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The Makapansgat Hominins: A Descriptive and Comparative Morphological Study

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THE MAKAPANSGAT HOMININS:

A DESCRIPTIVE AND COMPARATIVE MORPHOLOGICAL STUDY

by

Tafline Constance Arbor

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ABSTRACT OF THE DISSERTATION

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Professor Glenn C. Conroy, Chairperson

The primary focus of this thesis is to extensively describe the cranial, mandibular, and dental specimens from Makapansgat and to compare the assemblage to other South African early hominin samples. The fossils examined here include previously undescribed fossils from the fossiliferous *ex-situ* breccia piles of the Makapansgat Limeworks. Data analyses incorporated extant humans, gorillas, chimpanzees, and macaques to provide a comparative base with which to discuss intraspecific and interspecific variation in currently recognized taxa of South African *Australopithecus*. Results support previous assertions that the Makapansgat specimens share morphological similarities with both *Australopithecus africanus* and *Australopithecus robustus* and that these taxa exhibit considerable overlap in variation. The Makapansgat hominins are distinct in some features, but several competing scenarios are viable. These results are discussed in light of current knowledge and phylogenetic hypotheses for South African early hominin evolution. A taxonomic distinction for the Makapansgat hominins (*A.*

prometheus) is not recommended due to limitations of the small sample. However, these hominins compose the earliest known South African hominin sample and contribute a critical geographic and temporal element, as well as a biologically meaningful and unique pattern of morphological variation, for early hominin studies.

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Finally, I thank my husband for his support during what sometimes seemed like a never-ending process. Sage is an unrepentant optimist, a characteristic occasionally envied and frequently appreciated by me.

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There is a possibility but a rather remote one, in view of the divergences between the baboon at the 2 sites, that the faunal differences between Taungs and Makapansgat (or Sterkfontein) could be an impression of climatic rather than geological discrepancy. In that event we might be confronting at Makapansgat merely the adult form of the large-brained *Australopithecus africanus*. But… it seems more probable that the *Australopithecus* of Makapansgat, although closely akin, was a different species from that of Taungs; he certainly hunted bigger game and had a more varied dietary. Even if there were none of these differences the locality and the novel evidence it affords would justify reference of the specimen to a new species: *Australopithecus prometheus*.

– *Raymond Dart* (1948d)

INTRODUCTION

Raymond Dart introduced a new australopithecine species from the South African fossil site of Makapansgat (Afrikaans for "Makapan Cave") in 1948. Indeed, his comments were the opening remarks for a debate that carried on for decades (Broom, 1946, 1950; Tobias, 1967, 1978, 1980; Aguirre, 1970, 1972; Sperber, 1973; Howell, 1978; White *et al.*, 1981; Rak, 1983). The australopithecine (australopith) bearing Makapansgat Limeworks is in the Makapan Valley of South Africa's Northern Province. The site is well known for its extensive Pliocene mammalian fossil assemblage and early hominin sample. Dart (1948d) originally attributed the Makapansgat australopiths to the new species *Australopithecus prometheus*, but Robinson (1954a) [arguably P.V. Tobias (1967)] later subsumed the specimens into *Australopithecus africanus* (Dart, 1925a). Over the years, these specimens have played a vital part in numerous paleoanthropological studies. For instance, a subadult pelvis (MLD 7) was strong support for Le Gros Clark's hypothesis that early hominins were bipedal (Dart, 1949d). Moreover, the high frequency of broken skeletal elements and the skewed skeletal part profiles of the Makapansgat fossil assemblage led Dart to his theory of the Osteodontokeratic ("Bone-Tooth-Horn") Culture (Dart, 1957a), resulting in the subsequent explosion of more detailed taphonomic investigations (e.g. Vrba, 1975, Shipman and Phillips, 1976, Shipman and Phillips-Conroy, 1977; Maguire *et al.*, 1980; Brain, 1981; Reed, 1997; Latham *et al.*, 1999).

A total of 37 australopithecine specimens, representing at least 12 individuals, are currently reported from the Makapansgat Limeworks (Dart and Boné, 1955; Tobias *et al.*, 1977; see also Table 3-1). Out of these 37 specimens, a few have never been formally described aside from their inclusion in specimen lists for the site. In addition, two recently discovered and undescribed specimens augment the Makapansgat hominin sample to a total of 39 specimens.

All of the specimens from Makapansgat are currently attributed to *Australopithecus africanus*, although one adolescent mandibular specimen has sometimes been more closely aligned with *Australopithecus robustus* on the basis of its hyper-robustness (i.e. Aguirre, 1970, 1972). Many have debated which specimens should be included in the hypodigm of *A. africanus*, and some have highlighted differences between the Makapansgat and Sterkfontein samples (e.g. Broom 1946, 1950; Dart, 1948d; Tobias, 1967; Sperber, 1974; Rak, 1983). Others have argued that the Makapansgat and Sterkfontein australopiths belong to different species, genera, or subfamilies (e.g. Dart, 1948d; Broom, 1946, 1950).

The Makapansgat australopiths are primarily represented by craniodental specimens and range in ontogenetic age from infancy through old adulthood. Although the majority of these specimens were discovered *ex situ* (i.e., from the Limeworks fossil breccia piles or “dumps”), they were attributed to a geological age range of 2.8 - 3.2 million years ago on the basis of faunal seriation and U-Pb analysis of associated breccia (Vrba, 1985; McKee, 1995; McKee *et al.*, 1995; Crawford *et al.*, 2004; Warr *et al.*, 2009). More recently, however, paleomagnetic analysis of the cave deposits and *ex situ* associated breccia indicate an age of approximately 2.58 million years for the Member 4 MLD 37/38 specimen and approximately 2.7 million years for the *ex situ* fossils from Member 3 (Warr *et al.*, 2009; Warr, 2009). Despite the historical contributions of these fossils and debates surrounding both the Makapansgat hominins and the hypodigm of *A. africanus*, previous studies of the Makapansgat hominins have primarily focused only on particular skeletal elements (e.g. Dart, 1948a,b, 1949b,c; Boné, 1955a,b, 1956; Tobias, 1967; Reed *et al.*, 1993; Neubauer *et al.*, 2004). This will be the first study to attempt to systematically describe and compare the entire Makapansgat hominin assemblage to other South African hominin assemblages.

The main goals of this research can be summarized as follows: (1) to compile detailed morphological descriptions, photographs, and measurements of all of the Makapansgat craniodental specimens, (2) to qualitatively and quantitatively compare the morphology of the Makapansgat hominins to other South African australopithecines, and (3) to assess how inclusion of the Makapansgat hominin sample in the taxon impacts interpretations of the overall hypodigm of *A. africanus*. The Makapansgat assemblage provides a temporally and geographically confined sample with which to explore variation within the current hypodigms of *A. africanus* and *A. robustus*. The Makapansgat early hominin sample affords an obviously unique and valuable research opportunity.

Results from this project permit the exploration of numerous questions. For instance, does the variation exhibited by the Makapansgat sample exceed that expected for a single species? How do the Makapansgat hominins compare to *A. africanus* and *A. robustus* at other sites? Should the Makapansgat hominins be attributed to *A. africanus*?

Does the range of variation at Makapansgat exceed that of the Sterkfontein sample of *A. africanus*? How do the levels and patterns of variation within the Makapansgat sample compare to those for *A. africanus* at Sterkfontein? And, how does including the Makapansgat sample in the hypodigm of *A. africanus* impact interpretations of this species?

While answers to these questions are undoubtedly complicated, this is the first exploration of these issues with the complete Makapansgat sample. The Makapansgat hominins are critical for sorting out several broad paleoanthropological issues. In particular, results from this project contribute to (1) establishing whether the Makapansgat hominins represent a single population or a mixed-species assemblage, (2) assessing whether the Makapansgat and Sterkfontein samples represent different species or geographically and temporally distinct populations of an evolving species, (3) examinations of morphological variation in South African early hominins, and (4) focused discussions of variation within *A. africanus*.

PHYLOGENETIC AND TAXONOMIC ISSUES

South African Australopiths

Phylogenetic and Taxonomic Debate. In September 1947, James Kitching, an anatomy student at the University of the Witwatersrand, found the posterior part of a hominin calvaria in the Limeworks dumps (Dart, 1948d; Tobias, 1997). Assuming the blackened bones previously discovered at the site (Dart, 1925b) were the result of fire use by this early hominin, Dart attributed this specimen to the new species *Australopithecus prometheus*. Eventually, both the hominin specimens from Makapansgat attributed to *A. prometheus* and the hominin specimens from Sterkfontein attributed to *Plesianthropus* (*Australopithecus*) *transvaalensis* were subsumed into *Australopithecus africanus* by Robinson (1954a) [although incorrectly indicated by some to be Tobias (1967)].

Today, the Makapansgat australopiths are generally accepted as belonging to the species *A. africanus* (e.g. Clarke, 1977; White, 1977; Tobias 1978; White *et al.*, 1981; Rak, 1983), yet they appear to be distinct in at least some features from most specimens of *A. africanus* at Sterkfontein. Over the years, some authors have argued that one adolescent mandible from Makapansgat should be referred to the taxon *A. robustus* (i.e. Aguirre, 1970, 1972). Others have argued that the Makapansgat and Sterkfontein assemblages attributed to *A. africanus* belong to different species (e.g. Tobias, 1967, 1968, 1973). Several researchers have suggested on the basis of postcranial, dental, cranial, and craniofacial studies that there was significant size variation within the species *A. africanus* (e.g. Kimbel and White, 1988; Clarke, 1988; Reed *et al.*, 1993; Lockwood, 1999; Lockwood and Tobias, 1999; 2002; Plavcan, 2003; Moggi-Cecchi *et al.*, 1998; 2006). These high levels of variation within the hypodigm of *A. africanus* and, more specifically, within the Sterkfontein sample have spurred considerable debate regarding the number of species at Sterkfontein (e.g. Kimbel and White, 1988; Clarke, 1988; 1994; Calcagno *et al.*, 1999, Lockwood, 1999; Lockwood and Tobias, 2002; Moggi-Cecchi, 2003; Moggi-Cecchi *et al.*, 2006).

Controversy also surrounds the phylogenetic relationships of *A. africanus* and several competing hypotheses remain viable, where *A. africanus* is closely linked with: 1) *A. afarensis*, 2) *A. robustus*, 3) a robust australopith clade, 4) *Homo*, and 5) a sister taxon to *Homo* and robust australopiths.

<u>*A. afarensis*.</u> It is possible that the currently recognized species *A. afarensis* and *A. africanus* are geographic variants or subspecies of a single species, *A. africanus* by precedence (Boaz, 1979; Tobias, 1980). In this scenario, the variation within a combined sample of South African *A. africanus* and East African *A. afarensis* can be explained by geographic and temporal factors, without necessitating a species-level distinction. Alternatively, it is possible that the species *A. africanus* is a direct descendant of *A. afarensis* on the basis of more derived features of the cranium and dentition for members of *A. africanus* (many of which this taxon shares with "*Paranthropus*") (Rak, 1985; Skelton *et al.*, 1986; Skelton and McHenry, 1992; McHenry, 1992).

<u>*A. robustus*.</u> An ancestor-descendant relationship has been hypothesized where the species *A. africanus* is ancestral to *A. robustus* on the basis of craniofacial and dental features (e.g. anterior pillars, reduced anterior teeth, molarized premolars) (Rak, 1983;

1985). In some variations of this scenario, the species *A. robustus* is then ancestral to an even more robust *A. boisei*.

A robust australopithecine monophyly (i.e. *Paranthropus*). In these scenarios, the species *A. africanus* has been designated a member of a robust australopithecine clade (Chamberlain and Wood, 1987), a last common ancestor of a robust australopithecine and *Homo* clade (Skelton, 1986; Tobias, 1988; Skelton and McHenry, 1992), or ancestral or a sister group to a robust australopithecine clade (Johanson and White, 1979; White *et al.*, 1981; Rak, 1983; Grine, 1985). In each of these scenarios, craniodental specializations relating to a robust masticatory complex are treated as independent phylogenetic variables [see also discussions by McCollum (1999) and Collard and Wood (2001)].

Homo. The species *A. africanus* has been linked with the genus *Homo* in a number of scenarios. *A. africanus* has been subsumed into the genus *Homo* or into a clade of early *Homo* to the exclusion of the robust australopiths (Robinson, 1963; 1972; Lieberman *et al.*, 1996). Some researchers suggest that *A. africanus* is ancestral to *Homo* (Grine, 1988; Tobias, 1991), while others link *A. africanus* with both *A. robustus* and *Homo* (Walker *et al.*, 1986). Several craniofacial characters link *A. africanus* with *Homo* in these analyses.

A sister taxon to *Homo* and robust australopiths. This scenario stresses a few apomorphies for members of *A. africanus* and results from concerns regarding parsimony in phylogenetic analyses (Strait *et al.*, 1997; Asfaw *et al.*, 1999).

The numerous phylogenetic hypotheses that have been constructed for the hypodigm of *A. africanus* are an obvious source of confusion regarding the appropriate treatment of the Makapansgat hominins.

Research Questions

(1) Morphological description and comparative study. *What morphological features are exhibited by the Makapansgat hominins? How does the Makapansgat assemblage compare to other early hominin assemblages in South Africa?* The morphological features exhibited by the Makapansgat australopiths are examined in light of current knowledge of South African australopith variation. The early hominin fossils from the Makapansgat Limeworks have played a significant role in the history of paleoanthropological thought. Despite their importance in numerous shifts of thought concerning early hominin phylogenetic and behavioral reconstructions, detailed descriptions and comparison of the assemblage as a whole to other hominin assemblages have not been executed. This thesis research was not only undertaken to accomplish this task, but also to produce an extensive dataset for the Makapansgat hominins and make details of previously unpublished specimens available.

(2) Variation within A. africanus*. Does the morphological variation exhibited by the Makapansgat hominins exceed that expected for a single species? Does it fall within the range of variation known for* A. africanus *at other sites?* Long-standing debates regarding the appropriate treatment of the Makapansgat hominins are discussed in light of variation in other human and non-human primates. The rapid deposition of Makapansgat

Members 3 and 4 (Warr *et al*., 2009) indicates that the hominins from this site may be a good proxy of a biological population (or multiple contemporaneous populations). The Makapansgat hominins contribute an important geographic and temporal component to investigations of South African early hominins, particularly in light of Sterkfontein having produced more than half of the total australopithecine sample in South Africa. Results of this study will contribute to long-standing debate regarding the number of species in the Makapansgat hominin assemblage and whether they fall within the range of variation known for the sample of *A. africanus* at Sterkfontein. Moreover, they are a critical sample for in-depth studies on the magnitude and patterning of variation in *A. africanus.*

***(3) How do the results of (1) and (2) impact current phylogenetic hypotheses regarding* A. africanus?** Results are discussed in the context of hypotheses regarding the patterning of variables, where some variables may be effective sex-discriminators (e.g. crown breadth, canine size, several facial widths) and yet other variables may be effective at discriminating taxonomic units (e.g. crown length, cranial breadths, relative cusp sizes, root morphology) (e.g. Wood *et al.*, 1983; Abbott, 1984; Wood and Uytterschaut, 1987; Wood *et al.*, 1988; 1991; although see Collard and Wood; 2001). In addition, rather than producing yet another phylogenetic scenario to exclusively fit the results presented in the following chapters, results are discussed in light of current scenarios. The scenarios most compatible with results are highlighted in the discussion chapter.

(4) Taxonomy. *Given this in-depth examination of the South African australopithecines, what is the appropriate species attribution for the Makapansgat hominins?* Results from (1), (2), and (3) are weighed regarding the appropriate taxonomic

treatment of the Makapansgat and Sterkfontein samples in the final chapter. Regardless of the specific conclusions that are drawn, a focused investigation of the morphological variation within the Makapansgat early hominin sample has implications regarding early hominin phylogeny and taxonomy. Early hominin phylogenetic reconstructions and taxonomic attributions may need to reconsider the appropriate treatment of the hypodigm of *A. africanus*.

SITE HISTORY AND GEOLOGY

Makapansgat

A History of Makapansgat. The Makapansgat Limeworks (see Figure 3-1) is one of several cave sites located on the Makapansgat farm in the Northern Province of South Africa, some 16 kilometers east-northeast of Mokopane (formerly Potgietersrus). The Makapan Valley caves represent a unique paleontological spectrum for South Africa, with Pliocene and Pleistocene fossils known from several localities at Makapansgat (which includes the well known Limeworks site, as well as a number of other fossiliferous sites), Buffalo Cave, Peppercorn Cave, and Cave of Hearths, among other lesser known fossil-bearing localities.

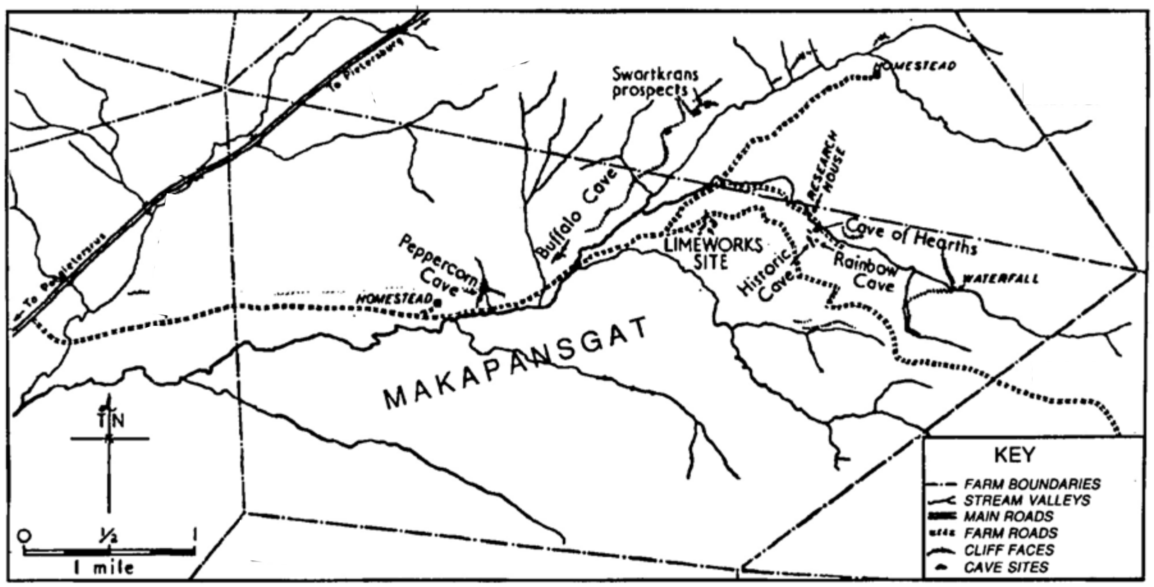
The Makapan Valley's cave sites first achieved notoriety in 1854 after the siege and slaughter of hundreds of Ndebele people of the Kekana lineage by the Boers in the Makapansgat Historic Cave (Hofmeyr, 1993; Tobias, 1997). It was over 60 years later, in the 1920's, that the Makapansgat caves earned fame in a scientific arena due to Wilfrid Eitzman (Tobias, 1997). Eitzman, a high school math and science teacher, visited the Makapan cave sites numerous times from 1922 through the 1930's (Eitzman, 1958). Eitzman discovered several outcrops of fossil-bearing red breccia [many of the South African "breccias" are actually conglomerates or sandstones] in the valley and, with the permission of the White Limes Company that was actively quarrying for limestone, collected samples to send to the South African Museum (Haughton, 1922; Malan, 1988; Tobias, 1997). These efforts were met with limited success, however (Tobias, 1997).

Following Raymond Dart's announcement of the Taung skull (Dart, 1925a), Eitzman piqued Dart's interest in Makapansgat by sending him several blackened fossil specimens and preliminary chemical test results to Dart at the University of Witwatersrand Medical School (Eitzman, 1958; Tobias, 1997). Dart relayed the specimens to a laboratory for further analysis and learned that the bones exhibited a high percentage of free carbon (Dart, 1925b; Tobias, 1997). On the basis of these results, Dart (1925b) suggested the bones must have been burned as a result of an early modern human occupation. Quarrying at the Limeworks ceased in 1935, although a company continued to remove low-grade limestone from the quarry dumps (Eitzman, 1958). The ensuing resorting of the Makapansgat Limeworks dumps is primarily responsible for only a small portion of the original fossil-rich breccia being recovered and, most likely, for much of the difficulty in attributing provenience information to the fossiliferous *ex situ* breccia piles.

Student expeditions to the Makapan Valley began in 1945, led by Phillip Tobias (Tobias, 1997). The first primate remains (*Papio darti*) were recovered from the Limeworks in the inaugural student expedition (Broom and Jensen, 1946) and the first early hominin remains were recovered two years later during a Bernard Price Institute for Palaeontological Research (BPI) funded project (Rubidge, 1997; Tobias, 1997). In subsequent years, the BPI supported further expeditions by James Kitching, Ben Kitching, Scheepers Kitching, and Alan Hughes that led to the discovery of several additional hominin specimens from the Limeworks *ex situ* fossil piles (Eitzman, 1958; Tobias, 1997; Rubidge, 1997). The vertebrate fossils removed from the dumps were central in Raymond Dart's early taphonomic studies. The prevalence of broken skeletal elements and skewed skeletal-part and taxon profiles of the Makapansgat fossil collection led Dart to develop his theory of an "Osteodontokeratic" (bone-tooth-horn) culture for early hominins (Dart, 1957). Dart hypothesized that the Makapansgat fossil assemblage accumulated entirely due to hunting and transport by early hominins and that the disproportionate preservation of various skeletal parts were best explained by hominin selection of the densest osteological elements for use as tools and weapons. Dart's taphonomic analyses supported his highly sensational theories of early hominin behavior (Dart, 1953), spurring an entire generation of researchers to more rigorous taphonomic analyses (e.g. Vrba, 1975, Shipman and Phillips, 1976; Shipman and Phillips-Conroy, 1977; Maguire *et al.*, 1980; Brain, 1981; Reed, 1997) and initiating modern cave taphonomy (see discussion in Brain, 1997).

The past decade has seen increased efforts to recover Plio-Pleistocene fossil material at the Limeworks. In 1993, the Hominid Paleoecology Research Program, led by J.K. McKee, began excavations of *in situ* Member 4 deposits to contribute to paleoecological reconstructions of the valley. However, the Makapansgat Field School is responsible for the recent sorting and preparing of fossils from the Limeworks. Since its inception in 1998, the field school has discovered three additional australopith specimens and numerous faunal remains. Most recently, I have been involved in collaborative efforts to sort out ongoing provenience problems at the Limeworks by excavating fossil-bearing breccia from *in situ* Member 2 and an adjacent, earlier deposit, to assist paleoecological reconstructions for these deposits [summarized by Crawford and colleagues (2004)]. In addition, it has recently become evident that provenience information can be attributed with confidence to fossil bearing breccias in the Limeworks *ex situ* fossil piles on the basis of the general appearance of the fossils and breccia (Latham *et al.*, 2007).

FIGURE 3-1: Map. Map of Makapansgat Limeworks location within the Makapansgat Farm property and modified from H.B.S. Cooke in Tobias (1997).



Stratigraphy, Taphonomy and Provenience. The Makapansgat Limeworks is one of several cave sites located on the Makapansgat farm in the Northern Province of South Africa, some 16 kilometers east-northeast of Mokopane (Potgietersrus). The complex of caverns in the Makapan Valley formed as a result of a combination of subsidence and solution weathering of the Precambrian Malmani Dolomite of the Transvaal Supergroup (Partridge, 1973; Latham *et al.*, 1999). Weathering of the soluble dolomite resulted in the development of extensive connected caverns, whose chambers were subsequently lined with speleothem flowstone and filled with fossil-bearing breccia and indurated silts (Latham *et al.*, 2003; Crawford *et al.*, 2004).

Partridge (1979) first described the Makapansgat stratigraphy in the form of a member system extending from the earlier, lower Member 1 to the later, higher Member 5 breccia deposits. Partridge's South African member system vastly oversimplifies complex cave stratigraphies into fairly simple ubiquitous layered successions for South African early hominin-bearing sites. In reality, the stratigraphy at Makapansgat is far more complex, where multiple repositories were simultaneously being filled with sediments and skeletal remains (Latham *et al.*, 1999; Crawford *et al.*, 2004). Nevertheless, until the actual depositional sequence is better understood following detailed paleomagnetic and chronostratigraphic mapping of the entire Makapan Cave, Partridge's member system provides a useful framework for discussion.

Member 1 is the earliest stratum and the lowest floor travertine that is deposited amid massive stalagmites (Partridge, 1979). The breccias of Member 1 bear little fossil material. This deposit is succeeded by a recently discovered deposit, which appears in much of the cave as thin subaqueous calcite flowstones coating Member 1. This newly identified deposit expands in other parts of the cave, where it indicates intermittent carbonate rich pools in which animals were trapped and subsequently deposited with fine silts (Latham, pers. comm.). A considerable species size bias appears to exist for this newly described deposit. Currently, local concentrations of small to medium sized mammals have been extracted from these deposits, including animals as large as small bovids such as *Makapani broomi* (Schrenck, 1984; Latham *et al.*, 2007; Crawford, pers. obs.).

Member 2, the Red Silts, contains local concentrations of fragmentary fossils indicating denning activity, but it is sparsely fossiliferous overall (Latham *et al.*, 1999; Crawford *et al.*, 2004). Recent excavations have concentrated on finding new *in situ* Member 2 fossil accumulations, although faunal analyses of excavated material are not yet completed (Crawford *et al.*, 2004). To date, no australopiths are known from this deposit.

Member 3, the Grey Breccia, is essentially a blackened calcite contaminated dense fossil bone deposit that was most likely accumulated by the extinct hyena, *Hyaena hyaena makapani* (Brain, 1981; Shipman and Phillips, 1976; Shipman and Phillips-Conroy, 1977; Reed, 1997), and porcupines (Maguire *et al*, 1985; Reed, 1997; Latham *et al.*, 1999). While this deposit at Makapansgat is the most prolific with regard to australopith specimens, they comprise only a small percentage of the Member 3 mammalian fauna. Instead, frugivorous (~15.0%) and arboreal (~5.5%) taxa make up relatively high percentages of the overall faunal assemblage (Reed, 1997). The habitat for the time period represented by Member 3 is reconstructed on the basis of mammalian community analyses as a mosaic habitat with riparian woodlands, bushlands, and edaphic grasslands nearby (Reed, 1997).

Member 4 was described by Partridge (1979) as a coarse pink breccia, although recent studies suggest that it may actually be composed of two different deposits, a lower chalky pink deposit and a higher large angular clast deposit, although both appear to have sediments originating from the same area (Latham, pers. comm.). The MLD 37/38 skull was discovered from *in situ* Member 4 deposits, specifically the higher clastic portion of this deposit. Australopiths make up a small percentage of the overall Member 4 fauna, although cercopithecine primates comprise more than 80% of the faunal remains from this deposit (Reed, 1997). Raymond Dart suggested a climatic shift between the time periods represented by Members 3 and 4 as indicated by a dramatic change in their preserved faunas (Dart, 1962b). Indeed, a higher percentage of frugivorous (~20%) and arboreal (~7%) taxa together suggest a more wooded habitat is indicated by Member 3 deposits, although it is possible that this may be the result of a sampling bias from accumulation by leopards and birds of prey (Reed, 1997). It is likely on the basis of both faunal studies and detailed stratigraphic studies indicating rapid continuing deposition that Members 3 and 4 are roughly contemporaneous (Reed, 1997; Latham *et al.*, 2007). Latham (pers. comm.) makes a convincing argument for a relatively rapid and seasonal deposition of Members 3 and 4.

Member 5 is a coarse brownish red sandy breccia for which few species, but no primates, are represented. Member 5 faunal analyses may indicate a more open habitat since frugivores have yet to be recovered from these deposits (Partridge, 1979; Reed, 1997).

Extensive U-Pb and paleomagnetic revisions are in progress for Makapansgat and other South African australopith-bearing sites by a number of authors. In fact, recent U-Pb and paleomagnetic analyses date Sterkfontein Member 2 StW 573, ‘Little Foot’, to 2.2 Ma, which is considerably younger than published age estimates of greater than 4 Ma, suggesting its contemporaneity with Sts 5, 'Mrs. Ples' (Walker *et al.*, 2006). Most recently, paleomagnetic analyses of fossil-bearing breccia by Warr (2009) indicate an age of approximately 2.6 – 2.7 million years for the Makapansgat specimens. These newest dates place the Makapansgat australopiths in the position of earliest human fossils currently known from southern Africa. These new age data could explain why the Makapansgat and Sterkfontein australopith assemblages are distinct, shedding light on debates regarding the taxonomic and phylogenetic position of *A. africanus*. Thus, the Makapansgat australopith specimens (regardless of species attributions) make up an important sample for australopith biogeography. These specimens are critical in efforts to reconstruct both the appearance of the earliest fossil hominins in South Africa and their phylogenetic relationship to East African early hominin species.

TABLE 3-1: List of hominin specimens from the Makapansgat Limeworks. This list includes all specimens claimed to have been hominin (Tobias *et al.*, 1977).

Specimen	Description	Condition	Age	Probable Sex	Descriptions
MLD 1	calvaria$^{\alpha}$ – includes posterior parts of parietals and majority of occipital	Very fragmentary	Adult	Female	Dart, 1948d; Robinson, 1954b
MLD 2	mandible – complete from symphysis to inferior rami; includes left P_3, (P_4), M_1, M_2, right I_1, I_2, (C_1), (P_3), dm_2, M_1, M_2		Adolescent (~12)	Male	Dart, 1948a,b,
MLD 3	right parietal		Infant		Dart, 1949; Boné, 1956
MLD 3a	endocast of MLD 3 – includes part missing on MLD 3 near lambda		Infant		Listed in Tobias *et al.*, 1977
MLD 4	Lower left M_3 (*same individual as MLD 18 and perhaps MLD 28*)				Dart, 1949a
MLD 5	Lower right dm_2		Juvenile	Male	Dart, 1949a
MLD 6	craniofacial fragment – includes right maxilla with right P^3, P^4, M^1, M^2 (*same individual as MLD 23 and perhaps MLD 1*)		Adult	Female	Dart, 1949a; Robinson, 1956;
MLD 6a	Impression of MLD 6				Listed in Tobias *et al.*, 1977
MLD 7	Left ilium (perhaps same individual as MLD 2)		Adolescent	Male	Dart, 1949c; Le Gros Clark, 1955; Robinson, 1972;
MLD 8	Right ischium – fragment (perhaps same individual as MLD 7)				Dart, 1949c; Robinson, 1972
MLD 9/12	Right maxilla– includes P^3, P^4, M^1, M^2, M^3, sockets of I^1, I^2, C^1, and right palatinum	Fragmentary	Adult	Female	Dart, 1949; 1955
MLD 9a	Breccia cast of MLD 9				Listed in Tobias *et al.*, 1977
MLD 10	"biparieto-occipitale"	Fragmentary	Young adult		Boné, 1955;
MLD 10a	Breccia cast of MLD 10				Listed in Tobias *et al.*, 1977
MLD 11/30	Maxilla – includes I^2, C^1, P^3, P^4, left palatinum and alveolar ridge with M^1 and P^4(?)				Dart, 1949;
MLD 13*	Isolated upper canine – very worn				Undescribed; listed in Tobias *et al.*, 1977

MLD 14*	Right humerus – distal part of diaphysis	Fragmentary			Boné, 1955c; Robinson, 1972
MLD 15*	Right radius – distal part of diaphysis	Fragmentary			Boné, 1955c
MLD 16	Right radius – proximal portion	Fragmentary			Boné, 1955c
MLD 17*	Femur – only includes head	Fragmentary			Boné, 1955c
MLD 18	Mandible – includes left I_1, I_2, C, P_3, P_4, right I_1, I_2, C, P_3, P_4, M_1, M_2, M_3 (*same individual as MLD 4 and probably MLD 28*)	Fragmentary	Adult	Female	Dart, 1954
MLD 19	Mandible – includes M_2 distal roots, M_3	Very fragmentary			Boné, 1955a
MLD 20*	Right clavicle – only acromial end	Fragmentary			Boné, 1955a; Robinson, 1972
MLD 20a	Breccia cast of MLD 20				Listed in Tobias *et al.*, 1977
MLD 21*	Ilium? Indeterminate	Very fragmentary			Tobias *et al.*, 1977
MLD 21a	Breccia cast of MLD 21				Listed in Tobias *et al.*, 1977
MLD 22	Mandible – includes left M_2, M_3 (*original specimen lost – cast only*)	Very fragmentary	Adult	Female	Dart, 1962
MLD 23	Left maxilla – includes I^2, P^3 (same individual as MLD 6)	Very fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 23a	Breccia cast of MLD 23				Listed in Tobias *et al.*, 1977
MLD 24	Isolated lower left M_2 – very worn				Dart, 1962
MLD 24a	Breccia cast of MLD 24				Listed in Tobias *et al.*, 1977
MLD 25	Left ilium	Fragmentary	Adolescent	Female	Dart, 1957b
MLD 26*	Frontal	Very fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 27	Mandible – includes symphysial region, sockets of left and right I_1, I_2, C_1, roots of left and right P_3 (*perhaps same individual as MLD 19*)	Very fragmentary	Adult		Dart, 1962
MLD 28	Right maxilla with palatinum and M^2, M^3 (probably same individual as MLD 4/18)	Very fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 29	Mandible – includes left P_4, M_1	Fragmentary	Adult	Male	Dart, 1962
MLD 31*	Right temporal – includes part of mastoids, posterior half of tympanic plate, exposed middle ear cavity				Undescribed; listed in Tobias *et al.*, 1977
MLD 32	Left radius – proximal portion	Fragmentary			Undescribed; listed in Tobias *et al.*, 1977

MLD 33*	Right parietal	Very fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 34	Mandible – includes roots of right M_2, M_3 (*perhaps same individual as MLD 22*)	Very fragmentary			Dart, 1962
MLD 35	Ilium? Indeterminate	Very fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 36*	Left clavicle – acromial end	Fragmentary			Undescribed; listed in Tobias *et al.*, 1977
MLD 37/38 "Makapansgat Skull"	Cranium with right and left maxillae – includes right M^1, M^2, M^3, left M^2	Fragmentary and very fragmentary	Adult	Female	Dart, 1959a,b, 1962;
MLD 39*	Right humerus – distal portion	Fragmentary			Dart, 1961
MLD 40	Mandible – left side with C_1, P_3, P_4, M_1, M_2, roots of M_3	Fragmentary	Old Adult		Dart, 1962
MLD 41	Isolated molar – broken	Fragmentary			Undescribed
MLD 42	Isolated upper right canine – very worn				Undescribed
MLD 43	Isolated upper right I^1				Undescribed
MLD 44	Isolated upper left molar – most likely M^3				Undescribed
MLD 45	Right maxilla with P^3 and roots of P^4	Fragmentary			Lockwood, 1997
MLD 46	Left femur – proximal portion	Fragmentary			Reed *et al.*, 1993
MLD 47	Mandible – left side with partial roots of M_2 and roots of M_3	Fragmentary			Undescribed
MLD 48	Mandible – right side with roots of P_4, M_1, and M_2	Fragmentary			Undescribed

*probably non-hominin
$^{\alpha}$holotype of *Australopithecus prometheus* (Dart, 1948)

MATERIALS

Data were collected from the crania, mandibles, and dentition of australopith and extant primate taxa. Every South African australopith specimen available for study was included (see Appendix 1 for a list). These australopiths provide critical comparative information with which to assess the Makapansgat hominin sample and elucidate potential population differences within the samples of *A. africanus*, as well as address possible issues of morphological and size changes over time. The primary sample for this thesis is the Makapansgat hominin collection, housed in the Department of Anatomy at the University of the Witwatersrand Medical School in Johannesburg, South Africa (see Table 4-1). Comparative fossil data were collected on material of *A. robustus*, *A. africanus*, and *Homo* from Sterkfontein (StW), and Coopers (COA, COB) at the University of the Witwatersrand Medical School and from Kromdraai (TM), Swartkrans (SK, SKW), and Sterkfontein (Sts, SE, TM) at the Transvaal Museum in Pretoria, South Africa.

Extant primate data were collected to aid comparative analyses of the South African australopiths and to serve as models from which to base estimates of australopith within-species variation. Researchers have attempted to account for temporal variation within fossil species by including multiple primate subspecies in their analyses (e.g. Richmond and Jungers, 1995), highly sexually dimorphic species in their samples (e.g. Lieberman *et al*., 1988; Wood, 1991b), or only a single subspecies per species (e.g. Lockwood *et al*., 2000).

Here, data on extant primate craniodental and mandibular morphology were collected for specimens of *Homo*, *Pan*, *Gorilla*, and *Macaca*. Extant primate data were collected from museum skeletal collections housed at the Smithsonian Institution's National Museum of Natural History (NMNH) in Washington D.C., the American Museum of Natural History (AMNH) in New York, and the Field Museum of Natural History (FMNH) in Chicago.

TABLE 4-1: Makapansgat Hominins[1]

Specimen No.	Element	Discovery (Year / Person / Location)
MLD 1	Calvaria	1947 / J Kitching / Dumps
MLD 2	Mandible with right P3, dp4, M1, M2, and left P3, P4(erupting), M1, M2 (Subadult)	1948/AR Hughes & J Kitching/ Dumps
MLD 3	Parietal	1948 / AR Hughes / Dumps
MLD 4	Left M3	1948 / AR Hughes / Dumps
MLD 5	Right M2	1948 / J Kitching / Dumps
MLD 6	Right craniofacial fragment with right P3-M2	1948 / B Kitching / Dumps
MLD 7	Left ilium (subadult)	1948 / J Kitching / BPI
MLD 8	Right ischium	1948 / J Kitching / BPI
MLD 9	Right maxilla	1948 / B Kitching / BPI
MLD 10	Biparieto-occipital fragment	1948 / B Kitching / BPI
MLD 11/30	Right maxilla with P4-M1 (subadult)	1949, 1956 / AR Hughes, J Kitching / BPI
MLD 12	Right M3	1949 / J Kitching / BPI
MLD 14	Distal humerus shaft fragment	1949 / AR Hughes / Dumps
MLD 18	Mandible with right P4 and right C1-left M3	1953 / AR Hughes / Dumps
MLD 19	Left mandible with M3	1955 / EL Boné / Dumps
MLD 22	Left mandible with M2-3	1955 / AR Hughes / Dumps
MLD 23	Left maxillary fragment with I2 and P3	1955 / AR Hughes / Dumps
MLD 24	Left M2	1955 / AR Hughes / Dumps
MLD 25	Left ilium	1956 / J Kitching / BPI
MLD 27	Mandible without associated teeth	1956 / AR Hughes / Dumps
MLD 28	Right maxilla with M2-3	1956 / AR Hughes / Dumps
MLD 29	Left mandible with P4-M1	1956 / B Kitching / BPI
MLD 34	Right mandible with M1-2 roots	1956 / J Kitching / BPI
MLD 37/38	Partial cranium with fragmentary right M1-3 and left M2	1956 / J Kitching / in situ Member 4 "Pink Breccia"
MLD 40	Left mandible with C1-M2 and M3	1961 / B Maguire / BPI

	roots	
MLD 41	Right M3	1977 / Unknown / BPI
MLD 42	Left C1	1975 / J Kitching / BPI
MLD 43	Left I1	1980 / D Johanson & T White / Unknown (BPI assumed)
MLD 44	Left M3	1983 / M Murase / Dumps
MLD 45	Right maxilla with P3	Unknown / Unknown / Unknown
MLD 46	Proximal left femur	Unknown / J Kitching / in situ Member 4, Upper Phase 1 "Pink Breccia"
MLD 47	Right mandible with M3 roots	2000 / Field School / Dumps
MLD 48	Left mandible with P4-M2 roots	1999 / Field School / Dumps

[1]Data provided by personal observation, Reed (1993), Crawford and Latham (in prep), Dart (1948d; 1949), and the Makapansgat Hominin Catalogue available at the University of Witwatersrand.

Australopith Sample

The australopith specimens were identified by site, likely species attribution, and specific deposits (see Appendix 1 for specimen numbers, sites, and species attributions; see also fossil sample size information provided in Table 4-2). Data were collected on original fossil specimens in virtually all cases. The only exceptions occurred when the original specimen provided an important comparative contribution to this investigation but was not available for study. Specifically, the Makapansgat MLD 22 mandibular fragment, SKX 268 (M^1) from Swartkrans, and StW 402 (M^1) from Sterkfontein were measured from high quality casts. The Taung skull has suffered rather significant damage to the dentition and alveolar bone over the past few decades of study, and as a result, is no longer generally available for study. It was, however, available for photography. Thus, dental morphometrics performed on occlusal photographs were based on the original specimen. The MLD 22 mandibular fragment has been misplaced since its initial discovery in 1955. The MLD 22 cast allows the examination of general morphology. Fine details of the occlusal surfaces of the preserved dentition, however, are not visible.

Regardless, the cast provides a means of assessing traits, measuring overall dimensions, and inclusion in dental morphometric analysis. The isolated upper molar casts from Swartkrans and Sterkfontein (SKX 268 and StW 402) were produced prior to the destructive sampling of the original specimens for use in isotopic analyses. Sex identifications were not recorded, as they are considered indeterminate by this author for all cranial and mandibular specimens from Makapansgat until South African australopith variation is better understood. However, arguments by others regarding sex designation are discussed.

TABLE 4-2: Fossil Fragment Sample Sizes by Site

Locality	Sample Size (N)
Makapansgat	
Crania	10
Mandibles	10
Upper Dental Arcades1	10
Lower Dental Arcades1	11
Sterkfontein	
Crania	20
Mandibles	14
Upper Dental Arcades1	99
Lower Dental Arcades1	115
Swartkrans	
Crania	26
Mandibles	19
Upper Dental Arcades1	110
Lower Dental Arcades1	70
Kromdraai	
Crania	3
Mandibles	3
Upper Dental Arcades1	9
Lower Dental Arcades1	7
Coopers	
Crania	0
Mandibles	0
Upper Dental Arcades1	2
Lower Dental Arcades1	0

[1]In this table, “dental arcades” refers to fossil specimens exhibiting a complete or partial dentition, as well as unassociated isolated teeth.
[2]The category “Crania” includes maxillae.

Taxonomic Designations. Taxonomic attributions for all fossils were based upon morphological assessments of the cranium, mandible, and/or complete dentition whenever possible. For the large number of isolated teeth, taxonomic attributions were based upon morphological assessments of the tooth crown where possible. In some cases, isolated teeth were not taxonomically assigned. Cranial fragments not permitting a reliable assessment of species were not assigned to taxonomic groups. References to taxonomic attributions are presented in the appendices, but it should be emphasized that many of these taxonomic attributions are debated in the literature. Considering the disagreement over the number of species at Sterkfontein (e.g. Kimbel and White, 1988; Clarke, 1988; 1994; Calcagno *et al.*, 1999, Lockwood, 1999; Lockwood and Tobias, 2002; Moggi-Cecchi,2003; Moggi-Cecchi *et al.*, 2006) and Swartkrans (e.g. Grine, 2004), taxonomic attributions should be considered tentative at best.

Anatomically Modern Human Sample

Specimens of anatomically modern *Homo sapiens* were examined and measured at the American Museum of Natural History in New York. Two pre-industrial populations were selected for the comparative modern human sample to provide a global sample of humans. The pre-industrial populations were selected on the basis of two requirements, specifically that each population must: 1) have inhabited a location within reasonable proximity of the tropics (subjectively restricted to within ~30 degrees north or south of the equator) and 2) be represented by large samples of both cranial and postcranial specimens (postcranial data were collected, but have been set aside for later analyses).

Western post-industrial populations are known for their relatively sedentary lifestyle and dietary reliance on highly processed foods. These Western cultural tendencies produce different biomechanical stresses during life which may alter human facial and mandibular mechanical properties. As a result, for this study humans were selected from pre-industrial archeological contexts to be assured that biomechanical strains and stresses more closely approximated those of our ancestors; that is, to assure that individuals consumed a less processed diet and engaged in greater locomotor activity. Data on extant humans were collected from archaeological assemblages from the Marquesas Islands and Egypt (see Table 4-3) for all cranial and mandibular analyses.

