
KNM-ER 806	14.3[33]		13.1[33]		13.1[8]		13.1[8]		14.7[33]	14[33]	12.1[33]	12.2[33]	12.4[8]	12.2[8]	12.3[8]	12.1[8]
KNM-ER 809																
KNM-ER 820																
KNM-ER 992	13[33]	13.2[33]	12.3[33]	12.5[33]	12.2[8]	12.2[8]	11.8[8]	12.2[8]	12.8[33]	13[33]	12.3[33]	12.1[33]	12.3[8]	12.1[8]	11.7[8]	10.8[8]
KNM-ER 1507																
KNM-ER 1808		13.6[8]		12[8]		12[8]		11.9[8]	13.6[34]		12[34]					
KNM-ER 1812									14.5[8]		12.5[8]		12.4[8]		12.5[8]	
KNM-WT	12.2[35]	12.4[35]	11.5[35]	11.4[35]												
OH 22		13[8]		11.7[8]		11.7[8]		11.4[8]								
OH 51																
SK 15		14.6[8]		13[8]		12.6[8]		12.9[8]	14.7[8]	14.6[8]	12.6[8]	12.2[8]	12.4[8]	12.2[8]	12.2[8]	12.3[8]

MD = Mesiodistal Crown Diameter. **BLMax** = Buccolingual Crown Diameter maximum distance, **BL1** = Buccolingual Crown Diameter from Protoconid - Metaconid, **BL2** = Buccolingual Crown Diameter from Hypoconid - Entoconid.

[1] Johanson *et al*., 1982b. [2] Kimbel *et al*., 2004. [3] Kimbel *et al*., 1994. [4] Alemseged *et al*., 2005. [5] White 1977. [6] White *et al*., 2000. [7] White *et al*., 1993. [8] Wood 1991. [9] Moggi-Cecchi *et al*., 2006. [10] Moggi-Cecchi *et al*., 1998. [11] Kuykendall & Conroy 1999. [12] Leakey & Walker 1988. [13] Coppens 1973a. [14] Coppens 1971. [15] Coppens 1973b. [16] Suwa *et al*., 1997. [17] Day *et al*., 1976. [18] Leakey & Walker 1985. [19] Howell 1969. [20] Keyser 2000. [21] Moggi-Cecchi *et al*., 2010. [22] Keyser *et al*., 2000. [23] Grine & Daegling 1993. [24] Grine & Strait 1994. [25] Grine 1988. [26] Thackeray *et al*., 2001. [27] Leakey & Wood 1974. [28] Leakey *et al*., 2012. [29] Bromage *et al*., 1995. [30] Prat *et al*., 2005. [31] Suwa *et al*., 2007. [32] Day & Leakey 1973. [33] Leakey & Wood 1973. [34] Brown & Walker 1993. [35] Brown *et al*., 1985.

Table 9.8 presents the stable carbon isotope results for each hominin analysed to date. Information includes the tooth the data was extracted from, the site and member the tooth was found, its estimated age, and the type of environment the specimen was reconstructed to have inhabited. The stable carbon isotope results highlight the changing environment over time, particularly in East Africa, shifting from a C_3 dominated diet to more of a C_4-based diet.

Table 9.8: Stable Carbon Isotope signatures and environmental reconstructions for each hominin specimen

Species	Specimen	Tooth	δ13C	Site	Age	Member	Environment	Reference
A. afarensis	A.L. 125-11	M1 in	-13	Hadar	3.42 - 3.26**	SH2	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	A.L. 207-17	**Lm3**	-4.3	Hadar	3.26 - 3.2**	DD2	Mixed habitats, woodland, bushlands, edaphic	Wynn *et al*. (2013) SOM
	A.L. 225-8	**M2 in**	-6.7	Hadar	3.42 - 3.26**	SH1	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	A.L. 249-27	P3 fragment	-10	Hadar	3.42 - 3.26**	SH1	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	A.L. 293-3	I1	-10.7	Hadar	3.26 - 3.2**	DD3	Mixed habitats, woodland, bushlands, edaphic	Wynn *et al*. (2013) SOM
	A.L. 309-8	M1 fragment	-6.4	Hadar	3.26 - 3.2**	DD3	Mixed habitats, woodland, bushlands, edaphic	Wynn *et al*. (2013) SOM
	A.L. 333-52	M1 fragment	-8.6	Hadar	3.26 - 3.2**	DD2	Mixed habitats, woodland, bushlands, edaphic	Wynn *et al*. (2013) SOM
	A.L. 411-1	**M2 in**	-7.7	Hadar	3.42 - 3.26**	SH2	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	A.L. 423-1	M1	-7.2	Hadar	3.42 - 3.26**	SH2	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	A.L. 432-1	**M3 fragment**	-4.3	Hadar	3.26 - 3.2**	DD3	Mixed habitats, woodland, bushlands, edaphic	Wynn *et al*. (2013) SOM
	A.L. 437-2	M2 fragment	-6.6	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 438-1h	RM1 fragment	-10.2	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 440-1	P4 fragment	-7.6	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 444-2	**M2/M3**	-8	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 452-18	M fragment	-2.9	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 462-7	**M3**	-6.4	Hadar	3.12 - 2.94**	KH2	Open woodland/ shrubland	Wynn *et al*. (2013) SOM
	A.L. 660-1	**M2 fragment**	-9.6	Hadar	3.42 - 3.26**	SH1	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	DIK2-1	M fragment	-4.3	Hadar	3.8 - 3.42**	BM	Mosaic of woodland and shrubland, near water	Wynn *et al*. (2013) SOM
	DIK40-1	LM1	-10.6	Hadar	3.42 - 3.26**	SH	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
	DIK49	P	-4.9	Hadar	3.42 - 3.26**	SH	Medium - open density woodland, grassland,	Wynn *et al*. (2013) SOM
A. africanus	MLD 12	**RM3**	-7.7	Makapansgat	2.9 - 2.6**	MAK 3	Mosaic habitat, riparian woodland, bushland,	Sponheimer & Lee-Thorp
	MLD 28	**RM3**	-8.1	Makapansgat	2.9 - 2.6**	MAK 3	Mosaic habitat, riparian woodland, bushland,	Sponheimer & Lee-Thorp
	MLD 30	RM1	-5.6	Makapansgat	2.9 - 2.6**	MAK 3	Mosaic habitat, riparian woodland, bushland,	Sponheimer & Lee-Thorp
	MLD 41	M	-11.3	Makapansgat	2.9 - 2.6**	MAK 3	Mosaic habitat, riparian woodland, bushland,	Sponheimer & Lee-Thorp

Species	Specimen	Tooth	δ13C	Site	Age	Member	Environment	Reference
	STS 31	**RM3**	-6.8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	Sponheimer *et al*. (2005a)
	STS 32	**RM3**	-7.8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	Sponheimer *et al*. (2005a)
	STS 2218	M	-5.9	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	Sponheimer *et al*. (2005a)
	STS 45	**RM2**	-4	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	Sponheimer *et al*. (2005a)
	STS 72	**RM3**	-9.7	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	Sponheimer *et al*. (2005a)
	STW 14	Lm1	-6.7	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 207	?	-2	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 211	M	-7.3	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 213i	Lm1	-1.8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 229	P	-5.8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 236	P	-3.7	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 252	RM1	-7.4	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 276	Lm1	-8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 303	**RM2**	-4.3	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 304	M	-7.4	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 309b (409)	Lm1	-6.1	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 315	Ldm2	-5.7	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
	STW 73	**RM2**	-8.8	Sterkfontein	2.65 - 2**	ST4	Open woodland, riparian forest, bushland and	van der Merwe *et al*. (2003)
P. boisei	KNM-ER 13750	m-frag	0.2	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1469	**Lm3**	-2.3	Turkana:	1.82	Upper	Open woodland, edaphic grasslands and	Cerling *et al*. (2013) SOM
	KNM-ER 1479A	**m3**	-2.3	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 15940	**Lm3**	-1.1	Turkana:	1.73	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1804	**LM3**	-1.2	Turkana:	1.73	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1806C	**Rm3**	-1.3	Turkana:	1.76	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 3952F	**LM3**	-1.2	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 732A	RP4	-0.1	Turkana:	1.78	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 810	p3	-3.4	Turkana:	1.73	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 816B	m-frag	-1.9	Turkana:	1.73	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1171C	Lm1	-0.6	Turkana:	1.59	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 15951F	m-frag	-3.3	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 1819	**m3**	0.9	Turkana:	1.6			Cerling *et al*. (2013) SOM
	KNM-ER 3737B	Rm1	-1.6	Turkana:	1.59	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 3887	**RM3**	-1.7	Turkana:	1.46	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM

