Craniodental Evidence for Population Variability within *Paranthropus Robustus*: Taxonomy and Phylogenetic Implications

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Bachelor's of Anthropology with Honours Masters of Arts

This thesis is submitted in total fulfilment of the requirements for a Doctorate of Philosophy

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> > February 2020

Statement of Authorship

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Chapter 2 of this thesis consists of an article by Herries et al. which has been submitted to and accepted by the journal *Science*. The following has been drawn from the manuscript and is also in Appendix 1 (I am referred to as "ABL"):

Author contributions: AIRH led the geology and dating program and undertook the palaeomagnetic analysis with TM. JMM, ABL, DS, SN, GS and CM undertook the analysis of the hominin remains. JWA, JM, DSR, CM and SB undertook faunal analysis and biochronology. GB and AIRH undertook stratigraphic analysis and interpretation. GB, AM, TE and TD undertook micromorphological analysis. RJB undertook the US-ESR dating. BA undertook spatial and GIS analysis. JH, JW and RP undertook studies of the archaeological material. ABL, SB, JMM and AIRH excavated the hominin crania. BJA and CW undertook video and imaging of the site. AIRH, SB, CM, and JMC directed excavations at different times that recovered the hominin material. CM initiated the dating program at Drimolen. All authors contributed to the writing of the paper. Research supporting this publication was undertaken by JM, ABL, AM, while completing a PhD at La Trobe University.

I am a co-first author on this article and further detail on my contribution can be found at the beginning of Chapter 2. Permission from *Science* to include this manuscript in my PhD thesis has been submitted with this thesis.

Chapter 3 of this thesis has been redacted.

Angeline B Leece

7/2/2020

Acknowledgements

This work was supported by a La Trobe University Full Fee Research Scholarship (LTUFFRS), a La Trobe Internal Research Grant Scheme, and by an Australian Research Council Grant (DP170100056) awarded to Prof. Andy Herries. This work was also supported by NECSA through use of their micro-CT equipment, the University of the Witwatersand for use of their micro-CT equipment and research facilities, the La Trobe University Archaeomagnetism Laboratory, Washington University, Monash University, and the University of Johannesburg. I want to thank my supervisors: Andy Herries, David Strait, Justin Adams, and Matt Meredith-Williams for their support.

In addition to these formal things, I want to thank my colleagues and friends from Australia, South Africa, the US, and Europe for their support through what was an arduous task filled with more obstacles than I could have anticipated. I want to thank Kheti and Nathi NKosi (N'Gomo Lodge) for putting their faith and trust in us. Thanks to Stephanie Baker who has been a friend through two degrees and many a field season. Most of all, I want to thank Jesse Martin without whom I likely wouldn't have completed this task and certainly wouldn't have maintained by sanity. I couldn't ask for a more supportive husband and colleague. And, of course, last but not least, thanks to my cats, Lilith and Tarzan, for sitting with me through yet another dissertation.

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Abstract

This thesis addresses the taxonomy of the Drimolen Main Quarry robust australopiths and their phylogenetic relationships to other Plio-Pleistocene hominins. Although originally attributed to multiple discrete taxa, all ~2.0-1.4 Ma South African robust australopiths are now attributed to one taxon: *Paranthropus robustus*. Cladistic analysis typically reconstructs *P. robustus* as being a member of a monophyletic *Paranthropus* clade that also includes the highly derived *P. boisei* and the more primitive *P. aethiopicus*. **Three sentences redacted**. Dental evidence extends beyond that of qualitative character traits, in that metrical analysis of the broader Drimolen Main Quarry dental sample has shown statistically significant differences from the Swartkrans dental sample. Phylogenetic analyses conducted here demonstrate that the Drimolen Main Quarry *P. robustus* material, **redacted**. This interpretation is consistent with geochronological analyses presented here suggesting that the Drimolen Main Quarry *P. robustus* material is geologically older than other South African *P. robustus* samples.

1. Introduction

1.1 Chapter Outline and Aims

Drimolen is a series of fossil bearing palaeocaves, approximately 7km north-west of the better-known sites of Sterkfontein and Swartkrans, within the Fossil Hominid Sites of South Africa UNESCO World Heritage Area (Keyser et al., 2000; Figure 1). Drimolen consists of 2 main fossil bearing palaeocaves: the older 2.6 Ma Drimolen Makondo (DMK), and the younger hominin bearing Drimolen Main Quarry (DMQ). The primary goal of this thesis is to understand how the DMQ robust australopith material contributes to our understanding of the systematics and palaeobiology of Paranthropus robustus and other robust australopith taxa. DMQ is one of the richest early hominin bearing palaeocaves from South Africa. Since discovery of the DMQ in 1992, it has yielded a collection of over 150 hominin specimens as of the end of 2019, including the almost complete DNH 7 cranium. DNH 7 is the most complete skull assigned to *P. robustus* and has been argued to represent the species' female bauplan based on comparisons with larger specimens from Swartkrans (Keyser, 2000; Lockwood et al., 2007). Only a portion of this assemblages, which consists predominately of isolated teeth, has been published (Keyser, 2000; Gommery et al., 2002; Lague and Menter, 2017; Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Gallagher and Menter, 2011; Vernon, 2013; Smith et al., 2015; Peterson, 2017; Towle et al., 2019). This thesis will present the unpublished DMQ hominin material and clarify the taxonomic and phylogenetic relationships of the South African robust australopiths in light of these new specimens, Redacted.

The current chapter will present an overview of relevant localities, dates and contexts, and concepts and theories. Research presented in Chapter 2 will assess the morphology, palaeobiology, and taxonomy of the DNH 152 and DNH 134 crania in light of the clarified chronology of Plio-Pleistocene South African hominin sites following the application of multiple dating techniques such as palaeomagnetism, electron spin resonance and uranium-lead. Chapter 2 will also discuss hypotheses regarding multiple hominin taxa occupying the South African landscape contemporaneously. Chapter 3 has been redacted. Chapter 4 of this

thesis will present and describe 53 new DMQ dental specimens and assign these specimens to taxa. Chapter 5 conducts dental metrical analysis with the aim of reassessing previously published hypotheses claiming to explain variability within the South African robust australopith samples. Chapter 6 presents an assessment of deciduous dental qualitative character traits and conducts a cladistic analysis with the aim of determining the phylogenetic relationships between the South and eastern African robust australopith taxa. Chapter 7 proposes the application of the archaeological theory of Time Perspectivism to palaeoanthropological research and discusses the research implications of such an application. In closing, Chapter 8 will discuss the overarching conclusions and implications of the research conducted here.

1.1.2 Historical Background to Research Aims

Between 1925 and 1947, a series of early hominin taxa were proposed to accommodate a range of fossils discovered within South African karst deposits (e.g. Sterkfontein, Makapansgat, Taung, Swartkrans and Kromdraai; Fig. 1; Dart, 1925; Broom, 1936; Dart, 1947; Broom and Robinson, 1952; Brain, 1958). Some of these taxa, such as Australopithecus africanus and Paranthropus robustus (Dart, 1925; Broom, 1936), remain in use today while others, such as Plesianthropus transvaalensis and Telanthropus capensis (Broom, 1936; Broom and Robinson, 1949), are no longer recognised, with the previously assigned fossils having been subsumed into other taxa. Others, such as A. prometheus, have fallen out of use only to be resurrected (Broom, 1947; Kuman and Clarke, 2000; Clarke, 2013; Clarke, 2019) following more recent discoveries of additional fossil specimens. These nomenclatural changes have been driven largely by an increased sample size leading to a greater understanding of population variation, geographic variation, and temporal variation. As this understanding expands further and as gaps in the hominin fossil record grow ever smaller, these taxa must again be reassessed.

P. robustus was originally defined based on fossils recovered from the palaeocave of Kromdraai B (Broom, 1936), located in the Gauteng exposures of the Malmani dolomite approximately 40km NW of Johannesburg (Murszewski et al., 2019). This

broader area is now designated as the 'Fossil Hominid Sites of South Africa' UNESCO World Heritage Site and is known locally as the 'Cradle of Humankind' (Fig. 1). Since that time, fossil specimens attributed to *Paranthropus* have been recovered from the palaeocaves of Swartkrans, Cooper's, Sterkfontein, Gondolin and Drimolen (Menter et al., 1999; Keyser et al., 2000; de Ruiter et al., 2009; Moggi-Cecchi et al., 2010; Grine et al., 2012; Pickering et al., 2019). Broom and Robinson (1952) suggested that a second species, *P. crassidens* was needed to accommodate the increased variation between *Paranthropus* specimens recovered from Kromdraai and the recently discovered Swartkrans specimens.

Historically, some researchers put forward hypotheses that explained these differences through taxonomic diversity with each deposit attributed to a different species or subspecies (Broom, 1950; Howell, 1978; Junger and Grine, 1986; Grine, 1982, 1985a, 1985b, 1988; Tobias, 1995). Today, the combined Swartkrans and Kromdraai B samples are generally subsumed within a single species (*P. robustus*) despite a relatively large degree of intraspecific variation (Keyser, 2000; Keyser et al., 2000; Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016). The addition of the DMQ sample expanded the variation attributed to *P. robustus* even further. Lockwood et al. (2007) have suggested that differences between the assemblages from Swartkrans and DMQ can be explained by marked sexual dimorphism, with the complete specimen from DMQ, DNH 7, representing the female of the species and specimens from Swartkrans (including SK 12, SK 46, and SK 48) representing males. The acceptance of a single highly variable species of *P. robustus* is largely predicated on accepting that the DMQ sample is mostly comprised of females, whereas the Swartkrans sample is largely comprised of males with systemic and pronounced sexual dimorphism accounting for size and other discrete morphological differences between the two samples. This argument, advanced by Lockwood (2007) runs counter to Broom and Robinson's (1952) original view that at least some of the Swartkrans specimens Lockwood et al. (2007) argues represent males are in fact females (Broom and Robinson, 1952).

Previous studies have been somewhat hampered by the fact that only a few relatively complete crania of *Paranthropus* have been discovered in South Africa and even fewer have well associated maxillary and mandibular dental remains

(Keyser, 2000; Clarke et al., 2019). **Four sentences redacted.** This thesis will also examine the better-represented dental record consisting of adult and juvenile teeth, to assess the taxonomy and phylogeny of *Paranthropus*.

1.1.2 Aims

The broad scale aims of this project are as follows:

- Reassess the hominin record of DMQ in light of new chronological estimates and context models of South African robust australopith samples (Chapter 2).
- Present new fossil material and assess current hypotheses regarding *Paranthropus* variation, taxonomy, and phylogeny in South African robust australopiths (Chapters 2, 3, and 4, and appendices).
- Assess hypotheses regarding population-level variation in *P. robustus* (i.e., Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016; Chapter 5).
- Assess phylogenetic hypotheses by conducting parsimony and bayesian analyses (i.e. Grine, 1985; Chapter 6).
- Identify morphological differences between samples and interpret variation, taxonomy, and phylogenetic relationships (Chapter 8).

1.2 An overview of relevant fossil sites

The majority of *P. robustus* material derives from the palaeocave localities of DMQ and Swartkrans with a smaller number of specimens recovered from Kromdraai B, Coopers, Sterkfontein Member 5, and Gondolin. All these *P. robustus* yielding localities formed within the Malmani Dolomite complex caves which sit within a 25km² area (Fig. 1 and 5). Consequently, geographic variation can be excluded as an explanatory factor regarding inter-sample variability. The sites of Makapansgat Limeworks and Sterkfontein have primarily yielded specimens attributed to *A. africanus* with a further particularly well-preserved specimen of this species recovered from Taung. In addition to *P. robustus* and *A. africanus*, this study will also discuss the depositional context, taxonomic history, and phylogenetic interpretations of *P. boisei, P. aethiopicus,* and *A. afarensis*. These species derive

from eastern Africa with most specimens recovered from Olduvai Gorge, the Turkana Basin, Laetoli, and Hadar (Fig. 1).



Figure 1: Map showing relevant hominin fossil sites in east and South Africa

This chapter will discuss the depositional ages and contexts from which specimens attributed to these taxa derive. As understanding of the depositional history and ages of these contexts changes, so must interpretation of the taxonomy and phylogeny of the hominins recovered from within them (contra Hawks, 2017). This chapter will also discuss previously and currently accepted taxonomic and phylogenetic hypotheses. This will provide a foundation for analyses presented in subsequent chapters and conclusions drawn throughout this study.

1.2.1 South Africa

1.2.1.1 Taung

The Taung Child specimen (Taung 1) was discovered within a large lime quarry known as the Buxton-Norlim Limeworks in 1924 (Dart, 1925). The deposit is located on the escarpment of the Ghaap Plateau, a large exposure of Malmani dolomite approximately 360 km SW from the Cradle of Humankind localities (Fig. 1). As the deposit was heavily mined, and the Taung specimen was brought to Dart in an ex situ block, the context of Taung 1 was difficult to ascertain. The Buxton-Norlim Limeworks contains fossil material dating to as early as the last few 1000 years (Kuhn et al., 2016). Early surveys concluded that the Taung specimen was discovered near what are now two remnant tufa pinnacles: The Dart (formerly Australopithecus) and Hrdlička pinnacles (Peabody, 1954). Interpreting the relationship between the Taung skull and deposits found within these two pinnacles has been the topic of much debate. Sedimentological analysis of the matrix of the skull shows it comes from a pink claystone unit (PCS; Partridge and, 1982; Hopley et al., 2013; Herries et al., 2013; Tobias et al, 1993), rather than a younger red sandstone unit (YRSS; Herries et al., 2013). Most researchers have concluded that the skull came from a cave, within the tufa (Gordon, 1925; McKee, 1993; Tobias et al.. 1993), however recent analysis suggests the PCS unit formed contemporaneously with the tufa itself, with the younger YRSS later filling caves formed through both the tufa and PCS (Herries et al., 2013; Hopley et al., 2013). Preliminary palaeomagnetic analysis combined with biochronology suggests the remnants of these units, and thus the Taung Child is dated to between 3.03 and 2.61 Ma (Herries et al., 2013; dates for reversals adjusted as per Singer, 2014). Given that more recent analysis by Herries et al (2013) suggests that the two remnant pinnacles were attached prior to mining activity and thus preserve identical temporal units, attributing Taung 1 to either of these pinnacles rather than an associated cave provides some certainty as to the specimen's date. Extensive mining of the site also means that no further hominin specimens have been discovered from the A. africanus type site, although this may also be related to the unusual depositional context within an active tufa formation rather than within a cave (Hopley et al., 2013). It has been argued that the Taung skull was deposited via an eagle (Berger and Clarke, 1995; Berger, 2006; Berger and McGraw, 2007) and so it is not necessarily likely that other specimens would have entered the deposit at all. Although Taung has yielded only one hominin specimen, dated to 3.03–2.58 Ma (Herries et al., 2013), the good preservation and relative completeness of this specimen warrants inclusion within the analyses presented here. As this specimen represents the earliest member of its taxon predating other specimens by as much as 1 million years, the inclusion of this specimen will also contribute to discussions herein regarding temporal change within hominin taxa.

The discovery of Taung 1 changed the field of palaeoanthropology. Before the publication of this specimen in 1925, palaeoanthropology had been largely Eurocentric, assuming the rise of humankind must have occurred in Europe or Eurasia. Additionally, the Piltdown Man was still weighing heavily on the interpretation of human evolution (see for example Keith, 1925a). Dart (1925) attributed the juvenile Taung specimen to a new taxon: Australopithecus africanus. Dart (1925) argued this bipedal 'ape-like man' provided evidence that humankind may have instead evolved in southern Africa, a hypothesis that was not readily or widely accepted until the late 1940's (Keith, 1947). Many palaeoanthropologists working in Europe at the time considered the Taung Child to represent an extinct species of non-hominin ape (Keith, 1925; Smith, 1925). Keith went as far as to assert that it was "preposterous" for Dart (1925) to claim that the Taung Child was a human ancestor and instead that "Australopithecus must be classified with the chimpanzee and gorilla" (Keith, 1925b, pp.462). When morphological similarities between the Taung Child and accepted hominin species were acknowledged, they were explained by homoplasy or 'parallelism' (Le Gros Clarke, 1950). It wasn't until developmentally mature specimens were discovered at the site of Sterkfontein that additional evidence could be brought to bear on the question of whether Taung represented an early ancestor of Homo sapiens (Broom and Schepers, 1946).

1.2.1.2 Sterkfontein Caves

The specimens recovered from Sterkfontein were originally attributed to *Australopithecus transvaalensis* (Broom, 1937). Although Broom (1937) considered these specimens to be morphologically distinct from the Taung Child, it was argued that there were sufficient similarities to attribute the fossils to the same genus. This theory was then retracted and the Sterkfontein specimens were attributed to a distinct genus: *Plesianthropus transvaalensis* (Broom, 1938). This

reattribution followed the discovery of further specimens at Sterkfontein and was based largely on the differences in the morphology of the mandibular symphysis between the Taung Child and these new specimens (Broom, 1938). In 1952, Broom and Robison argued that the *Plesianthropus transvaalensis* specimens from Sterkfontein did not represent a distinct taxon but rather the adult version of the Taung *A. africanus* skull, subsuming *Plesianthropus transvaalensis* into *A. africanus*. Gradually acceptance grew for the inclusion of the Taung Child and *A. africanus* into the hominin lineage even from Keith (1947), previously a staunch adversary to the proposition. Keith (1947) states that both he and Le Gros Clarke were convinced of the attribution of the australopiths to the hominin lineage by evidence provided by Broom and Schepers (1946). This evidence included a thorough description of the Sterkfontein material.

Sterkfontein (Fig. 1) is perhaps the most geologically complex of the South African hominin bearing sites. The site is located, within the Blaauwbank Stream Valley (Fig. 1) and is divided into a complex, and not entirely resolved, member system (Partridge, 1978; 2000). The majority of Australopithecus africanus specimens derive from Sterkfontein Member 4, dated to between ~2.61 and ~2.07 Ma (Broom, 1947; Pickering & Kramers, 2010; Herries et al., 2010, 2013; Herries & Shaw, 2011; Pickering et al., 2019). Fossils from the supposedly 4 Ma Jakovec Cavern may also belong to this species (Partridge et al., 2003; Beaudet et al., 2018). The age of Jakovec has been challenged on the basis of the fact that *Equus* occurs in the unit, which is only known in Africa from ~2.3 Ma (Reynolds and Kibii, 2011; Herries et al., 2013). The latest occurrence of A. africanus is generally considered to be the Sts 5 cranium from Sterkfontein Member 4 which is capped by a flowstone dated to ~2.07 Ma by uranium-lead (U-Pb) and palaeomagnetism (Broom, 1947; Pickering and Kramers, 2010; Herries et al., 2010; 2013; Pickering et al., 2019). However, Clarke (2013) has also suggested that StW 53 represents A. africanus, although it has more often been attributed to early Homo (Clarke, 1985; Kimbel et al., 1997; Curnoe and Tobias, 2006; Curnoe, 2010). U-Pb and palaeomagnetism suggest this is a unit intermediate in age between Member 4 and Member 5 at ~1.8-1.6 Ma (Herries and Shaw, 2011). It has also been suggested by a number of authors that a second species, may be present within Sterkfontein Member 4, although most of these studies did not agree on which fossils should be in which

species (see for example Clarke, 1985; Kimbel et al., 1997; Curnoe and Tobias, 2006; Curnoe, 2010). The more recent discovery of the StW 573 skeleton has further suggested a second species occurs at Sterkfontein, although the age of Member 2 where it was discovered (anywhere between 3.7 and 2.2 Ma), or Member 2's relationship to Member 4 has been highly debated (Partridge et al., 2003; Pickering and Kramers, 2010; Herries and Shaw, 2011; Herries et al., 2013; Granger et al., 2015; Kramers and Dirks, 2017). The Little Foot specimen (StW 573) recovered from Sterkfontein Member 2, has been argued to belong to *A. prometheus* and is dated to either ~3.67 Ma based on cosmogenic nuclide burial (Al/Be) dating, or 2.6-2.2 Ma based on combined uranium-lead and palaeomagnetic dating (Pickering and Kramers, 2010; Herries and Shaw, 2010; Herries and Shaw, 2011; Granger et al., 2015; Stratford et al., 2017).

While Clarke and Kuman (2019) attribute StW 573 (Little Foot) and the 'more robust' Sterkfontein specimens to *A. prometheus* rather than *P. robustus*, they nonetheless recognize morphological similarities between the non-*africanus* Sterkfontein Member 2 and 4 specimens and *Paranthropus robustus* by suggesting that the two samples probably share a close phylogenetic relationship. StW 573 and the other robust Sterkfontein specimens are alternatively hypothesised as belonging to *Paranthropus robustus*, *Australopithecus prometheus* or a third novel species belonging to either genus (Clarke, 1993, 1994, 2013; Clarke and Kuman, 2000). The potentially early date of StW 573 and close phylogenetic relationship with *P. robustus* has consequences for the reconstruction of *Paranthropus* phylogeny. Further discussion of *Paranthropus* phylogeny will be discussed below (Section 1.5).

Dating deposits at Sterkfontein is a perennial problem, well demonstrated by the fact that the division of Sterkfontein Member 5, both internally and from Member 4, is still hotly debated (see for example, Berger et al., 2002; Partridge et al., 2003; Pickering et al., 2019). Sterkfontein Member 5C, dated to 1.3-0.8 Ma (Herries et al., 2009), has yielded Acheulean stone technology and hominin specimens attributed to *Homo ergaster* and early *Homo* sp. (Tobias, 2000). Sterkfontein Member 5B, dated to 1.4-1.1 Ma by ESR (Herries and Shaw, 2011), or 2.18 ± 0.21 Ma by Al/Be dating (Granger et al., 2015), has yielded Oldowan stone technology

and hominin specimens attributed to P. robustus and Homo (alternatingly called Homo ergaster, Homo erectus, and early Homo sp.; Tobias, 2000; Kuman and Clarke, 2000). The oldest section of Sterkfontein Member 5a (Partridge, 1978, 2000) is the most heavily debated, in part because the controversial specimen StW 53 is derived from this part of the cave system. Kuman and Clarke (2000) argue that the stratigraphic layer containing this specimen is a younger part of Member 4 and so dates to ~2 Ma. Herries and Shaw (2011) and Herries et al. (2013), however, suggests that StW 53 instead derives from an infill layer between Members 4 and 5 and dates to 1.8-1.5 Ma based on U-Pb, ESR and palaeomagnetism. Additional debate surrounds the taxonomic attribution of this specimen. If StW 53 represents Australopithecus rather than early Homo (as suggested by Clarke, 2008, 2013; contra Curnoe, 2010 or Curnoe and Tobias, 2006) then this specimen would represent the last appearance date (LAD) for Australopithecus at 1.8-1.5 Ma (Herries and Shaw, 2011). However, if StW 53 is included instead within the genus Homo, the LAD of the genus Australopithecus is 1.98 Ma based on the first and last appearance date of Australopithecus sediba at Malapa (Fig. 1 and 2; Pickering et al., 2011a). The overarching theme of taxonomic and phylogenetic interpretations of Sterkfontein hominin material is the complex and disputed formational and depositional history of the karst complex. The determination of a clear depositional sequence, and so a sequence of hominin specimens on the landscape, would significantly impact the ability of researchers to interpret the taxonomy and phylogeny of the Sterkfontein hominins. Such an interpretation may, however, be impossible. The implications of such complexity will be discussed in Chapter 8.

1.2.1.3 Makapansgat Limeworks

The fossil site of the Makapansgat Limeworks (referred to commonly as 'Makapasgat'; Figure 1) was discovered on Makapansgat Farm (Dart, 1948) and is the only other hominin site in South Africa dating to >2.6 Ma. Like Taung, Makapansgat is a satellite site of the Fossil Hominid Sites of South Africa UNESCO world heritage area located some 260 km north of Sterkfontein, Swartkrans and DMQ. Like Taung and the Gaunteng Malmani sites, Makapansgat is formed within the Malmani dolomite and the valley contains a number of other fossil sites including the younger sites of the Cave of Hearths and Buffalo Cave (Latham and

Herries, 2004; Herries et al., 2006). As such, the literature is often unclear when reference is only made to 'Taung' or 'Makapansgat' because there are multiple fossil sites at each location spanning the Pliocene to Holocene (this is phenomenon also seen when other sites such as Sterkfontein or Swartkrans are discussed; see for example Conroy et al., 1990; Grine et al., 2010; Moggi-Cecchi et al., 2010).

The majority of the Makapansgat Limeworks fossil hominin material derives from a breccia dump, which has been associated with a 'grey breccia layer' (Dart, 1948; Brain, 1958). As breccia dumps are essentially mining debris, material derived from such areas cannot be confidently assigned to a depositional context. Despite this, all material from this 'grey breccia' have been assigned to Member 3 (Partridge, 1979). Three hominin fossils including an occipital / parietal fragment, MLD 37/38, has been recovered from Member 4 (Dart, 1959; Reed et al., 1993; Partridge, 2000). These hominin specimens are currently considered to belong to *A. africanus* (Robinson, 1954; see also Grine, 1985; Reed et al., 1993; Grine et al., 2013), although it has been hypothesised that more than one species is present at Makapansgat since the site's discovery, as at Sterkfontein (Grine et al., 2013). Makapansgat Limeworks Member 3 has been dated to between 3.03 to 2.61 Ma, with Member 4 dated close to 2.61 Ma making them penecontemporaneous with both the Taung Dart Pinnacle PCS deposits (Fig. 2; Herries et al., 2013).



Figure 2: Ages of relevant hominin fossil deposits. This does not purport to be a comprehensive representation of Homo within these deposits. The "Sterkfontein Member 5A (StW 53)" deposit is shown to contain Homo re the discussion on StW 53 in section 1.2.1.2.

Hominin specimens from the Makapansgat Limeworks Member 3 were originally attributed to *A. prometheus* (Dart, 1948; Broom, 1987, 1948; Kuman and Clarke, 2000; Clarke, 2013) but later subsumed into *A. africanus* (Robinson, 1954). While Clarke (2019) recently suggested the occurrence of two species at Makapansgat, resurrecting the species *A. prometheus*, most studies have concluded that this is not the case (Robinson, 1954; see also Grine, 1985; Reed et al., 1993; Grine et al., 2013), and others have pointed out the difficulty of using the species *A. prometheus* to refer to such a second species (Hawks and Berger, 2019). The name *A. prometheus* was originally attributed to these specimens because they were found in association with blackened faunal material, argued by Dart (1948) to be evidence that the species had control of fire and was thus behaviourally distinct from *Australopithecus africanus*. Recent evidence, however, suggests that the

black staining on the associated faunal material may be the result of a natural process rather than deliberate burning by hominins. Manganese oxides are commonly identified in soils and within various rock types on the broader South African landscape, as well as on the surfaces of fossilised bone. As rainwater flows through the sediment, it becomes saturated with manganese, which then precipitates onto materials it comes into contact with such as rock or bone (Fernandez-Jalvo and Andrews, 2016). Manganese oxide on the surface of bone material in palaeokarst Southern Africa has been, in the case of the Makapansgat Limeworks, mistaken for burning. The specimens recovered from the Makapansgat Limeworks were also the basis for Dart's (1957) erection of the Osteodontokeratic culture theory. Dart (1957) hypothesised a culture of internal violence amongst the South African australopiths. This hypothesis was based on what is now known as plastic deformation of cranial remains but Dart (1957) identified it as damage from a weapon. Additionally, Dart (1957) recovered osseous specimens preserved in such a way that one bone was lodged inside of another which he identified as tools or, more specifically, weapons. If recent analyses of the black staining on the Makapansgat faunal material are correct insofar as they posit a natural argent and moreover the material originally thought to represent tools is not necessarily as it seems (see Maguire et al., 1980), then much of the impetus for supposing that the specimens attributed to Australopithecus prometheus are behaviourally distinct from Australopithecus africanus is removed. As will be discussed in the next paragraph, the removal of a behavioural impetus for taxonomically separating the Australopithecus prometheus specimens from the Australopithecus africanus specimens requires that the argument for species level distinctiveness be made based on morphological difference alone.

It has been argued that the Makapansgat Limeworks *Australopithecus* specimens were more robust in mandibular morphology than the Taung Child and the penecontemporaneous *A. africanus* (*Plesianthropus transvaalensis*) specimens from Sterkfontein deposits (Dart, 1948). Indeed, it was suggested the *A. prometheus* may rival or even surpass some *P. robustus* specimens in robustness (Dart, 1948). It was also argued that *A. prometheus* differed from both of *P. robustus* and *A. africanus* (formerly *Plesianthropus transvaalensis*) in occlusal morphology of the postcanine dentition (Dart, 1948). More recently however, most

researchers agree that the Makapansgat Limeworks specimens can be accommodated within the variability represented within the *A. africanus* hypodigm (Robinson, 1954; see also Grine, 1985; Reed et al., 1993; Grine et al., 2013) thus expanding the degree of variability accepted within *A. africanus* even further. Indeed, the degree of temporal and morphological variability accepted within *A. africanus* is immense and has led to hypotheses regarding a distinct behavioural repertoire attributed to the species (see Chapter 8 for further discussion).

1.2.1.4 Swartkrans

Swartkrans is also located within the Fossil Hominid Sites of South Africa UNESCO World Heritage Site in the Gauteng Province, South Africa (Fig. 1). As will be discussed further in Section 1.3, the Swartkrans robust australopith material was originally attributed to *P. crassidens* before being subsumed into *P. robustus*. Swartkrans is divided into five main depositional and geological units: Member 1 (Member 1 Lower Bank and Member 1 Hanging Remnant), and Members 2 through 5 (Brain, 1993). P. robustus and Homo sp. have been recovered from Swartkrans Member Lower Bank, dating to sometime between 2.3 and 1.7 Ma based on U-Pb and (Al/Be) dating (Fig. 2; Gibbon et al., 2014; Pickering et al., 2019). Member 1 Hanging Remnant has been the source for most of the hominin material but no archaeology has been recovered from this deposit. Member 1 Hanging Remnant has been dated to between 2.3 and 1.8 Ma ESR and U-Pb dating, but likely dates to after 2 Ma based on the direct dating of fossils by ESR and evidence that the basal ~2.25 Ma flowstone has been heavily eroded before the deposition of the fossil deposits (Fig. 2; Pickering et al., 2011; Herries and Adams, 2013). Member 2 has yielded both early Homo and P. robustus specimens, dating less securely to ~1.7-1.5 Ma (Brain, 1993; Watson, 1993; Herries et al., 2009). Member 3 contains P. robustus and dates to between 1.3-0.6 Ma based on ESR and Al/Be dating, (Brain, 1993; Watson, 1993; Herries and Adams, 2013; Granger et al., 2015). P. robustus fossils have also been recovered from much younger Members where they are argued to be intrusive (de Ruiter, 2003). Herries and Adams (2013) have also questioned whether the same is true of the Member 3 hominin material. While *P. robustus* has been recovered from other Members, it is the Swartkrans Member 1 P. robustus material that is particularly suitable for comparison with the DMQ P. robustus material as it is the most temporally similar lithostratigraphic unit and there is an apparent lack of mixing. There is also a selection of material that cannot be reliably attributed to any member due to mining and the use of explosives during early excavation (Broom and Robinson, 1952; Dart, 1959). Further detail on both the Swartkrans deposits will be provided in Chapter 2.

1.2.1.5 Cooper's

Coopers A (Fig. 1) has also been reported to have yielded *P. robustus* however, this material has since been lost. Hominin materials recovered from Coopers D (Fig. 1), dated to less than 1.4 Ma based on U-Pb dating of the basal flowstone, are few (n=~3) and poorly preserved (Fig. 2; de Ruiter et al., 2009; Pickering et al., 2019). Due to the small sample size, *P. robustus* specimens from Coopers D have not been included in this study's analyses.

1.2.1.6 Kromdraai

Kromdraai (Fig. 1) is divided into two sites: Kromdraai A and Kromdraai B. Kromdraai A yields non-hominin faunal material while Kromdraai B yields eight *P. robustus* material and one suggested early *Homo* specimen (Braga and Thackeray, 2003; Lacruz, 2007). Kromdraai B Member 3 is suggested to date to 1.78-1.65 Ma (Fig. 2; Thackeray et al., 2002; Herries et al., 2009). It is from this member that all *in-situ* hominin material has been recovered, although Thackeray et al. (2002) has suggested the type specimen comes from the older, >1.95 Ma, Member 1 deposit based on associated breccia colour adhering to the specimen. Recent reanalysis of the stratigraphy of the site has questioned whether all the material comes from Member 3 and changed the sequencing of deposits and Members, as well as the context of the samples taken for palaeomagnetism (Bruxelles et al., 2016; Stammers et al., 2018). Due to this it is hard to assess the age of the deposits and the hominin material recovered therein.

1.2.1.7 Gondolin

Gondolin (Fig. 1) dated to ~1.8 Ma, has yielded only two hominin specimens as well as a large non-hominin faunal assemblage (Fig. 2; Menter et al., 1999; Adams and Conroy, 2005; Herries et al., 2006; Adams et al., 2007; Adams, 2010; Herries and Adams, 2013). The GDA-2 specimen was originally attributed to *Paranthropus*

sp. as it significantly exceeds the known size range of *P. robustus* and resembles size variation in *P. boisei* (Menter et al., 1999; Grine et al., 2012). While alone these specimens reveal nothing about demographics and populations, the large absolute size of one of the specimens (GDA-2) has led to the examination of possible indicators of secondary maturation in *P. robustus* (Lockwood et al., 2007; Grine et al., 2012). Although dental size would not be affected by an individual exhibiting secondary maturation, the existence of the GDA-2 lower second molar has compelled further examination of sexually dimorphic variation within *P. robustus*. It is possible, however, that sampling bias due to differential depositional processes at sites yielding *P. robustus* (such as Swartkrans and DMQ) has led to a lack of representation of large males within this taxon. Although this specimen is potentially informative when investigating *P. robustus* life history, the small sample size prevents inclusion within the study presented here.

1.2.1.8 Drimolen

The palaeocave site of Drimolen is part of a dolomitic palaeocave system within the Monte Cristo Formation of the Malmani Dolomite approximately 7 km north of other well-known sites such as Sterkfontein and Swartkrans (Fig. 1; Keyser et al., 2000). Drimolen is represented by two units: the 'Drimolen Main Quarry' (DMQ) and the 'Drimolen Makondo' (DMK). Excavations conducted since initial discovery have concentrated on the extensively mined 'Main Quarry' deposit and have produced a large faunal assemblage (Adams et al., 2016), as well as over 150 hominin specimens representing both Paranthropus robustus and early Homo (Keyser, 2000; Moggi-Cecchi et al., 2010). In 2014, a second deposit, the Drimolen Makondo, was explored and has produced fossils that are dated to around 2.6 Ma, but it has not yielded hominin remains (Herries et al., 2018). Unlike the other hominin-bearing sites in the region such as Sterkfontein and Swartkrans, formation processes at the DMQ have yielded a relatively simple deposit with few intrusions or mixing events (Keyser et al., 2000; Herries et al., 2020; Chap 2). After the formation of a basal speleothem, the central part of the Main Quarry Palaeocavern consists of a single, gradually accumulated talus cone formed beneath a vertical entrance, which has yielded all the hominin remains described here. The clastsupported breccia in the centre of the palaeocavern transitions laterally, first to matrix-supported breccia, and then into laminated siltstone and sandstone deposits

against the walls of the cavern. The transition from clast-supported breccia, through matrix-supported breccia to laminated siltstone and sandstone represents the effect of finer-grained sediment being winnowed from the central talus cone to the edge of the cavern and leaving in place the larger clasts that can't be transported by the energy of the flooding water. As such, the occurrence of the hominins within the central breccia as opposed to the siltstone and sandstone deposits, is not because they are a different age but because of the nature of deposition at the site. It is unlikely, given the sequence of deposition within the central talus cone, that it represents any significant time depth (i.e., not on the order of half a million years as suggested for Sterkfontein Member 4; Herries et al., 2018).

Mining for speleothem at the site at the turn of the 20th Century significantly disturbed the more eastern deposits of the palaeocavern, while the more western deposits remain largely in situ. Excavation at the Main Quarry over the last 20 years has been concentrated in the area around the block from which the DNH 7 P. robustus skull was recovered. Although his block is not in situ, site reconstruction suggests minimal displacement (Herries et al., 2020; Chap 2). The vast majority of the deposits excavated around the block are thus not in situ decalcified breccia, but likely a mixture of material that has decalcified and spalled off both the DNH 7 block as well as the western wall of the *in situ* breccia deposits that represent some of the oldest deposits at the site, dated to ~2.04 (maximally 2.28 Ma) and 1.95 Ma based on a combination of uranium-series electron spin resonance (US-ESR), palaeomagnetism and uranium-lead (U-Pb) dating (Herries et al., 2020; Chap 2). It also suggests that almost all of the deposits (including the DNH 7 block) were close to 1.95 Ma in age, or older. The apparent underestimation of the age of an ESR dated tooth from the DNH 7 block is likely related to the more complex history of post-depositional radiation exposure of this ex situ block, compared to those taken from the *in situ* deposits (Herries et al., 2020; Chap 2).

Unlike the DMK which consists of an older deposit that has not yet yielded hominin remains or archaeological material, the DMQ has produced both archaeology and hominin remains as well as a diverse range of faunal specimens (Adams et al., 2016). Both *P. robustus* (n=82) and early *Homo* (n=14) specimens make up the craniodental hominin sample along with Hominin sp. (n=32; Keyser, 2000; Keyser

et al., 2000; Moggi-Cecchi et al., 2010; Leece, 2016; Chapters 2, 3, and 4). The assemblage consists primarily of dental elements with only 27 of 155 specimens representing postcranial material. The DMQ *P. robustus* assemblage is morphologically distinct in multiple ways. The most notable specimen from this collection is DNH 7. This individual consists of a nearly complete cranium and mandible of a lightly built, putative female *P. robustus* (Keyser, 2000; Lockwood et al., 2007). Not only is this specimen the most complete example of the species to date, but it also differs from the sample of young adult putative males preserved at Swartkrans (Keyser et al., 2000; Lockwood et al., 2007; Moggi-Cecchi, 2009; Moggi-Cecchi et al., 2010). DNH 7 therefore potentially contributes to the understanding of intraspecific variation and sexual dimorphism within the species.

1.2.2 Eastern Africa

Unlike the South African cave sites, volcanic tufa layers bracket fossil-yielding deposits in eastern Africa. These tuffs can be directly dated using potassium-argon (K-Ar) or argon-argon (Ar-Ar) radiometric dating techniques. However, as fossil specimens rarely derive from the volcanic layers, dating of the specimens themselves are indirect and depend on the ability of researchers to relate specimens often collected off the surface to a tuff layer. Additionally, interpretation of these layers interbedded with fossil-bearing deposits has been complicated by geological uplift, erosion and reworking (McHenry and Stanistreet, 2018). Discussion of the deposition and context of eastern African sites will be limited to localities and strata from which material directly employed in analyses presented within this thesis derived (deciduous dentition; see Chapter 6). Robust australopith specimens relevant to this study derive from Tanzania, Kenya, and Ethiopia. Although specimens attributed to P. aethiopicus, P. boisei, and A. afarensis have been recovered from throughout these deposits, only a fraction of specimens preserve the deciduous dentition (as discussed in Chapter 6). Eastern African specimens included in the following analyses derive from Olduvai Gorge, Omo-Turkana basin, Koobi Fora, Laetoli, and Hadar.

1.2.2.1 Omo-Turkana Basin

Two deciduous dental specimens, L704-2 and L64-2, originally attributed to *P. boisei* (Wood, 1992; Wood and Constantino, 2007) were recovered from the Shungura formation of the Omo-Turkana basin. As a result of a taxonomic reassessment that occurred following the discovery of OMO-18 and KNM-WT 17000, L704-2 has been reassigned to *P. aethiopicus* (White et al., 1994; Wood and Leakey, 2011). The second, L64-2, has not been confidently assigned and has been argued to represent either *P. aethiopicus* or *P. boisei* and so has been excluded from this study. The remaining *P. aethiopicus* specimen, L704-2, derives from member 3 of Tuff D of the Shungura formation in the Omo-Turkana Basin. Tuff D3 has been dated to 2.52 Ma (Wood and Constantino, 2007). A reassessment by McDougall et al. (2012) dated Shungura tuff D3 to 2.44 \pm 0.05 Ma using palaeomagnetic methods (Fig. 2).

1.2.2.2 Koobi Fora

The Koobi Fora KBS formation has yielded two specimens attributed to P. boisei: KNM-ER 3886 and KNM-ER 1820. Wood and Constantino (2007) report that these specimens date to 1.87 Ma however context, ages, and interpretations of these specimens have been variable as the interpretation of the stratigraphy of the KBS tuff has changed with various studies (Lepre and Kent, 2015). Some of these changes came in quick succession changing the interpretation of the KBS formation and specimens deriving therein. Fitch and Miller (1970) dated the KBS tuff to 2.61 ± 0.26 Ma using K-Ar methods. Curtis et al. (1975) then dated the KBS tuff to between 1.82 ± 0.04 Ma and 1.60 ± 0.05 Ma also through the use of K-Ar methods. Shortly after, Fitch et al. (1976) redated the KBS tuff using K-Ar methods to 2.42 ± 0.26 Ma and Hurford et al. (1976) dated the same to 2.44 ± 0.08 Ma using fission track methods. Following a subsequent analysis by Feibel et al. (1989), the entirety of the Koobi Fora formation was thought to be approximately 1.78 Ma based on the location of the Olduvai Subchron. An analysis conducted by Gathogo and Brown (2006) changed the interpretation of this stratigraphy and concluded the Olduvai Subchron was located ~35 m lower than thought by previous researchers (Hillhouse et al., 1997, 1986; Feibel et al., 1989; and McDougall et al., 1992). McDougall et al. (2012) analysed three tuffs lying within the KBS member and concluded the Morutot tuff, essentially capping the member dated to 1.61 ± 0.02 Ma, the Orange tuff placed almost centrally dated to 1.76 ± 0.03 Ma, and the KBS tuff as the basal point of the member dated to 1.87 ± 0.02 Ma. The two *P. boisei* specimens do not derive from the KBS tuff itself but derive from Area 104 (Lepre and Kent, 2015). Area 104 has been attributed to the KBS member based in part on the identification of the White tuff. McDougall et al. (2012) dated the White tuff, and so the majority of Area 104, to 1.65 ± 0.05 Ma.

1.2.2.3 Olduvai Gorge

Two further *P. boisei* specimens, OH 3 and OH 30, have been recovered from Olduvai Gorge. The first was recovered from BK lower Bed II. Tuff IID is located directly below Olduvai BK Bed II and so can provide a maximum age. This tuff had been dated to approximately 1.2 Ma (Leakey, 1971; Hay, 1976) but reanalysis using 40 AR/³⁹AR dating moved this to 1.353 ± 0.035 Ma (Domínguez-Rodrigo et al., 2013). Tuff IID was also dated using its appearance in the Richard Hay Cliff resulting in an age of 1.321 ± 0.032 Ma (Fig. 2; Domínguez-Rodrigo et al., 2013). Domínguez-Rodrigo et al. (2013) used an average of these two results to report an age of 1.338 ± 0.024 Ma for tuff IID. This provides a maximum age for materials deriving from BK Bed II. The second specimen derives from a context dated to 1.7 Ma (Wood et al., 1994).

Specimens attributed to *Australopithecus* are also recovered from the BK Bed II. Although originally aligned most closely with *A. africanus* (Walker and Leakey, 1978), these specimens were later accepted as specifically distinct and reattributed to *A. afarensis*. Sixteen deciduous elements attributed to *A. afarensis* are relevant to this study. Four of these specimens derive from the site of Laetoli: LH 1 from Locality 1, LH 2 from Locality 3, and LH 3 and LH 6 from Locality 7. Locality 1 consists of the Upper Laetolil Beds, the Upper Ndolanya Beds, and the Olpiro Beds positioned between Tuffs 6 and 8 – although sits closer to Tuff 8 (Harrison and Kweka, 2011). Locality 2 consists of the Upper Laetolil and sits between Tuffs 7 and 8 (Harrison and Kweka, 2011). Locality 7 consists of the Upper Laetolil Beds between Tuffs 5 and 7 (Harrison and Kweka, 2011). K/Ar and ⁴⁰Ar/³⁹Ar dating has been used to date the Laetoli volcanic tuffs. The Upper Laetolil Beds have been dated to 3.85-3.63 Ma (Deino, 2011), the Upper Ndolanya Beds have been dated to 2.66 Ma (Deino, 2011), and the Olpiro Beds have been dated to .2057 Ma

(Deino, 2011). The summation of these dates mean that Locality 1 is dated to between 3.73 ± 0.09 Ma and 4.04 ± 0.08 Ma while Locality 3 and 7 date to between 3.85 and 3.63 Ma (Fig. 2; Deino, 2011).

1.2.2.4 Hadar

A further 12 A. afarensis deciduous dental specimens have been recovered from level 2 of the Denen Dora member of the Hadar formation: AL 43 a&b, AL 105, AL 30, AL 86, AL 66, AL 35, AL 77, AL 99, AL 104, AL 76, AL 68, and AL 67. This context has been dated to approximately 3.24-3.20 Ma using ⁴⁰Ar/³⁹Ar dating of tephra beds (Walter, 1994; Kimbel, 2004). The Denen Dora member is marked by five or more tephra beds and sits near the surface of the Hadar formation with only the Kada Hadar member sitting above it (Walter, 1994). Triple Tuff 4 is the most consistent marker bed within the Hadar formation and defines the border between the Denen Dora member and the underlying Sidi Hakoma member but cannot be directly dated due to a lack of datable components. A thin sand layer located between Triple Tuff 4 and Triple Tuff 5, however, was dated using fission-track methods and yielded an age of 3 ± 1 Ma to 24 ± 6 Ma (Walter et al., 1991). The Kada Hadar tuff is not as consistently identifiable but defines the border between the Denen Dora member and the overlying Kada Hadar member and has been dated to 3.18 ± 0.02 Ma – 3.17 ± 0.03 Ma (Fig. 2; Walter, 1994). During this analysis a single sample consisting of alkali feldspar returned a date of 24.4 ± 0.01 Ma indicating Miocene aged deposit contamination and likely explaining the extreme date range of the sand layer between Triple Tuff 4 and Triple Tuff 5 (Walter, 1994). A study of accumulation rates and dating ranges suggest that the ~30 m thick Denen Dora member bounded by Triple Tuff 4 and the Kada Hadar tuff likely accumulated in 40 ± 10 ka bounding the ages of the 12 A. afarensis deciduous specimens recovered from this context (Walter, 1994).

1.3 Background of the Paranthropus clade

The genus *Paranthropus* was established by Broom (1938) to accommodate robust, heavily built australopith-like specimens recovered from Kromdraai B in South Africa. Beyond the observation of the larger size of the Kromdraai specimens, specific argument for the distinction between *P. robustus* and the

Sterkfontein australopiths was not made at this time. Broom (1946) elucidated these differences noting reduced anterior dentition and enlarged postcanine dentition as compared to the Sterkfontein specimens, a concavity of the infraorbital plate resulting in a unique manifestation of orthognathism, a broader and more anteriorly positioned zygomatic root, and a broader zygomatic arch among other craniodental and mandibular differences. Many researchers did not consider the differences between these new specimens and previously discovered Australopithecus africanus (Taung) and Plesianthropus transvaalensis (the original designation of Sterkfontein A. africanus) specimens significant enough to warrant the establishment of a new genus (Washburn and Patterson, 1951; Le Gros Clark, 1955, 1964; Campbell, 1963). Through assessment of adaptive strategy using dental evidence, Robinson (1965) came to the inverse conclusion and supported the creation of the genus *Paranthropus* noting good evidence for clear differences in 'basic adaptation'. Leakey (1959, pp. 491) accepted 'Paranthropus' as a "valid" genera based primarily on differences present in the anatomy of the cranium citing many of the same morphological differences observed by Broom (1946). It must be noted, however, that Leakey (1960) erected a new genus, Zinjanthropus, to accommodate the eastern African robust australopiths and employed Paranthropus only when referring to South African specimens. Others were content to await future discoveries to clarify the question of whether both fossil hypodigms could be comfortably accommodated within a single genus (Mayr, 1963).

Further discoveries were made, particularly in eastern Africa, and more specimens were found to display robustness beyond that of the australopith taxa, thus building support for the naming of a distinct genus (Leakey, 1959; Arambourg and Coppens, 1968; Olsen, 1985; Walker et al., 1986). As with *P. robustus*, many specimens now attributed to *P. boisei* were originally placed in the genus *Australopithecus* although they were considered by most to be specifically distinct (Leakey at al., 1978). Thus, although originally considered to belong to the genus *Australopithecus*, these eastern African specimens were thought to represent a species not present in South Africa. This followed arguments that the eastern African robust australopiths resembled *A. afarensis* more closely than the South African *Paranthropus* specimens (Tobias, 1980). This dichotomy, plus disagreement about the phylogenetic position of the robust species relative to the

gracile species, led to the differential use of both *Australopithecus* and *Paranthropus* to refer to the robust species (i.e. *Paranthropus boisei* versus *Australopithecus boisei*; see for example Leakey, 1959, pp. 491 who concluded that "both genera are valid"). Use of both *Paranthropus* and *Australopithecus* to refer to these robust specimens is still common (see for example Grine, 1988) indicating that the genus question is still unresolved. This variation in preference is generally guided by two factors: phylogenetic interpretation based on the requirement of monophyly (de Queiroz and Gauthier, 1994) and interpretation of adaptive zones based on distinct behavioural repertoires (Wood and Collard, 1999). Both of these concepts will be discussed further below. The influence of eastern African species *P. boisei* and *P. aethiopicus* will be discussed in more detail below.

Disagreement regarding the genus to which the robust specimens ought to be attributed was mirrored by disagreement concerning the composition of such species. P. robustus was originally argued to be an endemic South African species comprised of the robust specimens from Kromdraai B (Broom, 1936). P. crassidens was erected to accommodate a subtly different robust morph of Australopith (Broom, 1949a, 1949b) found at the site of Swartkrans. Originally created by Broom (1949a), P. crassidens included dental and mandibular remains. The specimens attributed to P. crassidens shared several derived traits with P. robustus, but also shared several primitive traits with the Sterkfontein A. africanus specimens. Broom (1949a) reported that the specimens from Swartkrans differed from those recovered from Sterkfontein in dental morphology, both in the overall size and specifically in the morphology of the canine, and in mandibular morphology, primarily in overall size. Later that year, Broom (1949b) formalised this attribution and defined the morphology of P. crassidens as compared to A. africanus (Plesianthropus transvaalensis) and South African early Homo (*Telanthropus capensis*). In 1952, Broom and Robinson clarified that the urgency leading to the pre-emptory naming of a new taxon to accommodate the recently excavated Swartkrans material was due to their suspicion that another research team working at the site of Sterkfontein had discovered similar specimens and may beat them to naming the new taxon. Indeed in this manuscript, Broom and Robinson (1952) thoroughly described many morphological similarities between P.

robustus and *P. crassidens*, primarily in regards to permanent dental size and morphology, and reasserted a lack of similarity to the Sterkfontein material. Similarities between the Swartkrans *P. crassidens* material and the Sterkfontein material were primarily observed on deciduous dentition, pelvic morphology, and cranial capacity (Broom and Robinson, 1952).

Broom and Robinson (1952) noted that European colleagues asserted that the Paranthropus crassidens (Swartkrans) specimens represented an adult male morph of the Taung skull. This argument extended to proposing that Plesianthropus transvaalensis specimens from Sterkfontein also represented an adult morph of the Taung skull (a theory later accepted, subsuming *Plesianthropus* transvaalensis into A. africanus; Broom and Robinson, 1952). Differences between specimens from Kromdraai B and Swartkrans were explained by others as a subspecies level distinction (P. robustus robustus and P. robustus crassidens; Broom and Robinson, 1952; Robinson, 1954; Tobias, 1995; see also Grine, 1985). The concept of 'sub-species level distinction' is often unclear and inconsistently defined making such hypotheses difficult to test (see Chapter 3 for further discussion). It is now generally accepted that a single species, 'Paranthropus robustus', can accommodate the variation of both the Kromdraai B and Swartkrans specimens (see for example Cofran and Thackeray, 2010). As a result, *P. crassidens* has been subsumed within *Paranthropus robustus* and is no longer accepted by many as a distinct taxon. Additional fossil specimens recovered from the site of DMQ have been attributed to Paranthropus robustus expanding the accepted variation within this taxon even further (Keyser, 2000; Keyser et al., 2000; Lockwood et al., 2007; Moggi-Cecchi et al., 2010). It has been proposed that size and morphological differences between the Swartkrans P. robustus and the DMQ P. robustus dental assemblages may be the result of marked sexual dimorphism (Keyser et al., 2000; Lockwood et al., 2007; Moggi-Cecchi 2009; Moggi-Cecchi et al., 2010).

The discovery of robust australopith specimens in eastern Africa influenced interpretation of the South African robust australopiths. The 'robust' hominin skull OH 5 recovered from eastern Africa was first assigned to both a new genus and a new species, *Zinjanthropus boisei*, with Leakey (1959) asserting that these specimens were more distinct from *Australopithecus* and *Paranthropus* than either

of the genera was from each other. As further specimens were discovered, Zinjanthropus boisei was first reattributed to Australopithecus (Tobias, 1967) and later to Paranthropus (Leakey, 1978) creating a closer alignment between this robust eastern African form and the South African P. robustus specimens. Lastly, the eastern African specimen Omo-18-1968-18 originally named Paraustralopithecus aethiopicus (Arambourg and Coppens, 1968) was subsumed into the genus name that took priority, formally becoming Paranthropus aethiopicus (Olsen, 1985). The nearly complete KNM-WT 17000 cranium was attributed first to P. boisei (Walker et al., 1986) and later to P. aethiopicus (Kimbel et al., 1988). This specimen worked to solidify this taxonomic change by providing a larger amount of comparative anatomy.

1.4 Paranthropus alpha taxonomy

The attribution of hominin specimens to different species and genera first requires an acceptance of a particular species and genus concept and the kinds of evidence that may factor in identification of genera and species. Biological species concepts sensu lato agree on the principle that species are segments of metapopulation lineages that are distinct from one another. Most biological species concepts accept that reproductive isolation, howsoever biologically achieved, is a necessary additional quality of a species. However, the Unified Species Concept recognised reproductive isolation (and the myriad ways this can be achieved biologically) as contingent properties of a good species along with other contingent properties such as morphological distinctiveness. The Unified Species Concept has therefore recast all argued necessary qualities of a 'good species' as separate lines of evidence for lineage divergence (and therefore separate species status) of populations of organisms. For palaeoanthropological purposes, the Unified Species Concept has revitalised the relevance of morphological analysis and, in particular, morphological diagnosability as a way to provide discernible evidence as to whether a population represents one or two species.

Wood and Collard (1999) consider that a genus should be monophyletic (after Clayton, 1983) and comprise species that all share the same adaptive grade. Inversely, according to Wood and Collard (1999), species that occupy significantly

different adaptive niches should not be placed within the same genus. Therefore, based on Wood and Collard's (1999) adaptive grade argument, P. robustus, A. africanus, and early Homo in South Africa must have occupied different adaptive zones (perhaps for instance manifesting as drastically different in dietary behaviours) in order to be considered distinct genera. In line with this theory, it has been hypothesised that while the Paranthropus diet consisted mainly of tubers and other fibrous materials, the diet of early Homo included more meat (Pickering et al., 2008). The dental morphology required for slicing and tearing meat would, necessarily, be clearly distinct from the morphology required for crushing and grinding grasses or tubers. As new discoveries show that at least one species belonging to each of the Paranthropus, Australopithecus, and Homo genera all coexisted on the same landscape at the same time (Herries et al., 2020; Chap 2), for the implications inherent in Wood and Collard's (1999) argument to stand, Grine (1986) argues that clear adaptive distinctions must be observed between species also. This concept is referred to as the principle of competitive exclusion of Gause's Law (Gause, 1934; Mayr, 1950; Hardin, 1960; Wolpoff, 1971; Weiss, 1972; Swedlund, 1974; Grine, 1981; Pocheville, 2015; among others). The primary point of competitive exclusion is that two species existing contemporaneously on the same landscape cannot maintain an equivalently successful population while competing for the same resource (Hardin, 1960; Slobodkin, 1961; Wynne-Edwards, 1962; Walter, 1988; Pocheville, 2015). Such a situation would cause the decline of one species or an adaption to a different niche leading to the presumption that two species identified in the palaeo record must have occupied distinct adaptive niches.

Grine (1981, p.212), conversely, argued "there are no sound reasons to suppose a low probability of two or more hominid species coexisting." He argues that the theory of competitive exclusion relies on inadequate definitions of niches, tautological assertions, and post factum confirmations (Grine, 1981). Grine's (1981) argument was however, primarily targeted at those employing the theory of competitive exclusion to support single-species hypotheses and does not make invalid the assumption that two coexisting species would occupy two distinct niches and so exhibit distinct dietary-driven morphology; a pattern observed by Grine (1986). Contra the theory of competitive exclusion due to complex anatomical trends mentioned above, the morphological distinction between the dentition of South African hominin taxa, as well as their relationships with taxa outside South Africa, can be ambiguous. Internally, disagreement on the attribution of Kromdraai B specimen KB 5223 to either Homo or P. robustus demonstrates the lack of clarity even between contemporaneous species that should be diagnosably distinct (Braga and Thackeray, 2003; Lacruz, 2007). Multiple methods of assessment are employed in an attempt to untangle complex patterns for the purpose of determining taxonomic attribution and phylogenetic relationships. These include both qualitative and quantitative analyses. Although primary dental description does little to compare dental morphology in a quantitative manner, qualitative character traits can be informative. Metrical data presented with primary descriptions is most often limited to buccolingual and mesiodistal dimensions. Further quantitative analysis can be seen in the form of enamel thickness assessment, relative cusp sizes, and even 3D geometric morphometric analyses of enamel dentine junction and occlusal morphology (Skinner et al., 2008, 2018). Identifying quantitative differences, or similarities, of specific dental elements is extremely informative. Once identified, functional and biomechanical analyses can be conducted to determine the adaptive implications of morphological differences. Variability in the function of individual dental elements and the dental arcade as a whole has direct implications on dietary behaviours. Determining these behaviours can help to inform the extent to which niche separation might be invoked to explain generic- and specific-level distinctions.