Marquesas Island Sample. The Marquesas Islands are located in French Polynesia, some 1,371km from Tahiti. The Marquesas Island sample used in this study is composed of skeletal specimens from the islands of Nuku Hiva, ‘Ua Pou, and Tahuata, housed at the American Museum of Natural History. All of these specimens were recovered by H.L. Shapiro during his involvement in the 1934 Templeton Crocker Pacific Expedition and possibly the 1929 Bernice P. Bishop Museum Tuamotu Expedition (Stefan and Chapman, 2003). The islands of Nuku Hiva and ‘Ua Pou are located in the northwest Marquesas Islands, while Tahuata is located in the southeast Marquesas Islands. Despite linguistic, archaeological, craniometric, and cranial trait data suggesting subtle differences between the inhabitants of the northwest and southeast Marquesas

Islands (*e.g.* Linton, 1923, 1925; Green, 1966; Lavondés and Randall, 1978; Sinoto, 1979; Rolett, 1989; Hughes and Fisher, 1998; Stefan and Chapman, 2003), the three island samples available at the AMNH were combined into a single Marquesas Island population. All of these skeletal specimens are considered to be from pre-contact Marquesan inhabitants (Stefan and Chapman, 2003).

Evidence for interpersonal violence was apparent on several of the Marquesas Island skeletal specimens. For instance, the analyzed sample included one skull with a weapon embedded in the calvaria, multiple individuals had obvious healed fractures of the skull and/or skeleton, some skulls had postmortem drill holes in the calvaria, and a few skulls had cording attached to the calvaria and/or mandible in order, presumably, to be hung on exhibition. Damage to the basicranium was evident in several crania, probably relating to the occasional removal of the cranium from the vertebral column. Most likely as a result of cultural factors relating to interpersonal violence, the sample was skewed with more males than females and age at death was relatively young as determined by dental wear. In addition, the Marquesas Island samples exhibited high levels of both congenital absence and premortem loss of their maxillary and mandibular M3's.

A series of pelves were housed in a box labeled under the single specimen number of 99.1/1805. To avoid duplication of individuals within the Marquesas Island human pelvic sample, only left pelves were measured.

Egypt Sample. The Egyptian sample is composed of skeletal remains collected from archaeological excavations at Gizeh and El Hesa. The Lower Egypt Gizeh sample was excavated by von Luschan in 1889.

The Upper Egypt El Hesa sample is cited as being from the Roman Period, dating to approximately AD 200-400 (Irish, 2006). According to AMNH records, the skeletal remains were collected by the archeologist von Luschan in 1907-1908. These remains were excavated from a middle class late Roman cemetery on the Nile island of El Hesa, an "island" now submerged (Elliot Smith and Wood-Jones, 1910; Reisner, 1910; Irish, 2006). The original AMNH records from von Luschan, however, indicate that these skeletal remains date to the Egyptian 1st dynasty [contra Elliot Smith and Wood-Jones (1910), Reisner (1910), and Irish (2006)]. However, this study follows the treatment of these remains by Irish (2006). The crania from El Hesa exhibit considerable postmortem tooth loss and damage to the dental arcade, nasal cavity, and orbit as a result of their exposure to the mummification process. While some might presume the mummification process would diminish during the Roman Period, this period actually saw an intensification of the use of mummification and an increasing use of resin in the process (e.g. Aufderheide, 2003).

TABLE 4-3: Extant Human Sample Sizes

Extant Human Assemblage	Sample Size N (Males/Females/Unknown or Unrecorded)
Homo sapiens (Gizeh)	
Crania	17 (11 / 6 / 0)
Mandibles	7 (3 / 3 / 1)
Upper Dental Arcades1	11 (1 / 7 / 3)
Lower Dental Arcades1	12 (4 / 5 / 3)

Homo sapiens (El Hesa)	
Crania	10 (4 / 6 / 0)
Mandibles	17 (10 / 6 / 1)
Upper Dental Arcades1	22 (4 / 12 / 6)
Lower Dental Arcades1	33 (11 / 14 / 9)
Homo sapiens (Marques.)	
Crania	20 (13 / 7 / 0)
Mandibles	22 (13 / 4 / 3)
Upper Dental Arcades1	26 (11 / 4 / 11)
Lower Dental Arcades1	30 (16 / 7 / 7)

[1]In this table, "dental arcades" may refer to specimens exhibiting a complete or partial dentition.

Extant Non-Human Primate Sample

The extant non-human primate sample includes data for Chimpanzees (*Pan troglodytes*), Western Lowland Gorillas (*Gorilla gorilla gorilla*), Mountain Gorillas (*Gorilla gorilla beringei*), and Rhesus Macaques (*Macaca mulatta*). Only non-pathological bony regions of wild-caught specimens were measured and included in skeletal samples. This criterion limited the number of specimens available for study and made compiling a large extant primate comparative sample difficult. However, measurements were recorded and included in analyses for the dentition of captive primates. Sample sizes for each taxon are presented in Table 4-4 and data regarding locality and ages are presented in the appendices.

TABLE 4-4: Extant Non-Human Primate Sample Sizes

Taxon	Sample Size: N (Males / Females / Unrecorded)
Pan troglodytes ssp.	
Crania	39 (18 / 19 / 2)
Mandibles	46 (14 / 17 / 15)
Upper Dental Arcades1	39 (8 / 13 / 18)

Lower Dental Arcades1	45 (14 / 17 / 14)
Pan sp?	
Crania	1 (1 / 0 / 0)
Mandibles	1 (1 / 0 / 0)
Upper Dental Arcades1	1 (1 / 0 / 0)
Lower Dental Arcades1	0 (0 / 0 / 0)
Pan paniscus	
Crania	1 (0 / 0 / 1)
Mandibles	1 (0 / 0 / 1)
Upper Dental Arcades1	1 (0 / 0 / 1)
Lower Dental Arcades1	1 (1 / 0 / 0)
Gorilla gorilla beringei	
Crania	21 (11 / 10 / 0)
Mandibles	25 (14 / 9 / 2)
Upper Dental Arcades1	29 (15 / 9 / 5)
Lower Dental Arcades1	25 (14 / 9 / 2)
Gorilla gorilla gorilla	
Crania	25 (19 / 6 / 0)
Mandibles	42 (17 / 11 / 14)
Upper Dental Arcades1	33 (20 / 9 / 4)
Lower Dental Arcades1	36 (17 / 12 / 13)
Macaca mulatta ssp.	
Crania	26 (11 / 15 / 0)
Mandibles	34 (12 / 15 / 7)
Upper Dental Arcades1	26 (11 / 15 / 0)
Lower Dental Arcades1	33 (12 / 15 / 6)

Pan. Chimpanzee specimens were collected as wild-shot animals in Cameroon, Liberia, Rwanda, Zaire, Gabon, and Uganda. One collector from the Field Museum of Natural History, Heller, procured a series of chimpanzees from a site called “Walikali” which he described as being located 30 miles south of Kitunda Village. This same location (Walikali) was cited as being located in Zaire, Rwanda, and the “Belgian Congo” on different chimpanzee tags. It is assumed here that “Walikali” refers to the modern territory of Walikale in North Kivu, which is an eastern province of the current Democratic Republic of the Congo (formerly the Belgian Congo and Zaire). As Rwanda is located on the eastern periphery of the DRC (Democratic Republic of the Congo), it is impossible, but unessential, to determine within which modern geopolitical borders these specimens were attained.

Specimens of *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii*, and *Pan troglodytes* (not identified to subspecies) were combined into a single chimpanzee sample. Although chimpanzee subspecies are combined for the purposes of data analysis within this thesis, population-level variation was visually apparent. Most notably, some chimps from Cameroon exhibited unusually spherical braincases and the Liberian chimps exhibited more vertical mandibular symphyses than other chimp populations. This study's sample sizes do not provide sufficient statistical power to explore these observations. However, these observations indicate that research conducted on more extensive chimpanzee samples housed elsewhere might be able to distinguish populations on the basis of infraorbital variation, mandibular symphysis cross-sectional morphology, and/or braincase shape, among other cranial metric and non-metric variables. Previous studies have distinguished among subspecies of *Pan troglodytes* on the basis of geography, and dental, cranial, postcranial, and genetic variation (e.g. Shea and Groves, 1987; Shea and Coolidge, 1988; Groves *et al.*, 1992; Morin *et al.*, 1994; Uchida, 1996; Braga, 1998; Stone *et al.*, 2002; Taylor and Groves, 2003; Lockwood *et al.*, 2004; Pilbrow, 2006; Becquet *et al.*, 2007; Jabbour, 2008), although others indicate that cranial differences among the subspecies *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii* are primarily the result of size-related and allometric factors (Shea *et al.*, 1993).

Data were collected on the neurocranium of some chimpanzee specimens whose skull caps had been removed with a bone saw when bone loss at the cut edges were estimated to be minimal. When this was the case, the calvaria was repositioned and fastened by putty and measurements were taken according to the same procedure as utilized for specimens with intact calvaria.

Gorilla. Data were collected on Western Lowland Gorilla (*Gorilla gorilla gorilla*) and Mountain Gorilla (*Gorilla gorilla beringei*) specimens available at the FMNH, AMNH, and NMNH. Variation between these gorilla subspecies has been explored in many contexts and has been used to argue that the two subspecies actually belong in separate species (e.g. Shultz, 1934; Vogel, 1961; Taylor and Groves, 2003).

Behaviorally, lowland gorillas are known to be more arboreal and frugivorous than mountain gorillas (Nishihara, 1992; Remis, 1994; 1995; Tutin *et al.*, 1991; Tutin, 1996) and to be more chimpanzee-like in their ranging patterns and groupings (Tutin and Fernandez, 1984, 1985; Tuttle and Watts, 1985; Williamson *et al.*, 1990; Tutin *et al.*, 1991; Remis, 1994, 1995). Molecularly, the genetic variability of the two gorilla subspecies has been argued by some to exceed that of different chimpanzee species (Ruvolo *et al.*, 1991; Ruvolo, 1994). Craniodentally, lowland gorillas have been found to be differentiated from mountain gorillas on the basis of craniometrics, mandibular proportions, crown height, cusp sharpness, and transverse ridges (Groves, 1970; Uchida, 1996, 1998; Taylor and Groves, 2003). Postcranially, lowland gorillas exhibit differences in scapular proportions which can be interpreted as an adaptation to greater arboreality (Taylor, 1997b). In terms of sexual dimorphism, some authors suggest that lowland gorillas are more sexually dimorphic (with larger males and smaller females than mountain gorillas) (Jungers and Susman, 1984; Jungers 1985), while analyses of a much larger sample suggest that mountain gorillas are more sexually dimorphic (with no difference in female body mass, but larger males) (Taylor, 1997a).

Despite the above caveats, gorilla subspecies were combined into a single sample of *Gorilla gorilla* ssp. in order to increase statistical power for analyses. The combination of gorilla subspecies into a single sample is appropriate in this study as greater variation is to be expected for fossil species due to their greater temporal breadth. However, if the variation exhibited by the different gorilla subspecies is considered by the reader to be great enough to warrant species-level distinctions, this action would increase the likelihood of Type II Error. That is, it would increase the likelihood that the Makapan hominins could be found to be statistically indistinguishable from the Sterkfontein sample of *A. africanus* if they are, indeed, a distinct species.

The mountain gorillas, particularly, exhibited numerous gunshot wounds in a variety of stages of healing. Resorption indicating periosteal inflammation was apparent on several individuals. Only measurements on regions seemingly unaffected by injury or disease were recorded.

Macaca. Data were collected on Rhesus Macaque (*Macaca mulatta*) populations from India, China, Thailand, Nepal, Vietnam, and Pakistan housed at the FMNH and NMNH. The Rhesus Macaque is a diurnal, primarily terrestrial, partly arboreal species (Seth and Seth, 1986) with arguably the most widespread geographic distribution of any non-human primate (Wolfheim, 1983; Zhang *et al.*, 1991). Rhesus Macaque subspecies

(*Macaca mulatta mulatta*, *Macaca mulatta villosa*, and *Macaca mulatta* ssp.) were combined into a single Rhesus Macaque sample. Variation between the subspecies is known on the basis of mitochondrial DNA, behavior, and morphology (e.g. Fooden, 1976, 2000; Capitanio, 1986, Capitanio *et al.*, 1998; Clarke and O'Neil, 1999; Groves, 2001).

METHODS

Data Collection

Overview. Multiple data collection methods were utilized to obtain an extensive quantitative and qualitative dataset on the Makapansgat hominins and comparative samples. Elements for which only a single specimen is preserved at Makapansgat and for which the comparative fossil hominin material at Sterkfontein is absent or deficient were described and qualitatively compared to other hominin specimens, but no quantitative analyses ensued. Elements for which a large sample exists for Makapansgat and/or Sterkfontein were described and quantitatively assessed. While a variety of methods were employed to collect data on the South African hominins, the small Makapansgat sample limited the number of cranial, mandibular, and dental measurements recorded. Only non-pathological and wild-caught extant human and non-human primate specimens were measured, however, these criteria were relaxed for fossil specimens. All available fossil specimens were included to increase sample sizes. Details regarding pathology, postmortem distortion, preservation, and measurement repeatability are described whenever relevant in the following chapters.

Data collection for the dentition involved recording linear dental metrics with Mitutoyo digital calipers accurate to +/-0.2 mm and assessing shape variation from occlusal photographs. In addition, extensive trait data were compiled for dental, cranial, and mandibular specimens. Cranial and mandibular landmarks were recorded using a MicroScribe G2x 3-D digitizer accurate to =/-0.23 mm. Methods were devised to collect data while being as non-invasive as possible, to prevent measurement damage to valuable fossil and extant comparative collections. Plastic digital calipers, plastic (delrin) tips for the MicroScribe G2x 3-D digitizer, and occlusal photographs were used to record data for each specimen.

Terminology. Numerous dental, cranial, and mandibular terms and landmarks are employed here, following standard anatomical nomenclature and use in the paleoanthropological literature (e.g. Bräuer, 1988; Wood, 1991; Bailey, 2002; and others). Anatomical terms relating to the cranium, mandible, and dentition utilized in the following chapters are presented by anatomical region in Tables 5-1, 5-5, 5-9, 5-13, and 5-16. Figures 5-1 through 5-9 identify key morphological features and landmarks mentioned in the text.

Qualitative Descriptions. Each specimen from Makapansgat was described and compared to other South African early hominin specimens. The "Description and Results" chapters include detailed descriptions of the morphology of the Makapansgat hominins. In addition, photographs of major anatomical features are presented for each specimen from Makapansgat.

Age estimates were produced for the Makapansgat hominins by Dart (e.g. 1948a, b, d; 1949a; 1962a, b) and Mann (1975) on the basis of a human model of development, but are not presented in the specimen discussions. Early hominin age reassessments by a variety of authors have since indicated that a human model grossly overestimates age in these taxa, particularly since dental crown formation times were considerably shorter than extant humans and are apelike in their dental developmental timing (e.g. Bromage and

Dean, 1985; Smith, 1986, 1987; Beynon and Dean, 1987; Beynon and Wood, 1987; Bromage, 1987; Conroy and Vannier, 1987; Dean, 1987a,b; Dean *et al*., 2001; Lacruz and Rozzi, 2010). In fact, enamel apposition rates in the South African australopiths were found to be more rapid than both modern humans and apes, suggesting that the thicker enameled maxillary and mandibular molars of australopiths took equal or less time to form than extant apes (Lacruz and Bromage, 2006). Thus, age estimates are provided for each specimen on the basis of general developmental stages (infancy, early childhood, late childhood, young adulthood, and old adulthood). A table summarizing the Makapansgat specimen age estimates supported by this other and previous estimates is available in Table 9-1.

These descriptions, supplemented with basic analyses of the vast comparative extant primate and fossil hominin database acquired during data collection, compose the bulk of this study.

Traits. Nonmetric cranial and mandibular data were scored following Wood (1991), Bailey (2002), and Kimbel and colleagues (2004) and were supplemented by traits or characters specifically devised for this study. Traits for the cranium, mandible, and dentition are listed and defined in Tables 5-2, 5-6 and 5-10. These traits were only recorded for fossil specimens.

Cranial and Mandibular Linear Data. Linear dimensions were recorded both directly and secondarily, via extractions from landmark data. Landmark data provide a particularly flexible way to measure and analyze morphological variation (see landmarks in Tables 5-3, 5-7, 5-14, and 5-17). These landmark data were recorded using a

MicroScribe G2x 3-D digitizer with a plastic (delrin) tip, accurate to 0.23 mm, available from Washington University (ET). Linear dimensions were extracted from landmark data by calculation of the minimum distance (*d*) between 2 points [(x_1, y_1, z_1) and (x_2, y_2, z_2)] according to the following formula: $d = \text{sqrt}[(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2]$. Smaller linear dimensions, particularly some dimensions of the mandible and all dimensions of the dentition, were recorded using Mitutoyo plastic digital calipers to avoid problems with the lower accuracy of linear dimensions extracted from digitized landmarks.

Linear dimensions and cranial and mandibular landmarks for the Makapansgat and comparative specimens were recorded following Bräuer (1988), White and Johanson (1982), Wood (1991), Ackermann (1998), Lockwood (1999), and Krovitz (2000, 2003). Measurements of comparative specimens were recorded for dimensions preserved in the Makapansgat sample and for overall size where appropriate.

An effort was made to re-measure a portion of the comparative and fossil specimens to assess repeatability for caliper and digitized data (see "Data Analysis" below). For these specimens, statistical analyses were based upon the averages of the remeasured values. When both the right and left landmarks were preserved in a fossil specimen, the landmark was recorded for both sides. When extracted dimensions for the right and left sides are available, an average was used in analyses.

Data Collection – Cranium

Cranial Terminology. Anatomical terms relating to the cranium and employed in the following chapters are presented in Table 5-1.

TABLE 5-1: Cranial Terminology

	Feature		Feature
1	Anterior nasal spine	16	Infratemporal fossa
2	Articular eminence	17	Mastoid
3	Canine fossa	18	Maxillary tuberosity
4	Carotid canal	19	Occipital condyle
5	Crista petrosa	20	Palatine process
6	Digastric notch	21	Posterior nasal spine
7	External auditory meatus	22	Squamosal suture
8	Foramen magnum	23	Parietomastoid suture
9	Foramen ovale	24	Stylomastoid foramen
10	Frontal squama	25	Subnasale
11	Fronto-Zygomatic Junction	26	Superior orbital fissure
12	Incisive foramen	27	Temporal Squama
13	Inferior orbital fissure	28	Tympanic
14	Infraorbital foramen	29	Vaginal process
15	Infraorbital plate	30	Vomer-Sphenoid Junction

Cranial Traits. Extensive cranial traits were recorded on South African fossil specimens to aid descriptions (see Table 5-2). Cranial traits were recorded, with some modification, following Wood (1991) and Kimbel and colleagues (2004). Traits for the cranium, mandible, and dentition are listed and defined in Tables 5-2, 5-6 and 5-10.

TABLE 5-2: Cranial Traits

Trait	Coding
Posterior calvarial contour	0 = aligned with circle 1 = deviates from circle
Midfacial prognathism	0 = high 1 = intermediate 2 = low
Position of zygomatic angle	0 = below orbit 1 = at orbit

	2 = above orbit
Shape of squamosal suture	0 = flat 1 = arched
Relative height of squamosal suture	0 = low 1 = intermediate 2 = high
Infraorbital plate orientation	0 = vertical 1 = sloped 2 = extremely sloped
Infraorbital topography	0 = flat 1 = maxillary trigon 2 = nasomaxillary basin
Canine fossa	0 = present 1 = groove 2 = fossula 3 = absent
Subnasal contour	0 = biconvex 1 = straight/bi-concave 2 = straight, guttered
Interorbital width	0 = broad 1 = narrow
Sagittal compound temporonuchal crest	0 = yes 1 = no, some components present 2 = absent
Nuchal line emphasis	0 = lateral 1 = medial
Calvarial bone thickness	0 = thin 1 = thick 2 = very thick
Supraorbital corner	0 = angle 1 = rounded
Supraorbital thickness gradient	0 = medial to lateral (thickset medially) 1 = lateral to medial (thickest laterally)
Supraorbital surface	0 = undivided 1 = divided
Posterior temporal squama	0 = flattened 1 = vertical
Max. lateral projection of	0 = high

mastoid	1 = low
Mastoid tip position	0 = anterior 1 = posterior
Mastoid face	0 = single posterolateral 1 = discrete post and lat 2 = single lateral
Digastric notch	0 = confined 1 = posteriorly extended
Mandibular fossa depth	0 = shallow 1 = intermediate 2 = deep
Tympanic form	0 = tubular 1 = platelike
Vaginal process	0 = absent 1 = process
Nuchal plane form	0 = transversely convex 1 = flat
Dental arch shape	0 = posteriorly convergent 1 = intermediate 2 = posteriorly divergent
Zyg temp surface	0 = flat 1 = deeply excavated
Zygo frontal process lateral margin	0 = vertical 1 = laterally divergent
Frontal squama form	0 = sulcus 1 = flat 2 = concave
Palate depth	0 = shallow 1 = intermediate 2 = deep
Palate shape	0 = narrow 1 = intermediate 2 = broad

Cranial Landmarks. Numerous cranial landmarks were recorded for both fossil and extant taxa (see Table 5-3 and Figures 5-1 through 5-5). Cranial landmarks followed, with modification, Bräuer (1988), Ackermann (1998), White (2000), Krovitz (2000, 2003), and Whitehead and colleagues (2005). The majority of landmarks identify intersections of sutures or cranial foramina. Some landmarks indicate points of greatest breadth or minimum breadth, both of which could be argued to be more subjectively identified than sutural intersections or foramina.

The cranial landmarks were collected as indicated in Table 5-3. However, some individuals exhibited completely obliterated cranial sutures, making it difficult to precisely locate a few cranial landmarks. When this was the case, these points were not recorded. Some species-specific variation required minor modification of landmarks for relevant taxa. For instance, the landmark pterion was noted to be particularly variable within the chimpanzee sample. Although pterion was defined in this study as the intersection of the frontal, parietal, and sphenoid, this intersection was not present in all individuals. Since this configuration was not consistently present, pterion was also recorded as the intersection of the frontal, temporal, and sphenoid (if there was no frontal, parietal, and sphenoid intersection). This was particularly common for chimpanzees.

The landmarks defined as subnasale, nasospinale and anterior nasal spine were difficult to differentiate in macaques. As a result, dimensions surrounding macaque nasal apertures are expected to be highly variable. Mastoidale was also sometimes difficult to identify in macaques since the mastoids are insignificant in comparison to other taxa included. The landmark for the digastric groove was only apparent in hominins. For extant primates, this landmark was recorded as the deepest point medial to the mastoid whether a clear groove was present or not. This variable was not analyzed for the extant primate comparative sample.

TABLE 5-3: Cranial Landmarks

Ref.	Ab.	Landmark	Coding/Definition
A-9	al	Alare	Lateralmost point on nasal aperture, perpendicular to nasal height
A-11	av	Alveolare*	Inferiormost alveolar margin between central incisors at midline, taken externally (= infradentale superius)
A-23	ans	Ant nasal spine*	Anterior nasal spine
---	aps	Anterior pillar sup	Superiormost point of anterior pillar visible, taken along nasal margin
A-22	api	Anterior pillar inf	Inferiormost point of anterior pillar visible – or external alveolar margin at center of canine
I-16	aem	Articular eminence	Anteriormost point on the temporomandibular articular surface
L-17 (P-2)	ast	Asterion	Intersection of temporal, parietal, and occipital bones
L-12	au	Auriculare	Point above the center of the external auditory meatus at the root of the zygomatic process
I-3	bas	Basion*	Anterior margin of the foramen magnum on the midsagittal plane
A-1 (L-1)	br	Bregma	Intersection of sagittal and coronal sutures on external cranium
A-21	crt	Canine root	Superiormost point of canine root clearly visible through maxilla
I-12	car	Carotid canal	Posterolateral point of carotid canal
S-4	co	Coronale	Lateralmost point on frontal bone, taken on coronal suture.
L-6	d	Dacryon	Point of intersection of lacrimomaxillary suture and frontal bone
I-15	dig	Digastric groove	Deepest point in the digastric groove
A-15	ek	Ektoconchion	Lateralmost point on orbital margin

I-8	ekm	Ectomolare	Lateralmost point of external alveolar margin, typically at M2 in Homo sapiens
I-7	enm	Endomolare*	Medialmost point on inner surface of alveolar margin, often by center of M2 in Homo sapiens
P-1 (S-5)	eur	Euryon	Lateralmost point of parietal
I-11	fov	Foramen ovale	Posterolateral point of foramen ovale
L-8 (A-19)	fzt	Frontozygo temporale	Lateralmost point on zygomaticofrontal suture
A-16	fzo	Frontozygo orbitale	Point where the zygomaticofrontal suture intersects the inner rim of the lateral orbital margin
S-2	ft	Frontotemporale	Medialmost extension of temporal ridge/temporal line (wherever, not restricted to frontal)
A-3 (L-3)	g	Glabella*	Anteriormost projection of frontal bone along the midsagittal line
I-4	ho	Hormion	Posteriormost point of vomer in midsagittal plane
A-12	inc	Incision	Central point on occlusal surface between the upper central incisors
I-9	icf	Incisive foramen	Posteriormost point on incisive foramen
---	iof	Inferior orbital fissure	Lateralmost point of inferior orbital fissure
---	I^1a - M^3 a	I^1- M^3 lingual alveolar margins	For each tooth (I1- M3), the lingual alveolar margin in the middle of that tooth
---	I^2/Ca - M^2/M^3a	I^2/C - M^2/M^3 lingual alveolar margin	For each interproximal surface (I2/C -M2/M3), the lingual alveolar margin
---	M^3a (post)	M^3 lingual alveolar margin - posterior	The lingual alveolar margin posterior to M3
A-20	if	Infraorbital foramen	Inferolateral point of foramen (when multiple, taken on largest; when equal in size, taken on most superior)
I-10	it	Infratemporale	Medialmost point on convex infratemporal crest on sphenoid's greater wing

L-15	i	Inion*	Intersection of two superior nuchal lines, may coincide with base of external occipital protuberance
A-17 (L-9)	ju	Jugale	Deepest point in the notch between the zygomatic's frontal and temporal processes
L-7	la	Lacrimale	Point where the posterior lacrimal crest meets the frontolacrimal suture
P-3	lam	Lambda*	Where lambdoid and sagittal sutures meet on external skull; If precise location is difficult due to extrasutural bones, estimate point based on where the sutures would have intersected
L-13	ms	Mastoidale	Inferiormost point on mastoid process, when oriented in Frankfurt Horizontal
A-6 (L-5)	mf	Maxillofrontale	Point where the anterior lacrimal crest meets the frontomaxillary suture
L-2 (A-2)	m	Metopion	Point on frontal along midsagittal line, where frontal's elevation above the chord from nasion – bregma is greatest. This point is mechanically determined, not visually.
A-4 (L-4)	nas	Nasion*	Where frontonasal suture meets midsagittal plane
A-7	ns	Nasospinale*	A point on the midsagittal plane, taken along a line tangent to the inferiormost points along the curves of the inferior nasal aperture
---	cfma	Condyle – anterior	Anterior point of occipital condyle on margin of foramen magnum
I-2	cfmp	Condyle – posterior	Posterior point of occipital condyle on margin of foramen magnum
I-1	opn	Opisthion*	Posterior margin of foramen magnum in the midsagittal plane.
L-16	op	Opisthocranion*	Posteriormost point of skull in the midline – sometimes the external occipital protuberance.
I-6	ol	Orale*	Anterior margin of palate. Taken on the midline, where it intersect with a line through the posterior margins of the central incisor lingual alveoli.
A-14	orb	Orbitale	Inferiormost point on the orbital margin.
L-11	po	Porion	Superiormost point of external auditory meatus
A-10	pros	Prosthion*	Anteriormost point on alveolar process of maxilla in midsagittal plane
L-14	ptn	Pterion	Intersection of frontal, (temporal), parietal, and sphenoid

A-5	rhi	Rhinion	Inferiormost point on the internasal suture in the midsagittal plane
I-5	sta	Staphylion*	Point on midline of posterior portion of hard palate, on interpalatal suture, where midline crossed by a line tangent to the deepest part of the curves of the posterior margins of the palatine bones.
S-3	st	Stephanion	Point where the temporal line crosses the coronal suture
I-14	sty	Stylomastoid foramen	Posteriormost point on stylomastoid foramen
A-8	sn	Subnasale	Inferiormost point in the nasal cavity on the alveolar process
---	sof	Superior orbital fissure	Superiormost point of superior orbital fissure (medially)
I-17	tym	Tympanic	Posteriormost point of mandibular fossa
I-13	vaj	Vaginal process	Anteriormost point of vaginal process, taken on posterior aspect
A-18	zyg	Zygion	Lateralmost point of zygomatic arch
L-10	zm	Zygomaxillare	Inferiormost point on the zygomaxillary suture
A-13	zyo	Zygo-orbitale	Point of intersection of the orbital rim and zygomaticomaxillary suture

[1]Starred landmarks are midsagittal.

FIGURE 5-1: Cranial Landmarks – Anterior. Numbers correspond to descriptions in Table 5-3. Image modified from White (2000).

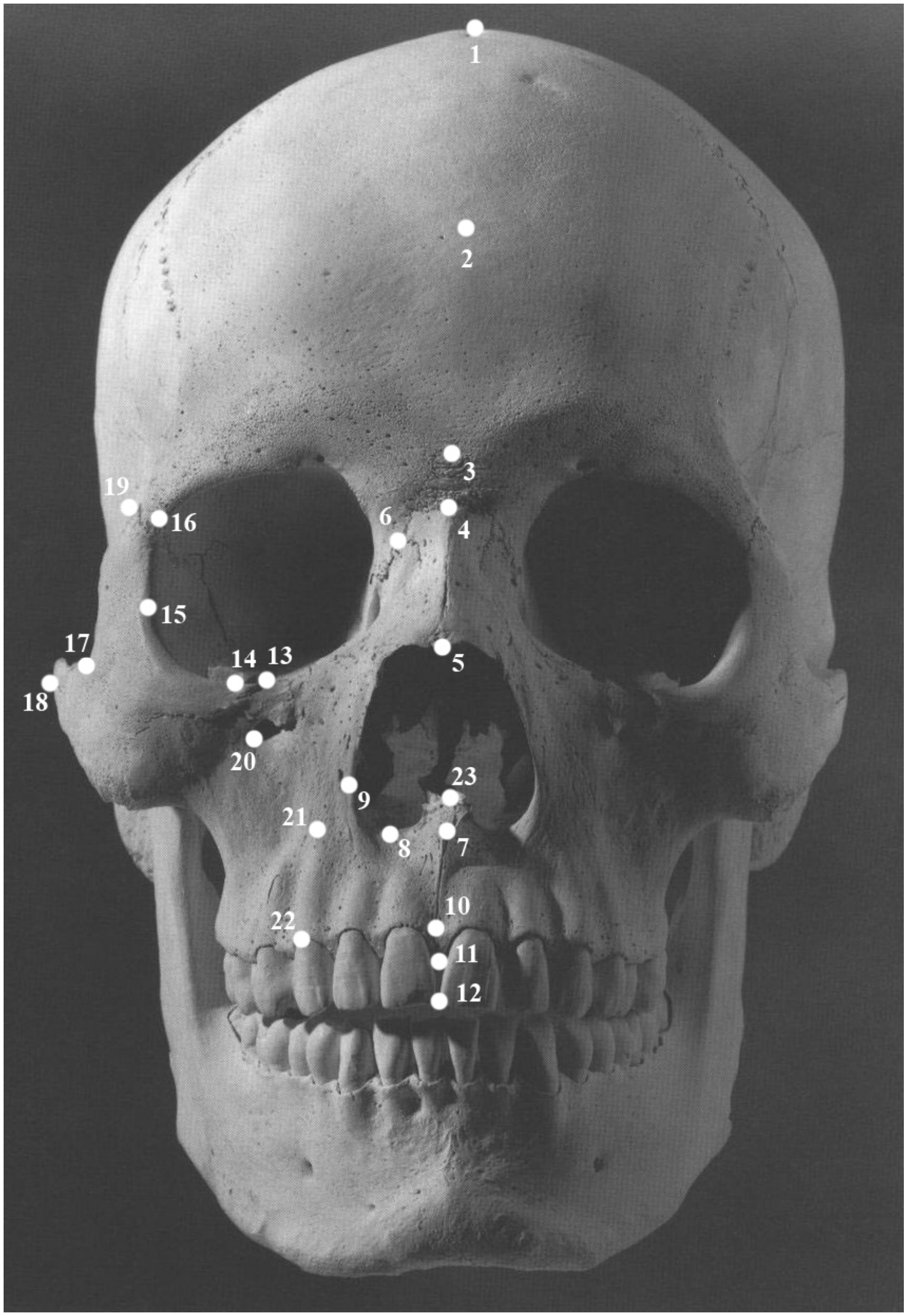


FIGURE 5-2: Cranial Landmarks – Posterior. Numbers correspond to descriptions in Table 5-3. Image modified from White (2000).

***FIGURE 5-3: Cranial Landmarks – Superior*.** Numbers correspond to descriptions in Table 5-3. Image modified from White (2000).

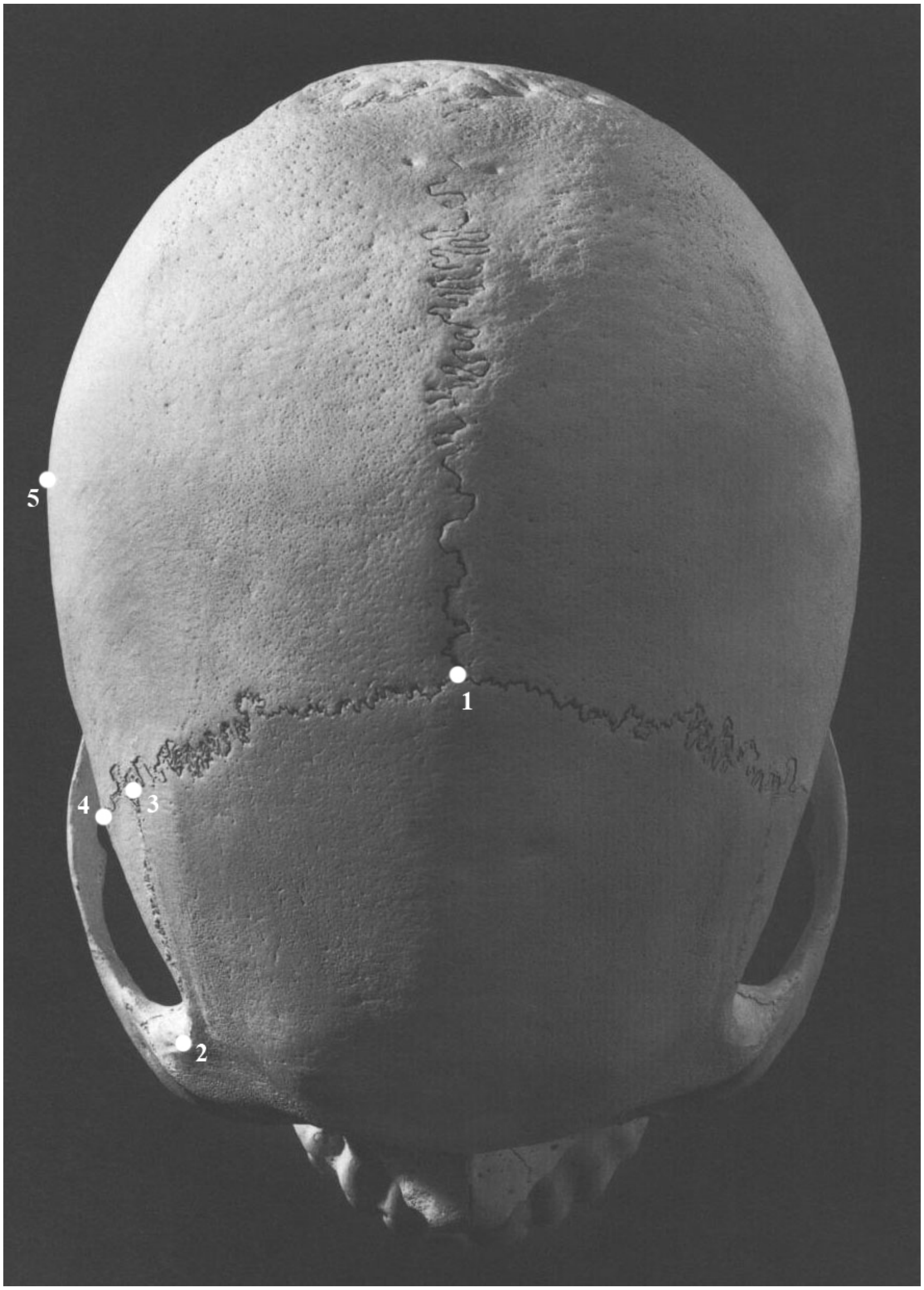


FIGURE 5-4: Cranial Landmarks – Inferior. Numbers correspond to descriptions in Table 5-3. Image modified from White (2000).

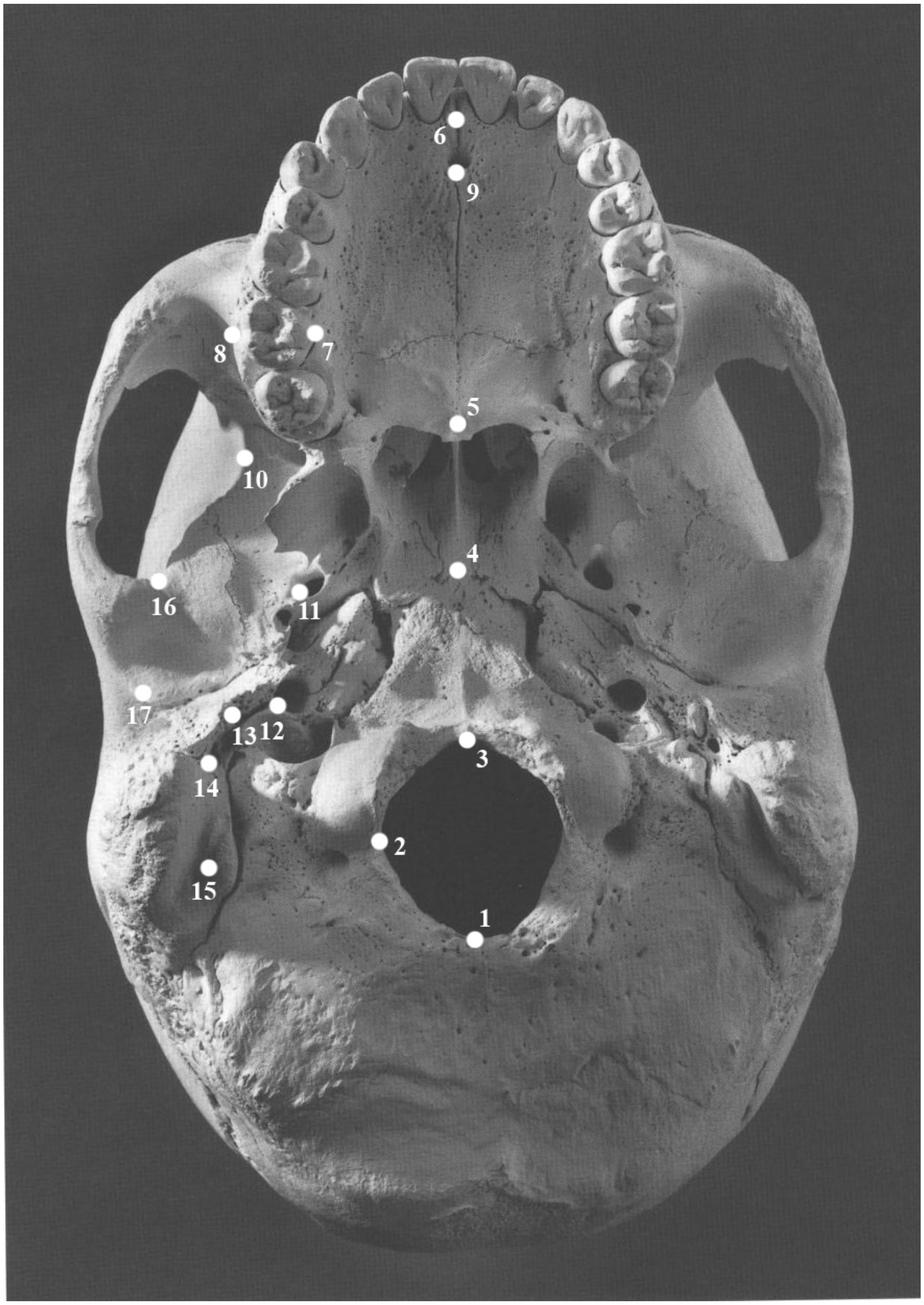
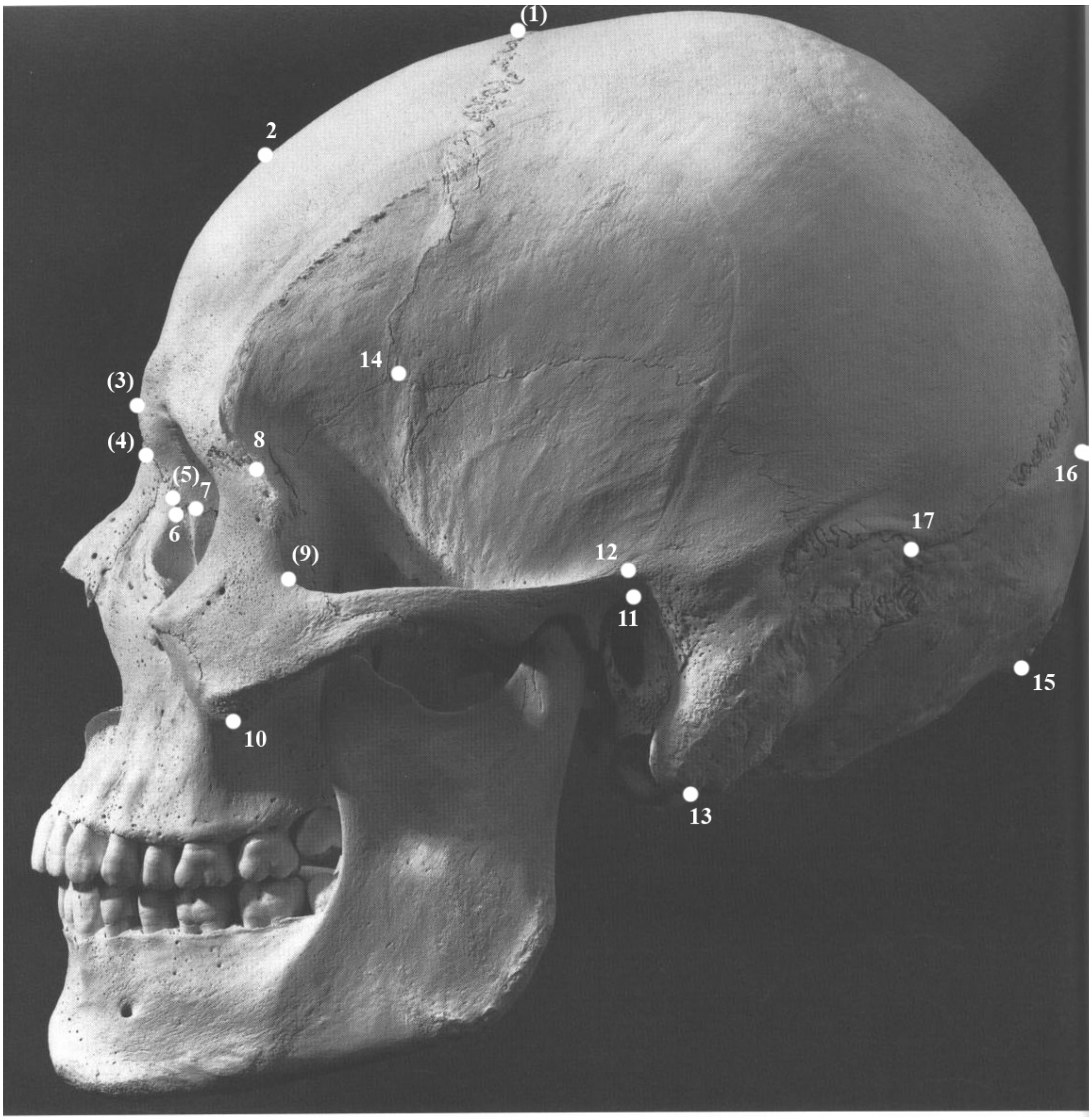


FIGURE 5-5: Cranial Landmarks – Lateral. Numbers correspond to descriptions in Table 5-3. Image modified from White (2000).



Cranial Metrics. Cranial metrics were recorded after extracting them from extensive landmark data (see Table 5-4). Most of the dimensions recorded here primarily follow Bräuer (1988), but also Howells (1973), Lockwood (1999), Wood (1991) and are supplemented by measurements added by the author.