Species	Specimen	Tooth	δ13C	Site	Age	Member	Environment	Reference
	KNM-ER 6080	**Rm2**	-2.2	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 6082	Lp3	-0.8	Turkana:	1.5	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 729	Lp4	0	Turkana:	1.53	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 733A	**Rm3**	-1.5	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 733D	LP4	-0.5	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 801C	**Lm3**	0.4	Turkana:	1.59	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 802D	Lm1	-0.1	Turkana:	1.59	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 802G	**m3**	-1.9	Turkana:	1.59	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 818	**Lm3**	0.7	Turkana:	1.5	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-WT 17396	**Lm3**	-1.9	Turkana:	1.77	Kaito:	Closed, wet woodland habitat	Cerling *et al*. (2013) SOM
	KNM-WT 37100	**m2 or m3**	-1.8	Turkana:	1.77	Kaito:	Closed, wet woodland habitat	Cerling *et al*. (2013) SOM
	KNM-WT 37748	**RM3**	-2.1	Turkana:	1.77	Kaito:	Closed, wet woodland habitat	Cerling *et al*. (2013) SOM
	OH5	**LM2**	-1.2	Olduvai	1.82	Bed I	Closed/ wet habitat. Palm and Acacia	van der Merwe *et al*. (2008)
	Peninj	**Lm2**	-0.7	Peninj	1.62	Humbu	Savannah grassland	van der Merwe *et al*. (2008)
	KNM-CH-302	m-frag	-1.3	Baringo	1.42			Cerling *et al*. (2011) SOM
P. robustus	SK 14000	**LM3**	-5.9	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SK 14132	**RM3**	-6.9	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SK 1512	P	-8.8	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (1994)
	SK 19	**Rm3**	-6.3	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SK 24605	**RM3**	-7.3	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2006a)
	SK 24606	**RM2**	-6.1	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2006a)
	SK 41	**LM3**	-6.7	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SK 57	**LM3**	-6.5	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SK 876	M	-6.7	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (2000)
	SK 878	Rp3	-6.8	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (1994)
	SK 879	M	-8.5	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (1994)
	SK 879	M	-8.1	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (1994)
	SKW 3068	**LM2**	-8.1	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SKW 4768	**LM2**	-7.4	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SKW 6	**LM3**	-7	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2005a)
	SKW 6427	M	-8.6	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2006a)
	SKX 1312	LM1	-8.1	Swartkrans	1.7 - 1.1**	SK2	Wooded grassland with wetlands	Lee-Thorp *et al*. (1994)
	SKX 333	Rm1	-10	Swartkrans	1.7 - 1.1**	SK2	Wooded grassland with wetlands	Lee-Thorp *et al*. (1994)

Species	Specimen	Tooth	δ13C	Site	Age	Member	Environment	Reference
	SKX 35025	RM	-7.9	Swartkrans	1.3 - 0.6**	SK3	Open edaphic grasslands with a river/ stream	Lee-Thorp *et al*. (1994)
	SKX 5015	**Lm3**	-9.6	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (1994)
	SKX 5939	M	-5.4	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Sponheimer *et al*. (2006a)
	TM 1600	**Lm2**	-7.9	Kromdraai	1.8 - 1.6**	KB3	Open grassland with riparian woodland	Sponheimer *et al*. (2005a)
H.habilis	KNM-ER 1483E*	m-frag	-7.5	Turkana:	1.89	Upper	Open woodland, edaphic grasslands and	Cerling *et al*. (2013) SOM
	KNM-ER 1802B*	**LM3**	-6.4	Turkana:	1.97	Upper	Open woodland, edaphic grasslands and	Cerling *et al*. (2013) SOM
	KNM-ER 1805*	Lm1	-7.7	Turkana:	1.76	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 3734*	**Lm3**	-5.8	Turkana:	1.95	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	OH 62	**LM2**	-8.3	Olduvai	1.8	Bed I	Closed/ wet habitat. Palm and Acacia	van der Merwe *et al*. (2008)
	OH 65	**LM3**	-5.2	Olduvai	1.8	Bed I	Closed/ wet habitat. Palm and Acacia	van der Merwe et al. (2008)
	OH 7	**Lm2**	-8.8	Olduvai	1.75	Bed I	Closed/ wet habitat. Palm and Acacia	van der Merwe *et al*. (2008)
H. ergaster	KNM-ER 730A*	Lm1	-2.6	Turkana:	1.54	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 820*	Ldm2	-3.5	Turkana:	1.51	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 992B*	Lc	-5	Turkana:	1.46	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 1808l*	m-frag	-2.6	Turkana:	1.59	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
Homo sp.	KNM-WT 42718	Rm1	-7.2	Turkana:	2.29	Kalochoro	Mosaic habitat, wet grassland, marsh or lagoon	Cerling *et al*. (2013) SOM
	KNM-ER 1478A	m-frag	-8.6	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1478A	**M2**	-8.1	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1593C	m1	-7.4	Turkana:	1.8	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 1814E	**m3**	-6.6	Turkana:	1.67	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 2599	p4	-9.9	Turkana:	1.86	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 2600	m-frag	-6.1	Turkana:	1.82	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 45501	m-frag	-5.8	Turkana:	1.85	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 45502	Lm1 or Lm2	-3.9	Turkana:	1.85	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 45503	**M2 or M3**	-8.6	Turkana:	1.85	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 62000	rM1	-7.2	Turkana:	1.97	Upper	Open woodland, edaphic grasslands and	Cerling *et al*. (2013) SOM
	KNM-ER 7330	RP3	-5.5	Turkana	1.83	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-WT 37745	Rp3	-6.4	Turkana:	1.75	Kaito:	Closed, wet woodland habitat	Cerling *et al*. (2013) SOM
	SK 27	**LM3**	-8.2	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (2000)
	SK 80/ 847	P	-7.1	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (2000)
	SK 2635	P	-9.2	Swartkrans	2.31 - 1.64**	SK1	Open habitat with a riverine woodland nearby	Lee-Thorp *et al*. (2000)
	KNM-ER 807	LM1	-5.6	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 807	**LM2**	-5.6	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM

Species	Specimen	Tooth	δ13C	Site	Age	Member	Environment	Reference
	KNM-ER 808G	RM1	-5.1	Turkana:	1.52	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 809A	Lm1	-5	Turkana:	1.53	Okote	Wetlands and edaphic grasslands	Cerling *et al*. (2013) SOM
	KNM-ER 3733	LM1	-4.6	Turkana:	1.65	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM
	KNM-ER 3733	**LM2**	-3.8	Turkana:	1.65	KBS	Grassland/ shrubland environment	Cerling *et al*. (2013) SOM

* SOM = Supporting Online Material. **Species and dates assigned based on information of specimen numbers and member information from Table 9.2-9.3. All environmental reconstructions use information from Table 9.2-9.3. Specimens in bold denote those using an M_2 or M_3.

Results

Tables 9.9-9.10 indicate that significant values were obtained between similar-sized monkeys consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the crown area variables. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did. Significant differences were also present on most of the Levene's tests for the Equality of Variance/ Homogeneity of Variance too. These results indicate that there are significant differences between similar-sized monkeys consuming different diets.