Within *P. robustus* it has been proposed that differences between the more gracile DMQ morph and the more robust Swartkrans morph can be explained by marked sexual dimorphism with DNH 7 representing a small female specimen while the Swartkrans assemblages consists of nearly all males (Keyser, 2000; Lockwood et al., 2000). It should be noted however, that prior to the discovery of the DMQ material, Broom and Robinson (1952) had argued there was marked sexual dimorphism observable within the Swartkrans sample. DMQ dental material sits in the lower range of mesiodistal (MD) / buccolingual (BL) dimensions as compared to the Swartkans sample (Constantino and Wood, 2004; Moggi-Cecchi et al.,
2010). Given this, dental evidence seems to support Lockwood et al.'s (2000) observation of systematic size differences based on cranial evidence. Keyser et al. (2000) and Moggi-Cecchi et al. (2010) claim that the DMQ dental specimens 'filled the gap' between the Swartkrans and Kromdraai assemblages, again citing marked sexual dimorphism within *P. robustus*. Others have suggested that the anatomical differences among the DMQ, Swartkrans, and Kromdraai B *P. robustus* hypodigms can be explained simply by population-level differences (Constantino and Wood, 2004).

1.5 Paranthropus Phylogeny

Australopithecus afarensis has been proposed as a progenitor species to both A. africanus and all other australopiths (Johanson et al., 1978). A. africanus itself has been found in different phylogenetic studies to represent the ancestor to the genus Homo (Tattersall and Eldredge, 1977; Wallace, 1978; Delson, 1978; Wolpoff, 1982), A. sediba (Berger et al., 2010), H. habilis (Skelton et al., 1986), and P. (A.) robustus (Johanson & White, 1978; White et al., 1981; Rak, 1983). Assessment of cranial features seems to support a clear distinction of A. africanus from Paranthropus and all Homo species, early and modern (Aiello and Dean, 1990). Recent 3D geometric morphometric studies on dental morphology (specifically enamel-dentine junction morphology) however, show that while the groups are shown to be morphologically distinct, the differences are quite subtle (Skinner et al., 2008). Interpreting these relationships becomes increasingly complicated as some researchers propose the inclusion of A. africanus in the genus Homo (Robinson, 1972; Olson, 1978; Curnoe, 2010). Creating Homo africanus would then move A. sediba out of Australopithecus and into Homo, so removing the presence of Australopithecus from South Africa. This hypothesis would, however, reflect A. africanus as the ancestor to all Homo species and would, presumably, move A. africanus further away, phylogenetically from Paranthropus.

Understanding of relationships within and between early hominin taxa is everevolving. In 1925, the discovery of *Australopithecus africanus* shifted the eye of palaeoanthropology away from Eurasia and into Africa (Tobias, 2005). Dart (1925) asserted that this species represented an early ancestor to previously discovered European species. Later discoveries from the site of Sterkfontein originally attributed to Australopithecus transvalensis and later changed to Plesianthropus transvalensis were later subsumed into A. africanus. A. africanus was a long-lived species, existing on the South African landscape from approximately 3.03 Ma to 2.07 Ma (Broom, 1947; Pickering and Kramers, 2010; Herries and Shaw, 2011; Herries et al., 2013; Pickering and Herries, 2020). The specifics of which South African specimens should be included in *A. africanus* however, are far from settled. As discussed above, Clarke (2013) proposed that some specimens previously attributed to A. africanus represented a second species should instead attributed to a previously named species, Australopithecus prometheus. A. prometheus was originally used to refer to specimens from the site of Makapansgat Limeworks (Dart, 1948) although these specimens were later subsumed into A. africanus. Clarke (2013) proposed reverting the Makapansgat Limeworks specimens to their original attribution and adding certain specimens from Sterkfontein that exhibited a more robust suite of cranial features than A. africanus but are still morphologically distinct from Paranthropus. This hypothesis moves select specimens from Sterkfontein out of the proposed Australopithecus – Homo lineage and instead into an Australopithecus - Paranthropus lineage. Additionally, variation between the Taung specimen and Sterkfontein specimens can be observed and has, on occasion, been interpreted as warranting a species-level distinction (Broom and Schepers, 1946; Broom et al., 1950; Grine, 1985; Chapter 6). It is possible that the large amount of variability observed within the A. africanus sample is due to change through time across it's almost one million years of existence. Alternatively, it is possible that an early population of A. africanus went through a cladogenetic event and this new species continued to exist alongside a remaining A. africanus population. Though these taxonomic debates are strictly unrelated to phylogenetic arguments, the inability to consistently identify operational taxonomic units (OTUs) certainly weighs on phylogenetic interpretations. For example, the inclusion or exclusion of potential 'second species' specimens from Sterkfontein from the A. africanus sample will influence observed synapomorphies within the OTU.

There are generally two competing, mutually exclusive hypotheses concerning *Paranthropus* phylogeny. The first is that *Paranthropus* is monophyletic. The second is that *Paranthropus* is polyphyletic, and therefore an invalid genus as

currently defined. The most common manifestation of this hypothesis is one in which *P. aethiopicus* is only ancestral to the east African *P. boisei*, whereas the South African robust australopiths descended from a South African gracile australopith such as *A. africanus* or *A. prometheus*. Some Sterkfontein hominins have been argued to be ancestral to younger *P. robustus* specimens, challenging the hypothesis that *P. robustus* is descended from *P. aethiopicus* (Clarke, 2013; Clarke and Kuman, 2019). Clarke and Kuman (2019) do, however, note that the *A. prometheus* specimens from Sterkfontein may represent parallel development within *Paranthropus* rather than the ancestor of *P. robustus*.

P. aethiopicus has been proposed as the ancestor to a monophyletic *Paranthropus* clade. This hypothesis is supported by the date of each *Paranthropus* taxon: *P. aethiopicus* preceding *P. robustus* preceding *P. boisei*. This trajectory would mean that morphological changes would have had to move broadly from a hyper-robust morph as seen in *P. aethiopicus*, to a less robust morph in *P. robustus*, and then return to a more robust morph in *P. boisei*. Derived reversals are certainly not unheard of and although this situation would appear to require a high degree of such reversals, this may be only superficial. That is, it is possible that while overall robustness demonstrates this trend, characters considered to carry high phyletic weight do not. This will be tested throughout this study.

As mentioned above, there are two competing, mutually exclusive hypotheses concerning *Paranthropus* phylogeny. The first is that *Paranthropus* is monophyletic, which generally is synonymous with the hypothesis that *P. aethiopicus* is ancestral to both the South African and eastern African robust australopiths (Fig. 3). The second is that *Paranthropus* is polyphyletic (and therefore an invalid genus as currently defined) with one manifestation of the hypothesis being that *P. aethiopicus* is only ancestral to the eastern African robust australopiths, whereas the South African robust australopiths descended from a South African gracile australopith (Fig. 3). While most formal phylogenetic analyses agree that *P. robustus, P. boisei,* and *P. aethiopicus* represent a monophyletic clade (see for example Kimbel 1988; Strait et al., 1997; Strait and Grine, 2004), acceptance of this does not necessarily clarify the relationships between robust australopith taxa, such as *P. boisei* and *P. robustus,* or the relationships between

different samples of a single taxon, such as Swartkrans and DMQ *P. robustus*. It is plausible that *P. aethiopicus* is ancestral to both *P. robustus* and *P. boisei* (Delson, 1986; Walker and Leakey, 1988; Grine, 1988; Kimbel et al., 1988).



Figure 3: Two dominant hypotheses regarding robust australopith phylogeny.

Wood and Collard (1999) argued that two criteria must be met for the definition of a genera: monophyly and the presence of a distinct adaptive grade. Although the requirement of monophyly was widely accepted prior to this (de Queiroz and Gauthier, 1994), Wood and Collard (1999) argued that an additional criterion was necessary for this concept to be applied to the fossil record and accommodate temporal factors. This additional criterion works to identify ecological divisions between what could otherwise be considered single genus with a large time depth. That is, as a monophyletic group consists of all descendants of a single ancestral species, a perfect fossil record could result in two species separated by millions of years being placed in a single genus. The criterion of the presence of distinct adaptive grades allows for the identification of divisions based on ecological niche differentiation. For example, although the *Homo* lineage likely rose from the australopithecines, presumed adaptive differences such as hunting or cooking creates a logical and natural generic division.

Based primarily on the presence of enlarged dentition with hyperthick enamel and heavily buttressed bony masticatory apparatus, both *P. robustus* and *P. boisei* appear to exist within the same adaptive grade and so meet this criterion. The matter of a shared common ancestor was, however, a subject of contention. Prior to the discovery of *P. aethiopicus*, it was hypothesised that the morphological similarities between these two taxa may be due to homoplasy or 'parallelism' (Le Gros Clark, 1950; Broom and Robinson, 1952; Wood and Chamberlain, 1987). It was hypothesised that *P. boisei* may represent a descendent population of *A. afarensis* while *P. robustus* represented a descendent population from *A. africanus*. If this hypothesis was supported, the erection of *Paranthropus* as a genus would violate the criterion of monophyly and so be invalid if both eastern and southern African taxa where included. It is for reasons of monophyly versus paraphyly and disagreement about adaptive grade separation between the robust and gracile australopiths that *P. robustus* and *P. boisei* were historically referred to as *Australopithecus robustus* and *Australopithecus boisei*.

One hypothesis that would remove the concern of generic monophyly is that differences between *P. robustus* and *P. boisei* morphology are due to geographic variation as a result of regional adaptation within a single species, rather than

variation between two species as the result of metapopulation lineage divergence (Wood and Chamberlain, 1987). Dietary isotopic studies have found a distinctly stronger presence of C₄ within *P. boisei* as compared to *P. robustus* (van der Merwe et al., 2008) suggesting clear dietary differences between the two taxa and supporting the possibility of regional adaption. If *P. boisei* and *P. robustus* stand as two different species, however, they must be descended from a common ancestor if monophyly of the genus *Paranthropus* is to be maintained. The discovery of *P. aethiopicus* and the placement of this taxon as an ancestral species to both *P. robustus* and *P. boisei* is the most common way to solve this issue (Olsen, 1985; Kimbel, 1988; Strait et al., 1997; Strait and Grine, 2004). Other studies, however, have argued that *P. aethiopicus* is not particularly closely related to either *P. robustus* or *P. boisei* (Skelton and McHenry, 1992). Despite these disagreements, most current research supports *Paranthropus* monophyly although, as aptly stated by Constantino and Wood (2004, pp. 147), this may be "more of an assumption than an empirically supported hypothesis."

Similarities between *P. robustus* and *A. africanus*, as originally suggested by Broom and Robinson (1952), challenge the hypothesis placing *P. aethiopicus* as the ancestor species of the paranthropine clade. Indeed, it has been proposed by some that *A. prometheus*, a contested South African hominin species best represented by the newly described StW 573 (Little Foot) specimen, is intermediate between *P. robustus* and *A. africanus* (Clarke and Kuman, 2019) although this suggestion has yet to be widely supported. Newly recovered specimens from the DMQ bring relationships within the *Paranthropus* clade further into question by highlighting both the differences between the DMQ and Swartkrans *P. robustus* samples (and further between southern and eastern African *Paranthropus* species) and the similarities between the DMQ *P. robustus* and Sterkfontein/Taung *A. africanus* samples. Analyses addressing this and related questions are presented in Chapters 2, 3, 5, and 6.

As outlined in this chapter, current understanding of the sites and contexts from which hominin specimens have derived is often far from the initial published observation. Most notably, ages of deposits and relationships between specimens have often altered significantly. These changes greatly effect interpretation of the taxonomy and phylogeny of these specimens. For example, if it was found that *P. boisei* was in fact penecontemporaneous to *P. aethiopicus*, it could no longer be hypothesised that the latter was ancestral to the former; at least not without projecting into the past an unfounded ghost lineage. It is for this reason that the variability in such evidences is so crucial for the subsequent analyses presented throughout this study.

1.7 Current hypotheses

Assessment of derived and primitive traits can inform both taxonomic attribution and phylogenetic interpretation. As morphological change is not guided by a teleological process (Mayr, 1982), there is no reason for supposing *a priori* that taxa will evolve in a particular direction or at a specific or constant tempo. One example of this is overall molar size. At 4.2 – 3.9 Ma, *A. anamensis* exhibits relatively small molar teeth as compared to taxa succeeding it and considered descendant (White et al., 2006; Haile-Selassie et al., 2019). Through time, molar tooth size increases as seen in *A. afarensis* at 3.85 – 2.95 Ma (White, 1995; Grine et al., 2006; Haile-Selassie et al., 2019) through *A. africanus* at 3.03 – 2.07 Ma (Blumenberg and Lloyd, 1983; Pickering and Kramers, 2010; Herries and Shaw, 2011; Herries et al., 2013; Stratford et al., 2015; Pickering et al., 2019; Fig. 4). As hominin species become more derived towards modern *Homo sapiens* however, this trend reverses – the pattern in all *Homo* species is decreasing molar tooth size .gthrough time (see for example Quam et al., 2009; Villmoare et al., 2015).



Figure 4: Mesiodistal (MD) and buccolingual (BL) size comparison of A. afarensis *and* A. africanus *lower second molars.*

There is a direct link between the morphology of the masticatory apparatus, including the dentition, and the dietary needs and feeding behaviours of a species (see for example Robinson, 1954; Jolly, 1970; Rak, 1983; Lieberman et al., 2004). Both dental microstructure and occlusal morphology have been linked to tooth function (Reid et al., 1998). The former influences the ability of the likelihood of abrasion or fracturing to occur when a tooth is subjected to masticatory load (Reid et al., 1998) and particularly relates to enamel thickness and cusp shape (Schwartz, 2000; Scott et al., 2005; Benazzi et al., 2013; Berthaume and Schroer, 2017). This is inclusive of morphological features such as enamel thickness, number of cusps or cuspules/cuspids, tooth size and shape, "crushing" versus "shearing" capacity, ect. The examination of these features can be useful in determining dietary behaviours of a species.

Following this logic, morphological differences between different samples of *P. robustus* may indicate behavioural, temporal, or taxonomic distinctions. Current theories for these disparities within the South African robust australopiths tend to

reference sexual dimorphism while older theories lean towards taxonomic differences as an explanation. Broom and Robinson (1952) discussed the possibility of sexual dimorphism between *P. robustus* from Swartkrans and Kromdraai B. Grine (1985) discussed the possibility of taxic diversity as an explanation of the morphological differences within this sample. Research conducted by Grine (1985) will be discussed further in Chapter 6.

Though these samples were later subsumed into a single *P. robustus* taxon, the addition of the DMQ sample caused this to be revisited. Both Lockwood et al. (2007) and Moggi-Cecchi et al. (2010) argued that the DMQ assemblage represents female *P. robustus* while the Swartkrans assemblage represents male *P. robustus*. The former study based this on a basic two-dimensional morphometric analysis of maxillae while the latter studied overall size (mesiodistal length x buccolingual width) of molar teeth. Moggi-Cecchi et al. (2010) went on to explain that a taphonomic process reflecting preferential hunting patterns of contemporaneous carnivores could have resulted in differential collection between the two deposits. Conclusions drawn from these two papers will be discussed further in Chapters 4 and 5.

More broadly, differences between *P. robustus* in South Africa and *P. boisei* in eastern Africa have been attributed to temporal and geological separation. Some researchers were inclined to accept a larger range of variation caused by temporal and geographic separation, within a single species (Wood and Chamberlain, 1987). Others argue the similarities may be result of homoplasy due to *P. robustus* and *P. boisei* occupying similar adaptive niches creating the need for enlarged dentition and buttressed masticatory apparatus (see Wood and Constantino, 2007). That said, the majority of studies agree on a species-level differentiation within a lineage. Differences between *P. aethiopicus* and the other robust australopiths are attributed to the former's greater age and presumed primitive, ancestral state. The following chapter will present new hominin specimens from the DMQ and discuss new interpretive possibilities for robust australopith and South African hominin phylogeny based on new geochronological evidence.

Manuscript: PUBLISHED

This manuscript has been modified (headings, figure numbering, and referencing style) to match the formatting within this thesis as closely as possible. All content matches the accepted manuscript verbatim. Supplementary material, acknowledgements, and all text that is not Main Body text, have been collated in Appendix 1. I contributed significantly to the following manuscript and, as such, am listed as a co-first author. I primarily excavated the hominin specimens presented within the following manuscript. I played a major role in the description and analysis of these specimens as well as in the formation of the arguments regarding the implications of the new dates presented herein on hominin phylogeny and taxonomy.

2. Drimolen crania indicate contemporaneity of *Australopithecus*, *Paranthropus* and early *Homo erectus* in S. Africa

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Understanding the extinction of *Australopithecus* and origin of *Paranthropus* and *Homo* in South Africa has been hampered by the perceived complex geological context of hominin fossils, poor chronological resolution, and a lack of well-preserved early *Homo* specimens. Here we describe, date and contextualize the discovery of two hominin crania from Drimolen Main Quarry in South Africa. At ~2.04-1.95 Ma, DNH 152 represents the earliest definitive occurrence of *Paranthropus robustus*, and DNH 134 represents the earliest occurrence of a cranium with clear affinities to *Homo* erectus. These crania also show that *Homo*, *Paranthropus* and *Australopithecus* were contemporaneous with at ~2 Ma. This high taxonomic diversity is also reflected in non-hominin species and provides evidence of endemic evolution and dispersal during a period of climatic variability

One Sentence Summary: Multiple hominin genera, including early *Homo erectus*, were present in South Africa at 2 Ma.

2.1 Introduction

Remnants of infilled and eroded cave systems (palaeocaves) formed within the Malmani dolomite in north-eastern South Africa have yielded one of the richest early hominin records in the world, including *Australopithecus africanus*, *A. sediba*, *Paranthropus robustus* and early *Homo* (Strait and Wood, 1999; Curnoe; 2010; Keyser, 2000; Berger et al., 2010; Herries and Adams, 2013; Herries et al., 2013). Most of these hominin species are endemic to southern Africa, with only the early *Homo* material being potentially conspecific with hominins in eastern Africa (Strait and Wood, 1999; Keyser, 2000; Berger et al., 2000; Berger et al., 2010; Curnoe, 2010), where the origins of *Homo* have been suggested to occur much earlier (Villmoare et al., 2010).

2015). However, the fragmented nature of most South African early *Homo* specimens (e.g., StW 53; SK 15; SK 847) makes the taxonomy of this group and its relationship to eastern African *Homo* uncertain, with many fossil specimens assigned to multiple species or genera (Curnoe, 2010). An alternative hypothesis is that *Australopithecus sediba* could be the ancestor of South African *Homo* (Berger et al., 2015), despite being known from only ~2 Ma (Dirks et al., 2010).

The majority of Early Pleistocene hominin specimens from South Africa come from the Sterkfontein, Swartkrans and Kromdraai B palaeocaves, located within 3 km of each other in the Blaauwbank Stream Valley, ~40 km north-west of Johannesburg in Gauteng Province (Strait and Wood, 1999; Curnoe, 2010; Herries and Adams, 2013; Herries et al., 2013). Prior to 1992, the only other early hominin fossils known from South Africa were the 40 specimens from the Makapansgat Limeworks (~260 km to the north), and the single specimen from the Buxton-Norlim Limeworks (Taung Child; 360 km to the southwest) (Herries et al., 2013). Moreover, all the discoveries of new early hominin fossils in the last 30 years have come from an area of karst roughly 40 km by 12 km (Figs. 1 & 5); referred to here as the 'Gauteng Malmani'. The pattern of hominin evolution in South Africa prior to ~1.1 Ma is thus biased geographically due to the limited extent of the Malmani dolomite karst from which all the fossils derive (Herries and Adams, 2013; Herries et al., 2013). Correlation of the South African hominin record to that in eastern Africa has been limited by the perceived stratigraphic complexity of many of the South African sites, as well as the historic difficulty in dating palaeokarst due to a lack of suitable material for radiometric dating (Herries and Adams, 2013; Herries et al., 2013). Until recently most dates for South African sites were based on biostratigraphic correlation with the better-dated eastern African sites some 3000 to 4000 km away (Herries and Adams, 2013; Herries et al., 2013).



Figure 5: The Location of the Drimolen Palaeocave Complex. (A): The location of Drimolen in comparison to other Homo erectus sites worldwide and their approximate maximal age. (B) The location of Drimolen within South Africa in relation to other early hominin fossil sites and the Gauteng Malmani sites. (C) The location of Drimolen within the Gauteng Malmani in relation to other hominin sites. The Blauubank Stream Valley is represented by sites running from Bolt's Farm (BF) to Kromdraai (KR) (CP, Coopers D; STK, Sterkfontein; SWT, Swartkrans; RS, Rising Star; GV, Gladysvale; ML, Malapa; HG, Haasgat; GD, Gondolin). Colours indicate the predominant genus or species represented (C) An aerial view of the Drimolen site and the relationship of the hominin bearing DMQ (2.04-1.95 Ma) and non-hominin bearing DMK (~2.61 Ma).

The stratigraphic sequences at most South African palaeocave sites have been defined based on a lithostratigraphic approach in which breccia deposits and siltstone deposits have been classified as sequential numbered Members, thought to represent different temporal phases of deposition (Butzer, 1976; Brain, 1976; Partridge, 2000; Bruxelles et al., 2016). In some cases, where stratigraphic contacts can be identified, older lithofacies having clearly collapsed, subsided, or been eroded by secondary cave formation processes before later lithofacies infilled the resulting space (Herries and Shaw, 2011). This often leads to complexities

such as deposits formed by reworking of older units, and thus mixing of fossil material (Herries and Shaw, 2011; Stratford et al., 2012; Herries and Adams, 2013). In other cases, where stratigraphic links are obscured, the relationship of different lithologies is less certain and the depth that deposits have been accumulated within the cave has often been used to suggest this also represents temporal depth, even when a continuous depositional sequence cannot be identified (Partridge, 2000; Herries et al., 2013). However, caves do not always conform to the law of superposition and deposits can be inverted, have reworking or intrusive events (Adams et al., 2007; Stratford et al., 2012; Herries and Adams, 2013; Herries et al., 2018; Bruxelles et al., 2019). At other sites, where mining or erosion has not obscured stratigraphic relationships it is clear that the different lithofacies represent different depositional processes happening in separate parts of the cave simultaneously, with grading between the different defined Members (Latham et al., 1999; Herries et al., 2018). The Members thus bear little relation to chronostratigraphy and there is profound lateral variation in lithology within what should strictly be defined as a single Member. Misinterpreting these complexities has led to much confusion when defining the stratigraphy of the sites, which often requires a well-resolved chronology for robust interpretation (Herries and Shaw, 2011; Stratford et al., 2012; Herries and Adams, 2013; Herries et al., 2013).

With the advent of uranium-lead (U-Pb) geochronology as a method for dating Pliocene and Pleistocene speleothems it became possible to date the flowstones that underlie and cap fossil bearing deposits, creating datable Flowstone Bound Units (FBUs; Pickering et al., 2007; Pickering et al., 2019). Dating of flowstones across the Gauteng Malmani revealed their contemporaneous formation in multiple caves between ~3.2 and ~1.3 Ma (Pickering et al., 2019). As such, flowstones can be used to derive a regional chronology in the same way as volcanic tuffs in eastern Africa (Pickering et al., 2019). However, due to mining and/or surface erosion at some sites capping and underlying flowstones have been removed (Herries et al., 2018), and the dating of flowstones alone may only provide broad age ranges for the associated fossil-bearing cave sediments between them (Pickering et al., 2019). It is therefore critical to combine U-Pb dating with other complementary methods such as Uranium-Series Electron Spin Resonance (US-ESR) dating and palaeomagnetism (Herries and Shaw, 2011; Herries and Adams, 2013; Herries et al., 2013).

al., 2013; Herries et al., 2019). As complex depositional situations can occur in caves, such as speleothem false floors, it is also important to show the nature of the contact between sediments and dated speleothem using micromorphology.

Recent geochronological work in the Gauteng Malmani suggests a transition occurs between ~2.3 and ~1.8 Ma from supposedly older sites containing *Australopithecus* (Malapa, Sterkfontein Member 4) to supposedly younger sites containing *Paranthropus* and *Homo*, together with the first bone and stone tools (Gondolin, Kromdraai B, Sterkfontein Member 5, Swartkrans Member 1; Backwell and d'Errico, 2008; Dirks et al., 2010; Herries and Shaw, 2011; Herries and Adams, 2013; Herries et al., 2013; Gibbon et al., 2014; Stammers et al., 2018; Pickering et al., 2019). At the same time there is a turnover in other fauna as South African environments became more arid (Vrba, 1999; Dupont et al., 2005; Hopley et al., 2007; Caley et al 2018). However, coarse chronological resolution and imprecise provenance of historically collected fossils (Herries and Adams, 2013) have limited interpretations of how and when faunal communities changed and whether *Paranthropus* and/or supposed early *Homo* fossils directly relate to earlier *Australopithecus* species, or dispersed into the region and ultimately replaced them.

Work on sites outside the Blaauwbank stream valley has expanded our understanding of the South African record and has revealed that not all palaeocave sites have complex multi-generational phases of karstification and infill (Dirks et al., 2010; Herries et al., 2018) as documented at sites like Sterkfontein, Swartkrans and Kromdraai (Herries and Shaw, 2011; Herries and Adams, 2013; Herries et al., 2013; Bruxelles et al., 2019). Discovered in 1992, the Drimolen palaeocave complex (Fig. 5) is one such site (Keyser et al., 2000). Drimolen has yielded over 155 hominin specimens (Keyser, 2000; Moggi-Cecchi et al., 2010) together with significant collections of other fauna (Adams et al., 2016), bone tools (Backwell and d'Errico, 2008), and a small assemblage of Mode 1 stone tools (Stammers et al., 2018). The younger part of the Drimolen system, known as Drimolen Main Quarry (DMQ), is best known for the 1994 discovery of the DNH 7 cranium, the most-complete *P. robustus* skull found to date (Keyser, 2000). Much of the rest of the

DMQ hominin material consists of isolated teeth (Moggi-Cecchi et al., 2010). However, in 2015 and 2018 two new hominin crania were discovered representing *Homo* (DNH 134) and *Paranthropus* (DNH 152) respectively. These recent fossil finds, together with a well-resolved chronology at DMQ, now make it possible to address in greater detail the complex period of change in hominin evolution that occurred around 2 Ma and sets a standard for dating fossil-bearing palaeokarst.

2.2 The DNH 134 Homo aff. erectus cranium

DNH 134 comprises a partial neurocranium (Fig. 6) preserving most of the occipital squama, parietals, and frontal squama with no evidence of plastic deformation. The cranial sutures are patent and at an early stage of fusion, indicating that the specimen is a juvenile. The metopic suture is fused externally and the anterior and posterior fontanelles are absent, indicating an age at death greater than 12-36 months according to modern human standards (Bajwa et al., 2013; Pindrik et al., 2014). The parietals exhibit two tables of bone separated by diploë, indicating that DNH 134 was ontogenetically older than the Mojokerto juvenile (Anton, 1997; Coqueugniot et al., 2004 but see Balzeau et al., 2005). To estimate cranial capacity we created a partial virtual endocast and used multivariate statistics based on three-dimensional landmark data of a reference sample (Fig. 7; see Appendix 1 [Supplementary Text]). The endocranial volume as predicted via linear regression is 538 cc with a 95% single prediction band from 514 to 564 cc. Estimates based on multiple thin-plate spline reconstructions have a larger range but are consistent with this estimate (484-593 cc). Thus, estimated brain size in the juvenile DNH 134 overlaps with the high end of the range of adult Australopithecus and Paranthropus but exceeds the brain sizes (275-410cc) of juvenile Australopithecus (Anton, 2003; Holloway et al., 2004; Berger et al., 2010). While extrapolation of an adult cranial capacity is not straightforward, it is clear that at this ontogenetic stage, DNH 134 has not reached adult size but possesses a cranial capacity at the lower range of adult variation of the population from which it was drawn. Assuming an age at death between two and three years, DNH 134 could have reached a cranial capacity between 588-661 cc or 551-577 cc according to a human or a chimpanzee growth model, respectively.



Figure 6: The DNH 134 Homo aff. erectus *neurocranium*. (*A*) *Superior view, anterior to the left.* (*B*) *Posterior view.* (*C*) *Right lateral view, anterior to right.* (*D*) *Left lateral view, anterior to the left. Scale bar = 10 mm.*



Figure 7: Endocranial volume estimation of DNH 134. (A) Endocranial landmark set used for ECV estimation. Each vertex of the surface is used as a landmark or semilandmark. Anatomical landmarks are shown as spheres, curve semilandmarks are connected as black lines. Measured versus predicted ECV [(B) regression-based, (C) pooled TPS-based, and (D) species-specific TPS-based estimates] for human (blue), H. erectus (red), gorillas (grey), orangutans (orange), chimpanzees (green).

The specimen preserves characters that align it morphologically with *H. erectus sensu lato* (including *H. ergaster*): its profile is "teardrop" shaped in superior view, its squamosal suture is nearly straight, sagittal keeling is present on the frontal and parietals, the cranial vault is long and low with strong sagittal occipital curvature and lambdoidal flattening, and although the anterior aspect of the foramen magnum is missing it is evident that a basion – bregma chord would have been short. These traits together distinguish DNH 134 from *A. africanus, P. robustus* (as preserved in DNH 7), *H. habilis, H. rudolfensis* and *H. naledi* (Benazzi et al., 2014). Individually, none of these traits is fully diagnostic of *H. erectus s.l.*, which is morphologically variable across time and space (Falk et al., 2005), yet collectively they strongly suggest an affinity with that species. Indeed, DNH 134 is strikingly similar to the Mojokerto *H. erectus* cranium in overall cranial shape (Fig. 8).



Figure 8: Comparisons of the DNH 134 cranium with the Mojokerto juvenile H. erectus cranium. DNH 134 (red) superimposed on the Mojokerto cranium (grey) after scaling both specimens to the same bregma – inion length. (A) Left lateral view, anterior to left. (B) Superior view, anterior to left. (C) Posterior view.

2.3 The DNH 152 Paranthropus robustus cranium

DNH 152 is a partial cranium preserving much of the left side of the parietal and frontal bones, a portion of the occipital, the right temporal, the lateral margin of the right orbit, as well as four teeth: left and right maxillary first and maxillary second molars (Fig. 9). The right dental elements are *in situ* within a portion of the maxilla while the left elements are isolated. The specimen preserves a number of characters that align it taxonomically with *P. robustus*. The supraglenoid gutter is partially preserved and would have been wide. The mastoid process is inflated lateral to the supramastoid crest, from which it is separated by a broad shallow groove. The external auditory meatus is large and nearly circular (11.8 mm by 11.5

mm), positioned lateral to the tip of the mastoid process, and nearly at the level of the suprameatal crest. The post-glenoid process is small and fused to the tympanic. Although the tips of the articular tubercle and entoglenoid process are missing, it is evident that the articular eminence was wide and that the glenoid fossa was deep. The digastric groove takes the form of a narrow notch. The superior temporal line on the frontal bone is a well-demarcated ridge, suggesting that a frontal trigon would have been present, but this cannot be directly observed. The sagittal crest bifurcates superior to lambda leaving a bare area on the occipital, and the temporal lines meet the nuchal line in the lateral third of its extent forming a short, partial compound temporonuchal crest. There are extensive striations and beveling on the inferior aspect of the left parietal bone, indicating that the overlap between the temporal and parietal bones at the squamosal suture was extensive. The inferior orbital margin is rounded laterally. Both molars evince a guadrangular occlusal outline with mesiobuccal extension, a deep and narrow central fossa and longitudinal fissure, and a thick distal marginal ridge typical of P. robustus. The left M¹ is fractured and shows 'hyper-thick' enamel. Based on these characteristics the cranium has been assigned to *P. robustus*.



Figure 9: The DNH 152 Paranthropus robustus cranium. (A) Superior, (B) Posterior, (C) Right Lateral, (D) Left Lateral, (E) Right Temporal, (F) Right Orbit, (G) Left M1 Occlusal, (H) Left M2 Occlusal, (I) Left M1 Buccal, (J) Left M2 Buccal, (K) Right M1 and M2 Buccal, (L) Right M1 and M2 Occlusal. Scale bar = 10mm.

2.4 Morphology of the Drimolen Main Quarry (DMQ) Palaeocavern

The Drimolen palaeocave system consists of at least two temporally and spatially distinct cave infills: the ~2.61 Ma Drimolen Makondo (DMK) deposit (Herries et al., 2018), and the hominin-bearing DMQ (Dupont et al., 2005; Hopley et al., 2007; Caley et al., 2018) (Fig. 5C). DMQ is a large palaeocavern (~20 m x 15 m) formed in one of the highest current exposures of the Gauteng Malmani (~1545 m amsl). Based on current topography, the palaeocavern had a very small watershed and acted as a vertical pothole sink for groundwater. The nearby Wonder Cave (aka: van Wyk's Main Cave; Brain, 1958) provides a good modern analogy. In contrast, cave sites in the Blaauwbank Valley, such as Sterkfontein and Plovers Lake act as valley bottom 'collecteur' caves, estavelles or exsurgences where underground

lakes occur either intermittently or permanently (Herries et al., 2019). While the landscape in the Gauteng Malmani has been altered over the last few million years due to erosion (Dirks et al., 2010), this would not have significantly changed the watershed of the Drimolen palaeocave due to its location near the top of a hill, rather than within an actively incised valley. Moreover, only ~10m of erosion is estimated per million years on the hill behind DMQ (Herries et al., 2019). If washed in, the sediments, fossils, and archaeology deposited in DMQ would have originated from a restricted landscape around the cave.



Figure 10: 3D laser scan of Drimolen Main Quarry. The location of the hominin fossils DNH 7, DNH 134 and DNH 152 are shown relative to the main stratigraphic sections (Warthog Cave, Italian Job, Jangi, Walls of Jericho) and features described in the text (WC, Warthog Cave; CEA, Central Excavation Area; WW, dolomite Western Wall of the palaeocavern).

Today, DMQ is a roughly subcylindrical karstic depression with vertical sides, about 5-8 m deep. Most of the ceiling and the upper parts of the DMQ cavern infill have been lost to erosion, breakdown and dissolution (Fig. 5, 10). The outline of the

current quarry was created through speleothem (lime) mining in the late 19th century. The pattern of mining indicates that speleothem deposition originated on the eastern side of the palaeocavern. Water forming these speleothems flowed down-slope along the bedding of the Malmani dolomite (to the north-west) to form a thinning flowstone floor on the south-western side of the cavern. The combination of natural erosion/dissolution and anthropogenic mining has produced a range of stratigraphic profiles that exposes the entire formational history of the cavern (Fig. 10-14).



Figure 11: Warthog Cave Section showing palaeomagnetic and uranium-lead (U-Pb) and sample locations: 1: dolomite bedrock; 2: flowstone (BFS); 3: clast-supported breccia (CSB); 4: sandstone/siltstone (WGSS); 5: recent decalcified sediment, mine dumps and displaced blocks; 6: U-Pb sample locations: BFS (DN39A; 2.673 \pm 0.103 Ma) and WCFS (DN09 1.789 \pm 0.104 Ma). Palaeomagnetic samples indicated by black (normal polarity) and white (reversed polarity) circles.



Figure 12: Jangi Buttress Section depicting DNH 134 find locus: JB - Jangi Buttress; EB -Eurydice Block; 1. CSB, with skeleton-supported structure, large chert and decalcified dolomite (grey dusty patches) blocks and preserved, microfauna-rich reddish layers; 2. MSB with unsorted chert and subordinate dolomite clasts (the lower half is decalcified); 3. mining rubble filling void cut underneath Jangi Buttress; dotted rectangle depicts DNH 134 Homo cranium dispersion area; DMQ-2 denotes the US-ESR date 2.041 ± 0.240 Ma (50cm scale).

The western part of DMQ consists of a 10m wide belt of in situ calcified palaeocave sediments adhering to the western dolomite wall of the DMQ palaeocavern and deposited over a remnant of basal flowstone. These in situ deposits consist of calcified sediment pinnacles up to 3 m high, shaped by subcutaneous secondary karstic dissolution. The spaces between these pinnacles (makondos; Herries et al., 2018) are filled by soft sediment that represents the in situ decalcified equivalent of the sediment in the pinnacles and articulated bone can be found embedded across the contact of both mediums (Herries et al., 2018). Both DNH 134 and 152 were recovered partly from decalcified and partly from lightly calcified breccia, and in close contact to solid breccia. Directly to the east of these in situ deposits, are a mixture of collapsed and decalcifying palaeocave deposits and miner's rubble that were the focus of excavations between 1992 and 2016 (Keyser et al., 2000). This 'Central Excavation Area' has yielded most of the fossil material, but it is mostly ex situ. This includes the DNH 7 P. robustus cranium (Keyser, 2000) that comes from a large block (Eurydice Block: Fig. 10) in the centre. Fossil material in this collapse zone, and in the centre of makondo features (Herries et al., 2018), often shows poorer preservation, which is likely why the majority of hominin fossils recovered to date consist of isolated teeth (Moggi-Cecchi et al., 2010). The collapse of this breccia was caused by the undermining of the *in situ* deposits during lime-mining forming the Inner Cave (Fig. 11). While secondary cave formation has also occurred at DMQ it is limited to the formation of Warthog Cave at the contact between the palaeocavern infill and the southern dolomite wall of the palaeocavern (Fig. 11). Warthog Cave has only slightly eroded into the palaeocave fill and the only fossil to have been recovered from the fill is an isolated Paranthropus molar (DNH 122) that lay very close to the contact with the palaeocave deposits. There is no evidence that this cave has affected the palaeocave deposits via other mechanisms such as collapse.



Figure 13: Italian Job Pinnacle. Photograph (left) and Section (right) showing stratigraphy and geochronometric data: 1. dolomite bedrock; 2. MSB,; 3. flowstone (WOJFS); 4. GSS; 5. decalcified sediment; 6. DMQ-3 denotes the US-ESR date 1.962 ± 0.107 Ma; red circle - DNH 152 Paranthropus skull location.



Figure 14: Walls of Jericho Pinnacle. Photograph (left) and Section (right) showing stratigraphy, palaeomagnetic polarity and geochronometric data: 1. dolomite bedrock; 2.

wad and other dolomite weathering products; 3. basal flowstone (BFS); 4. flowstone; 5. GSS: coarse sandstone /fine gravel; 7. decalcified sediment; 8. Walls of Jericho Flowstone (WOJFS) dated by U-Pb 1.962 ± 0.107 Ma. Palaeomagnetic data: black circles (normal polarity) grey circles (intermediate polarity); white circles (reverse polarity).

2.5 Stratigraphy of the Drimolen Main Quarry (DMQ) Palaeocavern

Here we outline the geochronology and stratigraphy of the DMQ palaeocavern as recorded in a number of key stratigraphic sections along the mined and excavated exposures of the in situ western wall palaeocave deposits (see also Appendix 1 [Supplementary Video 1]). The various lithofacies described in Table S1 have been identified by stratigraphic analysis and micromorphology (Stoops, 2013). The deposits represent a process of continuous accumulation, erosion and reworking of a single, large clast-supported talus cone breccia (CSB) that formed on a basal flowstone (BFS) beneath a vertical entrance. This talus cone was then subject to lateral winnowing during flooding to sequentially create matrix-supported breccia (MSB) and distal gravel, sandstone and siltstone (GSS; Fig. 15, 16; Table S1). Micromorphological observations (Table S1; Fig. 15A-B) indicate the in-washing of sediment derived from the erosion of colluvial soils previously developed outside the cave. A lengthy evolution for these soils is indicated by the intense weathering of minerals and rocks (Fig. 15B). The granular microstructure of the breccia sediment mass is generally rather loose (Fig. 15A), mostly in the upper part of the breccia cone, suggesting fast deposition and leaching of the fine particles, followed by rapid cementation of the sediments. Calcite is the most common cement for both breccias and sandstone/siltstones (Fig. 15D), with the most frequent crystalline pattern being mosaic calcite with anhedral crystals of variable size that cements the whole mass. Fragments and splinters of compact or cancellous bone, as well as microfauna, are often present throughout the breccia (Fig. 15C). The breccia also contains well-preserved fragments of vegetal tissue, which exhibit cellular patterns typical of large-size monocotyledon taxa, and were likely washed in (Fig. 15C). The shape of voids in the breccia are consistent with formation by roots and/or burrowers (Fig. S15C). These occur in samples from about 30 cm above the basal flowstone indicting the early opening of a reasonably wide entrance, and thus indicating that no upper cavern existed as previously suggested (Keyser et al., 2000).



Figure 15: Micromorphology of selected aspects of the DMQ infill. (A) HR scan of thin section of CSB (main talus cone) sample MM26, from WW, showing loose microstructure (LMs), chert (Ch) and dolomite (Ds) clasts, reworked soil/sediment aggregates (SA) sometimes showing crust-like features probably reworked from sandstone/siltstone sediments. (B) CSB sample MM04 from WW, with clay aggregate stained by amorphous Fe- and subordinately Mn-oxides; the lower third of the panel is under XPL, showing poorly developed stipple-speckled b-fabric (white arrows) in unstained areas. (C) CSB sample MM01 from WC, with bone fragment (Bf), monocoth-like wood fragment (white arrow), wide pores originated by biological activity (BV); the lower third of the panel is under XPL, showing xPL, showing anhedral sparite infills within pores. (D) Sample MM32 from WC; void with

"dusty" calcite coating (CC) probably deriving from recrystallisation of aragonite, and subsequent sparitic anhedral calcite infilling (CI). (E) HR scan of thin section of MSB (intermediate facies) sample MM18L from IJ; sequence of fining-upwards sequences with cm-size clasts at the base of each sequence; the bracket highlights the sequence in panel F. (F) Mosaic of microphotographs under PPL (left) and XPL (right), showing a f.u. sequence with thin clay crusts interbedded within the fine part. (G) HR scan of thin section of GSS (distal facies) sample MM12 from WOJ (above WOJFS), with fine grainsize fining-upwards sequences (black brackets), interbedded with a thin flowstone crust (FS); the red and yellow squares indicate respectively the areas in panels H and I. (H) very fine silt and clay crusts (Cr) topping f.u. sequences. (I) Columnar calcite flowstone (Fs) with multiple short growth hiatus marked with detrital caps on crystal tips. the flowstone is overlain by a f.u. sequence terminated by a clay crust (white arrow); the right side of the panel is under XPL.



Figure 16: Micromorphology of the Wall of Jericho Flowstone. (**A**) aspect and stratigraphy of the ~1.95 Ma WOJFS, as in the northern side of the Walls of Jericho pinnacle, showing that WOJFS formed during a stop in clastic deposition and is not intrusive into GSS; FBU1 and FBU2: Flowstone-Bounded Units 1 and 2, as in Figure 18; yellow rectangle: micromorphology samples. Scale = 5cm, (**B**) short range picture of the micromorphology sample detachment niche inside red rectangle of panel A. BFS: basal flowstone, (**C**) scan of thin section showing the distinct nature of sedimentation below and above WOJFS, with several fine speleothem crusts alternating with silt before the formation of the main flowstone. Coloured rectangles indicate spots described in the following panels; blue: panel D, green: E, amber: F, black: G; red: H, (**D**) top of WOJFS and upper contact (white arrow) with the overlying USS. Black arrow: subhedral sparitic calcite with rombohedron

faces indicating upwards crystal growth direction. The layer of anhedral calcite crystals between the arrows is recrystallised and the top surface has undergone dissolution due to contact with siltstone. Plane Polarised Light (PPL), (**E**) same as in D, showing a wide gulflike dissolution feature (DF) into the upper surface of WOJFS layer, due to contact with subsequently deposited silt. White arrows indicate remains of the upper layer (PPL), (**F**) high magnification of calcite within WOJFS, showing the remnant needle-like aragonite (black arrows) that was critical to the successful dating of the sample by U-Pb (PPL), (**G**) Thin flowstone crust (FS) underlying the main WOJFS, showing preserved upwards-growth pattern. Lens-like voids were subsequently infilled by anhedral calcite (CIV), (**H**) Precipitation of anhedral calcite spar (CIV) within channel voids.

2.5.1 Warthog Cave Section

Warthog Cave Section is the most southerly and deepest exposure of the DMQ palaeocavern fill (Fig. 11). The base of the 3m deep section consists of a 50 cm thick flowstone speleothem (which was thicker before mining) that contains no significant detrital material and formed before the cavern had an opening to the surface. This basal flowstone (BFS; -6.40 m below datum) has been U-Pb dated to 2.673 ± 0.103 Ma (DN39A; Pickering et al., 2019). The normal polarity of the flowstone limits its formation to older than the Gauss-Matuyama Boundary at 2.61 Ma (Singer, 2014), setting a lower age limit on the DMQ deposits. There is a sharp contact with an overlying fossil-bearing, clast-supported breccia (CSB) that formed the extreme southern toe of the talus cone down the westerly dipping flowstone and represents the oldest fossil bearing deposits at the site (Lower Cave Breccia). This unit is not noted elsewhere, has not been excavated, and is overlain by a series of well-stratified GSS deposits (Warthog GSS; Table S1). WGSS represents winnowing of fine-grained material from near-entrance talus deposits to the southern edge of the cavern during floods. WGSS was sampled for palaeomagnetic analysis and recorded a reversed polarity (Fig. 17; Table 1) consistent with being deposited between BFS and WCFS, between 2.61 and 1.95 Ma. WGSS filled the southern part of the palaeocavern to the low stepped roof that now forms the top of Warthog Cave. The top of WGSS has been eroded and capped by a 15 cm thick flowstone (Warthog Cave Flowstone; WCFS; -3.90 below datum), which infilled an erosional channel between the palaeocave deposits and the western dolomite wall of the palaeocavern. The flowstone dates to 1.789 ± 0.104 Ma by U-Pb (DN09; Pickering et al., 2019) and recorded a normal magnetic polarity (Fig. 17; Table 1) consistent with deposition during the Olduvai SubChron (1.95-1.78 Ma), and indicating its formation 170-60 ka after the deposition of the WGSS deposits on which it lies (Singer, 2014).



Figure 17: Palaeomagnetic data from DMQ. (Upper) Representative palaeomagentic data plots for DMQ (vector, stereographic, and demagetisation spectra). Open symbols on stereographic plots = negative inclination and closed symbols = positive inclination. (**A**) DN09 Normal Polarity >2.61 Ma Basal Flowstone, (**B**) DN27 Normal Polarity Siltstone from the top of the Walls of Jericho, (**C**) DNFS3 Intermediate Polarity ~1.95 Ma Walls of Jericho Flowstone, (**D**) DN29 Reversed Polarity Siltstone from base of the Walls of Jericho, (**E**) DN01 Reversed polarity siltstone from the Warthog Cave Section, (**F**) DN10 Rejected Basal Flowstone Sample with normal trend but with MAD >15. (Lower) Mineral magnetic results for the DMQ. (**G**) Unmixed coercivity contributions to a representative backfield curve with labelled remanence coercivities for each component (comp.). (**H**) FORC diagram with smoothing parameters listed (e.g., Sc0) and a hysteresis loop insert. (**I**) thermomagnetic curve with curie temperature estimate.

Sample	Location	Depth	Туре	Dec	Inc	К	Plat	Polarity	U-Pb/ESR (Ma)	Combined Date (Ma)	Fossil
DN09	WC	-3.90	FS	16.5	-63.7	141.4	66.5	N	1.79 ± 0.10	1.89-1.78	
DN27	WOJ	0.04	SS	11.7	-23.2	40.3	72.3	N		1.95-1.78	
DN24	WOJ	-0.45	SS	16.9	-21.0	149.3	68.0	N		1.95-1.78	
DN26	WOJ	-0.59	SS	42.7	-12.0	64.5	44.7	Ι		~1.95	
DNFS3	WOJ	-0.78	FS	242.1	-53.8	62.2	-5.8	Ι	1.96 ± 0.11	~1.95	
DN19	WOJ	-1.02	SS	222.3	28.6	174.7	-48.4	Ι	1.97 ± 0.15	~1.95	
DN21	WOJ	-1.55	SS	258.2	29.4	337.6	-17.0	Ι		~1.95	
DN29	WOJ	-1.71	SS	153.8	38.3	41.4	-65.7	R		2.28-1.95	
DN08	WOJ	-1.90	SS	156.9	29.6	56.0	-61.6	R		2.28-1.95	
DN01	WC	-3.33	SS	167.4	17.1	139.0	-69.0	R		2.28-1.95	DNH 152
DN03	WC	-4.36	SS	188.4	26.7	180.7	-75.8	R	2.04 ± 0.24	2.28-1.95	DNH 134
DN39	WC	-6.40-80	FS	26.5	-29.1	156.9	63.1	N	2.67 ± 0.10	2.77-2.61	

Table 1: Palaeomagnetic data, associated US-ESR and U-Pb ages and age ranges for the various deposits at DMQ. (FS = flowstone, SS = sandstone and siltstone).

2.5.2 Jangi Buttress

Jangi Buttress occurs just to the north of the Warthog Cave Section at the southwest edge of the Central Excavation Area, in the centre of the site (Fig. 12). The Jangi Buttress comprises a 3 m deep outcrop of clast-supported breccia (CSB; Table S1) representing a talus cone breccia formed from a vertical entrance and accumulated against the western wall of the palaeocavern overlain by matrixsupported breccia (MSB; Table S1). The breccia consists of large angular to subangular dolomite and chert blocks (up to ~40 cm) formed by entrance and roof collapse, with small pockets of fine-grained in-washed sediment, often with dense macrofossils, occurring between the blocks. A continuous outcrop of CSB extends from Jangi Buttress west to the Western Wall and then north to the Italian Job Pinnacle (see below; Fig. 10). Adhering to the Jangi Buttress on its northern side (western wall of Central Excavation Area) are decalcified remanets of CSB. Excavation of this decalcified material mimics the nature of the breccia with pockets of yellowish red micromammal rich sediment and ghost rock nodules consisting of the insoluble fraction of decalcified dolomite boulders and cobbles. The DNH 134 Homo cranium was recovered as a series of individual pieces at ~-5.31 m below datum (1.1 m above BFS) towards the base of the pinnacle (Fig. 12) during excavations in 2008, 2015, 2016 and 2019 (from the single piece from 2008 was not recognized as hominin until more of the cranium was recovered in 2015). The cranial pieces were partly recovered from lightly decalcified CSB and from decalcified sediment and collapse (since 2008 excavations) next to the pinnacle. These deposits also yielded adult Paranthropus teeth and bone tools. MSB and CSB of the Jangi Pinnacle is equivalent to the GSS deposits of the Warthog Cave section and represents the talus cone from which the WGSS deposits were winnowed. A US-ESR age from a bovid tooth next to the cranium gave an age of 2.041 ± 0.240 Ma (see below; Fig. 12), further confirming this association, and shows the WGSS and Jangi Buttress CSB sediments were deposited ~600-280 ka after BFS formed at >2.61 Ma.

2.5.3 The Italian Job Pinnacle Section

The Italian Job Pinnacle Section is located just to the northwest of the Central Excavation Area (Fig. 13) and occurs stratigraphically higher than the Jangi
Pinnacle, with which it is connected by *in situ* breccia that also connects both sections to the West Wall of the palaeocavern. The Italian Job Pinnacle consists of an intermediate facies of MSB (Table S1) that represents a vertical and lateral transition from CSB at the core of the central talus cone to MSB as fine sediment begins to dominate over large clast deposition during the vertical and westward expansion of the central debris cone. It also represents a lateral transition from MSB of the upper part of the central debris pile to GSS deposits that occur on the northern side of the Italian Job Pinnacle itself and in the Walls of Jericho Pinnacle on the northern edge of the palaeocavern (see below). This transition represents winnowing of fine-grained sediment from the central talus cone to the northern corner of the cavern during floods. A thin flowstone (Walls of Jericho Flowstone; WOJFS) occurs at -0.97 m below datum in the Italian Job Pinnacle and continues into and through the adjacent Walls of Jericho Pinnacle, suggesting a slight hiatus in deposition. US-ESR dating of a bovid tooth from ~18 cm below the flowstone at -1.15 m below datum produced an age of 1.965 ± 0.147 Ma (see below). The DNH 152 Paranthropus robustus cranium was recovered from the very base of the current excavated exposures of the Italian Job at a height of -3.15m below datum and ~2.18 m below the WOJFS.

2.5.4 The Walls of Jericho Pinnacle Section

The Walls of Jericho Pinnacle Section is the most northerly exposure of the DMQ palaeocavern infill (Fig. 14). Most of the section comprises GSS, representing finegrained sediments winnowed by medium-energy flow (Fig. 15E-F) from the central debris pile to the south. On the northern side of the pinnacle a steeply dipping flowstone is assumed to be equivalent to the basal flowstone in the Warthog Cave section (2.78-2.61 Ma) (DN39A; Pickering et al., 2019). As in the Warthog Cave section, there is a sharp contact between this basal flowstone and the overlying sediments. At -0.78m below datum the WOJFS occurs (~2cm thick) that has been U-Pb dated to 1.962 ± 0.107 Ma (DN26) (Pickering et al., 2019), consistent with the US-ESR age just below this flowstone in the Italian Job Pinnacle. Micromorphological analysis (Fig. 16) confirms this flowstone is not intrusive and formed during a hiatus in the deposition of GSS. GSS deposits below the WOJFS are well-laminated, whereas those above are more coarsely layered, with thin intercalated flowstones and silt crusts suggesting alternating hiatuses in clastic deposition and pooling of water (Fig. 15G-I). Palaeomagnetic analysis indicates a change from reversed to normal polarity up through the section with intermediate polarity occurring in the WOJFS as well as sediments above and below it, further confirming it formed during the deposition of the sediment sequence (see below). Based on the U-Pb and US-ESR ages this can be correlated to the reversal at the base of the Olduvai SubChron at ~1.95 Ma (Rivera et al., 2017).

2.6 Geochronology

US-ESR analysis was undertaken on an indeterminate medium-sized alcelaphin right maxillary third molar (right M3; DMQ-2) recovered from the lightly decalcified breccia of the Jangi Buttress in direct association with the DNH 134 cranium (Fig. 12); and, on another partial bovid tooth (DMQ-3) encased in breccia from the southern side of the Italian Job Pinnacle, 2 m above DNH 152 and around 20 cm below the WOJFS (Fig. 13). The Dose equivalents for DMQ-2 and DMQ-3 were estimated using the peak-to-peak T_1 -B₂ method at 1814 ± 57 and 2414 ± 76 respectively (2σ error) (Table S2) including an unstable radical component (NOCOR) of 21% and 16%, respectively (Joannes-Boyau and Grun, 2009; Joannes-Boyau and Grun, 2011; Joannes-Boyau, 2013). When integrated into the US-ESR dating modelling described by Shao et al. (2014), the ages of DMQ-2 and DMQ-3 are estimated to be 2.041 \pm 0.240 Ma and 1.965 \pm 0.147 Ma respectively (1o error; Table 2, S2). Both samples did not show any ratios above secular equilibrium, although the dental tissues were not extensively mapped. Nonetheless, the U-diffusion in DMQ-2 and DMQ-3 fits the open-system model, and the teeth did not exhibit obvious complex compound uranium diffusion episodes. However, the isotopic ratios between the enamel and dentine remain different, most likely indicating a more recent incorporation (uptake) of uranium in the dentine. With a U-uptake history model close to linear in most dental tissues (Table 2) as well as rather homogenous ratio over the analysed area, we were able to assume equilibrium in the uranium decay chain after ²³⁰Th (e.g., ²¹⁰Pb/²³⁰Th=1).

SAMPLE	DMQ-2	DMQ-3
ENAMEL		
Dose (Gy) ^a	1814±59	2414±76
U (ppm) ^b	1.43±0.15	2.07±0.18
234U/238U ^b	1.2841 ± 0.0587	1.0886 ± 0.0369
230Th/234U ^b	0.9220±0.0256	0.9731±0.0155
Thickness (m)	1354±189	1551±320
Water (%)	3±1	3±1
DENTINE		
U (ppm) ^b	$17.30{\pm}1.11$	19.31±1.05
234U/238U b	1.4110±0.0237	1.4183 ± 0.0109
230Th/234U b	0.9558±0.0201	0.8822 ± 0.0278
Water (%)	5±3	5±3
SEDIMENT		
U (ppm)	1.9±0.5	1.9±0.5
Th (ppm)	3.02±0.2	$3.02{\pm}0.2$
K (%)	$0.29{\pm}0.05$	$0.29{\pm}0.05$
Water (%)	15±10	$15{\pm}10$
EXTERNAL DOSE RATE SEDIMENT		
Beta dose (µGy a ⁻¹)	44±9	38±8
Gamma Dose (µGy a ⁻¹)	323±39	323±39
Cosmic (µGy a ⁻¹)	97±50	97±50
COMBINE US-ESR AGE		
Internal dose rate (µGy a ⁻¹) ^c	291±80	701±76
Beta dose dentine (µGy a ⁻¹) c	134±37	69±8
P enamel ^c	0.64±0.13	-0.45±0.01
P dentine ^c	0.03±0.02	1.46±0.15
Total dose rate (µGy a ⁻¹) ^c	889±109	1228 ± 100
AGE (ka) ^c	2041±240	1965±147

Table 2: US-ESR dating data for DMQ-2 and DMQ-3 fragments

^a Dose equivalent De obtained using McDoseE 2.0, with SSE (from Joannes-Boyau et al. (2018).