TABLE 5-4: Cranial Metrics

Metrics	Definition
Glabella – inion	Recorded as the distance between glabella and inion (extracted from landmark data).
Nasion – inion	Recorded as the distance between nasion and inion (extracted from landmark data).
Glabella – lambda	Recorded as the distance between glabella and lambda (extracted from landmark data).
Glabella – opisthocranion	Recorded as the distance between glabella and opisthocranion (extracted from landmark data).
Prosthion – inion	Recorded as the distance between prosthion and inion (extracted from landmark data).
Basion – bregma	Recorded as the distance between basion and bregma (extracted from landmark data).
Basion – nasion	Recorded as the distance between basion and nasion (extracted from landmark data).
Glabella – bregma	Recorded as the distance between glabella and bregma (extracted from landmark data).
Bregma – pterion	Recorded as the distance between bregma and pterion (extracted from landmark data).
Bregma – lambda	Recorded as the distance between bregma and lambda (extracted from landmark data).
Pterion – asterion	Recorded as the distance between pterion and asterion (extracted from landmark data).
Parietal lambdoid length	Recorded as the distance between lambda and asterion (extracted from landmark data).

Bregma – asterion	Recorded as the distance between bregma and asterion (extracted from landmark data).
Lambda – inion	Recorded as the distance between lambda and inion (extracted from landmark data).
Inion – opisthion	Recorded as the distance between inion and opisthion (extracted from landmark data).
Occipital sagittal length	Recorded as the distance between lambda and opisthion (extracted from landmark data).
Superior facial height	Recorded as the distance between nasion and prosthion (extracted from landmark data).
Basion – prosthion	Recorded as the distance between basion and prosthion (extracted from landmark data).
Alveolar height	Recorded as the distance between nasospinale and prosthion (extracted from landmark data).
Subnasale – prosthion	Recorded as the distance between subnasale and prosthion (extracted from landmark data).
Maxillofrontale – ektoconchion	Recorded as the distance between maxillofrontale and ektoconchion (extracted from landmark data).
Orbitale – zygomaxillare	Recorded as the distance between orbitale and zygomaxillare (extracted from landmark data).
Nasal height	Recorded as the distance between nasion and nasospinale (extracted from landmark data).
Rhinion – nasospinale	Recorded as the distance between rhinion and nasospinale (extracted from landmark data).
Rhinion – anterior nasal spine	Recorded as the distance between rhinion and anterior nasal spine (extracted from landmark data).
Sagittal length of nasal bones	Recorded as the distance between nasion and rhinion (extracted from landmark data).
Anterior nasal spine – nasospinale	Recorded as the distance between anterior nasal spine and nasospinale (extracted from landmark data).
Anterior nasal spine – alveolare	Recorded as the distance between anterior nasal spine and alveolare (extracted from landmark data).
Anterior nasal spine – prosthion	Recorded as the distance between anterior nasal spine and prosthion (extracted from landmark data).
Foramen magnum length	Recorded as the distance between basion and opisthion (extracted from

	landmark data).
Occipital condyle length	Recorded as the distance between anteriormost and posteriormost points on the occipital condyle (extracted from landmark data).
Palate length	Recorded as the distance between orale and staphylion (extracted from landmark data).
Porion – bregma	Recorded as the distance between porion and bregma (extracted from landmark data).
Glabella – porion	Recorded as the distance between glabella and porion (extracted from landmark data).
Nasion – porion	Recorded as the distance between nasion and porion (extracted from landmark data).
Rhinion – porion	Recorded as the distance between rhinion and porion (extracted from landmark data).
Subnasale – porion	Recorded as the distance between subnasale and porion (extracted from landmark data).
Alveolare – porion	Recorded as the distance between alveolare and porion (extracted from landmark data).
Ektoconchion – porion	Recorded as the distance between ektoconchion and porion (extracted from landmark data).
Zygoorbitale – porion	Recorded as the distance between zygoorbitale and porion (extracted from landmark data).
Opisthocranion – porion	Recorded as the distance between opisthocranion and porion (extracted from landmark data).
Zygomaxillare – porion	Recorded as the distance between zygomaxillare and porion (extracted from landmark data).
Anterior pillar height	Recorded as the distance between anterior pillar superior and inferior (extracted from landmark data).
Canine root – anterior pillar superior	Recorded as the distance between canine root and anterior pillar superior (extracted from landmark data).
Porion – opisthion	Recorded as the distance between porion and opisthion, parallel to the Frankfurt Horizontal (extracted from landmark data).
Prosthion – lingual alveoli (I^1-M^3)	Recorded as the distance between prosthion and each lingual alveolar margin (extracted from landmark data).
Prosthion – external alveoli (I^1-M^3)	Recorded as the distance between prosthion and each external alveolar margin (extracted from landmark data).

Prosthion – posterior M^3	Recorded as the distance between prosthion and the posterior alveolar margin of M3 (extracted from landmark data).

Data Collection – Mandible

Mandibular Terminology. Anatomical terms relating to the mandible and employed in the following chapters are presented in Table 5-5.

TABLE 5-5: Mandibular Terminology

	Feature		Feature
1	Coronoid process	9	Mandibular fossa
2	Lateral corpus hollow	10	Ramus
3	Mandibular condyle	11	Ramus root
4	Mandibular foramen	12	Symphysis

Mandibular Traits. Traits were recorded for the mandible and were modified from Wood (1991) and Kimbel and colleagues (2004). Mandibular traits are described and listed in Table 5-6. Unlike the cranial traits, mandibular traits were recorded for both extant and fossil taxa.

TABLE 5-6: Mandibular Traits

Trait	Coding
Position of mental foramen	Anteroposterior location of the mental foramen with respect to tooth position, for each foramen present (by tooth or interdental septum)
Mandibular foramen morphology	open V, horizontal oval, etc

Symphyseal axis (externally)	0 = strongly inclined 1 = intermediate 2 = upright
Ramus root ant position	Below which tooth the anteriormost root of the ramus is positioned
Ramus root vertical position	Through which tooth the anterior border of the vertical ramus crosses
Lateral corpus hollow	0 = very strong 1 = moderately strong 2 = weak 3 = absent
Dental arch shape	0 = posteriorly convergent 1 = intermediate 2 = posteriorly divergent
Occlusal wear	0 = strong ant postcanine gradient 1 = weak ant postcanine gradient

Mandibular Landmarks. Extensive mandibular landmarks were collected for the right and left sides of each fossil and extant primate mandible. These landmarks are available in Table 5-7 and are displayed in Figures 5-6 through 5-8. Mandibular landmarks follow, with modification, Bräuer (1988), Ackermann (1998), White (2000), Krovitz (2000, 2003), and Whitehead and colleagues (2005).

Species-specific variation affected the identification of the landmarks pogonion and mentale. Pogonion was recorded strictly as the anteriormost point on the labial aspect of the mandibular symphysis, whether this was inferiorly positioned (as is the chin in modern humans) or superiorly positioned (as is the prognathic subalveolar bone in chimpanzees). Mentale was recorded as the inferiormost point of the mental foramen. However, all of the extant and extinct samples contained some variation in the number of mental foramina on right and left mandibular corpora. Chimpanzees, gorillas, and macaques exhibited particularly variable numbers of mental foramina. When multiple foramina were patent, the largest foramen was recorded. In a couple of instances, multiple mental foramina were visible but were equivalent in size. When this occurred, the superiormost foramen was recorded.

TABLE 5-7: Mandibular Landmarks

Ref.	Ab.	Landmark	Coding/Definition
S-1	cdc	Condylion – centrale	Center point on the superior surface of the mandibular condyle
S-2	cdl	Condylion laterale	Lateralmost point on the mandibular condyle
S-3	cdm	Condylion mediale	Medialmost point on mandibular condyle
L-3	cr	Coronion	Superiormost point (tip) of the coronoid process
S-4	ge	Genion	Tip of the mental spine in the midsagittal plane (If multiple mental spines, taken on superior; if not a clear spine, yet muscle attachments visible, then superior part of attachment)
L-4	go	Gonion	Lateralmost point at the gonial region of the mandible (where the body and ramus meet)
P-2	gn	Gnathion/ I_1 base of mandible*	Most inferior point on the base of the mandible. Taken along the midsagittal line.
---	id	Infradentale*	A midsagittal point between the central incisors along the external alveolar margin
P-1	li	Linguale	The lingual alveolar margin between the central incisors
P-3	lg	Lingulare	Anterosuperior point of the mandibular lingula
L-2	ml	Mentale	Inferiormost point of the margin of the mental foramen (if multiple, then largest; if same size, then superiormost)
---	mfl	Mental foramen – external	The external alveolar margin at the mental foramen
---	mfb	Mental foramen – base of mandible	The inferiormost point at the base of the mandible, at the level of the mental foramen
L-1	pg	Pogonion	The anteriormost point on the mandible in midline (whether chin or alveolus – taken inferiorly on vertical symphyses)

L-5	ran (min)	Ramus - anterior (min)	Anterior point of the ramus at minimum breadth
L-6	rpn (min)	Ramus - posterior (min)	Posterior point of the ramus at minimum breadth
L-7	rax (max)	Ramus - anterior (max)	Anterior point of the ramus at maximum breadth
L-8	rpx (max)	Ramus - post (max)	Posterior point of the ramus at maximum breadth
---	I_2b- M_3b	I_2- M_3 base of mandible	For each tooth (I_2- M_3), the most inferior point on the base of the mandible at that tooth.

FIGURE 5-6: Mandibular Landmarks – Superior. Numbers correspond to descriptions in Table 5-7. Image modified from White (2000).

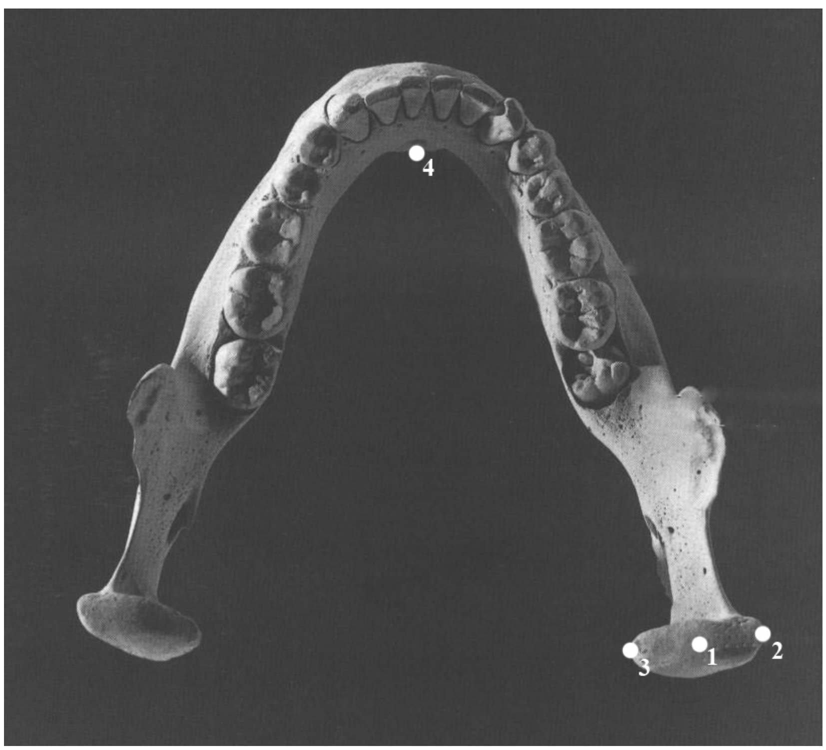


FIGURE 5-7: Mandibular Landmarks – Lateral. Numbers correspond to descriptions in Table 5-7. Image modified from White (2000).

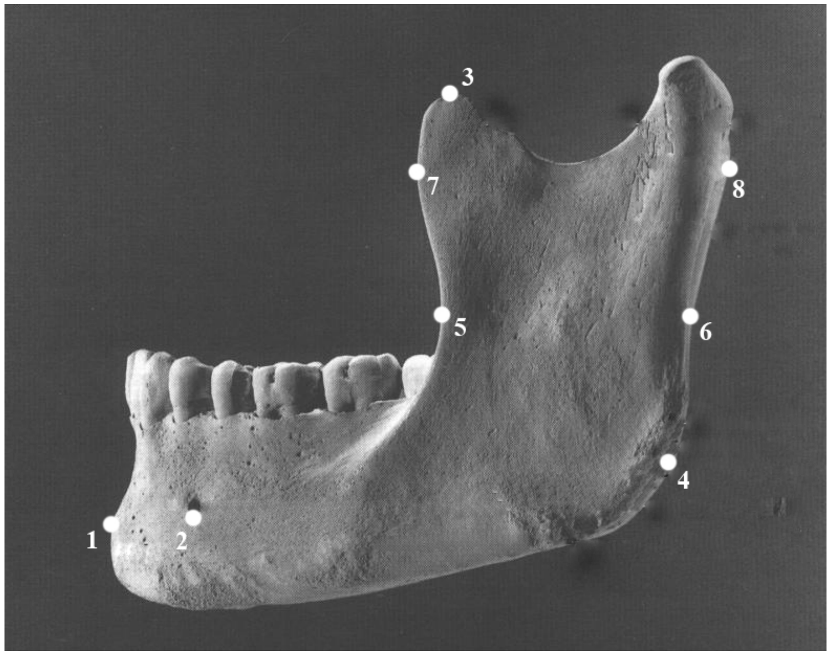
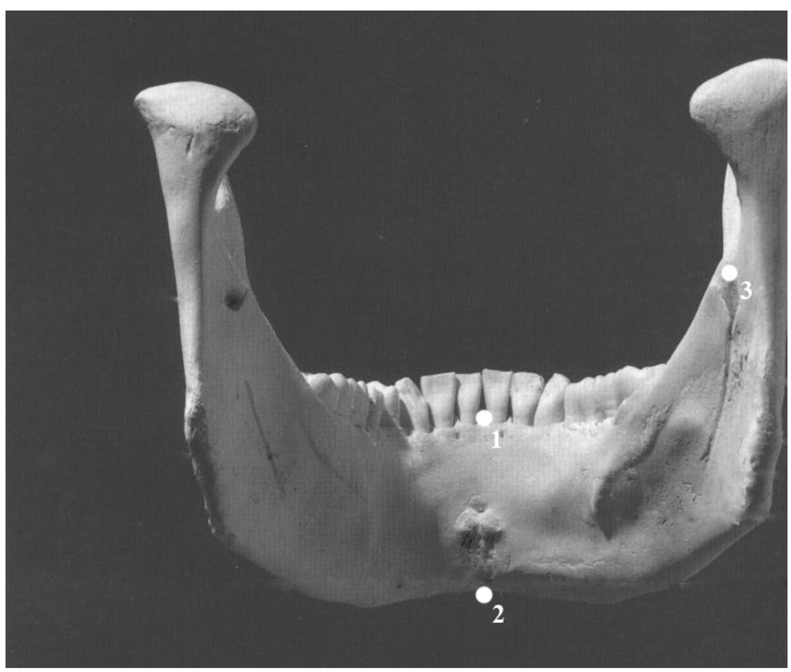


FIGURE 5-8: Mandibular Landmarks – Posterior. Numbers correspond to descriptions in Table 5-7. Image modified from White (2000).



Mandibular Metrics. Linear metrics for the mandible were recorded to the nearest tenth of a millimeter with plastic digital calipers and were extracted from data collected by the G2 MicroScribe. Some of these data were collected during a pilot study in 2004 and 2005 and were supplemented later. See Table 5-8 for a description of linear metrics used in this study. Mandibular metrics follow those of Bräuer (1988), but also Howells (1973) and Wood (1991).

TABLE 5-8: Mandibular Metrics

Metrics	Definition
Internal Corpus Height (symph)	Distance from the base of the mandible to the lingual alveolar margin at the symphysis. Gnathion to Infradentale (extracted from landmark data).
Internal Corpus Height (I_1-M_3)	For each tooth (I1-M3), the distance from the base of the mandible to the lingual alveolar margin at the midpoint of the relevant tooth (extracted from landmark data).
Internal Corpus Height (M_3 post)	Distance from the base of the mandible to the lingual alveolar margin posterior to M_3 (extracted from landmark data).
External Corpus Height (symph)	Base of mandible to external alveolar margin at the symphysis. Linguale to Gnathion (extracted from landmark data).
External Corpus Height (mental foramen)	Base of mandible to external alveolar margin above the midpoint of mental foramen (extracted from landmark data).
External Corpus Height (I_1-M_3)	Base of mandible to external alveolar margin at midpoint of relevant tooth (extracted from landmark data).
Caliper Corpus Height (I_1-M_3)	Base of mandible to internal alveolar margin at midpoint of relevant tooth. Taken as a maximum (calipers).

Caliper Corpus Height (mental foramen)	Base of mandible to internal alveolar margin above midpoint of mental foramen. (Taken as a maximum (calipers).
Corpus Width (symph)	Thickness of mandibular corpus at the mental foramen. Maximum width, measured perpendicular to corpus height (calipers).
Corpus Width (mental foramen)	Thickness of mandibular corpus at the mental foramen. Maximum width, measured perpendicular to corpus height (calipers).
Corpus Width (I_1-M_3)	Thickness of mandibular corpus at internal alveolar margin at midpoint of relevant tooth. Maximum width, measured perpendicular to corpus height (calipers).
Bi-Tooth Lingual Breadth	For each tooth (I1-M3), the distance between the right and left lingual alveoli at the tooth's midpoint (extracted from landmark data).
Bi-Tooth External Breadth	For each tooth (I1-M3), the distance between the right and left external alveoli at the tooth's midpoint (extracted from landmark data).
Bi-Tooth Mandibular Base Breadth	For each tooth (I1-M3), the distance between the right and left mandibular base points at the tooth's midpoint (extracted from landmark data).
Pogonion Height	Distance from Pogonion to Infradentale (extracted from landmark data).
Genion Height	Distance from Genion to Linguale (extracted from landmark data).
Ramus Breadth (max)	Maximum breadth of the mandibular ramus. Distance between points rax and rpx (extracted from landmark data).
Ramus Breadth (min)	Minimum breadth of the mandibular ramus. Distance between points ran and rpn (extracted from landmark data).
Mentale Height – Right	Distance from right Mentale to its external alveolar margin (extracted from landmark data).
Mentale Height – Left	Distance from left Mentale to its external alveolar margin (extracted from landmark data).

Mentale Position – Right	External symphysis to right Mentale. Measured here as the minimum distance from the right Mentale to a line passing through Infradentale and Gnathion (extracted from landmark data).
Mentale Position – Left	External symphysis to left Mentale. Measured here as the minimum distance from the left Mentale to a line passing through Infradentale and Gnathion (extracted from landmark data).
Mental Foramen - ML	Mediolateral dimension of mental foramen (calipers).
Mental Foramen – SI	Superoinferior dimension of mental foramen (calipers).
Mental Foramen – Area	Calculated from the previous 2 dimensions.
Superior Mandibular Length	Minimum distance from Infradentale to a line passing through the AP middles of the mandibular condyles. Measured here as the distance from Infradentale to a line passing through right and left Condylion Centrale (extracted from landmark data).
Inferior Mandibular Length	Minimum distance from infradentale to a line passing through right and left Gonion (extracted from landmark data).
Bicondylar Maximum Breadth	Maximum breadth from condyle to condyle. Distance between right and left Condylion Laterale (extracted from landmark data).
Bicondylar Minimum Breadth	Minimum breadth from condyle to condyle. Distance between right and left Condylion Mediale (extracted from landmark data).
Bicondylar Articular Breadth	Distance between the ML middles of the condyles. Distance between right and left Condylion Centrale (extracted from landmark data).
Condyle Breadth – Right	ML breadth of the condyle. Distance between Condylion Mediale and Condylion Laterale on the right mandible (extracted from landmark data).
Condyle Breadth – Left	ML breadth of the condyle. Distance between Condylion Mediale and Condylion Laterale on the left mandible (extracted from landmark data).
Bicoronoid Breadth	Distance between the coronoid processes. Measured as the distance between right and left Coronion (extracted from landmark data).

Bigonial Breadth	Distance between right and left Gonion (extracted from landmark data).
Dental Arcade Length	Minimum distance from Infradentale to a line passing through the posteriormost point of M3 on the internal alveolus. Distance from Infradentale to a line passing through right and left M3 post (extracted from landmark data).
Ramus Height – Right	Distance between the right Gonion and Condylion Centrale (extracted from landmark data).
	[*Note* – Gonion was identified as the widest part of the ramus in the gonial region. This means that this measure of ramus height will likely be variable (as the position of Gonion varies greatly in a superoinferior dimension).]
Ramus Height – Left	Distance between the left Gonion and Condylion Centrale (extracted from landmark data).
	[*Note* – Gonion was identified as the widest part of the ramus in the gonial region. This means that this measure of ramus height will likely be variable (as the position of Gonion varies greatly in a superoinferior dimension).]
Ramus Height – Right (base)	Minimum distance from the right Condylion Centrale to a line passing through the right mandibular base at M1 and M3 (extracted from landmark data).
	[*Note* – this measure of ramus height represents a purely SI dimension and extracts the ML portion of standard ramus height.]
Ramus Height – Left (base)	Minimum distance from the left Condylion Centrale to a line passing through the left mandibular base at M1 and M3 (extracted from landmark data).
	[*Note* – this measure of ramus height represents a purely SI dimension and extracts the ML portion of standard ramus height.]
Ramus Height – Right (M3)	Distance from the right Condylion Centrale to the right M3 base (extracted from landmark data).
	[*Note* – this measure of ramus height includes both SI and ML

	dimensions.]
Ramus Height – Left (M3)	Distance from the left Condylion Centrale to the left M3 base (extracted from landmark data). [*Note* – this measure of ramus height includes both SI and ML dimensions.]
Condyle Alveolar Height – Right	Minimum distance from alveolar plane to the superior surface of the condyle. Measured here as the minimum distance from the right Condylion Centrale to a line passing through external alveolar midpoints of right M2 and M3 (extracted from landmark data).
Condyle Alveolar Height – Left	Minimum distance from alveolar plane to the superior surface of the condyle. Measured here as the minimum distance from the left Condylion Centrale to a line passing through external alveolar midpoints of left M2 and M3 (extracted from landmark data).
Lingulare Height – Right	Right Coronion to right Lingulare (extracted from landmark data).
Lingulare Height – Left	Left Coronion to left Lingulare (extracted from landmark data).

Data Collection – Dentition

Dental Terminology. Anatomical terms relating to the dentition and employed in the following chapters are presented in Table 5-9.

TABLE 5-9: Dental Terminology

	Feature		Feature
1	Accessory Marginal Tubercles	19	Deflecting Wrinkle
2	Accessory Ridge Buccal Cusp	20	Distal Cuspule
3	Accessory Ridge Lingual Cusp	21	Distal Trigonid Crest
4	Buccal Essential Crest	22	Distal Accessory Ridge
5	Carabelli's Cusp	23	Distolingual Groove

6	Crista Obliqua	24	Groove Pattern
7	Cusp 1/Protocone	25	Medial Longitudinal Fissure
8	Cusp 2/Paracone	26	Median Longitudinal Fissure
9	Cusp 3/Metacone	27	Mesial Accessory Ridge
10	Cusp 4/Hypocone	28	Mesial Marginal Accessory Tubercle
11	Cusp 5/Distal Cuspule	29	Mesiobuccal Groove
12	Cusp 1/Protoconid	30	Protostylid
13	Cusp 2/Metaconid	31	Transverse Crest
14	Cusp 3/Hypoconid	32	Cusp 6/Entoconulid
15	Cusp 4/Entoconid	33	Cusp 7/Metaconulid
16	Cusp 5/Hypoconulid	34	Cusp 5/Hypoconule
17	Cusp 6/*Tuberculum Sextum*		
18	Cusp 7/*Tuberculum Intermedium*		

Dental Traits. Nonmetric dental data are particularly important for this study since the dentition provide the largest samples for the Makapansgat and comparative hominin samples. Dental traits were scored following the Arizona State University dental anthropology standards (Turner *et al*., 1991) and additional dental characters drawn, with modification, from Wood and Uytterschaut (1987), Wood (1991), Suwa (1991), Bailey (2002), Wood and colleagues (1988), and Kimbel and colleagues (2004). Collection of these data required visual inspection of specimens and recording of presence/absence or character states. Characters were scored for each tooth lacking extreme wear. Dental traits were recorded for fossil specimens, only. Trait frequencies were compiled using a modification of the individual count method (Scott and Turner, 1988). Due to the frequency of missing antimeric data for fossils, it was most efficient to analyze data from the more complete side of the dental arch and then supplement these data with values from preserved antimeres. Although Hlusko (2004) promotes a restrictive definition of protostylid in australopiths due to the common presence of a protoconid ridge whose covariance and developmental relationship is unclear, the presence of a protoconid ridge was used as indicative of protostylid formation in this work (e.g. Dahlberg, 1950).

TABLE 5-10: Dental Traits

Trait	Coding
$P^{3,4}$ occlusal wear	1 = unworn 2 = enamel wear only, no dentine exposure 3 = dentine exposed on one cusp only 4 = dentine exposed on 2 cusps 5 = lingually worn to roots 6 = lingually and buccally worn to roots
$P^{3,4}$ cusp number	1 = 1 2 = 2 3 = 3 A cusp is defined as an enamel feature with an independent apex; in worn teeth the occlusal fissures are used as a guide
$P^{3,4}$ median longitudinal fissure	1 = deep and uninterrupted (straight or undulating) 2 = evident, but interrupted by enamel ridges leading from the main cusps 3 = no fissure evident
Grooves	0 = absent 1 = weak 2 = weak groove, does not extend to cusp margin 3 = marked groove, does not extend to cusp margin 4 = strong groove, cuts through cusp margin Coded for each: mesiobuccal groove, distobuccal groove, mesiolingual groove, and distolingual groove
$P^{3,4}$ mesial accessory ridge buccal cusp	0 = absent 1 = weak 2 = intermediate 3 = marked
$P^{3,4}$ distal accessory ridge buccal cusp	0 = absent 1 = weak 2 = intermediate 3 = marked
$P^{3,4}$ mesial accessory ridge lingual cusp	0 = absent 1 = weak 2 = intermediate 3 = marked

$P^{3,4}$ distal accessory ridge lingual cusp	0 = absent 1 = weak 2 = intermediate 3 = marked
$P^{3,4}$ buccal essential crest	0 = absent 1 = single ridge 2 = bifurcated ridge 3 = bifurcated ridge, marked 4 = trifurcated (only if accessory ridge also present)
$P^{3,4}$ lingual essential crest	0 = absent 1 = single ridge 2 = bifurcated ridge 3 = bifurcated ridge, marked 4 = trifurcated (only if accessory ridge also present)
$P^{3,4}$ transverse crest presence	0 = absent 1 = weak (etched, but not fully cut by median longitudinal fissure) 2 = intermediate 3 = marked
$P^{3,4}$ transverse crest form	1 = single 2 = bifurcated Crest may be straight and uninterrupted or bifurcated with another ridge (distinct from distal or mesial accessory ridges)
$P^{3,4}$ accessory marginal tubercles	0 = absent 1 = present, mesial 2 = present, distal 3 = present, both Presence of mesial or distal accessory marginal tubercle in which sagittal sulcus is strongly bifurcated at the mesial and/or distal marginal ridge resulting in a bulge or free-standing accessory tubercle on marginal ridge
$P^{3,4}$ external grooves	0 = absent 1 = ill-defined with triangular depression 2 = trace groove, includes ill-defined at most occlusal crown 3 = intermediate 4 = strong groove Recorded for mesiobuccal, distobuccal, mesiolingual and distolingual aspects of non-occlusal crown.
$M^{1,2,3}$ occlusal wear	1 = unworn 2 = enamel wear only 3 = dentine exposed on one cusp only 4 = dentine exposed on two cusps 5 = dentine exposed on three cusps

	6 = dentine exposed on four cusps, but dentinal areas still discrete 7 = two dentinal areas coalesced, leaving two free areas 8 = three dentinal areas coalesced, leaving one free area 9 = all dentinal areas coalesced with small dentine island 10 = all dentinal areas coalesced, enamel rim complete 11 = all dentinal areas coalesced, enamel rim incomplete
$M^{1,2,3}$ crista obliqua	0 = no crista obliqua, the lingual ridge of the metacone and the distobuccal ridge of the protocone have not developed more strongly than the adjacent ridges on the protocone and paracone (after Korenhof, 1960) 1 = a similarly situated crest, but interrupted by the main longitudinal fissure 2 = continuous crest b/t the tips of the protocone and metacone, possibly with a vertical notch in the locality of the longitudinal main groove, but never fully cut through by the latter
$M^{1,2,3}$ Carabelli's complex	0 = absent 1 = pit or groove at the mesiolingual corner of the crown 2 = grooves and ridges running from the lingual groove to the mesiolingual corner 3 = definite shelf of enamel related to the protocone
$M^{1,2,3}$ distal cuspules/Cusp 5	0 = absent 1 = present 2 = 2 distal cuspules 3 = 3 distal cuspules 4 = 4 distal cuspules Cuspules are identified as having an apex, even if the surrounding grooves do not continue for the entire circumference of the cuspule.
$M^{1,2,3}$ mesial marginal accessory tubercles	0 = absent 1 = weak 2 = intermediate 3 = marked Presence of accessory tubercle of mesial marginal ridge complex
$P_{3,4}$ occlusal wear	1 = unworn 2 = enamel wear only, no dentine exposed 3 = dentine exposure minimal 4 = dentine exposure moderate with at least one large dentine patch but no coalescence 5 = coalescence of at least two dentine areas (may be rim with small island) 6 = dentine exposure extensive but with complete enamel rim, 7 = dentine exposure extensive, enamel rim incomplete 8 = roots exposed on occlusal surface
$P_{3,4}$ cusp number	The number of cusps was recorded as 2, 3, etc. A cusp is defined as an

enamel feature that has an independent apex and is defined by fissures; in worn teeth, a cusp is scored on the basis of the remaining fissure pattern. The two main cusps, the buccal and lingual are included in the score. Additional cusps are either extra lingual cusps, or cusp features elsewhere on the talonid

$P_{3,4}$ median longitudinal fissure	0 = no evident fissure 1 = deep and uninterrupted 2 = evident, but interrupted by enamel ridges leading from the main cusps 3 = evident, cuts through marginal ridges The above codes were not ordered, the above codes are ordered as 3 – 1 – 2 - 0
$P_{3,4}$ metaconid placement	0 = mesial 1 = medial 2 = distal Position of metaconid relative to mesial and distal crest of protoconid and position of protoconid apex
$P_{3,4}$ crown asymmetry	0 = symmetrical 1 = asymmetrical In occlusal view tooth crown outline is symmetrical or asymmetrical (with lingual cusp mesially truncated); recorded only with respect to lingual cusp's M-D placement
$P_{3,4}$ buccal essential crest	0 = absent 1 = single ridge 2 = bifurcated ridge 3 = bifurcated ridge, marked
$P_{3,4}$ lingual essential crest	0 = absent 1 = single ridge 2 = bifurcated ridge 3 = bifurcated ridge, marked
$P_{3,4}$ transverse crest	0 = absent 1 = weak 2 = intermediate 3 = marked Presence of crest or ridge connecting buccal and lingual cusps (central occlusal ridge)
$P_{3,4}$ transverse crest form	1 = single 2 = bifurcated Crest may be straight and uninterrupted or bifurcated with another ridge (distinct from distal or mesial accessory ridges)

$P_{3,4}$ grooves	0 = absent 1 = present, weak 2 = developed, does not extend to marginal ridge 3 = marked, extends to marginal ridge 4 = cuts marginal ridge Coded for each: mesiobuccal groove, distobuccal groove, mesiolingual groove, and distolingual groove
$P_{3,4}$ mesial accessory ridge	0 = absent 1 = present, weak 2 = intermediate 3 = marked Presence of accessory ridge on mesiolingual border of tooth. Recorded for buccal and lingual cusps.
$P_{3,4}$ distal accessory ridge	0 = absent 1 = present, weak 2 = intermed 3 = marked Presence of accessory ridge on distolingual border of tooth. Recorded for buccal and lingual cusps.
$P_{3,4}$ external grooves	0 =absent 1 = ill-defined with triangular depression 2 = trace groove, including ill-defined 3 = intermediate groove 4 = strong groove Recorded for mesiobuccal, distobuccal, mesiolingual and distolingual aspects of non-occlusal crown.
$P_{3,4}$ root form	1 = single root 2 = two roots, one is Tomes' root 3 = two roots, mesiobuccal and distal 4 = two roots, mesial and distal
$M_{1,2,3}$ cusp number	The number of cusps recorded as 5, 6, etc. The cusp number score reflects the presence of a C6 and/or a C7 (with a score of 2 or more, see C7 scoring) in addition to the five principal cusps. An area of enamel was interpreted as a cusp if it was delineated by fissures and, in unworn teeth, if an apex was present. In worn teeth a subjective assessment was made using the preserved morphology. Protostylids were not included in cusp number.
$M_{1,2,3}$ occlusal wear	1 = unworn 2 = enamel wear only, no dentine exposure 3 = dentine exposed on one cusp 4 = dentine exposed on two cusps 5 = dentine exposed on three cusps 6 = dentine exposed on four cusps

	7 = two dentinal areas coalesced 8 = three dentinal areas coalesced 9 = four dentinal areas coalesced 10 = all dentinal areas coalesced, but an enamel island, or peninsula, occupies part of the occlusal surface 11 = enamel rim completely surrounds the dentinal area 12 = enamel rim partially surrounds the dentinal area 13 = roots exposed on the occlusal surface
$M_{1,2,3}$ tuberculum sextum/distal cusp/C6	0 = absent 1 = fissure branches with small indistinct cusp-like feature 2 = one distinct distal cusp 3 = two distinct distal cusps 4 = three distinct distal cusps
$M_{1,2,3}$ tuberculum intermedium/lingual cusp/C7	0 = absent 1 = short fissure present, branching off the lingual fissure into the metaconid, but no identifiable cusp 2 = longer and more definite fissure, with a small cusp-like feature between them 3 = fissures clearly demarcate a well-developed lingual cusp 4 = two cusplike features at this site
$M_{1,2,3}$ protostylid	0 = absent 1 = shape and branching pattern of the mesiobuccal groove are suggestive of protostylid formation 2 = protostylid present as a small shelf of enamel below a distinct branch off the mesiobuccal groove 3 = well-developed protostylid present as a long and well-developed enamel shelf below a distinct groove passing across the buccal surface of the protoconid 4 = vertical grooves and ridges on the mesiobuccal surface of the protoconid 5 = extra cusp branching off mesiobuccal region, but from mesial groove 6 = extra cusp on mesiobuccal corner, not from mesial groove
$M_{1,2,3}$ distal trigonid crest	0 = absent 1 = present, but distinctly interrupted by the longitudinal fissure 2 = continuous crest, the mesial longitudinal fissure may course over it, but does not deeply incise it Crest connects the tips of the protoconid and metaconid
$M_{1,2,3}$ deflecting wrinkle	0 = absent 1 = medial ridge straight but constricted at midpoint 2 = medial ridge deflects distally but does not contact distolingual cusp 3 = medial ridge "L-shaped", contacts distolingual cusp present, but distinctly interrupted by the longitudinal fissure 3 = continuous crest, the mesial longitudinal fissure may course over it, but does not deeply incise it.
$M_{1,2,3}$ entoconid-hypoconulid	0 = absent

crest	1 = present, but distinctly interrupted by longitudinal fissure 2 = continuous crest, not deeply incised by longitudinal fissure
$M_{1,2,3}$ fissure pattern	0 = “Y”; contact between metaconid and hypoconid 1 = “+”; point contact between metaconid, protoconid, entoconid, and hypoconid 2 = “X”; contact between protoconid and entoconid
$M_{1,2,3}$ root form	1 = single root 2 = two roots, one is Tomes’ root 3 = two roots, mesiobuccal and distal 4 = two roots, mesial and distal
dm_1 shape	0 = BL narrow 1 = BL broad 2 = molarized
dm_1 mesial profile	0 = mesial marginal ridge (mmr) absent, protoconid anterior, anterior fovea (fa) open 1 = mesial marginal ridge slight, protoconid anterior, anterior fovea open 2 = mesial marginal ridge thick, protoconid = metaconid, anterior fovea closed

Dental Metrics. Linear dental metrics for the crown and cervix were recorded to the nearest tenth of a millimeter with plastic digital calipers (following Grine, 1981; Falk and Corruccini, 1982; Wood and Abbott, 1983; Wood, 1991; Suwa *et al*., 1994; Colby, 1996; Hillson, 1996; Hillson *et al*., 2005). Cervical dimensions are very useful in heavily worn teeth since dimensions are greatly affected by wear, especially the mesiodistal dimensions by interproximal wear. These data were collected, in part, during a pilot study at the University of the Witwatersrand and the Transvaal Museum in 2004 and 2005. Whenever available, data for antimeres in fossil specimens were collected and averages were used in analyses. Antimeres were not recorded for extant primate specimens. In order to maximize fossil sample sizes, isolated specimens were included in analyses despite the possibility that they may be an antimere of an included tooth.

The dental identifications and recorded dimensions of this study were compared to those published by Moggi-Cecchi and colleagues (2006). Specimens for which there were disagreements between studies, were reassessed and/or remeasured. This process revealed some differences in the treatment of particular specimens in this study. StW 450 is treated as a right M_1 (rather than a right M^1). StW 529 (formerly StW 534) is treated here as being a left M_2 (rather than a right). StW 307 is considered to be a right dp_3 (rather than a right dp_4). Images of these specimens, taken by the author, were used to reconfirm these identifications. However, it is possible that these isolated specimens may have been housed with the wrong identification label. For instance, comparison to published images indicates that the tooth identified here as StW 520 is not the same tooth identified as StW 520 in at least one other analysis. This tooth is included in analyses as "StW 520?". It remains a possibility that a fraction of the relatively few discrepancies between the specimen identifications employed here and elsewhere result from such limitations. As a few of the isolated specimens were not labeled on the tooth, it leaves the identification of specimen number reliant upon the specimen being housed with the correct label.

TABLE 5-11: Dental Metrics

Metrics	Definition
I^1-M^3 MD crown diameter	Mesiodistal dimension of the crown for each maxillary tooth.
I^1-M^3 LL/BL crown diameter	Labiolingual or buccolingual dimension of the crown for each maxillary tooth.
I^1-M^3 MD cervical diameter	Mesiodistal dimension of the cervix for each maxillary tooth.

I^1-M^3 LL/BL cervical diameter	Labiolingual or buccolingual dimension of the cervix for each maxillary tooth.
I^1-M^3 crown area (calc.)	Mesiodistal dimension multiplied by labiolingual/buccolingual dimension of maxillary tooth crown. Calculated.
I^1-M^3 cervical area (calc.)	Mesiodistal dimension multiplied by labiolingual/buccolingual dimension of maxillary tooth cervix.
I_1-M_3 MD crown diameter	Mesiodistal dimension of the crown for each mandibular tooth.
I_1-M_3 LL/BL crown diameter	Labiolingual or buccolingual dimension of the crown for each mandibular tooth.
I_1-M_3 MD cervical diameter	Mesiodistal dimension of the cervix for each mandibular tooth.
I_1-M_3 LL/BL cervical diameter	Labiolingual or buccolingual dimension of the cervix for each mandibular tooth.
I_1-M_3 crown area (calc.)	Mesiodistal dimension multiplied by labiolingual/buccolingual dimension of mandibular tooth crown. Calculated.
I_1-M_3 cervical area (calc.)	Mesiodistal dimension multiplied by labiolingual/buccolingual dimension of mandibular tooth cervix. Calculated

Dental Morphometrics. Photographs of occlusal morphology of the postcanine dentition were used to examine dental shape variation. Photographs were taken with a Konika Minolta Dimage A2, which is a 7 megapixel digital camera with macrophotographic capability. Each tooth was positioned in the center of the frame with the tooth surface parallel to the camera lens. In addition, a scale bar was positioned on the same plane as the occlusal surface of the specimen and as close as possible to the tooth of interest. The camera was leveled and positioned as far from the dental row as possible to minimize parallax, while maintaining a sufficiently high resolution for photo enlargement. Adobe Photoshop was used in order to crop all images and, when necessary, mirror-image dental photos so each tooth appears to be from the right. The latter action was taken since Morphologika 2.5 (O'Higgins and Jones, 2004) will rotate and translate coordinate data, but not flip them to account for the comparison of antimeres.

For individuals preserving both right and left teeth, only one side was included in analyses. Once processed as described above, occlusal photographs of the mandibular and maxillary premolars and molars for South African hominids from Kromdraai, Swartkrans, Sterkfontein, Taung, and Makapansgat were converted into TPS files using TpsUtil (Rohlf, 2008). These TPS files were then imported into TpsDig2 (Rohlf, 2006), where all dental semi-landmark and landmark coordinates were digitized. Semi-landmarks were recorded for both worn and unworn maxillary and mandibular teeth (see Table 5-12).

In TpsDig2, each tooth was enlarged to fill the entire screen for the digitizing of all landmarks. For worn and unworn premolars and molars, 50 semi-landmarks were digitized along the occlusal outline of the tooth (making estimates for interproximal wear and minor fossil damage). The first step in recording these occlusal landmarks was drawing a curve in TpsDig2 that carefully followed the occlusal outline of each tooth. Second, 51 points were resampled along this curve by equal length (the first and last points were overlaid). Finally, 50 landmarks were digitized from the curve points in order to evenly space them (the TpsDig2 CURVE command, itself, is not recognized in Morphologika 2.5) (see Figure 5-9). The first landmark was recorded at a clearly defined location on the mesial aspect of each tooth, as described in Table 5-12.

In addition, for reasonably unworn specimens, cusp tips were digitized for the primary cusps of each tooth. Accessory cusps were not digitized since Morphologika 2.5 cannot deal with missing data. These accessory cusps, however, would presumably impact the overall occlusal outline of most individual teeth. Each tooth (worn and unworn) was scaled by setting a 10 mm section of the photographed scale as equal to 10 mm in TpsDig2. For SK 100, a left P_4, the scale was set to 7 mm due to the limitations of the original photograph. These data (coordinates and scale information) were imported into Morphologika 2.5 (O'Higgins and Jones, 2004) where generalized Procrustes analysis (GPA) and principal components analysis (PCA) were executed. Please see "Data Analysis" below for details.

***FIGURE 5-9: Dental Semi-Landmarks and Landmarks**. An M^1 is displayed with semi-landmark and landmark data displayed in TpsDig2.*

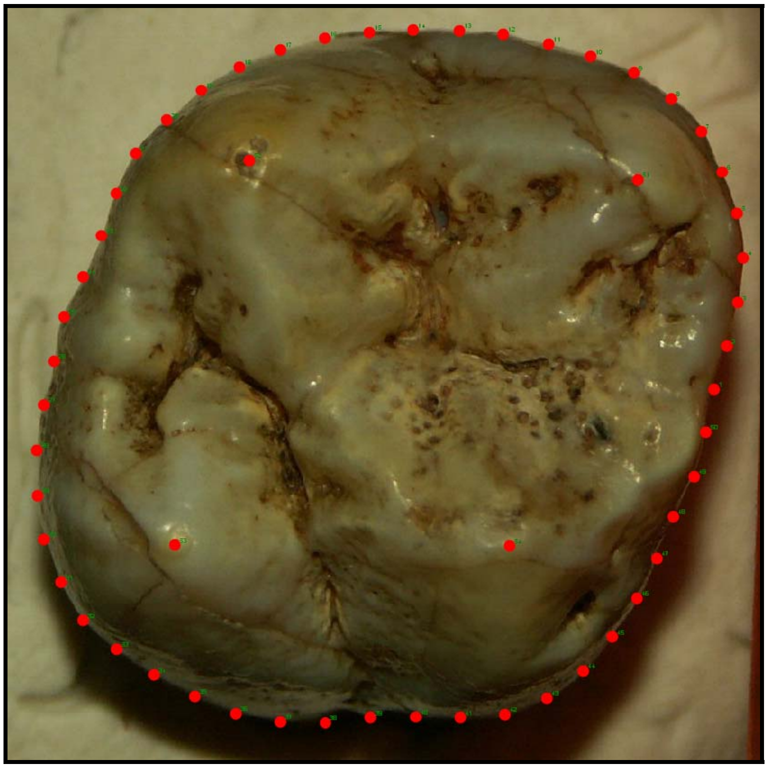


TABLE 5-12: Dental Semi-Landmarks and Landmarks

Teeth	Landmark(s)	Coding/Definition
P^3, P^4	1-50	Occlusal outline, where semi-landmark 1 was identified on the mesial surface of the tooth at approximately the level of central groove and continued in a counterclockwise direction. Semi-landmarks were digitized for both worn and unworn teeth.
	51	Buccal cusp. Landmark digitized for unworn teeth, only.
	52	Lingual cusp. Landmark digitized for unworn teeth, only.
M^1-M^3	1-50	Occlusal outline, where semi-landmark 1 was identified on the mesial surface of the tooth at the level of the mesial fossa and continued in a counterclockwise direction. Semi-landmarks were digitized for both worn and unworn teeth.
	51	Mesiobuccal cusp. Landmark digitized for unworn teeth, only.