Table 9.9: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using $P_4 – M_1$ Crown Area (CA)

Body size	Diet category	P_4 CA				M_1 CA			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	52.061	**0.000**	42.269	**0.000**	91.859	**0.000**	57.812	**0.000**
Large	Traditional Diet	17.529	**0.000**	-19.945	**0.000**	20.618	**0.000**	-21.765	**0.000**
Small	SpecClassCode DO*	14.989	**0.000**	38.906	**0.000**	10.511	**0.000**	82.759	**0.000**
Large	SpecClassCode DO	16.827	**0.000**	18.715	**0.000**	24.031	**0.000**	20.712	**0.000**
Small	Fruit DO	0.73	0.393	-5.983	**0.000**	0.109	0.742	-7.009	**0.000**
	Leaves DO	6.578	**0.011**	-5.003	**0.000**	15.474	**0.000**	-8.474	**0.000**
	Seeds DO	49.253	**0.000**	152.452	**0.000**	26.447	**0.000**	206.836	**0.000**
	Animals DO	78.729	**0.000**	146.054	**0.000**	157.121	**0.000**	256.618	**0.000**
Large	Fruit DO	16.827	**0.000**	-18.715	**0.000**	24.031	**0.000**	-20.712	**0.000**
	Leaves DO	15.297	**0.000**	0.768	0.444	86.449	**0.000**	-2.204	**0.030***
	Seeds DO	11.027	**0.000**	202.795	**0.000**	26.49	**0.000**	283.452	**0.000**
	Roots DO	7.611	**0.001**	131.508	**0.000**	15.852	**0.000**	205.578	**0.000**
Small	SpecClassCode FA	47.562	**0.000**	18.633	**0.000**	50.659	**0.000**	81.281	**0.000**
Large	SpecClassCode FA	1.141	0.322	11.571	**0.000**	8.552	**0.000**	31.296	**0.000**
Small	Fruit FA	14.938	**0.000**	22.021	**0.000**	20.363	**0.000**	46.43	**0.000**
	Leaves FA	36.152	**0.000**	278.456	0.097	40.234	**0.000**	275.598	**0.019***
	Seeds FA	178.388	**0.000**	109.089	**0.000**	187.868	**0.000**	220.38	**0.000**
	Animals FA	5.315	**0.005**	21.171	**0.000**	21.849	**0.000**	38.904	**0.000**
Large	Fruit FA	7.951	**0.001**	203.829	**0.000**	35.234	**0.000**	304.909	**0.000**
	Leaves FA	0.501	0.48	9.178	**0.000**	0.07	0.792	5.765	**0.000**
	Seeds FA	8.529	**0.000**	1.717	0.189	56.592	**0.000**	4.39	**0.016***
	Roots FA	10.499	**0.000**	217.991	**0.000**	32.402	**0.000**	325.689	**0.000**
	Animals FA	9.843	**0.000**	4.785	**0.012***	46.466	**0.000**	4.357	**0.017***
Overall (*n* = 23)	**Number significant**				**20**				**23**
Small (*n* = 11)	**% Significant**				**90.91%**				**100%**
Large (*n* = 12)	**% Significant**				**83.33%**				**100%**
Overall	**% Significant**				**86.96%**				**100%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis
Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.10: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using M_2 _ M_3 Crown Area (CA)

Body size	Diet category	M_2 CA				M_3 CA			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	96.165	**0.000**	296.424	**0.000**	103.949	**0.000**	528.491	**0.000**
Large	Traditional Diet	15.885	**0.000**	-21.392	**0.000**	15.774	**0.000**	-15.382	**0.000**
Small	SpecClassCode DO*	12.921	**0.000**	304.521	**0.000**	9.309	**0.000**	190.388	**0.000**
Large	SpecClassCode DO	16.838	**0.000**	20.048	**0.000**	16.626	**0.000**	15.03	**0.000**
Small	Fruit DO	1.364	0.243	-9.038	**0.000**	1.52	0.218	-7.974	**0.000**
	Leaves DO	15.813	**0.000**	-11.139	**0.000**	12.86	**0.000**	-14.664	**0.000**
	Seeds DO	22.739	**0.000**	212.033	**0.000**	18.117	**0.000**	205.989	**0.000**
	Animals DO	150.245	**0.000**	389.414	**0.000**	124.193	**0.000**	302.019	**0.000**
Large	Fruit DO	16.838	**0.000**	-20.048	**0.000**	16.626	**0.000**	-15.03	**0.000**
	Leaves DO	51.736	**0.000**	-1.279	0.204	31.274	**0.000**	-1.506	0.135
	Seeds DO	14.809	**0.000**	223.536	**0.000**	11.386	**0.000**	119.278	**0.000**
	Roots DO	10.636	**0.000**	175.874	**0.000**	6.58	**0.002**	113.964	**0.000**
Small	SpecClassCode FA	76.245	**0.000**	377.386	**0.000**	95.834	**0.000**	466.063	**0.000**
Large	SpecClassCode FA	1.502	0.226	24.316	**0.000**	0.401	0.671	20.361	**0.000**
Small	Fruit FA	32.625	**0.000**	42.958	**0.000**	39.308	**0.000**	40.027	**0.000**
	Leaves FA	13.779	**0.000**	231.827	**0.000**	0.483	**0.000**	151.194	**0.000**
	Seeds FA	180.014	**0.000**	229.823	**0.000**	156.688	**0.000**	261.292	**0.000**
	Animals FA	9.005	**0.000**	48.103	**0.000**	27.645	**0.000**	51.788	**0.000**
Large	Fruit FA	12.667	**0.000**	252.122	**0.000**	9.901	**0.000**	123.857	**0.000**
	Leaves FA	1.883	0.172	6.331	**0.000**	0.695	0.406	4.235	**0.000**
	Seeds FA	30.372	**0.000**	0.85	0.432	17.117	**0.000**	1.14	0.327
	Roots FA	15.38	**0.000**	252.237	**0.000**	10.492	**0.000**	124.233	**0.000**
	Animals FA	27.222	**0.000**	0.55	0.58	17.901	**0.000**	53.338	0.096
Overall (*n* = 23)	**Number significant**				**20**				**20**
Small (*n* = 11)	**% Significant**				**100%**				**100%**
Large (*n* = 12)	**% Significant**				**75%**				**75%**
Overall	**% Significant**				**86.9%**				**86.96%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.11-9.12 indicate that significant values were obtained on many variables between similar-sized monkeys consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the crown shape indices. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did. Significant differences were also present on many of the Levene's tests for the Equality of Variance/ Homogeneity of Variance too. These results indicate that there are significant differences between similar-sized monkeys consuming different diets.

Table 9.11: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using $P_4 – M_1$ Crown Shape Indices (CSI)