^b Uranium concentration values were obtained by LA-MC-ICPMS and LA-ICPMS on both teeth and both dental tissues.

^c The age was calculated using Shao et al. (2014), with the dose rate conversion factors of Guérin et al. (2011), the enamel and dentine density of 2.95 and 2.85 respectively from Grun (1986).

Palaeomagnetic analysis was performed on the GSS and U-Pb dated flowstones from the Warthog Cave and Walls of Jericho Sections (Table 1; Fig. 11, 14). Natural Remanent Magnetisation (NRM) intensities ranged from 8.94 to 0.57 Am²/kg¹ with a mean xLF (non-speleothem samples) of 186 x10⁻⁵ SI indicating sufficient ferromagnetic material for palaeomagnetic analysis. Mineral magnetic measurements (Fig. 17G-I) show that both low coercivity magnetite and maghemite occur in superparamagnetic (SP), stable single domain (SSD), and vortex state (formally referred to as pseudo-single domain) (Roberts et al., 2017) grain size ranges. Pigmentary hematite is also likely present as indicated by a low contribution antiferromagnetic component observed in backfield unmixing curves (Fig. 17G). This does not contribute to the NRM. A significant proportion of SP to viscous single domain (vSD) boundary grains are shown by high frequency dependence of magnetic susceptibility (xFD%; mean 11.75% for non-speleothem samples) and these are susceptible to more recent viscous re-magnetisation. First Order Reversal Curves (FORCs) show a predominance of single domain signals, which are ideal for palaeomagnetism, and are highlighted by closed concentric contours along the central ridge of the FORC diagram (Fig. 17H) (Roberts et al., 2000). Given that some of the central ridge coercivity distribution intersects with the Bu axis the SSD magnetisations are likely mixed with those of lower coercivity SP/vSD boundary grains (Pike et al., 2001) in line with χ FD% results. Such samples require caution when undertaking AF_D cleaning to ensure remanences associated with SSD particles are properly isolated from SP/vSD boundary overprints prior to their removal. FORCs also derive some influence from larger vortex state particles as shown by a spread of remanence away from the central ridge and weak lobe features, while there is no evidence for multi domain (MD) grains, which would be reflected by a greater remanence spread along the Bu axis (Roberts et al., 2017).

Final palaeomagnetic data for the 13 block samples are presented in Table 1 and Fig. 17. Viscous overprints associated with SP/vSD boundary grains were removed via AF_D typically between 12–15 mT or with TH_D at temperatures of 250–325 °C to reveal a single stable component of magnetisation comprised of low MADs (<10; Fig. 17A-F). This ChRM signal is removed via TH_D between 540–580 °C (and 5–40mT via AF_D), suggesting detrital magnetite (T_c = ~585°C) as the main remanence

carrier, corroborating T_c estimates of 561–586 °C derived from *M*/T heating curves (Fig. 17I). In isolated samples the ChRM wasn't removed until ~610 °C suggesting some minor maghemite contribution. Taken together, the overall stability of magnetisation to high temperature along with the occurrence of reversed polarities and directional consistency among different demagnetisation strategies indicates a primary remanence formed within SSD (to vortex state) magnetite and maghemite around the time of sediment deposition in the cave (i.e. depositional or post-depositional remanent magnetisation; DRM or pDRM). The occurrence of microlayers of flowstone within the sediments likely aided the quick lock in of magnetic remanence and reduced any effects of post-depositional remanent magnetisation. Final directions (Figs 11, 14, 17, 18; Table 1) indicate a series of polarity changes throughout the sequence. Normal polarity is observed in the basal and capping flowstones of the Warthog Cave section and the upper 60cm of the GSS of the Walls of Jericho Section. Reversed polarity is noted in the GSS of the Warthog Cave Section and base of the Walls of Jericho Pinnacle. The middle part of the GSS Facies (-1.55 to -0.59 m below datum) in the Walls of Jericho Section, as well as the WOJFS itself, record intermediate magnetic polarity that represents true intermediate geomagnetic behaviour occurring during a magnetic reversal. It is extremely rare to find evidence for such reversals in terrestrial sedimentary sequences and indicates this part of the sequence likely formed over a few to several 1000 years during the reversal itself.



Figure 18: Composite stratigraphy for DMQ. The Stratigraphic Sections (WC – Warthog Cave, JB – Jangi Buttress, IJ – Italian Job, WOJ – Walls of Jericho; m = metres below or above datum) and Dates (Ma) for DMQ compared against the Geomagnetic Polarity timescale and other early hominins in South Africa as well as global Homo erectus sites.

2.7 Chronostratigraphy and Flowstone Bound Units

Despite the perceived stratigraphic complexity of Gauteng Malmani palaeocaves, DMQ has a simple depositional history. Evidence suggests the site was a water sink (pothole) that infilled over a short timeframe and there is little evidence for secondary cave formation, natural reworking of fossils, or infills of significantly different ages. Putting all the geochronological data and stratigraphic information together, the DMQ sequence can be divided into two major flowstone-bound units (FBU; Fig. 18; Table 1). The thicker (~5.6 m thick) stratigraphically lower FBU (FBU1) occurs between the 2.673 ± 0.103 Ma (Stratford et al., 2012) Basal Flowstone (-6.40m below datum) that underlies the entire sequence of clastic deposits within the palaeocavern and the 1.962 ± 0.107 Ma Walls of Jericho Flowstone (-0.78 m below datum) that divides the Walls of Jericho and Italian Job Pinnacles (Fig. 16; Pickering et al., 2019). The thinner (~1.07m), upper FBU (FBU2) formed between the Walls of Jericho Flowstone and the 1.789 ± 0.104 Ma Warthog Cave Flowstone (Table 1; Pickering et al., 2019). The normal polarity of the Basal Flowstone indicates it formed prior to the Gauss-Matuyama boundary at ~2.61 Ma (Singer, 2014), while the sharp contact with overlying sediments and lack of detrital inclusions confirms the flowstone formed prior to an opening to the surface (as seen in base of Warthog Cave Section).

During the formation of FBU1 a large clast-supported breccia (CSB) was deposited beneath a vertical entrance in the western to central part of the palaeocavern (as seen in Jangi Buttress) and flooding winnowed fine-grained sediments (GSS) against the southern wall of the palaeocavern (as seen in Warthog Cave Section). Between the clasts within CSB fine-grained sediments (equivalent to GSS) and macrofossils occur in small pockets. In this early phase articulated skeletons are often found across more than a single pocket. This indicates deposition of the skeletons before or during the deposition of blocks rather than a mechanism whereby fossils and fine sediment have filtered down through a pre-existing structure of blocks. The reversed polarity of the Warthog Cave GSS and US-ESR age of 2.041 \pm 0.240 Ma for the oldest excavated CSB deposits from the Jangi Buttress indicate the oldest sediments, including *Homo* aff. *erectus* fossil DNH 134, entered the DMQ palaeocavern several 100,000 years after the Basal Flowstone

formed, and sometime between ~2.04 and 1.95 Ma, during the Matuyama reversed polarity Chron. Isolated teeth of Paranthropus robustus and bone tools have also been recovered from these layers. As the central talus cone continued to be deposited in the central part of the cavern it also expanded against the western dolomite wall of the cave. As the CSB of the talus central talus cone built up it also graded laterally to a more matrix supported breccia (MSB) in the western half of the cavern (as seen in the base of the Italian Job Pinnacle). At this time, when DNH 152 was deposited, the GSS deposits has already filled the cavern to the roof in its lower southern part and GSS deposits were now being winnowed against the northern wall where the cavern roof was higher (as seen on northern edge of Italian Job and in the Walls of Jericho Pinnacle). Like the top of the Warthog Cave Section, the oldest deposits in the Walls of Jericho Pinnacle record a reversed polarity. The DNH 152 P. robustus cranium was deposited during the middle part of FBU2 ~3.2 m above the basal flowstone, 2.2 m above DNH 134, 2.2 m below the WoJFS, and ~1.6 m below the beginning of the magnetic reversal in the Walls of Jericho (Singer, 2014; Rivera et al., 2017; Fig. 18).

The talus cone continued to form and as sediment was further winnowed into the northern edge of the cave (Italian Job to Walls of Jericho Section) the polarity of the GSS deposits changed from reversed to intermediate polarity, indicating the onset of a magnetic reversal. The US-ESR age of 1.965 ± 0.147 Ma for these deposits suggests this reversal is the onset of the Olduvai Subchron at ~1.95 Ma. This is confirmed by the 1.962 ± 0.107 Ma U-Pb age and intermediate polarity for the thin WoJFS (DN26; Stratford et al., 2012) that formed during a hiatus (shorter than the few to several 1000 years of a magnetic reversal) in deposition and caps the lower well-laminated GSS deposits in the northern part of the cavern (as shown in the WOJ; Fig. 14, 18). GSS continues to form after the WoJFS and again records intermediate polarity before transitioning to the normal polarity of the Olduvai Subchron just prior to GSS filling up to the roof of this part of the cavern (1.95-1.78) Ma) (Rivera et al., 2017). This indicates that the upper parts of the lower FBU, the WoJFS, and the lower part of the upper FBU were all deposited during the timeframe of the magnetic reversal at the base of the Olduvai Subchron at ~1.95 Ma. Reversals have been estimated to take between 4,000 and 22,000 years to complete (Singer et al., 2019). Significantly after this event, an erosional channel formed between the talus cone and the western dolomite wall, also eroding the top of the GSS sediments in the Warthog Cave section. This erosional channel was filled with the Warthog Cave Flowstone (WCFS) that has been U-Pb dated to 1.789 ± 0.104 Ma (DN09; Pickering et al., 2019) but whose age can be refined to between 1.89-1.78 Ma due to its normal polarity and correlation to the Olduvai Subchron (1.95-1.78 Ma). The WCFS caps FBU2, although most of the fossil-bearing sediments in FBU2 only occur in the top ~90cm of the Walls of Jericho and Italian Job Pinnacles (Fig. 18) and are formed immediately after the reversal at ~1.95 Ma. While a younger US-ESR age of 1.712 ± 0.538 Ma has been produced for a tooth from the Eurydice (DNH 7) block that may suggest deposition during FBU2, the ex situ nature of the block and its decalcification make dosimetry estimates more difficult. The Eurydice block consists of CSB and is consistent with deposition in FBU1 and the US-ESR age does overlap with the other ages from FBU1 within error. Moreover, comparisons between the ESR dating of teeth from calcified and decalcified breccia at other sites show that decalcification causes ages that are too young (Herries and Shaw, 2011). As such, it is critical to collect teeth from in situ calcified breccia when undertaking US-ESR analysis at such sites. The lack of any short magnetic reversal events, such as the ~2.07 Ma Huckleberry Ridge event (Singer, 2014) identified at other palaeocaves in the region (Dirks et al., 2010; Herries and Shaw, 2011) within deposits older than the reversal at DMQ suggests the deposits all formed post ~2.07 Ma, consistent with the median age of the US-ESR sample from the Jangi Buttress. The vast majority of hominin remains from DMQ, including DNH 134 and DNH 152, thus come from FBU1 maximally between 2.28 and 1.95 Ma, but most likely between ~2.04 and 1.95 Ma.

2.8 Biogeographic Interpretations of the Drimolen Main Quarry Faunas

There are several faunal species represented at DMQ (Adams et al., 2016) that support some level of non-endemic mammal dispersal into South African palaeoecosystems during the early Pleistocene, and/or temporal variation within South African phyletic lineages. The recovery of *Equus* cf. *quagga* ssp is consistent with the deposits having formed after ~2.3 Ma given the first appearance of the genus in eastern Africa at this time (Adams et al., 2016). *Equus* is first seen in South Africa at Sterkfontein Member 4 prior to ~2.07 Ma (Herries and Shaw, 2011;

Herries et al., 2013), as well as at Malapa just after ~2 Ma (Dirks et al., 2010). This indicates the relatively rapid expansion of this genus into the southern part of the continent, perhaps coinciding with environmental change and increasing aridity at this time (Dupont et al., 2005).

The papionin sample at DMQ (DN 403, 528, 541, 2160, 2162, 2344) is best attributed to Papio robinsoni. Diagnostic features include a prominent glabellar region, definitive anteorbital drop, definitive facial fossae, and a dorsally flattened rostrum with rounded maxillary ridges that are elevated superiorly to the nasal bones. They are distinct from *P. hamadryas*, which is found at penecontemporary sites such as Malapa (Gilbert, 2015), by the aforementioned rostral morphology, rounder maxillary ridges, and by having less excavated facial fossae. However, the specimens collectively share distinct facial fossae that depart from their conspecifics at Swartkrans Member 1. Specifically, the anterior extent of the maxillary fossae on the DMQ specimens are not as developed as the Swartkrans specimens SK555, SK557, and SK560. The infraorbital region is not as excavated by the maxillary fossae in the DMQ specimens. As the malar root approaches the alveolar bone in the Swartkrans material, it typically curves anteriorly (further defining the maxillary fossae; Gilbert et al, 2018) However, in nearly every DMQ specimen the malar root descends directly on the alveolar bone between the second and third molar. This variation may be explained by temporal variation between DMQ and Swartkrans Member 1, with the latter perhaps dating closer to 1.8 Ma (Herries and Adams, 2013). Other sites (e.g., Pit 23at Bolt's Farm) that have definitively yielded P. robinsoni remain undated (Edwards et al., 2019), making DMQ the earliest definitive evidence for this species (Gilbert et al., 2018).

The hunting hyaena *Lycyaenops* is first recorded in the early Pliocene of Europe as *L. rhomboideae* (Kretzoi, 1938) and appears by 3.85 - ~3.63 Ma as *L. cf. silberbergi* in the Upper Laetolil Beds at Laetoli (Werdelin et al., 2011), and in South Africa at Sterkfontein Members 2 and 4 between 2.61-2.07 Ma (Herries et al., 2013; Pickering et al., 2019). During this period *Lycyaenops* cohabits the South African ecosystems with *Chasmaporthetes*, a genus present in South Africa at Langebaanweg by ~5.15 Ma (Werdelin, 2010; Roberts et al., 2011). DMQ represents the last appearance of *Lycyaenops*, while the South African *C. nitidula* persists into the early Pleistocene (Herries and Adams, 2013). This suggests that any environmental conditions favouring the initial dispersal of *Lycyaenops* into South Africa may not have existed after DMQ.

The oldest occurrence of Dinofelis (D. cf. diastemata) is in South Africa at Langebaanweg ~5.15 Ma (Werdelin and Lewis, 2001; Roberts et al; 2011). By the end of the Pliocene Dinofelis is represented by D. aronoki in eastern Africa, and D. barlowi and D. darti in South Africa (Werdelin and Lewis, 2001). The only Dinofelis definitively known to be present in Africa after approximately 1.87 Ma is D. piveteaui (Werdelin and Lewis, 2001), with D. barlowi last known to occur at Malapa and now DMQ at ~2 Ma (Dirks et al., 2010; Adams et al., 2016). Moreover, Dinofelis barlowi and Dinofelis aff. piveteaui co-occur at DMQ (Hopley et al., 2007), marking the first time that these taxa have been found together at the same site. Historically, D. piveteaui has been interpreted as being directly descended from D. barlowi (Hemmer, 1965; Cooke, 1991; Werdelin and Lewis, 2001), but Werdelin & Lewis (2001) posited a close relationship between the eastern African D. aronoki and the later-occurring D. piveteaui. An ancestor-descendent relationship between D. aronoki and D. piveteaui suggests the expansion of a population of the east African D. aronoki, or a population transitional between D. aronoki and D. piveteaui, at some point just prior to 2.0 Ma. This population, possibly represented by the DMQ Dinofelis aff. piveteaui (Adams et al., 2016) and the Cooper's D Dinofelis sp. ~1.36 Ma (Lacruz et al., 2006; Pickering et al., 2019), may have displaced the South African endemic D. barlowi.

The dominance of the antilopin *Antidorcas recki* in the DMQ deposits (28.6% of the total bovid assemblage; Adams et al., 2016) may reflect movement by an earlier Neogene mammal population from outside South Africa into the evolving palaeocommunities of the region during the earliest Pleistocene. The species is present in the 3.44 Ma Shungura Formation Member B and younger deposits across eastern Africa, ultimately becoming common in terminal Pliocene deposits like the 2.66 Ma Upper Ndolyana Beds at Laetoli (Gentry, 2010). In contrast, the first South African *A. recki* specimens are not recovered until the modest sample (NISP: 5, MNI: 3) identified from the Sterkfontein Member 4 assemblage that formed between 2.61-2.07 Ma (with at least some of that fauna post-dating 2.33

Ma due to the occurrence of Equus; Vrba, 1995; Herries et al., 2013). The hypothesis that South African A. recki occurred only ~1 Ma after evolving in eastern Africa, draws support from two potentially interrelated factors. First, Antidorcas is notably absent from the large Makapansgat Member 3 assemblage (3.03-2.61 Ma, with faunal deposition close to the end of that period; Herries and Adams, 2013) in which the dominant antilopin and the second-most common bovid is Gazella vanhoepeni (NISP: 472, MNI: 55; Reed, 1996; Pickering et al., 2007; Gentry, 2010). Despite this abundant representation in Member 3, and potential relationship to the Langebaanweg Gazella (5.15 Ma; Reed, 1996) and extant Gazella species, G. vanhoepeni has not been definitively identified from the extremely sparse record of indeterminate Gazella from any subsequent early Pleistocene South African deposit (Watson, 1993; de Ruiter, 2003; de Ruiter, 2009; Gentry, 2010; Gibbon et al., 2014). Second, shortly after A. recki first appears at Sterkfontein Member 4, there is an adaptive radiation of Antidorcas in South Africa into at least two additional species (the extinct A. bondi and extant A. marsupialis). Collectively, species of Antidorcas are frequently recovered from early-mid Pleistocene palaeokarstic deposits in the region and form substantial components of the Swartkrans, Kromdraai and Cooper's D faunal assemblages (Watson, 1993; de Ruiter, 2003; de Ruiter, 2009; Adams et al., 2016). The apparent turnover in representation of antilopin genera from Gazella to Antidorcas coupled with rapid speciation in the latter group is suggestive of exploitation of changing regional palaeoecosystems in which Antidorcas species adapted to the progressive expansion of xeric South African Pleistocene palaeohabitats.

2.9 Conclusions and Impact

The geology of DMQ further highlights the inadequacies of the Member system still used at other South African sites (Butzer, 1976; Brain, 1976; Partridge, 2000; Bruxelles, 2016). As DMQ and other sites show (Latham et al., 1999; de Ruiter et al., 2009; Herries et al., 2013; Herries et al., 2019), these different lithologic units can form synchronously, and wherever a siltstone and sandstone unit occurs there is (or was) likely a paired breccia from which it was winnowed. The alternative, allostratigraphic criterion used here disentangles lithostratigraphy from chronology. The context and dating of the DNH 134 *H.* aff. *erectus* cranium and *P. robustus*

fossils to between ~2.04 Ma and 1.95 Ma shows how DMQ is now one of the best dated sites in South Africa, as well as how the integration of geomorphology, stratigraphy, and high-precision age determinations are resolving the South African fossil karstic record and providing critical insights into hominin evolution.

Australopithecus is last known to occur ~2 Ma at Malapa (Berger et al., 2010; Dirks et al., 2010) and perhaps as late as 2.07 Ma at Sterkfontein (Herries et al., 2013). Australopithecus thus persisted in southern Africa for roughly half a million years after it went extinct in eastern Africa (Shao et al., 2014). However, the precise timing of the first occurrence of Homo and Paranthropus, and whether it overlapped with Australopithecus, has been hard to resolve because of uncertainty in the depositional ages of fossils from Sterkfontein, Kromdraai and Swartkrans (somewhere between 2.3 and 1.8 Ma). At >1.95 Ma the DNH 152 cranium represents the oldest confirmed representative of Paranthropus robustus in South Africa (Fig. 9). The age and association of the Kromdraai B Paranthropus fossils are presently unknown, although preliminary palaeomagnetic analysis indicated an age of <1.78 Ma for the hominin-bearing Member 3 deposits (Herries and Adams, 2013), and thus younger than DMQ. While the Paranthropus fossils from Swartkrans Member 1 Hanging Remnant have been dated to sometime between ~2.3 and 1.8 Ma (Herries and Adams, 2013; Pickering et al., 2019), there is no firm evidence that they are >1.95 Ma (Herries and Adams, 2013). A number of studies have suggested the deposits are likely closer in age to the upper flowstone that was dated at 1.8 Ma, consistent with ESR dates (Curnoe et al., 2002) and faunal interpretations (Pickering et al., 2011); including the difference noted between P. robinsoni at DMQ and Swartkrans (Herries and Adams, 2013; Pickering et al., 2011).

At ~2.04 Ma (minimum age 1.95 Ma) DNH 134 is the most complete and oldest early Pleistocene *Homo* neurocranium (Fig. 6-8) in South Africa. DNH 134 is at least 100-150 ka older than *H. erectus s.l.* specimens from Dmanisi (Lordkipanidze et al., 2010) and over 300 ka older than the KNM-ER-3733 cranium from Kenya at ~1.63 Ma (Lepre and Kent, 2015). The KNM-ER-2598 occipital fragment from eastern Africa shows affinities to *Homo erectus* (Lepre and Kent, 2015). However, based on palaeomagnetic data, its location 4m below the KBS tuff (dated to 1.87 ± 0.02 Ma) would place KNM-ER 2598 within the Olduvai Subchron at <1.95 Ma (McDougall et al., 2006; Braun et al., 2010; McDougall et al., 2012). As such, DNH 134 also represents the oldest fossil with affinities to *Homo erectus* in the world. Despite this we do not assert that the species necessarily evolved first in southern Africa, especially given major geological biases in hominin finds across Africa. However, the dating of the DNH 134 cranium to >1.95 Ma substantially weakens the hypothesis that *H. erectus sensu lato* evolved outside of Africa (Lordkipanidze et al., 2010).

It has been postulated that *A. sediba* is a good candidate for the ancestor of *Homo* (Berger et al., 2010), although much older fossils attributed to *Homo* exist (Berger et al., 2015). *A. sediba* can only be ancestral to *Homo* in southern Africa if a population existed prior to DNH 134 for which there is no current evidence (Villmoare et al., 2015). An alternative scenario is that the *Homo*-like morphological elements in *A. sediba* (Berger et al., 2010) may instead represent homoplasy, evolved as local environmental pressures gave rise to convergent morphological features at ~2.0 Ma in a terminal population derived from *A. africanus* (Kimbel and Rak, 2017). Regardless, changing environmental conditions across Africa likely placed *Australopithecus* populations under selective pressures that led eventually to the evolution of divergent *Homo* and *Paranthropus* lineages (Ledogar et al., 2016; Joannes-Boyau et al., 2019).

Global climatic transitions have been suggested to occur at 3.0-2.5 Ma (with rapid global cooling and African landscape aridification) and 2.0-1.5 Ma (with the inception of the Walker Circulation in the Pacific governing tropical airflow and rainfall patterns across the continent; Hopley et al., 2007; deMenocal 2011). Evidence for a major environmental shift in at least parts of southern Africa comes from deep-sea cores off Namibia which indicate stronger climatically induced fluctuations between 2.7 and 2.2 Ma, with semi-arid environments more widespread during glacial periods (Dupont et al., 2005). Aridification and climate variability further increased significantly after 2.2 Ma (Dupont et al., 2005), although humid conditions occurred in the Limpopo basin between 2.0 and 1.75 Ma (Hopley et al., 2007). These climatic shifts are shown in the caves by changes from major phases of massive speleothem and tufa deposition in the Pliocene at the

Makapansgat Limeworks and Taung (Herries et al., 2013), to increasingly sporadic formation throughout the Pleistocene (Pickering et al., 2019). Some researchers have suggested that hominin evolution has been driven by long-term trends towards aridity (Potts, 1998), whereas others suggest the importance of short periods of extreme climatic change or variability (Maslin and Trauth 2009). When set within the regional record the DMQ sequence highlights that, while an overall trend towards aridity occurred, the period between 2.3 and 2.0 Ma was a critical period of major ecological change and dispersal that extensively modified South African faunal communities.

The changes seen in hominin taxa are mirrored in other fauna with DMQ representing a transitional faunal community overlapping between older, >2.1 Ma sites like Sterkfontein Member 4 and Makapansgat Limeworks Member 3 (Herries et al., 2013) and younger sites such as Swartkrans and Gondolin (Herries and Adams, 2013). The transitional faunal community recorded at DMQ reflects the larger turnover in mammal communities driven by major ecological changes in southern Africa that saw the extinction of South African endemic species, dispersal of new species, and adaptive radiation in the region. This suggests that South Africa was a centre for the evolution of mammalian lineages as well as a refuge for ancient lineages in the early Pleistocene. The high taxonomic diversity on the South African landscape around 2 Ma is likely a response of indigenous hominins and other fauna to climate and environmental shifts, in tandem with new immigrants that were part of a series of radiations across Africa that set the stage for hominins leaving the continent and inhabiting Asia sometime between 2.12 and 1.95 Ma (Zhu et al., 2018). We interpret the occurrence of Homo aff. erectus at this time in South Africa, and soon after at Dmanisi (Lordkipanidze et al., 2010) as evidence for a major range expansion of this species (covering at least 8000 km) both out of, and within Africa around 2.0 to 1.8 million years ago.

At ~2.04-1.95 Ma DMQ records a critically underrepresented time period in the evolution of South African faunas and palaeoecosystems and shows unequivocally that *Australopithecus sediba* (from Malapa at ~1.98 Ma) (Berger et al., 2010; Dirks et al., 2010), *Paranthropus robustus,* and *Homo* aff. *erectus* occurred contemporaneously within the ~250 km² of karst landscape NE of Johannesburg,

even though it cannot be demonstrated definitively that they were truly sympatric. With the last occurrence of *A. africanus* (Sts 5) potentially as late as ~2.07 Ma at Sterkfontein Member 4 the South African record has a very high diversity of hominins at ~2.1-1.9 Ma (Adams and Herries, 2013; Herries et al., 2013). We suggest that southern Africa served as an ecological refugium for *Australopithecus* until just after 2.0 Ma when either short- or long-term climatic variability would have finally driven *Australopithecus* to extinction. It is unclear whether biological or behavioural adaptations in *Australopithecus* (Joannes-Boyau et al., 2019) or competition with *Homo* and/or *Paranthropus* would have also contributed to the demise of the genus, but the dating of DNH 134 and DNH 152 to a period of overlap with *Australopithecus* now make this a possibility.

3. This chapter has been redacted.

Figures 19-22 redacted within chapter.

4. DMQ Dental Descriptions

DMQ dental specimens employed in analyses throughout this thesis have been described in various locations. Sixty-one specimens were published by Moggi-Cecchi et al. (2010) and 39 specimens were preliminarily described (draft or note form) by Leece (2016, Appendix 2). The descriptions of some of these specimens such as DNH 106, 107, and 108, were limited to tooth identification only. These 39 specimens have been described in full, rather than in their previous draft form, within this chapter. A further 14 specimens have been described herein, as well. This included detailed descriptions of dentition associated with DNH 152 (Herries et al., 2020; Chap 2) and **Redacted**. Descriptions presented here relate to the specimens that form the basis of analyses presented in Chapters 5 and 6.

4.1 Contexts

The specimens presented in this study have been identified between 1999 and 2018, with the material presented in Moggi-Cecchi et al. (2010) having been discovered between 1992 and 1999. As such, the collection was excavated by a number of different researchers and thus there have been a variety of different methods of excavation, recording, and curation employed for the material. However, despite this the majority of the collection has a square and height designation, or full 3D co-ordinates (Fig. 23).



Figure 19: Relative contexts of the DMQ fossil hominin material.

The majority of the DMQ hominin assemblage is represented by isolated dental elements, with notable exceptions including the nearly complete *P. robustus* crania, DNH 7 (Keyser, 2000; Moggi-Cecchi et al., 2010) and **Redacted**. This may relate to the greater survival of enamel in sediments that have undergone significant decalcification, as the greater survival of bone close to still-calcified breccia is clearly documented. DNH 7 and **Redacted** were notably recovered decalcifying out of solid breccia (Keyser et al., 2000; **Redacted**). However, it may also relate to the nature of deposition of the fossils at the site with fossils having been washed in down a vertical shaft (Keyser et al., 2000). DMQ thus conforms to the definition of a keyhole cave where the fossil accumulation will be partly filtered (see Herries et al., 2020; Chap 2 for further discussion). However, the occurrence of more complete crania and potential post-cranial elements may suggest a mixture of taphonomic factors occurring at the site or change through time as the morphology of the cave and cavern changes.

4.2 Descriptions

Dental descriptions and metrical data collection were performed following Wood (1991) and Moggi-Cecchi et al. (2010). It should be noted that the tooth identifications of certain specimens (DNH 90, 91, 93, 107, 128) described below differ from Leece (2016) as errors became clear through more detailed description. Further, the specimen described above as DNH 151 was previously referred to as DNH 77b by Leece (2016). The accession number of this specimen has been changed here as closer assessment indicated that association of this specimen by Moggi-Cecchi (*pers. coms.* 2016; see Leece, 2016, Appendix 2) with previously published DNH 77a (Moggi-Cecchi et al., 2010) was not likely. Differential states of wear between DNH 77a and DNH 151 do not support such an association.



Figure 20: DNH 27b, 27c, 85, 87, 88, & 151. (a-b) DNH 87, labial and lingual views; (c-e) DNH 27b, occlusal, buccal, and lingual views; (f-g) DNH 85, occlusal and distal views; (h-i) DNH 88, labial and lingual views; (j) DNH 151, lingual view; (k-m) DNH 27c, occlusal, buccal, and lingual views. Scale bar = 10mm.

DNH 27: (b) RP₄; (c) RM₁ (Fig. 24)

These two dental elements are being added to DNH 27 (LP_4 – relabelled as DNH 27a) published by Moggi-Cecchi et al (2010). DNH 27b is represented by a RM₁ and DNH 27c a RP₄.

RP_4

While differences in colour exist between DNH 27a and DNH 27b, overall morphology, wear, root morphology and number, and basic metrics suggest that these dental elements are antimerical. The molarisation of this tooth, as observed in the antimere DNH 27a, supports an attribution to *P. robustus*. Both the crown and the roots are well preserved aside from minor cracking through the enamel. The occlusal outline is almost square with a large talonid. On the buccal surface remnants of a deep distobuccal groove are evident. Enamel extensions are evident on the buccal and the lingual face. Detailed crown morphology is obscured by the moderately advanced state of wear seen on this element. The occlusal surface is worn flat with both the protoconid and the metaconid showing small dentine exposures. Dentine pits are also visible on the talonid. Mesial and distal interproximal contact facets (ICFs) are both present. Both ICFs are large and reach the occlusal surface, markedly reducing the original MD dimension. This premolar may have sat slightly out of alignment with the tooth row with the mesial ICF facing mesiolingually and the distal ICF facing distobuccaly. Both the mesial and distal roots are very long and thin and have two distinct canals, with the mesial root showing a slight distal leaning.

\mathbf{RM}_1

This element is well preserved aside from a fragment of the crown missing from the mesial face. While enamel extension is evident on the lingual face, moderate to heavy wear has obscured detailed morphological description. The occlusal surface is worn flat with dentine is exposed on all cusps. Advanced wear has resulted in a single large basin occupying the protocone, metaconid, hypoconid, and hypoconulid. Wear facets expose the thick occlusal enamel typical of *P. robustus.* The distal ICF is very large and occupies most of the face. The two mesial roots are thin with distal tilting at the apex. Although they are partially fused, two root canals are evident. The distal roots are completely fused, straight and the apex tilted distally.

79b: L_C (Fig. 24)

This specimen is being added to the previously published DNH 79 (R_c – relabelled as DNH 79a).

This unworn specimen is well preserved with one enamel flake missing from the lingual face along the cervical eminence. Overall morphology, root morphology, development stage, and basic metrics suggest that these dental elements are antimerical. Particularly, a clear hypoplastic line along the labial face matching that of DNH 79a supports these specimens as antimeres. As is true with DNH 79a, DNH 79b is unerupted and unworn. Light abrasion seen on the labial face would have occurred post-depositionally. The labial face is tall and convex both incisocervically and mesiodistally. The crown tip is centrally placed. The crown outline is asymmetrical with a shorter and less-steeply inclined mesial edge. The cervical eminence is moderately developed lingually and skewed distally relative to midline leading to a marked DMR. The MMR is faint and leads to an incipient stylid with a deep mesial furrow. The median lingual ridge is only lightly developed but presents a sharp crest forming a deep and V-shape cleft when combined with the DMR. The root is thick and oval in cross-section showing mesiodistal compression along the mesial face with a clear subvertical groove. This specimen compares moderately well with SK 27. This tooth is antimerical to DNH 79a attributed to *P. robustus* by Moggi-Cecchi et al. (2010) and morphological features such as the convexity near the cervical margin support this attribution. That said the presence of a distinct mesial stylid is reminiscent of A. africanus. As such a pattern was recognized by Martin et al. (in prep; Chap 3) regarding cranial traits of DMQ P. robustus specimens, such morphological features are not taken to contradict an attribution to P. robustus.

DNH 85: Molar fragment (Fig. 24)

This specimen preserves the distal face of the crown, a small portion of the distal occlusal surface, and a portion of the roots. The fragment is of a deciduous molar, likely a Ldm². The base of the roots is not preserved so no assessment of resorption can be made. The preserved portion of the hypocone is well developed and it has a wear facet on its cusp tip and the metacone is slightly worn. The fovea

posterior is deep. The DMR is low and thick with a centrally located incipient cuspule. The distal face shows a clear but slight oval-shaped ICF as well as small hypoplastic pits near the occlusal surface. The distobuccal root shows mesiodistal compression with a marked groove running down the mesial side. Although morphological traits reported here such as the deep and narrow fovea posterior and thick DMR support an attribution to *P. robustus*, the fragmentary nature of this specimen prevents confident attribution. It is instead reported in Table 3 as '*P. robustus*?' and has not been used in any subsequent analysis presented here.

DNH 86: RM₃ (Fig. 24)

This specimen is well preserved aside from the missing distolingual portion of the crown and the missing distal roots. Small enamel flakes are also missing from the mesiobuccal and the mesiolingual corners. The occlusal outline is ovoid, tapering distally. The occlusal surface is moderately worn, obscuring any detailed morphological description. The remnants of the central fovea and a distal groove perforating the MMR can be seen delineating the entoconid from all other main cusps. Small dentine exposures can be seen on both the protoconid and the hypoconid. It is possible a dentine exposure existed on the now-fractured metaconid. The mesial ICF is large and concave, occupying most of the mesial face. A deep mesiobuccal groove clearly delineates the protoconid and hypoconid. The mesial roots are long and thick with distal hooking in the lower third of the roots. Although fused, two mesial root canals are evident. Marked distal tapering and thick enamel visible at the fractured metaconid supports an attribution to *P. robustus*.

DNH 87: Ld_c (Fig. 24)

This specimen is well preserved deciduous tooth with light abrasion on the lingual side of the root. Both the labial crown outline and the cervical enamel line are slightly asymmetrical. On the lingual face, the cervical eminence presents weakly and is offset mesially. The MMR is thick and rounded while the DMR is thinner but still clearly present. Moderate wear has resulted in minor loss of crown height and a small dentine exposure apically. A wear facet is also visible on the mesial side of the occlusal edge. There is no mesial ICF while the distal ICF is large and reaches the occlusal edge. The root is conical in shape. Despite the open root apex, some

degree of resorption is visible on the labial face. This specimen compares well with DNH 44 attributed to *P. robustus* by Moggi-Cecchi et al. (2010).

DNH 88: Ldi1 (Fig. 24)

This is an isolated and well preserved deciduous tooth. The labial face is straight although only a portion is preserved as advanced wear has greatly reduced the crown height of this specimen. The outline of the lingual face is more triangular as well as asymmetrical, displaced distally in respect to the midline. A faint cervical eminence is present. A large rectangular dentine exposure can be seen on the incisal edge. The wear plane is tilted slightly labially but generally suggest an apical wear pattern. A large distal ICF is present. The mesial ICF has been lost through crown height reduction. The root is relatively thick and oval in cross-section showing only slight mesiodistal compression. Although no lower deciduous first incisors exist for the purposes of comparison aside from the damaged Taung di₁, the reduced nature of this tooth and the flat apical wear plane supports an attribution to *P. robustus*.



Figure 21: DNH 86, 89, & 90. (a-b) DNH 89, occlusal, buccal, and distal views; (d-e) DNH 86, occlusal, buccal, and lingual views; (g-h) DNH 90, labial and lingual views. Scale bar = 10mm.

DNH 89: Rdm¹ (Fig. 25)

This specimen is missing enamel from a large portion of the crown including over half of the mesial face, the entire mesiobuccal corner, the majority of the distal face, and a portion of the lingual face. Despite this, all four main cusps are evident although the relative size of the cusps cannot be assessed. A tapered, almost triangular, occlusal outline supports the attribution of this specimen to *P. robustus*. Due to moderate wear, some occlusal morphology has been obscured and the fovea anterior has been reduced to a shallow fissure. Dentine exposures are visible on all four cusps. The central fovea is wide and must have been deep to present as strongly as it does despite the moderate wear. Despite the wear, the crista oblique presents as a thick ridge of enamel. The fovea posterior is a long, deep, transverse fissure. On the buccal face, the distobuccal groove is faint but wide, ending gradually without a pit. There is no evidence of a Carabelli trait, however enamel loss obscures this identification. The roots are closed and diverge markedly. The buccal roots are relatively thick and mesiodistally compressed. A deep groove on the mesial face of both buccal roots suggests a double radicular canal. The lingual root is subtriangular in cross-section. All three roots show resorption.

DNH 90: L_C (Fig. 25)

Although referred to here as a lower canine, this specimen does not compare well to other lower canines from the DMQ (such as DNH 79aandb). This may be to a developmental anomaly. That said, this ambiguity prevents confident taxonomic attribution. Table 3 shows this specimen as '*P. robustus?*'. This specimen is well preserved crown aside from missing enamel apically. Despite this, it can be said that the labial crown outline is broadly symmetrical. The cervical enamel line is slightly asymmetrical, with the concavity located distally relative to midline. Hypoplastic bands can be seen on the upper portion of the labial face. The labial MMR and DMR are faint but grow more distinct apically. On the lingual face, the marked cervical eminence is skewed mesially, bearing an incipient cuspule. The lingual MMR and DMR are both thick and both present clefts located centrally. The median ridge is located mesially relative to the midline and projects sharply. A small mesial ICF is evident while no distal ICF can be seen. The root is thick and oval in

section with slight mesiodistal compression. On the labial face of the root tip, periradicular bands are clearly visible. Root formation is incomplete.

DNH 91: I² (Fig. 26)

This is an isolated and overall well preserved tooth. Although previously referred to as a lower canine (Leece, 2016), it is described here as an upper second incisor as the specimen compares well in overall shape to similar teeth within the Swartkrans *P. robustus* assemblage. That said, the ambiguous morphology observed on this specimen prevents confident taxonomic attribution. Table 3 shows this specimen as '*P. robustus*?'. The crown was broken in three pieces that have been glued back together. A tiny chip of enamel is missing on the cusp tip. A large but not marked mesial ICF is present. The distal ICF is an irregular oval, on the disto lingual edge. The labial outline is oval, with some mesioincisal extension. The labial face is tall, markedly convex both IC and MD. On the lingual face, the cervical eminence is weakly developed and placed slightly distal to the midline. The MMR is weakly expressed, whereas the DMR is more marked. The root is long and thick. It is subtriangular in section and MD compressed, with longitudinal grooves on the mesial and distal faces. Numerous periradicular bands are clearly visible. Root apex is still open.



Figure 22: DNH 91, 92, 93, 96a, 96b, 97, 98, & 99. (a-b) DNH 93, labial and lingual views; (c-e) DNH 92, occlusal, labial, and distal views; (f-g) DNH 91; labial and lingual views; (h-i) DNH 96a, occlusal and lingual views; (j-k) DNH 96b, occlusal and buccal views; (l-m) DNH 99, occlusal and buccal views; (n-p) DNH 97, occlusal, buccal, and lingual views; (q) DNH 98, labial view; (r-s) DNH 94, labial and lingual views. Scale bar = 10mm.

DNH 92: Indet. Premolar (Fig. 26)

This is an isolated specimen. Preservation is good, except for an area abraded near the cervical margin of the buccal face that affects the crown and the root. The root tip is broken. Attrition is minimal with a wear facet on the mesial edge of the buccal cusp. Two adjacent ICF of different size are evident on the buccal face: one smaller, facing mesially, the other larger, facing buccally. This condition suggests that the premolar was not correctly aligned in the tooth row. The occlusal outline is almost circular, with some buccal extension. The two main cusps are not clearly delineated. There is no fovea anterior. The central fovea is deep and broad. The talonid is large and bears three incipient cuspulids. Morphological details of the buccal face are obscured by wear. There is a single root, relatively long and very

thick. It is subtriangular in section and MD compressed, with longitudinal grooves on the mesial and distal faces. These suggest the presence of a double radicular canal.

The overall appearance suggests some kind of developmental alteration that affected crown morphology. MD and BL dimensions fall below the minimum for *P. robustus* and at the lower end of the South African *Homo* range. It cannot be determined whether, and to what extent, the developmental alteration also affected crown size. Taxonomic allocation is indet. Additionally, although previously referred so as a lower third premolar (Leece, 2016), it is described here as an unknown tooth position. Although this specimen likely represents a premolar, the degree of developmental alteration prevents confident identification.

DNH 93: LI¹ (Fig. 26)

This is a well preserved, isolated tooth although a large flake of enamel is missing from the incisal half of the lingual face and the incisal edge is not preserved. The labial outline is almost trapezoidal. The preserved portion of the labial face is slightly convex both MD and IC. The enamel line is almost straight. Perikimata as well as a large hypoplastic pit are evident on the labial face. On the lingual face, a weakly developed cervical eminence is visible with a groove on the distal side. Remnants of the mesial ICF are visible. The distal ICF is elongated and lingually displaced relative to midline. Damage to the crown precludes description of additional morphological details. The root is thick and subtriangular in cross-section showing mesiodistal compression. The crown outline and presence of a cervical eminence support an attribution to *P. robustus*. Additionally, this specimen compares well metrically to Swartkrans *P. robustus* upper first incisors.

DNH 94: Ldi¹ (Fig. 26)

This is an isolated and well preserved deciduous tooth. The crown is heavily worn, markedly reducing crown height. A large and concave area of dentine is exposed along the incisal edge. The labial face is convex MD and almost straight IC. The enamel line is almost straight. Hypoplastic pits are present centrally on the labial face. On the lingual face, the cervical eminence is marked and centrally located. A median eminence must have been present, as indicated by its sectioned profile at

the incisal margin. The mesial ICF is large and circular, occupying most of the mesial face and reaching the incisal margin. The distal ICF is large and concave. The root is thick, conical in shape and BL compressed with a lingual tilt apically. A longitudinal groove is present on the labial surface. The presence of a cervical eminence and strong comparison to SK 839/852 support an attribution to *P. robustus*.

DNH 96: L and Rdm¹ (Fig. 26)

This specimen comprises two isolated deciduous antimeres. The left tooth is very well-preserved, except for a tiny chip of enamel missing on the mesiolingual corner, near the cervical margin, and a minor crack crossing the lingual cusps. The right tooth has enamel missing from most of the mesial and distal faces, and also on the mesiolingual part on the occlusal surface of the protocone. The following description is drawn from the left tooth. The crown is worn, with small areas of dentine exposed on the mesial cusps and on the hypocone. The cusp tip of the metacone is rounded with no dentine exposure. The occlusal outline is almost square, with a marked mesiobuccal extension indicative of an attribution to P. robustus. All four main cusps are evident. The protocone is the largest, followed by the paracone and metacone of approximately similar size and then the hypocone. The fovea anterior is reduced to a fissure, bounded distally by an enamel ridge emanating from the tip of the paracone. There is a parastyle that merges with a thick MMR. The central fossa is small and deep, partly occupied by an enamel ridge connecting the paracone and the metacone. The crista obligua is present as a thick ridge of enamel. The fovea posterior is reduced to a shallow fissure by an enamel extension emanating from the hypocone. It is bounded by a worn and thick DMR. On the buccal face, a faint mesiobuccal groove delineates the parastyle. The distobuccal groove is faint, ending gradually. On the lingual face, the lingual groove is deep and terminates with no issue. No clear Carabelli trait is evident. The mesial ICF is circular in shape and buccally located relative to midline. The distal ICF is large and oval in shape, reaching the occlusal margin. It is located slightly lingually relative to midline. The MB root shows two radicular canals with a lingual curve at the tip. The DB root is straight and is oval in cross-section. The lingual root is conical in shape and widely divergent from the buccal roots. The DB and the lingual roots show resorption.

DNH 97: RM₃ (Fig. 26)

This is an isolated and overall well preserved tooth with enamel missing from most of the lingual face and the mesiolingual corner. The tooth is heavily worn. Dentine exposure on the protoconid, metaconid and hypoconid extend to create a single large basin. The remaining cusps are worn flat, with no dentine exposures. The occlusal outline is ovorectangular, with some distolingual extension supportive of an attribution to *P. robustus*. On the buccal face, a large hypoplastic area is evident in its central part. There is a large mesial ICF that encroaches the occlusal margin. The heavy wear precludes description of additional morphological details. The mesial roots are thick and tilted distally. Although fused, two radicular canals are evident. Similarly, the distal roots are fused, straight and distally oriented.

DNH 98: Rl¹ (Fig. 26)

This specimen is an isolated element with only a distal fragment of the crown preserved. On the crown fragment no morphological details can be described, aside from a distal ICF. The incisal edge is also damaged with very little preserved. The root has the tip broken and the labial face abraded. The preserved portion of the root is thick and subtriangular in cross-section. The fragmentary nature of this specimen prevents a confident taxonomic attribution.

DNH 99: RM¹ (Fig. 26)

This is an isolated, partial crown of a developing tooth. The mesiobuccal corner of the crown is missing, broken through the paracone. Additionally, enamel is missing from the mesial, lingual, and buccal faces just superior to the cervical margin. Only part of the distal face is preserved showing crown completion with no root formation. Occlusal outline appears to have been square, with the four cusps well delineated. This is supportive of an attribution to *Homo sp*. The remaining part of the fovea anterior is a short fissure, mesially placed to the paracone. The MMR is thick and well developed bearing two cuspules. The central fovea is large and deep. The crista oblique is thick and is intersected by the longitudinal fissure. The fovea posterior is a deep fissure with a trilobate shape, bounded distally by a low and not thick DMR. On the lingual face, the lingual groove is shallow, ending

gradually. There is no apparent Carabelli trait. No details of the buccal face can be described. This specimen compares well to Swartkrans *Homo* specimen SK 27.



Figure 23: DNH 100, 101, 102, 103, 104, & 105. (a-b) DNH 100, occlusal and buccal views; (c-d) DNH 102, lingual view of incisor, labial view of canine; (e) DNH 103, lingual view; (f-g) DNH 101, occlusal and buccal views; (h-i) DNH 104, occlusal and buccal views; (j-k) DNH 105, occlusal and internal fracture views.

DNH 100: LM₂ (Fig. 27)

This is an isolated and well preserved tooth bud. Crown formation is nearly complete with no root formation. Faint "pavement-cracking" is still visible on the lateral enamel faces. An enamel flake is missing on the central part of the lingual face near the cervical margin. The occlusal outline is ovorectangular with slight MD compression supportive of an attribution to *Homo sp*. The main cusps are well-developed with the metaconid being the largest followed by the protoconid and hypoconid of similar size. The cusps form a Y pattern. A well delineated C7 is present, reaching the longitudinal fissure. On the lingual face two shallow parallel furrows delimit the C7. The MMR is thick and low with incipient cuspulids present centrally. One of these cuspulids protrudes into the large and deep fovea anterior. A continuous distal trigonid crest is evident. The central fossa is broad and deep.

The distal fovea is small but deep, bounded by a thin and low DMR. On the buccal face the mesiobuccal groove is deep and broad, ending in a deep pit. A well developed protostylid is present. The distobuccal groove is deep and short, ending in a pit. This specimen compares well to DMQ *Homo* specimen DNH 67 in terms of cuspal anatomy despite the identification of DNH 67 as a lower first molar.

DNH 101: RM₂ (Fig. 27)

This specimen is represented by a developing crown. Crown formation is complete with few millimeters of root formed. Most of the disto-lingual portion of the tooth (the entoconid, the hypoconulid, and most of the hypoconid) is missing. The occlusal outline appears to have been rectangular. The main cusps are welldeveloped. The metaconid is the largest cusp although the relative size of the others is difficult to assess. The cusps form a Y pattern. On the metaconid, a faint groove delineates an incipient postmetaconid. The MMR is thick and low with a series of cuspulids and tiny pits. The base of the metaconid is separated at the lingual end of the MMR by a groove. The fovea anterior is reduced to a thin and deep fissure, bounded by a distal trigonid crest incised by the longitudinal fissure supportive of an attribution to *P. robustus*. The central fossa is broad and shallow, perforated by numerous grooves running from the longitudinal fissure. On the buccal face, both the mesiobuccal and the distobuccal groove are thin and deep. The mesiobuccal groove ends in a pit. The preserved portion of the lingual groove is faint. It should be noted that although this specimen is described as a lower second molar (and has been treated as such in subsequent analyses presented within this thesis) it is possible that it instead represents a lower third molar due to the marked distal tapering it exhibits.

DNH 102: (a) L_C; (b) Ll² (Fig. 27)

L_{C}

The crown of the Lc was still developing and shows immature enamel with "pavement-cracking". The crown outline is asymmetrical with the apex located distally relative to midline. The mesial edge is short and angled. The distal edge is much longer than the mesial edge and very steeply inclined. The labial face is markedly convex incisocervically and mesiodistally. The preserved portion of the

MMR is faint, whereas the remaining DMR is marked, giving rise to an incipient stylid with a broad furrow of the mesial side. The median lingual ridge is strongly developed, running distally from the cusp tip as a sharp crest.

 LI^2

The developing crown of the LI2 is only half formed, showing "pavement-cracking" on the cervical portion. The crown outline is asymmetrical, with the mesio-incisal corner being angulated while the distal corner is more rounded. The labial face is convex IC and MD. In lingual view, the incisal edge has several mamelons of different sizes. The MMR is very faint, whereas the DMR is thick but weakly expressed, ending in a tiny cuspule on the incisal edge. The lingual face is flat both MD and IC. Part of a faint median lingual ridge is also evident. This specimen compares moderately well with KNM-ER 808.

DNH 103: Indet. lower incisor (Fig. 27)

This specimen is represented by half crown of a developing lower incisor, possibly I_1 . Preservation is good on the remaining portion. The crown is short of completion. The labial face is tall and almost straight IC. Perikymata are clearly visible. On the lingual face a thick and low marginal ridge is evident. The preserved portion of the crown outline supports an attribution to *P. robustus*.

DNH 104: LM³ (Fig. 27)

This isolated tooth is broken just below the cervix with only the crown remaining. Preservation is good, except for a large flake of enamel missing from the cervical half of the mesial part of the lingual face. Wear has reduced the occlusal surface to an almost flat plane, with no dentine exposure. The occlusal outline is almost round in appearance due to a reduction of the distal cusps. This outline supports an attribution to *P. robustus*. The protocone is the largest cusp, followed by the paracone, hypocone and metacone. A deep central fossa is present also supporting an attribution to *P. robustus*. The crista obliqua is deeply incised. Although the crown is worn, a well developed C5 is still evident occupying the majority of the fovea posterior. A subvertical furrow on the mesiolingual corner of the crown suggests the presence of a Carabelli's trait. The mesial ICF is very large, flat and encroaches the occlusal margin.

DNH 105: Molar fragment (Fig. 27)

This is a fragment of the crown of a developing molar. The preserved surface shows no morphological details although enamel rods are clearly visible. The developmental stage and fragmentary nature of this specimen prevents a confident taxonomic attribution.



Figure 24: DNH 106. (a) third premolar, occlusal, mesial, and distal views; (b) second molar, occlusal, buccal, and lingual views; (c) first molar, occlusal, buccal, and lingual views; (d) maxillary fragment in breccia with articulated fourth premolar (occlusal view).

DNH 106: Isolated P_3 , P_4 in maxilla, isolated partial M_1 (mostly lingual cusps preserved, worn), and isolated M_2 crown. (Fig. 28)

LP^3

This element preserves only the crown as it has broken off the still-brecciated maxilla. The buccodistal enamel face is also missing. While both cusps are a similar size, the protocone is much taller than the paracone. The fovea anterior is a circular pit located buccally helping to delineate a distinct mesiostyle. A wide but shallow groove on the mesial portion of the buccal face also works to delineate the mesiostyle from the paracone. The central fovea is narrow but deep supporting an attribution to *P. robustus*. The fovea posterior is split into buccal and lingual sections by distally curving enamel extensions from both the protocone and

paracone. Despite fragmentation, a paramolar tubercle is also suggested distal to the paracone.

LP^4

This specimen is still articulated to the maxilla and so is greatly obscured by both preserved maxillary bone and adhering breccia matrix, limiting morphological description. As with the LP³, while both cusps are a similar size, the protocone is much taller than the paracone. The central fovea is large, joined with both the fovea anterior and the fovea posterior by a marked longitudinal groove. The DMR is thick, rising lingually to a paramolar tubercle.

LM^1

This specimen is highly fragmented. The crown has separated from the roots and preserved maxilla at the cervical margin and the paracone and a portion of the metacone are missing. The preserved protocone is moderately worn having lost nearly all crown height and the preserved hypocone shows heavy cusp polishing. The central fovea has been reduced to a faint and shallow basin by the advanced stage of wear. The fovea posterior appears deep and long, supporting an attribution to *P. robustus*, but is obscured by adhering breccia matrix. A lingual groove originating from the fovea posterior delineates the hypocone and terminates halfway down the lingual face. Only a small portion of the mesial ICF is preserved.

LM^2

This element is the best preserved of this specimen although it has detached from the roots and preserved maxilla. All four main cusps are well developed and multiple accessory cusps are present. The central fovea is deep but narrow, clearly delineating all present cusps. The fovea anterior is small but deep and positioned buccally. Two small but distinct mesiostyles are present on the MMR. A large epiconule of similar size to the main cusps is present mesiobuccally to the protocone, delineated by a deep mesiolingual groove terminating in a deep pit. A large plagioconule, also similar in size to the main cusps, is present centrally extending buccally from the protocone. Both the buccal and lingual grooves and wide and terminate just above the cervical margin. The fovea posterior is deep and large bounded by a poorly developed, low DMR. A small but distinct distostyle is present on the distal side of the metacone and a large postentoconule is present buccal to the fovea posterior.

Molarization of the two premolars, the occlusal outlines of the two molars, and the deep occlusal fovea present on both molars support an attribution to *P. robustus*.



Figure 25: DNH 107. (a-c) right lower dm2, occlusal, buccal, and lingual views; (d-e) right lower canine, labial and internal fragmented views; (f) indet. molar fragment; (g-h) left lower canine, labial and lingual views; (i-k) left lower dm1, occlusal, buccal, and lingual views; (l-n) right lower third premolar, occlusal, buccal, and lingual views; (o-p) right lower second incisor, labial and internal fragmented views; (q-s) right lower dm1, occlusal, buccal, and lingual views; ; (t-v) left lower third premolar, occlusal, buccal, and lingual views; (w-x) left lower second incisor, labial and lingual views; (y-z) lower first incisor, labial and internal fragmented views; (aa-cc) lower fourth premolar, occlusal and internal
fragmented views; (dd-ff) lower second molar, occlusal, buccal, and internal fragmented views; (gg-ii) right lower first molar; occlusal, buccal, and lingual views; (jj-ll) left lower dm2, occlusal, buccal, and lingual views. Scale bar = 10mm.

DNH 107: All isolated mandibular teeth. L and R dm1, L and R dm₂, RM₁ in mandibular fragment, L and R P₃, RP₄ (or upper molar), RM₂ (or M₃) L_C, R_C (half crown), RI₁, R and L I₂, labial face only. An indeterminate molar crown and root fragment are also present. (Fig. 29)

R and Ldm₁

The right element is missing the protoconid and the mesial root while the left element is missing the hypoconid and hypoconulid and a portion distal root. As such, the following description is composite from both antimeres. The specimens are heavily worn with a large dentine exposure occupying the hypoconid and hypoconulid, small dentine exposures on the protoconid and metaconid, and a tiny dentine exposure on the entoconid. A well developed mesioconulid also shows a very small dentine exposure. The central fossa is not pronounced although this is likely due to the advanced stage of wear. The buccal groove is faint but visible. The lingual groove is more distinct and runs to the cervical margin. The fovea anterior is short but deep. The MMR is cut by a well developed mesiconulid. A clear distal trigonid ridge bounds the fovea anterior on its distal side. The fovea posterior is obscured by the advanced stage of wear. The metaconid and entoconid are clearly delineated by a deep fovea. Both the mesial and distal ICFs are large and reach the occlusal surface. Both the mesial and the distal roots are fused but mesiodistal compression maked it clear that two idacular canals are present in both. Both roots show some resorption.