	52	Distobuccal cusp. Landmark digitized for unworn teeth, only.
	53	Distolingual cusp. Landmark digitized for unworn teeth, only.
	54	Mesiolingual cusp. Landmark digitized for unworn teeth, only.
P_3-P_4	1-50	Occlusal outline, where semi-landmark 1 was identified on the mesial surface of the tooth at approximately the level of the mesial fossa and continued in a clockwise direction (mesial – buccal – distal – lingual). Semi-landmarks were digitized for both worn and unworn teeth.
	51	Buccal Cusp. Landmark digitized for unworn teeth, only.
	52	Lingual Cusp (most prominent). Landmark digitized for unworn teeth, only.
M_1-M_3	1-50	Occlusal outline, where semi-landmark 1 was identified on the mesial surface of the tooth at approximately the level of the mesial fossa and continued in a counterclockwise direction (mesial – lingual – distal – buccal). Semi-landmarks were digitized for both worn and unworn teeth.
	51	Mesiolingual cusp. Landmark digitized for unworn teeth, only.
	52	Distolingual cusp. Landmark digitized for unworn teeth, only.
	53	Distobuccal cusp (most prominent). Landmark digitized for unworn teeth, only.
	54	Centrobuccal cusp. Landmark digitized for unworn teeth, only.
	55	Mesiobuccal cusp. Landmark digitized for unworn teeth, only.

Data Analysis

Overview. Quantitative analyses were rendered for elements with an adequate comparative sample. In order to deal with claims for multiple species at Sterkfontein and within *A. robustus*, analyses included: 1) the complete samples of *A. robustus* and *A. africanus* from Sterkfontein, and 2) when sample sizes permitted it, with the available samples of *A. robustus* treated separately (i.e. Kromdraai and Swartkrans). Contentious specimens attributed to *A. africanus* were discussed in terms of their placement within analyses (e.g. StW 252, StW 183, StW 255). Moreover, extreme outliers were examined for human error and are discussed in light of their impacts on results.

Numerous theoretical issues plague the measurement of variation in the fossil record and make statistical analysis of fossils complex. Fossils are fragmentary and few in number. Fossil samples often include non-random geographic and temporal variation resulting in an increase in intraspecific variation, sexual dimorphism, demographic and taphonomic biases, and multiple closely related taxa. In addition, the possibility for reticulate evolution in fossil species is a legitimate concern. Given all of these complexities, high Type II error rates were expected to result from small sample sizes. Moreover, non-normality must be assumed when dealing with the relatively small Makapansgat hominin sample and an overall hominin sample with non-random time variation, sexual dimorphism, age and demographic issues, and the possibility of multiple species. To minimize these concerns, non-parametric data analysis methods were used. Moreover, new specimens considerably augment previous studies of the Sterkfontein sample following the publication of Sterkfontein Member 4 fossils (Moggi-Cecchi *et al.*, 2006).

Attempts were made to remeasure approximately 10% of each extant sample in order to assess measurement repeatability. In addition, measurements were repeated for all of the specimens from Makapansgat. For these specimens, statistical analyses were based upon the averages of these values. Measurement repeatability data are presented in

Appendix 2. In addition, tables presenting the cross-correlation of measurements are presented as similarity matrices in Appendix 3. For fossils, when both sides were available, they were both measured and averages were presented, unless there was an indication of fossil deformation for one side. For each variable, descriptive statistics and scatterplots were examined. Outliers were explored to establish whether they were the result of computational or data input error. These specimens were either remeasured, removed from analyses, or (when not the result of researcher error) were included in analyses as discussed in the following chapters.

In addition to extensive qualitative comparisons, multivariate tests (PCA and DFA) were executed to assess clustering of data. Under conditions met with fossil samples and the questions posed, multivariate methods aid discussion of groupings and likely results, rather than provide conclusive answers. Multivariate methods are more powerful in testing species composition than bivariate methods (e.g. Godfrey and Marks, 1991; Plavcan and Cope, 2001). The few dimensions available for most of the individual Makapan specimens combined with the small comparative fossil samples for many dimensions limited the statistical analyses employed herein. Variables were selected in consideration of levels of cross correlation, biological meaning, and maximizing fossil sample sizes.

Principal components analyses (PCA) were produced in order to look at patterning in the variables among taxa, these analyses were repeated both with and without size-standardizations. Size standardizations were calculated using the geometric mean following the method of Darroch and Mossiman (1985).

Standard discriminant function analyses (DFA) were computed on raw data to assess fossil and extant species groupings for the dentition and mandibular corpora. DFAs assess how well groups can be distinguished on the basis of the variables included in analyses. The Makapansgat specimens were treated as ungrouped specimens. Data were not size-standardized for DFAs since these analyses are less impacted by issues of scaling of individual variables than PCAs. To increase fossil sample sizes, missing data were replaced for fossil specimens for up to half of the variables of interest in DFAs by the group mean. Variables were equally weighted to avoid skewing fossil specimens on the basis of replaced variables. The pooled within-groups correlations are presented to aid assessment of which variables contribute to discriminating among groups. Classification matrices are presented for grouped and ungrouped fossil specimens and were calculated on the basis of minimizing each specimen's distance to the group centroid.

Trait Data. Data analyses were not undertaken for the trait data, but may be the focus of future analyses. These data are presented in the form of character states and percentages for populations and comparison of the Makapansgat sample to other fossil samples.

Metric Data. Descriptive statistics (median, mean, standard deviation, coefficient of variation, and range) were recorded for all dimensions, areas, and indices. Scatterplots and boxplots with the median (line), 1st and 3rd quartiles (box), and range (bars) for each sample were examined for all of the variables. Numerous boxplots are presented and discussed in the following chapters. The graphical treatment of data provides an excellent method of assessing variation with small fossil samples, although sampling bias is carefully considered. These graphical methods also aid assessment of whether the Makapansgat fossils fall within the range of variation for other fossil samples.

Non-parametric tests (Mann-Whitney U) were employed in order to identify significant differences for the samples of *A. africanus* versus *A. robustus*, Makapansgat versus Sterkfontein (*A. africanus*), and Makapansgat versus *A. robustus* for the dentition and mandibles. These analyses were selectively applied in order to compare the fossil samples.

PCAs were employed to examine the patterning of variation among samples in raw variables and variables size standardized by the geometric mean (Darroch and Mosimann, 1985). The amount of variance explained by each PC is provided.

DFAs were calculated for select mandibular and cranial variables in order to assess groupings of specimens. Due to the fragmentary nature of many of the fossils, DFAs were selectively executed on variables that were considered both biologically meaningful and helped maximize fossil sample sizes. The group mean was used as a replacement for fossil specimens missing up to half of the variables of interest. Thus, a step-wise DFA was not undertaken. Equal weighting of the variables was selected in order to minimize the potential skewing of fossil sample groupings due to the replacement of missing variables. Extant primate specimens were excluded from analyses when they were missing variables. The statistically significant discriminant functions (DF) are plotted for visual examination of groupings and the explanatory power of each DF is discussed. In addition, tables provide the pooled within-groups correlations of variables for each significant DF and the classification matrices.

Dental Morphometrics. Comparisons of overall shape of the maxillary and mandibular premolars and molars and cusp locations for unworn specimens were made in order to assess the overall similarity of the shapes of the occlusal outlines of the various fossil specimens. The outlines included 25 equally spaced semi-landmarks and a landmark for each major cusp tip. Analyses were repeated with 50 equally spaced semi-landmarks for worn specimens, excluding cusp tips, in order to increase sample sizes. A smaller number of semi-landmarks were employed when cusp tip landmarks were included as a potential means of increasing the emphasis on cusp tip positions.

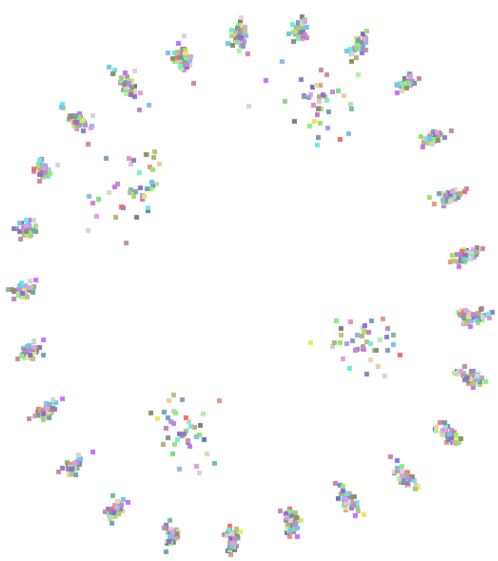
Morphologika (O'Higgins and Jones, 2006) was used to examine size and shape variation via generalized Procrustes analysis permitting the scaling, translation, and rotation of landmark and semi-landmark data (Figure 5-10a & b), followed by PCA of these transformed coordinate data. These analyses permit the exploration of shape after each tooth is scaled by centroid size (the square root of the sum of squared distances of a specimen's landmarks from their common centroid). In addition, centroid sizes can be used to examine differences in size.

Discussion. It has become clear in recent years that the patterning of variables differs between and within species, where some variables tend to be good sex-discriminators (e.g. crown breadth, canine size, several facial widths) and others tend to be good taxonomic discriminators (e.g. crown length, cranial breadths, relative cusp sizes, root morphology) (e.g. Wood *et al.*, 1983; Abbott, 1984; Wood and Uytterschaut, 1987; Wood *et al.*, 1988; 1991; although see Collard and Wood; 2001). Data are discussed in light of these hypotheses. In addition, the graphical treatment of data furnishes a powerful way with which to assess variation and species composition, particularly when dealing with small sample sizes. Thus, a phenetic approach is used to discuss phylogenetic hypotheses for Makapansgat. Results are weighed regarding the appropriate taxonomic treatment of the Makapansgat and Sterkfontein samples.

FIGURE 5-10a, b: Dental Landmark and Semi-Landmarks. *Procrustes Superimposed Landmarks before (a.) and after (b.) rotation, translation, and scaling.*

a.)

b.)



CRANIAL DESCRIPTIONS AND RESULTS

This and the subsequent two chapters present the morphology of the Makapansgat hominins and results of statistical analyses placing the Makapansgat australopiths in the context of both South African australopith and greater extant primate variation. Each hominin specimen from Makapansgat is described in the following chapters. These descriptions are followed by analyses and discussion of the entire Makapansgat and comparative sample for each anatomical region. The regional descriptions and analyses are divided into cranial, mandibular, and dental chapters. This first results chapter is devoted to the australopith cranial remains from Makapansgat. Age estimates are provided by this author utilizing the following categories: infancy, early childhood, late childhood, young adulthood, and old adulthood. More precise age estimates from a variety of authors are presented in the discussions where relevant (see also Table 9-1).

Crania

Descriptions. The Makapansgat hominins include 10 cranial specimens, ranging from small fragmentary specimens to the nearly complete MLD 37/38 neurocranium and the well-preserved MLD 6 maxillofacial fragment (see Figures 6-3a, b, c, and d). The cranial remains represent individuals of varying ages from the childhood MLD 11/30 maxilla to the adult MLD 9/12 maxilla, the latter exhibiting a particularly worn postcanine dentition. The craniofacial sample exhibits both morphological and size-related variation and differing authors have previously interpreted this variation in diverse ways (e.g. Clarke, 1988, 1994a, 2008; Kimbel and White, 1988; Lockwood, 1997, 2000; Moggi-Cecchi *et al.*, 1998; Tobias and Lockwood, 2000). The Makapansgat cranial specimens were originally described by Dart (1948a, 1948d; 1949a; 1949d; 1954b; 1959a, b; 1962a; 1962b; 1962c) and by Lockwood (1997). The descriptions below are based on a combination of these original treatments of the specimens, as well as the addition of numerous details contributed by this author.

MLD 1

Overview. The MLD 1 specimen is a partial calvaria with portions of the occipital and both parietal bones of a young adult (See Figures 6-1a, b, and c at the end of this section). The occipital condyles and the entire basioccipital region are not preserved. The maximum breadth spanning the right and left broken borders is 108.9 mm, taken perpendicular to the sagittal suture. The length of the fragment along the sagittal line from the anteriormost preserved portion of the sagittal suture to the posteriormost fragmentary border of the foramen magnum is 82.4 mm. The right side of MLD 1 appears to include a small fragment of the superior portion of the temporal bone (approximately 29.3 mm anteroposteriorly broad and 16.7 mm proximodistally long), although the precise boundaries of this temporal fragment are difficult to demarcate. The posteriormost portion of the temporal is not present as the breakages exhibited by MLD 1 on the right and left appear to coincide with the general location of the squamosal and parietomastoid sutures. The fragmented lateral border of the left parietal appears to preserve a small component of its contribution to the parietomastoid suture.

Parietals and Occipital. The preserved portion of the parietals extends 43.5 mm along the sagittal suture from lambda. There are several extrasutural bones at lambda and along portions of the lambdoidal suture. The largest of these extrasutural bones is 27.5 mm x 26.4 mm.

The parietals exhibit a hint of bossing, only slightly more apparent on the right parietal. The temporal lines converge anteriorly, at their closest preserved point they are only 5.9 mm apart. The temporal lines are strongly developed at the anteriormost portion of the specimen. The temporal and nuchal lines are barely visible as they converge posterolaterally, not nearly as apparent as those exhibited by many specimens of *A. afarensis*. The occipital protuberance is relatively small, considerably smaller than that of MLD 37/38. The superior and inferior nuchal lines are clearly visible, although unexceptional. The superior nuchal line and slopes of the nuchal and occipital planes contribute to a somewhat angled appearance to the occipital fragment when viewed laterally. This appearance is typical in australopiths.

Endocranium. Grooves for the posterior meningeal vessels are apparent on the endocranial surface of this specimen. The right posterior cranial fossa is relatively deep, while the left side preserves less of this region. Sulcal and sinus impressions are clearly reflected on the internal aspect of MLD 1. Grooves for the transverse sinus, confluence of sinuses, sagittal sinus, and occipital sinus are apparent. Compared with specimens of extant *Homo sapiens*, the position of the internal occipital protuberance and, thus, the location of the confluence of sinuses, transverse sinus and its attachments for the tentorium cerebelli, and sagittal sinus and its attachments for the falx cerebri are positioned far more inferiorly in MLD 1. In addition, the occipital sinus and the attachments for the falx cerebri (both indicated by the internal occipital crest) run a comparatively short length of the occiput. This is certainly as expected, considering the short cranial base morphology of all australopith species. Although a groove for the occipital sinus is apparent, it is not enlarged (Tobias and Falk, 1988). Instead the transverse sinus seems to dominate the endocranial aspect of this specimen. This is typical for specimens of *A. africanus*, with some exceptions (Tobias and Falk, 1988); an enlarged occipital and marginal sinus system is more prevalent in specimens of *A. robustus* (e.g. Kimbel, 1984; Falk and Conroy, 1983; Conroy *et al.*, 1990).

Cranial Vault Thickness. The thickness of the cranial vault was recorded in a number of locations. The vault thickness is 7.1 mm at the anteriormost portion of the sagittal suture, 6.3 mm at the anteriormost intersection of the right parietal and temporal, 6.1 mm at the temporal boundary (recorded more posteriorly than on the right), and 6.8 mm at the middle of the preserved right aspect of the foramen magnum.

Discussion. Originally discovered by James Kitching in 1947, MLD 1 was the first australopith specimen discovered at Makapansgat and the first that preserved the posterior aspect of the skull (Dart, 1948d). Dart presented a detailed description of this specimen in 1948. In it, he made an elegant argument for this specimen's closer affinities to modern humans than to gorillas or chimpanzees on the basis of a thick cranial vault [(although later it would be shown to be thin compared to specimens attributed to *A.*

afarensis (Kimbel *et al.*, 2004)], expanded occipital plane, inferior positioning of inion with respect to opisthocranion, moderately developed occipital torus, and presence of large wormian bones.

Dart argued that this specimen had once been fashioned into a skull bowl as part of the Osteodontokeratic Culture on the basis of its "form and the eroded nature of its broken bone edges, apparently as the result of great use…" (Dart, 1962c: 292). He (1948d: 277-278) also declared that the individual represented by MLD 1 succumbed to "major cranial violence" as, he argued, was frequently the case for australopiths. Modern taphonomic studies have essentially disproved Dart's evidence of violence and cannibalism and clearly indicate the skeletal-part profiles and fragmentary nature of the fossil remains from Makapansgat are likely the result of actions by denning animals, primarily hyenas and porcupines (Brain, 1981; Shipman and Phillips, 1976; Shipman and Phillips-Conroy, 1977; Reed, 1997; Maguire *et al.*, 1985). While many of his original interpretations are no longer considered valid, Dart's anatomical descriptions are still relevant.

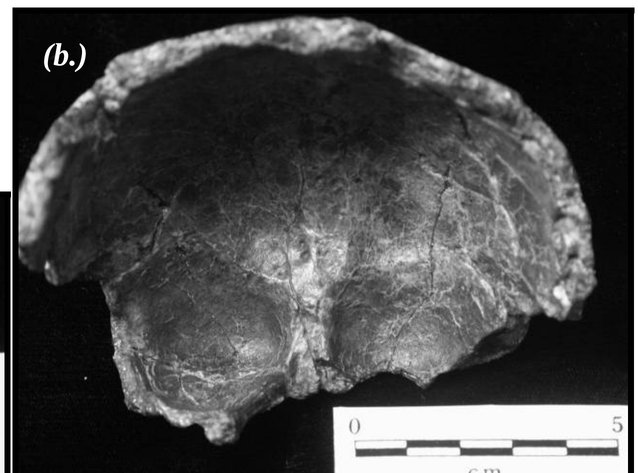
Zuckerman (1953, 1954) contended that MLD 1 is best reconstructed as a subadult due to its unfused lambdoidal and sagittal sutures (*contra* Dart, 1948d; Mann, 1975). Zuckerman's subadult interpretation is undoubtedly related to his view that MLD 1's foramen magnum was in an "apelike" position and that more apelike sagittal and nuchal cresting would have undoubtedly developed had this individual lived to adulthood (Zuckerman, 1954). Regardless, MLD 1 almost certainly represents an australopith adult on the basis of overall morphology and ectocranial suture fusion. This specimen exhibits partial fusion of the lambdoidal and sagittal sutures. The sagittal and lambdoidal sutures exhibit similar patterns of ectocranial fusion, whereby some portions are unfused and other portions are fused to obliteration. The sagittal suture is unfused at its posteriormost 24.8 mm, while the anterior portion is virtually obliterated. The lambdoidal suture is mostly unfused, although its lateralmost regions exhibit varying degrees of fusion. MLD 1 exhibits a similar degree of ectocranial suture obliteration compared to MLD 37/38 (see pages below). In modern *Homo*, this degree of fusion of the ectocranial sutures would indicate a likely age at death of greater than 17 years (McKern and Stewart, 1957), but does not provide a reliable means of discriminating age any further within extant humans (e.g. Hershkovitz *et al.*, 1997). The endocranial aspect of these sutures is essentially fully obliterated, bolstering an adult age estimate.

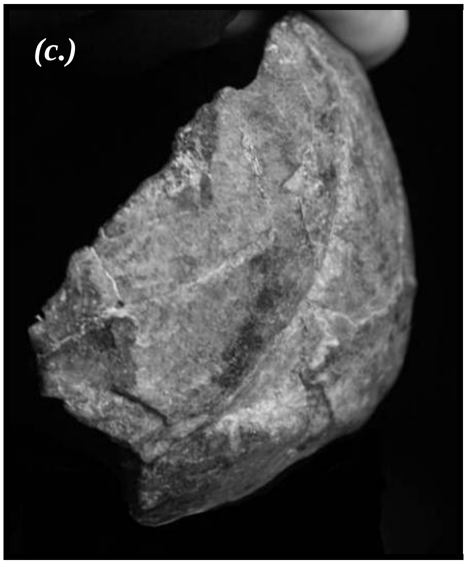
Visual examination of the preserved portions of the neurocranium suggests that its endocranial capacity was likely similar to that of MLD 37/38 (see below). Attempts have been made to reconstruct the endocranial volume with more precision for MLD 1 but have met with limited success (e.g. Holloway, 1972).

Some authors speculate this specimen represents a female on the basis of a possible association with MLD 6 (Dart, 1949a) and relatively gracile features (e.g. Dart 1948d; 1949a, 1962c, Tobias *et al.*, 1977), while others suggest this specimen represents a male on the basis of a possible sagittal crest indicated by temporal line positioning (e.g. Robinson, 1954b; Zuckerman, 1954; Dart, 1962a, b; Wolpoff, 1974). While the temporal lines are indeed closely positioned, it is unclear whether a sagittal crest would have been present. Regardless, this author considers current sex designations for the Makapansgat hominins to be dubious until a larger sample is collected or the sample is better understood within the context of South African australopith variation.

Based on the slopes of the nuchal and occipital planes and the moderately developed nuchal line, MLD 1 is more similar to samples of *A. africanus* than it is to samples of *A. robustus* (see also Robinson, 1954b). Even so, the morphology of both South African australopith species is similar and exhibits considerable overlap in variation of this region.

Figure 6-1a, b, & c: MLD 1. A fragment of an adult occipital and right and left parietals in posterior (*a*), internal (*b*), and left lateral (*c*) views.





MLD 3

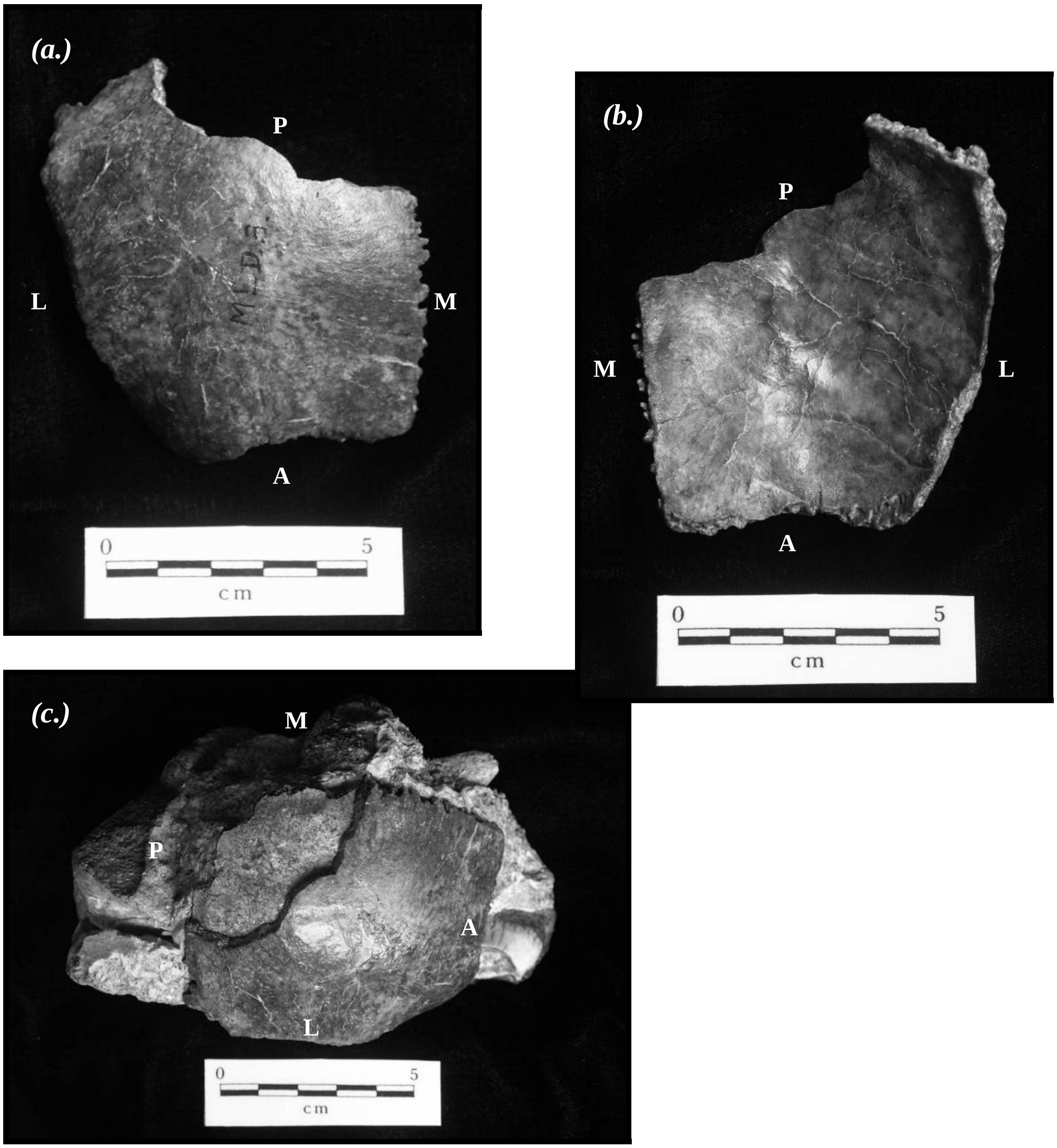
Overview. This specimen is a right parietal fragment of an infant or early child and retains the associated breccia, the latter being catalogued as MLD 3a (see Figures 6-2a, b, and c). The preserved portions of the MLD 3 parietal include the entire coronal border (47.8 mm long), approximately half of the anterior sagittal border (47.1 mm long), and approximately one-third of the lateral lambdoidal suture (25.8 mm long). The lateralmost portion of the parietal is intact and measures 74.2 mm from the squamosal suture's intersection with the coronal suture to the parietomastoid suture's intersection with the lambdoidal suture.

Parietal. Minor parietal bossing is apparent externally. A faint temporal line is discernable. The temporal line is far less developed than many of the South African australopith specimens and likely relates to the probable subadult status of this individual. In addition, the position of the temporal line is most sagitally positioned at its intersection with the coronal suture. Based upon doubling the distance from the temporal line to the sagittal suture, the minimum breadth between right and left temporal lines is 50.8 mm. The endocranial surface exhibits impressions of the anterior and posterior middle meningeal vessels and some sulcal morphology.

Cranial Vault Thickness. The thickness of the cranial vault at bregma is 5.2 mm, at the lateralmost portion of the coronal suture is 2.6 mm, and at the intersection of the parietomastoid and lambdoidal sutures is 5.9 mm. In comparison to data provided for other australopiths at bregma by Kimbel and colleagues (2004:147), the value for MLD 3 is close to the mean (5.1 mm) for a sample of *A. africanus* that includes Sts 5 (4.1 mm) and Sts 71 (6.0 mm). The cranial vault thickness at bregma is thin compared with that known for samples of *A. afarensis* and *Homo rudolfensis*, but within the known range of variation for specimens attributed to *A. africanus*, *A. boisei*, and *H. habilis*.

Discussion. The preserved regions of the coronal, sagittal, squamosal, and lambdoidal sutures are unfused. The earliest fusion of these sutures occurs during adolescence in extant humans (McKern and Stewart, 1957). Impressions of the vasculature and sulcus morphology are visible on the endocranial aspect of the specimen. In modern humans, these impressions first appear around the age of 1 year. Thus, MLD 3 almost certainly represents an infant or child at time of death (see also Dart, 1949; Boné and Dart, 1955; Boné, 1956; Mann, 1975; Tobias *et al.*, 1977). This specimen may represent the same individual as MLD 11 (Boné and Dart, 1955). Indeed, the comparable ages of these specimens support a possible association; however, the lack of adjacent or ipsilateral anatomical regions for MLD 3 and MLD 11 makes this possibility difficult to assess further. On the basis of temporal line development and positioning, this specimen resembles specimens of *A. africanus* more so than *A. robustus*. However, the young age of this specimen is certainly a causative factor in the position of the temporal lines and overall morphological appearance of the parietal.

Figure 6-2a, b, & c: MLD 3. The MLD 3 right parietal in external (*a*) and internal (*b*) views, where A is anterior, P is posterior, M is medial, and L is lateral. The MLD 3 fragment is repositioned on the associated MLD 3a breccia (*c*)



<u>MLD 6</u>

Overview. MLD 6 is a right craniofacial australopith fragment, preserving portions of the right and left nasals, lacrimals, ethmoid, sphenoid, frontal, right maxilla, right zygomatic, right P^3-M^2, and a portion of the roots of M^3 of a young adult (see Figures 6-3 a-d; see also Chapter 7 for descriptions of the dentition).

Orbital and Nasal Regions. The medial and inferomedial borders of the right orbit are preserved, along with the right infraorbital fissure. Only a small portion of the medial orbital wall is preserved for the left orbit, permitting the assessment of a minimum intraorbital breadth of 16.0 mm. The inferior aspect of the intraorbital region is relatively flat from the right infraorbital margin to the left, although postmortem deformation may have contributed to this appearance. A transverse infraorbital suture is visible on MLD 6 and Taung, SK 52, and Sts 52a, the latter three being juvenile australopiths (Braga, 1996). It is possible that this subadult characteristic persists in the MLD 6 individual anomalously, but future study may clarify its appearance in australopiths (Braga, 1996).

A large right lacrimal sinus is present. The right and left nasal bones and the right half of the nasal aperture are well preserved. The nasals narrow at their superior surface, although the frontonasal suture is difficult to demarcate in this individual. This morphology is well known for specimens of *A. africanus* (e.g. Clarke, 1977; Rak, 1983; Tobias, 1991). The nasals of MLD 6 curve sharply at the level of the superiormost lacrimal canal and, as also noted by Lockwood (1997), exhibit a faint median ridge. A median ridge has been identified in specimens of *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, and *Homo habilis* (Tobias, 1967, 1991; Clarke, 1977; Kimbel *et al.*, 1982, 1994, Franciscus and Trinkaus, 1988; Lockwood, 1997). A median ridge has also been identified in gorillas, although it provides support for an external *dorsum nasi* (Franciscus and Trinkaus, 1988). The margins of the nasal aperture project anterior to the base of the zygomatic arch. The nasal aperture is broadest near the proximodistal middle and exhibits blunt borders, common in specimens attributed to *A. robustus* (McCollum *et al.*, 1993).

Based on the appearance of the right half, the nasal aperture resembles a teardrop-shape or rounded inverted triangle. The nasal floor is flat and the small lateral portion of its junction with the nasoalveolar clivus indicates a stepped nasal floor, which aligns this specimen with the hypodigm of *A. africanus* rather than *A. robustus* (e.g. McCollum *et al.*, 1993). The transversely flattened nasoalveolar clivus is similar to specimens of *A. africanus* (but see Rak, 1983; White *et al.*, 1981; Lockwood, 1997). The rest of the nasoalveolar clivus is not preserved and thus does not permit further assessment. This is unfortunate, as ontogenetic characteristics of the nasoalveolar clivus are known to characterize specimens of *A. robustus* (Bromage, 1989). Specifically, the nasoalveolar clivus of *A. robustus* has been argued to resorb throughout ontogeny due to an exaggerated maxillary growth rotation; while this ontogenetic pattern is not the case for *A. africanus*. In a later study with a larger comparative sample (McCollum, 2008), it was argued that the pattern of remodeling (rather than the continued remodeling) is what distinguishes the robust australopith nasoalveolar remodeling.

The sagittal length of the nasal bones is one of the few cranial dimensions preserved across a large number of South African australopith specimens. Boxplots for this dimension were plotted for all samples (see Figure 6-4). The values for the MLD 6, SK 79 (*A. robustus*), and SK 80 (*Homo* from Swartkrans) specimens are essentially comparable and each of their values falls within the range for the sample of *A. africanus* from Sterkfontein.

Zygomatic Region and Palate. The zygomatic arch is mostly eroded away, exposing the right maxillary sinus. The maxillary sinus is partly filled with limestone infiltrate. This region exhibits a weak central facial hollow aligning this specimen with the hypodigm of *A. robustus* (e.g. Lockwood, 1997). The root of the zygomatic process is anteriorly positioned, between P^3/P^4. Such an anteriorly positioned zygomatic process root tends to appear more frequently in "robust" australopiths (Tobias, 1967, 1991; White *et al.*, 1981; Rak, 1983; Kimbel *et al*, 1984; Lockwood, 1997). However, there is great variability in the anterior positioning of the root of the zygomatic process across primates (Lockwood, 1997).

The infraorbital foramen is preserved as a large foramen angled inferiorly with a marked maxillary furrow, extending inferiorly towards the alveolar bone of P^3. Following the treatment by previous authors (Rak, 1983; Lockwood, 1997), the maxillary furrow is here distinguished from a maxillary sulcus, the latter essentially being a less developed maxillary furrow (without a crest-like boundary). A canine fossa is here considered an even less delimited development of these continuous characters (see discussions by Rak, 1983; Lockwood, 1997). The infraorbital foramen transmits the infraorbital neurovascular bundle in life and, presumably, is responsible for at least the superior portion of the maxillary furrow. A large anterior pillar contributes to the appearance of this region. It appears that, despite lacking some preservation in this region, a minor central facial hollow is also preserved (see also Lockwood, 1997). The large anterior pillar and prominent maxillary furrow in MLD 6 are, in combination, features defining the hypodigm of *A. africanus* (Rak, 1983; Lockwood, 1997; although see McKee, 1989; see also "Morphology" below).

A small portion of the true palate is preserved, indicating a somewhat deep palate. A groove for the greater palatine neurovascular bundle is apparent. The medialmost point of the lingual alveolar margin (endomolare) is by M^1, the lateralmost point of the external alveolar margin (ectomolare) is by M^3. The palate is anteriorly truncated, more similar to the palatal morphology of *A. robustus* (but also exhibited by the Sts 17 and Sts 71 specimens of *A. africanus*) (Kimbel *et al.*, 2004).

Endocranium. The endocranial aspect preserves the crista galli and cribriform plate of the ethmoid, a small portion of the margin of the posterior ethmoidal foramen, the orbital plate of the frontal, the lesser and greater wings of the sphenoid, a portion of the lateral pterygoid plate, the supraorbital fissure of the sphenoid (although it is obstructed with limestone within the orbit), the foramen rotundum for passage of the maxillary nerve (the second branch of the 5th cranial nerve, the trigeminal nerve), as well as portions of the anterior and middle cranial fossae.

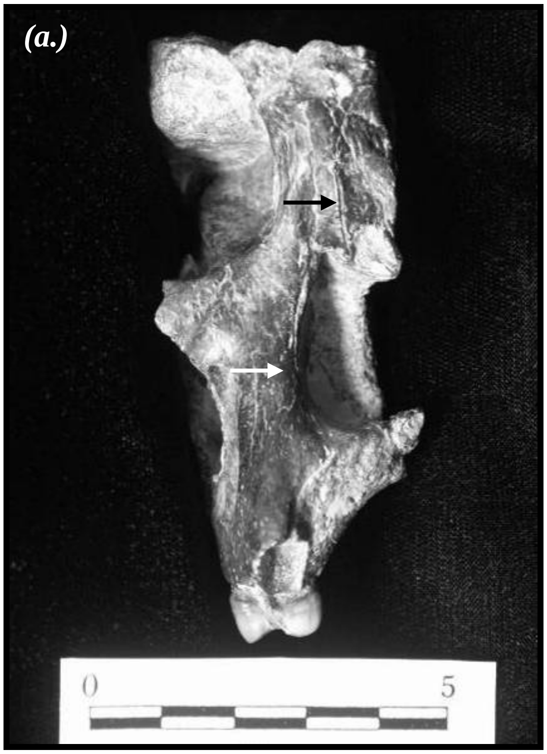
Discussion. It has been argued that MLD 6 represents the same individual as MLD 23 and MLD 1 (e.g. Dart, 1949a; Tobias *et al.*, 1977). According to Dart, "to judge from its proximity in the dump, it came from the same individual that furnished the [MLD 1] occiput" (1949a:189). It is important to note that these specimens were extracted *ex situ* from the fossil bone yards. The fossil bone yards are an area where loose fossiliferous breccias discarded by the limestone mine were later sorted by color into large piles (Dart, 1949a; Dart, 1954b; Tobias, 1997). These two specimens being discovered in near proximity among these piles of *ex situ* breccias alone would provide no solid indication of an association between the specimens. If the MLD 1 and MLD 6 specimens were extracted from the same breccia block, the association between these specimens would be more plausible. The strongest support for the supposition that MLD 1 and MLD 6 represent the same individual is that both specimens represent young adult australopith individuals at Makapansgat. The possible MLD 23 association is, however, considered probable by this author (see "MLD 23" on page 118 for a lengthier discussion of that possible association).

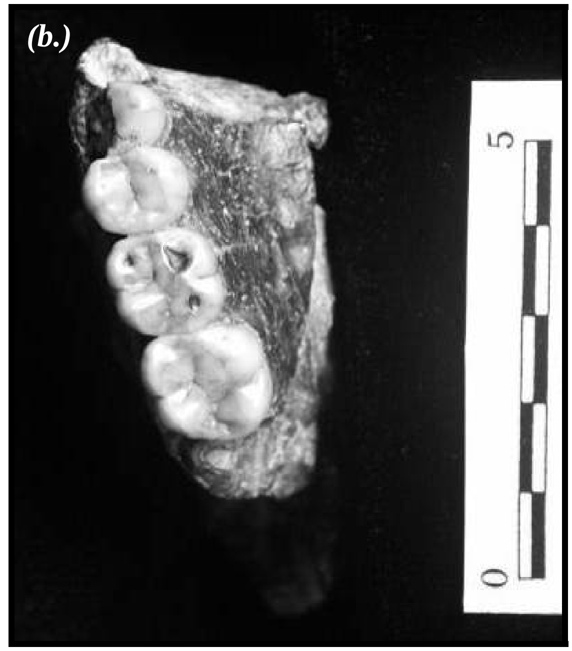
The anterior component of the incisive suture is incompletely closed, whereas its palatal contribution is completely closed (Braga, 1998). Braga asserts that specimens of *A. robustus*, like those of modern *Homo*, exhibit earlier anterior incisive suture closure than exhibited by specimens of *A. africanus*. Regardless, on the basis of the full eruption of M^3 and general dental wear for MLD 6, this individual is considered to represent a young adult. Some authors argue that this specimen belongs to a female individual on the basis of craniodental dimensions and infraorbital morphology (Dart, 1949a; Boné and Dart, 1955; Tobias *et al.*, 1977, Lockwood, 1999). Disagreement over the appropriate sex designation of Sts 5 is an appropriate cautionary testament to the difficulty with which sex designations are assigned to fossil specimens (e.g. Broom, 1947; Rak, 1983; Kimbel and White, 1988; Lockwood, 1999, Thackeray *et al.*, 2002).

The MLD 6 specimen has been described as relatively "squat" in its facial dimensions (Lockwood, 1997). It exhibits a number of features aligning it more closely with specimens of *A. africanus* than *A. robustus*. However, Dart saw great similarity in craniofacial form indicating an "intimate relationship" between the few craniofacial specimens then discovered at Taung, Makapansgat, and Kromdraai (Dart, 1949a:191). Dart (1949a) also argued that the MLD 6 specimen is more similar to specimens of *A. robustus* ("*Paranthropus*") than *A. africanus* specimens from Sterkfontein (Dart's "*Plesianthropus*", but essentially Sts 5) in its maxillary prognathism, but more prognathic overall than specimens of both *A. robustus* and *A. africanus* from Sterkfontein.

On the basis of subnasal morphology, MLD 6 aligns with the sample of *A. africanus* instead of *A. robustus*. Subnasal morphology was originally identified as distinguishing among Plio-Pleistocene hominins by Robinson (1953, 1954a) and later corroborated by others (e.g. McCollum *et al.*, 1993; McCollum, 2000, Bromage, 1989). Features this specimen exhibits that are more typical of the hypodigm of *A. africanus* include a stepped nasal floor, nasal bone morphology, and large anterior pillar combined with a marked maxillary furrow. The craniofacial features aligning MLD 6 more closely with the hypodigm of *A. robustus* are the anterior position of the root of the zygomatic arch, anteriorly truncated palate, central facial hollow, and blunt borders of the nasal aperture. Many of the features more closely aligning MLD 6 with either the hypodigm of *A. africanus* or *A. robustus* tend to be somewhat intermediate in appearance or are present in at least a few specimens of both species (e.g. nasal bone morphology, anterior pillar, anterior position of zygomatic arch root, anteriorly truncated palate, blunt borders of the nasal aperture).

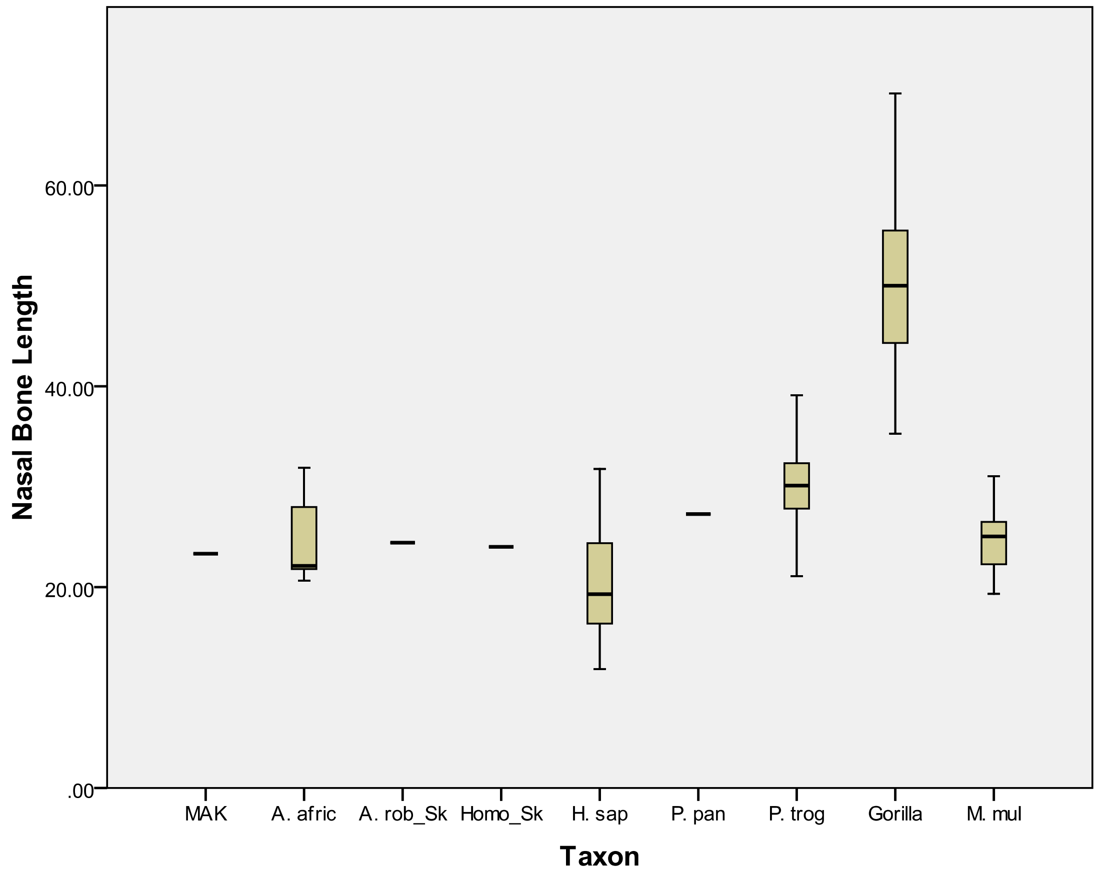
Figure 6-3a, b, c, & d: MLD 6. A well-preserved adult right craniofacial fragment in anterior (*a*), occlusal (*b*), right lateral (*c*), and left medial (*d*) views. Some of the features described in the text are indicated with arrows.






(d.)
0
5
cm

Figure 6-4: MLD 6 Nasal Bone Length. The median (line), 1st and 3rd quartiles (box), and range (bars) of the sagittal length of the nasal bones (nasion-rhinion) for MLD 6 in comparison to South African australopiths and a sample of extant primates. The fossil sample sizes for this analysis are: *A. africanus* (n = 5), Swartkrans *A. robustus* (n = 1), Swartkrans *Homo* (n = 1).