Body size	Diet category	P_4 CSI				M_1 CSI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	7.25	**0.000**	129.134	**0.000**	3.449	**0.016**	111.363	**0.000**
Large	Traditional Diet	0.688	0.408	2.973	**0.003**	1.355	0.246	-1.093	0.276
Small	SpecClassCode DO*	23.348	**0.000**	33.655	**0.000**	21.04	**0.000**	39.086	**0.000**
Large	SpecClassCode DO	1.605	0.204	8.21	**0.000**	1	0.319	1.506	0.134
Small	Fruit DO	31.542	**0.000**	1.487	0.138	30.976	**0.000**	1.076	0.282
	Leaves DO	4	**0.046**	-1.672	0.114	5.343	**0.021**	2.403	**0.029***
	Seeds DO	50.092	**0.000**	52.622	**0.000**	31.498	**0.000**	29.95	**0.000**
	Animals DO	96.145	**0.000**	17.788	**0.000**	55.562	**0.000**	15.105	**0.000**
Large	Fruit DO	0.902	0.344	2.645	**0.009**	1	0.319	-1.506	0.134
	Leaves DO	0.915	0.341	-4.308	**0.000**	3.942	**0.049**	-0.013	0.989
	Seeds DO	4.801	**0.01**	11.588	**0.000**	3.9	**0.023**	5.524	**0.008**
	Roots DO	3.45	**0.036**	2.002	0.148	0.225	0.799	5.017	**0.011**
Small	SpecClassCode FA	3.191	**0.024**	117.036	**0.000**	2.149	0.094	126.387	**0.000**
Large	SpecClassCode FA	1.605	0.204	8.929	**0.000**	1.235	0.294	5.207	**0.008**
Small	Fruit FA	14.399	**0.000**	27.161	**0.000**	21.636	**0.000**	28.539	**0.000**
	Leaves FA	64.733	**0.000**	3.761	**0.000**	25.187	**0.000**	20.089	**0.000**
	Seeds FA	37.047	**0.000**	38.169	**0.000**	31.975	**0.000**	22.65	**0.000**
	Animals FA	22.656	**0.000**	8.84	**0.001**	16.889	**0.000**	1.516	0.235
Large	Fruit FA	0.781	0.46	5.6	**0.007**	1.562	0.213	1.179	0.315
	Leaves FA	1.9	0.17	-2.9	**0.004**	1.903	0.17	-1.773	0.078*
	Seeds FA	0.421	0.657	14.408	**0.000**	2.043	0.133	4.347	**0.018**
	Roots FA	3.8	**0.024**	17.628	**0.000**	2.94	0.056	8.536	**0.001**
	Animals FA	0.947	0.391	17.712	**0.000**	2.811	0.064	4.402	**0.018**
Overall (*n* = 23)	**Number significant**				**20**				**15**
Small (*n* = 11)	**% Significant**				**81.82%**				**81.82%**
Large (*n* = 12)	**% Significant**				**91.67%**				**50%**
Overall	**% Significant**				**86.96%**				**65.22%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.12: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using M_2 – M_3 Crown Shape Indices (CSI)

Body size	Diet category	M_2 CSI				M_3 CSI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	6.743	**0.000**	91.604	**0.000**	4.769	**0.003**	39.963	**0.000**
Large	Traditional Diet	0.976	0.325	-2.719	**0.007**	0.08	0.778	-2.953	**0.004**
Small	SpecClassCode DO*	10.492	**0.000**	40.406	**0.000**	5.562	**0.000**	17.582	**0.000**
Large	SpecClassCode DO	0.932	0.336	3.044	**0.003**	0.124	0.725	3.253	**0.001**
Small	Fruit DO	6.292	**0.012**	2.523	**0.012***	6.454	**0.011**	4.498	**0.000**
	Leaves DO	5.902	**0.015**	7.107	**0.000**	5.772	**0.017**	16.111	**0.000**
	Seeds DO	26.823	**0.000**	24.523	**0.001**	9.107	**0.000**	19.954	**0.000**
	Animals DO	32.848	**0.000**	27.398	**0.000**	15.208	**0.000**	35.158	**0.000**
Large	Fruit DO	0.932	0.336	-3.044	**0.003**	0.124	0.725	-3.253	**0.001**
	Leaves DO	0.754	0.387	0.234	0.815	0.41	0.523	1.027	0.306
	Seeds DO	1.596	0.206	8.757	**0.001**	0.105	0.9	6.714	**0.003**
	Roots DO	0.248	0.781	8.696	**0.001**	0.665	0.517	4.955	**0.012**
Small	SpecClassCode FA	4.412	**0.005**	58.807	**0.000**	9.465	**0.000**	44.764	**0.000**
Large	SpecClassCode FA	0.964	0.384	4.729	**0.013**	1.86	0.159	2.242	0.116
Small	Fruit FA	15.412	**0.000**	39.753	**0.000**	4.041	**0.018**	4.814	**0.010***
	Leaves FA	18.635	**0.000**	0.792	0.1	24.155	**0.000**	1.351	**0.001***
	Seeds FA	26.315	**0.000**	12.67	**0.000**	18.329	**0.000**	24.349	**0.000**
	Animals FA	10.986	**0.000**	0.705	0.5	6.806	**0.001**	12.744	**0.000**
Large	Fruit FA	1.018	0.364	5.717	**0.006**	0.703	0.497	3.834	**0.029**
	Leaves FA	0.084	0.772	0.454	0.65	0.268	0.606	3.179	**0.002**
	Seeds FA	0.497	0.609	2.365	0.103	0.207	0.813	1.841	0.169
	Roots FA	1.102	0.335	9.674	**0.001**	0.208	0.813	3.945	**0.027**
	Animals FA	0.834	0.437	1.975	0.15	0.031	0.97	4.819	**0.012**
Overall (*n* = 23)	**Number significant**				**17**				**20**
Small (*n* = 11)	**% Significant**				**81.82%**				**100%**
Large (*n* = 12)	**% Significant**				**66.67%**				**75%**
Overall	**% Significant**				**73.91%**				**86.96%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.13-9.14 indicate that significant values were obtained on most variables between similar-sized monkeys consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the corpus size variables. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did. Significant differences were also present on most of the Levene’s tests for the Equality of Variance/ Homogeneity of Variance too. These results indicate that there are significant differences between similar-sized monkeys consuming different diets.

Table 9.13: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using Symphyseal Size (SS), P_4 – M_1 Corpus Size (CS)

Body size	Diet category	SS				P_4 CS				M_1 CS			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	38.298	**0.000**	14.052	**0.000**	76.543	**0.000**	45.092	**0.000**	91.086	**0.000**	54.689	**0.000**
Large	Traditional Diet	36.296	**0.000**	-15.1	**0.000**	18.163	**0.000**	-13.97	**0.000**	16.14	**0.000**	-12.808	**0.000**
Small	SpecClassCode DO*	19.953	**0.000**	55.545	**0.000**	15.193	**0.000**	86.185	**0.000**	18.709	**0.000**	80.785	**0.000**
Large	SpecClassCode DO	32.16	**0.000**	14.039	**0.000**	17.334	**0.000**	13.644	**0.000**	14.527	**0.000**	12.636	**0.000**
Small	Fruit DO	52.461	**0.000**	-11.011	**0.000**	63.826	**0.000**	-9.225	**0.000**	62.411	**0.000**	-8.765	**0.000**
	Leaves DO	1.867	0.172	-3.196	**0.001**	10.182	**0.002**	-4.462	**0.000**	8.924	**0.003**	-5.427	**0.000**
	Seeds DO	11.292	**0.000**	87.488	**0.000**	10.381	**0.000**	195.393	**0.000**	11.605	**0.000**	214.565	**0.000**
	Animals DO	86.792	**0.000**	171.646	**0.000**	115.842	**0.000**	136.249	**0.000**	127.43	**0.000**	127.586	**0.000**
Large	Fruit DO	32.16	**0.000**	-14.039	**0.000**	17.334	**0.000**	-13.644	**0.000**	14.527	**0.000**	-12.636	**0.000**
	Leaves DO	3.879	0.051	3.521	**0.001**	1.177	0.28	1.899	0.06	2.595	0.109	1.572	0.119
	Seeds DO	24.242	**0.000**	115.357	**0.000**	8.552	**0.000**	100.288	**0.000**	7.411	**0.001**	83.725	**0.000**
	Roots DO	21.73	**0.000**	70.812	**0.000**	10.884	**0.000**	66.637	**0.000**	8.627	**0.000**	57.834	**0.000**
Small	SpecClassCode FA	30.006	**0.000**	53.366	**0.000**	30.944	**0.000**	69.874	**0.000**	35.74	**0.000**	62.491	**0.000**
Large	SpecClassCode FA	4.757	**0.01**	0.193	0.825	0.963	0.384	2.4	0.1	0.54	0.584	2.97	0.060*
Small	Fruit FA	11.863	**0.000**	38.823	**0.000**	10.812	**0.000**	40.119	**0.000**	16.056	**0.000**	50.204	**0.000**
	Leaves FA	1.175	**0.000**	103.143	0.183	9.995	0.304	170.854	**0.022***	12.168	**0.000**	190.773	**0.002***
	Seeds FA	81.973	**0.000**	163.049	**0.000**	130.084	**0.000**	304.85	**0.000**	156.022	**0.000**	338.353	**0.000**
	Animals FA	12.265	**0.000**	26.593	**0.000**	62.786	**0.000**	27.092	**0.000**	93.981	**0.000**	29.305	**0.000**
Large	Fruit FA	21.858	**0.000**	116.254	**0.000**	9.025	**0.000**	96.786	**0.000**	8.361	**0.000**	81.154	**0.000**
	Leaves FA	13.515	**0.000**	6.691	**0.000**	3.361	0.069	6.562	**0.000**	1.353	0.246	5.819	**0.000**
	Seeds FA	2.196	0.115	6.566	**0.003**	0.609	0.545	1.788	0.176	1.568	0.212	1.219	0.303
	Roots FA	25.266	**0.000**	125.239	**0.000**	9.957	**0.000**	99.222	**0.000**	7.666	**0.001**	82.267	**0.000**
	Animals FA	2.761	0.067	13.594	**0.000**	0.591	0.555	7.845	**0.001**	1.656	0.195	5.139	**0.009**
Overall (*n* = 23)	**Number significant**				**21**				**20**				**20**
Small (*n* = 11)	**% Significant**				**90.91%**				**100%**				**100%**
Large (*n* = 12)	**% Significant**				**91.67%**				**75%**				**75%**
Overall	**% Significant**				**91.30%**				**86.96%**				**86.96%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.14: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using $M_2 – M_3$ Corpus Size (CS)