R and Ldm₂

Both elements are well preserved although the right element is missing portions of the entoconid and hypoconulid. The following description is drawn from the left element. This specimen is moderately worn with small dentine exposures visible on the protoconid, hypoconid, hypoconulid, and entoconid. The metaconid shows a fair degree of cusp polishing. A faintly developed metastylid (C7) is visible on the distal side of the metaconid delineated by a faint groove. The central fovea is deep and narrow supporting an attribution to *P. robustus*. The longitudinal groove is indistinguishable from the central fovea and is only stopped from joining with the fovea posterior by enamel extensions from both the entoconid and hypoconulid, nearly forming a postentocristid. The fovea posterior is a deep pit bounded by a thick DMR also supporting an attribution to *P. robustus*. The fovea anterior is narrow but deeply incised bounded by a thick MMR and a distal trigonid crest. The mesiobuccal groove is short and terminates abruptly in a deep pit. The distobuccal groove and the lingual groove are also short but do not terminate in a pit. The mesial ICF is large and reaches the occlusal surface. The distobuccal root is the only unbroken root on either antimere. This root shows some degree of resorption.

\mathbf{RI}_1

This specimen is well preserved and unerupted. The labial face is tall and straight comparing well to KB 5223/5383. Perikymata are clearly visible down the labial face. The lingual face shows only a weakly developed cervical eminence that is skewed slightly distally supporting an attribution to *P. robustus*. Both the MMR and the DMR are faint leaving a relatively straight and even lingual face. Three clear mamelons are visible along the incisal edge. The root is still incomplete and terminates 2.9mm from the cervical margin.

R and LI_2

Both antimeres are fractured mesiodistally with only the labial face preserving. These specimens are also unerupted although root development cannot be assessed due to fragmentation. Perikymata are clearly visible down the preserved labial face. Three faint mamelons are visible along the incisal edge.

R_C

This specimen is fractured labiolingually preserving only the mesial half of the crown. This specimen is unworn and root development is likely incomplete although fragmentation limits this assessment. There is no distinct MMR and the preserved portion of the lingual cervical eminence suggests a distal skew. The fragmentary nature of this specimen prevents further morphological description. It should be noted that Leece (2016) also referred to a left canine as an antimere to this tooth. This tooth has not been described here, however, as morphological

disparity indicates it is likely not antimerical. Although it is possible the tooth displays developmental abnormalities and does represent a left lower canine, it is more likely an upper second incisor (although association with this specimen is not confident).

R and LP_3

Both antimeres are well preserved although broken at the cervical margin preserving only the unworn crown. The following description is drawn from the left element. The protoconid is significantly larger than the metaconid. The fovea anterior is a deep pit bounded by a low by distinct MMR and a thin but high distal talonid ridge. The central fovea is joined with the fovea posterior by a wide and deep longitudinal groove forming a large, deep basin. The DMR is thick but low. A distinct buccal ridge that continues to the central fovea delineates the protoconid from a well developed talonid. A lingual extension of the central fovea delineates the metaconid from a well developed postmetaconulid. The molarization of these teeth is supportive of an attribution to *P. robustus*.

RP_4

This is a poorly preserved and fragmentary specimen. The mesial portion of the crown is missing. Crown formation is not yet complete and the specimen still exhibits "pavement cracking". The central fovea is deep and wide, occupying most of the preserved occlusal surface. The fovea posterior is deep and long bounded by a thick but long DMR and a thin postentocristid. Both distal cusps are well developed and clearly delineated from the preserved portions of the protoconid and metaconid. A shallow but wide groove runs down the buccal face terminating just short of the cervical margin.

$\mathbf{R}\mathbf{M}_1$

This is a well preserved specimen showing cusp polishing on all five major cusps. All five major cusps are well developed and similar in size. The central fossa is deep and narrow, supporting an attribution to *P. robustus*, clearly delineating all cusps. The fovea anterior is deep but small, bounded by a thick MMR and a weak distal talonid ridge. The fovea posterior is deep and of moderate size, bounded by a weak DMR that is perforated by a groove that continues down the distal face. A distinct postentocristid bounds the fovea posterior mesially. Both buccal grooves terminate halfway down the buccal face in pronounced pits. The lingual groove also terminates high but without a pit. A large enamel extension protrudes lingually from the hypoconid and occupies the central portion of the occlusal surface. Preserved mandibular bone obscures assessment of the lingual roots but the buccal roots are visible. Root development is incomplete.

RM_2

This element is poorly preserved with the entoconid and a portion of the hypoconulid missing. Crown development is incomplete with the specimen still exhibiting "pavement cracking". The central fovea is wide and indistinguishable from the longitudinal groove, clearly delineating the five main cusps. The fovea anterior is deep, bounded by a thick MMR and a distal talonid ridge. The mesiobuccal ridge is deep and well pronounced while the distobuccal ridge is faint.

Molar Fragment

A molar fragment is also associated with this specimen. It likely represents the upper M1 preserving what it potentially the mesial face. The fragmentary nature of this specimen precludes morphological description.



Figure 26: DNH 108. (a-b) right maxillary fragment with articulated upper canine and third premolar, occlusal and labial views; (c-d) upper first incisor, labial and lingual views; (e-g) left upper fourth premolar, occlusal, mesial, and distal views; (h-j) left upper third premolar, occlusal, mesial, and distal views; (k-m) left upper dm1, occlusal, mesial, distal views; (n-p) right upper fourth premolar, occlusal, mesial, and distal views; (q) right upper dm2, first molar, third premolar, and maxillary fragment in breccia; (r-t) left upper dm2, occlusal, mesial, and distal views; (u-v) left canine, labial and lingual views; (w-y) left upper first molar, occlusal, buccal, and mesial views. Scale bar = 10mm.

DNH 108: Right maxillary fragment with dm², M¹, M², R maxillary fragment with P³, ^c. Isolated teeth: Rdm¹, Ldm², RI¹, L^C, LP³, R and LP⁴, RP⁴, LP⁴, LM¹. (Fig. 30)

Ldm¹

This specimen is well preserved aside from a chip of enamel missing from the lingual side of the distal face and heavy wear leaving only the hypocone. The paracone, metacone and protocone are all obscured by one large dentine exposure, which has worn these three cusps down to the cervical margin. A small dentine exposure is also visible on the remaining hypocone. This advanced degree of wear greatly hinders morphological description. The distal ICF is large, occupying most of the distal face and contacting the occlusal surface. A faint and shallow ridge is present on the buccal face. The lingual root is greatly diverged from the buccal roots. All three roots show a degree of resorption.

R and Ldm²

The Ldm² is fragmentary with the distal half of the crown missing while the Rdm² is well preserved. On both specimens, the protocone is obscured by a large dentine exposure and a small dentine exposure is present on the paracone. The following crown description will be based in the right antimere. On the right element, a small dentine exposure is also visible on the hypocone. The fovea posterior is deep and short bounded by a thick DMR supporting an attribution to *P. robustus*. The central fovea is deep and extends buccally delineating the metacone from the paracone terminating halfway down the buccal face without a pit. The fovea anterior is faint and bounded by a thick MMR. A fracture runs through the lingual ridge obscuring any detailed morphological description. Both the mesial and distal ICFs are large with the former showing a distinct concavity. As the roots of the right antimere are obscured by breccia, detail here is drawn from the left antimere. The lingual root is greatly diverged from the buccal roots. Both lingual roots show compression internally. The mesiobuccal root is broken 5.6mm from the cervical margin.

L and RM¹

Both antimeres are well preserved but the right is obscured by breccia and the following description is drawn from the left. This specimen shows moderate wear with the protocone and hypocone greatly reduced in size and a fair degree of cusp polishing visible on the paracone and metacone. The central fossa is deep and large, supporting an attribution to *P. robustus*, and joins with both the anterior and fovea posterior. Deep and narrow foveae delineate the paracone from the metacone and the protocone from the hypocone. These foveae continue to

grooves on the buccal and lingual faces, both terminating halfway down the crown without pits. Short buccally oriented extensions are present from on the protocone and the hypocone terminating at the central fovea. A faint groove is present on the mesial side of the protocone delineating a moderately expressed epiconule. Faint hypoplastic pits are visible on the buccal face. The mesiobuccal root is missing and the lingual root is broken 9.3mm from the cervical margin.

$\mathbf{R}\mathbf{M}^2$

This element is obscured by both adhering breccia matrix and the remaining maxillary bone. The protocone is visible as is a weakly expressed hypocone. The distal portion of the metacone is also visible. The central fovea is shallow and wide, joining with the fovea posterior. The DMR is cut centrally by an accessory cuspule. The small hypocone is delineated by a groove running from the central fovea for the lingual face. Although obscured, root development appears incomplete.

R and LP⁴

Both antimeres are unworn and have broken at the cervical margin and do not preserve any roots. The left antimere is also missing the buccal half of the paracone and the following description is based on the right antimere. There is a well developed incipient cuspule on the distal side of the paracone delineated by a faint groove on the buccal face. The central fovea is deeply incised, supporting an attribution to *P. robustus*, and is joined with both the anterior and fovea posterior by a deep and narrow longitudinal groove. Both the MMR and DMR are large although the latter is higher than the former. An enamel extension protrudes distobuccaly from the protocone towards the fovea posterior.

R and LP³

Both antimeres are preserved but as the right element has a crack running mesiodistally through the paracone and is obscured by adhering breccia matrix and remaining maxillary bone, the following description is drawn from the left element. Both main cusps are well developed. The central fossa is deeply incised, supporting an attribution to *P. robustus*, and joins with the fovea anterior. The fovea posterior, although deep and large, is only separated from the central fossa by enamel extensions coming from both the protocone and paracone and nearly

joining. The MMR is extremely faint while the DMR is low but well developed. An incipient cuspule is present on the buccal side of the DMR. The lingual root is broken at the cervical margin. The buccal root is incomplete. The buccal root exhibits marked buccolingual compression with a clear groove running down its length.

R and L^C

Both antimeres are well preserved and unworn with a single crack running centrally through the crown. As the right element is obscured by adhering breccia and remaining maxillary bone, the following description is based on the left element. The labial crown outline is asymmetrical with the distal edge sloping more steeply than the mesial. A small but distinct ridge runs down the labial face just distal of midline. A clear hypoplastic line is visible on the lower 1/3 of the labial face. Both the DMR and the MMR are weakly developed. On the lingual face, the cervical eminence is small and located centrally. The presence of a cervical eminence supports an attribution to *P. robustus*.

RI^1

This element is well preserved with only the tip of the root missing. Heavy wear has left a large, rectangular dentine exposure occupying the majority of the incisal edge and greatly reducing crown height. In labial view, the incisal edge is dipped, creating a concave outline. Multiple hypoplastic lines are visible on the labial face. Only the lowest portion of the mesial ICF is preserved. On the lingual face, the faint cervical eminence is slightly mesial skewed. The presence of a cervical eminence supports an attribution to *P. robustus*. Neither the MMR nor the DMR are distinct leaving the lingual face with a slight concavity rather than with distinct bounding ridges. The root is broken 14.1mm from the cervical margin.



Figure 27: DNH 121, 122, 125, 126, 128, & 129. (a-c) DNH 121, occlusal, buccal, and lingual views; (d-f) DNH 125, occlusal, buccal, and lingual views; (g-i) DNH 122, occlusal, buccal, and lingual views; (j-l) DNH 126, occlusal, buccal, and internal fragmented views; (m-n) DNH 128, labial and lingual views; (o-q) DNH 129, occlusal, mesial, and distal views.

DNH 121: Ldm² (Fig. 31)

This is a fragmentary and heavily worn tooth preserving a small segment of the distobuccal root and the crown, excluding the mesial enamel. A large lingual dentine exposure occupies both the protocone and hypocone. This exposure flares buccally at its mesial extension and nearly joins a moderate dentine exposure on the paracone. Small dentine exposures are also present on the metacone and along the distal marginal ridge. The remaining occlusal surface is worn nearly flat.

Occlusal outline is square with a slight distal tapering as is traditionally observed in *P. robustus*. Although enamel cracking obscures the majority of crown morphology, a shallow fovea posterior is visible. The buccal groove is very faint although a clear fovea delineates the paracone and metacone. The distal interproximal contact facet is large and reaches the occlusal surface. It is not immediately clear whether the roots are broken near the cervical margin or if they have been almost completely resorbed to the point of tooth shedding.

DNH 122: LM₂ (Fig. 31)

This tooth preserves the crown, excluding a distal-lingual portion of the enamel between the entoconid and the hypoconid. The roots are also preserved excluding the extreme tips. Occlusal outline is rectangular with a slight mesiolingual extension and distinct distal tapering. Occlusal surface is worn mostly flat with a small dentine exposure on the protoconid. A small fovea anterior is visible distal to a thick mesial marginal ridge. The distal trigonid crest is broken by a small pit. Both the central fovea and the fovea posterior are pronounced despite advanced wear. The fovea posterior is intruded upon be enamel extensions originating from the hypoconid, entoconid, hypoconulid, and distal marginal ridge. The mesial interproximal contact facet is large, covering the majority of the mesial face and reaching the occlusal plane. Only a small portion of the distal interproximal contact facet is preserved, however it appears large and would likely have covered the majority of the distal face. A small enamel pit is visible on the buccal face between the hypoconid and the hypoconulid which may be a remnant of a high distobuccal groove. Another small pit is visible on the occlusal surface between the protoconid and the hypoconid and the buccal face shows multiple hypoplastic pits. The distal roots are fused completely to their point of breakage although mesiodistal compression suggests the presence of two distinct radicular canals. The mesial roots are fused for approximately ³/₄ of their length. The absolute size of this specimen as well as the relatively thick enamel seen along fractured surfaces support an attribution to *P. robustus* despite advanced wear obscuring occlusal morphology.

DNH 125: Ldm₁ (Fig. 31)

This is an isolated and well-preserved deciduous tooth. It is at crown completion and unerupted. The protoconid, metaconid, entoconid, and hypoconid are well developed while the hypoconulid is small yet distinct. A very small but clearly delineated distoconulid or C6 is evident. The occlusal outline is rectangular aside from a large, protuberant, mesioconulid. Indeed, the crown appears buccolingually compressed as is often observed within South African *Homo* specimens. The fovea anterior is deep, shifted slightly buccally, and bordered by a thin mesial marginal ridge rising to a large mesioconulid. This accessory cusp is delineated by faint grooves down both the buccal and mesial faces. The fovea posterior and the deep central fovea are joined by a deep longitudinal groove. The mesiobuccal groove is deep and extends down the buccal face to the cervical margin. The distobuccal groove is faint. A lingual groove is also evident down the lingual face. The mesial and distal roots are fused with marked mesiodistal compression. Both roots are in early stages of development and don't extend far from the cervical margin.

DNH 126: Maxillary molar fragment (Fig. 31)

This fragment only preserves part of the crown although it is possible this specimen represents an upper first molar. The metacone is almost completely preserved while only a small portion of the paracone and hypocone remain. Despite this specimen's fragmentary nature, a deep central fovea and a wide buccal groove are suggested. Further, thick enamel seen along the fracture plane indicates that this specimen should be attributed to *P. robustus*. The buccal and distal portions of the yet incomplete roots also preserve.

DNH 128: L^c (Fig. 31)

This is an isolated element with enamel missing from the mesial face and a fragment of the root missing on the distal side of the tip. Heavy apical wear has greatly reduced crown height and left a large dentine exposure covering the majority of the occlusal surface. The worn surface slopes linguo-distally. The mesial interproximal contact facet is not preserved while the distal interproximal contact facet is not preserved while the distal interproximal surface. Despite wear, an accessory ridge is evident mesial to the midline. The labial face preserves a well-developed distal ridge and the weak cervical eminence is skewed mesially. On the lingual face, the cervical eminence is pronounced and

markedly skewed mesially with a pronounced ridge on the distal edge. The root is long and tilted mesially with a groove along the distal face suggesting the possibility of a double radicular canal. The crown convexity below mid-crown is preserved and is consistent with *P. robustus* material.

DNH 129: RP₃ Fragment (Fig. 31)

The tooth is poorly preserved with only half the crown and a portion of the lingual root remaining. Wear is moderate with small dentine exposure on the metaconid. Mesial and distal interproximal contact facets both occupy their remaining faces and reach the occlusal surface. The lingual root is broken 4.8mm from the cervical margin. The mesiodistal metrics of this specimen as well as the relatively thick enamel visible on the broken surface support an attribution to *P. robustus*.



Figure 28: DNH 132, 133, 136, 138, 140, & 147. (a-c) DNH 132, occlusal, mesial, and distal views; (d-f) DNH 133, occlusal, mesial, and distal views; (g-i) DNH 136, occlusal, buccal, and lingual views; (j) DNH 143; (k-m) DNH 140, occlusal, buccal, and internal fragmented view; (n-o) DNH 138, labial and lingual views; (p-r) DNH 147, occlusal, buccal, and mesial views. Scale bar = 10mm.

DNH 132: Rdm² (Fig. 32)

This tooth is heavily fragmented, missing the entire distal face and most of the central crown, as well as large portions of all three roots and enamel along the entire mesial face and half of the buccal face. This tooth is heavily worn with dentine exposures on the paracone, metacone and hypocone. The protocone and hypocone are delineated by a deeply incised groove that continues down the superior portion of the lingual face. Due to the fragmentary nature of this tooth, much cuspal morphology has been lost. Despite the relatively large size of this specimen, the enamel is very thin supporting an attribution to *Homo*. The remaining roots are markedly splayed and display some signs of resorption.

DNH 133: RP⁴ (Fig. 32)

This well preserved tooth is approaching crown completion with minor pavement cracking and no root formation. The central fovea is deep with both buccal and lingual cusps large and pronounced. Both the mesial marginal ridge and the distal marginal ridge are distinct although not notably thick. In overall crown size, this tooth sits beyond the range previously seen at DMQ and instead falls within the range of Swartkrans *P. robustus*.

DNH 136: Rdm¹ (Fig. 32)

This isolated element is moderately well preserved with small cracks running through the protocone, paracone, and metacone. Only the bucco-distal root is preserved and is not yet at completion. Wear is minimal and only slight cusp polishing is evident. Neither the mesial or the distal interproximal contact facet is visible. The central fovea is deep and the buccal and lingual cusps are well delineated from one another. The occlusal outline is rhomboidal with a marked mesiobuccal extension. There is a strongly developed parastyle leading to a thick mesial marginal ridge. This parastyle is delineated by a short mesiobuccal ridge. A distobuccal groove is also evident. The lingual groove is long and deep. No Carabelli trait is evident. The posterior fovea is long and bounded by a moderately thick and high distal marginal ridge. Perikymata are clearly visible along the buccal face. The overall size of the crown and bulbous nature of the cusps as well as the deep and narrow nature of the cuspal furrows support an attribution to *P. robustus*.

DNH 138: L_C (Fig. 32)

This specimen is well-preserved with a small fragment of enamel missing at the occlusal edge of the labial face. Wear is heavy with a large amount of crown height loss and a large dentine exposure occupying the majority of the occlusal surface. Wear is angled lingually. Both the mesial and the distal interproximal contact facets are large with the superior portions absent due to wear. The root is long and straight exhibiting marked mesiodistal compression. Longitudinal grooves are present on both the mesial and distal faces. Some root resorption is evident. A marked hypoplastic line is visible on the labial surface just superior to a large cervical eminence. This specimen compares well metrically to DNH 7, supporting an attribution to *P. robustus*.

DNH 140: Molar Fragment (Fig. 32)

This molar fragment is heavily worn with dentine exposures suggested along the broken edges of the occlusal surface. The crown is broken at the cervical margin and no morphological details can be described. It is possible this specimen represents a lower molar with labial face preserved. Poor preservation prevents a confident taxonomic attribution beyond that of *Hominini indet*.

DNH 143: Enamel fragments (Fig. 32)

This specimen consists of five small enamel fragments. No morphological detail can be described. This specimen has been attributed to '*Cf. hominin?*' based on the thickness of the enamel flakes and its association with DNH 122.

DNH 147: RM³ (Fig. 32)

This specimen is poorly preserved with only one root and the buccal face remaining. A portion of the mesial interproximal contact facet is visible suggesting it was large and reached the occlusal surface. The preserved portion of the occlusal surface shows no morphology as the entire surface has been obscured by an extremely large dentine exposure. The preserved root is fused but mesiodistal compression suggests the presence of two radicular canals. The heavy wear on this specimen prevents confident taxonomic attribution.

DNH 151: R_C (Fig. 24)

This specimen was referred to as 'DNH 77b' by Leece (2016) however, differential wear stages prevent the association of this specimen with the previously published DNH 77a (Moggi-Cecchi et al., 2010). This specimen shows small amounts of damage: small enamel chips missing from the labial face, a single crack running from the tip of the root, up the labial face of the crown and across the occlusal surface, and a flake of cementum missing from the mesiolabial face of the root. This element also shows extreme wear. A large dentine exposure occupies the occlusal surface leaving only a thin edge of lateral enamel on the labial portion. Nearly all crown height has been lost but convexity at the cervical margin supports an attribution to *P. robustus*. The root is long and straight showing mesiodistal compression. Longitudinal grooves are present on both the mesial and distal faces. Lingual hooking can be seen at the root tip. The root also shows some degree of resorption.

DNH 152: LP⁴, LM¹, LM², RM¹, RM²; associated with the DNH 152 partial cranium (Fig. 9)

Left dental elements have fragmented out of the preserved cranium while right dental elements are still articulated. It should be noted that the fourth premolar described here has not been confidently attributed to the DNH 152 cranium and so is not referenced by Herries et al. (2020; Chap 2).

P4:

Only the left antimere is preserved. This element is lightly worn with the paracone showing cusp polish and the protocone showing a very small dentine exposure. The protocone is the largest followed by the paracone and the cusp apices are roughly parallel. Two accessory cusps are present on either side of the paracone. The mesiostyle is small while the paramolar tubercle is of a similar size to the paracone and may represent a true metacone having formed from the enamel dentine junction. The size of this cuspule adds a distal projection to the otherwise ovoid crown outline. These accessory cusps are delineated by mesial and distal buccal grooves as well as two buccal extension of the central fovea. The central fovea is deep and joins with the small but deep posterior fovea. A small, less well-delineated, accessory cusp is also present on the mesial side of the protocone.

The mesial marginal ridge is thick but low, interrupted only by the mesiobuccal accessory cusp. The distal marginal ridge is thick buccally but dips and nearly disappears lingually at the location of the posterior fovea. A thin, sharp ridge runs diagonally from the cervical margin to midway up the crown on the mesiobuccal surface, terminating just before the mesiobuccal accessory cusp. This ridge likely represents a developmental defect in the enamel and cannot be seen on the enamel dentine junction. Both the mesial and distal interproximal contact facets are located lingually suggesting a slight misalignment of this element in the tooth row. This would also contribute to lack of excessive wear as compared to other dental elements. Two roots are present although the buccal root is compressed and likely contains two radicular canals. Both roots show an enlarged band ~5.6mm from the cervical margin. Both roots are broken at the tip.

M1:

Though both left and right antimeres are persevered, the left element is described as disarticulation allows for better visibility. This element is moderately worn with a dentine exposure on the protocone and a small dentine exposure on the hypocone. The paracone and metacone are both worn flat. The occlusal outline is rhomboidal with a distinct mesiobuccal extension. The remnants of the central fovea suggest it was deep and narrow leading to a buccal groove terminating in a small pit halfway down the crown. A faint lingual groove is also preserved, terminating gradually halfway down the crown. The posterior fovea also appears to have been deep and narrow, bounded by a thick distal marginal ridge. The mesial interproximal contact facet is rectangular and offset towards the buccal side or the crown. The distal interproximal contact facet is large, centrally located, and occupies the majority of the distal crown face. Both buccal roots are broken ~6mm from the cervical margin. The lingual root is completely preserved with distinct lingual hooking at the tip. Buccal roots are preserved on the right antimere with the mesiobuccal root showing a distinct vertical groove and two radicular canals. The distobuccal root is broken apically.

M2:

This element is lightly worn with both mesial cusps worn almost flat. The occlusal outline is rhomboidal with a mesiobuccal extension and some distal tapering. The

protocone is the largest, followed by the paracone, then the metacone and hypocone of similar size. The central fovea is deep and moderately narrow, extending to a faint buccal groove which terminates gradually half way down the crown. The posterior fovea is also deep and narrow, extending to a faint lingual groove terminating similarly. The central and posterior foveae are delineated by a well-developed crista obligua that shows only faint remnants of a longitudinal groove. A faint, weakly developed, mesiostyle is visible buccally on the thick mesial marginal ridge. Both a hypostyle and a hypoconule are visible on the thick but short distal marginal ridge. Minor hypoplastic pitting can be seen on the distal and buccal faces of this element. The mesial interproximal contact facet is large, ovoid, and centrally placed. All three roots are broken. The lingual root preserves ~9mm and has a distinct vertical groove suggesting two radicular canals. The distobuccal root is broken ~12mm from the cervical margin. The mesiobuccal root is fused at the base and split before the breakage at ~12mm. The curvature of the two broken ends suggests this root was likely fused only near the cervical margin and became two separate roots further down.

DNH X: Description Redacted

4.3 Taxonomic attributions

Taxonomic attributions of all DMQ dental specimens described here, by Leece (2016), and by Moggi-Cecchi et al. (2010) are listed in Table 3. It must be noted that the attribution of DNH 90, 85, 92, 98, 125, and 129 as presented here contradicts the taxonomic attributions previously ascribed by Leece (2016). Further, a description of DNH 95 has not been included here despite previous preliminary description by Leece (2016) as this specimen has been determined to represent a non-hominin primate. Only specimens that have been confidently attributed to *P. robustus* in this chapter of by Moggi-Cecchi et al. (2010) and have been confidently assigned to a tooth position have been employed in subsequent analyses within this thesis. **Three sentences redacted.**

Catalogue Number	Element	Taxonomic Attribution
DNH 27	(b) LP4 (c) LM1	P. robustus
DNH 79	(b) Lc	P. robustus
DNH 85	Molar fragment	P. robustus?

DNH 86	LM3	P. robustus
DNH 87	Udc	P. robustus
DNH 88	Ldi1	P. robustus
DNH 89	Udm1	P. robustus
DNH 90	Uc	P. robustus?
DNH 91	UI2	P. robustus?
DNH 92	LP3	?
DNH 93	UI1	P. robustus
DNH 94	Udi1	P. robustus
DNH 96	U L and Rdm1	P. robustus
DNH 97	LM3	P. robustus
DNH 98	UI1	?
DNH 99	UM1	Ното
DNH 100	LM2	Ното
DNH 101	LM2	P. robustus
DNH 102	LI2 and Lc	Ното
DNH 103	I	P. robustus
DNH 104	UM3	P. robustus
DNH 105	Molar fragment	?
DNH 106	UP3, UP4, UM1, UM2	P. robustus
DNH 107	L L & R dm1, L L & R dm2, LM1, LM2, L L & R P3, LP4, L L & R C, LI1, L L& R I2, molar fragment	P. robustus
DNH 108	Udm1, U L & Rdm2, UI1, U L & R M1, UM2, U L & R P3, U L & R P3, U L & R P4 U L & R C,	P. robustus
DNH 121	Udm2	P. robustus
DNH 122	LM2	P. robustus
DNH 125	Ldm1	Ното
DNH 126	Molar fragment	P. robustus
DNH 128	UC	P. robustus
DNH 129	LP3	P. robustus
DNH 132	Udm2	Ното
DNH 133	UP4	P. robustus
DNH 136	Udm1	P. robustus
DNH 138	LC	P. robustus
DNH 140	Molar fragment	?
DNH 143	Enamel fragments	cf. hominin?
DNH 147	Indet. Molar	?
DNH 148	UM2	P. robustus
DNH 149	UI1	P. robustus
DNH 150	UM1	P. robustus
DNH 151		P. robustus
DNH 152		P. robustus
DNH X	Redacted	Redacted

4.4 Discussion

The descriptions presented here add an additional 31 specimens confidently attributed to P. robustus. These 44 specimens add 94 individual teeth to the DMQ assemblage. By comparison, only five additional specimens confidently attributed to *Homo sp.*, represented by six teeth, were added to the DMQ assemblage here. This continues the pattern of ~2 Ma assemblages containing a much higher frequency of *P. robustus* specimens as compared to *Homo*. This pattern was reported by Moggi-Cecchi et al. (2010) as well as noted by Brain (1993) regarding the Swartkrans assemblage. If the DMQ assemblage represents an accurate life assemblage, as proposed by Riga et al. (2019), as well as an assemblage with a short period of deposition, as proposed by Herries et al. (2020; Chap 2) and Malott (2015) the differential representation of P. robustus and Homo within the assemblage could be indicative of differential representation on the landscape at the time. That is, it is possible that this data suggests that *P. robustus* was more abundant on the landscape than Homo while the DMQ was forming. It is also possible that taphonomic or collection bias led *P. robustus* to be deposited in caves more frequently than Homo despite an equivalent or inverse number of individuals on the landscape. This explanation, however, seems unlikely as most deposits in eastern Africa also find Paranthropus specimens to be more numerous than Homo specimens despite vastly different depositional environments (Wood and Strait, 2004). Regardless of why the relative collection of these two taxa manifest as it does, the confident attribution of specimens to both Paranthropus and Homo works to confirm the contemporaneity of these taxa as proposed by Herries et al. (2020; Chap 2).

Herries et al. (2020; Chap 2) also presents DNH 134, a well preserved calotte most closely resembling *Homo erectus sensu latu*. Although a selection of South African specimens deriving from roughly the same time period have previously been attributed to *H. erectus sensu latu* (SK 847; *H. ergaster*: Clarke, 1977; Tobias, 1991; *H. habilis*: Leakey et al., 1964; Clarke and Howell, 1972; *H gautengensis*: Curnoe, 2010; StW 53: *H. habilis*: Clarke, 1985; Kimbel et al., 1997; Curnoe and Tobias, 2006; *H. gautengensis*: Curnoe, 2010), these attributions have not been

accepted uncritically. Indeed, the attribution 'South African early *Homo*' is sometimes treated nearly as a taxon itself insofar as it is used to refer to specimens as a single OTU. Debate surrounding the species attribution of these specimens is ongoing with some researchers asserting the identification of specimens belonging to *H. habilis, H. ergaster, Homo gautengensis,* or *Homo sp. nov.* (see for example Grine, 2005; Curnoe, 2006; Curnoe and Tobias, 2006; Grine et al., 2009). Moggi-Cecchi et al. (2010) asserted that there was little resemblance between the DMQ *Homo* specimens and species deriving from eastern Africa. Moggi-Cecchi et al. (2010, pp. 404) cited few similarities across tooth class saying, for example, "the M₁ sample shows similarities with *H. habilis* specimens from East African, but the differences with *H. ergaster* specimens are more marked."

The discovery of the new DNH 134 calvaria, however, which shows clear morphological similarities with *H. erectus sensu latu*, necessitates a reassessment of the DMQ *Homo* dental material. It is possible that two distinct *Homo* taxa are present within the DMQ assemblage. Such a hypothesis has been put forward by Schwartz and Tattersall (2003) as an explanation for variability within the *Homo* sample deriving from Swartkrans. It seems unlikely, however, that all *Homo* dental remains represent one species and the cranium another. It seems more likely that researchers do not yet understand the dental morphology of an early, ~2 Ma, *H. erectus* and many specimens currently attributed to 'South African early *Homo*' in fact belong to this group. Further study of dental specimens attributed to *Homo* at the DMQ will work towards answering such a question.

Variability between *P. robustus* samples is also explained in various ways, as discussed in Chapter 1. The additional 94 teeth, represented by 44 specimens, described here increases the DMQ *P. robustus* dental sample to 81 specimens and 223 teeth. Such an increase in sample size, particularly deriving from a well dated and temporally constrained sample, allows for further investigation into the question of *P. robustus* variability. Subsequent chapters presented within this thesis will employ this larger sample size in various analyses with the aim of assessing *P. robustus* variability. The possibility of intraspecific variability, manifesting as extreme sexual dimorphism (Lockwood et al., 2007; Moggi-Cecchi et al., 2010), taxonomic variability, either at the genus level (Broom and Robinson,

1952; Robinson, 1954), the species level (e.g. Grine, 1985), or at the sub-species level (e.g. Martin et al., *in prep*; Chap 3), or temporal variability (e.g. Herries et al., 2020; Chap 2; Martin et al., *in prep*; Chap 3) will be assessed.

5. Quantitative assessment of permanent tooth size

As the DMQ and Swartkrans Member 1 assemblages make up the majority of the Paranthropus robustus fossil record and consist largely of isolated teeth, Moggi-Cecchi et al. (2010) performed a statistical comparison of the mesiodistal and buccolingual measurements of the permanent teeth of these two samples. Three principal conclusions were drawn from that analysis: (1) the sample from DMQ represents two species, P. robustus and an "undetermined species of the genus Homo"; (2) P. robustus specimens from DMQ are generally smaller than specimens from Swartkrans while overlapping with the lower size range from the latter site; and (3) this size difference is representative of a "highly [sexually] dimorphic species," manifesting across the two sites as the result of depositional and site-use differences (Moggi-Cecchi et al., 2010 p.404). Since that analysis, a further 47 dental specimens have been recovered (see Chapters 2 [Herries et al., 2020], 3 [Martin et al., in prep], and 4; Leece, 2016, Appendix 2). Of these new specimens, 34 have been assigned to P. robustus and can be used to test the conclusion drawn in Moggi-Cecchi et al. (2010) regarding size disparities in the permanent teeth between DMQ and Swartkrans P. robustus. Further, both Lockwood et al. (2007) and Pickering et al. (2016) conclude that the degree of dimorphism between the DMQ and Swartkrans samples, both metrically and nonmetrically, is equal to or greater than that seen even in a highly dimorphic primate such as gorilla. Sentence redacted. Similarly, the conclusions regarding the highly dimorphic nature of *P. robustus* based on dental evidence drawn by Moggi-Cecchi et al. (2010) should be reassessed given the recovery of ~50 new dental specimens. The analyses presented in this chapter aim to address the hypothesis that dental size differences between DMQ and Swartkrans Member 1 P. robustus material represents sexual dimorphism within a single species (Keyser, 2000; Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016).

5.1 Materials and Methods

Analyses in this study include both descriptive and inferential statistics, as well as a series of bivariate and box plots to visualize differences between fossil assemblages. The DMQ *P. robustus* sample consists of specimens published by Moggi-Cecchi et al. (2010), specimens initially described in Leece (2016, Appendix 2), as well as new specimens described here (Chap 2 [Herries et al., 2020], Chap 3 [Martin et al., *in prep*], and Chap 4). The Swartkrans *P. robustus* sample consists of published material deriving from Member 1 deposits (Robinson, 1956; Grine, 1989; Wood, 1991; Pickering et al., 2016). The Swartkrans sample is limited to material derived from Member 1 to ensure that it is temporally constrained. Due to the small sample of dental elements available from Kromdraai B (Wood, 1991; Braga et al., 2016), comparisons with this assemblage will be limited. Basic metrical data (mesiodistal and buccolingual dimensions) were taken following the protocols of Wood (1991).

5.1.2 Descriptive Statistics

Descriptive statistics are provided following the methodology in Moggi-Cecchi et al. (2010). For all elements where $n \le 5$ but > 1, an adjusted Coefficient of Variation (CV*) was calculated following Sokal and Braumann (1980).

5.1.3 Bivariate and Box Plots

Comparisons of the *P. robustus* samples from DMQ, Swartkrans Member 1, and Kromdraai B have been visualised through bivariate scatterplots and box plots. As there are no canines or incisors present at Kromdraai B, bivariate and box plot comparisons of specimens from this locality were limited to the postcanine dentition.

5.1.4 Mann-Whitney U tests

Given that sample sizes for each tooth class rarely exceed 10, nonparametric Mann-Whitney U-tests were performed with the *p*-value set at p < 0.05. These analyses were conducted using IBM SPSS Statistics version 25. As the hominin dental sample from Kromdraai B is markedly small, specimens from this locality have not been included in the statistical analysis conducted here. Given the small number of incisors within the Swartkrans Member 1 and DMQ assemblages, statistical comparisons were limited to the permanent canine and postcanine teeth. The goal of this analysis was to evaluate the hypotheses that (1) metric differences in the dentitions between DMQ and Swartkrans Member 1 are the result of sexual dimorphism between sites, or (2) metric differences in the dentitions between DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween DMQ and Swartkrans Member 1 are the result of setween Sites, or (2) metric differences in the dentitions between Sites, or (3) metric differences in the dentitions between Sites, or (3) metric differences in the dentitions between Sites, or (3) metric differences in the dentitions between Sites, or (3) metric differences in the dentitions between Sites, or (4) metric differences in the

as suggested by analyses of craniofacial morphology (see Chapter 3). The statistical null hypothesis is that the DMQ and Swartkrans Member 1 assemblages do not differ significantly in any aspect of postcanine tooth size thus suggesting that the two samples are not demographically separated and instead represent a single homogenous taxon. Analyses yielding *p*-values below 0.05 would provide support for refuting this hypothesis and thus suggest a low likelihood that the DMQ assemblage means could be chosen at random from the Swartkrans Member 1 assemblage thus suggesting the two samples may be differentiated either taxonomically or by sex.

5.1.5 Inhibitory Cascade Model

Recently, an evolutionary-developmental model, termed the Inhibitory Cascade (IC) model, was discovered and relies on the presence of an activator-inhibitor network of molecular signalling molecules to determine the size and timing of sequentially developing tissues (Kavanagh et al., 2007). In particular, it is the balance of these activators (a) and inhibitors (i) that regulates the initiation and growth of sequentially-forming molars in mammals (Jernvall and Thesleff, 2000; Kavanaugh et al., 2007). As teeth develop within their bony crypts, the ratio a/i in dental epithelial cells creates an 'inhibitory gradient' that influences the size of subsequently developing teeth (Kavanagh et al., 2007). As a result, a simple mathematical correlate of the IC model is that the size of any molar in a tooth row should equal the average of the two molars on either side of it; this then implies a predictable pattern of sequential molar size variation. Variable degrees of support exist for the extension of the IC model (e.g., Kavanagh et al., 2007; Schroer and Wood, 2015; Evans et al., 2016), originally demonstrated in a mouse model, to explain patterns of molar size sequence variation across mammals, while other recent studies caution that the IC model in its current construction may not adequately model molar size variation (Hlusko et al., 2016; Roseman and Delezene, 2019)

Mammalian dental development is a complex spatiotemporal process. At its simplest, most mammals develop and erupt a set of deciduous teeth (incisors, canine, and molars) which is then replaced by a set of replacement teeth (the

permanent incisors, permanent canines, and permanent premolars) as well as a set of permanent molars. The permanent molars arise, in sequence, as a distal extension off of the dental lamina that gave rise to the deciduous molars (Schroeder, 1991). The permanent premolars, on the other hand, arise as secondary extensions off of the developing buds of the deciduous molars. As such, it was reasoned that any inhibitory effect on permanent molar development should come from the deciduous molars rather than from the permanent premolars (Evans et al., 2016). Recently, a study evaluated how well this simple developmental program fits patterns of molar size variation across hominin taxa, especially australopiths, as well as across early members of the genus Homo (Evans et al., 2016). Generally speaking, within the fossil hominin record, two broadly different molar size sequence patterns exist, with the australopiths exhibiting the size gradient dm1<dm2<M1<M2<M3 (where the permanent third molar represents the largest tooth) and with species of the genus Homo exhibiting predominantly a dm1<dm2<M1≈M2>M3 gradient (with the first or second permanent molar representing the largest tooth; Osborn, 1978; Wood and Collard, 1999; Evans et al., 2016). When viewed through the lens of the IC model, it is clear that these two distinct patterns of molar size variation are in fact two developmental consequences of the same underlying developmental program. In particular, the manner in which the IC model 'plays out' across the postcanine dentition is a direct function of overall M1 size: hominin species with much larger dm1s results in relatively increased activation, producing larger M1s, which in turn results in a size sequence pattern of ever-increasing tooth size towards the M3, or in other words, the australopith-like pattern. Conversely, the smaller deciduous molars in Homo results in an overall smaller permanent M1, which in turn results in the pattern of permanent molar sizes reducing, not increasing, towards M3 (Evans et al., 2016). These clear and consistent pattern differences between australopiths, on one hand, and members of the genus Homo on the other, allow for dm1-M3 tooth size to be predicted fairly confidently given information on the size of other dental elements within an individual, or on average for the species (Evans et al., 2016).

The hominin material from DMQ has been confidently attributed to *P. robustus*, but it possesses among the smallest molar size values for any robust australopith (Fig. 35). As such, it is useful to query whether the IC model fits this dentally small robust

australopith in the same manner that it fits all other australopiths. Therefore, the IC model will be applied here to the DMQ material. As Evans et al. (2016) focused solely on the application of the model to hominin mandibular teeth, it is these specimens that will be analysed here. Given the 'close fit' with which both australopiths and *Homo* follow predictions of the IC model, Evans et al. (2016, pp. 478) argued that a "tight association between tooth proportions and [adult mandibular] m1 size existed at the base of the hominin clade." Given that the DMQ sample has been assigned to *P. robustus*, patterns of metameric size variation in the sample should fit the australopith pattern more closely than it does the Homo pattern. Thus, prediction errors derived from the prediction formulae of Evans et al. (2016) should returning similar error rates to that of the *P. robustus* sample employed by Evans et al. (2016). Six DMQ specimens (DNH 7, DNH 8, DNH 19, DNH 44, DNH 60, and DNH 107) were included, all of which preserved at least three molar teeth. Crown area (mesiodistal length x buccolingual length) is employed here as in Evans et al. (2016). It should be noted that DMQ specimen DNH 7, DNH 8, DNH 19, DNH 44, and DNH 60 were included in the Evans et al. (2016) analysis and so errors found here will also be compared to that of P. boisei and A. africanus as well as the total error for Australopithecus as presented by Evans et al. (2016). DNH 8 and SK 6 were shown to differ somewhat in, the pattern of metameric tooth size variation by Evans et al. (2016). While both specimens exhibit a size reversal at M2, resulting in the very non-australopith pattern of M3 being smaller than M2, the degree and direction of this change is dissimilar (see Evans et al., 2016, Extended Data Fig. 2). For this reason, it is hypothesised here that the other five DMQ specimens will follow the same pattern as DNH 8. That is, the DMQ material should adhere to how most australopith taxa adhere to the inhibitory cascade model, exhibiting a pattern of M1<M2<M3 with a prediction error not significantly greater than that of P. boisei or A. africanus. Further, if the DMQ and Swartkrans *P. robustus* assemblages represent a single homogeneous taxon, the DMQ pattern should closely match that of Swartkrans. Dental metrics for DNH 7 and DNH 8 were taken from Keyser (2000), while metrics for DNH 19, DNH 44, and DNH 60 were taken from Moggi-Cecchi et al. (2010). Measurements for DNH 107, on the other hand, were taken by the author. The second molar of DNH 44 was not included as a metric assessment would have required advanced digital manipulation, including image segmentation. Resultant tooth areas were then

entered into the mandibular IC model published by Evans et al. (2016). An error between the predicted tooth size and the 'actual' tooth size was then calculated.

5.2 Results

Crown measurements of the new DMQ dental specimens are presented in Table 4, and descriptive statistics for the entire sample are presented in Tables 5 and 6.

Accession No	Element	MD	BL
DNH 27 (b)	LP4	9.8	12.6
DNH 79b	LC	7.4	8.4
DNH 86	LM3	17.2	14.2
DNH 87	Udc	6.3	5.2
DNH 88	Ldi1	3.8	3.5
DNH 89	Udm1	8.8	9.3
DNH 90	UC	8.6	8.1
DNH 91	LC	7.2	7.5
DNH 93	UI1	8.8	7.1
DNH 94	Udi1	6.3	4.2
DNH 96	Udm1	8.7	8.9
DNH 101	LM2	15.3	13.6
DNH 104	UM3	14	15.5
DNH 106	UM1	13.1	12.1
	UM2	15.3	13.7
	UP3	8.9	11.8
	UP4	10.0	15.4
DNH 107	LM1	15.0	13.7
	LM2	15.6	14.5
	LP3	10.0	13.6
	LC	8.1	9.4
	LI1	5.0	5.8
	LI2	5.9	-
	Ldm1	10.2	8.8
	Ldm2	12.6	11.3
DNH 108	Udm1	8.4	9.5
	Udm2	10.5	11.8
	UI1	8.7	6.2
	UM1	14.3	12.5
	UP3	8.8	12.5
	UP4	10.0	14.1
	UC	8.2	7.3

DNH 121	Ldm2	11.3	10.5
DNH 122	LM2	15.6	14.8
DNH 133	UP4	10.7	15.7
DNH 138	LC	6.2	7.5
DNH 148	UM1	13.1	15.2
DNH 149	UI1	7.6	7.3
DNH 150	UM1	12.6	13.4
DNH 152	UM1	12.0	14.8
	UM2	13.6	16.4
	UP4	11.3	15.3
DNH X	Redacted		

Table 4: Mesiodistal (MD) and buccolingual (BL) measurements of new DMQ dental specimens described in Chapter 4. Measurements in mm. "L" is lower; "U" is upper; deciduous teeth are indicated with lowercase letters.

	MD								DI						
	MD								BL						
	Mean	n	Std. Dev.	Min	Max	CV	CV*		Mean	n	Std. Dev.	Min	Max	CV	CV*
Maxillary								Maxillary							
I1	8.23	8	0.56	7.30	8.80	6.81		I1	6.90	6	0.56	6.20	7.70	8.11	
I2	5.70	4	0.54	5.00	6.30	9.46	10.46	I2	6.20	4	0.81	5.40	7.00	13.04	14.04
С	8.40	8	0.81	7.20	9.90	9.65		С	8.90	8	0.92	7.30	9.90	10.41	
P3	9.10	7	0.30	8.80	9.70	3.32		P3	12.70	7	0.59	11.80	13.40	4.69	
P4	10.20	9	0.53	9.50	11.30	5.27		P4	14.40	9	0.83	13.50	15.70	5.72	
M1	12.90	12	0.74	12.00	14.30	5.74		M1	13.90	12	1.01	12.10	15.20	7.28	
M2	13.50	8	1.17	11.90	15.30	8.64		M2	14.70	8	0.97	13.70	16.40	6.61	
M3	13.50	8	0.78	12.20	14.30	5.79		M3	15.20	8	0.78	14.20	16.30	5.10	
Mandibular								Mandibular							
I1	4.80	2	0.28	4.60	5.00	5.89	3.95	I1	6.00	2	0.21	5.80	6.10	3.57	2.78
I2	5.70	3	0.17	5.60	5.90	3.04	3.28	I2	6.20	2	0.42	5.90	6.50	6.84	4.42
С	7.40	7	0.64	6.20	8.10	8.68		С	8.20	7	0.71	7.20	9.40	8.62	
P3	10.00	6	0.64	8.90	10.90	6.42		P3	12.80	6	1.01	11.30	14.20	7.83	
P4	11.00	6	0.90	9.80	12.30	8.22		P4	12.80	6	0.59	11.90	13.60	4.63	
M1	14.10	8	1.11	12.2	15.70	7.85		M1	12.90	8	1.34	10.30	14.50	10.38	
M2	15.80	10	0.82	14.5	17.20	5.19		M2	14.30	10	0.67	15.20	14.30	4.72	
M3	16.50	9	1.35	14.3	18.80	8.14		M3	14.40	9	0.86	13.40	15.70	5.95	

Table 5: Summary of descriptive statistics (permanent). Measurements in mm.

	MD								BL						
-	Mean	п	Std. Dev.	Min	Max	CV	CV*	-	Mean	п	Std. Dev.	Min	Max	CV	CV*
Maxillary								Maxillary							
di1	6.15	2	0.21	6.00	6.30	3.45	2.72	di1	4.20	1		4.20	4.20	0.00	
di2	4.65	2	0.35	4.40	4.90	7.60	4.80	di2	3.70	1		3.70	3.70	0.00	
dc	6.30	2	0.07	6.20	6.30	1.13	1.57	dc	5.60	2	0.57	5.20	6.00	10.10	6.05
dm1	9.15	6	0.82	8.40	10.50	8.93		dm1	9.38	6	0.39	8.90	9.80	4.12	
dm2	11.25	4	0.58	10.50	11.80	5.16		dm2	11.62	5	0.80	10.50	12.70	6.92	
Mandibular								Mandibular							
di1	3.80	1		3.80	3.80	0.00		dil	3.50	1		3.50	3.50	0.00	
di2		0						di2		0					
dc	4.40	2	0.64	3.90	4.80	14.63	8.31	dc	4.90	2	0.00	4.90	4.90	0.00	1.00
dm1	10.25	4	0.61	9.40	10.70	5.99	6.99	dm1	8.50	4	0.54	7.70	8.80	6.30	7.30
dm2	12.19	8	0.72	11.30	13.20	5.94		dm2	10.49	8	0.50	9.90	11.30	4.77	

Table 6: Summary of descriptive statistics (deciduous). All measurements in mm.

5.2.1 Anterior dentition

No incisors are present within the Kromdraai assemblage limiting the analysis of incisors to the DMQ and Swartkrans Member 1 assemblages. Bivariate scatterplots and box plots show no clear size differences are present between the two assemblages, aside from a tendency for there being a different scaling relationship of length and width in the DMQ sample. Further interpretation of this data is limited by sample size.













Figure 29: Box plots of P. robustus *dentition. (MD = mesiodistal; BL = buccolingual).*














Figure 30: Bivariate plots of P. robustus *dentition. (MD = mesiodistal; BL = buccolingual).*

Both upper and lower canines were included in Mann-Whitney U-tests as well as in the bivariate plots (Fig. 34). A high *p*-value indicates a fair degree of metric overlap (Table 7). The bivariate plots, however, show that the canines are the only elements where the mean size is larger within the DMQ assemblage in at least one dimension. The box plots also show a large degree of overlap between the DMQ and Swartkrans Member 1 canine sample with the DMQ mean size slightly but consistently larger.

		MD <i>p</i> -value	BL <i>p-value</i>	DMQ n	Swartkrans <i>n</i>
Maxillary		•	•		
	С	0.826	0.608	8	21
	P3	0.002	0.000	7	19
	P4	0.050	0.027	9	25
	M1	0.111	0.047	11	19
	M2	0.300	0.002	8	19
	M3	0.004	0.001	8	21
Mandibular					
	С	0.682	0.220	7	11
	P3	0.930	0.028	6	13
	P4	0.972	0.806	6	17
	M1	0.051	0.212	8	20
	M2	0.027	0.091	10	17
	M3	0.140	0.571	9	19

Table 7: Results of Mann-Whitney U test of the Swartkrans P. robustus *versus the DMQ* P. robustus *samples. Significant p-values indicated in bold and italics.*

5.2.2 Premolars

All premolar elements were included in Mann-Whitney U-tests as well as in the bivariate plots. The two analyses yield different results. In the bivariate plot, the upper P4 of DMQ overlap almost entirely with the Swartkrans Member 1 assemblage, despite showing a high degree of separation between the sample means (Fig. 34). Mann-Whitney U-tests suggest significant differences in both mesiodistal and buccolingual dimensions (Table 7). Indeed, the same pattern is evident in the upper P3, with significant differences between the DMQ and Swartkrans Member 1 assemblages being present in both dimensions (p < 0.005 for both MD length and BL width; Table 7). Interestingly, the DMQ upper P3 distributions overlap only slightly with only the smallest Swartkrans Member 1

specimens (Fig. 34). The box plots show a similar pattern with only the tails of the Swartkrans Member 1 sample overlapping with the DMQ sample (Fig. 33).

The DMQ lower P3s clearly represent the largest specimens as shown in the bivariate plots (Fig. 34). Mann-Whitney U-test results also show a significant size difference in the buccal dimension of the DMQ and Swartkrans Member 1 *P. robustus* lower P3s (Table 7). The box plots show a tightly grouped MD measurement with very few differences across the samples while the BL measurement shows distinct differences, again suggesting variation in gross shape rather than raw size (Fig. 33). No significant difference is reported in the lower P4s and the bivariate and box plots shows a high degree of overlap with similar means between the samples (Fig. 33 and 34; Table 7).

5.2.3 Molars

All molar elements were included in Mann-Whitney U-tests as well as in the bivariate plots. Although the DMQ P. robustus assemblage contains the smallest molar, there is not a clear pattern of systematic differences of DMQ molars from the Swartkrans Member 1 material. Despite that, differences in sample means and degree of variation is clear in the box plots (Fig. 33). Both upper and lower M1s and M2s show a high degree of overlap (Fig. 34). Despite this overlap, however, the upper M1s and M2s both show statistically significant difference between the two assemblages in the buccolingual dimension while the lower M2s show significant differences in the mesiodistal dimension, with the DMQ molars being smaller in both cases (Fig. 34; Table 7). The lower M1 analysis does not reveal any statistical differences between assemblages (p = 0.051) however as the treatment of p < 0.05 as a significance threshold is an arbitrary determination, this result will be treated as statistically significant, as discussed by Wasserstein, Schirm, and Lazar (2019). Overlap in the lower M3 is complete to the point that both the largest and smallest individual is represented by M3s from the DMQ P. robustus assemblage and Mann-Witney U-tests resulted in no significant difference (Fig. 34; Table 7). Conversely, overlap within the upper M3s is minimal and significant differences were found in both the buccolingual and mesiodistal dimensions, with the DMQ M3s being significantly smaller (Fig. 33 and 34; Table 7).

5.2.4 Inhibitory cascade

Figure 35 shows the mean sizes of the DMQ dentition from the deciduous molars towards M3. The pattern for the DMQ sample does not differ markedly from the general australopith pattern, wherein all australopith taxa display the M1<M2<M3 pattern albeit to different degrees. In terms of absolute size, dental size in the DMQ sample is more similar to that of *A. africanus* than *P. boisei*, with the exception of dm2 and M3, as both the second deciduous molars and the third permanent molars are slightly larger in the DMQ sample than in the *A. africanus* sample. Conversely, the mean tooth area of the DMQ assemblage overlaps with the other *P. robustus* only at the dm1 position.



Figure 31: Mean sizes of dentition from the deciduous molars towards M3.

When the predictive algorithm was applied to the DMQ sample using the australopith model, a maximum error of 33.8% was found, compared to the

maximum error of 29.2% across all tooth positions of all australopith taxa (Table 8; see also Evans et al., 2016). For the entire sample studied here, the maximum error for the DMQ assemblage was found when dm2 size was predicted using dm1 size, while the maximum error in the Evans et al. (2016) study was found when M1 size was predicted using the M3. The average prediction error rate in the DMQ sample across all teeth was 12.8%, while average errors across all teeth from australopiths in Evans et al. (2016) was 7.9%. For comparison, the average error across all teeth in A. africanus and P. boisei is 10.7% for each taxon. It was expected that the highest error rate would be found when this method was applied to DNH 7 due to the marked smallness of this specimen (see results of overall tooth size from the prior section). That is, as DNH 7 consistently sits the farthest from the Swartkrans Member 1 size cluster, it could be hypothesised that perhaps this specimen would be the least likely to adhere to the IC model prediction rates for the Swartkrans P. robustus sample. By the same logic, DNH 8 was expected to adhere most closely to the australopith pattern, and demonstrate among the lowest error rates, although this was not the case. Maximum error rates by tooth class were instead found in DNH 8, DNH 44, and DNH 107. This result is counterintuitive in that all but one of the DMQ specimens included here were also included in Evans et al. (2016).

Mean Prediction Error					
Predicted Using	dm1	dm2	M1	M2	M3
dm1	-	15.17	9.52	22.49	
dm2	12.04	-	4.88	15.53	
M1	8.68	4.56	-	13.34	4.69
M2	17.85	13.06	11.26	-	16.89
M3			6.65	15.87	-
Maximum Prediction					
Error					
Predicted Using	dm1	dm2	M1	M2	M3
dm1	-	33.76	10.83	20.05	
dm2	25.25	-	8.49	17.45	
M1	9.77	7.83	-	21.41	5.5
M2	19.14	14.49	17.09	-	22.16
M3			10.73	28.48	-
SD of Prediction Error					
Predicted Using	dm1	dm2	M1	M2	M3

dm1	-	16.52	1.85	3.46	
dm2	11.92	-	5.1	2.72	
M1	1.53	4.62	-	6.9	1.15
M2	2.19	2.02	5.17	-	7.45
M3			3.66	11.49	-

Table 8: DMQ inhibitory cascade errors. Values represent percentages.

5.3 Discussion

Moggi-Cecchi et al. (2010) and Lockwood et al. (2007) have previously suggested that the size differences between the DMQ and Swartkrans P. robustus samples are the result of marked sexual dimorphism. Specifically, they hypothesised that the DMQ sample is dominated by females, whereas the Swartkrans sample is dominated by males. The results of the analysis presented here, which includes newly discovered specimens (e.g., redacted), do not support the sexual dimorphism hypothesis and instead support the hypothesis that the size differences between the two assemblages are the result of taxonomic differences within what is currently considered a single species, *P. robustus* (**Redacted**; Broom, 1950; Howell, 1978; Junger and Grine, 1986; Grine, 1982, 1985a, 1985b, 1988; among others). Four sentences redacted. Moggi-Cecchi et al. (2010) found seven tooth positions to be significantly smaller in size while this study found eight. It is based on these results that Moggi-Cecchi et a. (2010) concluded that P. robustus was a highly dimorphic species. This conclusion was in agreement with the Lockwood et al. (2007) conclusions of sexual dimorphism manifesting primarily with DMQ represented by females and Swartkrans represented by males.