MLD 9/12

Overview. MLD 9/12 is an adult right maxillary specimen with $P^3 – M^3$ (See Figure 6-5a, b; see also Chapter 7 for dental descriptions). This specimen is composed of two fossil fragments found in the fossil dumps a year apart. MLD 9 is a fairly complete right maxillary fragment with $P^3 – M^2$ and MLD 12 is a right maxillary fragment with M^3

and surrounding alveolar bone. Despite the loss of the anterior teeth, the lingual alveolar bone is preserved for right I^1-M^1 and M^3. The anteroposterior distance along the median palatine suture is 50.5 mm, from orale to the posteriormost portion of the preserved suture (at the posterior aspect of the M^2 roots).

Maxilla and Nasal Aperture. The inferior part of the base of the zygomatic arch is preserved, but only permits comparative assessment based upon the anterior positioning of the root of the zygomatic process (at P^4). This anterior positioning of the zygomatic process root is intermediate between specimens of *A. robustus* and *A. africanus*. While the infraorbital foramen is not preserved, there is a marked maxillary sulcus running inferiorly from its approximate location. Rak (1983) pointed out the morphological similarity between this region in MLD 9/12 and the subforamen divide (a connection between the anterior pillar and the root of the zygomatic process) exhibited by specimens of *A. robustus*. Lockwood (1997) similarly suggested that a maxillary fossula, more common in specimens of *A. robustus* than *A. africanus* (Rak, 1983), may have been demarcated by an extension of bone that is only partly preserved in MLD 9/12.

A large, long canine alveolus is exposed by the MLD 9/12 specimen and indicates that a significant canine jugum was most likely present. Just lateral to the exposed canine alveolus is a partially preserved, but significant anterior pillar. Rak (1983) and Clarke (1977) both agree with this author and suggest that the MLD 9/12 specimen exhibited a marked anterior pillar, although Lockwood (1997) suggests that its anterior pillar was broad and only somewhat prominent.

The maxillary sinus is partially exposed. The nasal floor is preserved and lacks a nasal sill (see also White *et al.*, 1981). The nasal cavity exhibits the classic "gracile" australopith stepped nasal floor and a gradual descent to alveolare. However, Lockwood (1997) correctly described the morphology of MLD 9/12 and StW 498 as extending more posteriorly and gradually into the nasal cavity before stepping down to the incisive fossa. This morphology is similar to that known for specimens of *A. afarensis* and a small number of specimens attributed to *A. africanus*, also including Sts 71, StW 183, and StW 391 (Lockwood, 1997; Kimbel *et al.*, 2004). Thus, although MLD 9/12 and StW 498 exhibit a stepped nasal floor, they deviate to some extent from the typical appearance of the nasal morphology in specimens of *A. africanus*. The nasoalveolar clivus is somewhat transversely flattened, similar to specimens of *A. africanus* and, to some extent, *A. afarensis* (see discussions in Rak, 1983; White *et al.*, 1981; Lockwood, 1997).

A simple comparison of alveolar height was made for this individual with all extant and fossil species (see Figure 6-6). The alveolar height of the MLD 9/12 specimen was found to be well below the range of all fossil species (*A. africanus*, *A. robustus*, and fossil *Homo*). The alveolar height of MLD 9/12 was found to be lower than that of essentially all other fossil specimens (see also Lockwood, 1997).

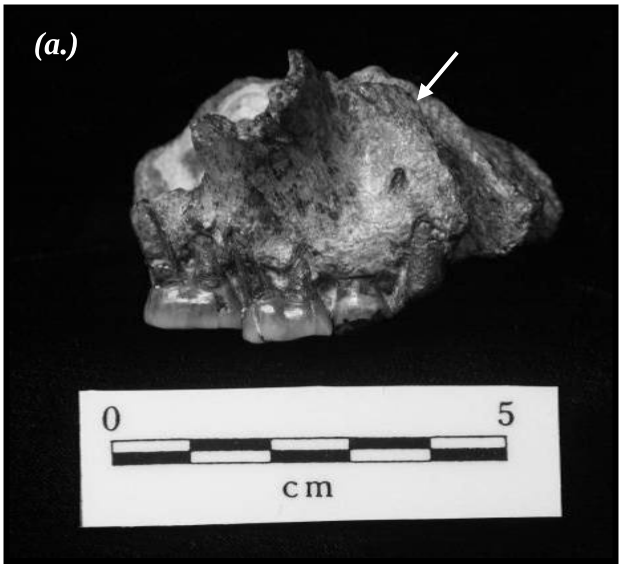
The incisive foramen is clearly preserved on the right and is large. The palate appears to be relatively shallow when compared with other South African australopiths, although the MLD 9/12 palate slopes gently to a deeper posterior aspect. In addition, the incisive canal appears to be anteriorly positioned. The palate fails to exhibit one common characteristic of *A. africanus*: the anterior shelving or steep slope from the incisal alveolar bone to the palate is lacking in MLD 9/12 (Lockwood, 1997). Also the palate, like that of MLD 6, is anteriorly truncated, a morphology that is used to described this region in specimens of *A. robustus* (with a few exceptions within the hypodigm of *A. africanus*) (Kimbel *et al.*, 2004). While a central facial hollow has been reconstructed for the MLD 9/12 specimen (Rak, 1985b), it seems tenuous to assume its presence based upon the minuscule portion of that region that is preserved.

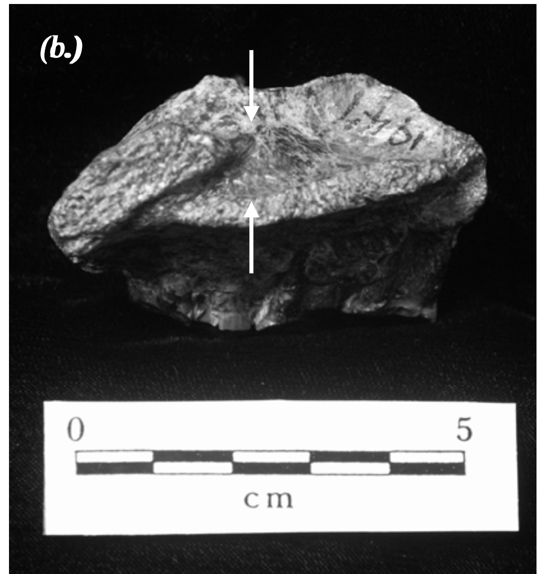
Discussion. This specimen represents an adult on the basis of the eruption of the M^3, as well as the significant wear exhibited by the postcanine dentition. This estimate is bolstered by the complete closure of the anterior and posterior components of the incisive suture (Braga, 1998). It has been argued that the MLD 9/12 specimen represents a female individual [presumably on the basis of dental and facial dimensions] (Dart, 1949d; Boné and Dart, 1955). However, on the basis of both large size and hypothesized male infraorbital morphology, Lockwood (2000) argued that MLD 9/12 represents a male. Indeed, the MLD 9/12 specimen appears to be relatively large for the Makapansgat sample, providing potential support to the male attribution by Lockwood. However, sex determinations cannot be established with confidence for the Makapansgat hominins.

Dart (1949d) found close anatomical similarities between MLD 9 (its MLD 12 complement had not yet been discovered upon his initial description) and MLD 6. This certainly remains the case for a number of features, including the anteriorly positioned base of the zygomatic arch, marked maxillary furrow or sulcus, anteriorly truncated palate, stepped nasal floor, and the large anterior pillar (presumed so in MLD 9/12). While some of these shared features are more common in the current sample attributed to

A. africanus (e.g. maxillary furrow or sulcus with large anterior pillar, and stepped nasal floor), other shared features align these specimens as either intermediate or more closely with the hypodigm of *A. robustus* (e.g. anteriorly positioned zygomatic and anteriorly truncated palate). While MLD 6 and MLD 9/12 are quite similar to each other, neither can be distinguished from the samples of *A. africanus* or *A. robustus*, and they are in many ways morphologically intermediate between the two species.

Figure 6-5a, b, & c: MLD 9/12. A right maxillary fragment with P_4-M_3 in right lateral (*a*), medial (*b*), and occlusal (*c*) views. *Note*: MLD 12 is not photographed in (*a*) or (*b*). Some of the major features described in the text are indicated with arrows.





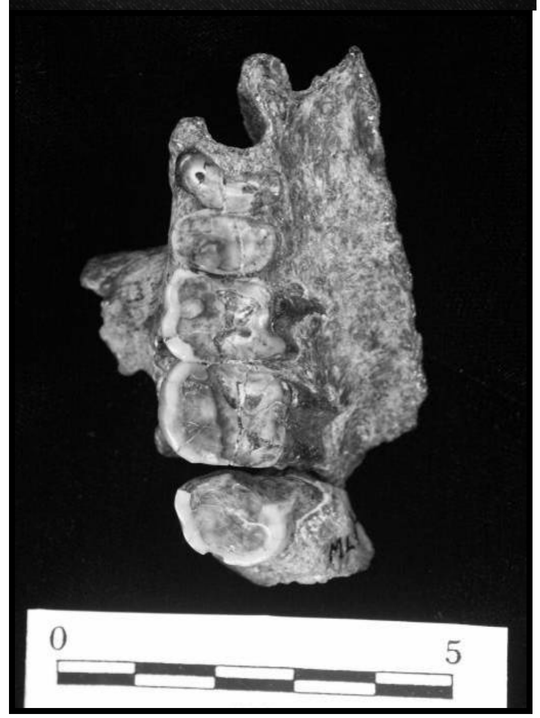
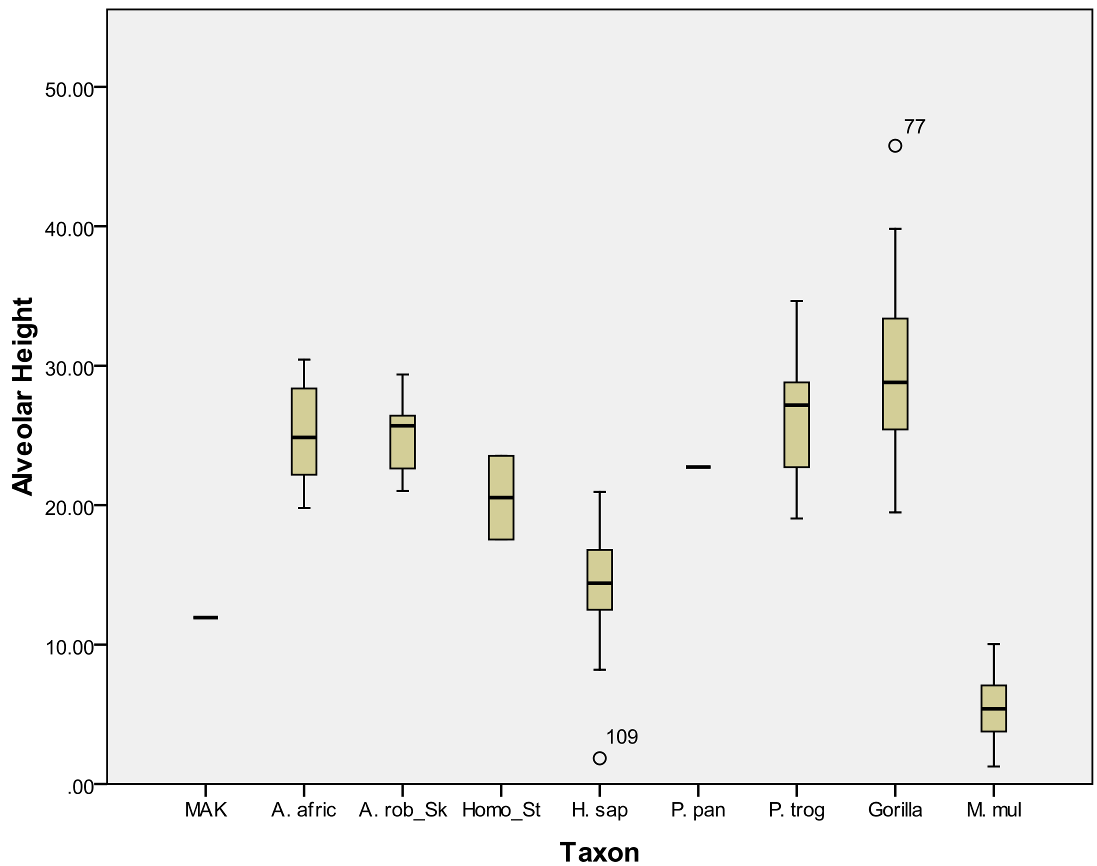


Figure 6-6: Alveolar Height. The median (line), 1st and 3rd quartiles (box), and range (bars) of Alveolar Height (Nasospinale-Prosthion) for MLD 9/12 in comparison to South African australopiths and a sample of extant primates. The extant gorilla and human samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: *A. africanus* (n = 10), Swartkrans *A. robustus* (n = 9), and Sterkfontein *Homo* (n = 1).



MLD 10

Overview. The MLD 10 specimen is an adult cranial vault fragment preserving portions of both parietals and the occipital (see Figures 6-7a, b). The fragment has a maximum breadth of 69.7 mm and a midsagittal length of 84.6 mm.

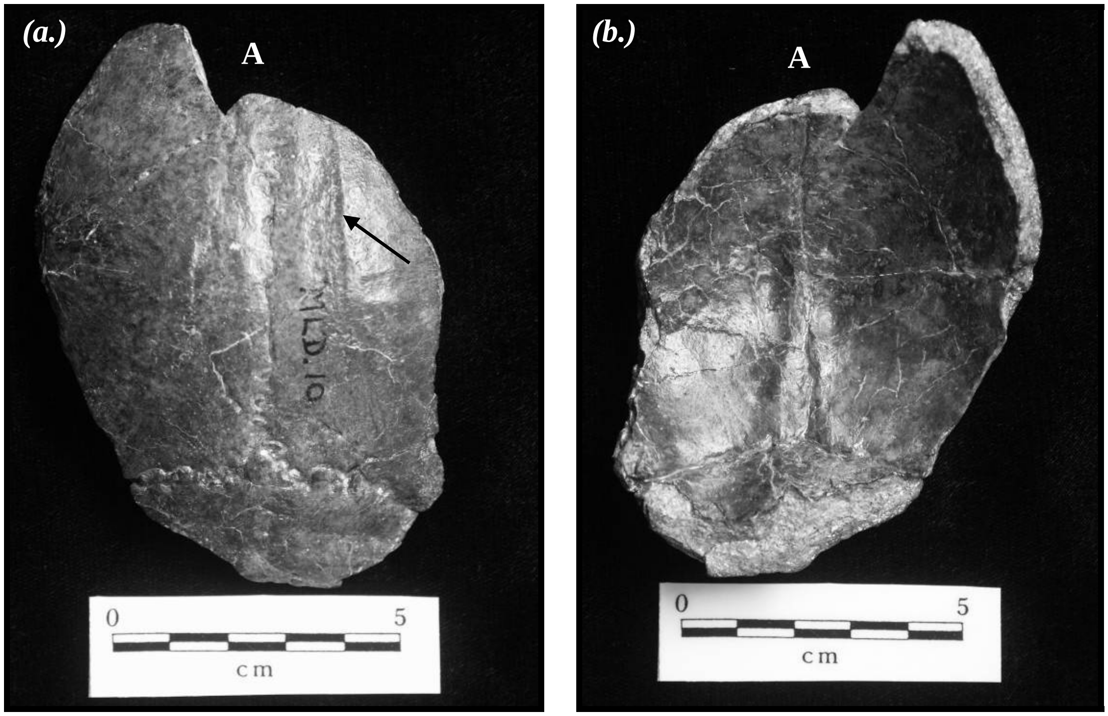
Ectocranium. The temporal lines for MLD 10 are clearly demarcated. They run somewhat parallel along the sagittal suture and then splay out laterally and inferiorly as they reach the lambdoidal suture. They are approximately 21.0 mm apart at their narrowest preserved point. This is far greater than seen in MLD 1, but considerably closer than seen in MLD 3. This difference is not an artifact of preservation since MLD 10 preserves more of the anteroposterior dimension of the parietals than MLD 1 and since MLD 3 preserves an equivalent length of the right temporal line. A short segment of the superior nuchal line is preserved on the right and left sides. The preserved superior portion of the nuchal attachments appears moderately developed.

Endocranium. The endocranial aspect of MLD 10 exhibits a series of Pacchioinian depressions (for arachnoid granulations) bilaterally along the posterior aspect of the sagittal suture. In addition, grooves for the middle meningeal vessels and the sagittal sinus are apparent. The portion of the preserved sagittal groove nearest to lambda exhibits attachment points for the falx cerebri. A few small Pacchioinian depressions are also visible in the region of lambda and just superior to the internal occipital protuberance. Although not typical, Pacchioinian depressions have also been recorded on the internal aspect of the occipital in some extant humans (e.g. Leach *et al.*, 2008).

Cranial Vault Thickness. Vault thicknesses were recorded as 7.5 mm at the anterior of the sagittal line, as 7.2 mm on the left parietal at the lateralmost preserved point, and as 7.4 mm on the right parietal at the lateralmost preserved point. Although these dimensions were not taken at equivalent regions in other australopiths, these dimensions generally indicate a somewhat thick cranial vault when compared to cranial vault data for *A. africanus* provided by Kimbel and colleagues (2004).

Discussion. The sagittal suture is unfused at the anteriormost and posteriormost borders of the preserved specimen. Where the sagittal suture is fused, it is not fully obliterated. The lambdoidal suture is unfused and exhibits an absence of extrasutural bones. Unfortunately, no part of the coronal suture is preserved. As a result of the degree of sagittal and lambdoidal suture fusion exhibited by MLD 10, this individual was likely an adult at time of death (McKern and Stewart, 1957; see also Boné, 1955; Mann, 1975; Tobias *et al.*, 1977). The positioning of the temporal lines (and absence of a sagittal crest) lends weak support for closer affinities of MLD 10 with specimens of *A. africanus*, although these characteristics are variable and also are used to distinguish sex within australopith samples.

Figure 6-7a & b: MLD 10. A cranial vault fragment with right and left parietals and occipital in external (*a*) and internal (*b*) views, where A is anterior. Some of the major features described in the text are indicated with arrows.



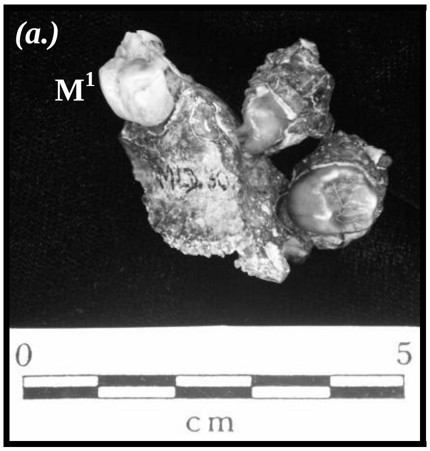
<u>MLD 11/30</u>

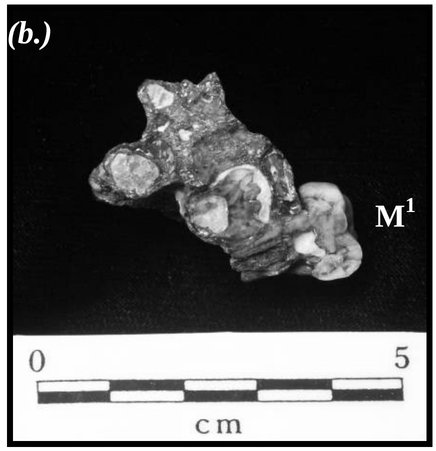
Overview. MLD 11/30 is a right maxillary specimen with C^1, P^3, and P^4 unerupted, M^1 in occlusion, I^2 at the starting phase of alveolar eruption, and I^1 in the crypt with only partial root formation (see Figure 6-8 a, b, c). The specimen was originally composed of two fragments: a right anterior maxillary fragment with a small fragment of P^3, approximately half of P^4, and M^1 (MLD 30) and a right maxillary fragment with I^1, I^2, C^1, P^3, and approximately half of P^4 (MLD 11). The original condition of the MLD 11 specimen is represented by a cast, as the original specimen suffered damage in 1956 by J.T. Robinson to access the teeth in their crypts (see Dart, 1962a). MLD 11/30 most likely represents an individual who died in late childhood.

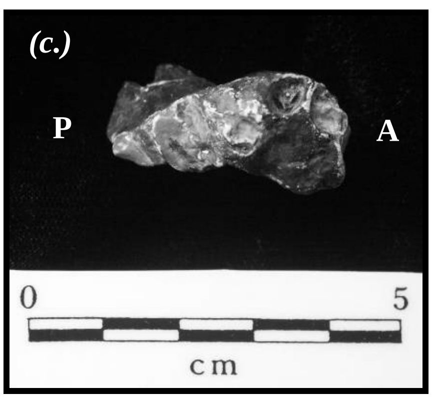
Maxilla. A bulge is visible superior to the canine alveolus. It is possible this is an incipient anterior pillar due to the subadult age of this individual at death. Posterolateral to this "anterior pillar" is a developed canine fossa appearing almost as an inferior continuation of the infraorbital canal (almost developed enough to be considered a maxillary sulcus). The younger Taung specimen exhibits a less developed "anterior pillar" and weaker canine fossa.

Discussion. The MLD 11/30 specimen represents an individual who died in late childhood. Mann's age at death estimate of 9 +/- 1 years was produced on the basis of a human developmental model (1975; See also Table 9-1). However, modern studies suggest an estimate of 5-6 years is more likely on the basis of a conversion of Mann's estimates using an ape model (Bromage, 1987). The right M^1 is in full occlusion, but the C^1-P^4 are in varying stages of development. The structure identified above as an incipient anterior pillar is positioned over the developing canine. The Taung skull exhibits similar positioning of its "anterior pillar". While it seems likely that a true (adult) anterior pillar results from modeling and remodeling in response to biomechanical forces transmitted via premolar masticatory loading (e.g. Rak, 1983; Strait *et al*., 2009), it is likely that in MLD 11/30 the child form results at least in part from the large developing canine. It is unclear what part premolar load resistance plays in the development of this morphology in subadult australopiths, although an analysis of the subadult South African australopiths would prove to be particularly interesting.

Figure 6-8a, b, & c: MLD 11/30. A right maxillary fragment with I^1- M^1 at varying dental developmental stages. Pictured below is MLD 30 in anteroinferior view with the P^3 and P^4 of MLD 11 in articulation (*a*), MLD 30 in a lateral, oblique view (*b*), and the MLD 11 cast in occlusal view as MLD 11 originally appeared (*c*), where A is anterior and P is posterior.







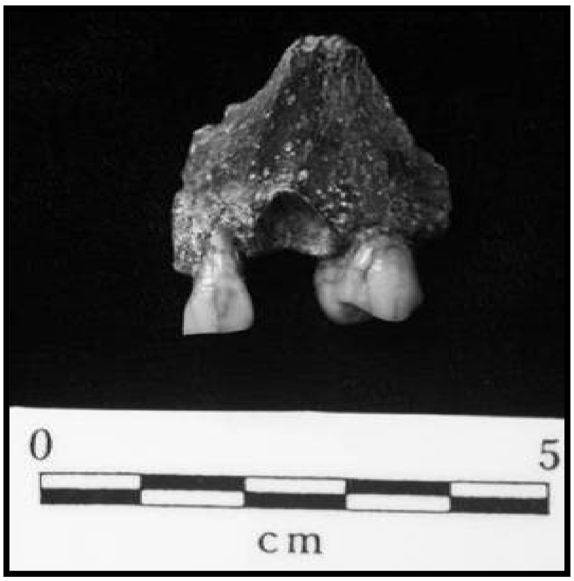
<u>MLD 23</u>

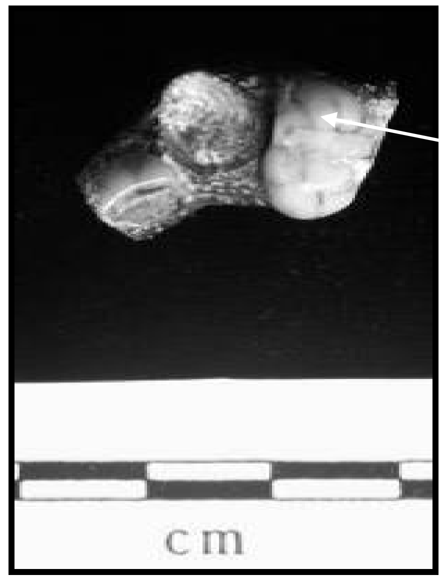
Overview. MLD 23 is a young adult's left maxillary fragment with I^2 and P^3 and the alveolus for C^1 (see Figures 6-9a, b, and c). This specimen preserves the alveolar bone surrounding I^2-P^3 and the inferior portion of an anterior pillar.

Maxilla. As is the case with MLD 6, there is evidence of a well-developed anterior pillar and canine jugum, as well as a marked inferior portion of a canine fossa (perhaps even a maxillary furrow) superior to the P^3. Issues of preservation limit any further assessment of this region.

Discussion. On the basis of the fully erupted, yet unworn I^2, C^1, and P^3 and visible perikymata, this specimen represents a young adult individual. This specimen may be associated with MLD 6 (Tobias *et al*., 1977; Lockwood, 1997, 1999), presumably on the basis of virtually identical premolar morphology and wear (yet nothing else has been cited to my knowledge to confirm this association). Examination of the perikymata of the MLD 23 P^3 and MLD 6 P^4 under 10x magnification provides evidence to support this association. Specifically, the P^4 of MLD 6 exhibits more visible perikymata than the P^3 of MLD 23, and would have presumably erupted later should they belong to the same individual regardless of whether a pongid or human-like developmental pattern were expected (see also Conroy and Mahoney, 1991; Conroy and Vannier, 1991a,b; Dean, 2000). Unfortunately, the buccal surface of the MLD 6 P^3 is not preserved to more directly assess this comparison. The preserved lingual surface, however, indicates equivalent developmental timing of enamel deposition in both MLD 23 and MLD 6. There is weak support to the contrary, however, in that the inferior portion of the maxillary furrow in MLD 6 is better demarcated than the comparable preserved portion in MLD 23. Overall, it seems reasonable to assume that MLD 23 and MLD 6 belong to the same individual. Certainly, a detailed analysis of perikymata would likely give a final conclusive answer.

Figure 6-9a, b, & c: MLD 23. This specimen is a left maxilla with I^2 and P^3 in buccal (*a*) and occlusal (*b*) views. Some of the major features described in the text are indicated with arrows.





<u>MLD 28</u>

Overview. This specimen is a young adult right maxillary and palatine fragment with M^2 – M^3 (see Figure 6-10). Only a small portion of the right maxilla and a miniscule portion of the horizontal part of the right palatine are preserved. The alveolar bone surrounding M^3 and the distal portion of M^2 and the inferior bony base of the maxillary sinus are preserved. In addition, the greater palatine foramen is apparent.

Maxilla. The lateralmost aspect of the posterior palate appears to be of moderate depth. Aside from the palate depth and dentition, there is little of morphological significance to this small maxillary fragment.

Discussion. The presence of a moderately worn M^2 and M^3 indicates this individual was a young adult at death. It has been suggested that MLD 28 represents the same individual as the MLD 18 mandible (Mann, 1975; Tobias *et al.*, 1977). This association appears likely on the basis of complementary dental morphology and wear.

Figure 6-10: MLD 28. This specimen is a right maxillary fragment with M^2 and M^3 visible in occlusal view.

MLD 37/38

Overview. The MLD 37/38 specimen is a young adult partial cranium, revealing a virtually complete neurocranium and basicranium and only the posterior portion of the palate with right M^1-M^3 and left M^2 (see Figure 6-11). This specimen is composed of two fragments that have been glued together: one preserves the majority of the neurocranium (MLD 37) and the other preserves the right lateral aspect of this same cranium (MLD 38). As a unit, MLD 37/38 preserves portions of the parietals, temporals, occipital, sphenoid, frontal, maxilla, palatines, and even a portion of the vomer. This specimen also preserves a fragmentary right M^1, M^2-M^3, and left M^2 (*contra* Dart, 1962b; *per* Tobias *et al.*, 1977) (although see below).

The anterior aspect of the MLD 37/38 specimen was presumably separated from the rest of the cranium after deposition, as the preserved portions of MLD 37/38 exhibit weathering from exposure to the elements. The fracture plane extends obliquely through the center of the right M^1, left M^2, and a somewhat coronal plane through the superior aspect of the cranium. Post-depositional deformation has had a subtle impact on the overall symmetry of the neurocranium and strongly affected the position of the maxilla with regard to the neurocranium. What remains of the neurocranium is generally well preserved and free of major distortion, although the zygomatics and to some extent the occipital condyles are not preserved. In addition, the right aspect of the basicranium suffered moderate damage. Along with Sts 5, MLD 37/38 is one of the best preserved basicranial specimens known for South African australopiths.

Neurocranium. The neurocranium of MLD 37/38 is somewhat gracile in appearance. The lambdoidal and sagittal sutures are unfused along the majority of their course. There is no sagittal crest and the temporal lines are not demarcated on this specimen. There is a weakly developed supramastoid crest extending posteriorly from above the external acoustic meatus. A compound temporonuchal crest is not evident. In many ways the neurocranium is quite gracile in appearance and somewhat primitive.

The dimension bregma-lambda was compared across all specimens preserving this region (see Figure 6-12). For the fossil australopith sample, only MLD 37/38 and the SK 54 specimen attributed to *A. robustus* were available. The medians are quite distinct among the extant samples. The two australopiths, however, were comparable in their values of bregma-lambda and both had values that fell within the range of the gorillas.

One of the overall dimensions of the neurocranium, basion-bregma, was compared across all fossil and extant species (see Figure 6-13). The only fossils for which this measurement was recorded include the Makapansgat MLD 37/38 and the Sterkfontein Sts 5 "Mrs. Ples" crania. Although a range of variation is not available for either the Sterkfontein or Makapansgat samples, the MLD 37/38 and Sts 5 specimens exhibit basion-bregma lengths that are essentially equivalent.

Basicranium. The sample of *A. africanus* at Sterkfontein displays an essentially primitive cranial base with regard to basal mastoid morphology, narrow cranial base, more sagittally oriented petrous bones, and transverse orientation of the tympanic plate (Tobias, 1967; 1991; Clarke, 1977; Dean and Wood, 1982; Spoor, 1993, Spoor, 1997b; Kimbel and White, 1988b; Kimbel *et al.*, 2004). However, it must be noted that there is considerable variation in basicranial morphology within the hypodigm of *A. africanus*, particularly with regard to the orientation of the petrous bones and tympanic plate (e.g. Dean and Wood, 1982; Kimbel *et al.*, 2004). MLD 37/38 is like basicranial specimens of *A. africanus* in most features, although it must be pointed out that basicranial morphology in specimens of *A. robustus* and *A. africanus* are also rather similar (e.g. Kimbel and White, 1988b). A couple of primary basicranial distinctions between *A. robustus* and *A.*

africanus in South Africa are in the greater breadth across the tympanic plates and less sagittally oriented petrous axes in specimens of the former (Dean and Wood, 1982).

One major exception with regard to the overall basicranial similarity of Sts 5 (and Sts 25) and MLD 37/38 is noticeable in the petrous portion of the temporal. The MLD 37/38 petrous axis is somewhat less oriented in a sagittal plane (Tobias, 1967, 1991; Dean and Wood, 1982; Kimbel and White, 1988a). This is not true for comparisons of MLD 37/38 against Sts19, however, in which the latter exhibits an even less sagittally oriented petrous axis. A less sagittally oriented petrous axis is derived, with humans less, and apes more, sagittally oriented (Dean and Wood, 1982).

It has long been clear that the tympanic is variable within australopiths (e.g. Dean and Wood, 1981, 1982). Examination of available South African australopiths reveals that even within the Sterkfontein assemblage, tympanic morphology ranges from a primitive clearly tubular tympanic to a derived, vertical morphology. On the other hand, the MLD 37/38 tympanic is intermediate in morphology, displaying a derived and vertical, but not tubular tympanic (Kimbel and White, 1988a; Kimbel *et al.*, 2004).

The mastoid region is preserved for MLD 37/38 and is morphologically similar to the comparable region exhibited by Sts 5, although the MLD 37/38 specimen is arguably slightly more primitive, having been likened to both African apes (Kimbel *et al.*, 1985) and specimens of *A. afarensis* in this region (Kimbel *et al.*, 2004). MLD 37/38 exhibits derived characters in its glenoid region, which have been described in detail by Kimbel and colleagues (2004). These authors note that compared to specimens of *A. afarensis* of similar mandibular fossa breadth, MLD 37/38 exhibits an anteroposteriorly lengthened mandibular fossa. In addition, unlike specimens attributed to *A. africanus* from Sterkfontein, MLD 37/38 exhibits a continually sloping articular eminence with an apex at the posterior border of the temporal foramen. The apex of the articular eminence in Sterkfontein australopiths rests posterior to the edge of the temporal foramen and divide the eminence, as it does in great apes and *A. afarensis*. MLD 37/38 shares with Sts 19 and A.L. 444-2, however, a notch on the posterior portion of the temporal foramen (Kimbel *et al.*, 2004).

The orientation of the articular eminence is also distinct in MLD 37/38, where it twists around its transverse axis in inferior view and exhibits a posteriorly facing medial portion and an inferiorly facing lateral portion (Kimbel *et al.*, 2004). This morphology results in a posteriorly positioned entoglenoid process whose anterior surface is essentially flat and meets the steeply inclined preglenoid plane at a sharp angle (Kimbel *et al.*, 2004). Specimens of *A. robustus* tend to exhibit larger, deeper mandibular fossae, but in most respects are similar to specimens of *A. africanus* (Kimbel *et al.*, 2004). MLD 37/38 is somewhat distinct from specimens of *A. africanus* and *A. robustus* in its glenoid morphology. The unusual glenoid morphology of MLD 37/38 even has been argued to be more similar to specimens of *A. boisei* than *A. africanus* (Kimbel *et al.*, 2004).

The infratemporal crest is unusual in appearance in MLD 37/38 in that it s somewhat elongate and triangular, as is seen in some macaque specimens. The external occipital protuberance of MLD 37/38 is more marked than that preserved for Sts 5, although considerable within-species variation of the external occipital protuberance is acknowledged within modern human and Sterkfontein samples. An occipital foramen is evident in the MLD 37/38 specimen (Braga and Boesch, 1997). The presence of an occipital foramen is variable across South African australopiths (Braga and Boesch, 1997), thus this foramen appears to have little phylogenetic value. The anteroposterior length of the occipital condyle of MLD 37/38 was compared to other available specimens of *A. africanus* and *A. robustus* (see Figure 6-14). While the ranges of the samples of *A. africanus* and *A. robustus* overlap, the MLD 37/38 specimen falls below both samples. The occipital condyle length appears low for MLD 37/38, but it does not appear distinct enough to be of diagnostic value. Presumably, larger samples of *A. africanus* and *A. robustus* would expand their ranges of variation enough to encompass the MLD 37/38 value.

Endocranium. Although the endocranium of MLD 37/38 is filled with a calcium-carbonate rich cement, some aspects of the endocranium can be described as a result of CTs analyses of this specimen (e.g. Conroy *et al.*, 1990; Braga and Boesch, 1997; Neubauer *et al.*, 2004). A major feature of MLD 37/38 is the absence of the occipital-marginal venous sinus that is common in specimens of *A. robustus* (Conroy *et al.*, 1990; Braga and Boesch, 1997; Neubauer *et al.*, 2004). The occipital-marginal venous sinus system is also common in samples of *A. afarensis* and *A. boisei* and is present in the Taung child (e.g. Kimbel, 1984; Tobias and Falk, 1988; Conroy *et al.*, 1990; Braga and Boesch, 1997).

Palate. The posterior aspect of the palate is very deep. The anterior portion of the palate is not preserved.

Cranial Vault Thickness. The thickness of the frontal in the midsagittal plane and just anterior to the coronal suture was measured as 5.5 mm. Measurements of cranial vault thickness at bregma for fossil hominins (Gauld, 1996:413) indicate that the MLD 37/38 cranial vault at bregma falls within the low end of the range known for the hypodigm of *A. africanus*.

Discussion. The MLD 37/38 cranium is one of only a handful of specimens recovered from *in situ* deposits at Makapansgat. Alan Hughes and James Kitching first discovered a relatively complete australopith cranium from *ex situ* blocks in the fossil bone yard. With this specimen in mind, they returned to the *in situ* deposits at Makapansgat and searched for the remaining (right lateral) portion of the australopith cranium. They met with success when they found a large block of pink breccia within Member 4 with the posterior aspect of the same australopith cranium (Dart, 1959a).

MLD 37/38 represents an adult individual at time of death, based on the fully erupted M^3 and the fusion of the sphenoccipital suture. The lack of M^3 dental wear and the unfused ectocranial sutures suggest this individual may have been a young adult at death, although Dart estimated an age at death of approximately 50 years based upon a human model and the presumption of the M3 as a supernumerary tooth(1962a). Dart suggested that this cranium represents a female australopith (1962b).

In line with Dart's somewhat sensational behavioral reconstructions for South African australopiths, he once suggested the MLD 37/38 individual was subjected to a slashing injury to its head (in the region of the temporal) and decapitated prior to fossilization (1962b). That said, the bony evidence of the temporal and basicranium to which Dart refers is the result of taphonomic processes acting on the skull rather than a cause of death. It is not difficult to imagine the slight misalignment of the temporal bone being the result of geological processes. Nor is it difficult to envision (as bland in comparison as it may be) that the erosion of the condyles and right mastoid were the result of hyena gnawing rather than decapitation.

In Dart's original anatomical description of the MLD 37/38 specimen, he argued that the left M^3, right M^2-M^3, and a supernumerary right molar are preserved. He was mistaken in this description, as the teeth are the right M^1-M^3 and left M^2. This assertion is also supported by the MLD 37/38 entry by Tobias and colleagues in the *Catalogue of Fossil Hominids* (Tobias *et al.*, 1977). It must be assumed that Dart described the right M^3 as a supernumerary molar on the basis of the extreme wear exhibited by the M^1 and M^2 in comparison to the minor wear of the M^3. It is also possible that the strongly crenulated occlusal surface drove him to treat the molar as supernumerary. This certainly skewed his extremely high age at death estimate of 50 years for MLD 37/38.

Although a number of individuals have estimated endocranial capacity for the MLD 37/38 fragmentary cranium (e.g. Dart, 1962b; Holloway, 1970, 1972), the most reliable estimates have been provided by Conroy and colleagues (1990) and Neubauer and colleagues (2004) of 425 cm^3 and 440 cm^3, respectively. The differences in these two estimates for cranial capacity rest in their estimates for the preserved and missing portions of the MLD 37/38 neurocranium. These authors estimate a small to moderate australopith cranial capacity for the MLD 37/38 specimen and describe the transverse and sigmoid sinuses, but both papers confirm that an expanded marginal sinus groove is absent. This groove is lacking in virtually every specimen attributed to *A. africanus* (Kimbel, 1984; Conroy *et al.*, 1990), although see Tobias and Falk (1988) for a discussion of its unusual morphological appearance and presence in the Taung child. A large occipital marginal sinus system is known for some australopiths, most notably including the hypodigm of *A. robustus* (e.g. Kimbel, 1984). Regardless, a later study found that these differences, once considered the result of changes in blood volume between species relating to encephalization, are not reflected by differences in the dimensions of basicranial foramina (Braga and Boesch, 1997). Considerable debate has focused upon the functional and phylogenetic utility of morphological variation in the sinus venous system (e.g. Falk and Conroy, 1983; Kimbel, 1984, Falk, 1990; Tobias and Symons, 1992; Braga and Boesch, 1997), but remains unresolved.

In his most detailed description of the MLD 37/38 specimen, Dart pointed out its great similarity to Sts 5 in bicranial dimensions (Dart, 1962b). He noted minor differences in the basicranium, however, including a less projecting postglenoid process, weak nuchal crest, and an "incurved inion" (1962b:126). With these characters in mind, he stated "while these differences appear to characterize the male as well as the female australopithecines at Makapansgat there seems to be no justification now for regarding them or any other known differences between the Sterkfontein and Makapansgat australopithecines as having more than variety value" (1962b: 126). Indeed, the MLD 37/38 specimen is similar to specimens of both *A. africanus* from Sterkfontein and *A. robustus*. In many aspects of the basicranium and glenoid, however, MLD 37/38 stands alone. Moreover, the combination of features this specimen exhibits makes it distinct from other currently known South African australopith specimens.

Figure 6-11: MLD 37/38. This specimen is a partial cranium visible in anterior (*a*), posterior (*b*), inferior (*c*), and right lateral views (*d*). Some of the major features described in the text are indicated with arrows.

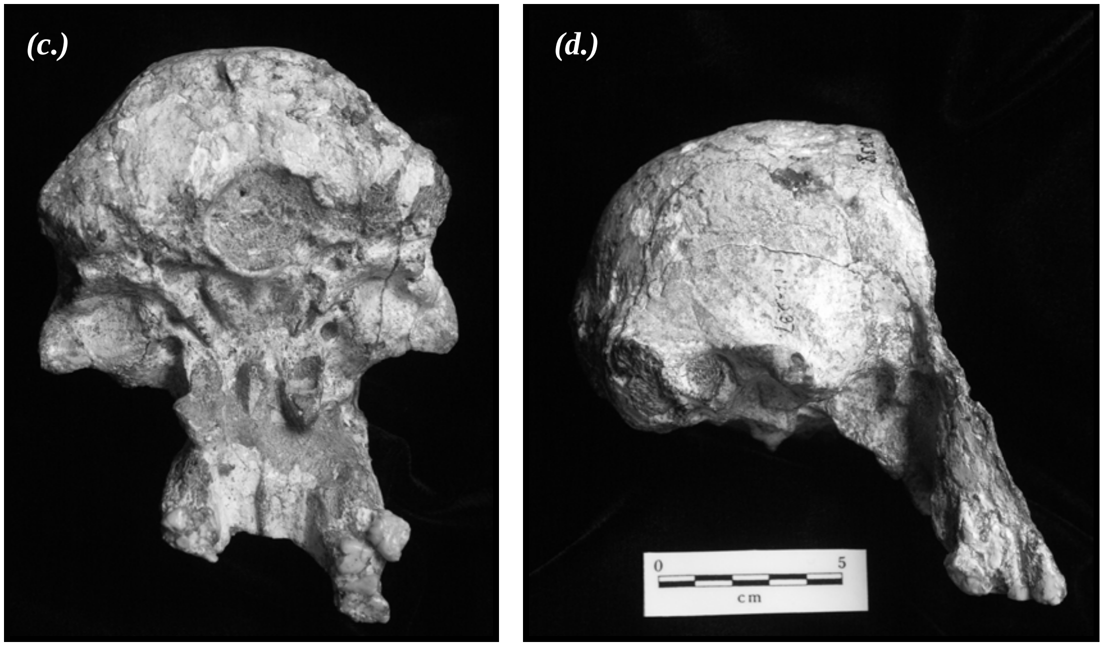

(c.)
(d.)
0
5
cm

Figure 6-12: Bregma-Lambda. The median (line), 1st and 3rd quartiles (box), and range (bars) of bregma-lambda for MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant human, chimpanzee and gorilla samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: Swartkrans *A. robustus* (n = 1).

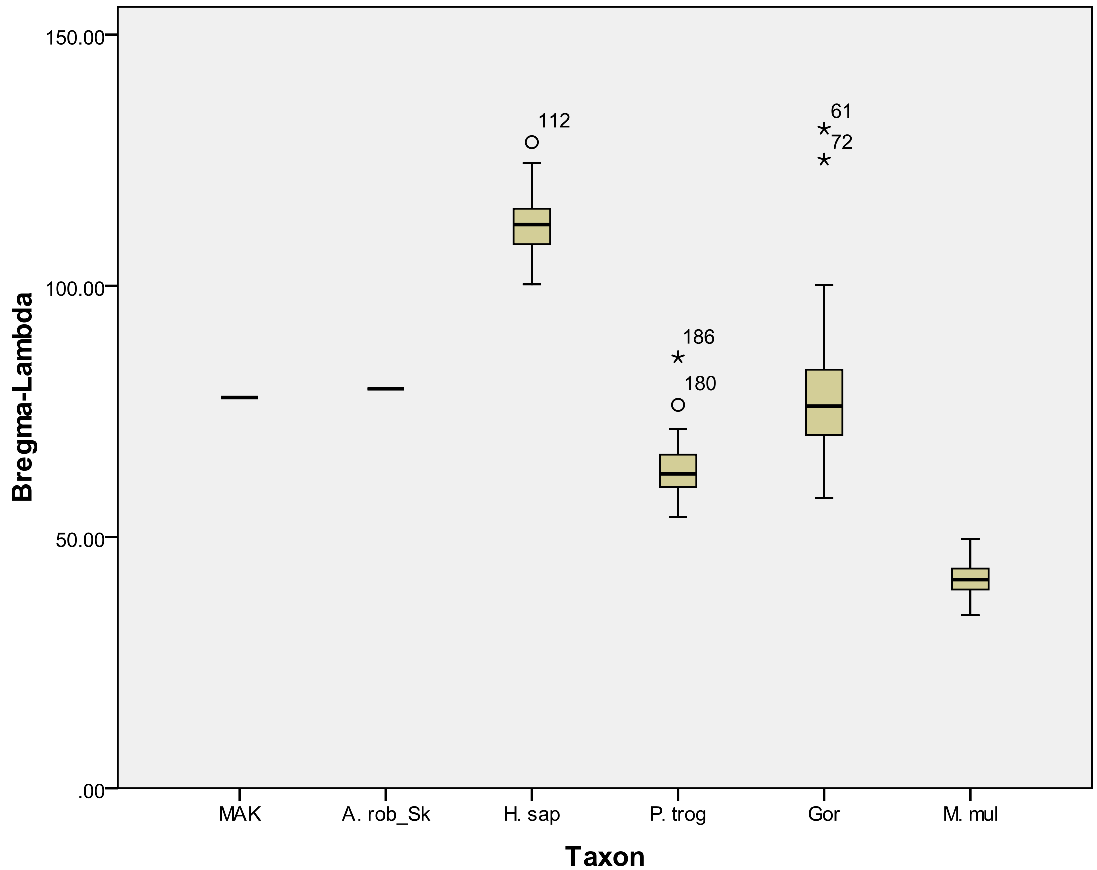


Figure 6-13: Basion-Bregma. The median (line), 1st and 3rd quartiles (box), and range (bars) of basion-bregma for MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant chimpanzee and human samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: *A. africanus* (n = 1).