Body size	Diet category	M_2 CS				M_3 CS			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	90.238	**0.000**	58.718	**0.000**	99.972	**0.000**	57.771	**0.000**
Large	Traditional Diet	8.238	**0.005**	-9.849	**0.000**	7.93	**0.005**	-8.778	**0.000**
Small	SpecClassCode DO*	20.147	**0.000**	81.634	**0.000**	21.62	**0.000**	101.673	**0.000**
Large	SpecClassCode DO	7.247	**0.008**	9.629	**0.000**	6.711	**0.011**	8.463	**0.000**
Small	Fruit DO	62.804	**0.000**	-8.577	**0.000**	81.632	**0.000**	-8.876	**0.000**
	Leaves DO	9.673	**0.002**	-6.91	**0.000**	10.267	**0.001**	-6.389	**0.000**
	Seeds DO	14.893	**0.000**	196.656	**0.000**	14.213	**0.000**	222.717	**0.000**
	Animals DO	124.527	**0.000**	124.726	**0.000**	120.05	**0.000**	121.415	**0.000**
Large	Fruit DO	7.247	**0.008**	-9.629	**0.000**	6.711	**0.011**	-8.463	**0.000**
	Leaves DO	1.19	0.277	1.029	0.305	4.997	0.027	-0.581	0.563
	Seeds DO	4.228	**0.017**	48.827	**0.000**	4.95	**0.008**	38.079	**0.000**
	Roots DO	3.445	**0.036**	36.641	**0.000**	2.672	0.074	35.874	**0.000**
Small	SpecClassCode FA	42.322	**0.000**	56.374	**0.000**	39.432	**0.000**	71.124	**0.000**
Large	SpecClassCode FA	0.717	0.49	3.542	**0.036**	0.636	0.525	9.472	**0.000**
Small	Fruit FA	23.019	**0.000**	54.506	**0.000**	28.348	**0.000**	59.368	**0.000**
	Leaves FA	15.729	**0.000**	230.471	**0.001***	22.67	**0.000**	234.969	**0.004***
	Seeds FA	197.376	**0.000**	360.791	**0.000**	197.357	**0.000**	421.533	**0.000**
	Animals FA	97.648	**0.000**	29.718	**0.000**	111.405	**0.000**	30.319	**0.000**
Large	Fruit FA	3.995	**0.02**	48.391	**0.000**	3.549	**0.031**	41.714	**0.000**
	Leaves FA	0.505	0.478	5.671	**0.000**	1.403	0.238	6.877	**0.000**
	Seeds FA	0.741	0.478	0.656	0.523	2.828	0.062	0.859	0.429
	Roots FA	4.432	**0.013**	49.427	**0.000**	4.454	**0.013**	40.087	**0.000**
	Animals FA	0.805	0.449	3.332	**0.043***	3.685	**0.028**	1.011	0.371
Overall (*n* = 23)	**Number significant**				**20**				**20**
Small (*n* = 11)	**% Significant**				**100%**				**100%**
Large (*n* = 12)	**% Significant**				**75%**				**75%**
Overall	**% Significant**				**86.96%**				**86.96%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.15-9.16 indicate that significant values were obtained on most variables between similar-sized monkeys consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the corpus robusticity indices. The smaller species obtained significant differences on the parametric and non-parametric tests slightly more often than the larger species did. Significant differences were present on most of the Levene’s tests for the Equality of Variance/ Homogeneity of Variance for the smaller species but not the larger species. These results indicate that there are significant differences between similar-sized monkeys consuming different diets.

Table 9.15: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using Symphyseal Robusticity Index (SRI), P_4 – M_1 Corpus Robusticity Indices (CRI)

Body size	Diet category	SRI				P_4 CRI				M_1 CRI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	4.535	**0.004**	3.035	**0.034**	3.089	**0.027**	107.666	**0.000**	0.992	0.396	62.388	**0.000**
Large	Traditional Diet	1.522	0.219	-4.316	**0.000**	0.197	0.657	3.82	**0.000**	0.847	0.359	4.654	**0.000**
Small	SpecClassCode DO*	2.927	**0.013**	5.64	**0.000**	8.858	**0.000**	27.763	**0.000**	9.283	**0.000**	23.493	**0.000**
Large	SpecClassCode DO	1.092	0.298	4.585	**0.000**	0.117	0.733	-4.455	**0.000**	0.696	0.406	-4.908	**0.000**
Small	Fruit DO	11.057	**0.001**	-2.637	**0.009**	17.498	**0.000**	3.998	**0.000**	12.606	**0.000**	-8.765	**0.000**
	Leaves DO	0.833	0.362	-2.644	**0.008**	0.048	0.827	0.076	0.939	2.428	0.12	0.308	0.758
	Seeds DO	0.497	0.609	17.626	**0.000**	13.324	**0.000**	14.236	**0.000**	3.671	**0.026**	4.301	**0.016***
	Animals DO	4.131	**0.017**	7.734	**0.001**	28.35	**0.000**	28.382	**0.000**	10.135	**0.000**	11.576	**0.000**
Large	Fruit DO	1.092	0.298	-4.585	**0.000**	0.117	0.733	4.455	**0.000**	0.696	0.406	4.908	**0.000**
	Leaves DO	0.855	0.357	0.843	0.401	0.266	0.607	-2.932	**0.004**	0.254	0.615	-3.355	**0.001**
	Seeds DO	3.274	**0.041**	11.581	**0.000**	0.586	0.558	11.87	**0.000**	1.137	0.324	12.083	**0.000**
	Roots DO	1.226	0.564	12.745	**0.000**	0.046	0.955	14.816	**0.000**	1.093	0.339	8.134	**0.001**
Small	SpecClassCode FA	5.874	**0.001**	2.412	0.07	2.782	**0.041**	143.405	**0.000**	1.116	0.343	82.334	**0.000**
Large	SpecClassCode FA	6.359	**0.002**	2.871	0.066	1.621	0.201	2.524	0.09	3.907	**0.022**	2.657	0.078
Small	Fruit FA	0.286	0.751	3.147	**0.047***	10.089	**0.000**	15.715	**0.000**	3.941	**0.02**	3.543	**0.032***
	Leaves FA	5.929	0.304	13.699	**0.021***	4.153	**0.000**	33.304	**0.002**	6.96	**0.000**	45.062	**0.003**
	Seeds FA	2.509	0.083	6.295	**0.002**	21.284	**0.000**	29.556	**0.000**	21.923	**0.000**	30.693	**0.000**
	Animals FA	2.107	0.123	1.923	0.162	18.438	**0.000**	8.969	**0.001**	10.851	**0.000**	6.282	**0.005**
Large	Fruit FA	1.915	0.151	11.06	**0.000**	0.339	0.713	12.15	**0.000**	1.156	0.317	12.27	**0.000**
	Leaves FA	1.407	0.237	2.374	**0.019**	1.576	0.211	0.414	0.68	0.326	0.569	-2.238	**0.027***
	Seeds FA	1.074	0.344	0.384	0.683	0.127	0.88	6.604	**0.003**	1.422	0.244	8.387	**0.001**
	Roots FA	4.558	**0.012**	11.501	**0.000**	0.763	0.468	12.28	**0.000**	1.381	0.254	9.184	**0.000**
	Animals FA	1.759	0.177	0.28	0.757	0.233	0.792	2.154	0.127	1.39	0.253	7.848	**0.001**
Overall (*n* = 23)	**Number significant**				**15**				**20**				**20**
Small (*n* = 11)	**% Significant**				**63.64%**				**90.91%**				**81.82%**
Large (*n* = 12)	**% Significant**				**72.73%**				**83.33%**				**91.67%**
Overall	**% Significant**				**65.22%**				**86.96%**				**86.96%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis.

Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.16: *T*-test and ANOVA tests on monkeys and body size, grouped by dietary categories using $M_2 – M_3$ Corpus Robusticity Indices (CRI)

Body size	Diet category	M_2 CRI				M_3 CRI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Small	Traditional Diet	1.855	0.136	51.511	**0.000**	4.548	**0.004**	23.111	**0.000**
Large	Traditional Diet	0.804	0.371	2.725	**0.007**	6.043	**0.015**	1.849	0.075
Small	SpecClassCode DO*	3.352	**0.005**	31.451	**0.000**	1.967	0.082	26.085	**0.000**
Large	SpecClassCode DO	0.534	0.466	-3.234	**0.002**	5.109	**0.025**	-2.426	**0.022**
Small	Fruit DO	0.536	0.464	3.38	**0.001**	1.231	0.268	2.821	**0.005**
	Leaves DO	1.792	0.181	-0.15	0.881	0.029	0.866	-1.795	0.073
	Seeds DO	0.916	0.401	23.078	**0.000**	3.058	**0.048**	33.095	**0.000**
	Animals DO	7.874	**0.000**	21.901	**0.000**	12.875	**0.000**	15.846	**0.000**
Large	Fruit DO	0.534	0.466	3.234	**0.002**	5.109	**0.025**	2.426	**0.022**
	Leaves DO	1.299	0.256	-3.929	**0.000**	1.087	0.299	-3.74	**0.000**
	Seeds DO	0.37	0.692	14.462	**0.000**	2.444	0.091	11.493	**0.000**
	Roots DO	0.084	0.919	2.836	0.069	2.146	0.122	1.299	0.282
Small	SpecClassCode FA	5.109	**0.002**	30.314	**0.000**	5.343	**0.001**	2.628	0.054
Large	SpecClassCode FA	2.274	0.106	6.515	**0.003**	0.121	0.886	9.315	**0.000**
Small	Fruit FA	4.859	**0.008**	13.34	**0.000**	4.368	**0.013**	7.736	**0.001**
	Leaves FA	5.136	**0.026**	69.135	**0.002**	5.272	0.588	47.263	0.508
	Seeds FA	8.88	**0.000**	48.87	**0.000**	1.747	0.176	15.624	**0.000**
	Animals FA	0.696	0.499	13.216	**0.000**	1.769	0.172	13.567	**0.000**
Large	Fruit FA	0.693	0.501	11.83	**0.000**	2.637	0.075	10.718	**0.000**
	Leaves FA	0.86	0.355	-1.808	0.073	3.059	0.082	-0.596	0.552
	Seeds FA	0.686	0.505	12.161	**0.000**	0.611	0.544	12.868	**0.000**
	Roots FA	4.242	**0.016**	5.644	**0.006**	3.913	**0.022**	2.845	0.067
	Animals FA	0.296	0.745	17.295	**0.000**	0.186	0.83	17.169	**0.000**
Overall (*n* = 23)	**Number significant**				**21**				**16**
Small (*n* = 11)	**% Significant**				**90.91%**				**72.73%**
Large (*n* = 12)	**% Significant**				**91.67%**				**66.67%**
Overall	**% Significant**				**91.30%**				**69.57%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis.
Blue variables = ANOVA. Black variables = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.17-9.18 indicate that significant values were obtained on most variables between similar-sized apes consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the crown area variables. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did. Significant differences were rarely obtained on the Levene's tests for the Equality of Variance/ Homogeneity of Variance. These results indicate that there are significant differences between similar-sized apes consuming different diets.

Table 9.17: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using P_4 – M_1 Crown Area (CA)

Body size	Diet category	P_4 CA				M_1 CA			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.004	0.951	3.263	**0.000**	1.515	0.221	1.118	0.266
Small	SpecClassCode DO	0.037	**0.848**	8.665	**0.000**	0.091	0.763	6.64	**0.000**
Large	SpecClassCode DO	0.038	0.846	3.189	**0.002**	1.102	0.297	2.311	**0.024**
Large	Fruit DO	0.038	0.846	3.189	**0.000**	1.102	0.297	2.311	**0.024**
Small	SpecClassCode FA	0.2	0.655	17.59	**0.000**	0.077	0.782	15.492	**0.000**
Large	SpecClassCode FA	1.33	0.251	2.127	**0.035**	0.633	0.428	4.713	**0.000**
Small	Fruit FA	0.2	0.655	17.59	**0.000**	0.077	0.782	15.492	**0.000**
	Leaves FA	7.456	0.001	194.514	**0.000**	13.068	**0.000**	148.914	**0.000**
	Roots FA	0.978	0.324	-20.792	**0.000**	0.643	0.424	-17.511	**0.000**
Large	Fruit FA	1.091	0.339	4.41	**0.023**	0.518	0.597	10.96	**0.000**
	Leaves FA	1.33	0.251	-2.127	**0.035**	0.633	0.428	-4.713	**0.000**
	Seeds FA	0.003	0.957	-3.292	**0.001**	1.531	0.218	-1.143	0.255
	Roots FA	3.589	0.061	-0.35	0.727	0.303	0.583	-4.057	**0.000**
Overall (*n* = 13)	**Number significant**				**12**				**11**
Small (*n* = 5)	**% Significant**				**100%**				**100%**
Large (*n* = 8)	**% Significant**				**87.50%**				**75%**
Overall	**% Significant**				**92.31%**				**84.62%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances.
SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis
Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Table 9.18: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using $M_2 – M_3$ Crown Area (CA)

Body size	Diet category	M_2 CA				M_3 CA			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.571	0.451	1.974	0.051	0.023	0.879	1.127	0.262
Small	SpecClassCode DO	0.406	0.525	6.615	**0.000**	0.079	0.779	6.608	**0.000**
Large	SpecClassCode DO	0.211	0.647	2.961	**0.004**	0.035	0.851	1.689	0.096
Large	Fruit DO	0.0211	0.647	2.961	**0.004**	0.035	0.851	1.689	0.096
Small	SpecClassCode FA	2.356	0.126	13.759	**0.000**	6.351	**0.012**	14.333	**0.000**
Large	SpecClassCode FA	0.312	0.578	4.777	**0.000**	0.087	0.769	2.746	**0.007**
Small	Fruit FA	2.356	0.126	13.759	**0.000**	6.351	**0.012**	12.495	**0.000**
	Leaves FA	9.18	**0.000**	92.279	**0.000**	10.811	**0.000**	79.842	**0.000**
	Roots FA	4.043	**0.045**	-14.318	**0.000**	7.941	**0.005**	-13.673	**0.000**
Large	Fruit FA	0.17	0.843	11.139	**0.000**	0.108	0.898	3.657	**0.041**
	Leaves FA	0.312	0.578	-4.777	**0.000**	0.087	0.769	-2.746	**0.007**
	Seeds FA	0.604	0.439	-2.005	**0.047**	0.022	0.882	-1.152	0.252
	Roots FA	0.453	0.502	-3.551	**0.001**	0.142	0.707	-2.116	**0.037**
Overall (*n* = 13)	**Number significant**				**12**				**9**
Small (*n* = 5)	**% Significant**				**100%**				**100%**
Large (*n* = 8)	**% Significant**				**87.50%**				**50%**
Overall	**% Significant**				**92.31%**				**69.23%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis
Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences.