Overall size differences alone, however, do not exclusively support a hypothesis of sexual dimorphism. Moreover, when dental size deviates drastically within a single species of non-hominin primates as the result of sexual dimorphism, there is a specific and predictable pattern of such size variation. For instance, in baboons, sexual dimorphism drives metrical differences in the maxillary and mandibular canines, third premolars, second, and third molars to the exclusion of other tooth positions (Lauer, 1975; Plavcan, 2001). Similarly, metric differences are present in the maxillary and mandibular canines as well as third molars, third premolars, and to a lesser extent, second molars of gorillas, despite that species

being less sexually dimorphic than baboons (Lauer, 1975). Differences in canine and postcanine tooth size between the DMQ and Swartkrans Member 1 specimens that are patterned similarly to that seen in dimorphic primates would be evidence supporting a hypothesis of sexual dimorphism being present between the two *P*. *robustus* assemblages.

As discussed previously (Chap 1), differences in maxillary morphology between P. robustus samples have been argued to represent both sub-specific and specific variation (Broom, 1950; Robinson, 1954; Howell, 1978; Grine, 1982, 1985; among others) although the criteria for these conclusions is often unclear. Results presented by Lockwood et al. (2007) may also support such a hypothesis though such an interpretation would run contra to the conclusion put forward by Lockwood et al (2007). For this reason, it is crucial to investigate potential differences in the maxillary dental arcade. Results reported here demonstrate a clear pattern wherein statistically significant differences in size (in at least one dimension) are present for all postcanine maxillary teeth, whereas no such pattern exists for the mandibular arcade. In fact, differences in size (BL width) were only found to occur in the I¹, P³, and M². As there is no extant population in which sexually dimorphic size differences manifest clearly in just one dental arcade, the hypothesis of sexual dimorphism explaining size differences between the DMQ and Swartkrans Member 1 samples, as has been put forward by Moggi-Cecchi et al. (2010), receives little, if any, support from the analyses presented herein. More specifically, the 'silverback effect' that has previously been hypothesised to account for P. robustus size variability (Lockwood et al., 2007) should result in increased upper molar, upper canine, and lower P3 size – a pattern clearly exhibited in extant sexually dimorphic primates (Lauer, 1975; Plavcan, 2001) - but one that is not present between the Swartkrans Member 1 and DMQ samples.

It has been reported that sexually dimorphic dental size differences are more exaggerated in dental elements surrounding the canine and are less noticeable for other tooth positions (Garn et al., 1966; Plavcan, 2001). These differences can manifest as up to at a 10% difference in size (Garn et al., 1966; Plavcan, 1990, 2001; Cochard, 1985). Results presented here show no such pattern between the DMQ and Swartkrans Member 1 material (Fig. 33 and 34; Table 7). Significant metric differences between the two *P. robustus* assemblages are present primarily

in the postcanine dentitions and exclude the mandibular dentitions. Size differences between the DMQ and Swartkrans Member 1 average at ~6% although some dental elements are as high as 16% and other as low as <1%.

Intraspecific variation differs greatly across primate species – for example, 21 species of Cercopithecus were found to vary less than four subspecies of Papio hamadryas (Plavcan and Cope, 2001). This weakens the reliability of any assessment of coefficient of variation (CV) between the DMQ and Swartkrans Member 1 assemblages. Additionally, Plavcan and Cope (2001) warn against the comparison of temporally disparate palaeo-populations. That is, as temporal variation will be observed within fossil assemblages and not within living populations, testing a fossil assemblage against standard CV values of a living sample is not an analogically strong piece of evidence. The presence of temporal variation will inflate the expected CV of any fossil taxon as specimens within the sample derived from differing temporal horizons (Simpson, 1961; Plavcan, 1993; Cope, 1993; Plavcan and Cope, 2001). That said, the DMQ represents a temporally constrained palaeo population (Chapter 2) with a mean CV of 6.8 across DMQ dental elements (Tables 5 and 6) – a value consistent with a single species with low degrees of sexual dimorphism (Plavcan and Cope, 2001). Indeed, the highest CV within the DMQ is for the maxillary I2 and mandibular M2 – a pattern inconsistent with size differences related to sexual dimorphism (Lauer, 1975; Plavcan, 2001).

In the absence of a similar extant analogue for sexually dimorphic dentitions and, with the presence of new dates clarifying the relationship of the DMQ and Swartkrans Member 1 deposit, it is suggested that the marked size variability can be most simply explained in terms of evolutionary change through time. Indeed, the IC model presented in Figure 35 demonstrates broad systematic differences between the DMA and Swartkrans Member 1 samples rather than differences in individual teeth. Although the mandibular dentitions of the DMQ and Swartkrans Member 1 assemblages are statistically identical in terms of size, natural selection pressures seem to be increasing the size of the DMQ mandibular dentitions towards the Swartkrans Member 1 *P. robustus* morph. The difference between the DMQ mandibular dentition (which is statistically the same size as Swartkrans

Member 1 dentition) and maxillary dentition (which is statistically significantly smaller than the Swartkrans Member 1 dentition) may be related to evolutionary constraints which acted to prevent the DMQ maxillary dentition from enlarging as quickly as the mandibular dentition. This may be because an increase in the size of maxillary dentition requires the restructuring of the entire splanchocranium and portions of the neurocranium to allow for changes in the maxillary arcade. This suggests that dental rearrangement towards the *P. robustus* morph sampled at Swartkrans Member 1 can be seen within the DMQ assemblage.

6. A cladistic assessment of deciduous dental character traits

While many studies have attempted to clarify the phylogenetic relationships within and between the southern and eastern African robust australopiths (White et al., 1981; Grine, 1985; Kimbel, 1988; Strait and Grine, 2004), all prior studies were conducted without the inclusion of the more recently discovered DMQ specimens. **Six sentences redacted. Subsequest sentences modified for continuity.** Three hypotheses will be tested in this study: 1) *P. robustus* from Swartkrans/Kromdraai and *P* robustus from DMQ are sister taxa, 2) *P. robustus* is paraphyletic such that the Swartkrans Member 1 *P. robustus* material will be the sister taxon to *P. boisei* (after Grine, 1983; 1985), while the DMQ *P. robustus* material will be the sister taxon to a clade including both the Kromdraai B and Swartkrans Member 1 *P. robustus* samples as well as *P. boisei* (after Martin et al., *in prep*; Chap 3) and, 3) robust australopiths are polyphyletic such that *P. robustus* and *A. africanus* form a clade distinct from an eastern African robust australopith clade (e.g., Walker et al., 1986; Kimbel et al., 1988).

Grine (1985) attempted to reconstruct the phylogeny of early hominins by assessing the deciduous dentition of A. africanus, P. robustus, P. boisei, and A. afarensis. Although the species now conventionally recognized as P. aethiopicus had already been identified (the holotype of which is OMO 18-1968-18 [Arambourg and Coppens, 1968]), the KNM-WT 17000 cranium had not yet been discovered nor had any deciduous dentition been attributed to this taxon, thus its exclusion by Grine (1985). Grine defined seven Operational Taxonomic Units (OTUs), six of which were site-specific: "Laetoli, Hadar, Sterkfontein + Makapansgat, Taung, Kromdraai, and Swartkrans" (Grine, 1985 pp. 164). The seventh was P. boisei. These divisions were intended to allow an examination of fine-grained phylogeny. For example, the splitting of Kromdraai and Swartkrans allowed him to evaluate previous phylogenetic arguments asserting that *P. robustus*, represented by the robust australopiths at Kromdraai, was intermediate between A. africanus and P. crassidens, the robust australopiths at Swartkrans (Broom and Robinson, 1952; Grine, 1982, 1985). Grine (1985) also assessed the Taung, Sterkfontein, and Makapansgat A. africanus specimens separately due to their original attribution to three different sub-species, species, or genera (Broom, 1946, 1950; Robinson, 1954, 1956). Despite studies showing differences between these samples (Tobias, 1967; Rak, 1983), they have generally been accepted into a single species: *A. africanus* (For example see Robinson, 1954; Clarke, 1977; Tobias, 1978, 1980; Strait and Grine, 2004). Grine (1985) reported no significant variability between Makapansgat and Sterkfontein and so treated them as a single sample. Grine (1985) left Taung separate due to a few differences between that specimen and those from Sterkfontein and Makapansgat. Consequently, although Grine (1985) believed that the Taung, Makapansgat, and Sterkfontein australopith specimens likely all represented a single species, the former was kept separate for the purposes of his analysis due to a small amount of differentiation. As Taung is represented only by a single specimen this similarity might be artificial as there is no possibility of capturing variability within the sample.

Grine (1985) concluded that deciduous dental evidence supported the hypothesis that the Hadar and Laetoli specimens represented a single species (*A. afarensis*) distinct from *A. africanus* as proposed by Johanson et al. (1978). Grine (1985) also found support for the argument that *P. boisei* represented a species distinct from the South African robust australopiths due to several identifiable autapomorphies (as discussed by Tobias, 1967; Howell, 1978; Rak, 1983). In relation to South African *P. robustus*, however, Grine (1985) supported a species level distinction between the Kromdraai and Swartkrans samples due to "multitudinous features" that distinguish the deciduous dentition of these two robust australopiths. Additionally, Grine (1985) suggested that *A. africanus* or an *A. africanus*-like morph was likely ancestral to the robust australopith clade although, again, these conclusions were drawn before the discovery of KNM-WT 17000 and the positioning of *P. aethiopicus* at this basal position by subsequent phylogenetic analyses (Kimbel, 1988).

Grine (1985) identified some morphological features that exhibited a high level of intra-sample variability and excluded these from his analysis. That is, if the expression of the tuberculum sextum, for example, was highly variable within samples such as Laetoli *A. afarensis* or Swartkrans *P. robustus*, this character was excluded from the study due to its limited ability to distinguish populations from one another. Instead, the study was limited to morphological traits that were consistent within the samples and so interpreted to be of 'high phyletic weight' (Robinson,

1960; Mayr, 1969; Grine, 1985). Thus, rather than fully characterizing the variability within each OTU, Grine's (1985) methodology aimed to identify characters that might reveal phylogenetic relationships and so removed highly variable traits. As any morphological traits found to be internally variable were excluded, OTUs employed by Grine (1985) are recorded as showing no variability in any included morphology. This resulted in 52 traits across all deciduous dental elements. Of these, 49 have been employed here to assess the relationship of the DMQ deciduous sample and other australopithecines. The three traits identified by Grine (1985) that have not been included in this study are the 'cuspal size' of the lower dm1, the 'incisal margin' of the lower di2 which refers to both the degree of bevelling present of the slope of the incisal edge, and the disposition of the 'median lingual ridge' of the upper dc. The 'cuspal size' trait has been excluded as it is thought by the author to be overly subjective and too vulnerable to inter-observer error. Both the 'incisal margin' of the lower di2 and the 'median lingual ridge' of the upper dc have been excluded due to a lack of representation within the DMQ P. robustus sample. The 'shape of anterior fovea of the lower dm2' as identified by Grine (1985), was split into two traits (see L15 'Presence or Absence of Accessory Trigonid Crest on the Lower dm2' and L16 'Angulation of the Distal Margin of the Anterior Fovea on the Lower dm2' below). This resulted in 50 deciduous traits employed in this analysis. Deciduous dental traits are described in detail below (Section 6.1.3).

6.1 Materials and Methods

6.1.1 Ingroup taxa

Text in the following paragraphs has been modified to accommodate the redaction.

The ingroup of this analysis includes *A. afarensis, A. africanus, P. robustus, P. boisei,* and *P. aethiopicus.* Within and across these taxa, OTUs have been variously divided in the six analyses presented here to follow various taxonomic hypotheses. Further detail is provided in Section 6.1.4. In some analyses conducted here, *A. africanus* has been split into two Operational Taxonomic Units (OTUs): a Taung sample and a joint Makapansgat/Sterkfontein sample following Grine's (1985) analysis. In other analyses a single *A. africanus* OTU is recognized

and includes Taung, Makapansgat, and Sterkfontein. In some analyses conducted here, *P. robustus* has been split into three OTUs: *P. robustus* Kromdraai B, *P. robustus* Swartkrans Member 1, and *P. robustus* DMQ. The treatment of the Kromdraai B and Swartkrans (Member unspecified) material here reflects the Grine (1985) analyses. In other analyses, *P. robustus* has been split into two OTUs: *P. robustus* Swartkrans/Kromdraai and *P. robustus* DMQ.

Specimens belonging to these taxa recovered prior to 1985 were drawn from Grine (1985). Although the dental specimens included within Grine's (1985) study had each been assessed by him, the author reassessed all of these specimens prior to adding any new specimens to the study to ensure that the two assessments by the two separate researchers broadly agreed. The author also examined specimens recovered more recently and added these data to the morphological matrix. South African specimens were examined via an in-person assessment while specimens recovered from eastern Africa were assessed via the published literature.

The *Homo sapiens* sample has been drawn predominately from morphology reported by Grine (1983) and includes Bantu specimens collected by Raymond Dart, specimens collected by taking casts of living San, as well as a limited sample of specimens described by him as "Mongoloid" and "Caucasoid". Modern humans were not included in the Grine (1985) cladistics analysis but are included here in the ingroup.

Unfortunately, not all of the deciduous teeth are represented within all samples. Most detrimental to this study is the fact that only one deciduous dental specimen attributed to *P. aethiopicus* is known, resulting in an extremely limited sample in which only 10 out of 50 character traits can be scored and even these have no room to display any intraspecific variability. Secondarily, the lack of any maxillary deciduous dentition from the Kromdraai sample creates a considerable limitation. While it is of course not ideal that no maxillary traits can be assessed from the Kromdraai assemblage, the mandibular traits that can be scored are moreover each represented by no more than a single specimen, again removing the possibility of observing intraspecific variation. All dental elements except maxillary anterior teeth are represented within the Swartkrans sample. The DMQ *P. robustus*

sample consists of the eight deciduous specimens included in Moggi-Cecchi et al. (2010) as well as ten previously undescribed specimens. All deciduous teeth are represented within the DMQ, Sterkfontein/Makapansgat, and Taung samples. The Swartkrans Member 1 sample preserves all deciduous dental positions excepting the upper first incisor. The *P. boisei* and *A. afarensis* samples preserve all deciduous dental positions except the upper first and second incisors.

6.1.2 Outgroup taxa

Both *Pan troglodytes* and *Gorilla gorilla* were included as outgroups in this study. Extant ape data were collected in consultation with Gary Schwartz and Amber Jaeger of Arizona State University using specimens curated at the American Museum of Natural History.

6.1.3 Character selection and scoring

Deciduous dental traits selected for this analysis follow Grine (1985) although some have been excluded or modified. Forty-nine traits drawn from Grine (1985) have been employed in this study. All traits have been scored qualitatively into discrete character states (e.g. 'Development of Distal Stylid': 'strong' 'weak' 'absent'). Some traits such as the aforementioned 'Development of Distal Stylid', although relative, can be accurately assessed in this manner due to the simplicity of the categories and trait expression. Other traits such as 'Cusp Size' have been excluded from this analysis because the author considered qualitative assessment to poorly capture observed variability. Such a trait should instead be assessed quantitatively.

Of the 50 deciduous characters drawn from Grine (1985), only 17 were not altered in this study. As a wider range of morphology must be accommodated in this study due to the inclusion of *Homo sapiens, Gorilla gorilla,* and *Pan troglodytes,* character states have been added to those described by Grine (1985) or have been changed. Of the other 33 characters, a 'variable' state was added to 18 to accommodate the morphology of the new DMQ *P. robustus* sample. Two further 'variable' states were added to accommodate Kromdraai *P. robustus* specimens discovered after the Grine (1985) publication. Still four more 'variable' states were

amalgamation created to accommodate the of the Taung and Sterkfontein/Makapansgat samples in a selection of analyses preformed in this study. Four 'variable' states were created to accommodate new A. afarensis specimens. Finally, one 'variable' state was created to accommodate the changes in taxonomic attribution of *P. boisei* specimens that took place after the Grine (1985) publication. Seven 'absent' states were created to accommodate morphology observed when two extant ape species were added to the sample. For example, while character L4 refers to the morphology of the lingual end of the mesial marginal ridge, the deciduous dentition of G. gorilla and P. troglodytes does not possess a mesial marginal ridge, making this state distinct from an absence of the described feature. Although a small amount of variability was observed within both G. gorilla and P. troglodytes, in all but one instance this variability fit within 'variable' states already created leading to only one further 'variable' state being added. One character, defined by Grine (1985) as the 'shape of the anterior fovea of the lower dm2', was split into two characters (L15: Presence or Absence of Accessory Trigonid Crest on the lower dm2 and L16: Angulation of the Distal Margin of the Anterior Fovea on the lower dm2) when the morphology described was found not to co-vary within the DMQ sample. In most instances, character definitions provided by Grine (1983, 1985) were adopted. In others, such as L24 (Expression of the Tuberculum Molare of the upper dm1), definitions were created or clarified by the authors and are provided on Morphobank.

Characters adapted from Grine (1985) and modified and defined from by the author have been labelled L. The characters employed are described and scored as follows:

L1 Position of the Protoconid of Lower dm1

Grine (1985) defines this character as the position of the protoconid relative to the metaconid. The states are (0) protoconid mesial to metaconid (2) protoconid and metaconid are aligned transversely. The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L2 Proportional Mesiodistal Length of the Trigonid of Lower dm1

This trait was defined by Grine 1985 as to whether the trigonid or the talonid is mesiodistally dominant. We have determined this trait by taking measurement 1 from the mesial side of the mesial marginal ridge (MMR) to the distal side of the trigonid basin. Measurement 2 is taken from the distal side of the trigonid basin to the distal side of the distal marginal ridge (DMR). If measurement 1 is larger than the 'trigonid is mesiodistally dominant over the talonid' (state 0), and if measurement 2 is larger than the 'talonid is mesiodistally dominant over the trigonid' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L3 Depth of Buccal Groove of Lower dm1

This trait was defined by Grine 1985 as being either a 'deep distinct fissure' (state 1) or a 'shallow to moderate groove' (state 2). State 0 (buccal groove absent) was added to accommodate variation in *Pan troglodytes* and *Gorilla gorilla*.

L4 Lingual End of Mesial Marginal Ridge (MMR) of Lower dm1

Grine 1985 defined this trait as either 'low' (state 1) or 'high' (state 2). We consider that when the MMR is approximately the same height as the cusps (or greater) that this represents the 'high' state. State 0 (MMR absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*.

L5 Completeness of MMR of Lower dm1

Grine 1985 identified two states to characterise the topography of the MMR. State 1 was 'separated from the metaconid by a distinct fissure' and state 2 was 'completely encloses anterior fovea'. We have simplified this characterisation into 'open' (state 1) and 'closed' (state 3).

L6 Position of Anterior Fovea of Lower dm1

Grine 1985 described this character as having two states 'anterior fovea skewed to the lingual side' (state 1) and 'anterior fovea symmetrically positioned' (state 2). The DMQ material exhibits a pattern not previously observed by Grine 1985, in that that the anterior fovea is skewed to the buccal side. We have thus created a further character trait 'anterior fovea skewed to the buccal side' (state 3) to accommodate the DMQ sample. We have also classified this as an unordered trait as it is not

clear what the evolutionary progression of this trait would have been. State 0 (Anterior fovea absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*. This trait has been re-coded as unordered.

L7 Shape of Anterior Fovea of Lower dm1

Grine 1985 defined this trait as manifesting as either a 'triradiate or broad triangular basin' or a 'single buccolingually oriented fissure'. We have accordingly attributed the following character states after Grine 1985: 'triradiate or broad triangular basin' (state 1) and 'single buccolingually oriented fissure' (state 3). Grine 1985 treated the Taung 1 specimen and the Skerkfontein / Makapansgat samples as being separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *A. africanus*) which has resulted in the need for an additional 'variable' (state 2) state. This is because the anterior fovea of the Taung 1 specimen represents state 1 whereas the anterior fovea of the Sterkfontein / Makapansgat sample represents state 2. The combined *A. africanus* OTU therefore is attributed the 'variable' (state 2) state. This trait has been re-coded as unordered.

L8 Tuberculum Molare Expression on the Lower dm1

Grine 1985 identified three states for the expression of this trait; strong, weak, and absent. However, Grine 1985 did not define the 'tuberculum malare' and thus we have adopted a definition based on our interpretation of this character. We consider the tuberculum malare to be a swelling at the base of the protoconid in the mesiobuccal corner of the tooth, near to the cervical margin which can manifest as either 'strong' (state 0), 'weak' (state 2), or 'absent' (state 3). We consider a strongly expressed tuberculum malare to be the ancestral (and thus state 0) condition because this is the state observed in *A. afarensis*. The 'variable (both strong and weak present)' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present. State 0 (Anterior fovea absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*. Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the need for an additional 'variable (both weak and present)'. This additional variable state has

become state 3 in analyses 2, 3, 5, and 6 and the 'absent' expression has become state 4.

L9 Relative Cusp Height of Lower dm1

Grine 1985 identified three states for this character; protoconid and metaconid markedly higher than the hyperconid and the entoconid (state 0), protoconid and metaconid slightly higher than the hyperconid and entoconid (state 1), and all cusps at a similar height (state 2). We have adopted these character states as defined by Grine 1985. The assessment of this character is greatly influenced by the degree of wear that is exhibited on the subject teeth. Thus we have excluded a large number of teeth (both from the DMQ sample and, where possible, Grine 1985's original sample) as we consider that for heavily worn dentition it is not possible to confidently assess what the unworn cusp topology would have been. Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable; states 1 and 2 present' state (state 3).

L10 Mesioconulid (Plesioconulid) Expression on the Lower dm1

Grine 1983 defines this character as being a small cuspulid on the mesial marginal ridge of the lower dm1 that can manifest as either absent (state 0) or present (state 1). We note that there are potentially multiple morphologies of this trait that are all rolled into the 'present' condition. Consequently, we consider any expression of this trait as equivalent to the 'present' state. Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). In these analyses, the 'present' state has become state 2.

L11 Length of the Buccal Groove on the Lower dm1

Grine 1985 describes this character as having two states; 'buccal groove terminates halfway down the crown' (state 1), and 'buccal groove continues to the cervical margin (state 2). State 0 (Buccal groove absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*.

L12 Hypoconulid Expression on the Lower dm1

Grine 1985 identifies two states for this character; 'weak' (state 1), and 'strong' (state 3). The 'variable' (state 2) condition was added to accommodate the DMQ *P. robustus* sample as both state 1 and state 3 are present. State 0 (Hypoconulid absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*.

L13 Position of the Protoconid on the Lower dm2

Grine (1985) defines this character as the position of the protoconid relative to the metaconid. The states are (0) protoconid mesial to metaconid (1) protoconid and metaconid are aligned transversely. The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L14 Relative Height of the Protoconid to the Metaconid of the Lower dm2

Grine 1985 observed three states for the character; 'protoconid and metaconid markedly different heights' (state 0), 'protoconid and metaconid slightly different heights' (state 1), and 'protoconid and metaconid at a similar height' (state 2). The assessment of this character is greatly influenced by the degree of wear that is exhibited on the subject teeth. Thus we have excluded a large number of teeth (both from the DMQ sample and, where possible, Grine 1985's original sample) as we consider that for heavily worn dentition it is not possible to confidently assess what the unworn cusp topology would have been.

L15 Presence or Absence of Accessory Trigonid Crest on the Lower dm2

This character is equivalent to Grine 1985 'shape of anterior fovea of the lower dm2'. Grine 1985 describes a 'subdivided' or 'undivided' anterior fovea however we consider this character as characterising the presence or absence of a ridge, rather than characterising the morphology of the anterior fovea itself. We thus define this character as the presence (state 0) or absence (state 1) of a ridge that divides the anterior fovea into mesial and distal sections. The 'variable' (state 1) condition was added to accommodate the Kromdraai *P. robustus* sample as both state 0 and state 2 are present.

L16 Angulation of the Distal Margin of the Anterior Fovea on the Lower dm2

Grine 1985 describes the angulation of the distal fossid of the anterior fovea of the lower dm2 as being either 'transverse' or 'oblique (mesiolingual distobuccal)'. We consider that this trait is a characterisation of the distal margin of the anterior fovea, whether or not the fovea is subdivided by an accessory trigonid crest (see character L15). We therefore redefine this trait as being the angulation of the distal margin of the anterior fovea, whether or not that fovea is subdivided as per L15. In support of this definition, Grine 1985 characterised *P. boisei* as having a transverse anterior fovea despite the fact that this fovea is undivided in this taxon. We therefore recognise two states after Grine 1985 to characterise the angulation of the distal margin of the anterior fovea as 'oblique' (state 0) or 'transverse' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L17 Relative Expression of the Accessory Trigonid Crest and the Distal Trigonid Crest of the Lower dm2

Grine 1985 describes this character as exhibiting two states; 'accessory trigonid crest less well developed than distal trigonid crest' and 'accessory trigonid crest more well developed than distal trigonid crest'. We have identified two further character states as 'both state 0 and state 2 present' (state 1) (or 'variable' as is the case for the DMQ sample) and 'accessory trigonid crest absent (state 3) to characterise the *P. boisei* sample. In relation to state 3, we have the view that the absence an accessory trigonid crest may be a function of the merger of the accessory trigonid crest and the distal trigonid crest. This is because where the absence of an accessory trigonid crest is observed in *P. boisei*, the distal trigonid crest is swollen and thickened relative to taxa that exhibit both a distinct accessory trigonid crest and a distal trigonid crest. Furthermore, the anterior fovea in P. boisei manifests as a narrow, compressed fissure most similar to the mesial fossid of a subdivided anterior fovea. Thus we hypothesise that the absence of an accessory trigonid crest (as is the case for P. boisei) may in fact be better characterised as the merging of the accessory trigonid crest and the distal trigonid crest. We therefore recognise four character states: 'accessory trigonid crest less well developed than distal trigonid crest' (state 0), 'both state 0 and state 2 present in

OTU' (state 1), 'accessory trigonid crest more well developed than distal trigonid crest' (state 2), and 'accessory trigonid crest absent' (state 3).

L18 Primary Occlusal Fissure Shape of the Lower dm2

Grine 1985 describes this character as exhibiting two states; 'a Y shaped fissure' (state 0), and 'mesiobuccal and lingual fissures are nearly straight, transverse lines' (state 2). We have interpreted state 2 to be synonymous with the H shaped fissure pattern described by Grine 1985. We have thus attributed state 2 as being 'H shaped fissure'. The 'variable' (state 1) condition was added to accommodate the Kromdraai *P. robustus* sample as both state 0 and state 2 are present.

L19 Expression of the Tuberculum Intermedium (C7) on the Lower dm2

Grine 1985 identified three states for this character; 'absent' (state 0), 'weak' (state 2), and 'strong' (state 3). Grine 1983 defines the tuberculum intermedium. The 'variable' (state 1) condition was added to accommodate the *A. afarensis* sample as both state 0 and state 2 are present. The 'variable' (state 4) condition was added to accommodate the DMQ *P. robustus* sample as state 0, state 2, and state 3 are all present. This trait has been re-coded as unordered.

L20 Expression of the Tuberculum Sextum (C6) on the Lower dm2

Grine 1985 identified three states for this character; 'absent' (state 0), 'weak' (state 1), and 'strong' (state 2). Grine 1983 defines the tuberculum sextum. The 'variable; both absent and weak present' (state 3) condition was added to accommodate the DMQ *P. robustus* sample as state 0, state 1, and state 2 are all present. Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable; both weak and strong present' state 4. This trait has been recoded as unordered.

L21 Expression of the Distal Marginal Ridge (DMR) on the Upper dm1

Grine 1985 identifies two states for this character; 'thin' (state 2), and 'thick' (state 3). State 0 (DMR absent) was added to accommodate variation within *Gorilla*

gorilla. State 1 (variable; absent and thin present) was created to accommodate variation within *Pan troglodytes*.

L22 Morphology of the Lingual Side of the Protocone on the Upper dm1

Grine 1985 identified three states for this character; 'strong bevelling, no inflation' (state 0), 'moderate bevelling, some inflation' (state 1), and 'no bevelling, strong inflation (nearly horizontal)' (state 2). State 3 (no bevelling; no inflation) was added to accommodate for variation within *Gorilla gorilla* and *Pan troglodytes*. This trait has been re-coded as unordered.

L23 Relative Size of the Paracone and Metacone on the Upper dm1

Grine 1985 recognised two states for this character; 'paracone noticeably larger than metacone' (state 0), and 'paracone and metacone similar size' (state 1).

L24 Expression of Tuberculum Molare of the Upper dm1

Grine 1985 identified three states for the expression of this trait; strong, weak, and absent. However, Grine 1985 did not define the 'tuberculum malare' and thus we have adopted a definition based on our interpretation of this character. We consider the tuberculum malare to be a swelling at the base of the protoconid in the mesiobuccal corner of the tooth, near to the cervical margin which can manifest as either 'strong' (state 0), 'weak' (state 1), or 'absent' (state 2). We consider a strongly expressed tuberculum molare to be the ancestral (and thus state 0) condition because this is the state observed in *A. afarensis*.

L25 Orientation of the Distal Trigon Crest of the Upper dm1

Grine 1985 observed two states for this character; 'distal trigon crest is at an oblique (approximately 45 degree) angle to the mesiodistal axis', and 'distal trigon crest is transverse'. We therefore recognise two states after Grine 1985 as 'oblique' (state 1) and 'transverse' (state 3). The 'variable' (state 2) condition was added to accommodate the DMQ *P. robustus*, Swartkrans *P. robustus*, and *P. boisei* samples as both state 1 and state 3 are present. State 0 (Distal trogon crest absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*.

L26 Expression of the Mesiobuccal Groove on the Upper dm1

Grine 1985 recognised two states for this character; 'weak' (state 1), and 'strong' (state 3). The 'variable' (state 2) condition was added to accommodate the DMQ *P. robustus* sample as both state 1 and state 3 are present. State 0 (absent) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*.

L27 Expression of V-shaped Furrow on Buccal Depression on the Upper dm1

Grine 1985 describes the buccal depression as a shallow V shaped depression within which the buccal grooves sit. He recognises two states for this character; 'absent' (state 0), and 'present' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L28 Expression (Height) of the Buccal Side of the Distal Marginal Ridge (DMR) on the Upper dm2

Grine 1985 recognised two states for this character, 'low and narrow' and 'tall and thick'. The DMQ sample indicates that lowness/tallness and narrowness/thickness do not necessarily covary because the DMQ sample is characterised by being low and thick. We have therefore split this character into two new characters (see L29). We have thus amended this character to refer only to the height (lowness/tallness) of the buccal side of the DMR and recognise two states; 'low' (state 0), and 'tall' (state 2). The 'variable' (state 1) condition was added to accommodate the *A. afarensis* sample as both state 0 and state 2 are present.

L29 Expression (Thickness) of the Buccal Side of the Distal Marginal Ridge (DMR) of the Upper dm2

This character was previously conflated by Grine 1985 with DMR height (see L28). We recognise two states for this character; 'narrow' (state 0), and 'thick' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L30 Accessory Lingual Cuspule / Lingual Groove on Upper dm2

Grine 1985 recognised two states for this character; 'uninterrupted lingual groove' (state 0), and 'accessory cuspule present within fissure' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L31 Occlusal Outline of the Upper dm2

Grine 1985 recognised two states for this character; 'quadrangular' (state 0), and 'asymmetrical' (state 2). Grine 1985 further characterised an asymmetrical occlusal outline as being driven by the presence of a mesiobuccal projection of the paracone. The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L32 Crown Shape Index Value

Grine 1985 recognised two states for this character; 'buccolingual length exceeds mesiodistal length' (state 0), 'mesiodistal length exceeds buccolingual length' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present. The index values are calculated according to the following formula: [(BL / MD) x 100]. Specimens are considered to exhibit state 0 if the crown shape index is greater than 100% and were considered to exhibit state 1 if the crown shape index is less than 100%.

L33 Size of the Hypocone of the Upper dm2

Grine 1985 recognised two states for this character; 'large' (state 0), and 'small' (state 2). The 'variable' (state 1) condition was added to accommodate the combined Taung, Sterkfontein, and Makapansgat *A. africanus* sample in analyses 2, 3, 5 and 6 as both state 0 and state 2 are present.

L34 Completeness of the Epicrista of the Upper dm2

Grine 1985 recognised two states for this character; 'incised' (state 0), and 'complete' (state 1).

L35 Expression of the Trigon Basin of the Upper dm2

Grine 1985 recognised two states for this character; 'mesial fissure better developed than distal limb' (state 1), and 'distal limb better developed than mesial

fissure' (state 2). State 0 (No limbs present) was added to accommodate variation within *Pan troglodytes* and *Gorilla gorilla*. This trait has been re-coded as unordered.

L36 Expression of the Talon Basin of the Upper dm2

Grine 1985 recognised two states for this character; 'buccal limb dominant over lingual limb' (state 0), and 'lingual limb equal to or dominant over buccal limb' (state 2). The 'variable' (state 1) condition was added to accommodate the DMQ *P. robustus* sample as both state 0 and state 2 are present.

L37 Expression of the Accessory Distobuccal Fissure of the Upper dm2

Grine 1985 recognised two states for this character; 'absent' (state 0), and 'present' (state 1).

L38 Occlusobuccal Margin of Trigon Basin of the Upper dm2

Grine 1985 recognised two states for this character; 'buccal limb cuts deep V shaped notch at margin' (state 0), and 'bulbous crest forms a high wall from the paracone to the metacone' (state 2). The 'variable' (state 1) condition was added to accommodate the *A. afarensis* sample as both state 0 and state 2 are present.

L39 Incisal Wear Facet of the Upper di1

Grine 1985 recognised three states for this character; 'strong linguo- and disto-cervical bevelling' (state 0), 'weak bevelling' (state 2), and 'no bevelling' (state 3). The 'variable' (state 1) condition was added to accommodate the DMQ *P*. *robustus* sample as both state 0 and state 2 are present.

L40 Lingual Shape of the Upper di2

Grine 1985 recognised two states for this character; 'shovelling' (state 0), and 'little to no shovelling' (state 1). These distinctions are made as per Hanihara 1954.

L41 Crown Shape of the Upper dc

Grine 1985 recognised two states for this character; 'symmetrical' (state 0), and 'mesial edge nearly horizontal' (state 1).

L42 Distal Apical Edge of Lower dc

Grine 1985 recognised two states for this character; 'elongate and vertically inclined' (state 0), and 'shorter and more shallowly (obliquely) inclined' (state 1).

L43 Lingual Cingulum Disposition of the Lower dc

Grine 1985 recognised two states for this character; 'only slightly higher mesially than distally' (state 0), and 'markedly higher mesially than distally' (state 1). Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). The 'markedly higher mesially than distally' expression has become state 2 for these analyses.

L44 Height of Mesial Crown Convexity of Lower dc

Grine 1985 recognised two states for this character; 'maximum mesial convexity below mid-crown' (state 0), and 'maximum mesial convexity above mid-crown' (state 1). Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). The 'maximum mesial convexity above mid-crown' expression has become state 2 for these analyses.

L45 Position of Apex of Lower dc

Grine 1985 recognised two states for this character; 'apex centrally located' (state 0), and 'apex displaced mesially' (state 1). Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). The 'apex displaced mesially' expression has become state 2 for these analyses.

L46 Degree of Lingual Surface Relief of Lower dc

Grine 1985 recognised two states for this character; 'weak' (state 0), and 'strong' (state 1). Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). The 'strong' expression has become state 2 for these analyses.

L47 Expression of Distobuccal Groove of Lower dc

Grine 1985 recognised two states for this character; 'weak' (state 0), and 'strong' (state 1).

L48 Expression of Distal Stylid of Lower dc

Grine 1985 recognised two states for this character; 'weak' (state 0), and 'strong' (state 1).

L49 Depth of the Mesiobuccal Groove of Lower dc

Grine 1985 recognised three states for this character; 'absent' (state 0), 'shallow' (state 1), and 'deep' (state 2). Grine 1985 treated the Kromdraai and the Swartkrans samples separate OTU's. These two samples have been combined in analyses 2, 3, 5, and 6 (as they both represent populations of *P. robustus*) which has resulted in the creation of an additional 'variable' state (state 1). The 'shallow' expression has become state 2 and the 'deep' expression has become state 3 for these analyses.

L50 Expression of Mesial Stylid of Lower dc

Grine 1985 recognised two states for this character; 'present' (state 0), 'absent' (state 2). The 'variable' (state 1) condition was added to accommodate the combined Taung, Sterkfontein, and Makapansgat *A. africanus* sample in analyses 2, 3, 5 and 6 as both state 0 and state 2 are present.

In addition to the deciduous dental traits described above, cranial and mandibular character traits have been drawn from Martin et al. (*in prep*; Chap 3) and employed in some analyses (3 and 6) presented here.

6.1.4 Phylogenetic Analyses

Six phylogenetic analyses were performed:

- Analysis 1: Parsimony analysis of deciduous dental traits using OTUs following Grine (1985). That is, *A. afarensis*, Taung *A. africanus*, Sterkfontein/ Makapansgat *A. africanus*, *P. robustus* Kromdraai B, *P. robustus* Swartkrans, and *P. boisei* with *P. aethiopicus* and *P.* robustus DMQ added. This analysis tests how new fossil discoveries affect the phylogenetic analysis of Grine (1985).
- 2. Analysis 2: Parsimony analysis of deciduous dental traits using OTUs corresponding to commonly recognized species. That is, *A. afarensis, A. africanus* as a single OTU, *P.* robustus Kromdraai B and *P.* robustus Swartkrans as a single OTU '*P. robustus* Swartkrans/Kromdraai', *P. boisei, P. aethiopicus*, and *P. robustus* DMQ as a separate OTU. This analysis assesses the phylogenetic relationships of *P. robustus* DMQ using a conventional taxonomic framework.
- 3. Analysis 3: Redacted.
- 4. Analysis 4: This repeats Analysis 1 but uses Bayesian analysis to recover the most credible trees.
- 5. Analysis 5: This repeats Analysis 2 but uses Bayesian analysis to recover the most credible trees.
- 6. Analysis 6: Redacted

The parsimony analyses were run using TNT v1.5 (Goloboff and Catalano, 2016). The analyses were set to allow for 10,000 tree iterations and employed implicit enumeration to identify the shortest trees due to the small number of included taxa. Bremer support was calculated for the purposes of assessing node support of suboptimal trees. Steps were increased gradually to ten until a hominin polytomy was produced. Bootstrapping was conducted via symmetric resampling with P=33

set at 5,000 replicates and group present/contradicted frequency (GC) values were produced for the resultant consensus tree. This consensus tree was produced as a strict (Nelson) tree.

The Bayesian analyses were run using MrBayes v3.2.6 (Ronquist et al., 2012) using the Markov Chain Monte Carlo (MCMC) sampling method. An undated Mkv analysis was performed with ingroup and outgroup definitions as the only constraints. The analysis was set to two runs of four chains for 20 million generations resulting in a halfcompat 50% majority rule consensus tree. Priors were set to a standard gamma clock with *Gorilla gorilla* set as the most distant outgroup.

6.2 Results

6.2.1 Analysis 1

This analysis produced three equally parsimonious trees (Fig. 36). All three find that the Taung and Sterkfontein/Makapansgat OTUs are sister taxa, that *A. afarensis* and *H. sapiens* are sister taxa, and that these four OTUs comprise a clade. All three trees also recover a *Paranthropus* clade, although relationships within the clade vary. However, this variability depends entirely on *P. aethiopicus*. Putting that taxon aside, whose variable phylogenetic position is almost certainly related to the fact that it is represented in only ten of the fifty deciduous dental traits, of the remaining four OTUs *P. robustus* from Swartkrans Member 1 is always in a clade with *P. boisei*, *P. robustus* from Kromdraai B is the sister taxon of that clade, and *P. robustus* from DMQ is the basal member of the clade. The consistency Index (CI) of each tree is 0.720 and the Retention Index (RI) of each tree is 0.730. Bootstrapping revealed very weak support for all nodes within a hominin clade (GC values of 13, 14, and 21) except for the sister group relationship between the two *A. africanus* OTUs (GC value of 82).



Figure 32: Three equally parsimonious trees from Analysis 1.

6.2.2 Analysis 2

This analysis produced two equally parsimonious trees differing only in the position of *P. aethiopicus,* which is reconstructed as being either the sister taxon of *P. boisei* or the clade including *P. robustus* Swartkrans/Kromdraai and *P. boisei* (Fig. 37). Both trees find that *A. africanus* is the sister taxon of a clade including *H.* sapiens
and *A. afarensis,* that Paranthropus is monophyletic, and that *P. robustus* DMQ is the sister taxon of a clade including *P. robustus* Swartkrans/Kromdraai, *P. aethiopicus,* and *P. boisei.* Bootstrapping finds reasonable support for a *Paranthropus* clade (GC value of 72). The consensus tree of the two most parsimonious trees shows a length of 133, a Cl of 0.74, and a Rl of 0.7.



Figure 33: Two equally parsimonious trees from Analysis 2.

6.2.3 Analysis 3 Redacted

Figure 34: Redacted.

6.2.4 Analysis 4

The Mkv model produced by this analysis identified a *Paranthropus* clade with *P. robustus* DMQ as the basal member (Fig. 39). All other robust australopiths were placed in a monophyletic polytomy. These nodes both show a high posterior probability (basal node BPP of 75.57%; derived node BPP of 87.49%; Fig. 39). The split Taung and Sterkfontein/Makapansgat samples are positioned as sister taxa with a posterior probability of 80.91%.



Figure 35: Mkv model from Analysis 4. Posterior probability values shown at nodes.

6.2.5 Analysis 5

The Mkv model produced by this analysis also identified a *Paranthropus* clade with *P. robustus* DMQ as the basal member (BPP of 54.9%; Fig. 40). *Paranthropus aethiopicus* is placed as the sister taxon of a *P. boisei* + *P.* robustus Swartkrans/Kromdraai (BPP of 90.45%) clade (BPP of 62.83%). The clade containing these three OTUs is very well supported.



Figure 36: Mkv model from Analysis 5. Posterior probability values shown at nodes.

6.2.6 Analysis 6 Redacted

Figure 37: Redacted.

6.3 Discussion and Implications

As noted above, three hypotheses were tested in this study: 1) *P. robustus* Swartkrans/Kromdraai and *P robustus* DMQ are sister taxa, 2) the robust australopiths are paraphyletic such that the Swartkrans Member 1 *P. robustus* material will be the sister taxon to *P. boisei* (after Grine 1983; 1985), while the DMQ *P. robustus* material are the sister taxon to a clade including both the Kromdraai B and Swartkrans Member 1 *P. robustus* samples as well as *P. boisei* (after Martin et al., *in prep*; Chap 3) and, 3) robust australopiths are polyphyletic such that *P. robustus* australopith clade.

Results were not consistent with Hypothesis 1. Rather, the OTUs conventionally assigned to *P. robustus* were paraphyletic in all six analyses, with *P. robustus* DMQ consistently branching off near or at the base of the *Paranthropus* clade, and *P.*

robustus from Swartkrans Member 1 being the sister taxon of either *P. boisei* or an eastern African *Paranthropus* clade.

Results are generally consistent with Hypothesis 2, except insofar as *P. aethiopicus* rather than *P. robustus* from Swartkrans Member 1 is sometimes found as the sister taxon to *P. boisei.* However, the Swartkrans and Kromdraai samples are always more closely related to *P. boisei* than they are to *P. robustus* DMQ.

Results are inconsistent with Hypothesis 3. There is no evidence that *Paranthropus* is polyphyletic, or that any of the *P. robustus* OTUs have any special relationship with *A. africanus*.

Paragraph redacted.

Of the six analyses conducted here, four relied solely on deciduous dental character traits. Interpretation of results from these analyses are somewhat limited by missing data. The *P. robustus* sample deriving from Kromdraai B does not include any maxillary deciduous teeth, leaving the taxon represented by only 29 of 50 character traits. *P. aethiopicus* is represented by a single deciduous molar and so only 10 out of 50 characters could be assessed. This results in instability in the placement of this OTU that would likely be resolved by the addition of more deciduous tooth positions. **Sentence redacted.** In Analyses 1 and 4 the Taung and Sterkfontein/Makapansgat *A. africanus* samples are treated as separate OTUs. While these two taxa are consistently found as sister taxa, the Taung *A. africanus* OTU is, of course, limited by the presence of only one individual and so, while every tooth position is represented, the sample lacks variability.

Paragraph redacted.

Analyses 1, 2, 4 and 5 differ from Analyses 3 and 6 regarding the placements of the gracile australopiths and *H. sapiens*. Specifically, these taxa form a clade in the former analyses, but do not in the latter. Using parsimony to reconstruct character states in Analysis 1, this clade is supported by four derived character states: a strong tuberculum molare on the dm₁ (character L8), protoconid and

metaconid at slightly different heights on the dm₂ (character L14), accessory trigonid crest less well developed than the distal trigonid crest on dm₂ (character L17), and a strong tuberculum molare on dm¹ (character L24). Analyses 1, 2 4 and 5 all reflect the phylogenetic signal of the deciduous dentition, but insofar as different anatomical region may provide slightly different phylogenetic information, a total evidence approach should be preferred. Thus, Analyses 3 and 6, which are based on characters from across the cranium, mandible, adult dentition and deciduous dentition this suite of anatomical characters themselves may not necessarily fully reflect are more likely to provide a more accurate view of the evolution of deciduous dental traits. Because **redacted**, those derived traits would be interpreted as being homoplasies rather than synapomorphies in the most parsimonious / most credible trees of those analyses.

Four sentences redacted. It is difficult to assign function or adaptive significant to these traits individually, but collectively they suggest that derived changes in size and occlusal morphology of the postcanine dentition in gracile australopiths relative to pre-australopiths manifested themselves not only in the adult dentition but in the deciduous dentition as well. It is hypothesised that many of these changes may be related to consumption of foods that may have been mechanically challenging to process (e.g., Jolly, 1970; Peters, 1987; Teaford and Ungar, 2000; Strait et al., 2009, 2013).

Table 9: Redacted.

The *Paranthropus* + *Homo* clade is supported by three deciduous dental synapomorphies (Table 9). These include a variable or closed mesial marginal ridge on the dm₁ (character L5), paracone and metacone of similar size on the dm¹ (character L23), and a variable distal trigon crest on the dm¹ (character L25). Thus, deciduous dental traits provide only modest support for this clade, although the clade is well supported by 11 other craniodental synapomorphies.

The *Paranthropus* clade is supported by only four deciduous dental synapomorphies (Table 9), although this clade is very strongly supported by 24 other craniodental and mandibular synapomorphies. The deciduous dental traits include: an anterior fovea manifesting as a single buccolingually oriented fissure on the dm₁ (character L7), a variable tuberculum molare on the dm₁ (character L8), a weak strong tuberculum molare on the dm¹ (character L8), and a variably thick buccal side of the distal marginal ridge on the dm².

A clade including *P. robustus* Swartkrans/Kromdraai, *P. boisei* and *P. aethiopicus* is supported by 18 deciduous dental synapomorphies (Table 9) and only 4 other cranial and mandibular synapomorphies. The derived deciduous dental traits include: protoconid and metaconid aligned transversely on the dm_1 (character L1), a high mesial marginal ridge on the dm_1 (character L4), a variably weak or absent tuberculum molare on the dm₁ (character L8), all cusps at similar height on the dm₁ (character L9), a strong hypoconulid on the dm₁ (character L12), protoconid and metaconid aligned transversely on the dm₂ (character L13), variably present accessory trigonid crest on the dm₂ (character L15), accessory trigonid crest more well developed than the distal trigonid crest on the dm_2 (character L17), variable occlusal fissure shape on the dm₂ (character L18), thick distal marginal ridge on the dm¹ (character L21), no bevelling and strong inflation of the lingual side of the protocone on the dm¹ (character L22), tall buccal side of the distal marginal ridge on the dm² (character L28), thick buccal side of the distal marginal ridge on the dm² (character L29), lingual limb of taloned basin equal to or dominant over buccal limb 181

on the dm² (character L36), bulbous crest forms a high wall from the paracone to the metacone of the trigon basin on the dm² (character L38), variably disposed lingual cingulum of lower dc (character L43), variable height of the mesial crown convexity of lower dc (character L44), and variable position of apex lower dc (character L45). The very large number of derived deciduous dental traits that are present in this clade but absent in *P. robustus* DMQ provides compelling evidence both for the taxonomic separation of *P. robustus* DMQ and *P. robustus* Swartkrans/Kromdraai, and for the positioning of *P. robustus* DMQ as the basal member of the *Paranthropus* clade.

Thus, in summary, a consideration of deciduous dental morphology provides strong support for the hypotheses that *Paranthropus* is monophyletic rather than polyphyletic, and that *P. robustus* DMQ is the basal member of the *Paranthropus* clade.

7. Time Perspectivism

7.1 The Problem: the nature of the palaeo record

Whereas anthropologists and biologists studying living organisms can directly observe the behaviours of a subject group, palaeo-researchers must infer behaviour and biological phenomena from osteological and/or archaeological remains. Consequently, archaeologists and palaeo-researchers are obliged to work with the data that a particular site preserves, rather than the data that would be optimal for the purposes of answering the research questions that they are interested in. Limiting factors regarding preservation in the palaeo-sciences primarily fall into the area of taphonomy. Taphonomy pertains broadly to all of the processes that are involved with transforming a living, breathing, behaviourally complex organism into a fossil. The field of taphonomy, although originally relating to the process of fossilisation (Efremov, 1940), has developed to include the study of how pre- and post-depositional processes cause fossil assemblages to provide biased representations of past biomes. Moreover, only a small number of individuals existing at any one point in time are preserved in the fossil record, thereby limiting the inferences that palaeoanthropologists concerned with understanding the organismic diversity of extinct ecosystems, species diversity, or variability within palaeo-populations of species, are able to make.

All transformative processes, including taphonomic agents, are bracketed or truncated by the temporal depth of a deposit. It is issues related to temporal depth that will be discussed here. Though all fossil assemblages are time averaged, conducting analyses as though this has a homogeneous effect of fossil samples must be avoided. Assemblages such as the DMQ with a maximum time depth of ~90,000 years will be referred to here as a 'temporally shallow' deposit. Assemblage such as Sterkfontein Member 4 with a time depth of >500,000 years will be referred to here as a 'temporally deep' deposit. This distinction is being made for the purposes of defining and identifying different biological processes or phenomena that may affect the deposit in question. For example, a process such as 183

as anagenic change is unlikely to present itself as markedly in a temporally shallow deposit such as the DMQ as compared to a temporally deep deposit. Terms such as 'shallow' and 'deep' are, of course, relative. For example, while the DMQ deposit is likely too temporally shallow to clearly observe evolutionary change, it would be too temporally deep to assess questions regarding specific cultural activity. It will be argued here that the archaeological theory of time perspectivism is well suited to addressing time depth limitations within the palaeo record. The application of the theory of time perspectivism to palaeo research should both help to resolve long-standing research questions as well as prevent the aforementioned errors from being committed in future research. As defined by Bailey (1983, pp. 103), time perspectivism is *"the belief that differing timescales bring into focus different features of behaviour, requiring different sorts of explanatory principles"*.

Early in the history of palaeo-studies, most researchers were trained as anatomists or naturalists and so possessed no theoretical background with which to address resultant limitations of working with fossil assemblages. Those parts of archaeological theory which deal with the conceptual framework associated with understanding palimpsestic deposits are equally applicable to the palaeontological palimpsestic deposits with which palaeoanthropologists work and has indeed been applied by palaeontological researcher such as Jablonski (2007) and Bennington and Aronson (2012) among others. A palimpsest is defined as something reused or altered but still bearing visible traces of its earlier form and is a term originally applied to scrolls or manuscripts that have been written-over. The field of archaeology co-opted the term and used it to refer to an object made or worked upon for one purpose and later reused for another, for example a stone axe later repurposed as a scraper. The term is also used in archaeology to refer to a deposit such as a campsite that has been utilized repeatedly in such a way that the distinction between each event is unclear. Time perspectivist approaches have been utilized by some when interpreting archaeological assemblages for over two decades (see for example Stern, 1993). The application of such a term to the fossil 184

record is simple in that all fossil-bearing deposits represent more than a single moment in time and so are, by definition an amalgamation of events. Indeed, palaeontologists have employed this theory of interpretation to non-hominin assemblages (see for example Jablonksi 2007 or Bennington & Aronson 2012). Despite this, the field of palaeoanthropology has not broadly adopted this framework.

Bailey (2007) defines five categories of palimpsests: 1) true palimpsests where all earlier traces have been obliterated by later activities, 2) cumulative palimpsests where material traces of different time periods are mixed together, 3) spatial palimpsests where narrower assemblages of shorter time depth are aggregated across space, 4) temporal palimpsests where, though one 'event' is represented, the individual material constituents possesses different 'temporalities' [dates], and 5) palimpsests of meaning where a single object (i.e. a 'scraper') started life as a different object (i.e. an axe). Of these, it is the cumulative palimpsest and the spatial palimpsest that are immediately relevant to palaeo-research. Whereas palimpsests of meaning accrue as the result of anthropogenic processes, this study focuses on palimpsests that accrue as the result of depositional processes and the effect that this has on research questions addressed via analysis of data derived from such deposits.

It could be argued that nearly all deposits represent cumulative palimpsests at least to a degree. Indeed, even a campsite occupied once by a single camper represents a cumulative palimpsest. If, for example, a research question is designed around assessing the contents of said camper's breakfast, a campsite utilized for a single day will still contain an amalgamation of food remains representing breakfast, lunch, and dinner. Early archaeologists would use ethnographies as a tool for direct interpretation of archaeological deposits (Schiffer, 1976). Specifically, ethnoarchaeologists would go to camps of traditionally living people, record material remains, return to an archaeological deposit, and interpret preserved materials with the view that any missing materials were the result of an imperfect record (Schiffer, 1976). Regarding the campsite example, this would mean that if a researcher discovered the remains of three food types and desired to study breakfast behaviours at this campsite, the researcher would go to an active campsite and observe which of the recovered food discard most closely resembled that eaten for breakfast by living people. Or, if only two food types were recovered and neither resembled the breakfast behaviours of the living people, it would be assumed that the 'correct' food type did not preserve.

All palaeo-deposits are, by nature, extreme examples of cumulative palimpsests, and recent dating work has shown that the time spans involved in their accumulation can be very different. For example, a single flowstone dating to ~2.6 Ma based on uranium-lead dating formed at the base of Sterkfontein Member 4, DMQ and DMK (Pickering et al., 2019) but subsequent deposition and fossil accumulation differed between these localities. At DMK and Sterkfontein Member 4 electron spin resonance (ESR) dating conducted on fossil teeth suggest that sediments and fossils were accumulated soon after the formation of this flowstone (Herries and Shaw, 2011; Herries et al., 2018). At DMK, palaeomagnetism and ESR suggests the deposit that remains at the site were deposited in a short temporal window around 2.61 Ma based on the occurrence of a magnetic reversal that likely covered <20 ka, whereas at Sterkfontein Member 4 deposition of sediments began almost immediately and continued until after at least 2.3 Ma and perhaps as late as 2.07 Ma (Pickering and Herries, 2020). In contrast, DMQ did not deposit the first fossils and sediments until approximately half a million years after the \sim 2.6 Ma flowstone formed, with fossil bearing deposits forming between \sim 2.04 and 1.95 Ma. While these deposits are well constrained in terms of their period of deposition, many sites are not. Kromdraai lacks any secure dates, whereas Swartkrans Member 1 has only broad dates of somewhere between 2.3 and 1.8/1.7 Ma based on the bracketing ages of underlying and capping flowstones (Pickering et al., 2011). Herries and Adams (2013) have noted that the basal flowstone 186

underneath the Hanging Remnant of Member 1 at Swartkrans has been majorly truncated before the deposition of sediments over the top of it. As such, it would seem likely the sediments were deposited closer in time to the capping flowstone rather than the basal flowstone. This is further supported by ESR ages. A similar situation can be seen at the *Paranthropus* site of Gondolin, with the age of the deposit closer in age to a capping 1.78 Ma flowstone (Adams et al., 2007). As such, it is always important to view age ranges for the deposits in light of such factors. Deposits in caves that are often used for dating, such as speleothems, can form from the very early life-history of the cave and do not denote an open cave entrance that can accumulate sediments and fossils. Large, clean (sediment free) basal flowstones are very common amongst the Gauteng Malmani cave sites and suggest the formation of thick basal speleothem in closed cave conditions. Further, not every speleothem that underlies a deposit is a 'basal speleothem'. While the ~2.6 Ma speleothem has been identified as forming in numerous caves in the region (Sterkfontein, DMQ, DMK, Makapansgat Limeworks, Aves Cave at Bolt's Farm; Herries et al., 2013; 2018; 2020; Pickering et al., 2019) the nature of formation can be quite different. At DMQ, DMK and Aves Cave it formed as part of a seemingly thick basal flowstone, whereas at Sterkfontein and the Makapansgat Limeworks it formed as a thinner flowstone over the or between clastic cave fill (capping the Australopithecus africanus bearing Member 3 at the Makapansgat Limeworks, and forming between Members 3 and 4 at Sterkfontein as defined by Partridge [2000]). The reason for this difference is that the basal flowstones of DMQ, DMK and Aves likely formed over a long time period and incorporate speleothem episodes of different ages. Specifically, it is likely that they incorporate the ~2.6 Ma, ~2.8 Ma and ~3.1 Ma phases of flowstone formation identified by Pickering et al. (2019) and appear as a single unit. This is because there is no entrance allowing sediment accumulation between these phases. The simple reason they have been dated to 2.6 Ma is that studies have targeted the upper layers of the basal flowstones to get maximum ages for overlying clastic cave fill and also because lime-mining often removed the older portions. At sites that were

already open to sediment deposition these phases occur as shorter episodes within clastic cave fill. Given that speleothem appear to form in different caves at the same time across the Gauteng Malmani, it is now possible to use them like volcanic tuffs in eastern Africa to build up a regional picture. It is also possible to infer the age of undated speleothems within certain cave sequences. For example, the undated capping flowstone at Gondolin GD2 (Herries et al., 2006) is likely the ~1.8 Ma flowstone dated at Swartkrans, Waypoint 160 at Bolts Farm, between Members 4 and 5 at Sterkfontein, and at DMQ itself. The occurrence of a magnetic reversal at Gondolin, interpreted originally as the 1.78 Ma upper Olduvai reversal, supports this (Adams et al., 2007).