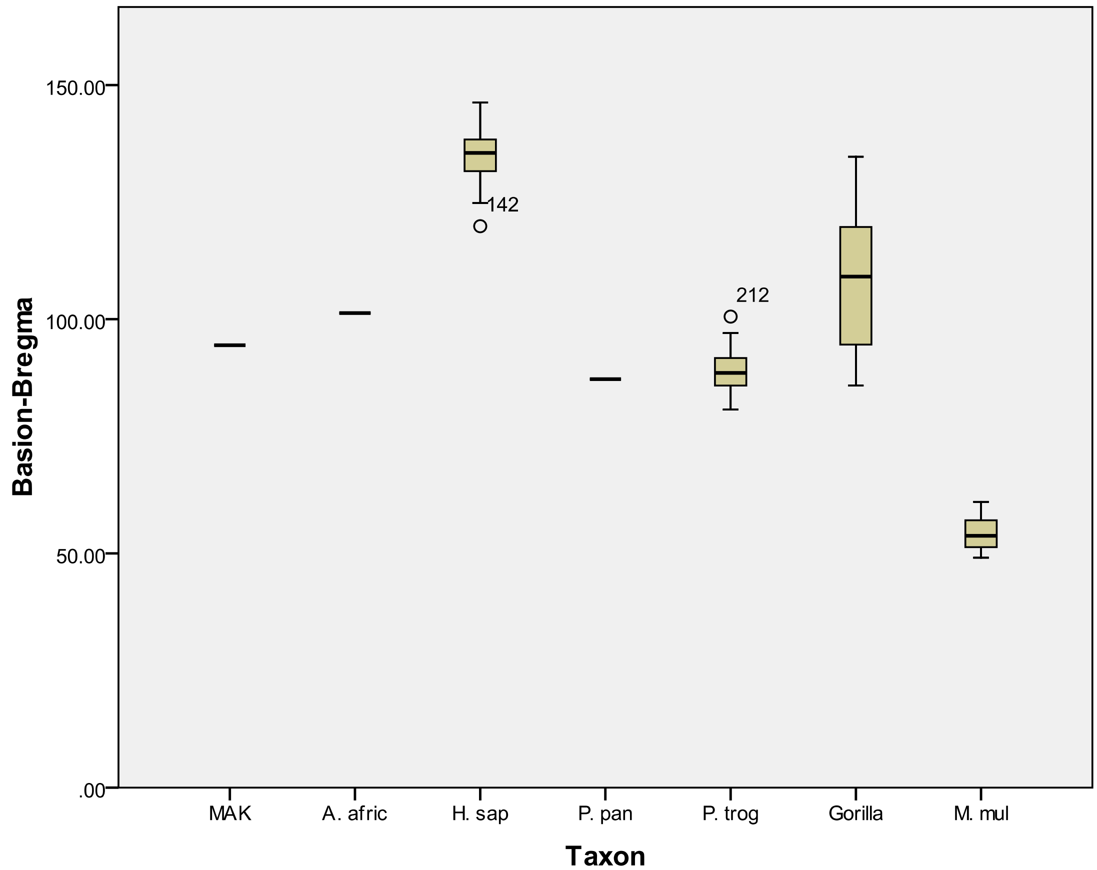
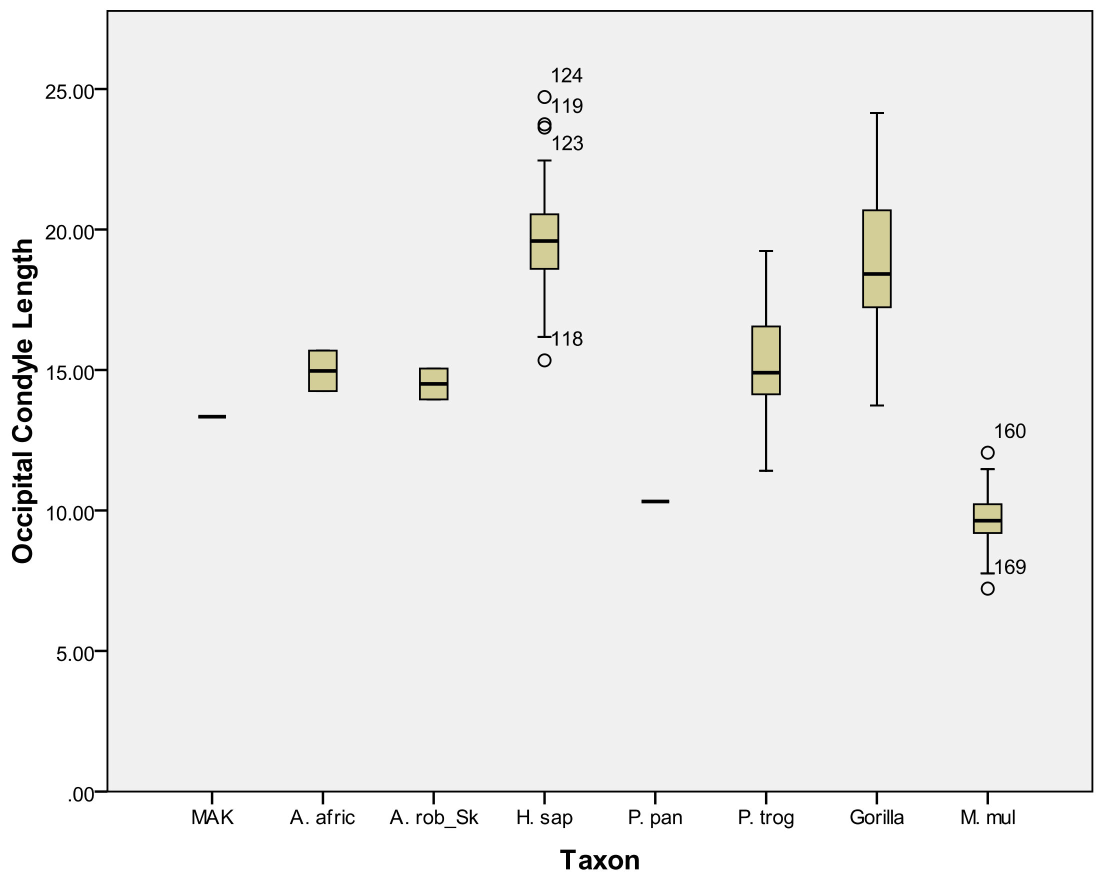


Figure 6-14: Occipital Condyle Length. The median (line), 1st and 3rd quartiles (box), and range (bars) of occipital condyle length (cfma-cfmp) for MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant human and macaque samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: *A. africanus* (n = 2) and Swartkrans *A. robustus* (n = 2).



MLD 45.

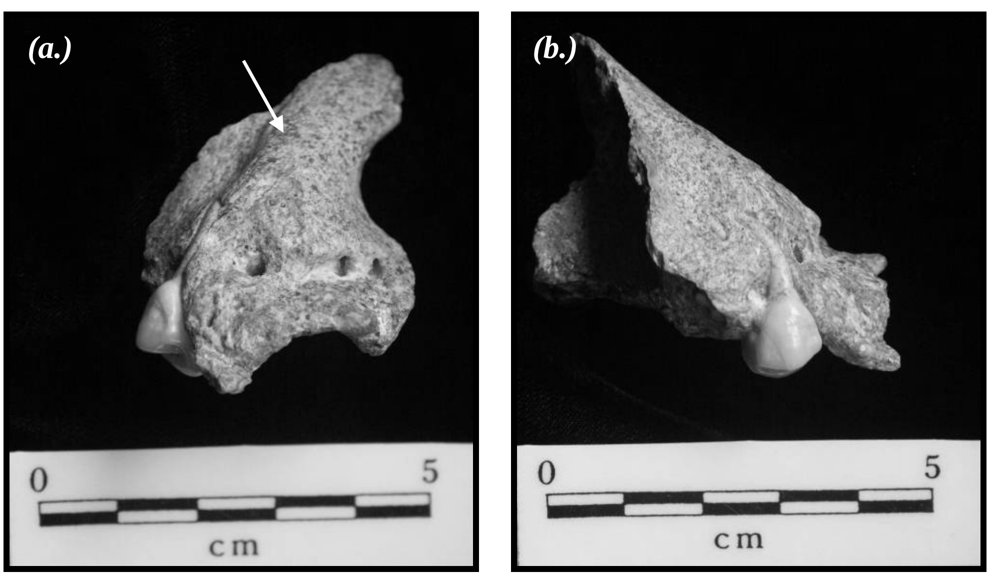
Overview. MLD 45 is an adult right maxilla with P^3, preserving portions of the maxilla around the nasal aperture and palate. With the exception of the P^3, the alveolar aspect of this specimen preserves little of morphological significance. The anterior teeth are not preserved. Portions of the mesial and lingual roots of P^4 are exposed in the maxillary sinus, no other part of the P^4 is exposed. The roots of P^3 are partially visible on the external surface of the maxilla, although it is difficult to assess whether this was the case premortem or if this appearance is an artifact of preservation.

Nasal Aperture and Palate. Although the midsagittal aspect of the maxilla is not preserved in its entirety, the nasal aperture appears somewhat narrow. The borders of the nasal aperture are blunt, as is common in specimens of *A. robustus* (McCollum *et al.*, 1993). In addition, MLD 45 exhibits the stepped nasal floor of the South African non-robust australopiths. Both a moderate anterior pillar and a weak canine fossa are present in this specimen, although the canine crown is not preserved. It is unclear externally whether any portion of a canine root is preserved. The palate appears moderately deep and exhibits the anterior shelving typical of specimens of *A. africanus* and unlike that of MLD 9/12 (see also Lockwood, 1997). The root of the zygomatic process is preserved well enough to estimate its position at approximately P^4. An equally anteriorly positioned root of the zygomatic process occurs in both South African australopith species (and MLD 9/12), but more frequently in specimens attributed to *A. robustus*. Finally, the incisive suture is incompletely closed at the anterior component (Braga, 1998).

Discussion. MLD 45 likely represents an adult at death on the basis of the size and appearance of the maxilla, partial closure of the incisive suture, and the full occlusion and minor wear of the P^3. Lockwood first described this specimen in 1997. In his original description, he provided a minimum alveolar height estimate of approximately 24 mm while cautioning that the clivus is fragmented (thus the height is likely an underestimate).

This author reaffirms Lockwood's minimum estimate of approximately 24 mm for a minimum alveolar height, which is within the range of values for specimens of both *A. africanus* and *A. robustus*. Lockwood (1999) argued that this individual represents a male on the basis of infraorbital morphology and size. Overall, MLD 45 is similar to MLD 6 and MLD 9/12 in being intermediate in morphology between specimens of the two South African australopiths. Specifically, MLD 45 exhibits the stepped nasal floor and anterior shelving of the palate that typify specimens of *A. africanus*, but the anteriorly positioned zygomatic root and blunt borders of the nasal aperture that are more common in specimens of *A. robustus*.

Figure 6-15: MLD 45. This specimen is a right maxilla with P^3 in anterior (*a*), right lateral (*b*), inferomedial (*c*), and inferior (*d*) views. Some of the major features described in the text are indicated with arrows.



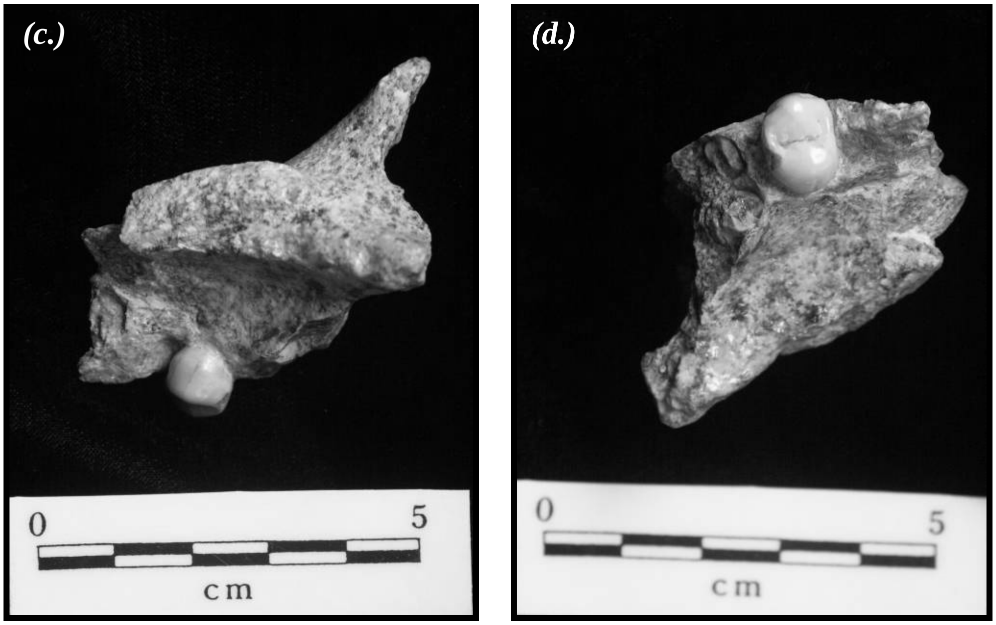
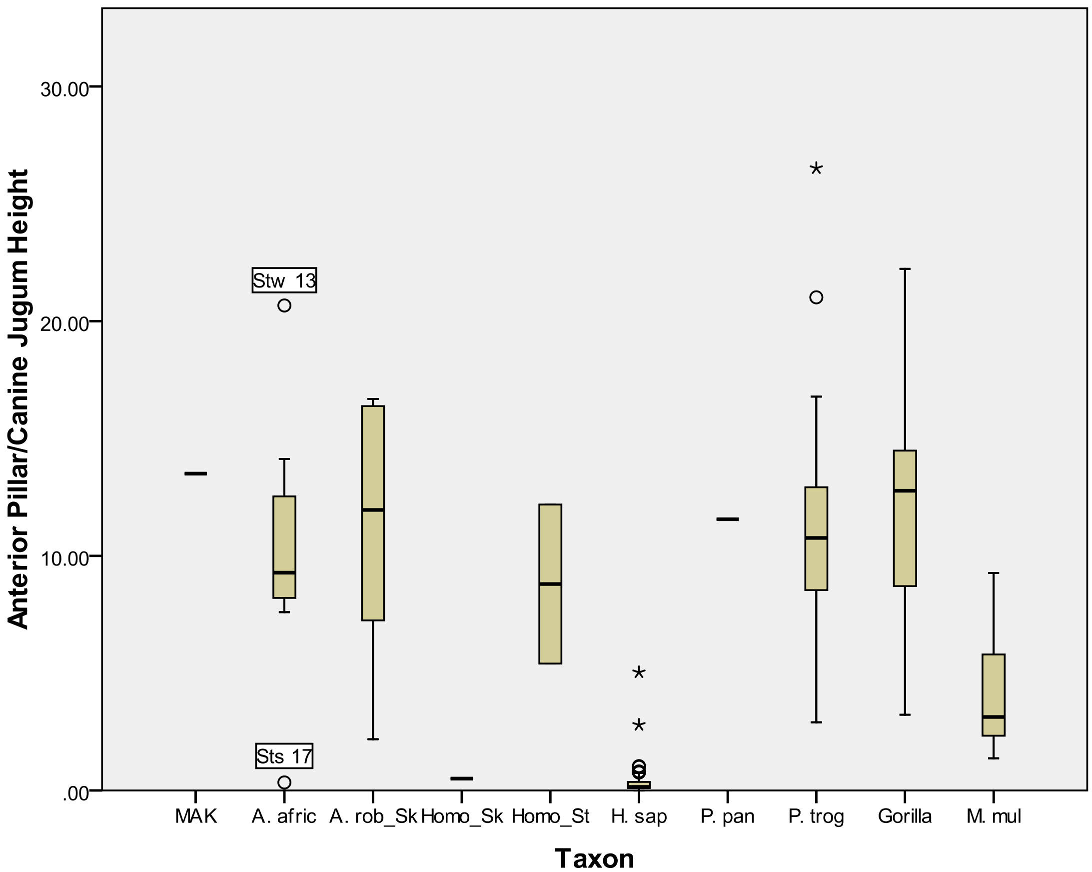

(c.)
0
5
cm
(d.)
0
5
cm

Figure 6-16: Anterior Pillar/Canine Jugum Height. The median (line), 1st and 3rd quartiles (box), and range (bars) of Anterior Pillar/Canine Jugum Height (canine root – anterior pillar superior) for MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The *A. africanus* and extant chimpanzee and human samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: *A. africanus* (n = 8), Swartkrans *A. robustus* (n = 6), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 2).



Cranial Traits. Cranial trait data indicate intraspecific variation for a variety of traits in South African australopiths (see Table 6-1). Many of these variants can be assumed to result from the coding of continuous traits as discrete character states (e.g.

shallow, intermediate, deep). Traits that were coded as intra-specifically variable include midfacial prognathism, position of the zygomatic angle, appearance of the canine fossa, interorbital width, sagittal compound temporonuchal crest, nuchal line emphasis, calvarial bone thickness, supraorbital corner, supraorbital thickness, supraorbital surface, mandibular fossa depth, tympanic form, nuchal plane form, dental arch, zygomatic temporal form, zygomatic frontal process lateral margin, frontal squama, palate depth, and palate shape. Several variables, including canine fossa appearance, nuchal line emphasis, calvarial bone thickness, nuchal plane form, and palate depth, are variable even within the small Makapansgat sample.

The Makapansgat sample is distinct from samples of both *A. africanus* and *A. robustus* from elsewhere in South Africa on the basis of its posterior calvarial contour, where the Makapansgat sample deviates from a circle. This morphology is the result of a broader petrous portion in the Makapansgat hominins. The Makapansgat sample is also distinct from specimens of *A. africanus* in infraorbital topography, although it must be cautioned that this distinction may be the result of sampling error as only a single specimen was recorded for each of these samples. Within this small cranial trait dataset, Makapansgat is more similar to *A. africanus* and can be differentiated from *A. robustus* in canine fossa appearance and calvarial bone thickness bolstering some of the descriptions presented above. The Makapansgat sample is not linked to the sample of *A. robustus* to the exclusion of *A. africanus* by these cranial trait data. However, small sample sizes and low statistical power do not permit statistical analysis of these data or conclusions to be drawn on the basis of cranial trait data alone. The tympanic form trait was excluded. The digastric notch trait does not correspond with this feature in other analyses (e.g. Kimbel *et al*., 2004), which reflects differences in the identification of its character states.

TABLE 6-1: Cranial Traits

Trait	Mak n / %	A. afric n / %	A. rob n / %	Fossil Homo n / %
Post calvarial cont				
0	0 / 0	3 / 100	1 / 100	0 / 0
1	2 / 100	0 / 0	0 / 0	0 / 0
2	0 / 0	0 / 0	0 / 0	0 / 0
Midfacial prog				
0	0 / 0	1 / 8	0 / 0	0 / 0
1	0 / 0	10 / 83	1 / 17	0 / 0
2	1 / 100	1 / 8	5 / 83	0 / 0
Pos zyg angle				
0	0/ 0	0 / 0	2 / 67	0 / 0
1	0 / 0	2 / 100	1 / 33	0 / 0
2	0 / 0	0 / 0	0 / 0	0 / 0
Squam suture shape				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	3 / 100	2 / 100	3 / 100	0 / 0
Rel ht squam				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	1 / 100	0 / 0	0 / 0
2	0 / 0	0 / 0	0 / 0	0 / 0
Infraorbital plate orientation				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	1 / 100	0 / 0	0 / 0
2	0 / 0	0 / 0	0 / 0	0 / 0
Infraorbital topography				
0	1 / 100	0 / 0	0 / 0	0 / 0
1	0 / 0	1 / 100	0 / 0	0 / 0
2	0 / 0	0 / 0	0 / 0	0 / 0
Canine fossa				
0	2 / 67	4 / 33	0 / 0	0 / 0

1	1 / 33	3 / 25	4 / 44	0 / 0
2	0 / 0	5 / 42	3 / 33	0 / 0
3	0 / 0	0 / 0	2 / 22	0 / 0
Subnasal contour				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	3 / 100	11 / 100	8 / 100	1 / 100
2	0 / 0	0 / 0	0 / 0	0 / 0
Interorbital width				
0	0 / 0	2 / 50	1 / 50	0 / 0
1	1 / 100	2 / 50	1 / 50	0 / 0
Sag compound temporonuch crest				
0	0 / 0	3 / 43	0 / 0	1 / 100
1	3 / 100	2 / 29	1 / 100	0 / 0
2	0 / 0	2 / 29	0 / 0	0 / 0
Nuchal line emph				
0	1 / 50	2 / 40	0 / 0	0 / 0
1	1 / 50	3 / 60	1 / 100	1 / 100
Calvarial bone thickness				
0	1 / 25	1 / 14	0 / 0	0 / 0
1	3 / 75	5 / 71	4 / 100	1 / 100
2	0 / 0	1 / 14	0 / 0	0 / 0
Supraorbital corn				
0	0 / 0	2 / 50	1 / 50	0 / 0
1	0 / 0	2 / 50	1 / 50	1 / 100
Supraorbital thick				
0	0 / 0	2 / 50	2 / 100	1 / 100
1	0 / 0	2 / 50	0 / 0	0 / 0
Post temp sq				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	2 / 100	2 / 100	1 / 100	0 / 0
Dig notch				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	2 / 100	3 / 100	1 / 100	1 / 100
Mandib fossa depth				
0	0 / 0	1 / 20	0 / 0	0 / 0
1	1 / 100	2 / 40	1 / 33	0 / 0
2	0 / 0	2 / 40	2 / 67	0 / 0

Vaginal process				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	1 / 100	0 / 0	0 / 0
Nuchal plane form				
0	1 / 50	1 / 25	0 / 0	0 / 0
1	1 / 50	3 / 75	0 / 0	0 / 0
Dental arch				
0	0 / 0	1 / 8	0 / 0	1 / 100
1	0 / 0	3 / 25	1 / 10	0 / 0
2	1 / 100	8 / 67	9 / 90	0 / 0
Zygo temp form				
0	1 / 100	1 / 33	3 / 100	0 / 0
1	0 / 0	2 / 67	0 / 0	0 / 0
Zygo fro proc lat				
0	0 / 0	0 / 0	1 / 50	0 / 0
1	0 / 0	2 / 100	1 / 50	0 / 0
Front sq				
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	3 / 100	1 / 33	0 / 0
2	0 / 0	0 / 0	2 / 67	0 / 0
Palate depth				
0	0 / 0	0 / 0	3 / 25	0 / 0
1	4 / 67	7 / 58	4 / 33	1 / 100
2	2 / 33	5 / 42	5 / 42	0 / 0
Palate shape				
0	0 / 0	3 / 25	0 / 0	1 / 50
1	2 / 100	9 / 75	11 / 100	1 / 50
2	0 / 0	0 / 0	0 / 0	0 / 0

Cranial Landmark Data. The small sample sizes for both the Makapansgat and comparative australopith samples limited statistical analyses.

A few comparisons of cranial dimensions permitted examination of multiple specimens from Makapansgat to South African australopith species samples. While bregma-pterion and bregma-asterion are highly correlated ($r^2 = 0.9$), they are both presented because these regions are preserved for different specimens (see Figures 6-17 and 6-18). For the dimension bregma-pterion, the Makapansgat median falls within the low end of the confidence interval for the sample of *A. africanus* but is not preserved in specimens of *A. robustus*. The similar dimension bregma-asterion was recorded for only one specimen of both *A. robustus* and *A. africanus* and the Makapansgat specimens MLD 3 and MLD 37/38 fall between the preserved species values. These dimensions of the neurocranium are unlikely to contribute much to distinguishing among South African australopiths beyond estimates of cranial capacity and the South African australopiths are known to overlap even in this characteristic.

The dimension inion-opisthion is preserved in MLD 1 and MLD 37/38 and reflects both cranial base length and nuchal line positioning (see Figure 6-19). The Makapansgat range falls entirely within that of the specimens attributed to *A. africanus* from Sterkfontein and overlaps with the lower end of the range for specimens attributed to *A. robustus*.

Figure 6-17: Bregma – Pterion. The median (line), 1st and 3rd quartiles (box), and range (bars) of bregma - pterion for MLD 3 and MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant chimpanzee and human samples display outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis is: *A. africanus* (n = 2).

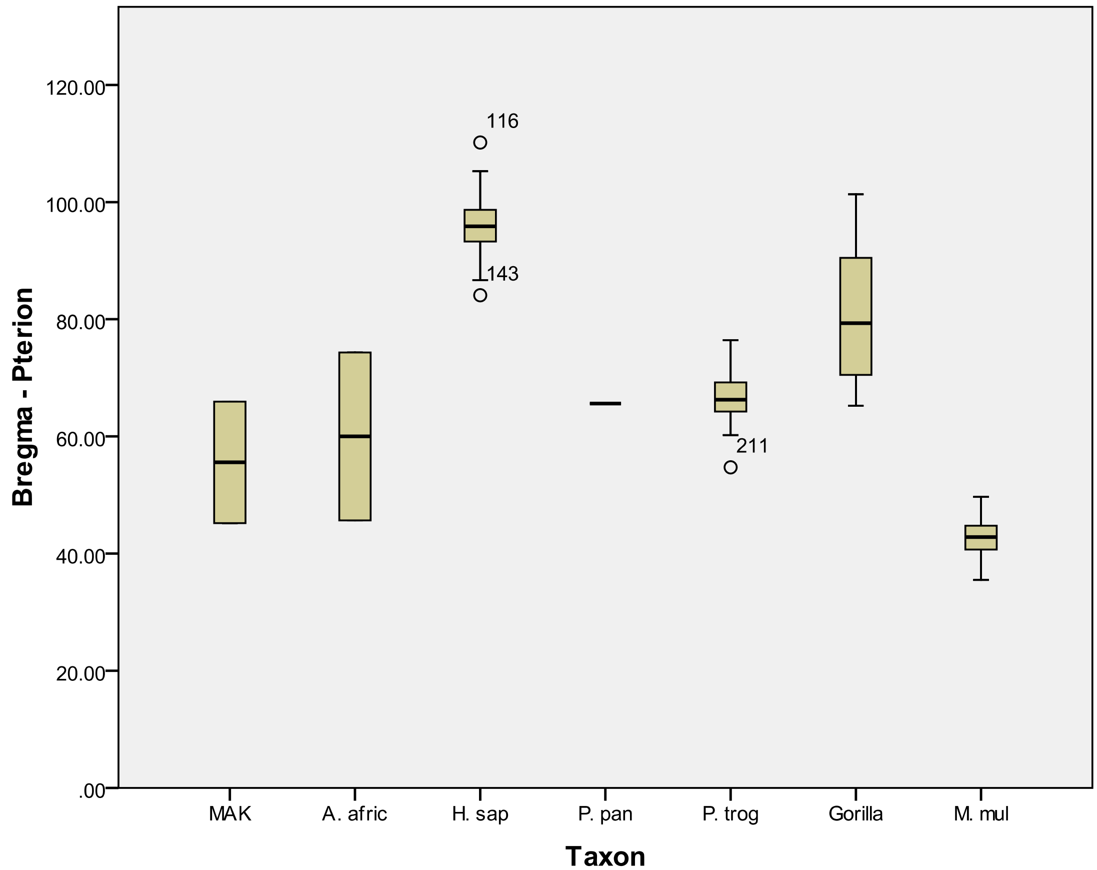


Figure 6-18: Bregma – Asterion. The median (line), 1st and 3rd quartiles (box), and range (bars) of the external symphyseal height (linguale-gnathion) for MLD 3 and MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant human sample displays outliers (the numbers identify the specific individuals). The fossil sample sizes for this analysis are: *A. africanus* (n = 1) and Swartkrans *A. robustus* (n = 1).

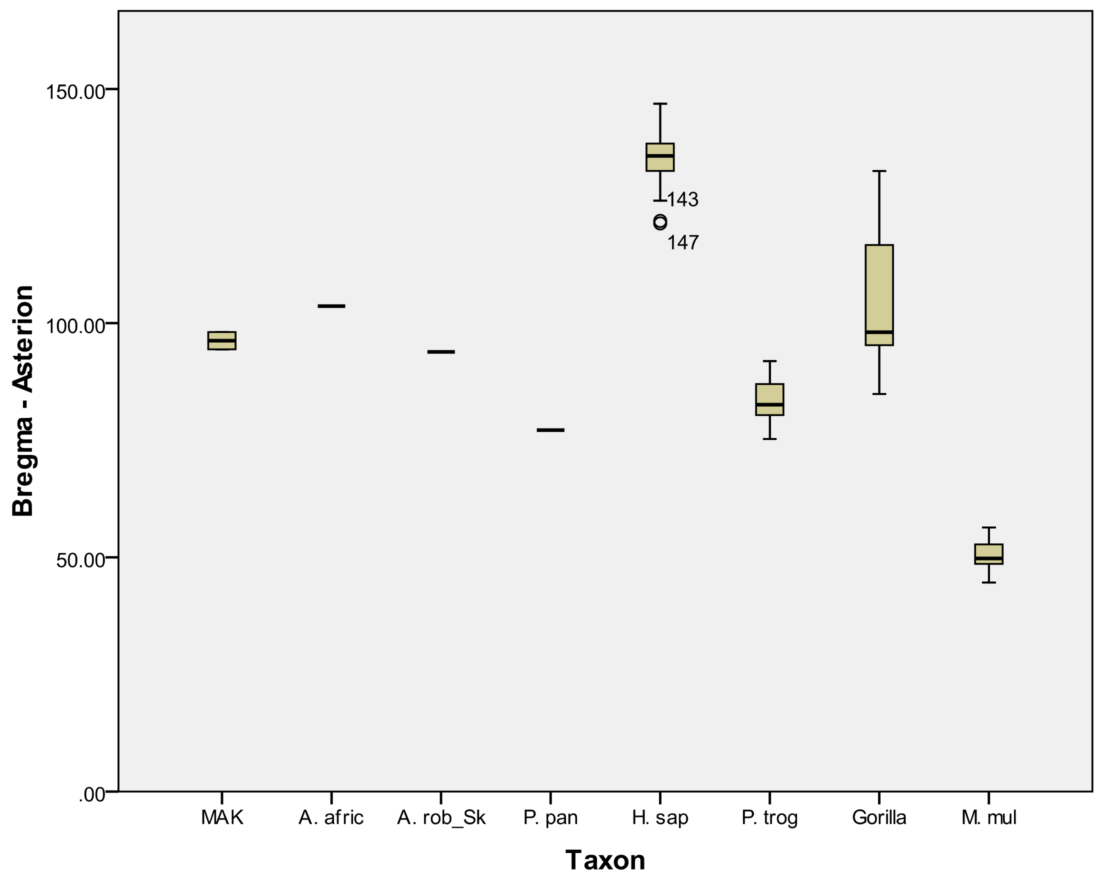
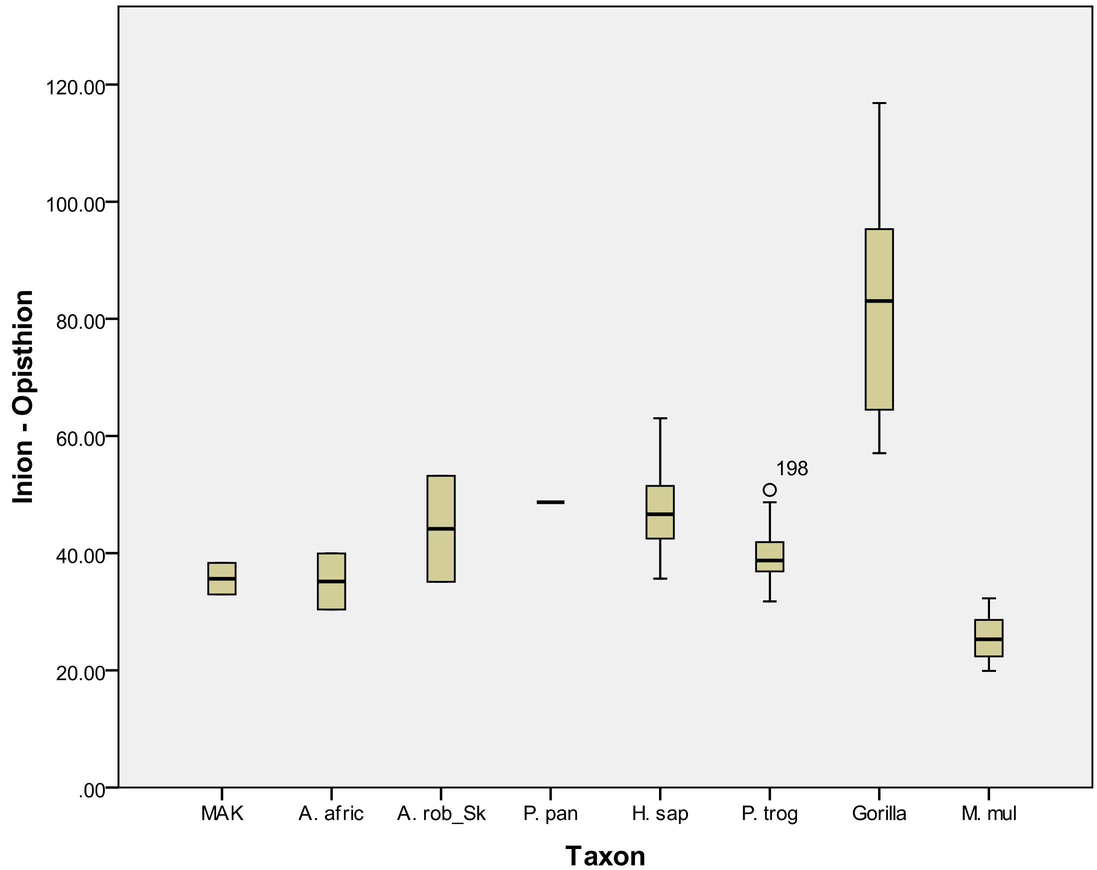


Figure 6-19: Inion – Opisthion. The median (line), 1st and 3rd quartiles (box), and range (bars) of inion – opisthion for MLD 1 and MLD 37/38 in comparison to South African australopiths and a sample of extant primates. The extant chimpanzee sample displays an outlier (the number identifies the specific individual). The fossil sample sizes for this analysis are: *A. africanus* (n = 2) and Swartkrans *A. robustus* (n = 2).



Non-parametric analyses were not analyzed for the cranial variables simply because extremely small sample sizes do not permit sufficient statistical power. Multivariate analyses were executed on extant and fossil cranial specimens because they provide a powerful means of assessing a small sample within the context of much larger fossil samples. Discriminant function analysis was executed as a means to deal with missing data (see discussion in Methods). Variables were selected by those reflecting overall dimensions of the skull and on the basis of preservation within the Makapansgat sample. Multivariate analysis permits assessment of grouping of results.

A DFA of a series of neurocranial variables was executed for all taxa and discriminated both extant humans and macaques from all other taxa (see Figure 6-20 and Tables 6-2 and 6-3). The extant specimens were predicted correctly in virtually every case (chimps and gorillas were occasionally placed in the wrong taxon due to their overlap in morphology). The Makapansgat and Sterkfontein australopiths were as frequently attributed to *P. troglodytes* as to *A. africanus*. In addition, no robust australopiths preserved enough variables to be included in this analysis. Unfortunately, this analysis provided little explanatory value with regard to the fossil samples.

A DFA of a series of cranial variables of the subnasal region was computed for all comparative and fossil taxa (see Figure 6-21 and Tables 6-4 and 6-5). The discrimination and prediction of extant humans and macaques was excellent. The distribution of chimps and gorillas are essentially entirely overlapping and hindered predictions for these taxa. The South African australopiths were essentially indistinguishable from chimps and gorillas and a large number of fossils were incorrectly predicted. MLD 9 stands out as being more extant humanlike in its subnasal morphology.

Figure 6-20: DFA of Cranial Variables. Variables include bregma-pterion, bregma-asterion, pterion-asterion, and nasospinale-prosthion, where DF 1 explains 77% and DF 2 explains 21% of the variance in these data.

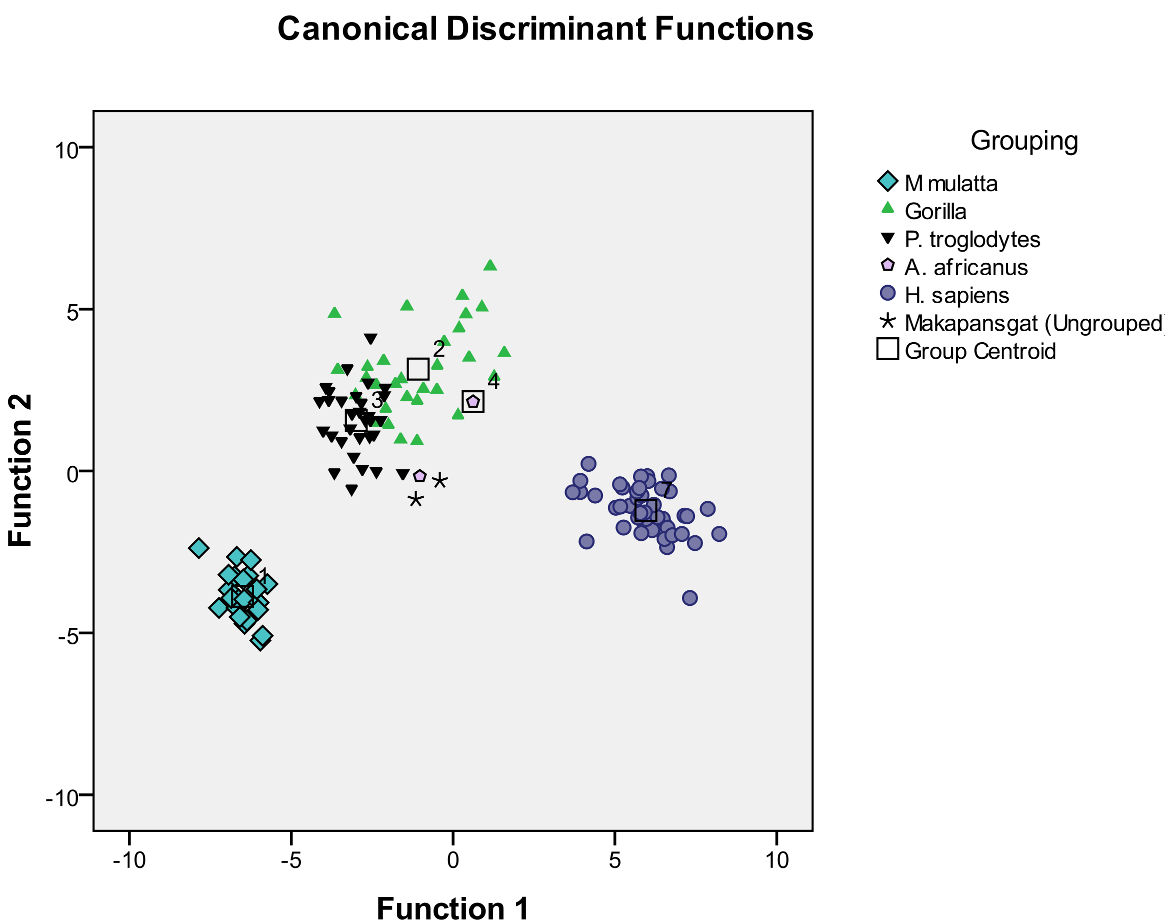


TABLE 6-2: Pooled Within Group Correlations for DFA of Cranial Variables. Variables include bregma-pterion, bregma-asterion, pterion-asterion, and nasospinale-prosthion, where DF 1 explains 77% and DF 2 explains 21% of the variance in these data.

Variable	DF 1	DF 2
Bregma - Asterion	0.870	0.340
Nasospinale - Prosthion	-0.018	0.935
Pterion - Asterion	0.340	0.551
Bregma – Pterion	0.573	0.332

TABLE 6-3: Classification Matrix for DFA of Cranial Variables. Variables include bregma-pterion, bregma-asterion, pterion-asterion, and nasospinale-prosthion, where DF 1 explains 77% and DF 2 explains 21% of the variance in these data. Only data for fossil specimens are presented.

Specimen Number	# of Missing Values	Actual Group	1st Predicted Group	*p*	2nd Predicted Group	*p*
MLD 3	0	Ungrouped	*A. africanus*	0.00	*P. troglodytes*	0.45
MLD 37/38	1	Ungrouped	*P. troglodytes*	0.01	*A. africanus*	0.25
Sts 71	2	*A. africanus*	*P. troglodytes*	0.00	*A. africanus*	0.27
StW 505	0	*A. africanus*	*A. africanus*	1.00	*P. troglodytes*	0.00

Figure 6-21: DFA of Subnasal Variables. DFA of cranial variables of the subnasal region: subnasale-prosthion, anterior nasal spine – nasospinale, anterior nasal spine – alveolare, anterior nasal spine – prosthion, where DF 1 accounts for 88% and DF 2 10% of the variance in these data.

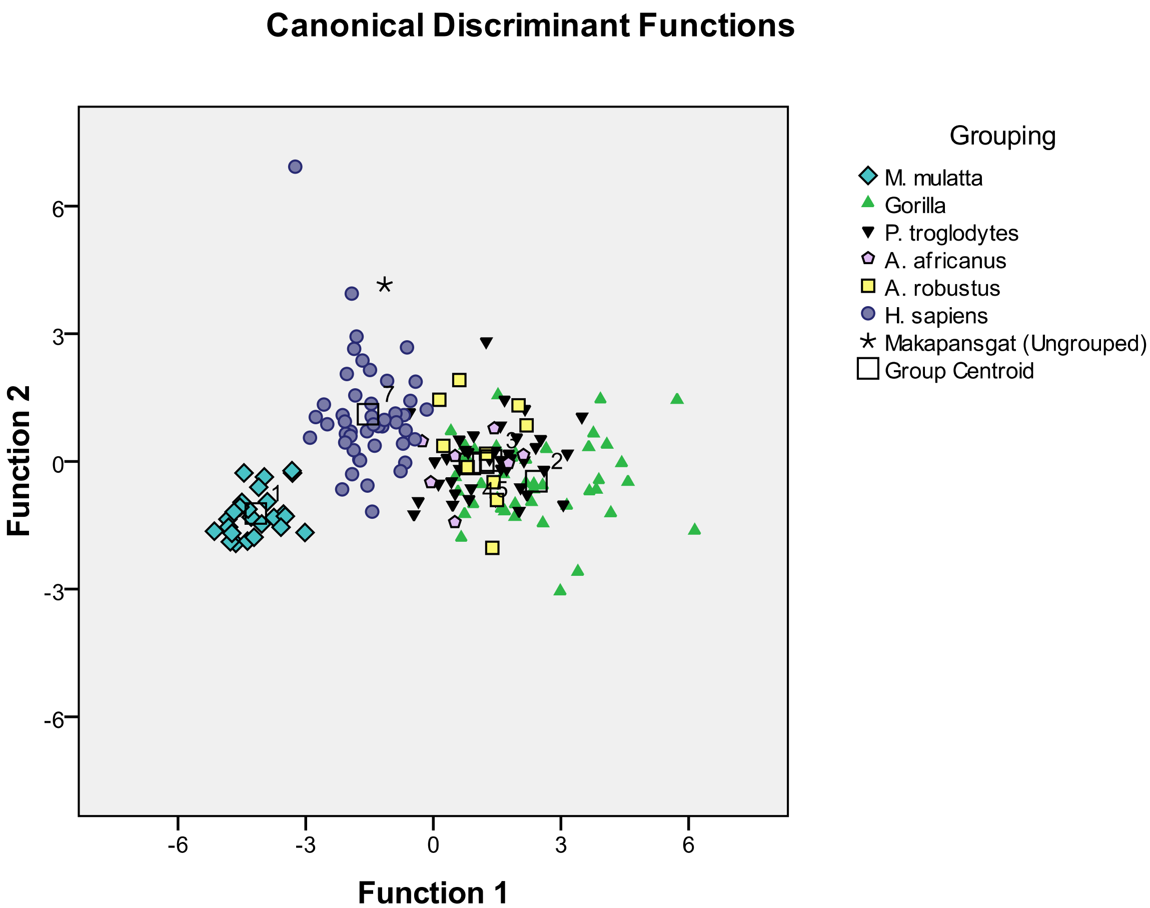


TABLE 6-4: Pooled Within Group Correlations for DFA of Cranial Variables. Variables include bregma-pterion, bregma-asterion, pterion-asterion, and nasospinale-prosthion, where DF 1 explains 88% and DF 2 explains 10% of the variance in these data.