Tables 9.19-9.20 indicate that significant values were rarely obtained between similar-sized apes consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the crown shape indices, M_3 CSI appears to be the only exception to this pattern with significant differences reported between most of the dietary categories. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did for P_4 CSI and M_3 CSI, but the reverse was true for M_1 CSI. Significant differences were rarely obtained on the Levene's tests for the Equality of Variance/ Homogeneity of Variance. These results indicate that there are some significant differences between similar-sized apes consuming different diets.

Table 9.19: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using P_4 – M_1 Crown Shape Indices (CSI)

Body size	Diet category	P_4 CSI				M_1 CSI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	1.627	0.205	-1.11	0.269	0.194	0.661	0.636	0.526
Small	SpecClassCode DO	1.177	0.28	-0.289	0.773	0.438	0.509	-0.084	0.933
Large	SpecClassCode DO	1.951	0.167	-0.706	0.483	1.123	0.293	1.412	0.162
Large	Fruit DO	1.951	0.167	-0.706	0.483	1.123	0.293	1.412	0.162
Small	SpecClassCode FA	7.652	**0.006**	-2.708	**0.007**	2.022	0.156	0.654	0.514
Large	SpecClassCode FA	0.776	0.38	1.11	0.269	1.989	0.161	2.375	**0.019**
Small	Fruit FA	7.652	**0.006**	-2.708	**0.007**	2.022	0.156	0.654	0.514
	Leaves FA	4.05	**0.019**	7.124	**0.001**	1.027	0.36	1.862	0.16
	Roots FA	10.707	**0.001**	2.817	**0.005**	3.398	0.067	-0.36	0.719
Large	Fruit FA	0.993	0.374	1.598	0.223	0.983	0.377	2.582	0.096
	Leaves FA	0.776	0.38	-1.11	0.269	1.989	0.161	-2.375	**0.019***
	Seeds FA	1.655	0.201	1.096	0.276	0.205	0.651	-0.65	0.517
	Roots FA	0.012	0.912	-1.783	0.077	1.467	0.228	-2.053	**0.042***
Overall (*n* = 13)	**Number significant**				**4**				**3**
Small (*n* = 5)	**% Significant**				**80%**				**0.00%**
Large (*n* = 8)	**% Significant**				**0.00%**				**37.50%**
Overall	**% Significant**				**30.77%**				**23.08%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances.
SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis
Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.20: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using $P_4 – M_1$ Crown Shape Indices (CSI)

Body size	Diet category	M_2 CSI				M_3 CSI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.463	0.498	-0.169	0.866	2.823	0.096	-0.495	0.622
Small	SpecClassCode DO	2.397	0.124	-0.869	0.386	0.057	0.812	-1.253	0.212
Large	SpecClassCode DO	0.34	0.561	-0.339	0.735	0.921	0.34	-1.614	0.111*
Large	Fruit DO	0.34	0.561	-0.339	0.735	0.921	0.34	-1.614	0.111*
Small	SpecClassCode FA	2.534	0.113	-0.261	0.794	5.883	**0.016**	-5.425	**0.000**
Large	SpecClassCode FA	0.041	0.839	-0.888	0.376	0.006	0.941	-4.783	**0.000**
Small	Fruit FA	2.534	0.113	-0.261	0.794	5.883	**0.016**	-5.425	**0.000**
	Leaves FA	3.842	**0.023**	0.053	0.949	5.206	**0.006**	16.016	**0.000**
	Roots FA	4.492	**0.035**	0.341	0.776	4.288	**0.039**	5.428	**0.000**
Large	Fruit FA	0.318	0.729	0.403	0.673	0.729	0.485	11.691	**0.000**
	Leaves FA	0.041	0.839	0.888	0.376	0.006	0.941	4.783	**0.000**
	Seeds FA	0.438	0.509	0.135	0.892	2.944	0.089	0.452	0.652
	Roots FA	0.369	0.545	0.836	0.405	0.147	0.702	4.601	**0.000**
Overall (*n* = 13)	**Number significant**				**0**				**9**
Small (*n* = 5)	**% Significant**				**0.00%**				**100%**
Large (*n* = 8)	**% Significant**				**0.00%**				**50.00%**
Overall	**% Significant**				**0.00%**				**69.23%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis
Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.21-9.22 indicate that significant values were obtained between similar-sized apes consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for most of the corpus size variables, with the exceptions of specific classification coding by faecal analysis and leaf and root consumption by faecal analysis in the larger species, all of which never obtained a significant value on their *t*-tests. The smaller species obtained significant differences on the parametric and non-parametric tests more often than the larger species did. Equality of Variances/ Homogeneity of Variances were assumed for the majority of the corpus size variables, but not for the symphysis size. These results indicate that there are significant differences between similar-sized apes consuming different diets that manifest more in the corpus than in the symphysis.

Table 9.21: *T*- test and ANOVA tests on apes and body size, grouped by dietary categories using Symphyseal Size (SS), P_4 – M_1 Corpus Size (CS)

Body size	Diet category	SS				P_4 CS				M_1 CS			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.793	0.375	1.096	0.275	0.014	0.905	2.051	**0.042**	0.256	0.614	2.519	**0.013**
Small	SpecClassCode DO	8.764	**0.004**	4.028	**0.007**	1.224	0.27	6.057	**0.000**	1.504	0.222	6.78	**0.000**
Large	SpecClassCode DO	0.112	0.738	1.418	0.16	0.032	0.859	2.058	**0.043***	0.099	0.754	2.503	**0.015**
Large	Fruit DO	0.112	0.738	1.418	0.16	0.032	0.859	2.058	**0.043***	0.099	0.754	2.503	**0.015**
Small	SpecClassCode FA	28.188	**0.000**	11.414	**0.000**	2.103	0.148	9.219	**0.000**	4.14	**0.043**	11.381	**0.000**
Large	SpecClassCode FA	4.104	**0.045**	1.053	0.295	1.17	0.282	0.752	0.454	0.681	0.411	0.768	0.444
Small	Fruit FA	28.188	**0.000**	8.008	**0.000**	2.103	0.148	9.219	**0.000**	4.14	**0.043**	9.903	**0.000**
	Leaves FA	21.814	**0.000**	31.886	**0.000**	6.473	0.002	34.973	**0.000**	7.343	**0.001**	48.765	**0.000**
	Roots FA	32.746	**0.000**	-9.185	**0.000**	2.042	0.154	-10.456	**0.000**	4.499	**0.035**	-11.217	**0.000**
Large	Fruit FA	3.51	**0.033**	1.261	0.3	0.715	0.491	2.394	0.111	0.339	0.713	3.87	**0.034**
	Leaves FA	4.104	**0.045**	-1.035	0.295	1.17	0.282	-0.752	0.454	0.681	0.411	-0.768	0.444
	Seeds FA	0.784	0.378	-1.118	0.266	0.008	0.929	-2.066	**0.041**	0.242	0.624	-2.541	**0.012**
	Roots FA	6.643	0.011	-0.416	0.679	1.262	0.264	0.387	0.699	0.358	0.551	0.625	0.533
Overall (n = 13)	**Number significant**				**5**				**9**				**10**
Small (n = 5)	**% Significant**				**100%**				**100%**				**100%**
Large (n = 8)	**% Significant**				**0.00%**				**50.00%**				**62.50%**
Overall	**% Significant**				**38.46%**				**69.23%**				**76.92%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.22: *T*- test and ANOVA tests on apes and body size, grouped by dietary categories using $M_2 – M_3$ Corpus Size (CS)