The key to understanding the age of the fossil bearing sediments themselves, and whether they represent a 'deep' or 'shallow' site, is identifying when landscape erosion caused an entrance to form and opened a site up for deposition. Sites such as Sterkfontein, Swartkrans, and Kromdraai are low topography valley-side cave systems that have long life histories and so they are very complex (Stratford et al., 2012; Bruxelles et al., 2014; Herries et al., 2019). In contrast, high topographic water input points like Drimolen tend to have shorter life histories related to erosion and the changing topography and hydrology of the upland landscape (Herries et al., 2019; 2020). This is likely the reason that many of the newly discovered, northern Gauteng Malmani sites such as Drimolen and Malapa appear to cover a very short time frame of deposition (Pickering et al., 2011; Herries et al., 2020).

Both shallower and deeper temporal deposits are often described homogeneously as being 'time averaged' and attendant analyses are cautioned to consider the effects that such averaging may have on the testing of biological hypotheses. However, as the situation noted above shows, to treat both temporally shallower (Swartkrans; formed over perhaps a few 100,000 years close to 1.8 Ma) and temporally deeper deposits (Sterkfontein; formed over up to 500,000 years between 2.6 and 2.1 Ma) as equivalently and equally 'time averaged' obscures 188 several ways in which such deposits are substantively different and the fossil data from them can be interpreted.

Firstly, while both a deposit accumulated over 20,000 and one deposited over 200,000 years are 'time averaged' the degree and extent of averaging, as well as the biological processes and phenomena that may be visible through the period of their deposition, are not the same across both deposits. Intra-sample variability cause by biological phenomena such as sexual dimorphism can be observed in the shortest time depth samples - moment in time, modern assemblages - while variability caused by a phenomenon such as evolutionary change only occurs through time and so can be expected to vary in degree across samples of differing time depths. In terms of the example given above, the DMQ assemblage represents at most ~90,000 years of time averaging (a relatively shallow temporal deposit), the Swartkrans Member 1 assemblage (including Lower Bank and Hanging Remnant) represent between 500 and 200,000 years of time averaging (a relatively deep temporal deposit), and the Sterkfontein Member 4 assemblage represents up to 500,000 years of time averaging (a relatively deep temporal deposit). So, while all these assemblages all represent 'time averaged' deposits, the time depth of each deposit is different. The implication then for interpreting such assemblages is that those explanatory factors that are considered consequently must also vary. If different processes require different time scales to operate so must different time scales be required for these processes to be observed. In general terms, it is reasonable to suppose that less of the variability between specimens recovered from a deposit formed across ~90,000 years will be due to evolutionary change through time than would be the case for specimens from a deposit formed over 500,000 years. Alternatively, while an explanatory factor such as sexual dimorphism likely exists within an assemblage with a ~500,000 year time depth, factors such as evolutionary change through time must be carefully considered and likely obscure short-term factors such as sexual dimorphism that operate through a shorter time period.

Specimens deriving from Sterkfontein Member 4 have alternatively been attributed to A. africanus or are considered to represent two separate species (the other being A. prometheus; Dart, 1948; Clarke, 1993, 2013). This situation can be interpreted in multiple ways. Allowing for the purposes of discussion that A. prometheus is a justified taxon, it is possible that both A. africanus and A. prometheus coexisted at Sterkfontein over the entirety of the half a million years it took to form. It is possible that the occupation of Sterkfontein by one of either A. africanus or A. prometheus preceded the occupation by the other. It is possible that a mixture of these scenarios occurred with A. africanus and A. prometheus only coexisting at Sterkfontein for a short time period within the half a million years it was deposited. It is also possible that A. africanus and A. prometheus alternated occupation of Sterkfontein over ~500,000 years without crossing paths (i.e. summer occupation versus winter occupation). Or it is possible that any morphological distinction between A. africanus and A. prometheus is the result of anagenetic change through time rather than the presence of two separate hominin lineages and if the deposit could be defined into two shorter and sequential time periods, only one taxon would be found in each with a morphological 'midpoint' in between. The occurrence of A. africanus older than 2.6 Ma at Taung and Makapansgat Limeworks Member 3, the later potentially in tandem with A. prometheus, and the apparent occurrence of the two species in Sterkfontein Member 4 post 2.6 Ma would argue against this however, and would suggest there is at least some temporal overlap. A very similar situation now occurs with A. anamensis and A. afarensis in that the two have been considered by some to be part of a temporal lineage, while the recent discovery of the MRD-VP-1/1 A. anamensis fossil, and it's dating to approximately 3.9 Ma, overlapping with early A. afarensis (Haile-Selassie et al., 2019). This has been argued to suggest they are different species and not part of the same lineage (Haile-Selassie et al., 2019). However, it is always possible that evolution from A. anamensis to A. afarensis only occurred in certain populations under selective pressure, while other populations did not undergo such change.

Without the means to disentangle such complexities, it is virtually impossible to validate one of these theories over all others. For reference, the period of deposition represented at Sterkfontein is the same as that encompassing Modern humans, *Homo naledi, Homo erectus, Homo floresiensis, Homo neanderthalensis, Homo heidelbergensis, Homo erectus,* the Denisovans, and possibly a variety of other purported taxa. To continue the campsite analogy, Sterkfontein M4 would be as if the campsite had had two occupants instead of one and the research question was designed around *which* occupant ate *what* for breakfast and whether or not they ate together.

Palaeo-researchers must work with the reality that aggregated palaeo-deposits will always have a time depth that cannot be resolved to specific moments in time, even if individual events that occur quickly are represented. Assuming a deposit represents a true moment in time event is referred to as the 'Pompeii Premise' and is a fallacy that must be avoided (Ascher, 1961). As per the campsite analogy above, even Pompeii does not represent a moment in time event. Though it is true that the city of Pompeii and many of its inhabitants were buried under ash in a very short time period, this did not occur instantaneously. Further, though the remains preserved represent a snapshot of the city in the moments it was buried, the remains themselves are a temporal palimpsest in the same way the remains of a single day's meals represents such a palimpsest at our campsite. For this reason it is more useful to refer to events as moments of time rather than moments in time. These moments of time can occur across variable temporal resolutions and time depths. Researchers with differing research questions may have a different concept of what represents a suitable moment of time, or adequate temporal resolution, for their purposes.

Even with an example such as the nearly complete Little Foot (StW 573) skeleton, the death of whom likely occurred over minutes, the specimen's deposition itself

represents a short temporal event. That is, the specimen can present data accumulated across the time period of its life and death (such things may include dental wear, healed skeletal injuries, carnivore bite marks, etc). The subsequent transfer of this individual into the fossil record would have also occurred across a relatively short time period and has been suggested to represent an example of natural mummification (Clarke and Partridge, 2002). However, even then the fossil has become disarticulated as deposits around it were eroded and later speleothem and breccia deposits infilled the holes made by these erosive events (Bruxelles et al., 2014).

Further, the event itself can only be roughly dated. For example, though it is true that StW 573 entering the Silberberg Grotto at Sterkfontein, either by will or accident, and dying represents a short temporal event, the specimen can only be dated to either 3.67 ± 0.16 Ma based on cosmogenic nuclide burial dating (Granger et al., 2015) or 2.6-2.2 Ma based on combined uranium-lead and palaeomagnetic dating (Pickering and Kramers, 2010; Herries and Shaw, 2011). This means that the single event of deposition can only be viewed through a time depth resolution of 320,000 to 400,000 years. What can be inferred from this specimen, however, is the morphology of that taxon at that moment in time. The StW 537 specimen can provide morphological data regarding nearly all skeletal elements in such a way that researchers can be confident this data all derives from the same event. That is, in the absence of a complete skeleton, researchers will derive information regarding, for example, a femur from one specimen and information regarding a tibia from another. If these same fossil elements were recovered from a deposit with a deep time depth of 500,000 years, such as Sterkfontein Member 4, it is only an assumption that researchers are aggregating morphological data from the same time point. Assessing a femur from a Homo sapiens individual alive today and a tibia from a Homo heidelbergensis individual from 400,000 years ago and presenting this data as the morphology of a single species would be equivalent to this.

Another significant issue that must be addressed in these deposits, as highlighted by the StW 573 situation, is that if erosion and infill features are not identified when excavations take place (often over several decades ago) then material of different ages can be mixed together due to the way material is excavated, or sometimes due to past geological processes. Several examples exist of this in the South African record. A good example of this is the SK 15 mandible that is most often associated with Swartkrans Member 1 (Schwartz and Tattersall, 2003), however, when it was excavated it was actually found within a dark 'chocolate' breccia apparently infilling the older Member 1 unit. While Robinson and others have suggested this was contemporary with Member 1, Brain suggests it is actually infiltration from the younger Member 2 (Brian, 1981). At the Taung Pinnacles Type site the Taung Child and other fossils were deposited within an older pre 2.61 Ma PCS deposit, formed synchronously with the formation of the Thabaseek Tufa (Hopley et al., 2013; Herries et al., 2013). At a later period, post 2.61 Ma caves formed through the PCS deposits and tufa and became infilled with the YRSS deposit (Herries et al., 2013). When this occurred some of the older material within PCS was eroded around quite significantly and YRSS sediments deposited in a manner that makes them appear to occur partly in PCS and partly in YRSS (Herries et al., 2013). In some cases, material may have been completely dislodged from the older to the younger unit, while in other cases excavation techniques may have led the excavators to believe they come from the wrong unit (Kuhn et al., 2016). At Sterkfontein ESR dates for Member 4 originally included samples with ages as young as ~1.2 Ma (Herries and Shaw, 2011). However, an analysis of the 3D plots of these samples indicate that these younger ages come from areas close to the contact with the younger Member 5 and were likely mixed into Member 4 material during excavation (Herries and Shaw, 2011). This would also mean younger fossil material could have been mixed into the older unit assemblages. In other cases, older material has been argued to have been reworked into younger units at both

Sterkfontein and Swartkrans. Fossil material suggested to represent early *Homo* is found in the Lincoln Cave deposits at Sterkfontein that are only a few 100,000 years old (Reynolds et al., 2007). The same thing may explain younger occurrences of Paranthropus robustus in Swartkrans Member 3 at ~1 Ma (Herries and Adams, 2013).

Spatial palimpsests are also common within the palaeo record. The nature of palaeo deposits, particularly palaeocave sites as seen in the South African Malmani, is such that accumulated material is aggregated across the site often in an indecipherable manner. Simply, vertical entrance cave strata form like sediments in an hourglass creating an upwards projecting talus cone with sediments deposited low on the edges of the cave contemporaneous with those much higher in the central talus cone (Gillieson, 1996; Herries et al., 2020; Chap 2). In cave deposits, fine-grained sediments such as silts are washed to the edges of the cavern while course-grained, blocky material tends to move less in the deposit and so remain within the central talus cone (Moriarty et al., 2000; Pickering et al., 2007; Herries et al., 2020; Chap 2). If, for example, a small light object such as a distal phalanx was deposited in the same moment as a larger heavier object such as a cranium, it is possible that the cranium will remain in the central talus cone near to where it originally landed while the phalanx is transported, by water movement or simply by gravity, to a lower point at the edges of the deposit. This winnowing could occur some time after the initial deposition and be part of an ongoing process of skeletal disarticulation. Once a cave is completely infilled and stratigraphic layering and age distinction is obscured, identification of these strata by excavators can be difficult and often leads to the naming of inaccurate grainsize based members (Herries et al., 2020; Chap 2). While lateral facies change is a well documented geological occurrence (see for example Latham et al., 1999), there is a disconnect between these processes and the subsequent interpretation of fossil contexts. Members based on criterion such as 'fine-grained silt' versus

'block-supported matrix', for example, would artificially distinguish the cranium from the phalanx due to their immediate depositional surroundings (Fig. 42).



Figure 38: Cave infill model. Each blue layer represents a depositional context with a different date while the area between the broken line represents a single excavational spit. The skull and long bone demonstrate how specimens deriving from distinct depositional contexts can become conflated.

Another way in which differing time depths can affect research is through the creation of unequal categories. That is, though it may seem valid to directly compare two samples of a single taxon from two different deposits, differences in the time depth (relatively shallow or relatively deep) of each site may preclude such a study. For example, both DMQ and Swartkrans yield *P. robustus* specimens. The two deposits are approximately 7 km apart (Keyser et al., 2000) thus excluding any chance of regional variation. Studies assessing similarities and differences between these two assemblages have most often attributed any dissimilarity to sexual dimorphism and have reported a higher degree of variability within the Swartkrans hominin assemblage (Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016). Problematically for these comparisons, DMQ and Swartkrans have only been dated recently (Pickering et al., 2011; Herries et al., 2020) and indicate that they have drastically different time depths. While the DMQ deposit has a relatively shallow time depth of <90,000 years (Mallett, 2015; Herries et al., 2020; Chap 2), Swartkrans has a relatively deep time depth of perhaps a million years covering the P. robustus bearing Members 1 to 3 (Pickering et al., 2011; Herries and Adams, 2013). Swartkrans Member 1 itself cannot be resolved beyond saying that it formed sometime between 2.3 and 1.8 Ma (Pickering et al., 2011; Gibbon et al., 2014) and in fact Member 1 is perhaps best viewed as two separate deposits (Lower Bank and Hanging Remnant). Herries and Adams (2013) have suggested that the Hanging Remnant formed closer in age to 1.8 Ma based on the fact the underlying ~2.25 Ma flowstone was heavily truncated prior to the deposition of fossil bearing sediments.

A further limitation for palaeo-research is disparate dates in that all palaeo-deposits differ in age to some degree. Even those sites that overlap in chronometrically dated age ranges are unlikely to overlap entirely or indeed at all. For example, Sterkfontein Member 4 has been dated to 2.61 – 2.07 Ma (Pickering and Herries, 2020) and Swartkrans Member 1 HR has been dated to sometime between 2.3 – 1.8 Ma (Pickering et al., 2011). These dates mean that the deposits have the ¹⁹⁶

potential to have overlapped in time by 230,000 years. While it is possible to interpret this to mean individuals within the Swartkrans Member 1 LB deposit existed at the same time as those within the Sterkfontein M4 deposit, as discussed above, it is equally as possible that all individuals existed in the non-overlapping portion of the date ranges. Further, there are situations where samples of the same taxon exist at non-overlapping dates. For example, the Taung and Makapansgat Limeworks *A. africanus* fossils have been dated to sometime between 3.03 and 2.61 Ma (Herries et al., 2013) while the Sterkfontein M4 *A. africanus* deposit has been dated to between 2.61 - 2.07 Ma (Pickering and Kramers, 2010; Herries and Shaw, 2011). Although it is possible that the Taung skull and all Sterkfontein M4 individuals existed at exactly 2.61 Ma, it is equally as possible that the former predates the latter by as much 940 ka.

Researchers can and have responded to these realities in different ways from ignoring them (or arguing they are irrelevant) to attempting to reverse engineer or remove their influence. Some researchers such as Val et al. (2014) simply ignore limitations caused by depositional time depth. Val et al. (2014) conducted a taphonomic study of the hominin-bearing cave site of Cooper's D to assess cave utilization of the large-bodied primates found at the site (three extinct non-hominin primates and *P. robustus*). The premise of this research question comes into conflict with the aforementioned limitations. That is, Cooper's D has only been dated to less than the age of the basal flowstone at 1.375 ± 0.113 Ma (maximum) age of 1.488 Ma; Pickering et al., 2019). As such, the precise age of the fossil material, or its time range is not known for the site and yet, the research question assumes all the taxa were occupying the landscape at the same time. Val et al. (2014) concludes that the accumulation is likely representative of a sleeping or living site collection. This conclusion was drawn due to a limited amount of evidence for carnivore activity within the cave and an apparent natural death profile of the primate remains (Val et al., 2014). This, however, requires the researcher to accept the assumption that the primate samples from Cooper's D are representative of 197

discrete populations and excludes any temporal mixing or differing depositional agents. Moreover, it has already been shown how long fossil bearing material can often be deposited after a basal flowstone has formed. If the ages for Swartkrans Member 3 are correct at 0.96 ± 0.09 Ma (Gibbon et al., 2014), and the *P. robustus* material has not been reworked from older deposits (Herries and Adams, 2013) then there is a potential for several 100,000 years of deposition at Cooper's D.

This error was repeated by Riga at al. (2019) in a study assessing the demographic profile of *P. robustus* from the DMQ. Similar to Val et al. (2014), Riga et al. (2019) concluded the DMQ hominin assemblage likely represented a sleeping or living site, as the demographics most closely resembled that of living apes. In addition to ignoring limitations of time depths discussed regarding the Val et al. (2014) study, the Riga et al. (2019) study also committed a further error regarding unequal categories. That is, the premise of the Riga et al. (2019) study was to compare the demographic profile of the DMQ hominins to that of living apes and that of the Swartkrans hominins. The Riga et al. (2019) study does not limit the Swartkrans assemblage to a particular member or deposit. Consequently, the demographic profile of a single, family group (extant apes) was meaninglessly compared to a deposit with a time depth of less than 90,000 years (DMQ; Herries et al., 2009; Riga et al., 2019), and to a deposit with a time depth of greater than 1 million years (Swartkrans; Herries et al., 2009; Pickering et al., 2011; Herries and Adams, 2013).

The treatment of *Homo naledi* is another example of researchers ignoring dates. Prior to the publication of any dates for the *H. naledi* material, Thackeray (2015) conducted a morphometric analysis of cranial specimens attributed to *H. naledi*, found they were most similar to those of *H. habilis*, and concluded that *H. naledi* must date to ~2 Ma and must be ancestral to the *Homo* lineage. Dembo et al. (2016) conducted a bayesian analysis employing a 'morphological clock' meant to determine the age of *H. naledi* using the assumption of a predictable and constant rate of morphological change. Dembo et al. (2016) concluded that *H. naledi* dated 198 to 912 ka and that H. antecessor, H. erectus, H. floresiensis, H. habilis, H. sapiens, and A. sediba were all possible sister taxa. Once OSL, US-ESR, palaeomagnetic, and U-Th dating methods placed *H. naledi* at 335 – 236 ka (Dirks et al., 2017), Hawks (2017) argued that dates should hold no sway over phylogenetic interpretations claiming that "a young date for some fossils doesn't bar them from membership in a species with much older fossil representatives." Hawks (2017) asserts that only morphological evidence rather than geological or temporal evidence should inform taxonomic attribution and phylogenetic attribution. Using this way of thinking, Berger et al. (2017) places Homo naledi as ancestral to Homo habilis, and the entire Homo lineage, despite H. naledi having only been sampled ~1.5 million years after the first appearance of *H. habilis*. Instead Berger et al. (2017) assert that the *H. naledi* specimens recovered from Rising Star represent surviving members of a taxon that arose "at the earliest stages of diversification within Homo." While, of course, it is morphology that is inherited, and so it is morphology that is directly examined for the purposes of phylogenetic reconstruction, the dates of the OTU's must be taken into account when cladistic results are interpreted.

7.2 The solution: time perspectivism

Time perspectivism influences palaeo research by highlighting the need to craft research questions around the data that is available. Depositional resolution is the motivation of the theory of time perspectivism. Different phenomena operate over different time depths and at different dates and so can only be addressed sufficiently if the requisite data is preserved. As discussed by Bennington and Aronson (2012), a mismatch between the temporal scale of fossil data versus the temporal scale of processes of interest to a researcher represents an inherent problem in palaeo analyses. That is, a research question aimed at examining population-level variation, for example, cannot be answered by a data set with a million year time depth (temporally deep). Equally, a research question aimed at 199

a time depth of only a few tens of thousands of years (temporally shallow) as has been attempted in the fundamentally flawed research mentioned above. Comparing multiple such deposits of different dates yielding the same taxon however, can be utilized in answering this question. The summation of this is that rather than trying to force the coarse-grained nature of a deposit to answer finegrained questions, research questions must be tailored to the site and the data available.

The importance of applying time perspectivism to palaeo research is also reflected in site deposition of both the South African cave sites and the east African rift valley. There are some basic assumptions made about site formation and stratigraphy. The first key assumption is that of the rule of superposition in a section, asserting that lower strata are older than higher strata. The second assumption is that the depth of the strata is indicative of shallow or deep time depths. The first assumption can very rarely be applied to cave sites such as those found within the Gauteng Malmani. As discussed above (Fig. 42) and in Chapter 2 (Herries et al., 2020), the manner in which talus cones form can lead to difficulty in identifying contemporaneous strata, especially when the laterally equivalent units have been disconnected by mining or erosion and lateral tracing of units cannot be undertaken. For example, Sterkfontein Members 2 and 4 may well be contemporaneous despite being found at different depths (Pickering and Kramer, 2010). The problem is that no stratigraphic section occurs linking the two deposits. In almost all caves a talus cone breccia will have a laterally equivalent fine-grained unit produced by winnowing. Defining these as separate Members that formed at different time becomes problematic. For example, it has been proposed that the speleothem found in association with Sterkfontein specimen StW 573 is, in fact, a later intrusion and so not reflective of the age of the specimen (Bruxelles et al., 2014). The occurrence of strata inversion, as frequently occurs in caves, demonstrates how stratigraphic sections in caves do not always follow the rule of superposition in that sediments found higher up can be older than sediments found 200

lower. This can also be the product of younger caves forming within older palaeokarst deposits, where the palaeokarst is treated as the host rock. This is seen both in the South African caves and in Australia at places like Wellington Caves (Osbourne, 2007). If the palaeokarst becomes decalcified during this process, identification can be difficult. Many of the South African palaeocaves have undergone multiple phases of karstification such as this that have added to this complexity. For example, at Sterkfontein multiple periods of deposition occur where older units have been subsided, collapsed and/or been eroded before a later phase was deposited in the same cavity (Herries et al., 2009, 2013, 2019; Stratford et al., 2012). This creates a high potential for mixing between these different units (Reynolds et al., 2007).

It is also assumed that depth within a stratigraphic section between datable units, such as volcanic tuffs in eastern Africa, or speleothems in South Africa, represents constant time deposition. The above discussion about when speleothems form compared to the sediments outlines clear issues with this assumption in the South African palaeocaves. In the case of tuffs, despite being reasonably deep in places, represent a single 'moment in time' event. Of course, while this seems to be a situation in which the Pompeii premise could be applied accurately, fossil material rarely derives from these tufa layers and specimens are instead dated by their assumed relationship with the volcanic strata. The time between the 'event' and the incorporation of remains into the record cannot be known due to the potential for depositional or erosive breaks in the sequence. The dating of the Herto H. sapiens specimens, for example, includes debates surrounding whether the fossils were deposited closer in age to the underlying or overlying volcanic tufa (Faupl et al., 2003; Clarke et al., 2003). However, depositional-rate age estimates are still used very widely in the eastern African record. Conversely, in cave deposits, fine-grained sediments such as silts are washed to the edges of the cavern while coursegrained, blocky material tends to move less in the deposit. This process creates a deep and apparently homogenous stratum of fine silts or sands that in reality can

consist of materials spanning the entirety of the deposit's temporal breadth. Equally, sealed or mostly sealed caves can result in deposits with very thin strata representing markedly deep time depths as only minimal deposition can occur. Further, as demonstrated by Stern (1993), the presence of a rapid depositional process such as a flooding event does not confirm the presence of a moment-intime event and so can obscure the pattern of strata width and time depth again violating the geological assumptions which guide most research. In the South African caves, the horizontally bedded sandstone and siltstone units that form at the edge of the caverns show clear stratification, and can be used to estimate the temporal depth of deposits, especially if certain layers are dated. However, closer to the entrances where the talus cones occur, depth can have less meaning as talus cones are dynamic moving environments and clast heterogeneity can allow smaller fossils to penetrate deeper into the talus cone. Vertical entrance talus cones with large drops from the surface are perhaps the most susceptible to this. They are, in this sense, the epitome of a palimpsest and in some cases no interpretation of internal age structure should be made beyond maximum and minimum ages derived from it, or associated lateral sediments, unless certain geological conditions exist. For example, if a clear stratigraphic layering can be determined with intervening speleothem layers. The formation of speleothem tends to stabilise the talus cones and can create clear separation of different parts of the talus cone. Methods such as micromorphology can be critical in making such determinations.

Processes such as decalcification and later activity such as lime mining, which was very prevalent across Cradle sites, cause obvious disturbance within fossil deposits. Even without any further disturbance, the original nature of these deposits (i.e. talus cone stratigraphy resulting in 'stratification without strata') can create a situation where disentanglement of reworking can be impossible. The regularity in which simple geological and archaeological interpretive frameworks are complicated in palaeo deposits, highlight the importance of the application of the theory of time perspectivism. Further, without recognising the importance of such

information, researchers may be inclined to omit relevant information such as the member from which specimens derive and just refer to, for example, 'Swartkrans' or 'Sterkfontein' (this is phenomenon also seen when other sites, such as Makapansgat, are discussed; see discussion in Chap 1; see for example Conroy et al., 1990; Grine et al., 2010; Moggi-Cecchi et al., 2010).

Time perspectivism is also made necessary in palaeo-research due to the unavoidable abundance of sampling bias and unequal categories. Ignoring the theory of time perspectivism is an easy trap to fall into, as there are a multitude of assumptions one must apply when analysing an imperfect fossil record. It is sometimes necessary to accept assumptions regarding site date overlap and potential temporal mixing. For example, any analysis purporting to assess variability between two deposits containing the same taxa must accept the assumption that the samples are internally consistent. That is, in this situation, the researcher must assume that neither deposit contains specimens that vary due to temporal changes. In a more specific example, many studies have compared the Swartkrans P. robustus sample to the Kromdraai P. robustus sample for the purposes of determining the taxonomic and phylogenetic relationships of the two. These studies must take into account that Swartkrans Member 1 has been dated to 2.3-1.8 Ma (Pickering et al., 2011; Herries and Adams, 2013) and Kromdraai B M3 has been weakly dated to 1.78-1.65 Ma (Thackeray et al., 2002; Herries et al., 2009; see discussion in Chap 1). Here it should be noted that there is little confidence that the Kromdraai B material dated relates to the fossil material. This means two things for any ensuing study: 1) the samples could have anywhere from 80,000 to 650,000 years disparity between them and 2) the individual samples themselves could have, respectively, 600,000 and 13,000 years disparity internally. Either situation greatly weakens any conclusions drawn from such a study.

Understanding the potential disparity between deposits creates a situation where any variability between the two localities could be attributed to population-level 203 variability (80,000 years) or represent morphological change through time (650,000 years). The potential internal disparity can lead to results then becoming a topic of 'lumping' or 'splitting' depending on the researcher's preference regarding the degree of variability allowed within a single species. The second point is more complicating. While it is possible that the entirety of the Swartkrans Member 1 Hanging Remnant sample accumulated at one point in time between 2.3 and 1.8 Ma, cosmogenics suggests that sediment deposits as old as 2.19 \pm 0.08 Ma and as young as 1.80 \pm 0.09 Ma may occur within the Member 1 Hanging Remnant (Gibbon et al., 2014). As such, it is just as probable that there is nearly as much time between two specimens deriving from Swartkrans Member 1 as a whole, or within Hanging Remnant, than there is between a specimen from Swartkrans Member 3. As both of these realities are equally possible, research that ignores time perspectivism in order to assume one to be true over the other is fundamentally flawed.

While accepting assumptions such as internal homogeneity is sometimes necessary, it is important to tailor research questions to the data available. Herries et al. (2020; Chap 2) and Mallett (2015) conclude that the DMQ deposit represents a relatively fast accumulation of <90,000 years. In other terms, while it is possible that specimens within the deposit are separated by up to this much time and likely do not represent a 'population' as biologists or anthropologists would recognize, it is reasonable to exclude temporal change as an explanation of any internal variability. Instead it is possible to design a finer-grained research question such as an assessment of sexual dimorphism within *P. robustus* DMQ. While the DMQ and Swartkrans specimens may have, in theory, been deposited over an equivalent timespan, research can only work at the level of the Minimum Identifiable Temporal Unit. That is, the DMQ material was deposited over as much as 500,000 years. Even if all specimens recovered from DMQ existed as one family group over decades, the most fine-grained assessment is still limited to less than 90,000 years

due to dating error ranges and the nature of the geological processes resulting in the incorporation of these specimens into the record. Accordingly, despite the possibility, these specimens cannot be treated as representing a moment-in-time and may equally have been deposited over the full 90,000-year period. Time perspectivism argues, logically, that this must be taken into account when formulation new research questions and hypotheses.

Errors regarding unequal comparisons are exacerbated by methodology employed during excavation and recording. Herries et al. (2020; Chap 2) discusses in depth the problems with the Member System traditionally employed to define strata in South African palaeo-cave deposits. This system is a holdover from before site formation processes were well understood for the South African sites. Often defined by sediment colour or grain-size, the member system can result in strata that unify multiple temporally disparate deposits while also erroneously splitting single depositional events. For example, as just discussed, a member defined based on fine-grained silts or sands will consist of nearly the entire depositional history. The theory of time perspectivism urges researches to consider the depositional processes, in this case the contemporaneity of fine-grained sediments and some blocky sediments, rather than relying solely on easily identifiable members.

Another common problem has to do with false precision of recording methods. With all the confounding factors discussed thus far, there can be less impact of the accuracy of recording methods. When a site has been mined with dynamite, incised with later formations, and formed without distinct stratigraphy, the difference between 3mm and 5mm accuracy becomes irrelevant. In fact, recording methodologies that insist on traditional techniques of 1m by 1m squares, excavated in 10mm spits, and recorded by a theodolite with a three-second accuracy, can harm interpretation. Hence employing these standards without critically assessing their relevance, can create the impression of spatial precision that far outstrips what the nature of the deposit makes possible. The effects of these digging methods further misconstrue the samples that palaeo researchers can study and such limitations must be considered through the lens of time perspectivism.

7.3 Implications for Research

When proposing the application of the theory of time perspectivism, Bailey (1983, 2008) discusses the dichotomy of short time scales for the examination of cultural and behavioural actors and long time scales for the examination of ecological and environmental actors. Bailey (1983, 2008) argues that this divide relates to time scales studied by researchers with these particular interests. It is also argued that an inverse situation where cultural and behavioural actors are studied across a long time scale and ecological and environmental actors are studied across a short time scale, is poorly explored. Paleoanthropological research in southern Africa is well suited to test this inverse. Slow-moving adaptation of tool traditions or bony morphology relating to locomotion or mastication cannot be observed on a short time scale and can only be studied due to the extensive timeframe of which palaeodeposits occur in South Africa ($\sim 3.7 - 0.3$ Ma) (Refs? - Dirks et al., 2011; 2017; Herries and Shaw, 2011; Herries et al., 2018; 2020; Pickering et al., 2011b; 2019). While it is not often possible to recreate a single moment such as a knapping event within the palaeo-record (See for example Boxgrove [Smith, 2013]), more recent archaeological assemblages should be regarded as a palimpsest, albeit a shorter one. Therefore, reconstructions and broad scale behavioural and cultural interpretations should be carried out cautiously. In addition, the inverse is also true when considering ecological and environmental actors. Though geological time is considered extensive (i.e. long time scale), there are many instances where geological events occur relatively rapidly (volcanic eruptions, glaciation, flooding and/or changes alluvial regimes).

One can see the need for a time perspectivist lens when examining research questions asked of the palaeo record. For example, it is a common approach to $\frac{206}{206}$

compare the variability of taxa of interpreting alpha taxonomy. Often, studies will assess the variability present within a fossil assemblage as compared to modern humans and extant apes. If the variability within the sample is near to the variability in living populations, this is taken as support for the presence of a homogenous species. A. africanus is often noted as being highly variable while H. naledi, for example, has been noted to be distinctly invariable (Clarke, 2013; Grine et al., 2013; Berger et al., 2015; see also for example, stable isotope studies such as Sponheimer and Lee-Thorp, 1999). While the question why is taxon X so highly variable while taxon Y is not? is not an uncommon one, when viewed through the lens of time perspectivism, the answer becomes clear. A. africanus is a taxon that has been recorded across ~940 ka to ~1.4 Ma while *H. naledi* has been sampled across a maximum of 99,000 years. The time depth of A. africanus can be assumed to include variability due to change through time and so is an incompatible comparison to variability in extant apes or modern humans. P. robustus has also been considered a highly variable hominin taxon with sexual dimorphism beyond that seen in Gorilla gorilla (an extremely variable creature) often identified as an explanation (Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016). Reassessment by Martin et al. (in prep; Chap 3) as well as in Chapter 5 of this thesis however, indicate that once the *P. robustus* sample is divided into finergrained, shallower, time depths and differing dates are taken into account, it can be concluded that the variability within this taxon can be attributed to evolutionary change through time seen through different deposits containing the taxon. Moreover, the variability of any of these smaller *P. robustus* samples fall well within that of living human and ape populations (Martin et al., *in prep*; Chap 3). When time perspectivism is considered, it becomes clear that the variability of A. africanus and H. naledi cannot be compared as the differential time depth of the two samples becomes a confounding variable.

This claim of higher than expected variability can also be levelled at *H. erectus*. **Three sentences redacted.** This allows for finer-grained research questions than

could be asked of a single, highly variable taxon spanning nearly 1.5 million years. In some cases such as *A. africanus*, the unhappy answer to this problem may be that it is unresolvable and research questions must be tailored to accommodate that as well as other limitations discussed above.

Paleo research is plagued by inherent limitations such as sampling biases, variable and deep time depths, differing dates, violations of geological heuristics, and incomplete preservation. These flaws greatly limit the credibility of past conclusions built on erroneous assumptions. The future of palaeo research can and must resolve these flaws by employing a theory originally designed for archaeology. Time perspectivism compels researchers not to force conclusions out of ill fit data but to base research questions on what can be reliably discovered from the data available. Applying time perspectivism in palaeo research will create a more robust body of research for the field to expand upon.

7.3.1 Time Perspectivism and the DMQ

The theory or viewpoint of time perspectivism has heavily influenced both analyses conducted within this thesis and interpretations drawn from subsequent results. The decision to, where possible, limit the Swartkrans comparative sample to specimens deriving from Member 1 only, is a direct result of the adherence to this concept. This decision was made for the purposes of limiting the temporal range of the Swartkrans sample in two ways. The first was to limit the temporal variability between the Swartkrans and DMQ samples in that the Swartkrans Member 1 material has been dated to the closest timepoint to the DMQ material as compared to other Swartkrans members (Pickering et al., 2019; Herries et al., 2020; Chap 2). The second goal was to limit the degree to which the Swartkrans sample employed was affected by time averaging. As Swartkrans Member 1 has been dated to 2.3 Ma to 1.8 Ma (Pickering et al., 2011; Herries and Adams, 2013; Pickering et al., 2019) the maximum temporal depth across which the assemblage could be averaged is ~500,000 years. Further, as geological evidence pertaining to heavy 2008

weathering of the basal flowstone below the Hanging Remnant indicates (Pickering et al., 2019; Herries et al., 2020; Chap 2), the true time depth of that part of the Member 1 deposit is likely less than this. If *P. robustus* specimens derived from any Swartkrans member were included in analyses presented herein, the degree of time averaging would increase markedly and instead represent a deep time depth of up to 1.4 Ma (Pickering et al., 2011; Herries and Adams, 2013; Granger et al., 2015; Pickering et al., 2019; Herries et al., 2020; Chap 2).

Indeed, the geochronological and biochronological evidence from the DMQ and Swartkrans Member 1 has implications for the sexual dimorphism in *P. robustus* hypothesis. The DMQ, dated to ~2.04 – 1.95 Ma (Herries et al., 2020; Chap 2), and Swartkrans Member 1 HR, dated to 2.3 – 1.8 Ma but likely closer to 1.8 Ma (Pickering et al., 2019; Herries et al., 2020; Chap 2), may yet overlap temporally based on these dates. As it is unknown how much time passed to produce the heavy weathering on the Swartkrans Member 1 basal flowstone (Herries and Adams, 2013), it cannot be known how much after 2.3 Ma the deposit began to collect. Further, ESR dating performed on a series of bovid dentition found in situ in sequence within the Swartkrans Member 1 HR deposit suggests that the hominin fossil assemblage dates closer to 1.8 Ma (Herries and Adams, 2013; Chap 2). Faunal evidence, such as differences seen in the *P. robinsoni* material (Herries et al., 2020; Chapter, 3), also indicates that the Swartkrans Member 1 assemblage is likely younger than the DMQ assemblage. Some of the taxa recovered from the DMQ assemblage do not persist into the time period of the Swartkrans Member 1 assemblage and, inversely, taxa deriving from the Swartkrans Member 1 assemblage do not yet exist at the DMQ time period (Adams et al., 2016; Herries et al., 2020; Chap 2). This conclusion is relatively reliable as both sites yield significant faunal assemblages. Thus, temporal overlap between the localities is extremely unlikely. This supports a conclusion that sexual dimorphism cannot at all explain morphological and metrical variation between the DMQ and Swartkrans Member 1 assemblages. Indeed, this reasoning would support a return to

conclusion drawn by (Broom and Robinson, 1952) that smaller specimens within the Swartkrans Member 1 assemblage, such as SK 48, represent females.
8. Discussion

This thesis has assessed multiple lines of evidence regarding the taxonomy and phylogeny of the DMQ robust australopithecine specimens via statistical size comparisons, qualitative character trait assessment, and cladistic analysis. Previously, the DMQ hominin material has been attributed to Paranthropus robustus (n=48), or to early Homo (n=8) (Keyser, 2000; Keyser et al., 2000; Moggi Cecchi et al., 2010). While it has been previously noted that the DNH 7 cranium from DMQ is morphologically distinct compared to other *P. robustus* crania, notably from Swartkrans, this distinctiveness was attributed to sexual dimorphism, with DNH 7 representing an adult female (Keyser, 2000; Lockwood et al., 2007). However, since the Lockwood et al. (2007) analysis positing sexual dimorphism as the explanation for the unique *P. robustus* morphology discovered at DMQ was published, 34 new dental specimens have been discovered and attributed to this taxon thus increasing the sample size substantially and adding to our understanding of variability within the sample. Moreover, the recent discovery of two hominin crania, Redacted and DNH 152, has shown that adult male crania from DMQ are morphologically similar to DNH 7 and are also diagnosably distinct from other *P. robustus* crania from Swartkrans Member 1 and Kromdraai B. A study of the extended dental remains from DMQ identifies some *P. robustus* derived traits present in all three samples but also confirms that the DMQ material is diagnosably distinct from the Swartkrans and Kromdraai B dental remains (Chap 4). None of these differences are consistent with analogous patterns of sexual dimorphism (Chap 5).

Previously, Broom (1949) suggested that differences between the Swartkrans and Kromdraai material represented differences which, while still belonging to the same genus, warranted species level differentiation in which *P. crassidens* referred to the Swartkrans material and *P. robustus* referred to the Kromdraai B material. Given the differences between the DMQ and Swartkrans Member 1 material and the diagnosably distinct nature of the samples, it may be appropriate to reconsider the 211

taxonomic treatment of these site samples. This chapter will discuss these issues and outline other potential hypothesis for explaining the differences between these assemblages.

Specifically, the following hypotheses have been tested herein: 1) all of the robust australopith specimens from South Africa can be accommodated within one highly variable species previously designated as *P. robustus*, 2) the morphological differences observed within *P. robustus* and between the sites of Swartkrans and DMQ reflect differences between males and females in a highly sexually dimorphic population, 3) *P. robustus* forms part of a monophyletic clade with other *Paranthropus* species from eastern Africa. A fourth set of alternative hypotheses are advanced and tested which, when combined, postulate the existence of at least two sub-species currently subsumed within *P. robustus* and that these sub-species level differences are the result of anagenic lineage change through time.

8.1 Diagnosably distinct P. robustus samples

Paragraph redacted

Quantitative assessment of the permanent dentition described in detail in Chapter 5 demonstrates that the DMQ maxillary dentition is statistically significantly smaller than the Swartkrans Member 1 maxillary dentition. That said, very little statistical significance was found when the mandibular dentition was compared. Indeed, the DMQ represented the largest individuals in the joint sample in both the third premolar and the third molar. Robust australopith material from Kromdraai B could not be included in the statistical analysis conducted in Chapter 5 due to the small sample size. As such, comparison was limited to material deriving from the DMQ and from Swartkrans Member 1. Though bivariate plots showed a high degree of overlap between the two samples, nearly all maxillary dentition was found to be statistically significantly different by Mann-Whitney U-tests. **Sentence redacted.** Although the Kromdraai B sample could not be included in the statistical analysis, ²¹²

bivariate plots show the few preserved specimens placed at a point of overlap between the DMQ and Swartkrans Member 1 samples.

Qualitative assessment of deciduous dental traits, after Grine (1985), presented in Chapter 6 also demonstrates that the DMQ assemblage is diagnosably distinct from the Swartkrans Member 1 and Kromdraai B assemblages. Despite representing a relatively short deposition, the DMQ deciduous dental material shows a pattern of variable traits not observed in the other two *P. robustus* samples. The characters observed to be variable in *P. robustus* DMQ are variable because sometimes they represent the gracile australopith character state and sometimes they represent character states of the other robust australopith taxa. The Kromdraai B assemblage, although most similar to the Swartkrans Member 1 assemblage, displays character states observed in the DMQ material rather than the Swartkrans Member 1 assemblage. This pattern is consistent with the results of other analyses presented within this thesis as the DMQ assemblage is shown to be more primitive than other P. robustus samples and consistent with other dental analyses presented within this thesis in that the Kromdraai B material is shown to be intermediate between the DMQ and Swartkrans Member 1 assemblages, although more similar to the latter.

8.2 P. robustus sexual dimorphism

As discussed previously, metrical and qualitative morphological differences between the DMQ and Swartkrans (members unspecified in analyses) assemblages has been explained as extreme sexual dimorphism within the species (Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2016). Central to this hypothesis is the postulate that the DMQ assemblage represents mostly females and the Swartkrans assemblage represents mostly males. It was proposed that differential taphonomic collection processes resulted in this extreme sample bias (Brain, 1981; Moggi-Cecchi et al., 2010; Pickering et al., 2016). For observed craniofacial differences to be explained by such a hypothesis, the degree of sexual 213

dimorphism must exceed even that seen in extant gorillas (Lockwood et al., 2007). **Six sentences redacted.**

Regarding the size differences observed within the permanent dentition, although the disparity between the maxillary and mandibular dentitions is unexpected, it does not resemble any analogous pattern of sexual dimorphism as proposed by Moggi-Cecchi et al. (2010). Sexual dimorphism manifesting in dentition is a well-observed phenomenon within extant primates. Specifically, the 'silverback effect' that has previously been hypothesised to account for *P. robustus* size variability (Lockwood et al., 2007) should result in increased upper molar and lower P3 size – a pattern clearly exhibited in extant sexually dimorphic primates (Lauer, 1975; Plavcan, 2001) – but one that is not present between the Swartkrans Member 1 and DMQ samples.

8.3 Taphonomy or geographic range

Explanations surrounding geographic variability as a result of adaption to differential environmental pressures cannot be supported. The DMQ and Swartkrans localities are located only ~7km apart. Both localities exist at a similar altitude with similar surrounding landscapes. Thus, there is no evidence to indicate differential pressures affecting the individuals within each respective deposit.

As mentioned above, it has been proposed that the DMQ and Swartkrans Member 1 assemblages are the result of two distinctly different collection processes. As has been discussed in Chapter 5, the hypothesis that the variability between the DMQ and Swartkrans *P. robustus* samples represents sexual dimorphism relies heavily on the existence of a taphonomic process that almost exclusively preserves males at Swartkrans and females at DMQ. Though metrical and morphological evidence presented within this thesis does not support the sexual dimorphism hypothesis, it nonetheless remains plausible that different taphonomic agents acting across both sites have led to biased assemblages. For instance, it has recently been proposed 214 that the DMQ assemblage represents a living assemblage and so includes specimens that died naturally in the cave (Riga et al., 2019). This has been proposed as a way of explaining the high frequency of juvenile *P. robustus* specimens and in way of supporting the hypothesis that nearly all adult specimens represent female individuals. It seems more likely, however, that the DMQ assemblage contains a higher frequency of juvenile individuals due to differential excavation methods including sieving to 1mm as these individuals are often represented by deciduous dentition measuring as small as 3.5mm (DNH 88).

Alternatively, it has been proposed that the Swartkrans Member 1 assemblage is the result of a carnivore accumulation (Brain, 1981; Brain, 1993; Pickering et al., 2008, 2016, 2018). This hypothesis was driven primarily by the high frequency of carnivore tooth marks and gnawing on fossil specimens (Brain, 1981; Brian, 1993). The carnivore accumulation hypothesis has also been employed to explain the assertion that nearly all *P. robustus* remains represent male individuals. Behaviour observed in extant baboons, specifically the inclination of dominant males to confront predators, has been cited in support of this hypothesis. Even if there was evidence for assuming the *P. robustus* behavioural repertoire approximated that of extant baboons, it is unlikely that any taphonomic agent would act consistently and solely across any palimpsestic deposit.

As discussed by Adams and Rovinsky (2018), the contents of fossil assemblages can be heavily impacted by non-taphonomic agents. That is, while the assemblage of a modern carnivore den looks distinctly different to that of a modern primate living site (Altmann et al., 1977; Hill et al., 2001; Carlson and Pickering 2003; Bronikowski et al., 2011), these collection agents are not the only factors impacting a fossil assemblage. Factors such as time averaging and collection / sampling bias will greatly affect a fossil assemblage (Adams and Rovinsky, 2018). As an example of the latter, *P. robustus* deciduous incisors can measure only 3.5mm (buccolingual measurement of DNH 88 lower di1) as compared to the average adult

measurement of 6.1mm (average of Swartkrans Member 1 and DMQ lower I1s). Although details regarding the methods undertaken in the early years of excavations are sparse, there is every indication that far coarser grained excavation and sieving protocols were employed as compared to modern methodology. Indeed, manual collection of visible specimens was commonplace. Given this, small specimens such as deciduous hominin dentition may have been missed. In contrast, as the DMQ locality was discovered much more recently, sampling has benefited from more modern excavation methodology. The DMQ excavation, for example, sieves all excavated sediments to 1mm. It is more likely that, although some specimens within the deposit may be the result of carnivore predation, a multitude of processes are responsible for the entirety of the Swartkrans Member 1 assemblage.

8.4 P. robustus locality dates and temporal depth of deposition

One factor that early researchers such as Broom were not able to take into account is the geological age of the various *Paranthropus* bearing deposits or the length of time over which the various units were deposited (as discussed in Chapter 7). Before recent geochronological studies refined the dates of the DMQ, it was thought that the deposit dated to 2.0 - 1.5 Ma based on faunal evidence (Keyser, 2000; Keyser et al., 2000). Recent geochronological analysis has shown this date to be 2.04 – 1.95 Ma (Herries et al., 2020; Chap 2). Swartkrans Member 1 (LB/HR) has been dated to 2.3 – 1.7 Ma (Pickering et al., 2011; Herries and Adams, 2013; Gibbon et al., 2014; Pickering et al., 2019). Though these date ranges allow for temporal overlap between the two deposits, geological and faunal evidence suggest otherwise. The Swartkrans Member 1 Hanging Remnant material is formed over a flowstone dated to ~2.25 Ma, however this flowstone has been heavily truncated before the deposition of the fossil bearing sediments suggesting that fossils deriving from this context likely date closer to the ~1.8 Ma capping flowstone (Herries and Adams, 2013). Linear uptake and US-ESR ages of less than 2.0 Ma also support this younger age (Curnoe et al., 2001; Herries et al., 2009; 216

Herries and Adams, 2013). The DMQ assemblage, conversely likely dates closer to ~2 Ma based on ESR analysis conducted in sequence within the Jangi Buttress surrounding the DNH 134 cranium and the presence of faunal taxa no longer on the South African landscape in the Swartkrans Member 1 time period (Adams et al., 2016; Herries et al., 2020; Chap 2). This leaves open the potential for the DMQ and Swartkrans Member 1 material examined here to be separated by up to ~200,000 years.

Rather than the hypotheses discussed above that assume, or even require, contemporaneity between the DMQ and Swartkrans Member 1 assemblages, it is possible the variation within the South African robust australopith samples is the result of a process such as anagenic evolutionary change that would not be noticeable between contemporaneous samples. The alternative hypothesis proposed here is that morphological differences between the samples, such as statistically smaller maxillary dentition and a less robust masticatory apparatus, represent a temporal cline towards increased robustness within the *P. robustus* lineage. With the dating of DMQ to 2.04-1.95 Ma, *Paranthropus* can be seen to have existed in South Africa for ~600,000 to ~1 million years. This is easily enough time to see lineage variation as recognized in other taxa, such as *A. anamenisis/afarensis* and *H. neanderthalensis* (incorporating the Sima de Los Huesos fossils; Bischoff et al., 2003; Bischoff et al., 2007).

As discussed in Chapter 1, researchers such as Grine (1982, 1983, 1985) treated each sample as a distinct species. Further, Grine (1985) hypothesised that *P. robustus*, represented by the Kromdraai B robust australopiths, was likely ancestral to *P. crassidens*, represented by the Swartkrans (member unspecified) robust australopiths. Although this is an assessment of morphological variability interpreted to be the result of temporally distinct populations undergoing anagenic change, Grine (1985) did not have the advantage of new higher-resolution geochronological data that allows for a finer-grained assessment of the

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relationships of these samples. The new dates for DMQ mean that the hypothesis that the inter-site variability of the *P. robustus* samples is the result of temporal change within a single evolving lineage through time cannot be rejected a priori. Because the ages of fossil sites and variation in the amounts of time over which deposits form are not biological questions, palaeoanthropological researchers rarely consider context as a factor that can influence the testing of biological hypotheses. For instance, because the Cradle of Humankind *P. robustus* sites are all located within a constrained geographic area, and the original dates for these sites all overlapped as a consequence of poor dating resolution, palaeoanthropologists could not explain variability between site samples as being the result of geographically distinct populations or temporally distinct populations. Consequently, hypotheses designed to explain variability between P. robustus samples have tended to fall into one of two mutually exclusive categories: 1) the combined sample represents a single species, highly variable as a consequence of extreme sexual dimorphism and attendant social structures, or 2) that multiple species (at least two) are present. For those researchers that concluded that the South African robust australopith samples represent a single species, sexual dimorphism is most often hypothesised to explain morphological distinctions (Lockwood et al., 2007; Moggi-Cecchi et al., 2010; Pickering et al., 2008, 2016). Each earlier hypothesis represents a different interpretation of variability within the fossil record. By demonstrating that, while geographically constrained, the P. robustus bearing Cradle sites are likely different geological ages, this thesis offers a new hypothesis that reconciles species-level variability between site samples with a single species lineage hypothesis.

Assemblages from different sites that are the same or a similar age bring into focus different biological processes compared to assemblages from different sites that are not especially similar with regard to their geological ages. That is, examination of temporally shallow assemblages is limited to hypotheses regarding taphonomic agents, intraspecific variation such as sexual dimorphism, or taxonomic variation 218

manifesting as cladogenesis or lineage separation. Examination of temporally deep assemblages can be influenced by all aforementioned agents as well as evolutionary change within and between lineages. As all deposits are palimpsestic in nature, assemblages are never truly temporally static. Two or more deposits may, however, overlap in date and so occupy the same temporal envelope. The comparison of such deposits may be considered an assessment of temporally static variation.

Results from analyses presented in Chapter 6 show the DMQ robust australopith material consistently nested at or near the most basal point of the *Paranthropus* clade. *P. boisei* is consistently shown at the most derived point while the Swartkrans Member 1 robust australopith material is found either as a derived sister taxon to *P. boisei* or at an intermediate point within the *Paranthropus* clade. The Kromdraai B robust australopith material is treated as a distinct OTU in analyses 1 and 4 and is consistently found nested in a position intermediate to the DMQ and Swartkrans Member 1 samples.

One sentence redacted. Rather than sexual dimorphism, an alternative hypothesis positing evolutionary change through time is suggested as being the principal agent explaining the variability in both size and morphological character traits between the DMQ and Swartkrans Member 1 *P. robustus* samples. If correct, this would imply that natural selection pressures operating on the southern African *P. robustus* population between ~2.04 Ma and ~1.8 Ma resulted in an increase in size in the maxillary dentition and, more broadly, an increase in the robusticity of the masticatory apparatus. Given the plethora of hypotheses that have been advanced regarding the adaptive strategy of *P. robustus* in terms of its megadontic dentition and heavily buttressed bony architecture (see for example Lockwood et al., 2007; Strait et al., 2009; Cofran, 2014), a trend towards increased size and robustness over time coupled with stasis in the mandibular dental size, or a change

predating the DMQ assemblage, may help to elucidate bio-mechanical interpretations of *P. robustus* adaptive strategy.

If P. robustus DMQ is ancestral to all other Paranthropus taxa, a reassessment of Grine's (1985) hypothesis that the ancestor to *Paranthropus* would be *A. africanus* or an *A. africanus*-like morph, must be re-examined. Of course, Grine's (1985) analysis was conducted before the discovery of KNM-WT 17000 and the subsequent placement of *P. aethiopicus* at this ancestral node. Further, while the cladistic analyses presented in Chapter 6 do not necessarily support the hypothesis that *P. aethiopicus* is the most primitive member of the *Paranthropus* clade, the taxon is poorly represented by deciduous dentition. One sentence redacted. Specimens attributed to P. aethiopicus, however, have been dated to ~2.7 Ma. Though dates have no influence of cladistic analyses, such information is crucial to the interpretation of cladistic results. The result above, for example, can be interpreted in multiple ways. The first interpretation is that the dating of P. aethiopicus is erroneous and the taxon represents a highly derived member of the Paranthropus clade and is potentially descended from either P. robustus or P. boisei. The second interpretation is that the phylogenetic tree is erroneous and missing data from *P. aethiopicus* or incorrect character interpretation has produced an unreliable result. The third is that the dates or sampling of both *P. robustus* and P. boisei are erroneous and both taxa existed long before current data shows. A third interpretation of such inconsistent and counterintuitive results is that KNM-WT 17000 does not, in fact, represent a hominin ancestor and instead belongs in the great ape lineage (Verhaegen, 1994).

The placement of the Kromdraai B *P. robustus* sample is not easily resolved. Grine (1985) concluded that there was substantial evidence for the separation of the Kromdraai B and Swartkrans samples into distinct species based on an assessment of deciduous dental character traits. Qualitative assessment performed here in Chapter 6 shows that there is more separation between the DMQ

and Kromdraai B samples than between the Kromdraai B and Swartkrans samples. However, the Kromdraai B sample size is very small, and it now seems probable based on currently available evidence that this sample overlapped in time with that of Swartkrans. Thus, the case for discriminating the Swartkrans and Kromdraai robust australopith samples at the subspecies level is tenuous.

Two sentences redacted. However, the Kromdraai B *P. robustus* morph is poorly represented both cranially and dentally. Further, little chronological evidence is available for the clarification of the Kromdraai B sample. Based on palaeomagnetic analysis Thackeray et al. (2002) argued that Member 1 and 2 were dated to slightly older than ~1.95 and ~1.78 Ma. While Thackeray et al. (2002) have argued that TM1517 comes from Member 1 and Partridge (1986, 2000) have stated that all the hominin fossils come from Member 3, thus based on the stratigraphy of Partridge (1982, 2000) Herries et al. (2009) interpreted the age of the fossils as between 1.78 Ma (the lower age limit of Member 2) and 1.65 Ma based on biochronology. This would make the hominins younger than Swartkrans Member 1 but perhaps similar in age to Swartkrans Member 2 (Herries and Adams, 2013) and older than those from Coopers D (<1.4 Ma; Pickering et al., 2019). However, Bruxelles et al. (2016) and Braga et al. (2017) have reinterpreted the stratigraphy of the site and state that the hominin fossils do not all come from a single unit but perhaps from different members of quite different time periods. This means that the original age determinations of Thackeray et al. (2002) and Herries et al. (2009) should not longer be considered valid and that no good age ranges exist for the deposits beyond biochronology, some of which may suggest an age equivalent to DMQ, but other estimates are younger and more equivalent to Swartkrans Member 1. Given the complexity of the deposits at Kromdraai B it is therefore possible that Paranthropus fossils of both DMQ and Swartkrans Member 1 age may exist and thus a mixture of the two morphs, rather than Kromdraai B representing an intermediate morph.