Variable	DF 1	DF 2
Subnasale - Prosthion	0.959	0.236
Anterior nasal spine – Prosthion	0.946	-0.181
Anterior nasal spine – Alveolare	0.925	0.017

Anterior nasal spine – Nasospinale	0.222	-0.068

TABLE 6-5: Classification Matrix for DFA of Cranial Variables. Variables include bregma-pterion, bregma-asterion, pterion-asterion, and nasospinale-prosthion, where DF 1 explains 88% and DF 2 explains 10% of the variance in these data. Only data for fossil specimens are presented.

Specimen Number	# of Missing Values	Actual Group	1st Predicted Group	*p*	2nd Predicted Group	*p*
MLD 9	0	Ungrouped	*H. sapiens*	0.03	*A. robustus*	0.01
SK 11	1	*A. robustus*	*A. africanus*	0.00	*A. robustus*	0.03
SK 12	2	*A. robustus*	*H. sapiens*	0.00	*A. robustus*	0.25
SK 13/14	0	*A. robustus*	*P. troglodytes*	0.98	*A. africanus*	0.31
SK 46	0	*A. robustus*	*A. robustus*	0.98	*P. troglodytes*	0.23
SK 48	0	*A. robustus*	*A. robustus*	0.93	*P. troglodytes*	0.27
SK 79	0	*A. robustus*	*P. troglodytes*	0.79	*A. robustus*	0.25
SK 83a,b	0	*A. robustus*	*A. robustus*	0.32	*H. sapiens*	0.22
SKW 11	0	*A. robustus*	*Gorilla*	0.26	*A. robustus*	0.28
SK 52/SKW 18	0	*A. robustus*	*A. robustus*	0.99	*P. troglodytes*	0.29
SKX 265	0	*A. robustus*	*A. africanus*	0.93	*P. troglodytes*	0.29
Sts 5	0	*A. africanus*	*P. troglodytes*	0.95	*A. africanus*	0.28
Sts 52	0	*A. africanus*	*P. troglodytes*	0.95	*A. africanus*	0.31
Sts 71	0	*A. africanus*	*A. africanus*	0.83	*A. robustus*	0.32
StW 13	0	*A. africanus*	*P. troglodytes*	0.93	*A. robustus*	0.25
StW 498	0	*A. africanus*	*A. africanus*	0.17	*P. troglodytes*	0.09
StW 73	0	*A. africanus*	*A. africanus*	0.79	*P. troglodytes*	0.26
Sts 53	0	*A. africanus*	*H. sapiens*	0.66	*A. robustus*	0.24

Morphology of the Makapansgat Cranial Sample. The Makapansgat sample provides some general characteristics of the cranium. These features are discussed by individual specimen above and by region in the next few pages. Unfortunately, few regions and even fewer dimensions of the cranium are preserved in multiple individuals at Makapansgat. This paucity of overlapping regions limits many analyses and firm conclusions from being drawn from the cranial sample alone.

Facial Morphology. The facial morphology of *A. africanus* and *A. robustus* has been the focus of a number of in-depth treatments, most notably by Rak (1983) and Lockwood (1997, 1999; Lockwood *et al*., 2007). In his seminal work, Rak (1983) defined a number of features variably present in the face of *A. africanus*, including the anterior pillar, maxillary furrow, concave transverse facial cross-section, zygomatic prominence, zygomatic frontal process that is widest inferiorly, flat nasoalveolar clivus, and infraorbital region that meets the alveolar plane at an obtuse angle. In another study (Lockwood *et al*., 2007), craniofacial specimens of *A. robustus* males were argued to be larger in older aged adults as well as to display better developed anterior pillars and maxillary trigons, while females were argued to reach full skeletal growth by adulthood.

One of the earliest comparative analyses suggested that facial prognathism is greater in specimens attributed to *A. africanus* than *A. robustus* (Robinson, 1956), although a generic separation on this basis was explicitly discouraged. Variation in facial prognathism within the hypodigm of *A. africanus* has been presumed to be the result of sexual dimorphism, where males are considered to be more prognathic (e.g. Schultz, 1962; Wood, 1976; Kimbel *et al.*, 1984). As originally discussed by Dart (1948a), MLD 6 exhibits less maxillary prognathism than Sts 5. This is also true for MLD 9/12, both of which exhibit a level of maxillary prognathism more common in specimens of *A. robustus*.

The maxillary furrow and anterior pillar, together, have been considered to be characteristic of the hypodigm of *A. africanus* (Rak, 1983; Kimbel and Rak, 1993). Their collective presence in the Makapansgat cranial sample (MLD 6 and MLD 9/12) supports an affinity with the hypodigm of *A. africanus*. The MLD 45 specimen, however, exhibits an anterior pillar and a canine fossa (a less demarcated depression of this region than a maxillary furrow). In addition, McKee (1989) pointed out that these features are variable in both presence and morphological appearance within the sample of *A. africanus*. In many ways, the differentiation of an anterior pillar has been treated uniquely by a number of authors. Certainly the anterior pillar has been indicated as present for both South African australopith hypodigms (e.g. McKee, 1989; Tobias, 1991; Skelton and McHenry, 1992; pers. obs.). The anterior pillar has even been identified as weakly present in specimens attributed to *H. habilis*, most notably OH 24 (McKee, 1989; Tobias, 1991). However, Tobias (1991) pointed out that the appearance of the anterior pillar in OH 24 (and StW 53) is distinct from its appearance in specimens of *A. africanus*, because the latter specimens exhibit a flatter maxilla adjacent to the nasal aperture. These authors argued based on variation of the anterior pillar, that this character should not be included in character lists discriminating early hominin species (McKee, 1989; Tobias, 1991).

McCollum and colleagues (1993) suggest that a rounded lateral margin of the nasal aperture may better discriminate the subtle differences in infraorbital morphology (although even these authors caution this may be an oversimplification). The hypodigm of *A. africanus* is well known to have the greatest frequency of anterior pillars, when compared to both *A. robustus* and *H. habilis* (e.g. Rak, 1983; Kimbel and Rak, 1993).

Lockwood (1997), however, pointed out that subtle features of the anterior pillar in relation to the nasal aperture and overall appearance of the infraorbital region just lateral to the anterior pillar better discriminate between the South African hominin species than the anterior pillar alone.

Rak (1983) first suggested that the anterior pillar developed in relation to premolar expansion, molarization, which he posited was selected for as a result of feeding behaviors during human evolution. He contended that australopiths developed a series of morphological characters that worked in concert to reduce stresses during premolar loading. These features include the presence of an anterior pillar, flattened nasoalveolar clivus, and an anteriorly positioned root of the zygomatic process (Rak, 1983). In addition, authors put forward potential hominin feeding behaviors that might have resulted in strong selection for premolar loading (and premolar molarization). Two of the most prominent scenarios were that premolar loading evolved as a result of selective forces due to a diet of small, hard seed-like objects (Jolly, 1970) or for distributing large quantities of food across the dentition (Walker, 1981).

It appears likely that despite previous assertions, premolar loading rather than canine size is a determinant of anterior pillar prominence. The premolar loading hypothesis was recently tested using finite element analysis of simulated bite forces (Strait *et al.*, 2009). These authors found that when compared with macaques, the craniofacial morphology of a reconstruction of *A. africanus* (based upon Sts 5 and Sts 52) was heavily affected by forces transmitted during chewing [although an excellent critical review of this study by Grine and colleagues (2010) casts some doubt on these interpretations]. Their assessment of premolar loading in macaques and South African *A. africanus* suggests that the craniofacial morphology of *A. africanus* may have been biomechanically selected to resist premolar loads. Additional support for Rak's (1983) hypothesis included the assessment of Strait and colleagues (2009) that the absence of anterior pillars in their reconstructed cranium of *A. africanus* would likely increase strains, particularly shear, during feeding.

On the basis of sample size and preservation issues, it is difficult to directly compare many regions of the Makapansgat australopith face to those of specimens of *A. africanus* from Sterkfontein. Even so, the facial morphology of the Makapansgat hominins can be described as somewhat *A. africanus*-like in many features. However, the Makapansgat sample (as a group) is distinct from the sample of *A. africanus* from Sterkfontein in some features. Most notably, the position of the zygomatic process is more anteriorly positioned in the Makapansgat sample than is typically the case for the Sterkfontein sample. The position of the zygomatic process in the MLD 6, MLD 9/12, and MLD 45 specimens is somewhat intermediate for the current samples of *A. africanus* and *A. robustus* (varying between P^4 and P^3/P^4). The Makapansgat sample is more anteriorly positioned than typical for specimens of *A. africanus* and more posteriorly positioned than typical for specimens of *A. robustus*.

The MLD 6 specimen is the only Makapansgat specimen to preserve a portion of the area with regard to a central facial hollow, considered a derived condition of *A. robustus* (Rak, 1983). In this feature MLD 6, again, exhibits an intermediate morphology between specimens of *A. africanus* and *A. robustus* (Lockwood, 1997). The infraorbital region does not contribute much to this discussion as one specimen (MLD 45) is most similar to specimens of *A. africanus*, while other specimens (MLD 6 and MLD 9/12) fit comfortably within the range of variation for either species (Lockwood, 1997). In addition, on the basis of size, Lockwood (1997) pointed out that the overall facial variation at Makapansgat is similar in magnitude to that exhibited by the sample of *A. africanus* from Sterkfontein, whereby the MLD 6 specimen appears to be the smallest specimen from Makapansgat and the MLD 45 specimen seems to be the largest. Lockwood, in his classic evaluation of the craniofacial morphology of the hypodigm of *A. africanus*, stated that "craniofacial morphology lends some support to removing the Makapansgat hominin material from *A. africanus* and replacing it in *A. prometheus* as it was classified by Dart" (1997: 293). However, it seems possible with the latest dates for the Makapansgat sample that the morphological distinctions in facial morphology between the Sterkfontein and Makapansgat specimens could relate to temporal variation in an evolving species.

Neurocranium. The neurocranial features of the Makapansgat hominins are somewhat unexceptional. They generally appear similar to non-"robust" australopiths. The position of the temporal lines is variable, but there is no evidence of the presence of a sagittal crest in any of the Makapansgat specimens (*contra* Robinson, 1954b; Wolpoff, 1974). A compound temporonuchal crest is not present in any of the specimens. On the basis of the gracile features of the neurocranium, the Makapansgat hominins appear more similar to specimens of *A. africanus*.

Basicranium. Australopith specimens from Sterkfontein and Makapansgat are considered to be similar in their basicranial morphology, whereby both samples are generally regarded as ancestral (Tobias, 1967, 1991; Clarke, 1977; Dean and Wood, 1982; Spoor, 1993). Regardless of its primitive morphology, the basicranium of the hypodigm of *A. africanus* is considered to vary greatly (Kimbel and White, 1988). MLD 37/38, however, presents an exception to its essentially primitive basicranium. In particular, its petrous axis is considered to be less sagittally oriented than the few specimens available at Sterkfontein (Dean and Wood, 1982; Tobias, 1967, 1991). Moreover, the MLD 37/38 glenoid has been considered morphologically intermediate between the primitive morphology of *A. africanus* and the more derived morphology of *A. robustus*. The glenoid of specimens of *A. africanus* are quite variable, most notably the tympanic plate ranges from the shallow and tubular tympanic of *A. afarensis* to the derived and vertical tympanic of Sts 19 (Kimbel and White, 1988).

Hominins have long been known to exhibit a high degree of basicranial flexion. This is the case for the MLD 37/38 specimen as well as a number of Sterkfontein specimens, but South African robust australopiths have been considered to exhibit even more marked basicranial flexion than specimens of *A. africanus* (e.g. Holloway, 1988). However, it has been well established that basicranial flexion is positively correlated with relative brain size in primates (e.g. Gould, 1977; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997b; Strait and Ross, 1999; Ross *et al.*, 2004). Brain size has been found to better predict basicranial flexion than even head and neck posture (Strait and Ross, 1999). Upon visual assessment, the degree of basicranial flexion in Sts 5 appears less than that of modern humans (Broom *et al.*, 1950; Le Gros Clark, 1967; Laitman *et al.*, 1979; Dean, 1986). Despite this, some researchers argue that Sts 5 has the amount of basicranial flexion expected within the Order Primates, and modern humans are less flexed than expected (Ross and Henneberg, 1995), while others question whether differences in the degree of basicranial flexion between Sts 5 and modern humans are significant (e.g. Ross and Henneberg, 1995; Spoor, 1997b). Regardless, recent research has indicated that modern humans have a less flexed basicranium than predicted on the basis of relative brain size across primates (Ross *et al*; 2004).

Although their ranges overlap, the reconstructed cranial capacity of specimens of *A. robustus* [476 cc for SK 1585 (Falk *et al.*, 2000), 500cc for SK 5 (Beals *et al.*, 1984), and a debatable 650 cc for KB (Tobias, 1971)] tend to be greater than those reconstructed for specimens attributed to *A. africanus* [515 cc for StW 505 (Conroy *et al.*, 1998), 436 cc for Sts 19 (Holloway, 1975), 428 cc for Sts 71 and Sts 60 (Holloway, 1975), and 485 cc for Sts 5 (Holloway, 1975)]. The relationship between brain size and basicranial flexion could account for the greater basicranial flexion of a larger-brained robust australopith. However, there is evidence that the basicranium and brain are morphologically integrated (e.g. Moss and Young, 1960; Enlow, 1968; Cheverud, 1982; Sperber, 1989; Enlow and Hans, 1996; Lieberman *et al.*, 2000), and that basicranial morphology (specifically maximum breadth) impacts cranial proportions and facial shape due to its effect on the developing brain (Lieberman *et al.*, 2000). Regardless, it is unlikely that the integration of the basicranium and brain can account for all of the differences in the face of the South African australopith species.

Cranial Vault Thickness. The thickness of the Makapansgat MLD 1, MLD 3, MLD 10, and MLD 37/38 cranial vaults are presented in the descriptions above; however, these specimens do not appear to provide any diagnostic characteristics as a group. Although statistical analyses on cranial vault thickness were not executed here, the cranial vault thicknesses of a sample of fifteen specimens attributed to *A. africanus* were found to exhibit a similar patterning to that of modern *Homo sapiens* based upon allometric study of catarrhine primate cranial vault thicknesses (Gauld, 1996). The sample of *A. africanus* analyzed in this study included the MLD 1 specimen, for which only maximum occipital thickness was recorded. The MLD 1 specimen exhibited the thickest occiput of all the specimens included in the sample of *A. africanus*. In fact, it was so thick that the values for MLD 1 fall within the occipital thickness values reported for *Homo erectus* (Gauld, 1996:413).

Summary

The Makapansgat early hominin cranial sample is represented by 10 specimens of varying age, size, and morphology. Cranial specimens from Makapansgat exhibit features aligning them with both *A. africanus* and *A. robustus*, although many of these features are variable within the current hypodigms of *A. africanus* and *A. robustus*. In several features, however, the Makapansgat hominin cranial specimens appear intermediate or distinct.

MANDIBULAR DESCRIPTIONS AND RESULTS

Mandibles

Descriptions. The Makapansgat mandibles include 10 specimens, ranging in age from the nearly adolescent MLD 2 specimen to several adult mandibles exhibiting significant dental attrition (most notably MLD 22 and MLD 27). The Makapansgat mandibles exhibit variable preservation and morphology. All of these specimens are generally included in the hypodigm of *A. africanus*, although the MLD 2 mandible has been considered so robust that it has been attributed to the hypodigm of *A. robustus* (Aguirre, 1970). Unlike the Makapansgat crania, and excluding Dart's descriptions of MLD 2, MLD 18, and MLD 40, the Makapansgat australopith mandibular specimens have not been described in great morphological detail (1954a, b; 1962a). This chapter was written to attempt to rectify this lack of descriptive detail surrounding the majority of the Makapansgat mandibles and presents preliminary morphological analyses.

Estimates of age at death are given for each specimen. As previously discussed, many of the earlier age estimates for the Makapansgat specimens are based upon early work using a human model (e.g. Dart, 1948a, b, 1949; Mann, 1975). As australopiths almost certainly had a more rapid rate of dental development compared to humans and apelike dental development, in general, age estimates based upon a human model likely overestimate the actual age of death of these individuals (see Bromage and Dean, 1985; Smith, 1986, 1987; Beynon and Dean, 1987; Beynon and Wood, 1987; Bromage, 1987; Conroy and Vannier, 1987; Dean, 1987a,b; Dean *et al*., 2001; Lacruz and Rozzi, 2010).

A summary of current and previous age estimates for the specimens are provided in a summary table (see Table 9-1).

MLD 2

Overview. This specimen is a well-preserved mandible with right C_1 visible in the crypt but not emerged to the level of the alveolar crest; right P_3 erupted but not fully into occlusion; right dp_4, right and left M_1, right and left M_2 and left P_3 in full occlusion; and left P_4 with buccal cusp tip just above the alveolar crest (see Figures 7-1a, b, c, and d). The mandibular rami are not preserved and the left mandibular corpus exhibits some distortion. A buccally situated crack extends posteroinferiorly from the left P_4 through the posteriormost preserved portion of the corpus. This has resulted in a part of the buccal aspect of the left mandibular corpus being displaced by a calcium carbonate infilling by approximately 1.0 mm superoanteriorly and 4.8 mm posteroinferiorly. This mandible represents an individual in late childhood on the basis of the presence of both deciduous and permanent teeth in varying stages of eruption.

Symphyseal Region. The symphysis is completely intact. There is no indication of a mental trigone or mental protuberance, instead, the external symphyseal region slopes gently to the base of the mandible. As originally described by Dart (1948a:391), MLD 2 is undoubtedly a “chinless” mandible. There is a short, low-lying symphyseal ridge extending from the external alveolar bone inferiorly for approximately 12.6 mm. Incisive fossae are present lateral to this external symphyseal ridge for attachment of the *levator labii inferioris*. Dart (1948a) described the anterior aspect of the symphysis from inferior view as exhibiting a distinct inverted triangular area with its apex at the mandible's base, its base at the incisal alveoli, and its walls delimited by the canine juga. Despite the subadult status of this mandible, there are clear canine juga.

The internal symphyseal region exhibits a shallow sublingual (subalveolar) fossa. In addition, a small spine, weak vertical ridge, and some additional rugosity are present internally for attachment of the genial muscles (i.e. the genioglossus and geniohyoid). As also noted by Dart (1948a), a genioglossal fossa and an apelike genial pit are absent. This internal symphyseal morphology is distinct from variably deep genial pits exhibited by other South African australopiths, including the Taung child, all other mandibles from Makapansgat preserving this region (e.g. MLD 18, MLD 27, and MLD 29), as well as many specimens of *A. africanus* from Sterkfontein and some specimens of *A. robustus*. There is no clear distinction between a superior and inferior mandibular torus in MLD 2 (see also Dart, 1948a). Instead, the internal aspect appears strongly proximodistally curved, or convex. The external symphyseal height of the MLD 2 mandible lies outside of the range of variation known for all other South African australopiths (see Figure 7-2). Virtually the entire robust sample overlaps with the sample of *A. africanus* from Sterkfontein, while MLD 2 lies just below the Sterkfontein range. This morphology likely relates to the subadult age assignment for the MLD 2 mandible, but also contributes to the appearance of mandibular robustness in this specimen. In measured thickness, the subadult MLD 2 mandibular corpus at each tooth is one of the thinnest represented by the Makapansgat sample (only thicker than MLD 22 at M_1 and MLD 34 at M_1 and M_2).

Corpus Morphology. The mandibular corpus appears thick compared to other hominins from Makapansgat. There is a distinctly bulbous lateral prominence at the level of the distal interproximal surface of M_1, which coincides here with the root of the ramus. Part of this thick appearance, however, is due to the subadult nature of the mandible. The basal margin of the mandible angles distosuperiorly with respect to the alveolar plane, giving the mandible a somewhat slanted appearance from P_3-M_3 (as is also the case in MLD 18).

Multiple mental foramina are apparent bilaterally. There are 3 mental foramina on the right and 4 mental foramina on the left. The mental foramina are positioned at P_3 on the right and between P_3 and P_4 on the left. In extant humans, the mental foramen typically transmits the mental nerve, artery, and vein via a single foramen on the right and left mandibular corpora. Extant humans are known to have a relatively high incidence of multiple mental foramina unilaterally, but a low incidence of multiple mental foramina bilaterally (Jaffar *et al.*, 2002). It is doubtful for there to be any taxonomic or functional utility to examining the number of mental foramina in hominins. Multiple foramina likely result from a more proximal splitting of the neurovascular bundle along its course.

The external oblique lines are visible extending from the canine alveolar bone posteriorly. The base of the mandible has a blunt edge and exhibits marked impressions for attachment of the anterior belly of the right and left digastric muscles. On the right, the digastric fossa is bounded by a very small tubercle relating to this complex. The mylohyoid groove is visible bilaterally on the internal aspect of the corpus. In addition, there is a strong mylohyoid ridge extending much of the length of the corpus. Bilaterally at the middle of M_2, there is a marked expansion or rugosity of the alveolus forming almost a vertical ridge extending superiorly from the mylohyoid ridge. Below the mylohyoid ridge is a clear and strongly externally angled, but shallow, submandibular fossa.

Ramus Morphology. The vast majority of the mandibular ramus is not present. Only the anteriormost root of the vertical ramus is preserved. The root originates at the middle of M_1, although this positioning would have most likely changed as the subadult individual aged.

Discussion. This specimen was discovered *ex situ*, but approximately 20 feet from the discovery location of the MLD 1 occiput (Dart, 1948a). The proximity of the two discovery sites and the comparable ages of these specimens have been used to argue that they represent the same individual (e.g. Dart, 1948a). While this remains a possibility, the evidence cited in support of this supposition is weak. Except in calculating a MNI (minimum number of individuals) for the site, it seems premature to assume MLD 1 and MLD 2 represent the same individual on these bases.

In line with his Osteodontokeratic Culture and violent reconstructions of australopith behavior, Dart argued that the mandible exhibits evidence that the individual died by “manually applied violence” (1948a:393). The absence of rami, the cracks in the corpus, and the supposed expulsion of the incisors were explained by Dart by rapid death by bludgeoning, which involved a crushing blow to the face. Dart noted the absence of evidence for remodeling at the fragmentary borders as support for his hypothesis. Today, the absence of remodeling in fragmentary specimens is well known to typically result from postdepositional processes acting over time. This is almost certainly the case with MLD 2. Part of his evidence for the hominin status of the MLD 2 mandible includes his citing of research that placed this specimen with bimolar breadth/bicanine breadth (Maire-Heintz, 1958; see Dart, 1962).

When originally published, this specimen was speculated to represent a male and noted to be more ape-like in its eruption pattern (Dart, 1948a, 1962; although see Koski and Garn, 1957; Conroy and Vannier, 1991). Dart presumed a humanlike delayed infancy on the basis of extensive wear of the deciduous dentition as support for his age estimate of 12 years (based on a human model) over his estimate of 6.5 years (based on a chimpanzee or gorilla model). More recent work by a variety of authors have indicated that australopiths exhibit a life history more similar to apes than to modern humans (e.g. Bromage and Dean, 1985; Bromage, 1987; Smith, 1986; 1991, 1994a,b; see also previous discussions). This would indicate an age estimate based upon a primate model, thus the much younger estimate of approximately 6.5 years is more appropriate. Recent work has produced age estimates of 6.6 years for this individual on the basis of assessment of dental developmental stages (Bromage, 1987; Conroy and Vannier, 1991). Thus, MLD 2 represents an individual in late childhood and likely close to 6.6. years of age at death.

Dart noted the robustness of the MLD 2 mandible in his initial descriptions of this specimen. He compared a robustness (robusticity) index of 87.5 for this juvenile specimen with 70.6 for a specimen of "*Paranthropus*" (*A. robustus*). Indeed, the MLD 2 mandible appears relatively robust compared with many South African australopith specimens. The mandibular robustness indices for M_1 (90.15) and M_2 (92.92) indicate that MLD 2 is one of the most robust hominin mandibles from South Africa, although part of these results can be attributed to the anterior positioning of the lateral prominence. Tobias (1971b), with regard to the Cave of Hearths mandible, noted that mandibular robustness indices tend to be high for subadult mandibles. He argued for an ontogenetic pattern of decreasing mandibular robustness with age, resulting from a marked increase in mandibular height at M_1 coupled with little or no increase in increased mandibular thickness. This ontogenetic pattern appears to be at play within the MLD 2 mandible. Comparison of the mandibular height at M_1 reveals that low corpus height values (M1 external height = 24.07; M2 external height = 24.73) drive the unusually high robustness index for this mandible, rather than mandibular corpus thickness.

On the basis of the morphology of the MLD 2 mandible (and teeth), Dart suggested the species it represents to be "more closely allied with the human stock than either of its other known adult relatives, *Plesianthropus* and *Paranthropus*" (1948a:392). In stark contrast to Dart's initial treatment of the Makapansgat hominins as a separate species, Aguirre (1970) argued that this Makapansgat specimen should be included as part of the hypodigm of *A. robustus*. Most authors, however, have treated MLD 2 as part of the hypodigm of *A. africanus*.

Figure 7-1 a, b, c, & d*: *MLD 2. The subadult mandible MLD2 in occlusal (*a*), inferior (*b*), right lateral (*c*), and posteroinferior (*d*) views.

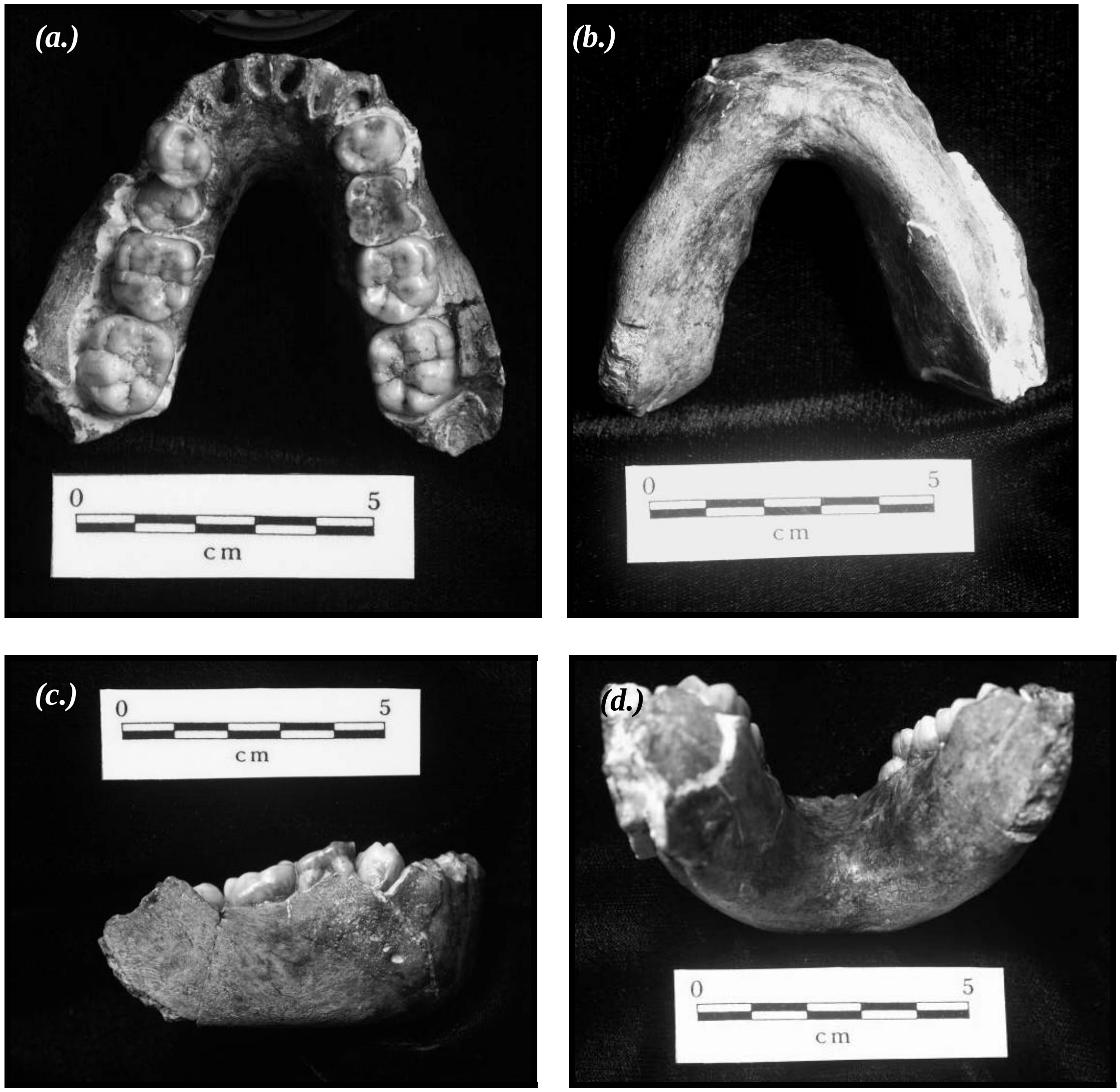
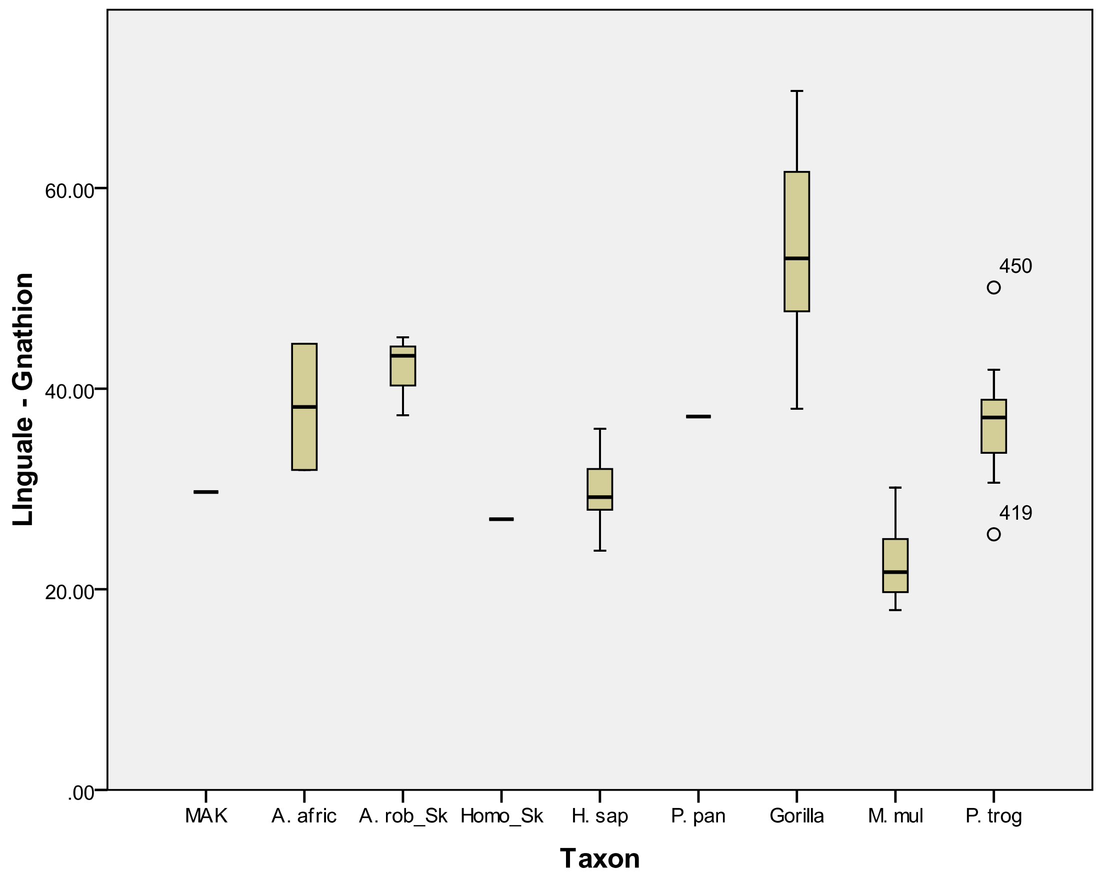


Figure 7-2: MLD 2 External Corpus Height – Symphysis. The median (line), 1st and 3rd quartiles (box), and range (bars) of the external symphyseal height (linguale-gnathion) for MLD 2 in comparison to South African australopiths and a sample of extant primates. The chimpanzee sample includes two biological outliers (the numbers identify the individual specimens). The fossil sample sizes for this analysis are: *A. africanus* (n = 2), Swartkrans *A. robustus* (n = 3), and Swartkrans *Homo* (n = 1).



MLD 18

Overview. MLD 18 is a young adult mandible with left I_1-C_1 and P_4, and right I_1-M_3 (see Figures 7-a, b, & c). The majority of the right mandibular corpus, the superior aspect of the symphysis, and small portion of the anterior left mandibular corpus are preserved. Only the root of the ramus and a small portion of the masseteric fossa are preserved on the right side. This specimen represents an adult individual on the basis of the full complement of teeth and their display of wear. No distortion is apparent for the preserved portions of the specimen.

Symphyseal Morphology. Only the superior portion of the external symphyseal region is preserved. This small region exhibits little superoinferior curvature and angles only slightly posteriorly. This region also exhibits a low ridge at the midline of the symphysis, known as a median alveolar jugum. Lateral to this, the incisive fossae are extremely well demarcated. There is a transverse symphyseal ridge extending along the external aspect of the mandible from the C/P_3 to the ipsilateral side. This ridge is faintly visible as a bony extension across the inferiormost preserved portion of the external symphysis. In addition, it meets the bony canine jugum extending inferiorly from the alveolar bone in the C/P_3 region and an inferior expansion of the median alveolar jugum extending inferiorly from the central incisors. This expansion of the median alveolar jugum creates what Dart termed a "typical" mental trigone (1962a:321), although the broken inferior portion of the symphysis would almost certainly continue to slope posteroinferiorly and not resemble a true "chin". Presumably, the expansion of the median alveolar jugum relates to muscle attachments for the *levator labii inferioris*.

The internal symphyseal region is somewhat better preserved. The incisal subalveolar region appears as a shallow shelf. In large part, this is due to the moderately developed superior transverse torus. Below the superior transverse torus is a deep fossa with two genioglossal pits at its base. The region inferior to these pits is not preserved, restricting further assessment of attachment points for the genial musculature. While the region of the inferior transverse torus is not preserved on the internal aspect, its presence can be reconstructed due to an external inferior torus and a genioglossal depression. The *planum alveolare* is broad and moderately deep, extending posteriorly to approximately P_3/P_4.

Corpus Morphology. The mandibular corpus does not appear as thick as many of the specimens from Makapansgat (including the subadult MLD 2 mandible, MLD 40, MLD 22, MLD 34, and MLD 47). However, this specimen is thicker at M_2 and M_3 than many of the specimens from Sterkfontein, although not all (e.g. the M_2 of STS 52 and STS 7). Despite claims that this specimen is shorter and less robust than the MLD 2 mandible (as well as other mandibles) (Dart, 1954a), the MLD 18 is the most robust mandible at the M_3 of all of the South African australopiths included in this study on the basis of a robustness index (with a value of 91.41). Mandibular robustness indices at M_1 and M_2 place the MLD 18 mandible on the low end of the range of values (more in line with specimens attributed to *A. africanus*). It should be noted, however, that the position and prominence of the lateral eminence (at M_2 and M_3) and the anteroinferior aspect of the ramus contributes considerably to measures of mandibular thickness.

A single large mental foramen is present at the level of P_4/M_1 [although below P_4, according to Dart (1962a)]. There is a significant lateral prominence at the level of M_2, just inferior to the root of the ramus. A superior lateral torus extends above the anteriormost extent of the ramus root towards the canine jugum [or premolar-canine alveolar jugum (Dart, 1962a)]. The posterior aspect of the marginal torus, or inferior lateral torus, is preserved and suggests a clear sulcus between superior and inferior lateral tori. The extramolar sulcus between the M_2, M_3 and the ramus indicates the possibility that the buccinators muscle required a large attachment area. This broad and moderately deep extramolar sulcus is typical to specimens of *A. africanus*. Dart identified a structure he referred to as a supreme lateral torus to describe the thickening of bone extending from the anterior base of the ramus to the M_1 alveolus, which is commonly found in extant humans (Dart, 1962a). The supreme lateral torus thus demarcates a lateral mandibular depression anteroinferiorly (inferior to P_4/M_1), and is distinct from the common presence of a swelling in robusts (Dart, 1962a).

The mylohyoid ridge is faintly visible along most of its course. It is most apparent inferior to M_3. A relatively strong submandibular fossa is evident, which is partly formed by an inferior expansion of the mandible (*contra* MLD 2). A crista pharyngea is evident and continues to a swelling inferior to M_3. The base of the mandible is broad and exhibits a rounded surface.

Ramus Morphology. The root of the ramus is most anteriorly positioned at M_2. The region of the ramus extending posteriorly from the anterior ramal root thins rapidly in the mediolateral dimension. The anterior portion of the masseteric fossa is preserved and exhibits rugosity for muscle attachment. The portion of the external oblique line for attachment of the *depressor labii inferioris* is not preserved, while that for the *depressor anguli oris* is diffuse and indistinct. The mandibular angle clearly extends posteroinferiorly (as is common in hominins).

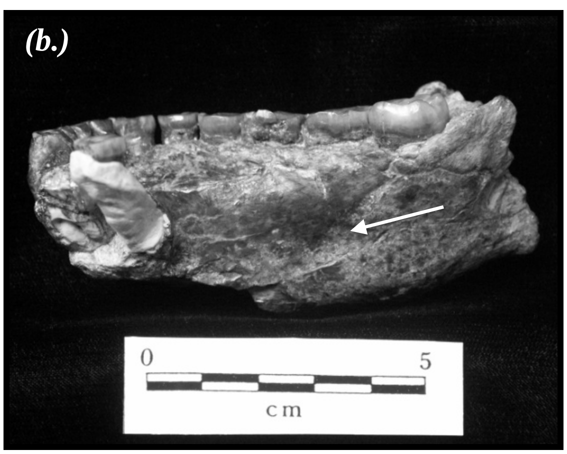
Discussion. This specimen was originally discovered by Alan Hughes in 1953. Dart's original description of the MLD 18 mandible includes a left P_3 as part of the dental arch, although that tooth is no longer stored with the MLD 18 mandible. This is a strange discrepancy as his original illustrations of the MLD 18 mandible also include a left P_3 as part of the dental arch (1954b). Presumably, the tooth was misplaced since Dart's original descriptions.

This specimen represents an australopith individual who reached adulthood with a complete dental complement indicating essentially no markers of poor health (see also Table 9-1). This specimen was originally described as representing an adult (most likely) female individual (Dart, 1954b); however, sex attributions are considered dubious.

Dart reconstructed a modern hominin symphysis for this specimen that is vertically oriented, but thicker than in modern humans. MLD 18 has been argued to represent the same individual as the MLD 4 M_3 (Dart, 1954b; Boné and Dart, 1955) and perhaps also the MLD 24 M_2 (Dart, 1962). The MLD 4 M_3 is almost certainly associated with MLD 18 on the basis of their similar morphology, wear, and size. However, the MLD 24 association is dubious as the left M_2 specimen exhibits less cuspal and interproximal wear than the MLD 18 right M_2.

Dart's original interpretation of the taphonomic processes working upon the mandible includes a crushing injury subjected at or near the time of death (Dart, 1954b). He emphasized damage to the mandible posterior to the M_3's (Dart, 1962), which most likely would be explained today by carnivore gnawing.

Figure 7-3a, b, & c: MLD 18. The MLD 18 mandible is visible in superior (*a*), medial (*b*), and lateral (*c*) views. Some of the major features described in the text are indicated with arrows.



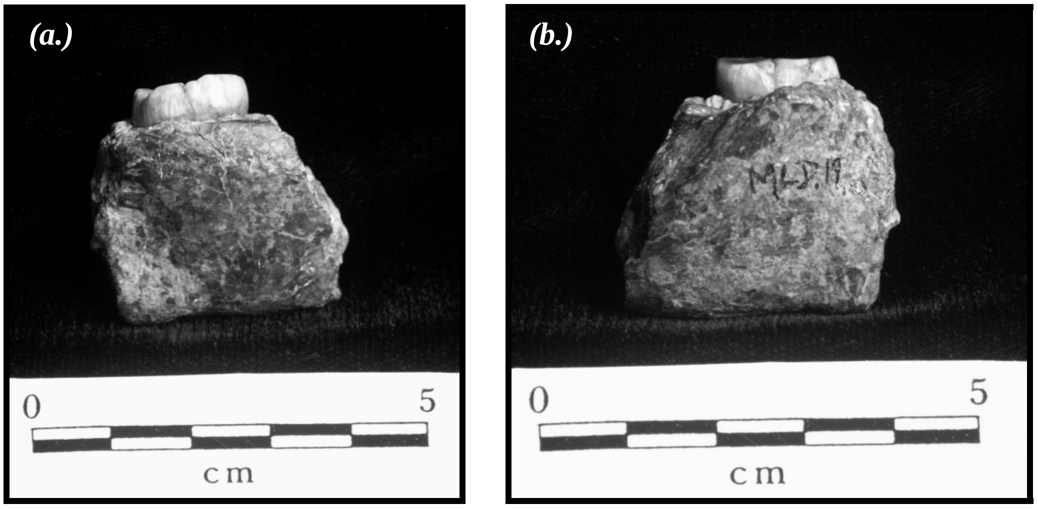
<u>MLD 19</u>

Overview. This specimen is an adult left mandibular fragment with M_3 and root fragments of M_2 (see Figure 7-4a & b). A sliver of the root of the ramus is preserved, but does not permit comparative assessment.

Corpus Morphology. The mandibular corpus at M_3 is not as thick as that of MLD 18 or MLD 40, even taking into account the lack of preservation of the ramus at M_3 in this specimen. The anteriormost attachment of the lateral pterygoid muscle is patent. The posterior portion of the mylohyoid ridge is also visible on its internal aspect of the mandibular corpus. The mylohyoid groove is not preserved. The extramolar surface between the buccal alveolar crest and the ramus is broad, suggesting the potential for a large buccinator muscle.

Discussion. The MLD 19 specimen was discovered in 1953. It was originally described as an adult and most likely a female individual. Its adult status is confirmed by the presence of a fully erupted M_3, but sexual identification is considered indeterminate.

Figure 7-4a & b: MLD 19. The MLD 19 left mandibular fragment visible in medial (*a*) and lateral (*b*) views.



<u>MLD 22</u>

Overview. This specimen is currently only known from a cast as the original specimen was discovered to be missing on April 7, 1962 in the Makapansgat Limeworks Catalogue. All measurements and descriptions were recorded from a cast produced by the anatomical casting facility in the Department of Anatomy of the University of Witwatersrand in Johannesburg, South Africa. It must be noted that the process of casting frequently results in casts that exhibit minor shrinkage in comparison to the original specimen. With these caveats in mind, the MLD 22 cast represents a fossil hominin left mandibular corpus with M_2 and M_3 and alveoli for P_4 and M_1 (see Figure 7-5a & b). The buccal alveolar wall for the M_1 has been eroded. This specimen represents an old adult individual at death.