Body size	Diet category	M_2 CS				M_3 CS			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.109	0.742	3.367	**0.001**	0.386	0.536	2.85	**0.005**
Small	SpecClassCode DO	4.056	**0.046**	7.662	**0.000**	5.449	**0.021**	8.231	**0.000**
Large	SpecClassCode DO	0.299	0.586	3.376	**0.001**	0.073	0.788	2.48	**0.015**
Large	Fruit DO	0.299	0.586	3.376	**0.001**	0.073	0.788	2.48	**0.015**
Small	SpecClassCode FA	8.481	**0.004**	12.679	**0.000**	7.177	**0.008**	13.738	**0.000**
Large	SpecClassCode FA	0.157	0.693	1.777	0.078	0.771	0.382	0.35	0.727
Small	Fruit FA	8.481	**0.004**	10.756	**0.000**	7.177	**0.008**	12.241	**0.000**
	Leaves FA	12.515	**0.000**	57.983	**0.000**	10.718	**0.000**	76.288	**0.000**
	Roots FA	10.814	**0.001**	-12.036	**0.000**	10.482	**0.001**	-13.594	**0.000**
Large	Fruit FA	0.511	0.601	5.509	**0.01**	1.341	0.266	3.138	0.061*
	Leaves FA	0.157	0.693	-1.777	0.078	0.771	0.382	-0.35	0.727
	Seeds FA	0.105	0.747	-3.395	**0.001**	0.405	0.526	-2.875	**0.005**
	Roots FA	1.628	0.205	0.05	0.96	2.57	0.112	1.238	0.218
Overall (*n* = 13)	**Number significant**				**10**				**10**
Small (*n* = 5)	**% Significant**				**100%**				**100%**
Large (*n* = 8)	**% Significant**				**62.50%**				**62.50%**
Overall	**% Significant**				**76.92%**				**76.92%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Tables 9.23-9.24 indicate that significant values were rarely obtained between similar-sized apes consuming different diets using both the parametric (*t*-tests and ANOVA) and non-parametric (Mann-Whitney U and Kruskal-Wallis) tests of difference for the corpus and symphyseal robusticity indices. Where significant differences did occur, they mainly manifested in the P_4 and M_1 corpus and only in the smaller species. Equality of Variances/ Homogeneity of Variances were assumed for all of the corpus robusticity indices. These results indicate that there are some significant differences between similar-sized apes consuming different diets that manifest more in the anterior corpus.

Table 9.23: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using Symphyseal Robusticity Index (SRI), $P_4 – M_3$ Corpus Robusticity Indices (CRI)

Body size	Diet category	SRI				P_4 CRI				M_1 CRI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.002	0.961	1.444	0.151	0.205	0.652	0.334	0.739	0.037	0.848	1.399	0.164
Small	SpecClassCode DO	0.371	0.543	-1.291	0.199	2.055	0.154	-2.219	**0.028***	0.74	0.391	-2.244	**0.026**
Large	SpecClassCode DO	0.204	0.653	1.706	0.092	0.228	0.635	0.256	0.799	0.014	0.906	1.454	0.15
Large	Fruit DO	0.204	0.653	1.706	0.092	0.228	0.635	0.256	0.799	0.014	0.906	1.454	0.15
Small	SpecClassCode FA	0.497	0.482	-4.287	**0.000**	0.006	0.939	-3.606	**0.000**	2.22	0.137	-3.373	**0.001**
Large	SpecClassCode FA	5.74	**0.018**	2.444	**0.016**	0.108	0.743	-0.192	0.848	1.996	0.16	0.365	0.716
Small	Fruit FA	0.497	0.482	-4.287	**0.000**	0.006	0.939	-3.606	**0.000**	2.22	0.137	-3.373	**0.001**
	Leaves FA	2.796	0.063	14.158	**0.000**	0.015	0.985	6.238	**0.003**	0.964	0.383	7.951	**0.001**
	Roots FA	1.364	0.244	4.733	**0.000**	0.068	0.794	4.719	**0.000**	1.947	0.164	4.197	**0.000**
Large	Fruit FA	3.454	**0.035**	2.929	0.072*	0.121	0.886	0.121	0.887	0.818	0.444	1.007	0.38
	Leaves FA	5.74	**0.018**	-2.444	**0.016**	0.108	0.743	0.192	0.848	1.996	0.16	-0.365	0.716
	Seeds FA	0.006	0.938	-1.446	0.151	0.182	0.671	-0.343	0.732	0.036	0.851	-1.422	0.158
	Roots FA	7.155	**0.009**	-1.747	0.083	0.022	0.881	0.393	0.695	1.221	0.271	0.43	0.668
Overall (*n* = 13)	**Number significant**				**8**				**5**				**5**
Small (*n* = 5)	**% Significant**				**100%**				**100%**				**100%**
Large (*n* = 8)	**% Significant**				**37.50%**				**0.00%**				**0.00%**
Overall	**% Significant**				**61.54%**				**38.46%**				**38.46%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.

Table 9.24: *T*-test and ANOVA tests on apes and body size, grouped by dietary categories using M_2 – M_3 Corpus Robusticity Indices (CRI)

Body size	Diet category	M_2 CRI				M_3 CRI			
		F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA	F/ Levene Statistic	EoV/ HoV	t/ F	*t*-test/ ANOVA
Large	Traditional Diet	0.095	0.758	0.826	0.411	0.124	0.725	-0.739	0.461
Small	SpecClassCode DO	0.719	0.398	-1.32	0.189	1.072	0.302	-0.448	0.655
Large	SpecClassCode DO	0.065	0.799	1.287	0.202	0.08	0.778	-0.474	0.637
Large	Fruit DO	0.065	0.799	1.287	0.202	0.08	0.778	-0.474	0.637
Small	SpecClassCode FA	0.226	0.635	-0.867	0.387	0.132	0.717	1.111	0.268
Large	SpecClassCode FA	3.335	0.07	1.781	0.077	0.002	0.967	0.593	0.555
Small	Fruit FA	0.226	0.635	-0.867	0.387	0.132	0.717	1.111	0.268
	Leaves FA	0.43	0.651	1.352	0.263	0.085	0.918	1.921	0.152
	Roots FA	0.401	0.527	1.374	0.171	0.365	0.546	-0.748	0.455
Large	Fruit FA	2.011	0.139	1.59	0.224	0.084	0.919	0.564	0.576
	Leaves FA	3.335	0.07	-1.781	0.077	0.002	0.967	-0.593	0.555
	Seeds FA	0.086	0.77	-0.844	0.401	0.122	0.727	0.711	0.478
	Roots FA	3.502	0.064	-1.336	0.184	0.117	0.733	-1.019	0.31
Overall (*n* = 13)	**Number significant**				**0**				**0**
Small (*n* = 5)	**% Significant**				**20%**				**0.00%**
Large (*n* = 8)	**% Significant**				**0.00%**				**0.00%**
Overall	**% Significant**				**0.00%**				**0.00%**

* EoV = Levene's test of Equality of Variances. HoV = Levene's test of the Homogeneity of Variances. SpecClassCoding =Specific Classification Coding. DO = Direct Observation. FA = Faecal Analysis

Blue dietary categories = ANOVA. Black dietary categories = t-tests. Numbers in bold denote those that obtained significant differences on their tests, and those in red did not obtain significant differences. Numbers with * denote those that obtained different results on the parametric and non-parametric tests.