Analyses conducted within this thesis all indicate that the DMQ robust australopith sample likely represents an adaptive midpoint. That is, as the *Paranthropus* clade is broadly defined by increasing robusticity, it can be hypothesised that an earlier temporal morph would be more gracile than a later temporal morph. When the possibility that variation between *P. robustus* samples may be due to through-time variability, a pattern of metrical and morphological difference that doesn't follow any sexual dimorphism analogies becomes less problematic. Palaeo-environmental studies suggest that a major climatic shift occurred ~2.1 Ma (Hopley et al., 2007; deMenocal, 2011; Caley et al., 2018). Such an event would be consistent with morphological evidence suggesting a period of relatively rapid adaptive change following a period of relative adaptive stability. Specifically, this pattern can be observed in Chapter 6 where qualitative character assessment shows a markedly higher degree of change between the three primary P. robustus samples than between the Taung and Sterkfontein A. africanus samples despite the former representing ~600,000 years of change (Herries and Adams, 2013; Pickering et al., 2019; Herries et al., 2020; Chap 2) and the latter representing ~1.4 million years of change (Clarke, 2013; Herries et al., 2013; Pickering et al., 2019).

8.5 Conclusions

Historically, it has been suggested that the variation between *P. robustus* samples from the sites of DMQ, Swartkrans, and Kromdraai either represents male and female specimens drawn from a single highly sexually dimorphic species (Lockwood et al., 2007; Moggi-Cecchi et al., 2010) or distinct temporal populations **Redacted** drawn from a single anagenically evolving lineage (Grine, 1983, 1985). The contribution of this thesis has been to analyse new cranial and dental evidence and dating evidence from the DMQ which has provided evidentiary support for the hypothesis that the variation between *P. robustus* samples is the result of temporal change within a single lineage segment. Further, as new evidence presented here confirms the disparate ages of these samples, they cannot be indisputably interpreted as competing taxa and instead should be interpreted as a single

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lineage. Dental size analysis indicates a temporal cline towards increasing robustness with the DMQ material representing the Paranthropus taxon with the least robusticity. This trend of robustness appears to deviate from the expected pattern in that there is a disparity in the rate of change between both the maxillary and mandibular dentition and between the mandibular dentition and the bony mandibular morphology. Craniodental and deciduous dental evidence both independently support a hypothesis in which the DMQ material represents a more primitive morph of *P. robustus* as compared to the other South African robust australopith samples. Additionally, these analyses both support a hypothesis in which the DMQ material represents the most basal member of the Paranthropus clade in a position ancestral to all other robust australopithecines. Both analyses found that *P. aethiopicus* nests in a highly derived position rather than as a highly primitive member of this clade. Although the DMQ P. robustus material exhibits far more A. africanus-like traits than other robust australopith taxa, the relationship between A. africanus and the Paranthropus clade remains unresolved. It must be noted, however, that there are more morphological similarities between the DMQ material and this taxon than between the DMQ material and *P. aethiopicus*.

8.6 The influence of temporality on phylogenetic interpretation

Rather than approaching analysis of the combined Swartkrans and DMQ *P. robustus* samples as one homogenous palaeo-population, the results of this study suggest that future analyses ought to treat DMQ and Swartkrans Member 1 as two temporally distinct *P. robustus* populations. **Six sentences redacted.**

Three sentences redacted. The treatment of the three primary *P. robustus* samples as a single OTU results in a time averaged joint assemblage. As discussed in Chapter 6, it is Sterkfontein and *A. africanus* that make the perfect example of the effects of time averaging. As a specific example, Sterkfontein Member 4 formed over more than half a million years. The variability within this deposit has alternatively been accepted as intraspecific variability or thought to represent two ²²³

different species (Clarke, 1993, 2013). Once sentence redacted. That is, it is possible that an assemblage with over half a million years of time averaging consists, in truth, of specimens representing variable time points within the same lineage. In terms of the taxon itself, A. africanus is often discussed as a highly variable species although it is rarely noted that this species is thought to have existed for up to ~1.4 million years based on ages of 3.03-2.61 Ma for Taung and Makapansgat (Herries et al., 2013) and dates as late as ~2.07 Ma (Pickering and Herries, 2020), maybe even 1.8-1.6 Ma if Clarke (2013) is correct about the assignment of StW 53 to A. africanus). Indeed, A. sediba has been found to be contemporaneous with *P. robustus* from the DMQ assemblage (Herries et al., 2020; Chap 2) and is considered by some to represent a late occurring member of the A. africanus lineage and is "probably descended from Australopithecus africanus" (Berger et al., 2010, pp. 195), thus expanding the temporal footprint of this taxon even further. Given this, the marked variability observed within this species likely represents through-time rather than temporally static variability. This same effect has influenced interpretation of *P. robustus* resulting from the general acceptance of the multiple samples into a single taxon. If all samples of South African robust austalopiths are treated as a single taxon, the resultant assemblage would span over 1 million years (2.04 Ma as the oldest date of the DMQ to 0.8 as the youngest date of Swartkrans Member3; Herries and Adams, 2013; Herries et al., 2020; Chap 2). This is a complicating factor that was identified by Clarke (1985) when discussing the variability of hominin material deriving from Sterkfontein Member 4. Clarke (1985, pp. 171) stated that the large degree of morphological variability observed across A. africanus "should be expected" as the deposit "embraces a long period of time" and so may represent temporal variation. The treatment of all A. africanus specimens as a single sample, then, may result in microevolutionary temporal change to be overlooked. Indeed, Clarke (2013) later argued that the degree of variability observed was significant enough to warrant species level delineation. This principle must be considered regarding all other taxa with such a time depth.

Given this, it is unsurprising that cladistic analyses produce drastically disparate results when given a single P. robustus OTU as compared to temporally distinguished OTUs. Phylogenetic analyses prior to the discovery of KNM-WT 17000 and the acceptance of *P. aethiopicus* as a highly primitive *Paranthropus* species most commonly hypothesised that A. africanus was ancestral to the South African robust austalopiths (White et al., 1981; Grine, 1985; among others). After the naming of *P. aethiopicus*, some researchers such as Walker et al. (1986) still hypothesised that A. africanus was ancestral to the South African robust australopiths while this new taxon represented the ancestor of only the eastern African robust australopiths. Others such as Delson (1986) attributed A. africanus to a basal node of the Homo clade and hypothesised that P. aethiopicus was ancestral to both South African P. robustus and eastern African P. boisei. Kimbel et al. (1988, pp. 266) further clarified that P. aethiopicus "represents a link between A. afarensis and A. robustus and/or A. boisei." Though remaining agnostic about whether both South African and eastern African robust australopiths represented descendants of *P. aethiopicus*, Kimbel et al. (1988) concluded that it was unlikely that A. africanus could be ancestral to either.

At the time of these studies, the South African robust australopiths were treated as a single OTU. This treatment produces a highly variable OTU including both more primitive and more derived morphologies. Additionally, the DMQ material had not yet been discovered at the time of these analyses. Cladistic studies conducted following the discovery of the DMQ material included this sample within the *P. robustus* OTU. The inclusion of the DMQ robust australopith material as a distinct OTU has produced phylogenetic trees showing *P. aethiopicus* as nested within the *Paranthropus* clade as the sister taxon of *P. boisei* (**Redacted**; Chap 6).

8.7 Future Work

The clarification of dates throughout the Cradle of Humankind and the confirmed contemporaneity of *Paranthropus, Australopithecus,* and *Homo* (Herries et al., 2020; Chap 2) has implications for behavioural interpretation. Athough all three of these genera likely existed on the South African landscape at the same time, there is little to no evidence that more than one species belonging to each genus co-existed. *P. robustus* DMQ, *A. sediba,* and a South African morph of *H. aff. erectus* have all been recovered from temporally and geographically constrained samples. If they co-occurred, there is reason to think that they may have partitioned their habitats according to the principle of competitive exclusion of Gause's Law (Gause, 1934; Mayr, 1950; Hardin, 1960; Wolpoff, 1971; Weiss, 1972; Swedlund, 1974; Grine, 1981; Pocheville, 2015).

The pattern of variability evinced between the DMQ and Swartkrans samples likely represents a trajectory of evolutionary change through time, and therefore has significance for biomechanical analysis and adaptive strategy reconstructions of the *P. robustus* masticatory apparatus. In particular, rather than approaching analysis of the combined Swartkrans Member 1 and DMQ P. robustus samples as one homogenous palaeo-population, the results of this study suggest that future analyses ought to treat DMQ and Swartkrans Member 1 as two temporally distinct *P. robustus* populations, adept for the purposes of elucidating change in adaptive strategy and biomechanical adaptation through time. The distinctly separate temporal envelope of the DMQ and Swartkrans Member 1 P. robustus populations, combined with their geographic proximity to one another, will allow studies to adopt the *a priori* assumption that variability between the two populations is not the consequence of temporally static geographic diversity. Unlike studies that contrast taxa and palaeo-populations separated by thousands of kilometres, further analysis of the DMQ and Swartkrans Member 1 P. robustus material will allow for a finegrained assessment of the trajectory of evolutionary change through time of this enigmatic member of the hominin family tree. Particularly, as the Paranthropus

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clade is broadly defined as showing a trend of increasing robusticity evolving for particular dietary requirements, the study of two samples which remove geographic and ecological variation, will be particularly informative.

Paragraph redacted.

As discussed in Chapter 6, further cladistic studies must be conducted. Firstly, a broader assessment of the deciduous dentition may work to clarify results found here. That is, the high degree of morphological variability observed within the DMQ material suggests that rather than data structured to remove intra-specific variability, a more inclusive selection of character traits may elucidate taxon-specific patterns of variability. Such patterns would likely assist in interpretations of lineage change trajectory. Secondly, such an analysis must be applied to permanent dentitions. A study of permanent dentitions would yield larger samples of each taxon and so better characterize the variability within them. It could also be argued that permanent dental morphology is more tied to, and so more informative of, dietary adaption. An assessment of such morphology employing temporally separated OTUs will work to inform adaptive trajectories along distinct hominin lineages.

Finally, newly discovered material from the DMQ along with highly refined dates indicating that the entire assemblage was deposited across less than 90,000 years or less allows for novel research questions surrounding hominin palaeopopulations. Rather than comparing the DMQ *P. robustus* material to the Swartkrans *P. robustus* material, internal comparison of DMQ material will allow for assessment of temporally static variability. **Sentence redacted.** Additionally, as the DMQ assemblage contains a high number of juvenile specimens and through-time variability is not a factor, more detailed studies of ontogeny or dental development and eruption may be conducted.

References

- Adams, JW 2010 'Taphonomy of the Gondolin GD 2 in situ deposits and its bearing on interpretations of South African Plio-Pleistocene karstic fossil assemblages.' *Journal of Taphonomy*, vol. 8, no. 2, pp. 79-114.
- Adams, JW, Conroy, GC 2005, Plio-Pleistocene faunal remains from the Gondolin GD 2 in situ assemblage, North West Province, South Africa, Interpreting the Past: Essays on Human, Primate and Mammal Evolution in Honor of David Pilbeam, Brill Academic Publishers Inc., Boston, pp. 243-261.
- Adams, JW, Herries, AIR, Kuykendall, KL & Conroy, GC 2007 'Taphonomy of a South African cave: geological and hydrological influences on the GD 1 fossil assemblage at Gondolin, a Plio-Pleistocene paleocave in the Northwest Province, South Africa.' *Quaternary Science Reviews*, vol. 26, pp. 2526-2543.
- Adams, JW, Olah, A, McCurry, MR, Potze, S 2015 'Surface model and tomographic archive of fossil primates and other mammal holotype and paratype specimens of the Ditsong National Museum of Natural History, Pretoria, South Africa.' *PLoS ONE*, vol. 10, 10:e0139800.
- Adams, JW, Rovinsky, DS, Herries, AIR, Menter, CG 2016, 'Macromammalian faunas, biochronology and palaeoecology of the early Pleistocene Main Quarry hominin-bearing deposits of the Drimolen Palaeocave System, South Africa.' PeerJ 4: e1941.
- Aiello, L, Dean, C 1990, *An introduction to human evolutionary anatomy*. Academic Press, London.
- Alemseged, Z, Spoor, F, Kimbel, WH, Bobe, R, Geraads, D, Reed, D, Wynn, JG 2006 'A juvenile early hominin skeleton from Dikika, Ethiopia.' *Nature*, vol. 443, pp. 296-301.

- Altmann, J, Altmann, SA, Hausfater, G, McCuskey, SA 1977 'Life History of Yellow Baboons: Physical Development, Reproductive Parameters, and Infant Mortality.' *Primates*, vol. 18, no. 2, pp. 315-330.
- Antón, SC 1997 'Developmental age and taxonomic affinity of the Mojokerto child, Java, Indonesia.' *American Journal of Physical Anthropology*, vol.102, pp. 497-514.
- Antón, SC 2003 'Natural History of *Homo erectus*.' Yearbook of Physical Anthropology, vol. 46, pp. 126-170.
- Arambourg, C, Coppens, Y 1968 'Decouverte d'un australopithecien nouveau dans les gisements de l'Omo (Ethiopie).' *South African Journal of Science*, vol. 64, pp. 58-59.
- Backwell, L, de Errico, F 2008 'Early hominid bone tools from Drimolen, South Africa.' *Journal of Archaeological Science*, vol. 35, pp. 2880–2894.
- Bailey, GN 1983 'Concepts of time in quaternary prehistory.' *Annual Review of Anthropology*, vol. 12, pp. 165-192.
- Bailey, GN 2007 'Time perspectives, palimpsests and the archaeology of time.' *Journal of Anthropological Archaeology*, vol. 26, pp. 198-223.
- Bailey, GN 2008 'Time perspectivism: origins and consequences.' *Journal of Anthropological Anrchaeology*, vol. 26, pp. 198-223.
- Bajwa, M, Srinivasan, D, Nishikawa, H, Rodrigues, D, Solanki, G, White, N 2013 'Normal fusion of the metopic suture.' *Journal of Craniofacial Surgery*, vol. 24, pp. 1201-1205.
- Balzeau, A, Grimaud-Hervé, D, Jacob, T 2005, 'Internal cranial features of the Mojokerto child fossil (East Java, Indonesia)', *Journal of Human Evolution,* vol. 48, pp. 535-553.

- Benazzi, S, Gruppioni, G, Strait, DS, Hublin, JJ 2014, 'Technical note: virtual reconstruction of KNM-ER 1813 Homo habilis cranium.' American Journal of Physical Anthropology, vol. 153, pp. 154-160.
- Benazzi, S, Ian, RG, Gruppioni, GWW & Kullmer, O 2013 'Comparison of occlusal loading conitions in a lower second premolar using three dimensional finite element analysis', *Clinical Oral Investigations*, DOI: 10.1007/s00784-0973-8.
- Bennington, JB & Aronson, MFJ 2012 'Reconciling scale in paleontological and neontological data: dimensions of time, space, and taxonomy.' In *Paleontology in ecology and conservation*, Louys, J (Ed), Springer, Berlin, Heidelberg, pp. 39-67.
- Berger, L 2002 'Australopithecus sediba and the earliest origins of the genus Homo.' Journal of Anthropological Sciences, vol. 90, pp. 117-131.
- Berger, LR, Hawks, J, Dirks, PHGM, Elliott, M, Roberts, EM 2017 '*Homo naledi* and Pleistocene hominin evolution in subequatorial Africa.' *eLife*, 6:e24234, DOI: 10.7554.
- Berger, LR 2006, 'Brief communication: Predatory bird damage to the Taung type-skull of Australopithecus africanus Dart 1925.' *American Journal of Physical Anthropology*, vol. 131, no. 2, pp.166-168.
- Berger, LR, Clarke, RJ 1995, 'Eagle involvement in accumulation of the Taung child fauna.' *Journal of Human Evolution*, vol. 29, no. 3, pp. 275-299.
- Berger, LR, de Ruiter, DJ, Churchill, SE, Schmid, P, Carlson, KJ, Dirks, PHGM, Kibii, JM 2010, 'Australopithecus sediba: A New Specie of *Homo*-Like Australopith from South Africa', *Science*, vol. 328, pp. 195-204.
- Berger, LR, Hawks, J, de Ruiter, DJ, Churchill, SE, Schmid, P, Delezene, LK, Kivell, TL, Garvin,
 HM, Williams, SA, DeSilva, JM, Skinner, MM, Musiba, CM, Cameron, N, Holliday, TW,
 Harcourt-Smith, W, Ackermann, RR, Bastir, M, Bogin, B, Bolter, D, Brophy, J, Cofran, ZD,

Congdon, KA, Deane, AS, Dembo, M, Drapeau, M, Elliot, MC, Feuerriegel, EM, Garcia-Martine, D, Green, DJ, Gurtov, A, Irirsh, JD, Kruger, A, Laird, MF, Marchi, D, Meyer, MR, Nalla, s, Negash, EW, Orr, CM, Radovcic, D, Schroeder, L, Scott, JE, Throckmorton, Z, Tocheri, MW, VanSickle, C, Walker, CS, Wei, P & Zipfel, B 2015, 'Homo naledi, a new species of the genus Homo from the Dinaledi Chamber, South Africa', *eLIFE*, DOI: 10.7554/eLife.09560.

- Berger, LR, McGraw, WS 2007, 'Further evidence for eagle predation of, and feeding damage on, the Taung child.' *South African Journal of Science*, vol. 103, no. 11-12, pp.496-498.
- Berthaume, MA, Schroer, K 2017 'Extant ape dental topography and its implications for reconstructing the emergence of early *Homo*.' *Journal of Human Evolution*, vol.112, pp. 15-29.
- Bischoff, JL and Shamp, DD 2003, 'The Sima de los Huesos Hominids Date to Beyond U/Th Equilibrium (>350 kyr) and Perhaps to 400-500 kyr: New Radiometric Dates.' *Journal of Archaeological Science*, vol. 30, pp. 275-280.
- Bischoff, JL, Williams, RW, Rosenbauer, RJ, Aramburu, A, Arsuaga, JL, García, N, Cuenca-Bescós, G 2007, 'High-resolution U-series dats from the Sima de los Huesos hominids yields 600^{+∞}-₆₆ kyrs: implications for the evolution of the early Neanderthal lineage.' *Journal of Archaeological Science*, vol. 34, pp. 763-770.
- Blumenberg, B, and Lloyd, AT, 1983, '*Australopithecus* and the origin of the genus *Homo*: Aspects of biometry and systematics with accompanying catalog of tooth metric data.' *BioSystems*, vol. 16, pp. 127-167.
- Braby, MF, Eastwood, R & Murray, N 2012, 'The subspecies concept in butterflies: has its application in taxonomy and conservation biology outlived its usefulness?' *Biological Journal of the Linnean Society*, vol. 106, pp. 699-71.

- Braga, J, Fourval, LB, Lans, B, Bruxelles, L, Thackeray, JF 2016 'Evolutionary, chrono-cultural and palaeoenvironmental backgrounds to the Kromdraai site: A regional perspective.' *Excavation of the Kromdraai, in the Cradle of Humankind World Heritage Site*, pp. 1.
- Braga, J, Thackeray, JF 2003, 'Early Homo at Kromdraai B: probabilistic and morphological analysis of the lower dentition.' *Comptes Rendus Palevol,* vol. 2, no. 4, pp. 269-279.
- Brain, C 1993, 'A taphonomic overview of the Swartkrans fossil assemblages', in Brain, C (ed.), *Swartkrans: a cave's chronicle of early man*, Pretoria, Transvaal Museum, pp. 257-264.
- Brain, CK 1976, 'A re-interpretation of the Swartkrans Site and it remain' *South African Journal of Science*, vol. 72, pp. 141–146.
- Brain, CK 1958, *The Transvaal Ape-Man-Bearing Cave Deposits: An overview of the sites at Sterkfontein, Kromdraai, Swartkrans and Makapan.* Transvaal Museum, Pretoria.
- Braun, DR, Harris, JWK, Levin, NE, McCoy, JT, Herries, AIR, Bamford, M, Bishop, I, Richmond,
 BR, Kibunjia, M 2010, 'Early hominin diet included diverse terrestrial and aquatic animals
 1.95 Ma ago in East Turkana, Kenya' *PNAS*, vol. 107, pp. 10002-10007.
- Bronikowski, AM, Altmann, J, Brockman, DK, Cords, M, Fedigan, LM, Pusey, A, Stoinski, T, Morris,
 WF, Strier, KB, Alberts, SC 2011, 'Aging in the Natural World: Comparative Data Reveal
 Similar, Mortality, Patterns Across Primates', vol. 331, pp. 1325-1328.
- Broom, R, Schepers, GWH 1946, *The South African Fossil Ape-Men The Australopithecinae*. Transvaal Museum, Pretoria.
- Broom, R, Robinson, JT, Schepers, GWH 1950, *Sterkfontein Ape-Man* Plesianthropus, Transvaal Museum, Pretoria.
- Broom, FRS and Robinson, JT 1952, *Swartkrans Ape-Man* Paranthropus crassidens, Transvaal Museum, Pretoria.

- Broom, R 1946, *The occurrence and general structure of the South African ape-men. Part 1.* Transvaal Museum, Pretoria, No. 2, pp. 7–153.
- Broom, R 1950 'The genera and species of the South African fossil ape-men.' *American Journal of Physical Anthropology*, vol. 8, pp. 1–13.

Broom, FRS 1936, 'New fossil anthropoid skull rom South Africa', *Nature*, vol. 138, pp. 486-488.

Broom, FRS 1937, "The fossil ape newly found in South African is probably closer to man than the living apes." *Scientific American*, pp. 85.

Broom, R 1938, 'The Pleistocene anthropoid apes of South Africa', Nature, vol. 142, pp. 377-379.

Broom, R 1947, 'Discovery of a new skull of the South African ape-man, *Plesianthropus*', *Nature*, vol. 159, pp. 672.

Broom, R 1949a 'Another New Type of Fossil Ape-Man.' Nature, vol. 164. no. 4132, pp. 57.

Broom, R 1949b, 'Sterkfontein ape-man Plesianthropus', no. 4, Transvaal Museum.

Broom, R, Robinson, JT 1949 'A new type of fossil man', Nature, vol. 164, no. 4164, pp. 322-323.

- Bruxelles, L, Maire, R, Couzens, R, Thackeray, JF, Braga, J 2016, 'A revised stratigraphy of Kromdraai.' In: Braga, J, Thackeray, JF (eds.), *Kromdraai: a Birthplace of Paranthropus in the Cradle of Humankind*. Sun Press, South Africa, pp. 31–48.
- Bruxelles, L, Stratford, DJ, Maire, R, Pickering, TR, Heaton, JL, Beaudet, A, Kuman, K, Crompton, R, Carlson, KJ, Jashashvili, T, McClymont, J 2019 'A multiscale stratigraphic investigation of the context of StW 573 "Little Foot" and Member 2, Sterkfontein Caves, South Africa.' *Journal of Human Evolution*, vol. 133, pp. 78-89.

- Bullock, PN, Fedoroff, N Jongerius, A 1985 '*Handbook for soil thin section description*.' Waine Research Publ., Wolverhampton, U.K.
- Butler, PM 1939 'Studies of mammalian dentition. Differentiation of the post-canine dentition.' *Proceedings of the Royal Society London*, vol. 109, pp. 1-36.
- Butzer, K, 1976, 'Lithostratigraphy of the Swartkrans Formation.' *South African Journal of Science*, vol. 72, pp. 136–141.
- Caley, T, Extier, T, Collins, JA, Schefuß, E, Dupont, L, Malaizé, B, Rossignol, L, Souron, A, McClymont, EL, Jimenez-Espejo, FJ, García-Comas, C, Eynaud, F, Martinez, P, Roche, DM, Jorry, SJ, Charlier, K, Wary, M, Gourves, PY, Billy, I, Giraudeau, J 2018 'A two-million-year-long hydroclimatic context for hominin evolution in southeastern Africa.' *Nature*, Vol. 560, pp. 76-79.
- Campbell, B., 1963 'Quantitative taxonomy and human evolution.' In *Classification and human evolution*, vol. 37, Aldine, Chicago, pp. 50-74.
- Carlson, KJ, Pickering, TR 2003 'Intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages.' *Journal of Human Evolution*, vol. 44, pp. 431-450.
- Catt, JA 1990 'Palaeopedology manual.' Quaternary International, vol. 6, pp- 1-95.
- Clarke, RJ. Howell, FC 1972 'Affinities of the Swartkrans 847 hominid cranium.' *American Journal of Physical Anthropology*, vol. 37, no. 3, pp. 319-335.
- Clarke, RJ 1985 'Australopithecus and early Homo in southern Africa.' In: Delson, E (ed.), Ancestor, the Hard Evidence, Alan R Liss, New York, pp. 171-177.

- Clarke, RJ 2019 'Excavation, reconstruction and taphonomy of the StW 573 Australopithecus prometheus skeleton from Sterkfontein Caves, South Africa.' Journal of human evolution, vol. 127, no. 41.
- Clarke, RJ, Partridge, TC 2002 'On the unrealistic "revised age estimates" for Sterkfontein.' *South African Journal of Science*, vol. 95, no. 9, pp. 415-419.
- Clarke, RJ 1977 'A juveline cranium and some adult teeth of early *Homo* from Swartkrans, Transvaal.' *South African Journal of Science*, vol. 73, pp. 46-49.
- Clarke, RJ 2008 'Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*.' *South African Journal of Science*, vol. 104, pp. 443-449.
- Clarke, RJ 2013 'Australopithecus from Sterkfontein Caves, South Africa.' In: Reed, KE, Fleage, JG & Leakey, RE (eds.), *The Paleobiology of* Australopithecus, Springer Dordrecht, Heidelberg, New York, London, pp. 105-123.
- Clarke, RJ 2019 'Australopithecus prometheus was validly named on MLD 1.' American journal of physical anthropology, vol. 170, no. 4, pp. 479-481.
- Clarke, RJ, Kuman, K 2019 'The skull of StW 573, a 3.67 Ma Australopithecus prometheus skeleton from Sterkfontein Caves, South Africa.' *Journal of Human Evolution*, vol. 134, 102634.

Clayton, WD 1983 'The genus concept in practice.' Kew Bulletin, issue 38, pp. 149-153.

Cochard, LR 1985 'Ontogenetic allometry of the skull and dentition of the rhesus monkey (Macaca mulatta).' In: Jungers, WL (ed.), Size and Scaling in Primate Biology, Plenum Press, New York, pp. 231-256.

- Cofran, Z, Thackeray, FJ 2010 'One or two species? Amorphometry comparison between robust australopithecines from Kromdraai and Swartkrans.' *South African Journal of Science*, vol. 106, no. 1/2, pp. 40-43.
- Cofran, Z 2014, 'Mandibular development in *Australopithecis robustus*.' *American Journal of Physical Anthropology*, vol. 154, pp. 436-446.

Constantino, P, Wood, B 2004 'Paranthropus paleobiology.' Paleontropologia, vol. 3, pp. 137-151.

- Cooke, HBS 1991 '*Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African expedition.' *Palaeontologica Africana*, vol. 28, pp. 9-21.
- Cope, DA, 1993 'Measures of dental variation as indicators of multiple taxa in samples of sympatric Cercopithecus species.' In *Species, species concepts and primate evolution*, Springer, Boston, MA, pp. 211-237.
- Coqueugniot, H, Jublin, JJ, Veillon, F, Houët, F, Jacob, T 2004 'Early brain growth in Homo erectus and implications for cognitive ability.' *Nature*, vol. 431, pp. 299 302 (2004).
- Cracraft, J 1983 'Species concepts and speciation analysis.' *Current Ornithology*, vol. 1, pp. 159-187.
- Curnoe, D, Grun, R, Thackeray, JF 2002 'Electron Spin Resonance dating of tooth enamel from Kromdraai B, South Africa.' *South African Journal of Science*, vol. 98, pp. 540.
- Curnoe, D 2010 'A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.).' *Journal of Comparative Human Biology*, vol. 61, pp. 151-177.
- Curnoe, D, Tobias, PV 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*, vol. 50, pp. 36-77.

- Curtis, GH, Drake, Cerling, T, Hampel 1975 'Age of KBS tuff in Koobi Fora Formation, East Rudolf, Kenya.' *Nature*, vol. 248, pp. 395-398.
- Dahlburg, AA 1945 'The changing dentition of man.' *Journal of the American Dental Association*, vol. 32, pp. 676-690.
- Dart, R 1957, *The Osteodontokeratic Culture of* Australopithecus prometheus, Transvaal Museum, Pretoria.
- Dart, RA 1925 'Australopithecus africanus: the man-ape of South Africa.' Nature, vol. 115, pp. 195-199.
- Dart, RA 1948 'The Makapansgat proto-human *Australopithecus prometheus*.' *American Journal of Physical Anthropology*, vol. 6, no. 3, pp. 259-284.

de Menocal, PB 2011, 'Climate and Human Evolution.' Science, vol. 311, pp. 540-541.

- de Queiroz, K 1998 'The general lineage concept of species, species criteria, and the process of speciation a conceptual unification and terminological recommendations' In: Howard, DJ, Berlocher, SH (eds.), Endless Forms: Species and Speciation, Oxford University Press, New York, pp. 57-75.
- de Queiroz, K 2007, 'Species concepts and species delimitation.' *Systematic Biology*, vol. 56, pp. 879-886.
- de Queiroz, K, Gauthier, J 1994, "Toward a phylogenetic system of biological nomenclature." *Trends in Ecology & Evolution*, vol. 9, no. 1, pp. 27-31.

- de Ruiter, DJ 2003 'Revised faunal lists for Members 1-3 of Swartkrans, South Africa.' *Annals of the Transvaal Museum*, vol. 40, pp. 29-41.
- de Ruiter, DJ, Pickering, R, Steininger, CM, Kramers, JD, Hancox, PJ, Churchill, SE, Berger, LR
 & Backwell, L 2009 'New Australopithecus robustus fossils and associated U-Pb dates from Cooper's cave (Gauteng, South Africa).' *Journal of Human Evolution*, vol. 56, no. 5, pp. 497-513.
- DeSilva, J, Lesnik, J 2006 'Chimpanzee neonatal brain size: implications for brain growth in *Homo erectus*.' *Journal of Human Evolution*, vol. 51, pp. 207-212.
- Deino, AL 2011 '40Ar/39Ar dating of Laetoli, Tanzania.' In: Harrison, T (ed.), Vertebrae Palaeobiology and Paleoanthropology, Paleontology and Geology of Laetoli: Human Evolution in Context: Volume 1: Geology, Geochronology, Palaeoecology and Palaeoenvironment, Springer, Netherlands, pp. 77-97.
- Delson, E 1978, "Models of early hominid phylogeny." In: Jolly, CJ (ed.), Early hominids of Africa, London, Duckworth, pp. 517-41.
- Dembo, M, Radovčić, D, Garvin, HM, Laird, MF, Schroeder, L, Scott, JE, Brophy, J, Ackermann, RR, Musiba, CM, de Ruiter, Dj, Mooers. AØ & Collard, M 2016, 'The evolutionary relationships and age of *Homo naledi*: An assessment using dated Bayesian phylogenetic methods', *Journal of Human Evolution*, vol. 97, pp.17-26.
- Dirks, PMDH, Kibii, JN, Kuhn, BF, Steininger, C, Churchill, SE, Kramers, JD, Pickering, R, Farber, DL, Mériaux, SA, Herries, AIR, King, GCP & Berger, LR 2010 'Geological setting and age of Australopithecus sediba from southern Africa', *Science*, vol. 328, pp. 205-208.
- Dirks, PHGM, Roberts, EM, Hilbert-Wolf, H, Kramers, JD, Hawks, J, Dosseto, A, Duval, M, Elliot,M, Evans, M, Grun, R, Hellstrom, J, Herries, AIR, Joannes-Boyau, R, Makhubela, TV,Placzek, CJ, Robbins, J, Spandler, C, Wiersma, J, Woodhead, J, Bergerm LR 2017 'The

age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa.' *eLife*, vol. 6, pp. 1-59.

- Dominguez-Rodrigo, M, Pickering, TR, Baquedano, E, Mabulla, A, Mark, DF, Musiba, C, Bunn, HT, Uribelarrea, D, Smith, V, Diez-Martin, F, Pérez-González, A 2013 'First partial skeleton of a 1.34-million-year-old Paranthropus boisei from Bed II, Olduvai Gorge, Tanzania.' *PLoS One*, vol.8, no. 12, e80347.
- Dupont, LM, Donner, B, Vidal, L, Perez, EM, Wefer, G 2005 'Linking desert evolution and coastal upwelling: pliocene climate change in Namibia.' *Geology*, vol. 33, pp. 461-464.
- Duval, M, Grün, M 2016 'Are published ESR dose assessments on fossil tooth enamel reliable?' *Quaternary Geochronology*, vol. 31, pp. 19-27.
- Edwards, TR, Armstrong, BJ, Birkett-Rees, J, Blackwood, AF, Herries, AIR, Penzo-Kajewski, P, Pickering, R, Adams, JW 2019 'Combining legacy data with new drone and DGPS mapping to identify the provenance of Plio-Pleistocene fossils from Bolt's Farm, Cradle of Humankind (South Africa).' *PeerJ* 7, e6202.
- Efremov, JA 1940 'Taphonomy: New branch of paleonotology.' *The Pan-American Geologist*, vol. 74, pp. 81-93.
- Egli, R 2013 'VARIFORC: an optimized protocol for calculating non-regular first-order reversal curve (FORC) diagrams.' *Global Planetary Change*, vol. 110, pp. 302–320.
- Evans, AR, Daly, ES, Catlett, KK, Paul, KS, King, SJ, Skinner, MM, Nesse, HP, Hublin, JJ, Townsend, GC, Schwartz, GT, Jernvall, J 2016 'A simple rule governs the evolution and development of hominin tooth size.' *Nature*, vol. 530, pp. 477- 490.
- Evans, AR, Jernvall, J 2009 'Patterns and Constraints in Carnivoran and Rodent Dental Complexity and Tooth Size.' *Journal of Vertebrate Paleontology*, vol. 29, pp. 24A.

- Falk, D, Hildebolt, C, Smith, K, Morwood, MJ, Sutikna, T, Brown, P, Jatmiko, Saptomo, EW, Brunsden, B, Prior, F 2005 'The brain of LB1, *Homo floresiensis.*' Science vol. 308, pp. 242-245.
- Feibel, CS, Brown, FH, McDougall, I 1989 'Stratigraphic Context of Fossil Hominids from the Omo Group Deposits: Northern Turkana Basin, Kenya and Ethiopia', American Journal of Phsyical Anthropology, vol. 78, pp. 595-622.
- Fernández-Jalvo, Y & Andrews, P 2016 'Discoloration and Staining.' In Atlas of taphonomic identifications, Fernández-Jalvo, Y & Andrews, P (Eds), Springer, Dordrecht, pp. 155-166.
- Fisher, R 1953 'Dispersion on a sphere.' *Proceedings of the Royal Society of London. Series A: Mathematical and Physical Sciences,* vol. 217, pp. 512–515.
- Fitch, FJ, Miller, JA 1970 'New Hominid Remains and Early Artefacts from Northern Kenya: Radioisotopic Age Determinations of Lake Rudolf Artefact Site.' *Nature*, vol. 226, pp. 226-228.
- Fitch, FJ, Hooker, PJ, Miller, JA 1976 ⁴⁰Ar/³⁹Ar Dating of the KBS Tuff in Koobi For a Formation, East Rudolf, Kenya.' *Nature*, vol. 263, pp. 740-744.
- Fu, Q, Hajdinjak, M, Moldovan, OT, Constantin, S, Mallick, S, Skoglund, P, Patterson, N, Rohland,
 N, Lazaridis, I, Nickel, B, Viola, B 2015 'An early modern human from Romania with a recent Neanderthal ancestor.' *Nature*, vol. 524, pp. 216-219.
- Gallagher, A, Menter, CG 2011 'DNH 109: A fragmentary hominin near-proximal ulna from Drimolen, South Africa.' *South African Journal of Science*, vol. 107, no. 5/6, pp. 1-4.
- Garn, SM, Kerewsky, RS, Swindler, DR 1966 'Canine "field" in sexual dimorphism of tooth size.' *Nature*, vol. 212, no. 5069, pp.1501-1502.

Gathogo, PN, Brown, FH 2006 'Revised stratigraphy of Area 123, Koobi Fora, Kenya, and new age estimates of its fossil mammals, including hominins.' *Journal of human evolution*, vol. 51, no. 5, pp.471-479.

Gause, GF 1934, 'The Struggle for Existence.' Dover Publications, Phoenix.

- Gentry, A 2010 'Cenozoic mammals of Africa.' In: Werdelin L, Sanders W, (eds.), *Bovidae*, Berkeley, University of California Press, pp. 741–796.
- Gibbon, RJ, Pickering, TR, Sutton, MB, Heaton, JI, Kuman, K, Clarke, RJ, Granger, DE 2014 'Cosmogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa.' *Quaternary Geochronology*, vol. 24, pp. 10-15.
- Gilbert, CC, Frost, SR, Pugh, KD, Anderson, M, Delson, E 2018 'Evolution of the modern baboon (Papio hamadryas): A reassessment of the African Plio-Pleistocene record'. *Journal of Human Evolution,* vol.122, pp. 38-69.
- Gilbert, CC, Steininger, CM, Kibii, JM & Berger LR 2015 'Papio Cranium from the Hominin-Bearing Site of Malapa: Implications for the Evolution of Modern Baboon CranialMorphology and South African Plio-Pleistocene Biochronology.' *PLoS ONE*, vol. 10, 8:e0133361. doi:10.1371/journal.pone.013336.
- Goloboff, PA, Catalano, SA 2016 'TNT version 1.5, including a full implementation of phylogenetic morphometrics.' *Cladistics*, vol.32, no. 3, pp.221-238.
- Gordon, GB 1925 'Discussion on the calcareous tufa deposits of the Campbell Rand.' *Transactions of the Royal Society of South Africa*, vol. 28.
- Gordon, AD, Nevell, L, Wood, BA 2008 'The *Homo floresiensis* cranium (LB1): size, scaling and early *Homo* affinities.' *PNAS*, vol.105, pp. 4650-4655.

- Granger, DE, Gibbon, RJ, Kuman, K, Clarke, RJ, Bruxelles, L, Caffee, MW 2015 'New cosmogenic burial ages for Sterkfontein Member 2 Australopithecus and Member 5 Oldowan.' Nature, vol. 522, no. 7554, pp. 85.
- Grine, FE 1981 'Trophic differences between 'gracile' and' robust' australopithecines: A scanning electron microscope analysis of occlusal events.' *South African Journal of Science*, vol. 77, no. 5, pp.203-230.
- Grine, FE 1982. 'A new juvenile hominid (mammalia: primates) from Member 3, Kromdraai Formation, Transvaal, South Africa.' *Annals of the Transvaal Museum*, vol.33, no.11, pp.165-239.
- Grine, FE 1988 'New craniodental fossils of Paranthropus from the Swartkrans formation and their significance in 'robust' Australopithecine evolution.' In *Evolutionary history of the "robust" Australopithecines*, Aldine de Gruyter, New York, pp. 223-243.
- Grine, FE 1983 'The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene hominids.' PhD thesis, University of the Witwatersrand, Johannesburg.
- Grine, FE 1985a 'Australopithecine evolution: the deciduous dental evidence.' In: Delson, E (ed.), Ancestors: The Hard Evidence, Alan R. Liss, New York, pp. 153-167.
- Grine, FE 1986 'Dental Evidence for Dietary Difference in *Australopithecus* and *Paranthropus:* a Quantitative Analysis of Permanent Molar Microwear.' *Journal of Human Evolution,* vol. 15, pp. 783-822.
- Grine, FE 1989 'New hominid fossils from the Swartkrans formation (1979-1986 excavations): craniodental specimens', *American Journal of Physical Anthropology*, vol. 79, pp. 409-449.
- Grine, FE, Deagling, DJ 1993 'New mandible of *Paranthropus robustus* from Member 1, Swartkrans Formation, South Africa.' *Journal of Human Evolution*, vol. 24, pp. 319-333.

- Grine, FE, Delanty, MM, Wood, BA 2013 'Variation in Mandibular Postcanine Dental Morphology and Hominin Species Representation in Member 4, Sterkfontein, South Africa.' In: Reed, K, Fleagle, J, Leakey, R (eds.), *The Paleobiology of* Australopithecus, Springer, Dordrecht Heidelberg New York London, pp. 125-146.
- Grine, FE, Sponheimer, M, Ungar, PS, Lee-Thorp, J, Teaford, MF 2012 'Dental microwear and stable isotopes inform the paleoecology of extinct hominins.' *American Journal of Physical Anthropology*, vol. 148, no. 2, pp. 285-317.

Grün, R 1986 'Beta dose attenuation in thin layers.' Ancient TL., vol. 4, pp. 1-8.

- Guérin, N, Mercier, G, Adamiec 2011 'Dose rate conversion factors: update.' *Ancient TL*., vol. 29, pp. 5-8.
- Haile-Selassie, Y, Latimer, BM, Alene, M, Deino, AL, Gibert, L, Melillo, SM, Saylor, BZ, Scott, GR, Lovejoy, CO 2010 "An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia." *PNAS*, vol. 107, no. 22, pp. 121212-12126.
- Haile-Selassie, Y, Melillo, SM, Vazzana, A, Benazzi, S, Ryan, TM 2019 'A 3.8-million-year-old hominin cranium from Woranso-Mille, Ethiopia.' *Nature*, vol. 573, pp. 214-219.
- Hanihara, K 1954 'Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids: deciduous incisors.' *Journal of the Anthropological Society of Nippon*, vol. 63, pp. 168-185.

Hardin, G 1960 'The Competitive Exclusion Principle.' Science, vol. 131, pp.1292-1297.

Harrison, T, Kweka, A 2011 'Paleonotological localities of the Eyasi Platau, including Laetoli.' In:
Harrison, T (ed.), Paleontology and Geology of Laetoli: Human Evolution in Context.
Volume 1: Geology, Geochronology, Paleoecology, and Paleoenvironment, Vertebra
Paleobiology and Paleoanthropology, Springer, Netherlands

- Harrison, RJ, Feinberg, JM 2008 'FORCinel: an improved algorithm for calculating first-order reversal curve distributions using locally weighted regression smoothing.' *Geochemistry, Geophysics, Geosystems,* vol. 9, Q05016, doi:10.1029/2008GC001987.
- Hawks, J 2017 'Arguing about species: Is it evidence, or ego?' *John Hawks Weblog*, blog post, 03 August, 06 November 2019, <johnhawks.net/weblog/topics/taxonomy/species-argumentevidence-ego-2017.html>.
- Hawks, J & Berger, LR 2019 'Reply to Clarke," Australopithecus prometheus was validly named on MLD 1".' *American journal of physical anthropology,* vol. 170, no. 4, pp. 482.
- Hemmer, H, 1965, Zur Nomenklatur und Verbreitung des Genus Dinofelis Zdansky, 1924 (Therailurus Piveteau 1948).
- Herries, AIR, Martin, JM, Leece, AB, Adams, JW, Boschian, G, Jaonnes-Boyau, R, Edwards, TR, Mallett, T, Massey, J, Murszewski, A, Neuebauer, S, Pickering, R, Strait, DS, Armstrong, BJ, Baker, SE, Caruana, MV, Denham, T, Hellstrom, Moggi-Cecchi, J, Mokobane, S, Penzo-Kajewski, P, Rovinsky, DS, Schwartz, GT, Stammers, RC, Wilson, C, Woodhead, J, Menter, C *in press* 'Drimolen crania indicate contemporaneity of *Australopithecus*, *Paranthropus* and early *Homo erectus* in S. Africa.'
- Herries, AI, Adams, JW, Joannes-Boyau, R, Armstrong, B, Baker, S, Blackwood, AF, Boshian, G, Caruana, MV, Penzo-Kajewski, P, Murszewski, A, Rovinsky, DS 2019 'Integrating palaeocaves into palaeolandscapes: An analysis of cave levels and karstification history across the Gauteng Malmani dolomite, South Africa.' *Quaternary Science Reviews*, vol. 220, pp.310-334.
- Herries, AIR, Adams, JW 2013 'Clarifying the context, dating and age range of the Gondolin hominins and *Paranthropus* in South Africa.' *Journal of Human Evolution*, vol. 65, pp. 676-681.

- Herries, AIR, Adams, JW, Kuykendall, KL, Shaw, J 2006 'Speleology and magnetobiostratigraphic chronology of the GD 2 locality of the Gondolin hominin-bearing paleocave deposits, North West Province, South Africa.' *Journal of Human Evolution*, vol. 51, no. 6, pp. 617-631.
- Herries, AIR, Curnoe, D, Adams, JW 2009 'A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa.' *Quaternary International*, vol. 202, pp. 14-28.
- Herries, AIR, Hopley, PJ, Adams, JW, Curnoe, D, Maslin, MA 2010 'Letter to the Editor: Geochronology and palaeoenvironments of southern African hominin-bearing localities— A reply to Wrangham et al., 2009. "Shallow-water habitats as sources of fallback foods for hominins".' *American Journal of Physical Anthropology*, vol. 143, pp. 640-646.
- Herries, AIR, Murszewski, A, Pickering, R, Mallett, T, Joannes-Boyau, R, Armstrong, Adams, JW, Baker, S, Blackwood, A, Penzo-Kajewski, P, Kappen, P, Leece, AB, Martin, J, Rovinsky, D, Boshian, G 2018 'Geoarchaeological and 3D visualisation approaches for contextualising in situ fossil bearing palaeokarst in South Africa: A case study from the ~2.61 Ma Drimolen Makondo.' *Quaternary International*, vol.483, pp. 90-110.
- Herries, AIR, Pickering, R, Adams, JW, Curnoe, D, Warr, G, Latham, AG, Shaw, J 2013 'A multidisciplinary perspective on the age of *Australopithecus* in southern Africa.' In: Reed, KE, Fleagle, JG, Leakey, RE (Eds), *The paleobiology of* Australopithecus, Springer, New York, pp. 21-40.
- Herries, AIR, 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*, vol. 60, pp. 523-539.
- Hill, K, Boesch, C, Goodall, J, Pusey, A, Williams, J, Wrangham, R 2001 'Mortality rates among wild chimpanzees.' *Journal of Human Evolution,* vol. 40, pp. 437-450.

- Hillhouse, JW, Ndombi, JWM, Cox, A, Brock, A 1977 'Additional results on palaeomagnetic stratigraphy of the Koobi Fora Formation, East of Lake Turkana (Lake Rudolf), Kenya.' *Nature*, vol. 265, pp. 411-415.
- Hillhouse, JW, Cerling, TE, Brown, FH 1986 'Magnetostratigraphy of the Koobi Fora Formation, Lake Turkana, Kenya.' *Journal of Geophysical Research*, vol. 91, pp. 11581-11595.

Hlusko et al., 2016/2019 PNAS (the integration of quantitative genetics, palaeontology...)

- Holloway, RL, Broadfield, DC, Yuan, MS 2004 'The human fossil record.' *Brain Endocasts*, vol. 3, Wiley, New York.
- Hopley, PJ, Herries, AIR, Baker, SE, Kuhn, BF, Menter, CG 2013 'Brief communication: Beyond the South African cave paradigm-Australopithecus africanus from Plio-Pleistocene paleosol deposits at Taung.' American Journal of Physical Anthropology, vol. 151, no. 2, pp. 316-324.
- Hopley, PJ, Marshall, JD, Weedon, GP, Latham, AG, Herries, AIR, Kuykendall, K 2007 'Orbital forcing and the spread of C4 grasses in the late Neogene: stable isotope evidencefrom South African speleothems.' *Journal of Human Evolution*, vol. 53, pp. 620-634.
- Howell, FC 1978 'Hominidae.' In: Maglio, VJ, Cooke, HBS (eds.), *Evolution of African Mammals*, Harvard University Press, Cambridge, pp. 154-248.

Hublin, JJ 2009 'The origin of Neanderthals.' PNAS, vol.106, pp.16022-16027.

- Huelsenbeck, JP, Ronquist, F 2001 'MRBAYES: Bayesian inference of phylogenetic trees.' *Bioinformatics*, vol. 17, pp. 754-755.
- Isler et al 2008 'Endocranial volumes of primate species: scaling analysis using a comprehensive and reliable dataset.' *Journal of Human Evolution*, vol. 55, pp. 967-978.
- Hurford, AJ, Gleadow, AJW, Naeser, CW 1976 'Fission-track dating of pumice from the KBS Tuff, East Rudolf, Kenya.' *Nature*, vol. 253, pp. 738-740.
- Jablonski, D 2007 'Scale and hierarchy in macroevolution.' *Palaeontology*, vol. 50, no. 1, pp. 87-109.
- Jernvall, J, Thesleff, I 2000 'Reiterative signalling and patterning during mammalian tooth morphogenesis.' *Mechanisms of Development*, vol. 92, no. 1, pp. 19-29.
- Joannes-Boyau, R, Adams, JW, Austin, C, Arora, M, Moffat, I, Herries, AI, Tonge, MP, Benazzi, S, Evans, AR, Kullmer, O, Wroe, S 2019 'Elemental signatures of *Australopithicus africanus* teeth reveals seasonal dietary stress.' *Nature*, vol. 572, pp. 112-115.
- Joannes-Boyau, R 2013 'Detailed protocol for accurate non-destructive direct dating of human remains.' *Geochronometria.* vol.40, pp. 322-333.
- Joannes-Boyau, R, Grün, RA 2009 'Thermal behavior of orientated and non-orientated CO2-radicals in tooth enamel.' *Radiation Measurements*, vol. 44, pp. 505-511.
- Joannes-Boyau, R, Grün, RA 2011, 'Comprehensive model for CO2- radicals in fossil tooth enamel: implications for ESR dating,' *Quaternary Geochronology*, vol. 6, pp. 82-97.
- Joannes-Boyau, RJ, Duval, M, Bodin,T 2018 'MCDoseE 2.0 A new Markov Chain Monte Carlo program for ESR dose response curve fitting and dose evaluation.' *Quaternary Geochronology*, vol. 44, pp. 13-22.
- Johanson, DC, White, TD 1978 'A systematic assessment of early African hominids.' *Science*, vol. 203, pp. 321-330.
- Johanson, DC, Masao, FT, Eck, GG, White, TD, Walterm RC, Kimbel, WH, Asfaw, B, Manega, P, Ndessokia, P, Suwa, G 1987 'New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania.' *Nature*, vol. 327, pp. 205-209.

- Jolly, CJ 1970 'The seed eaters: A new model for hominid differentiation based on a baboon analogy.' *Man*, vol. 5, pp. 5–26.
- Jungers, WL, Grine, FE 1986 'Dental Trends in the Australopithecines: The Allometry of Mandibular Molar Dimensions.' In: Wood, B, Martin, L, Andrews, P (eds.), *Major Topics in Primate and Human Evolution,* Cambridge University Press, Cambridge, pp. 203, 219.
- Kavanagh, KD, Evans, AR, Jernvall, J 2007 "Predicting evolutionary patterns of mammalian teeth from development." *Nature*, vol. 449, DOI: 10.1038.

Keith, A 1947 'Australopithecinae or Dartians.' Nature, vol. 159, no. 4037, pp.377-377.

Keith, A 1925a "The Taungs Skull." Nature, vol. 116, pp. 11.

- Keyser, AW 2000 'The Drimolen skull: the most complete australopith cranium and mandible to date.' South African Journal of Science, vol. 96, pp. 189-193.
- Keyser, AW, Menter, CG, Moggi-Cecchi, J, Pickering, TR, Berger, LR 2000 'Drimolen: a new hominid-bearing site in Gauteng, South Africa.' South African Journal of Science, vol. 96, pp. 193-197.
- Kimbel, WH, Johanson, DC, Rak, Y 1997 'Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia.' *American Journal of Physical Anthropology*, vol. 103, pp. 235-262.
- Kimbel, WH 1984 'Variation in the pattern of cranial venous sinuses and hominid phylogeny.' *American Journal of Physical Anthropology*, vol. 63, no. 3, pp.243-263.
- Kimbel, KH, Rak, Y, Johanson, DC 2004, *The Skull of* Australopithecus Afarensis, Oxford University Press, Oxford.

- Kimbel, WH & Rak, Y 2017 'Australopithecus sediba and the emergence of Homo: Questionable evidence from the cranium of the juvenile holotype MH 1.' Journal of Human Evolution, vol. 107, pp. 94-106.
- Kimbel, WH, Lockwood, CA, Ward, CV, Leakey, MG 2006, 'Was Australopithecus anamensis ancestral to A. afarensis? A case of anagenesis in the hominin fossil record.' Journal of Human Evolution, vol. 51, pp. 134-152.
- Kimbel, WH, Villmoare, B 2016 'Australopithecus to Homo: the transition that wasn't.' Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, vol. 371, pp. 1-10.
- Kimbel, WH, Rak, Y 1993 'The importance of species taxa in paleoanthropology and an argument for the phylogenetic concept of the species category.' In: Kimbel, WH, Martin, LB (eds.), Species, Species Concepts, and Primate Evolution, Plenum Press, New York, pp. 461-484.
- Kimbel, WH, White, TD, Johanson, DC 1988 "Implications of KNM-WT 17000 for the evolution of 'robust' Australopithecus." In: Evolutionary History of the "Robust" Australopithecines.Grine, FE (Ed). University of New York at Stony Brook, New York, pp. 259-258.
- Kirschvink, JL 1980 'The least-square line and plane and the analysis of palaeomagnetic data.' *Geophysical Journal, Royal Astronomical Society,* vol. 62, pp. 699–718.
- Kretzoi, M, 1938, Die Raubtiere von Gombaszög nebst einer übersicht der Gesamtfauna (Ein beitrag zur stratigraphie des Altquartaers). In *Annales Musei Nationalis Hungarici*, vol. 31, pp. 88-157.
- Kuhn, BF, Herries, AIR, Price, GJ, Baker, SE, Hopley, P, Menter, CG, Caruana, MV 2016 'Renewed inverstigations at Taung; 90 years after the discovery of *Australopithecus africanus.' Palaeoanthropologia Africana*, vol. 51, pp. 10-27.

- Kuman, K, Clarke, RJ 2000 'Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5.' *Journal of human evolution,* vol. 38, pp. 827-847.
- Lacruz, R S 2007 'Enamel microstructure of the hominid KB 5223 from Kromdraai, South Africa.' *American Journal of Physical Anthropology,* vol. 132, no. 2, pp. 175 182.
- Lacruz, R, Turner, A, Berger, LR 2006 'New *Dinofelis (Carnivora: Machairodontinae)* remains from Sterkfontein Valley sites and a taxonomic revision of the genus in southern Africa.' *Annals of the Transvaal Museum*, vol. 43, pp. 89–106.
- Latham, AG, Herries, AIR 2004 'The Formation and Sedimentary Infilling of the Cave of Hearths and Historic Cave Complex, Makapansgat, South Africa.' *Geoarchaeology*, vol. 19, no. 4, pp. 323-342.
- Latham, AG, Herries AIR, Quinney, P, Sinclair, A, Kuykendall, K 1999 'The Makapansgat Australopithecine Site from a Speleological Perspective.' In: Pollard, AM, (ed.), Geoarchaeology: exploration, environments, resources. Royal Geological Society, London.Special Publications, vol. 165, pp. 61-77.
- Lauer, C 1975 'A Comparison of Sexual Dimorphism and Range of Variation in *Papio cyncephalus* and *Gorilla gorilla* dentition.' *Primates,* vol. 16, pp. 1-7.
- Le Gros Clarke, WE 1950 'New Palaeontological evidence bearing on the evolution of the hominoidea.' *The South African Archaeological Bulletin*, vol. 5, no. 18, pp. 82.
- Leakey, MD 1978 'Olduvai fossil hominids: their stratigraphic positions and associations.' In: *Early Hominids from Africa*, pp.3-16.
- Leakey, LSB, Tobias, PV, Napier, JR 1964 'A new species of the genus *Homo* from Olduvai Gorge.' *Nature*, vol. 202, pp. 7-9.

- Leakey, MG, Spoor, F, Brown, FH, Gathogo, PN, Kiarie, C, Leakey, LN and McDougall, I 2001 'New hominin genus from eastern Africa shows diverse middle Pliocenelineages.' *Nature,* vol. 410, pp. 433-440.
- Leakey, LSB 1960 'The newest link in human evolution: the discovery by L.S.B. Leakey of *Zinjanthropus boisei.*' *Current Anthropology*, vol. 1, issue 1, pp. 76-77.
- Ledogar, JA, Smith, AL, Benazzi, S, Weber, GW, Spencer, MA, Carlson, KB, McNulty, KP, Dechow, PC, Grosse, IR, Ross, CF, Richmond, BG 2016 'Mechanical evidence that Australopithecus sediba was limited in its ability to eat hard foods.' *Nature Communications*, vol. 7, no. 10596.
- Leece, AB, Kegley, ADT, Lacruz, RS. Herries, AIR, Hemingway, J, Kgasi, L, Potze, S, Adams, JW, 2016 'The first hominin from the early Pleistocene paleocave of Haasgat, South Africa.' *PEERJ*. 4:e2024
- Lehmann, J & Boesch, C 2003, 'Social influences on ranging patterns among chimpanzees (Pantroglodytes) in the Tai National Park, Côte d'Ivoire.' *Behavioural Ecology*, vol.14, pp. 642-649.
- Leonhardt, R 2006 'Analyzing rock magnetic measurements: the RockMagAnalyzer 1.0 software.' *Computers and Geosciences,* vol. 32, pp. 1420–1431.
- Lepre, CJ, Kent, DV 2015 'Chronostratigraphy for KNM-ER 3733 and other Area 104 hominins from Koobi Fora.' *Journal of Human Evolution,* vol. 86, pp. 99-111.
- Lieberman DE, Krovitz GE, Yates FW, Devlin M, St. Claire M, 2004 'Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face.' *Journal of Human Evolution*, vol. 46, pp. 655–677.

- Lockwood, CA, Tobias, PV 1999 'A large male hominin cranium from Sterkfontein, South Africa, and the status of *Australopithecus africanus*.' *Journal of Human Evolution*, vol. 36, pp. 637-685.
- Lockwood, CA, Kimbel, WH, Johanson, DC 2000 'Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*.' *Journal of Human Evolution*, vol. 39, no. 1, pp. 23-55.
- Lockwood, CA, Menter, CG, Moggi-Cecchi, J, Keyser, AW 2007 'Extended male growth in a fossil hominin species.' *Science*, vol. 318, pp. 1443-1446.
- Lordkipanidze, D, Ponce de León, MS, Margvelashvili, A, Rak, Y, Rightmire, GP, Vekua, A & Zollikofer, CPE 2010 'A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early Homo.' *Science*, vol. 342, no. 6156, pp. 326-331.
- Maguire, JM, Pemberton, D, Collett, M 1980 'The Makapansgat limeworks grey breccia: hominids, hyaenas, hystricids or hillwash?' *Paleontologia Africana*, vol. 23, pp. 75–98.
- Mallett, T 2015 'Magnetostratigraphy of the Drimolen Main Quarry early hominin -bearing palaeocave deposits, South Africa.' Honours Thesis, La Trobe University.

Marchand, F 1902 'Ueber das Hirngewicht des Menschen.', (B.G. Teubner, Leipzig).

- Martin, JM, Schwartz, G, Herries, AIR, et al., *in prep* 'Juvenile hominin specimens from the Drimolen Main Quarry, South Africa.'
- Martin, JM, Leece, AB, Neubauer, S, Baker, SE, Mongle, CS, Boschian, G, Strait, DS, Herries, AIR **REDACTED**
- Maslin, MA, Trauth, MH 2009 'Plio-Pleistocene East African Pulsed Climate Variability and its influence on Early Human Evolution.' In: Grine, FE, Fleagle, JG, Leakey, RE (eds.), *The*

First Humans: Origin and Early Evolution of the Genus Homo, Springer, New York, pp. 151–158.

- Mayr, E 1950 'Isolation, Dispersal, and Evolution.' *Evolution, InternationI Journal of Organic Evolution*, vol. 4, no. 4, pp. 363.
- Mayr, E 1963, *Animal Species and Evolution*, Harvard University Press, Cambridge, Massechusetts.
- Mayr, E 1969, *Principle of Systematic Zoology*, McGraw-Hill, New York.
- Maxbauer, DP, Feinberg, JM, Fox, DL 2016 'MAX UnMix: a web application for unmixing magnetic coercivity distributions.' *Computers and Geosciences,* vol. 95, pp. 140–145.
- McDougall, I, Brown, FH, Cerling, TE, Hillhouse, JW 1992 'A reappraisal of the geomagnetic polarity time scale to 4 Ma using data from the Turkana Basin, East Africa.' *Geophysical Research Letters*, vol. 19, no. 23, pp. 2340-2352.
- McDougall, I, Brown, FH 2006 'Precise 40Ar/39Ar geochronology for the upper Koobi For a Formation, Turkana Basin, northern Kenya.' *Journal of the Geological Society,* vol. 163, pp. 205–220.
- McDougall, I, Brown, FH, Vasconelos, PM, Cohen, BE, Thiede, DS. Buchanan, MJ 2012 'New Single Crystal ⁴⁰AR/³⁹AR ages improve time scale for deposition of the Omo Group, Omo-Turkana basin, East Africa.' *Journal of the Geological Society*, vol. 169, pp. 213-226.
- McHenry, L, Stanistreet, IG 2018 'Tephrochronology of Bed II, Olduvai Gorge, Tanzania, and placement of the Oldowan-Acheulean transition.' *Journal of Human Evolution*, vol. 120, pp. 7-18.
- McKee, JK 1993 'Faunal dating of the Taung hominid fossil deposit.' *Journal of Human Evolution,* vol. 25, no. 5, pp. 363-376.

- Menter, CG, Kuykendall, KL, Keyser, AW, Conroy, GC 1999 'First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa.' *Journal of Human Evolution*, vol. 37, pp. 299-307.
- Moggi-Cecchi, J 2009 'The life histories of fossil hominins.' *Journal of Anthropological Sciences*, vol. 87, pp. 3-5.
- Moggi-Cecchi, J, Menter, C, Boccone, S, Keyser, A, 2010 'Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa.' *Journal of Human Evolution*, vol. 58, pp. 374-405.
- Mongle, CS, Strait, DS, Grine, FE 2019 'Expanded character sampling underscores phylogeneticstability of *Ardipithecus ramidus* as a basal hominin.' *Journal of Human Evolution*, vol.131, pp. 28-39.
- Moskowitz, BM 1981 'Methods for estimating curie temperatures of titanomagnetites from experimental Js-T data.' *Earth and Planetary Science Letters,* vol. 53, pp. 84–88.
- Murszewski, A, Edwards, TR, Cruden, AR, Armstrong, B, Boschian, G, Herries, AIR 2019 'Regional geological formation and speleogenesis of the "Fossil Hominis Sites of South Africa" UNESCO Wolrd Heritage Site.' *Earth Science Reviews*, vil. 188, pp. 498-513.
- Neubauer, S, Gunz, P, Hublin, JJ 2009, 'The pattern of endocranial ontogenetic shape changes in humans.' *Journal of Anatomy*, vol. 215, pp. 240-255.
- Neubauer, S, Gunz, P, Weber, GW, Hublin, JJ 2012 'Endocranial volume of Australopithecus africanus: New CT-based estimates and the effects of missing data and small sample size.' *Journal of Human Evolution,* vol. 62, pp. 498-510.

- Neubauer,S, Gunz, P 2018 'Endocasts and the evo-devo approach to study human brain evolution.' In: Bruner, E, Ogihara, N, Tanabe, H, (eds.), Digital Endocasts: From Skulls to Brains, Springer, Tokyo, pp. 173-190.
- Neubauer, S, Hublin, JJ, Gunz, P 2018 'The evolution of modern human brain shape.' *Science Advances,* 4,eaao5961.
- North American Commission on Stratigraphic Nomenclature (NACSN), 1981, Draft North American Stratigraphic Code: Canadian Society of Petroleum Geologists, Calgary, 63 p. North American Stratigraphic Code: *American Association of Petroleum Geologists Bulletin,* vol. 67, pp. 841-875 (1983).
- O'Regan, HJ & Menter, CG 2009 'Carnivora from the Plio-Pleistocene hominin site of Drimolen, Gauteng, South Africa', *Geobios* vol.42, pp. 329–350.
- Olsen, TR 1985 'Cranial morphology and systematics of the Hadar Formation hominids and "Australopithecus" africanus.' In: Delson, E (ed.), Ancesrtors, The Hrad Evidence, Alan R. Liss, New York, pp. 102-119.
- Olson, TR 1978, 'Hominid Phylogenetics and the Existence of *Homo* in Member 1 of the Swartkrans Formation, South Africa.' *Journal of Human Evolution*, vol. 7, pp. 159-178.
- Osborn, JW 1978 'Morphogenetic gradients: fields versus clones.' In: Butler, PM, Joysey, KA (eds.) Development, function and evolution of teeth, Academic Press, San Francisco, pp. 171-201.
- Osborne, RAL 2007 'Cathedral Cave, Wellington Caves, New South Wales, Australia. A multiphase, non-fluvial cave.' *Earth Surface Processes and Landforms: The Journal of the British Geomorphological Research Group*, vol. 32, no. 14, pp. 2075-2103.
- Partridge, TC 1979 'Re-appraisal of lithostratigraphy of Makapansgat Limeworks hominid site.' *Nature*, vol. 279, no. 5713, pp.484-488.

- Partridge, TC 2000 'Hominid-bearing cave and tufa deposits.' In: Partridge, TC, Maud, P.R. (eds), The Cenozoic in Southern Africa, Oxford Monographs on Geology and Geophysics, Oxford University Press, Oxford, pp. 100–125.
- Partridge, TC, Granger, DE, Caffee, MW, Clarke, RJ 2003 'Lower Pliocene hominid remains from Sterkfontein.' *Science*, vol. 300, pp. 607-612.
- Peabody, FE 1954 'Travertines and cave deposits of the Kaap Escarpment of South Africa, and the type locality of Australopithecus africanus Dart.' *Geological Society of America Bulletin*, vol. 65, no. 7, pp.671-706.
- Pickering, R Hancox, PJ, Lee-Thorp, JA, Grün, R, Mortimer, GE, McCulloch, M, Berger, LR 2007 'Stratigraphy, U-Th chronology, and paleoenvironments at Gladysvale Cave: insights into the climatic control of South African hominin-bearing cave deposits.' *Journal of Human Evolution*, vol. 53, pp. 602-619.
- Pickering, R, Herries, AIR 2020 'A new multidisciplinary age of 2.61-2.07 Ma for the Sterkfontein Member 4 Australopiths.' In; Zipfel B, Richmond B, Ward, C (eds.), Hominin Post-Cranial Remains from Sterkfontein, South Africa, 1936-1995. Oxford University Press. ISBN: 9780197507667.
- Pickering, R, Herries, AIR, Woodhead, JD, Hellstrom, JC, Green, HE, Paul, B, Ritzman, T, Strait, DS, Schoville, BJ, Hancox, PJ 2019 'U-Pb-dated flowstones restrict South African early hominin record to dry climate phases.' *Nature*, vol. 565, pp. 226-238.
- Pickering, R, Kramers, JD 2010 'Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa.' *Journal of Human Evolution*, vol. 59, no. 1, pp. 70-86.

- Pickering, R, Kramers, JD, Hancox, PJ, de Ruiter, DJ, Woodhead, JD 2011 'Contemporary flowstone development links early hominin bearing cave deposits in South Africa.' *Earth and Planetary Science Letters*, vol. 306, pp. 23-32.
- Pickering, TR, Egeland, CP, Domínguez Rodrigo, M, Brain, CK, Schnell, AG 2008 'Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa: hominid cave use and subsistence behaviour in the Early Pleistocene.' *Journal of Anthropological Archaeology*, vol. 27, no. 1, pp. 30-45.
- Pickering, TR, Heaton, JL, Sutton, MB, Clarke, RJ, Kuman, K, Senjem, JH, Brain, CK 2016 'New early Pleistocene hominin teeth from the Swartkrans Formation, South Africa.' *Journal of Human Evolution*, vol. 100, pp. 1-15.
- Pike, CR, Roberts, AP, Verosub, KL 2001 'First-order reversal curve diagrams and thermal relaxation effects in magnetic particles.' *Geophysical Journal International*, vol. 145, pp. 721–730.
- Pindrik, J, Ye, X, Ji, BG, Pendleton, C, and Ahn, ES 2014 'Anterior fontanelle closure and size in full-term children based on head computed tomography.' *Clinical Pediatrics*, vol. 53, pp. 1149-1157.
- Plavcan, JM 1993 'Canine size and shape in male anthropoid primates.' *American Journal of Physical Anthropology*, vol. 92, no.2, pp. 201-2016.
- Plavcan, JM 2001 'Sexual Dimorphism in Primate evolution.' *Yearbook of Physical Anthropology,* vol. 44, pp. 25-53.
- Plavcan, JM, Cope, DA 2001 'Metric Variation and Species Recognition in the Fossil Record.' *Evolutionary Anthropology*, vol.10, no. 6, pp.204-222.

- Pocheville, A 2015 'The ecological niche: history and recent controversies.' In: Heams, T, Huneman, P, Lecointre, G, Silberstein, M (eds.), *Handbook and Evolutionary Thinking in the Sciences*, Springer.
- Potts, R 1998 'Environmental hypotheses of hominin evolution.' *Yearbook of Physical Anthropology,* vol. 41, pp. 93–136.
- Quam, R, Bailey, S, Wood, B 2009 'Evolution of M¹ crown size and cusp proportions in the genus *Homo.' Journal of Anatomy*, vol. 214, no. 5, pp. 655-670.
- Rak, Y 1983, *The Australopithecine Face,* Academic Press, New York.
- Reed, KE 1996 'The paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities.' D. Phil. Thesis, State University of New York at Stony Brook.
- Reed, KE, Kitching, JW, Grine, FE, Jungers, WL, Sokoloff, L 1993 'Proximal femur of Australopithecus africanus from Member 4, Makapansgat, South Africa.' American Journal of Physical Anthropology, vol. 92, pp. 1-15.
- Reid, DJ, Schwartz, GT, Dean, CM, Chandrasekera, MS 1998, 'A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*', *Journal of Human Evolution*, vol. 35, pp. 427-448.
- Reynolds, S, Kibii, J 2011 'Sterkfontein at 75: review of paleoenvironments, fauna, and archaeology from the hominin site of Sterkfontein (Gautang Province, South Africa,).' *Palaentologica Africana*, vol. 46, pp. 59-88.
- Riga, A, Mori, T, Pickering, TR, Moggi-Cecchi, J, Menter, CG 2019 'Ages-at-death distribution of early Pleistocene hominin fossil assemblage from Drimolen (South Africa).' American Journal of Physical Anthropology, DOI: 10.1002, pp. 1-5.

- Rivera, TA, Darata, T, Lippert, PC, Jicha, BR, Schmitz, MD 2017 'The duration of a Yellowstone super-eruption cycle and implications for the age of the Olduvai subchron.' *Earth and Planetary Science Letters,* vol. 479, pp. 377–386.
- Roberts, AP, Almeida, TP, Church, NS, Harrison, RJ, Heslop, D, Li, Y, Li, J, Muxworthy, AR,
 Williams, W, Zhao, X 2017 'Resolving the Origin of Pseudo-Single Domain Magnetic
 Behavior.' *Journal of Geophysical Research: Solid Earth,* vol. 122, pp. 9534–9558.
- Roberts, AP, Pike, CR, Verosub KL 2000 'First-order reversal curve diagrams: a new tool for characterizing the magnetic properties of natural samples.' *Journal of Geophysical Research: Solid Earth*, vol. 105, pp. 461–475.
- Roberts, D, Matthews, T, Herries, AIR, Boulter, C, Scott, L, Dondo, C, Ntembi, P, Browning, C, Smith, R, Haarhoff, P 2011 'Regional and Global Palaeoenvironmental and Sea Level Context of the Late Cenozoic Langebaanweg (LBW) Palaeontological Site: West Coast of South Africa.' *Earth-Science Reviews*, vol. 106, pp. 191-214.

Robinson, JT 1965, The Dentition of the Australopithecinae, Transvaal Museum, Pretoria.

- Robinson, JT 1972 'The bearing of East Rudolf fossils on early hominid systematics.' *Nature*, vol. 240, pp. 239-240.
- Robinson, JT 1960 'Affinities of the new Olduvai australopithecines.' *Nature*, vol. 186, pp. 456-458.

Robinson, JT 1954 'Prehominid dentition and hominid evolution.' *Evolution*, vol. 8, pp. 324–334.

Robinson, JT 1954 'The genera and species of the Australopithecinae.' *American Journal of Physical Anthropology*, vol.12, pp.181-200.

Robinson, JT 1956, The dentition of the Australopithecinae, No. 9, Transvaal Museum, Pretoria.

Ronquist, F, Teslenko, M, Van Der Mark, P, Ayres, DL, Darling, A, Höhna, S, Larget, B, Liu, L, Suchard, MA, Huelsenbeck, JP 2012 'MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space.' *Systematic biology*, vol. 61, no. 3, pp.539-542.

Schroeder, HE 1991 'Oral structure and biology.' Thieme: Stuttgart, pp. 424.

- Schroeder, L, Roseman, CR, Cheverud, JM, Ackermann, RR 2014 'Characterizing the evolutionary path(s) to early *Homo*.' *PLoS ONE*, 9, e114307.
- Schroer, K, Wood, B 2015 'Modeling the dental development of fossil hominins through the inhibitory cascade.' *Journal of Anatomy,* vol. 226, pp. 150–162.
- Schwartz, GT 2000 'Taxonomic and Functional Aspects of the Patterning of Enamel, Thickness Distribution in Extant Large-Bodied Hominoids.' *American journal of Physical Anthropology*, vol. 111, pp. 221-244.
- Scott, RS, Ungar, PS, Bergstrom, TS, Brown, CA, Grine, FE, Teaford, WF, Walker, A 2005 'Dental microwear texture analysis shows within-species diet variability in fossil hominins.' *Nature*, vol. 436, pp. 693-695.
- Shao, Q, Bahain, JJ, Falgueres, C, Dolo, JM, Garcia, T 2014 'U-series dating of tooth enamel.' *Quaternary Geochronology*, vol. 10, pp. 406-411.

Simpson, GG 1961, *Principles of Animal Taxonomy*, Columbia Press, New York.

Simpson, GG 1951 'The species concept.' *Evolution*, vol. 5, pp. 285-298.

Singer, BS 2014 'A quaternary geomagnetic instability time scale.' *Quaternary Geochronology,* vol.21, pp. 29–52.

- Singer, BS, Jicha, BR, Mochizuki, N, Coe, RS 2019 'Synchronizing volcanic, sedimentary, and ice core records of earth's last magnetic polarity reversal.' *Science Advances*, vol.5, eaaw462.
- Skelton, RR, Mchenry, HM, Drawhorn, GM, Bilsborough, A, Chamberlain, A, Wood, BA, Vancata, V 1986 'Phylogenetic Analysis of Early Hominids.' *Current Anthropology*, vol. 27, no. 1, pp.21-43.
- Skelton, RR, McHenry, HM 1992 'Evolutionary relationships among early hominids.' *Journal of human evolution*, vol. 23, no. 4, pp.309-349.
- Skinner, MM, Gunz, P, Wood, BA, Hublin, JJ 2008 'Enamel-dentine junction (EDJ) morphology distinguishes the lower molars of *Australopithecus africanus* and *Paranthropus robustus.*' *Journal of Human Evolution*, vol. 55, no. 6, pp.979-988.
- Skinner, MM, Bailey, SE, Gunz, P, Kimbel, WH, Alemseged, Z, Delezene, LK, Menter, C, Moggicecchi, J, Kupczik, K 2018 'Below the crown; examining interspecies variation in postcanine enamel thickness, EDJ, and root form in the Paranthropus clade.' paper presented at The Annual Meeting American Association for Physical Anthropologists, Austin, USA, 11-14 April 2018 <Kar.kent.ac.uk/77911/>.
- Slobodkin, LB 1961 'Preliminary ideas for a predictive theory of ecology.' *The American Naturalist*, vol. 95, no. 882, pp.147-153.

Eliott-Smith, G 1925 'The fossil anthropoid ape from Taung.' Nature, vol. 115, pp. 236.

Smith, AB 1994, Systematics and the fossil record, Blackwell Scientific, Oxford.

Smith, GM 2013 'Taphonomic resolution and hominin subsistence behaviour in the Lower Palaeolithic: differing data scales and interpretive frameworks at Boxgrove and Swanscombe (UK).' *Journal of Archaeological Science*, vol. 40, no. 10, pp. 3754-3767.

- Sokal, RR, Braumann, CA 1980 'Significance tests for coefficients of variation and variability profiles.' *Systematic Biology*, vol. 29, no, 1, pp. 50-66.
- Spoor, F, Gunz, P, Neubauer, S, Stelzer, S, Scott, N, Kwekason, A, Dean, MC 2015
 'Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*.' *Nature*, vol. 519, pp. 83-86.
- Stammers, RC, Caruana, MV, Herries, AIR 2018 'The first bone tools from Kromdraai and stone tools from Drimolen, and the place of bone tools in the South African Earlier Stone Age.' *Quaternary International*, vol. 495, pp. 87-101.
- Stammers, RC, Herries, AI, Spry, C, Armstrong, BJ, Caruana, MV 2017 'Holocene LSA archaeology from Equus Cave, Buxton-Norlim Limeworks, South Africa: an analysis of the bone tool assemblage.' *The South African Archaeological Bulletin*, vol. 72, no. 206, pp.103-115.
- Stern, N 1993 'The structure of the lower Pleistocene archaeological record: a case study from the Koobi For a Formation.' *Current Anthropology*, vol. 34, pp. 201-205.
- Stiles, DN, Partridge, TC 1979 'Results of Recent Archeological and Paleo-Environmental Studies at the Sterkfontein Extension Site.' South African Journal of Science, vol. 75, no. 8, pp. 346-352.
- Stoops, G 2003, *Guidelines for analysis and description of soil and regolith thin sections*, SSSA, Madison, WI.
- Strait, DS, Weber, GW, Neubauer, S, Chalk, J, Richmond, BG, Lucas, PW, Spencer, MA, Schrein, C, Dechow, PC, Ross, CF, Grosse, IR, 2009 'The feeding biomechanics and dietary ecology of Australopithecus africanus.' Proceedings of the National Academy of Sciences, vol. 106, no. 7, pp.2124-2129.

- Strait, DS 2001 'Integration, phylogeny, and the hominid cranial base.' *American Journal of Physical Anthropology*, vol. 114, pp. 273-297.
- Strait, DS, Grine, FE 2004 'Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa.' *Journal of Human Evolution,* vol. 47, pp. 399-452.
- Strait, DS, Grine, FE, Moniz, MA 1997 'A reappraisal of early hominid phylogeny.' *Journal of Human Evolution*, vol. 32, pp. 17-82.
- Strait, DS, Weber, GW, Neubauer, S, Chalk, J, Richmond, BG, Lucas, PW, Spencer, MA, Schrein,
 C, Dechow, PC, Ross, CF, Grosse, IR, Wright, BW, Constantino, P, Wood, BA, Lawn, B,
 Hylander, WL, Wang, Q, Byron, C, Slice, DE 2008 'The feeding biomechanics and dietary
 ecology of *Australopithecus africanus.' PNAS*, vol. 106, no. 7, pp. 2124-2129.

Strait, DS, Wood, BA 1999 'Early hominid biogeography.' PNAS, vol. 96, pp. 9196-9200.

- Stratford, D, Bruxelles, L, Clarke, RJ, Kuman, K 2012 'New stratigraphic interpretations of the fossil and artefacts-bearing deposits of the Name Chamber, Sterkfontein.' South African Archaeological Bulletin, vol.67, pp. 159-167.
- Stratford, D, Granger, DL, Bruxelles, L, Clarke, RJ, Kuman, K, Gibbon, RJ 2017 'Comments on "The age of fossil StW573 ('Little Foot')": an alternative interpretation of 26Al/10Be burial data.' South African Journal of Science, vol. 113, no. 5/6, pp. 1–3.
- Suwa, G 1996 'Serial allocations of isolated mandibular molars of unknown taxonomic affinities from the Shungura and Unso Formations, Ethiopia, a combined method approach.' *Human evolution*, vol. 11, no. 3-4, pp.269-282.
- Swedlund, AC 1974 'The use of ecological hypotheses in australopithecine taxonomy.' *American Anthropologist*, vol. 67, no. 3, pp. 515-529.

- Tatersall, I, Eldredge, N 1977 'Fact, theory, and fantasy in human paleontology.' *American Scientist*, vol. 65, pp. 204-211.
- Thackeray, JF 2015 'Estimating the age and affinities of *Homo naledi.' South African Journal of Science*, vol. 111, pp. 11-12.
- Thackeray, JF, Kirschvink, JL, Raub, TD 2002 'Palaeomagnetic analyses of calcified deposits from the Plio-Pleistocene hominid site of Kromdraai, South Africa.' *South African Journal of Science*, vol. 98, no. 11/12, pp. 537-540.
- Tobias, PV, Vogel, JC, Oschadleus, D, Partridge, TC, McKee, JC 1993 'New isotopic and sedimentological measurements of the Thabaseek deposits (South Africa) and the dating of the Taung hominid.' *Quaternary Research*, vol. 40, pp. 360-367.
- Tobias, PV 1978 'The place of Australopithecus africanus in hominid evolution.' *Recent advances in primatology*, vol. 3, pp.373-394.
- Tobias, PV 1991, *Olduvai Gorge: The Skulls, endocasts and teeth of* Homo habilis, Cambridge University Press, Cambridge.
- Tobias, PV 2000 'The fossil hominids.' In: Partridge, TC, Maud, RR (eds.), *The Cenerzoic of Southern Africa, Oxfords Monographs on Geology and Geophysics*, Oxford University Press, Oxford, pp. 252-276.
- Tobias, PV 2005 'Eighty years after the discovery of the Taung skull revolutionised palaeoanthropology.' *Anthropologie*, vol 43, pp. 121-128.
- Tobias, PV 1967, Olduvai Gorge vol. II. The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei, Cambridge University Press, Cambridge.
- Tobias, PV 1980 "*Australopithecus Afarensis*" and *A. africanus*: Critique and an Alternative Hypothesis.' *Palaeontologia Africana*, vol. 23, pp. 1-17.

- Val, A, Taru, P, Steininger, C 2014 'New Taphonoomic Analysis of Large-Bodied Primate Assemblage From Cooper's D, Bloubank Valley, South Africa.' South African Archaeology Bulletin, vol. 69, pp. 49-58.
- van der Merwe, NJ, Masao, FT, Bamford, MK 2008 'Isotopic evidence for constrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania.' *South African Journal of Science*, vol. 104, pp. 153-155.
- Villmoare, B, Kimbel, WH, Seyoum, C, Campisano, CJ, DiMaggio, E, Rowan, J, Braun, DR, Arrowsmith JR, Reed, KE 2015 'Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia.' *Science*, vol. 347, pp. 1352-1355.
- Vrba, ES 1985 'Ecological and adaptive changes associated with early hominid evolution.' In: Delson, E (ed.), *Ancestors: The Hard Evidence*, Alan R. Liss, New York, pp. 63-71.
- Vrba, ES 1995 'The fossil record of African antelopes (Mammalia, Bovidae) in relation to humanevolution and paleoclimate.' In: Vrba E, Denton G, Partridge T, Burckle L, (eds.), Paleoclimate and evolution with emphasis on human origins. New Haven: Yale UniversityPress, pp. 385–425.
- Walker, A, Leakey, RE 1988 'The evolution of *Australopithecus boisei*.' In: Grine, FE (ed.) *Evolutionary History of the "Robust" Australopithecines*, Hawthorne, New York, pp. 247-258.
- Walker, A, Leakey, RE, Harris, JM, Brown, FH 1986 '2.5 Myr *Australopithecus boisei* from West of Lake Turkana, Kenya.' *Nature*, vol. 322, no. 6079, pp.517-522.
- Wallace, J 1978 'Evolutionary trends in the early hominid dentition.' In: Jolly, CJ (ed.), Early hominids of Africa, London: Duckworth, pp. 285- 310.

- Walter, RC, Manegam PC, Hay, RL, Drake, RE, Curtis, GH 1991 'Laser-fusion ⁴⁰AR/³⁹AR dating of Bed I, Olduvai Gorge, Tanzania.' *Nature*. Vol. 354, pp. 145-149.
- Walter, RC 1994 'Age of Lucy and the first family: single-crystal ⁴⁰Ar/³⁹Ar dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia.' *Geology*, vol. 22, no. 1, pp.6-10.
- Walter, GH 1988 'Competitive Exclusion, Coexistence and Community Structure.' *Acta Biotheretica*, vol. 37, pp. 281-313.
- Washburn, SL, Patterson, B 1951 'Evolutionary importance of the South African 'manapes'.' *Nature*, vol. 167, no. 4251, pp.650-651.
- Watson, V 1993, 'Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented.' In: Brain C, (ed.) *Swartkrans: a cave's chronicle of early man.* Pretoria: Transvaal Museum, South Africa, pp. 35–74.
- Weiss, KM 1972 'A generalized model for competition between hominid populations.' *Journal of Human Evolution*, vol. 1, pp. 451-456.
- Werdelin, L, Dehghani, R 2011 'Paleontology and geology of Laetoli: Human evolution in context.' In: Harrison, T (ed.), *Carnivora*, Springer, Netherlands, pp. 189–232.
- Werdelin, L, Lewis, ME 2001, 'A revision of the genus Dinofelis (Mammalia, Felidae).' Zoological Journal of the Linnean Society, vol. 132, pp. 147–258, DOI 10.1111/j.1096-3642.2001.tb02465.x.
- Werdelin, L, Peigné, S 2010 'Cenozoic Mammals of Africa.' In: Werdelin L, Sanders WJ, (eds.), *Carnivora*, University of California Press, Berkeley, California, pp. 603–658.
- White, TD 1995, *Paleoclimate and Evolution, with Emphasis on Human Origins*, Vrba, E, Denton, G, Partridge, T, Burkle, L (eds.), Yale Univ. Press, NewHaven, pp. 369–384.

- White, TD, Johanson, DC, Kimbel, WH 1981 'Australopithecus africanus: its Phyletic Position Reconsidered.' South African Journal of Science, vol. 77, pp. 445- 468.
- White, TD, WoldeGabriel, G, Asfaw, B, Ambrose, S, Beyene, Y, Bernor, RL, Boisserie, JR, Currie,B, Gilbert, H, Haile-Selassie, Y, Hart, WK, Hlusko, LJ, Howell, FC, Kono, RT, Lehmann, T,Louchart, A, Lovejoy, CO, Renne, PR, Saegusa, H,
- Vrbe, E 1995 'The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and palaeoclimate.' In: Vrba, E, Denton, G, Partridge, T, Burckle, L (eds.), *Palaeoclimate and Evolution with Emphasis on Human Origins*, New Haven, Yale University Press, pp. 385-425.
- Vrba, ES, Wesselman, H, Suwa, G 2006 'Asa Issie, Aramis and the origin of *Australopithecus*.' *Nature*, vol. 440, DOI: 10.1038.
- Walker, A, Leakey, RE 1978 'The hominids of east Turkana.' *Scientific American*, vol. 239, no. 2, pp.54-67.

Wolfpoff, Milford H. 1982a, 'Australopithecines: The unwanted ancestors,' In: Reichs, KJ, Hominid Origins, University Press of America, Washington, D.C., pp. 109-26.

- Wolpoff, M.H., 1971. Competitive exclusion among lower Pleistocene hominids: the single species hypothesis. *Man*, pp.601-614.
- Wood, BA, Chamberlain, AT 1987 'The nature and affinities of the "robust" australopithecines: a review.' *Journal of Human Evolution*, vol. 16, no. 7-8, pp.625-641.
- Wood, B, Wood, C, Konigsberg, L 1994 '*Paranthropus boisei*: an example of evolutionary stasis?' *American Journal of Physical Anthropology*, vol. 95, no. 2, pp.117-136.

- Wood, BA, Abbott, SA, Uytterschaut, H 1988 'Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine root morphology.' *Journal of anatomy*, vol. 156, p.107.
- Wood, B 1991 'A Palaeontological Model, for Determining The Limits of Early Hominid Taxonomic Variability.' *Palaeontologia Africana*, vol 28, pp.71-77.
- Wood, B 1992 'Early hominid species and speciation.' *Journal of Human Evolution*, vol. 22, pp. 351-365.
- Wood, B, Collard, M 1999 'The Human genus.' Science, vol. 284, pp. 65–71.
- Wood, B, Constantino, P 2007 '*Paranthropus boisei:* Fifty Years of Evidence and Analysis.' *Yearbook of Physical Anthropology,* vol. 50, pp. 106-132.
- Wood, B, Leakey, M 2011 'The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa.' *Evolutionary Anthropology*, vol. 20, pp. 264-292.
- Wood, BA 1991, *Koobi Fora Research Project, Volume 4, Hominid cranial remains*, Clarendon Press, Oxford.
- Wynne-Edwards, VC 1962, Animal dispersion: in relation to social behaviour, No. QL752 W9 1962a.
- Zhu, Z, Dennell, R, Huang, W, Wu, Y, Qiu, S, Yang, S, Rao, Z, Hou, Y, Xie, J, Han, J, Ouyang, T
 2018 'Hominin occupation of the Chinese Loess Plateau since about 2.1 million years ago.'
 Nature, vol. 559, pp. 608–612.
- Zuckerman, S 1928 'Age-changes in the chimpanzee, with special reference to growth of brain, eruption of teeth, and estimation of age; with note on the Taungs ape.' *Proceeds of the Zoological Society of London*, vol. 98, pp. 1-42.

Appendix 1

Supplementary Material from Herries et al. (2020), Chapter 2.

This manuscript has been modified (headings, figure numbering, and referencing style) to match the formatting within this thesis as closely as possible. All content matches the accepted manuscript verbatim.



Supplementary Materials for

Title: Drimolen crania indicate contemporaneity of *Australopithecus*, *Paranthropus* and early *Homo erectus* in S. Africa

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Tables S1 to S3 Movie S1

Table S1

Micromorphological Observations of Drimolen Lithofacies: A) General description of the 3 main clastic lithofacies; B) Detailed micromorphological descriptions of Drimolen lithofacies.

A.

Talus Cone Clast Supported Breccia (CSB) Facies

This facies is composed of unsorted dolomite and/or chert clasts, from granule- to small boulder size (up to 40-50 cm), embedded in reddish silty loam matrix cemented by calcite and aragonite (CaCO3). The shape of the skeleton clasts is lithology-controlled, with dolomite elements usually equant and subangular to subrounded, while chert clasts are generally platy and angular or slightly subangular when strongly altered. In most cases, clasts are randomly oriented within the sediment, and only in some cases they are oriented parallel to the depositional surfaces. The structure varies from clast-supported to subordinately matrix-supported, the latter occurring more frequently in the upper horizons; openwork does not occur. The matrix is reddish-brown, with medium to fine granular aggregation, grain-size ranges from clay to coarse sand; however, these characteristics are commonly masked by subsequent CaCO₃ cementation. At micromorphological scale, the fine component (i.e. the matrix) of the "Central Talus Cone" deposits (Fig. 11, A) includes silt- to fine sand-size granular aggregates of clay and amorphous iron oxides, with subordinate manganese oxide (Fig. 11, B).

Talus Cone: Intermediate Gravel, Sandstone and siltstone with Blocks; Matrix Supported Breccia (MSB) Facies

Finely layered sediments have often been referred to incorrectly as breccia (13) or in more recent literature (30) as "siltstone". These deposits are in fact characterised by wider grain-size ranges, from clay- to granule- and very fine gravel-size; the term sandstone/siltstone is therefore more appropriate. However, finely layered sediments often include large chert and/or dolomite blocks (up to 40-50cm), even if fewer than in the Central Talus Cone Breccia. These deposits have thus sometimes been referred to as matrix supported breccia (MSB). This aspect is typic of the intermediate facies of talus winnowing, which characterises the intermediate part of the talus cone. The structure is matrix-supported, the wide spaces among blocks being filled by sandstone/siltstone, which sometimes includes very fine gravel and/or granules. The fine fraction is organised in coarse laminae, sometimes with cross-bedding or scour-and-fill features that appear also at microscope scale (Fig. 11, E, F). The grain-size of these laminae often grades upwards and may be terminated by a fine silt to clay crust that indicated very low energy flow or puddling (Fig. 11, E, F).

The same components seen in the breccia can be observed microscopically within the sandstone and siltstone sediments, with differences mainly being in size and fabric. The fine fraction includes mainly mono- or polycrystalline quartz, chert, and very subordinate mica or micaceous metamorphic rock grains; the shape is mainly equant (excluding mica flakes), almost always angular. Clay aggregates, heavily stained by amorphous Fe-oxides are dominant within the finer fraction, but occur also within the coarsest one. Finer soil aggregates are in accordance with lower-energy transport and deposition of the winnowed sediment, with some evidence of pooling. Cyclical processes are indicated by stacks of fining-upwards laminae, with wide packing voids due to subsequent washing-out of fine particles from among larger grains.

Distal Gravel, Sandstone and Siltstone (GSS) Facies

These units (GSS) are rather homogeneous throughout the palaeocave infill, with minor changes and variations mostly related to energy sorting of the grain-size. For the same reason the average grain-size is smaller than in the intermediate facies and the size of the particles seldom exceeds fine sand. These sediments are rhythmically organised in laminae and layers from 0.5-1 to 3-4 cm thick, straight plane and (sub)horizontal; fining- upwards sequences are common, often terminated by a thin crust of fine clay that indicates pooling (Fig. 11, G-I). Very short hiatuses in clastic deposition processes are indicated by thin speleothem crusts interbedded within the siltstone (Fig. 11, G, I). This stabilisation of the underlying sediments greatly aids magnetic remanence lock in and accounts for the good palaeomagnetic data from the DMQ deposits (see below). Fine siltstone generally fills in spaces between breccia units and palaeocave walls. In general, sediments overlying the WOJFS are characterised by finer texture, fewer evidence of fining-upwards laminae and rare indicators of (relatively) high energy and sediment wash-out. This change may derive from a different organisation of the inner spaces of the cavern, as the deposition area was closer to the top of the breccia cone; however, a decrease in rainfall cannot be excluded

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R	Grain-size	Shape	Sedimentary structures	Formation process	Sedimentary environment	Location at Drimolen
Flowstone Speleothe m (FS Facies)		More or less continuous layers of aragonite, calcitised and calcite, with acicular to columnar crystal shape. Variable thickness.		Typical karst processes. Chemical deposition due to carbonate-rich water percolation.	Cave, generally not (or poorly) communicating with the outside. Humid environment.	 Forms as three distinct phases that form 2 FBUs Basal flowstone that was mined and now only survives in section below the Warthog Cave section where it is dated by U-Pb to ~2.64 Ma and at the base of the Walls of Jericho Section (BFS). A thin flowstone dated to ~1.95 Ma that separates lower FBU1 from upper FBU2 in the Walls of Jericho and Italian Job Sections, as well as on the Western Wall (WOJFS). Flowstone that caps the siltstone and sandstone of the Warthog Cave section after a phase of significant erosion and dated to ~1.79 Ma (WCFS).
Talus Cone : Clast Supported Breccia (CSB) Facies	Unsorted coarse skeleton, from fine gravel to blocks (up to 40- 50cm). The fine component consists of reddish to brownish sandy to silty loam matrix. Strong CaCO ₃ cementation. Skeleton comprises platy angular chert clasts and subequant subangular to subrounded dolostone, variously altered.	Cone-like when situated in central areas of the cave; half-cones when along the walls.	Crude layering, high- angle dipping, defined by grain- size variation or iso- orientation of platy skeleton clasts.	Discontinuous and laterally inhomogeneous accumulation of large ceiling breakdown clasts; in- wash of red soil sediment. Erosion of cone sides.	Cave, open to the outside. Moderate to medium energy flow or mass transport due to rainfall water entering the cave.	 In central part of palaeocavern in both FBU1 and FBU2, although FBU1 consists of denser, larger clasts. 1. Jangi Buttress (FBU1) associated with DNH 134 2. DNH 7 Block (FBU1) 3. Marcel Pinnacle 4. Base of Italian Job Pinnacle in FBU1 (associated with DNH 152) 5. Western Breccia.
Talus Cone: Intermediate Gravel, Sandstone and siltstone with Blocks; Matrix Supported Breccia (MSB) Facies	Unsorted coarse skeleton, from coarse gravel (rarely finer) to blocks. Reddish to brownish sandy to silty loam matrix, sometimes including fine gravel. Strong CaCO ₃ cementation. Skeleton comprises platy angular chert clasts and subequant subangular to subrounded dolostone, variously altered.	Wedge-like, steeply to moderately dipping.	Fine to laminated layering of matrix among stones; frequent alternating fine and coarse (fine gravel) layers. Scour-and-fill structures, filled by cross- bedded silt to fine gravel.	Erosion of fine components from the talus cones and re- deposition on the sides and proximal toe of the cone. Gravitational displacement of coarse skeleton.	Cave, open to the outside. Intermediate side of the talus cone. Moderate- to low-energy flow of rainfall water entering the cave.	 Italian Job Pinnacle in both upper FBU1 and FBU2. Jangi Buttress (FBU1) (above the CSB including DNH134).

Distal	Reddish to orange sand to silty	Tabular,	Parallel layering of	Re-deposition of fine	Side areas of cave (open to	1. Southern side of palaeocavern in Warthog
Gravel, Sandstone and Siltstone (GSS Facies)	clay loam, rarely very fine gravel; strong CaCO ₃ cementation.	parallel layering, subhorizont al.	thin layers and laminae; frequent fining-upwards sequences.	particles winnowed from the talus and from the intermediate facies.	the outside); talus toe and over. Low-energy flow of rainfall water entering the cave.	 Southern side of palaeocavern in Warthog Cave Section in FBU1 (WGSS). Northern side of palaeocavern in Walls of Jericho Section in both FBU1 and FBU2 On northern side of Italian Job Pinnacle in FBU1 Remnants against the West Wall of the
						Palaeocavern in FBU1

Table S2

Uranium values obtained on samples DMQ2 and DMQ3 using the MC-ICPMS and ICPMS quadrupole. Average values are consistent across several areas of the enamel and dentine measured by separate ICPMS (<2%).

Sample	Dental	U	0.1110 H	220/224		224/229	
	tissues/Instrument	(ppm)	(ppm) error		error	234/238	error
	Enamel (MC-						
	ICPMS)	1.43	0.15	0.9220	0.0256	1.2841	0.0587
	Dentine (MC-						
DMQ2	ICPMS)	17.3	1.1	0.9558	0.0201	1.411	0.0237
	Enamel (ICPMS)	1.62	0.39				
	Dentine (ICPMS)	18.22	0.81				
DMQ3	Enamel (MC-						
	ICPMS)	2.07	0.18	0.9731	0.0155	1.0886	0.0369
	Dentine (MC-						
	ICPMS)	19.31	1.05	0.8822	0.0278	1.4183	0.0109
	Enamel (ICPMS)	2.42	0.40				
	Dentine (ICPMS)	18.85	1.03				

Table S3

Summary of the dosimetry results for DMQ. All in situ measurements were obtained using a portable gamma spectrometer Inspector 1000. "Modelled breccia" represents the average value approximated from measurements were the probe was partially covered. Those values were not used for US-ESR age calculations. "Fractured breccia" are values obtained in natural fractures in the breccia. Decalcified breccia was obtained on the sediment from the same stratigraphic unit as the sample. Sediment content was obtained using ICPMS solution on a small fraction of the decalcified breccia around the tooth.."

Samples	Dose rate (mGy/ky)		Error		
Modelled Breccia*	218		64		
Fractured Breccia	281		24		
Decalcified Breccia	357		45		
	U (ppm)	Th (ppm)		K (weight %)	
Sediment (ICPMS)	1.88 (+/-0.5)	3.02 (+/-0	.2)	0.29 (+/-0.05)	

Movie S1

Movie describing the Drimolen site, its stratigraphy, sampling locations and age.

Supplementary Text

Materials and Methods

Reconstruction of endocranial volume

Based on surface scans of the original fossil acquired through use of the Artec Spider scanner following methodology outlined in Adams et al. (2015), we extracted the preserved endocranial surface of DNH 134 and generated a partial virtual endocast by smoothly filling in missing regions. We used a symmetric human template of an endocranial landmark configuration (935 landmarks and sliding semilandmarks; Fig. 8; see also Neubauer et al., 2009; Neubauer and Gunz, 2018), and defined which landmarks and sliding semilandmarks are preserved and which are missing. Semilandmarks were slid to the symmetric template configuration to gain point-to-point correspondence between individuals using the bending energy of the thin-plate-spline algorithm as a minimization criterion. Endocranial (semi)landmarks were also captured for an extant reference sample including 90 humans, 27 chimps, 39 gorillas and 44 orangutans, as well as for four African and four Asian *H. erectus* individuals (KNM-ER-3733, KNM-ER-3883, KNM-WT-15000, OH9, Sambungmacan 3, Sangiran 2, Ngandong 14, Nwagi; Spoor et al., 2015).

On the basis of the extant reference sample, a multiple linear regression model was established to estimate endocranial volume from the endocranial form of the preserved regions of DNH 134 as captured from the landmarks (e.g., Spoor et al., 2015). Pretending that the same regions as in DNH 134 are missing in each of the reference individuals as well as the listed *H. erectus* individuals and using the same methodology to estimate their endocranial volume allows comparison of the estimated and actual endocranial volume and therefore an interpretation of how the choice of the reference sample influences the estimates (eg., Neubauer et al., 2012; Spoor et al., 2015). This analysis (Fig. 8) shows that predicted and actual endocranial volumes are highly correlated without a taxon-dependent bias towards over- or underestimation so that DNH 134's endocranial volume can be estimated reliably.

Additionally, the missing portions of DNH 134's endocranial surface were reconstructed based on thin-plate-spline warping of the extant reference sample and the reconstructions' endocranial volumes were measured. The average or most common value and the range of estimates based on different reference individuals can be interpreted as the most

probable value and estimation uncertainty, respectively (Neubauer et al., 2012; Kimbel and Villmoare, 2016). Assuming that the same regions as in DNH 134 are missing in each of the reference individuals as well as the listed *H. erectus* individuals, we estimated their endocranial volumes as well and compared them to their measured cranial capacities (Fig. 8). If the pooled reference sample including humans and apes is used, the endocranial volume of smaller individuals (apes) is predicted too small. A good estimate is possible if the "correct" reference sample (i.e. the same species) was used (Fig. 8). Using humans and apes in a pooled reference sample to reconstruct DNH 134 might therefore lead to (slight) over- or underestimation of its endocranial volume. However, our results show that endocranial volume estimates based on thin-plate spline reconstructions (484-593 cc) are consistent with regression-based estimates (514-564 cc).

As a two-to-three-year-old individual, DNH 134 has not reached its adult brain size when it died, although it was likely approaching the adult population range of variation. We computed Gompertz growth curves for ontogenetic data of human and chimpanzee data from the literature for comparison (Marchand, 1902; Zuckerman, 1928; DeSilva and Lesnik, 2006; Alemseged et al., 2006; Isler et al., 2008; Neubauer et al., 2009; Neubauer et al., 2012). A two-year-old individual with a cranial capacity of 538 cc would grow into an adult of 661 cc and 577 cc according to the human and the chimpanzee growth curve, respectively, while a three-year-old individual would grow into an adult of 588 cc and 551, respectively. Despite its juvenile status, we therefore suggest that DNH 134 documents small brain size in this population.

Stratigraphy and Micromorphology

The characteristics of the sediments were observed and described on natural profiles (dissolution shapes), old quarry cuts, and recent excavation profiles and surfaces. Descriptions were carried out following Catt (Catt, 1990). Emphasis was given to texture, boundaries, sedimentary structures and, more generally, to the architecture of the sedimentary bodies, to reconstruct the stratigraphy of the cave infill. Litho- and allostratigraphic units (NACSN) were used in assessing the stratigraphic sequence and then lumped into chronostratigraphic Flowstone Bound Units (Pickering et al., 2007). Texture data were inferred from field observations and the measurement of clasts in exposed profiles, on freshly broken sections of hand samples, and from micromorphological samples in thin section under polarising microscope. Micromorphological observations were carried out on undisturbed sediment samples. Oriented blocklets were detached from natural or excavation profiles; their coordinates were recorded by a total station, and by far-field and macrophotography. The samples were air-dried in laboratory at 35° C in ventilated oven, and impregnated, including the cemented samples, by epoxy resin under medium vacuum and let polymerise. The resulting samples were cut by diamond saw, polished, glued on 90x60 or 60x45 mm microscope slides and ground to 30 µm on abrasive disks, using petroleum for lubrication. The resulting slides were protected by standard cover slides and labelled. Observations were carried out following the standard formalised by Bullock et al. (Bullock et al., 1985) and Stoops (Stoops, 2003). Thirty-eight monoliths were collected from locations selected to represent the most relevant aspects of the various lithologic units, as well as local peculiarities.

Coupled Uranium series and Electron Spin Resonance (US-ESR)

For each tooth a small fragment of dentine and enamel was removed using a hand-held saw, with a 300 µm thick diamond blade. The small fragment was then cut in half exposing a flat surface of dentine and enamel for U-series analyses. Internal dose rate was calculated using U-series values obtained via LA-MC-ICPMS on a Thermo Neptune plus coupled to ESI NW193 and ICPMS guadrupole Agilent 7700 for concentration correction of ²³⁸U. The values measured in the enamel and the dentine, are consistent across the measured area. An average value was calculated for each dental tissue and used for the US-ESR model. Baseline and drift were corrected using a NIST 612 glass disc, while a fossil hippopotamus tooth of know U-series concentration was used to correct ²³⁴U/²³⁸U and ²³⁰U/²³⁸U ratios and assess the accuracy of measurements. Concentration obtained by LA-MC-ICPMS were compared to quadrupole ICPMS analyses on the same dentine and enamel fragments (Table S2). To account for tailing effects, measurements were carried out at half-masses of 229.5 and 230.5 for ²³⁰Th and 233.5 and 234.5 for ²³⁴U. The other half was used for ESR measurements, by separating the different dental tissues. Both DMQ-2 and DMQ-3 enamel fragments removed from each sample and used for the ESR measurements were directly in contact with the dentine on one side and directly in contact with the sediment on the other side (no cement). The outer surface of the enamel (in contact with the surrounding sediment) and the dentine directly attached to it were removed using a diamond blade rotary tool. Simultaneously, 100 µm on each side was removed to avoid alpha particle contribution.

ESR dating for Drimolen fossil teeth was performed on a Freiberg MS5000 X-band spectrometer at 1G modulation amplitude, 2mW power, 100G sweep, and 100KHz modulation frequency, coupled to a Freiberg X-ray irradiation chamber, which contains a Varian VF50 x-ray gun at a voltage of 40KV and 0.5mA current. Each tooth fragment was mounted onto a teflon sample holder, allowing the fragment to be exposed directly to the x-ray source with no shielding (except for a 200µm aluminium cover). To estimate the ESR equivalent dose (De), each fragment was irradiated nine times, following exponentially increasing irradiation times (i.e. 90s, 380s, 1080s, 1800s, 3600s, 7200s, 14700s, 28800s and 63300s, with an average dose rate for DMQ-2 and DMQ-3 of 0.22Gy/s 0.25Gy/s respectively). The x-ray emission received by the bovid teeth was calibrated using added known gamma irradiation dose performed at the Australia's Nuclear Science and Technology Organisation (ANSTO). During each irradiation step, the output of the x-ray gun was recorded, to allow an accurate determination of the dose received by the sample at each irradiation steps. Fitting procedures were carried out with the McDoseE 2.0 software that uses a Bayesian framework approach, where the solution is a full probability distribution on the dose equivalent (Joannes-Boyua et al., 2018). The dose response curves (DRCs) were obtained by averaging the peak-to-peak T_1 - B_2 ESR intensities recorded for each irradiation dose over 180 degree (10° step) measurements and merged into a single spectrum (Joannes-Boyau, 2013). Isotropic and baseline corrections were applied uniformly across the measured spectra (Joannes-Boyau and Grün, 2011). The final D_E values were obtained by fitting a single saturating exponential (SSE) through the ESR intensities and by selecting the appropriate maximum irradiation dose (D_{max}) in order to avoid dose estimation inaccuracy (Duval and Grün, 2016).

The external dose rate (Table S3) was calculated using the U, Th and K content of sediment collected from the site as well as measured directly using a portable gamma-spectrometer Inspector 1000. Measurements were made in places were breccia was already fractured. Some results where the probe could not be fully surrounded by 30cm of sediment were modelled using the sedimentary geometric configuration around the probe (*Modelled breccia*), but represent poorly constraint measurements and therefore removed from calculation. The Drimolen cosmic dose rate was estimated, considering the site variation over the burial time as detailed in this study. With an estimated cover of about 30m of dolomite (using 2.85±0.03 g.cm⁻³ average density value) in the original context and

a gradual denudation rate of 10 meters per million years. The large error takes into consideration sudden collapse of parts of the dolomite instead of a gradual denudation rate (Table S3).

<u>Palaeomagnetism</u>

A series of 11 independently oriented samples (Table 2) were taken from the Drimolen palaeocave deposits targeting clastic siltstone sequences and flowstones. These were taken as block samples and were oriented in situ using a Suunto magnetic compass and clinometer. Subsequent corrections were made for the local dip of the stratigraphy and the declination of the local field according to the International Geomagnetic Reference Field (IGRF), accessed through the British Geological Survey (http://www.geomag.bgs.ac.uk/data service/models compass/igrf form.shtml). Block samples were drilled and cut into standard 20 x 25 mm palaeomagnetic subsamples using water-cooled preparation equipment. Palaeomagnetic experiments were undertaken at TAAL, with additional mineral magnetic tests performed at the University of Liverpool Geomagnetism Laboratory (ULGL; UK) and Institute for Rock Magnetism (IFRM), University of Minnesota (US). Mass specific magnetic susceptibility measurements at low (χLF) and high (χHF) frequency were undertaken using a Bartington MS3 system for frequency-dependant, room-temperature analysis. Isothermal Remanent Magnetization (IRM) acquisition curves and backfields, hysteresis loops and thermomagnetic curves (*M*/T) were run on a Magnetic Measurements Variable Field Translation Balance (VFTB) at ULGL, with additional IRMs imparted using a MMPM10 Pulse Magnetiser at TAAL. Curie temperatures (T_c) were calculated from *M*/T heating curves using the Moskowitz et al. protocol (Moskowitz, 1981) smoothed with a 3-point running average in RockMagAnalyizer 1.1 (Leonhardt, 2006). First-order reversal curves (FORCs) were measured on a Princetown Micromag Vibrating Sample Magnetometer at IFRM and processed using FORCinel 3.0 (Harrison and Feinberg, 2008) and VARIFORC smoothing (Elgi, 2013). Hysteresis backfield curves were de-convoluted using MAX UnMix (Maxbauer et al., 2016). Palaeomagnetic samples primarily underwent a 16-point thermal demagnetisation (TH_D) using a shielded Magnetic Measurements MMTD80a Thermal Demagnetiser in a zero-field cage. Alternating field demagnetisation (AF_D) was also undertaken for comparative purposes using a Molespin alternating field demagnetiser and an Advanced Geoscience Instruments Company (AGICO) LDA5 Alternating Field Demagnetizer. An additional hybrid demagnetisation strategy was employed incorporating

low field AF_D steps (e.g., to 8–12 mT) prior to standard TH_D which has shown to be useful in removing viscous overprints in palaeokarst deposits (Adams et al., 2007; Dirks et al., 2010; Herries et al., 2018). All remanence measurements were made using an AGICO JR6 spinner magnetometer at TAAL. Subsample characteristic remanent magnetisation (ChRM) directions were isolated using principle component analysis (Kirschvink, 1980) and were accepted with median angle of deflections (MAD) of <15°. Final directions for each block sample were calculated from between 3 and 7 subsample ChRMs using Fisher (1953) statistics. Polarity directions were assigned based on virtual geomagnetic pole latitudes of +90 to +60 (normal), +60 to -60 (intermediate), and -60 to -90 (reversed).

Acknowledgments: Thanks to the student excavators from the La Trobe University (LTU) Drimolen Palaeoanthropology & Geoarchaeology Field School and University of Victoria Field School, as well as the University of Florence Archaeological Mission to Drimolen. In particular we thank LTU PhD student Richard Curtis who first found parts of the DNH 134 cranium. We thank D. and J. Smith and Khethi Nkosi, the landowners at Drimolen at various stages, and who granted our permission to work at the site in conjunction with the South African Heritage Resources Agency (SAHRA). The DNH 152 cranium is named after the landowner (Khethi) as he excavated with us on the field school and discovered the first tooth. We want to say a special thanks to our co-author Simon Mokobane for his many years of work at the site. Simon recently passed away due to cancer and he will be remembered fondly by many generations of people who have worked at Drimolen. In recognition of this we have named the DNH 134 cranium after him (Simon). This work would not have been possible without him. We thank Dario Bilardello, Mike Jackson and Joshua Feinberg for their help and advice while measuring at the Institute of Rock Magnetism. Thanks to Bernhard Zipfel for facilitating access to the hominin collections at the University of the Witwatersrand.

Funding: The bulk of this research was funded by Australian Research Council Future Fellowship Grant FT120100399 to AIRH and ARC Discovery Grant DP170100056 to AIRH, JWA, DSS, and RJB. The U-Pb analysis was funded by ARC DECRA DE120102504 to RP. The US-ESR dating was supported by ARC DP140100919 to RJB. Work at the site by the Italian Archaeological Mission was supported by a series of grants by the Italian Ministry of Foreign Affairs to JMC. CM thanks the National Research Foundation (African Origins Platform) for grants that supported the excavation and research at Drimolen. This work was also supported by a La Trobe University Postgraduate Research Scholarship and La Trobe University Internal Research grant to ABL, AM, BA, TE, TM and RS, and a Society of Antiquaries London research grant to JMM. Components of the palaeomagnetic work were conducted during a Visiting Research Fellowship to TM at the Institute for Rock Magnetism, University of Minnesota, supported through the National Science Foundation, USA.

Author contributions: AIRH led the geology and dating program and undertook the palaeomagnetic analysis with TM. JMM, ABL, DS, SN, GS and CM undertook the analysis of the hominin remains. JWA, JM, DSR, CM and SB undertook faunal analysis and

biochronology. GB and AIRH undertook stratigraphic analysis and interpretation. GB, AM, TE and TD undertook micromorphological analysis. RJB undertook the US-ESR dating. BA undertook spatial and GIS analysis. JH, JW and RP undertook uranium-lead dating and associated contextual analysis. MC and RCS undertook studies of the archaeological material. ABL, SB, JMM and AIRH excavated the hominin crania. BJA and CW undertook video and imaging of the site. AIRH, SB, CM, and JMC directed excavations at different times that recovered the hominin material. CM initiated the dating program at Drimolen. All authors contributed to the writing of the paper. Research supporting this publication was undertaken by JM, ABL, AM, while completing a PhD at La Trobe University.

Competing interests: Authors declare no competing interests.

Data and materials availability: All data are available in the main text or the supplementary materials. The fossils are curated at the University of the Witwatersrand hominin vault. Access for research is granted through the hominin access committee (<u>Bernhard.Zipfel@wits.ac.za</u>), including requests for the 3D scan data.
Appendix 2

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