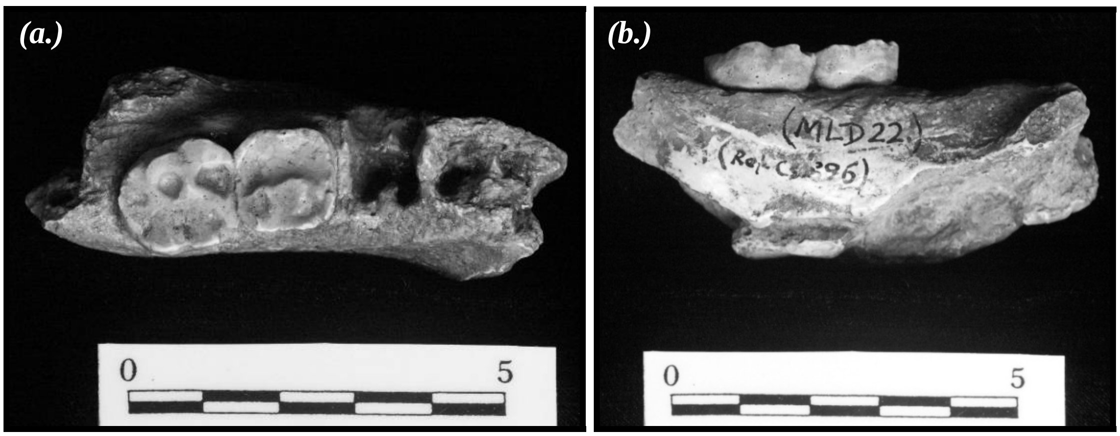
Corpus Morphology. The external aspect of the corpus preserves a single large mental foramen exhibiting abrasion of the external rim. The mental foramen is located beneath P_4. The external oblique line is prominent, extending anteriorly from the anterior root of the ascending ramus to the inferior broken edge of the external corpus. The superior part of a lateral prominence is preserved, as is the posterosuperior part of the submandibular fossa. The extramolar sulcus between the buccal alveolar crest at M_3 and the eroded root of the ramus is broad and exhibits some rugosity, which coincides with the location of the muscular attachment of the buccinator muscle. This identification cannot be made with confidence, however, considering these observations were restricted to a cast.

The internal aspect of the corpus preserves a sharp bony crest extending transversely from inferior to the distal interproximal space of M_2 to distal to M_3. This crest is likely related to either the position of the mylohyoid groove or the mylohyoid crest. It is unclear which is responsible for this bony morphology.

The preserved portion of the mandible permits an assessment of mandibular thickness at M_2 (23.7) and M_3 (26.1) with confidence.

Discussion. The MLD 22 mandible was discovered in 1955 by Alan Hughes in the Makapansgat fossil bone yards. It initially was argued to have been used for a long period as a tool, trophy, or sentimental item prior to fossilization on the basis of comparison to the MLD 34 specimen in the appearance of weathering (Dart, 1962). Obviously, this reconstruction is no longer considered valid. The considerable wear of the dentition indicates an adult age for this individual. This appears to be one of the oldest specimens known from Makapansgat on the basis of dental wear. This specimen was presumed to represent a female (Dart, 1962), a reconstruction that is considered premature with the small sample from the site. This specimen was also argued to have been potentially associated with MLD 34 (Dart, 1962). Unfortunately, little can be said with certainty regarding this specimen as a result of recent observations being restricted to a cast of the original specimen.

Figure 7-5a, b: MLD 22. The MLD 22 mandibular specimen in superior (*a*) and medial (*b*) views.



MLD 27

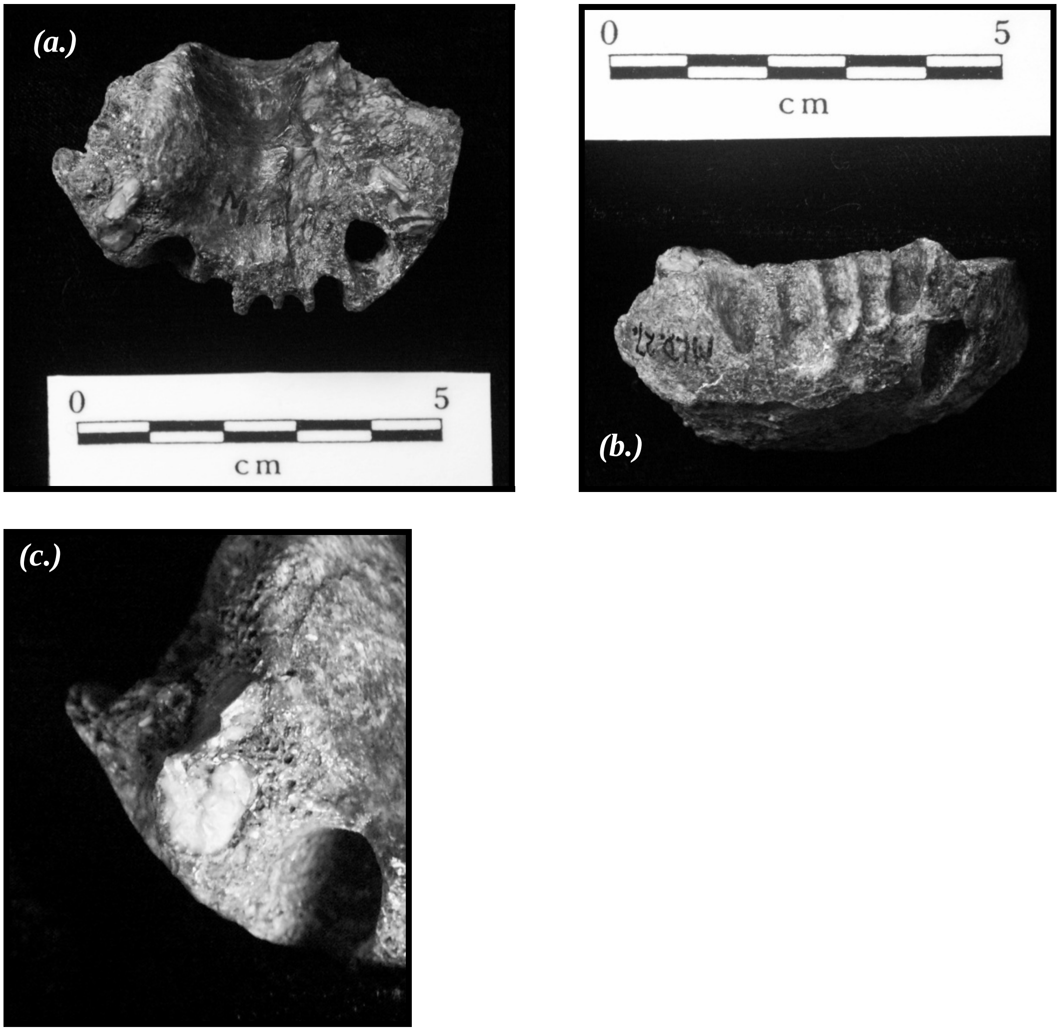
Overview. This specimen is an adult mandibular symphyseal fragment preserving alveoli for the right C_1-left C_1, root of both P_3s, and the mesial portion of the root socket for the right P_4 (see Figure 7-6a, b, & c). The base of the mandible and the external symphysis, with the exception of the external alveolar region, are not preserved.

Symphyseal morphology. The external symphyseal region preserves little bone. Where the superior portion of the symphysis is preserved, a small midline fossa is visible at the level of the tip of the I_1 roots (the location of the root tips are visible due to the abraded buccal alveolar wall). The internal symphyseal region preserves an incisal subalveolar plane that is shallow, but steeply oriented. This region exhibits a clear, but unexceptional superior transverse torus. A short, poorly developed inferior transverse torus is also visible. Between the superior and inferior transverse tori is a large, deep depression and inferior to this depression is a partially eroded mental spine, both for attachment of the genial musculature. The internal symphyseal region is acutely angled transversely. A small portion of a marked digastric fossa is preserved on the left.

Corpus Morphology. The canine alveoli appear large and may be evidence of long, thick canine roots for MLD 27. The right canine alveolus is particularly well preserved, alleviating some concerns regarding the impact of postdepositional processes on the size and appearance of alveoli in tooth root reconstruction. Caution is advised whenever evaluating characteristics of a tooth from canine alveoli, as numerous premortem and postdepositional processes contribute to the appearance of fossil alveoli.

Discussion. This specimen represents an adult on the basis of an adult-sized mandible with strong attachments for genial musculature and permanent P_3 roots. The absence of teeth makes it difficult to assign a more precise age estimate to this specimen (see also Table 9-1). Dart (1962a) suggested this specimen most likely represents a male on the basis of mandibular morphology (most likely symphyseal thickness), although this is currently considered tenuous.

Figure 7-6a, b, & c*: *MLD 27. The mandibular symphyseal specimen, MLD 27, in superior (*a* & *b*) and anterior (*c*) views.



<u>MLD 29</u>

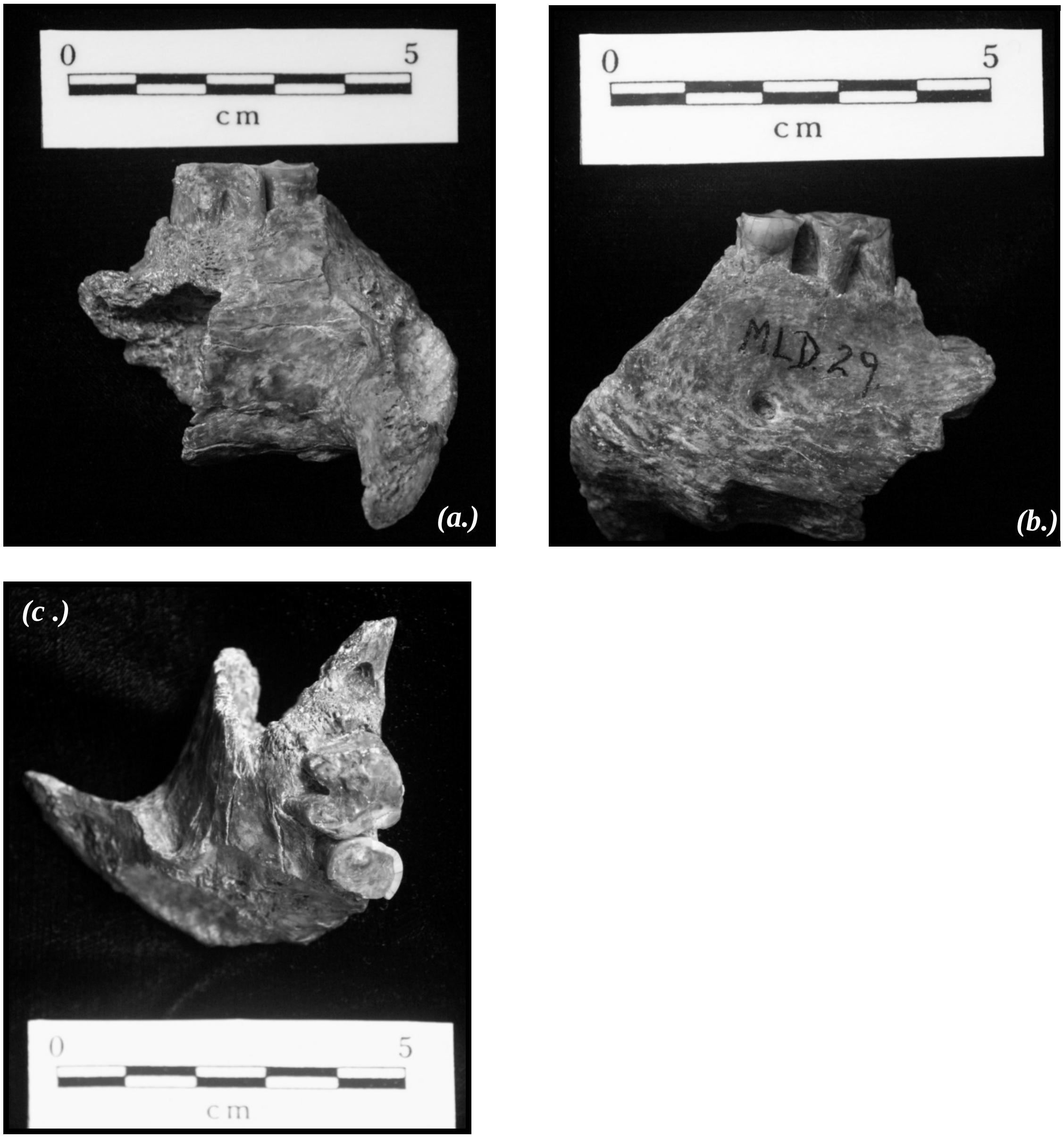
Overview. MLD 29 is an adult mandibular corpus fragment with left P_4 and M_1 and part of the alveolus for M_2 (see Figures 7-7a, b, & c). The inferior portion of the symphysis is intact, as is the left mandibular corpus to a point just distal to M_1. Most of the right mandibular corpus is missing. Portions of the roots of the left C_1-P_3 are preserved within the angled fracture plane of the mandible, extending from the inter-alveolar space of the left P_3 and P_4 and the base of the right mandibular corpus at approximately the level of M_1.

Symphyseal Morphology. The external symphysis preserves little bone, but indicates a broad symphyseal base. The internal aspect of the symphysis appears strongly transversely angled and preserves the attachments for the genial musculature. Although the region of the superior transverse torus is not preserved, the region just inferior to it exhibits a marked depression. In addition, a hint of an inferior transverse torus is present, as well as a poorly developed mental spine.

Corpus Morphology. The mandibular corpus at M_1 appears moderately thick. The external aspect of the corpus exhibits a single large mental foramen beneath P_4. The mandibular corpus inferior to M_1 exhibits the anterior development of a mylohyoid ridge. The base of the mandible is anteroposteriorly expanded and exhibits ridges for the attachment of the anterior belly of the digastric. Alveolar resorption is apparent around the cervical margin of the preserved dentition and within the preserved alveoli.

Discussion. This specimen was originally discovered in 1956 and was presumed to be male on the basis of size (Dart, 1962). MLD 29 is considered here to represent an old adult, on the basis of the heavily worn adult P_4 and M_1. While Dart noted that the specimen was damaged significantly by mining activities, he also reconstructed that premortem damage to the mandible was the result of smashing and spongy bone near the left M_2 had been “gouged out” prior to deposition in the fossil record (1962:272). This postmortem damage is likely the result of hyena gnawing or postdepositional processes.

Figure 7-7a, b, & c: MLD 29.



MLD 34

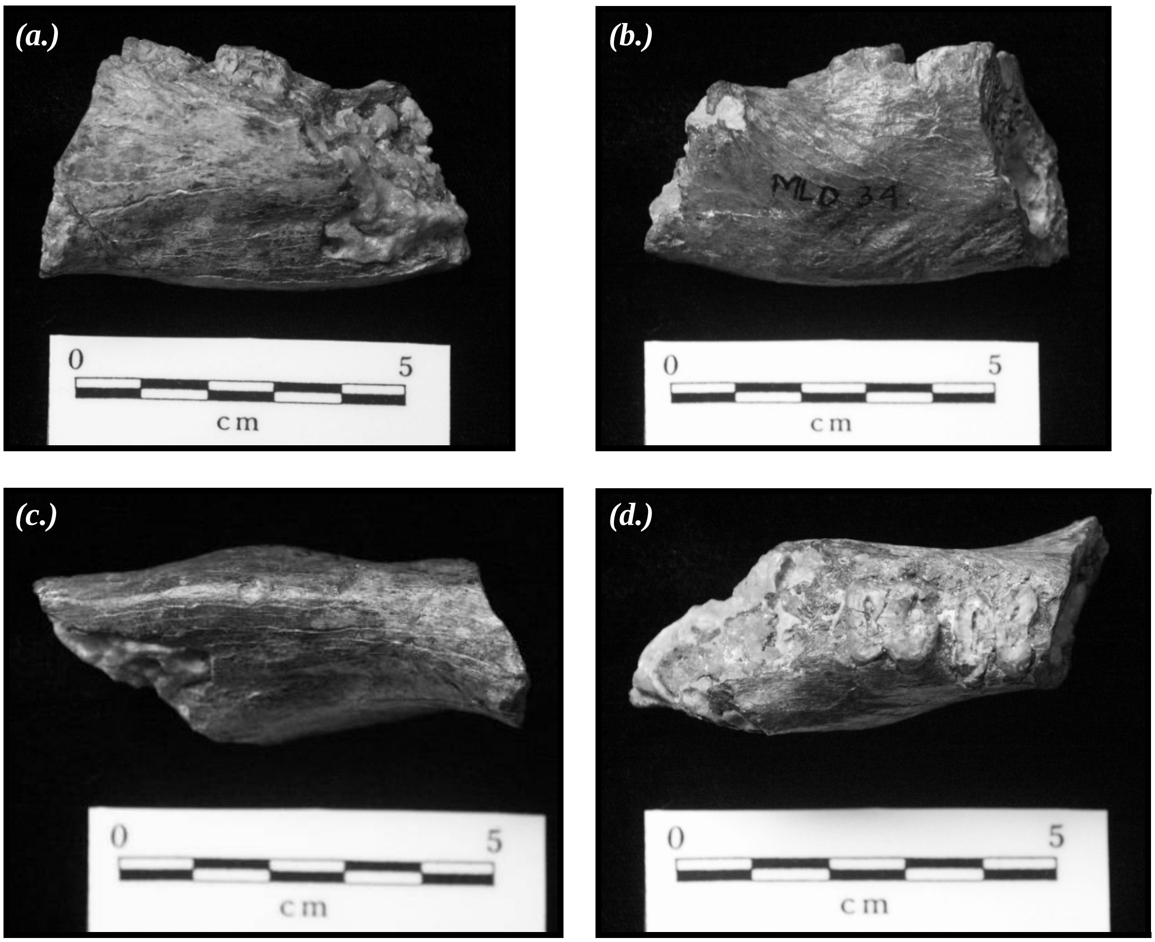
Overview. This specimen is a right mandibular corpus fragment at the level of M_1-M_3. The crowns of M_1 and M_2 are not preserved, although their roots and a small mesiodistal sliver of P_4's roots are preserved in their respective alveoli. A small portion of the root of the ramus is preserved. There appears to be some tooth marks from carnivoran or rodent gnawing on the external aspect of the corpus near the base of the mandible. This specimen represents a probable adult on the basis of the full occlusion of the M_1 and M_2.

Corpus Morphology. The mandible is not as thick at the level of M_2 and M_3 as MLD 40, but is thicker than MLD 18. The greatest mandibular thickness is preserved at approximately the region of the lateral prominence. The mental foramen is not preserved but must have been positioned anterior to M_1. The external oblique line is visible extending from the root of the ramus, as well as a moderate lateral prominence at the level of M_2/M_3. The internal aspect of the corpus exhibits a moderate submandibular fossa and weak mylohyoid ridge, the latter being visible anteriorly. The inferior border of the mandible is sharper than other mandibles from Makapansgat, particularly at M_2. The posteriormost portion of the preserved mandible exhibits some rugosity, presumably for attachment of the masseter.

Discussion. This specimen was originally discovered in 1960. MLD 34 is considered an adult on the basis of the occlusion of the M_1 and M_2, but further precision is considered unreliable. This specimen was originally presumed to belong to a female australopith (Dart, 1962), but is considered indeterminate until the specimens can be placed into a more precise comparative and evolutionary framework. In addition, MLD

34 may represent the same individual as MLD 22 on the basis of morphology and fossil coloration.

Figure 7-8a, b, c, & d: MLD 34.



MLD 40

Overview. This is a well-preserved nearly complete left mandible with C_1-M_3 and alveolus for I_2 (see Figures 7-9a, b, c, & d). The crown of M_3 is not preserved, although the roots are still embedded within the mandible. The ramus is preserved, with the exception of the gonial angle and the posterior border of the ramus. The region of the mandibular symphysis is absent. This mandible belonged to an adult on the basis of the M_3's in full occlusion and the wear level of the posterior dentition.

Corpus Morphology. The mandibular corpus is thick, particularly at the level of M_2/M_3 both superiorly and inferiorly. This thickness of the mandibular corpus results from the convergence of an enormous external swelling inferior to M_2 and M_3, which also envelops the marginal torus (or inferior lateral torus). For every measured position from C-M_3, the MLD 40 mandible is the thickest of all of the Makapansgat mandibles. The mandibular thickness values for MLD 40 either fit comfortably within the range or are at close to the top of the range of values for specimens of *A. robustus*. The base of the MLD 40 mandible (not surprisingly) exhibits a broad, rounded edge. A marked attachment site exists for the anterior belly of the digastric extending mesial from the base of the mandible at the level of P_3.

The external aspect of the mandibular corpus exhibits a marked lateral prominence and an anterior portion of the external oblique line that clearly exhibits attachments for the *Depressor Labii Inferioris* and the *Depressor Anguli Oris* musculature. Even the region at which the platysma attaches appears rugose in MLD 40. The extramolar sulcus between the buccal alveolar wall at M_3 and the ramus is broad. In addition, the external bony surface inferior to the M_1 and M_2 alveolar walls appears rugose and may indicate a particularly well-developed buccinator in this individual. The anterior portion of the preserved external corpus exhibits an incisive fossa inferior to I_2

and a prominence of the mandible near the inferior edge at the level of the C_1. A single moderately-sized mental foramen exists at the level of P_4/M_1. A single moderately sized mental foramen is present. The lateral prominence is located in the region of M_2/M_3 and is particularly broad.

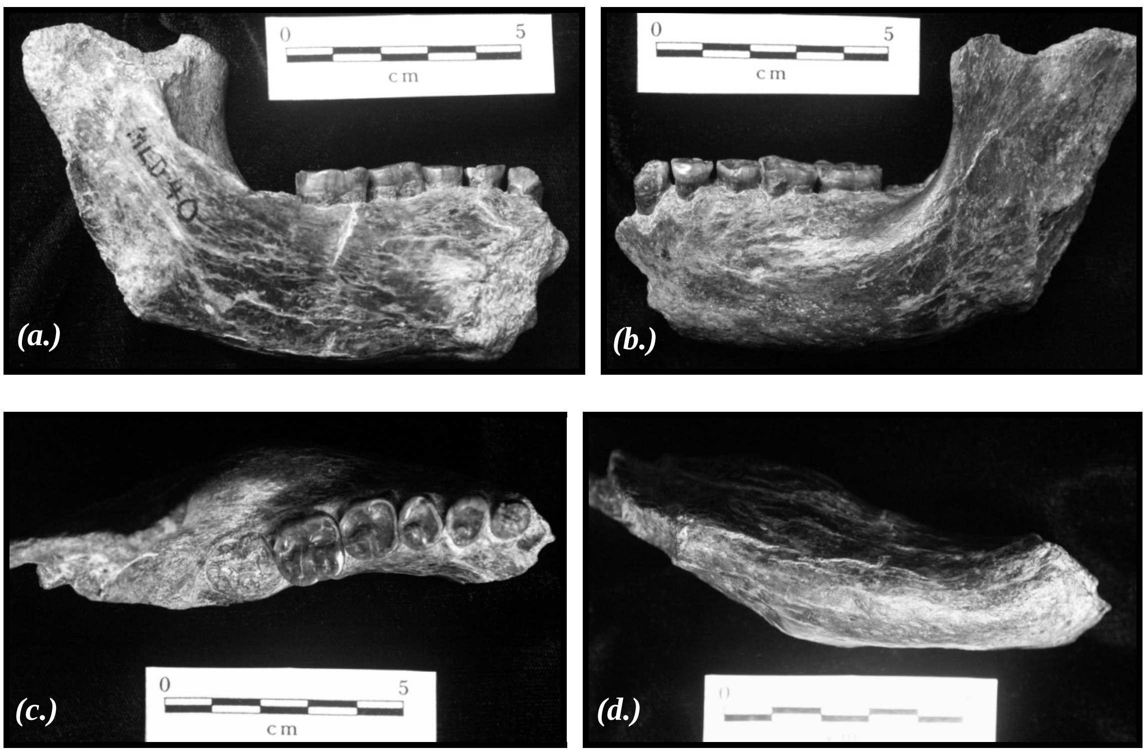
The internal aspect of the mandible has only minimal erosion. The large inferior alveolar foramen for passage of the inferior alveolar neurovascular bundle exhibits eroded borders. The mylohyoid groove is well demarcated and extending anteriorly from it is a small crest of bone marking its continuation (as well as the path of the nerve to the mylohyoid). There is a second fainter groove running superior to the groove for the mylohyoid, presumably this groove relates to the arterial supply to the mylohyoid muscle. The mylohyoid ridge is marked for a short length, extending from M_3 to M_2 and reappearing at the level of M_1. The crista pharyngea extends posterosuperiorly towards a partially preserved triangular torus. Rugosity for attachment of the internal pterygoid is visible posteroinferior to the mylohyoid groove. In fact, a slight ridge of bone demarcates the anterior border of the internal pterygoid attachment site. A clear submandibular fossa is apparent. There appears to be some buttressing inferior to P_4/M_1, although it is unclear to what this morphology relates. The alveolar prominence is broad and just inferiorly, there is a clearly demarcated subalveolar fossa. The *planum alveolare* is partially preserved, extending medially from the lingual aspect of the C_1. The lingual subalveolar bone at I_2 exhibits a shelf, similar in development to the other Makapan mandibles.

Ramus Morphology. The mandibular ramus does not preserve the gonial angle, posterior border, the superiormost coronoid process, or the mandibular condyle. The sigmoid notch is present, although the post-depositional processes that affected the coronoid process and condyle do not permit assessment of these regions. The bony surface for attachment of the masseter is rugose and is anteriorly bounded by the large lateral prominence. The attachment areas of the masseter are clearly demarcated for both insertions of this muscle. The attachment of the deep head is larger than the surface for the superficial head of the masseter (Dart, 1962a). Overall, the ramus preserves rugose attachments for powerful muscles of mastication in MLD 40. The anterior border of the ramus crosses the third molar, which is more posteriorly positioned than it is in MLD 18. The ramus appears slender, even in the region of the mandibular angle, particularly when compared with the broad corpus.

Discussion. The MLD 40 mandible was discovered in 1961. Dart's original attribution of sex (male) was based on the "massiveness" of the mandibular corpus (1962a). This specimen has been argued to potentially belong to the MLD 1 individual on the basis of sex (Dart, 1962a). The original interpretation of postdepositional processes acting on the mandible was driven by the notion of an Osteodontokeratic Culture, involving perimortem splitting of the symphysis and fracturing of the left condyle (Dart, 1962a).

This mandible was identified as being quite similar to specimens of *A. robustus* in some features and in mandibular area at M_1 (e.g. SK 6) and M_3 (e.g. SK 12) (Dart, 1962a). Indeed, Dart made numerous comparisons of this mandible to those of *A. robustus*, finding them similar in mandibular corpus robusticity and corpus breadth. However, he found MLD 40 to be more similar to specimens of *A. africanus* on the basis of ramus morphology and overall dimensions (e.g. Sts 52b and Sts 36) (Dart, 1962). On the basis of comparisons between the presumed female MLD 18 and male MLD 40 specimens, Dart indicated there was likely little sexual dimorphism within the sample (1962a), although he fails to clearly discuss how he attributes specimens to male or female on any basis other than size.

Figure 7-9 a, b, c, & d: MLD 40. This is a well-preserved left mandibular specimen with C1-M2 and M3 roots in lingual (*a*), buccal (*b*), occlusal (*c*), and inferior views (*d*).



<u>MLD 47</u>

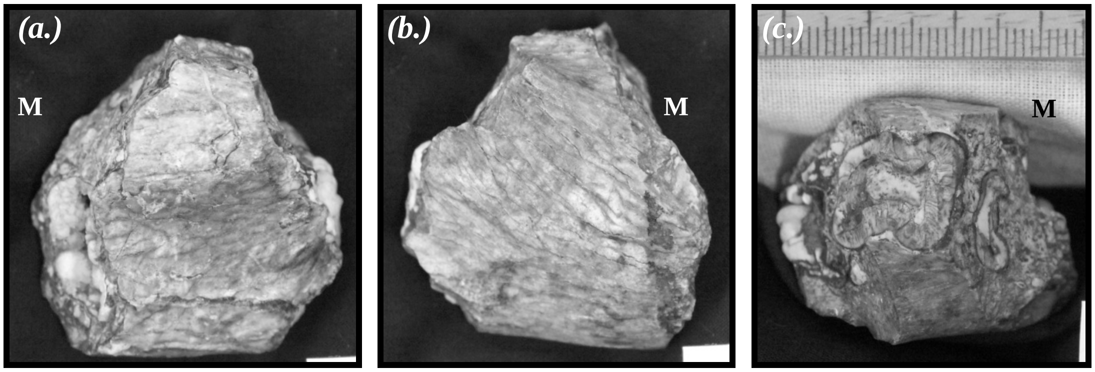
Overview. This adult specimen is a right mandibular corpus fragment preserving a small portion of the root of the ramus (see Figure 7-10). The crowns of the M_2 and M_3 are not preserved, although the roots of M_3 and a small portion of the posterior roots of M_2

are visible. The teeth were identified as M_2 and M_3 on the basis of comparison to the ramus and corpus morphology of MLD 18 and MLD 40. In MLD 47, the anterior part of the ramus crosses the dentition in the middle of the questioned tooth (presumed to be M3). In MLD 18 and MLD 40 this same region of the ramus crosses the dentition at M3. In addition, the mandibular corpus cross section supports this assessment on the basis of the position of the lateral prominence (at M_2), and the rapidly decreasing mediolateral thickness of the corpus extending posteriorly from this region.

Corpus Morphology. The mandibular corpus is moderately thick, with a maximum thickness of 29.2 mm. The extramolar sulcus is moderate and indicates a moderate buccinator. The lateral prominence, although not fully preserved, appears moderate. The anteriormost aspect of the ramus root is preserved. The internal aspect of the corpus preserves a clear mylohyoid attachment and submandibular fossa. A small portion of the anteriormost attachment of the internal pterygoid is preserved.

Discussion. This specimen was first discovered by the Makapansgat Field School in 2000. This specimen represents an adult on the basis of the presence of a fully erupted M_3.

Figure 7-10 a, b, & c: MLD 47. A right mandibular fragment with the roots of M_1, M_2, and a small part of P_4 in lingual (*a*), buccal (*b*), and occlusal (*c*) views, where M is mesial.



MLD 48

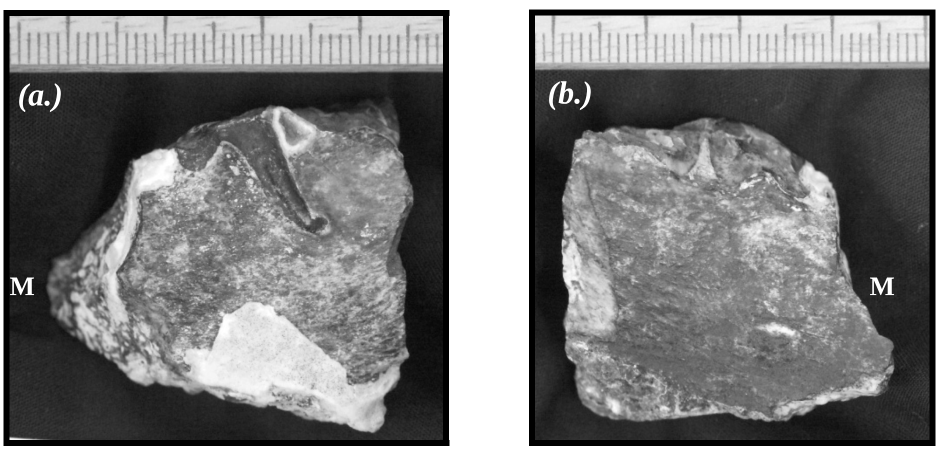
Overview. This specimen is a probable adult left mandibular corpus fragment with an overall length of 37.6 mm (see Figure 7-11), preserving the roots of the distalmost P_4, and M_1 and M_2 (*contra* Kuykendall and Kegley, unpublished manuscript). The small portion of the P_4 roots that are preserved may instead be a flowstone filling a fossilized imprint of the roots. The roots, the cervix, and a sliver of the distobuccal crown of the M_1 are preserved. The distal majority of the distolingual and a small portion of the distolabial roots of M_2 are preserved, but no part of the crown is preserved due to post-depositional fragmentation of the mandible and exposed dentition. The anterior portion of the fragment extends inferiorly from the lingual P_4/M_1 interproximal region at a slight anterior angle. The posterior margin of the fragment extends from the posterior aspect of M_2 inferiorly and slightly anteriorly. The base of the mandible is not preserved. In addition, flowstone calcite still clings to the fragmentary inferior border.

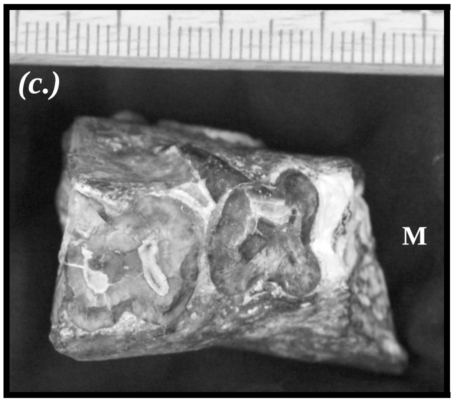
Corpus Morphology. The corpus is moderately thick in comparison to other specimens from Makapansgat. Externally, a portion of the external oblique line is preserved at the anteriormost root of the ramus, at the level of M_1/M_2. The distolabial M_1

root was exposed premortem and exhibits a root tip that curves distally. A small, but distinct fossa is apparent distal to the exposed distolabial root. The mental foramen is not preserved. Internally, the internal alveolar border is partially eroded. The inferior aspect of the fragment appears to preserve the anterosuperior periphery of a submandibular fossa.

Discussion. This specimen was first discovered by the Makapansgat Field School in 2001. MLD 48 most likely represents an adult on the basis of the M_1 and M_2 in full occlusion on the basis of the fully erupted cervical region.

Figure 7-11a, b, & c: MLD 48. This is a left mandibular fragment with roots of M_1, M_2 and a distal root fragment of P_4. The images below are of this specimen in lingual (a), buccal (b), and occlusal (c) views, where M is mesial.





Mandibular Traits. Mandibular trait data, like the previously discussed cranial trait data, indicate extensive intra-specific variation in South African australopith mandibles (see Tables 7-1 to 7-4). Traits that were coded as intra-specifically variable for the South African australopiths include the position of the mental foramen, mental foramen morphology, anterior position of the ramus root, and vertical position of the ramus root. More importantly, all of these are variable even within the Makapansgat sample. The Makapansgat sample cannot clearly be distinguished from the samples of neither *A. africanus* nor *A. robustus* in the position or morphology of the mental foramen, nor the vertical positioning of the ramus root.

The mental foramen is most frequently positioned at or slightly anterior to P_4 in all three of the South African australopith samples. This is also the case for the samples of *Gorilla*, *Pan* and extant *Homo*, while that of *Macaca* exhibits a more posteriorly positioned mental foramen. The Makapansgat sample tends to exhibit more posteriorly positioned mental foramina than the other South African australopiths (71% at or posterior to P_4), particularly the robusts (22% at or posterior to P_4). See also Figure 7-21 and further discussion below. A posterior position of the mental foramen (at M_1) has been identified as an autapomorphy of Neandertals (e.g. Stringer *et al.*, 1984; Condemi, 1991), although Trinkaus (1993) convincingly argued this status on the basis of polymorphism within the Neandertal and archaic and modern comparative samples and complex underlying ontogeny of this variable. In reality, the position of the mental foramen relative to the dentition is dependent upon developmental aspects of the corpus, inferior alveolar nerve, and dentition. To what extent the morphology of these regions contributes to the position of the mental foramen is unclear.

The morphology of the mental foramen does not exhibit clear patterning in the South African australopiths. The only discernible pattern within these fossil taxa suggests that the Makapansgat mandibles more frequently exhibit an anteroposteriorly elongated oval morphology of the mental foramen, while the South African robusts more frequently exhibit a circular morphology. The sample attributed to *A. africanus* appeared intermediate in this feature. Functionally, the mental foramen merely serves to transmit the mental neurovascular bundle and consistent variations in its shape within a particular taxon are not likely to be biologically meaningful.

The number of mental foramina exhibited by fossil and extant taxa varied. While each of the South African australopith samples exhibited mostly single mental foramina (56% for *A. robustus*, 83% for *A. africanus*, and 88% for Makapansgat), virtually all of the much larger samples of macaques (96%), chimpanzees (100%), and extant humans (97%) exhibited single mental foramina. The gorilla mandibles exhibited a relatively low frequency of single mental foramina (58%) similar to that of *A. robustus*.

The anterior position of the ramus root, below which tooth the anteriormost root of the ramus is positioned, appears more anteriorly positioned in the sample of *A. robustus* than that of *A. africanus*. Specifically, 70% of the sample of *A. robustus* exhibits an anterior root position anterior to M_2, while only 33% of the sample of *A. africanus* is positioned anterior to M_2. In this trait, the Makapansgat sample appears to be most like the robusts with 60% of the sample positioned anterior to M_2. While this trend is visible, sample sizes do not permit the statistical assessment of these data. The more anterior positioning of the ramus root, possibly shared by the samples of Makapansgat and *A. robustus*, is considered to be a derived feature in hominin mandibles.

The vertical positioning of the ramus root, through which tooth the anterior border of the ramus crosses, is most frequently at M_3 for all of the fossil and extant samples examined. This trait is virtually identical in frequency for the 3 South African australopith samples with a position at M_3 or anterior in every case. All of the extant comparative samples but chimpanzees exhibited a vertical position of the ramus root most frequently at M_3 or posterior. In fact, none of the extant humans and few of the other extant primates exhibited a vertical ramus root position anterior to M_3.

The mandibular trait data presented here do not provide much assistance in differentiating the three South African australopith samples examined in this study. Only the anterior position of the ramus root provides any indication of a possible closer association of the Makapansgat fossils with one of the fossil species to the exclusion of the other. A larger sample size might better permit the identification of patterns within the South African australopiths, particularly in the biomechanically significant positioning of the ramus root.

One could argue that the greatest significance of these data presented in Tables 7-1 through 7-4 is how obviously the inclusion of the Makapansgat sample in the hypodigm of *A. africanus* skews the sample of specimens available for analyses of the mandibular morphology of *A. africanus*. In each mandibular trait presented, the inclusion of the Makapansgat sample would almost double the sample size of *A. africanus*. For these data, the inclusion of the Makapansgat sample as part of the hypodigm of *A. africanus* would have as much an impact on the mandibular morphology attributed to *A. africanus* as the Sterkfontein sample. This sample size issue must be heavily considered in any analysis of mandibles of *A. africanus*.

TABLE 7-1: Position of Mental Foramen

	Mak N = 7 n / %	*A. afric* N = 6 n / %	*A. rob* N = 9 n / %	Fossil *Homo* N = 2 n / %	Extant *Homo* N = 38 n / %	*Pan* N = 28 n / %	*Gorilla* N = 47 n / %	*Macaca* N = 26 n / %
C/ P_3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	9 / 19	0 / 0
P_3	1 / 14	1 / 17	1 / 11	0 / 0	0 / 0	1 / 4	8 / 17	0 / 0
P_3/P_4	1 / 14	2 / 33	6 / 67	1 / 50	15 / 39	11 / 39	18 / 38	7 / 27
P_4	4 / 57	2 / 33	2 / 22	0 / 0	15 / 39	12 / 43	9 / 19	7 / 27
P_4/M_1	1 / 14	1 / 17	0 / 0	1 / 50	8 / 21	3 / 11	3 / 6	11 / 41
M_1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 4	0 / 0	1 / 4

TABLE 7-2: Mental Foramen Morphology

	Mak N = 5 n / %	*A. afric* N = 7 n / %	*A. rob* N = 11 n / %	Fossil *Homo* N = 1 n / %	Extant *Homo* N = 37 n / %	*Pan* N = 29 n / %	*Gorilla* N = 47 n / %	*Macaca* N = 26 n / %
Oval – horiz, single	3 / 60	3 / 50	0 / 0	1 / 100	15 / 41	24 / 83	25 / 53	10 / 38
Oval – horiz, multiple	1 / 20	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	10 / 21	0 / 0
Oval – vert single	0 / 0	0 / 0	1 / 9	0 / 0	1 / 3	0 / 0	1 / 2	0 / 0
Round, single	1 / 20	2 / 33	6 / 55	0 / 0	20 / 53	5 / 17	1 / 2	14 / 54
Round, multiple	0 / 0	2 / 33	4 / 44	0 / 0	1 / 3	0 / 0	10 / 21	1 / 4
V-shaped, single	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 4

TABLE 7-3: Ramus Root - Anterior

	Mak N = 5 n / %	*A. afric* N = 6 n / %	*A. rob* N = 10 n / %	Fossil *Homo* N = 2 n / %	Extant *Homo* N = 36 n / %	*Pan* N = 27 n / %	*Gorilla* N = 47 n / %	*Macaca* N = 24 n / %
M_1	2 / 40	2 / 33	4 / 40	1 / 50	3 / 8	1 / 4	0 / 0	0 / 0
M_1/M_2	1 / 20	0 / 0	3 / 30	0 / 0	7 / 19	10 / 37	5 / 11	0 / 0
M_2	2 / 40	3 / 50	3 / 30	0 / 0	24 / 67	15 / 56	20 / 43	1 / 4
M_2/M_3	0 / 0	1 / 17	0 / 0	1 / 50	2 / 6	1 / 4	18 / 38	4 / 17
M_3	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	4 / 9	18 / 75
M_3-post	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 4

TABLE 7-4: Ramus Root - Vertical

	Mak N = 7 n / %	*A. afric* N = 8 n / %	*A. rob* N = 13 n / %	Fossil *Homo* N = 2 n / %	Extant *Homo* N = 29 n / %	*Pan* N = 26 n / %	*Gorilla* N = 47 n / %	*Macaca* N = 24 n / %
M_2	1 / 14	1 / 13	2 / 15	0 / 0	0 / 0	2 / 8	0 / 0	1 / 4
M_2/M_3	2 / 29	2 / 25	2 / 15	0 / 0	0 / 0	2 / 8	1 / 2	0 / 0
M_3	4 / 57	5 / 63	9 / 69	2 / 100	22 / 76	22 / 85	41 / 87	6 / 25
M_3-post	0 / 0	0 / 0	0 / 0	0 / 0	7 / 24	2 / 8	5 / 11	16 / 67

Mandibular Landmark Data. Non-parametric analyses were executed on mandibular landmark data. Variables were selected on the basis of sample size. Mandibular height dimensions and robustness indices were recorded at each tooth on both the lingual and buccal aspects of the mandibles, but only the variable with the largest sample size is presented and discussed. However, when the overall sample size between two equivalent variables [such as buccal mandibular height at M_1 (M1eM1b) and lingual mandibular height at M_1 (M1lM1b)] was identical, the variable selected was that which included a larger sample of non-robust specimens (as the sample of *A. robustus* is the largest mandibular fossil sample included in this study). All analyses were based on 2 tailed tests with $\alpha = 0.05$. A Bonferroni correction was not implemented as the small samples and temporal and geographic variation make significance testing with Bonferroni or sequential Bonferroni adjustments to α-levels overly conservative. It has been argued that the best way to deal with multiple statistical tests is to discuss the results in light of p-values, statistical power, and trends within the results rather than to use traditional corrections that increase Type II errors to unacceptable levels [see discussions in Moran (2003) and Nakagawa (2004)]. In consideration of the low sample sizes of the fossils analyzed in this study, it is probably more biologically meaningful to discuss the actual p-values, trends, and sample sizes produced than it is to restrict discussions to only those variables that exceed conservative and rigid α-levels.

Non-parametric Mann-Whitney U analyses were executed to assess 1) Makapansgat and specimens of *A. africanus* from Sterkfontein and 2) Makapansgat and a pooled sample of *A. robustus*. Results of these analyses and sample sizes are presented in Table 7-5. The Makapansgat mandibles were found to be statistically indistinguishable from the sample of *A. africanus* in mandibular thickness. The Makapansgat mandibles were found to be significantly different from the sample of *A. robustus* in the thickness of the mandible at M_1 ($p = 0.05$, $N = 19$) and approached significance in the lower powered test of the thickness of the mandible at M_2 ($p = 0.07$, $N = 15$). The samples of *A. africanus* and *A. robustus* were significantly different in mandibular thickness at M_1, M_2, and M_3 ($p_1 = 0.003$, $N_1 = 21$; $p_2 = 0.02$, $N_2 = 18$; and $p_3 = 0.01$, $N_3 = 10$) and approached significance at P_4 ($p = 0.07$, $N = 16$). In terms of trends, the mandibular thickness data are somewhat inconsistent for Makapansgat. The Makapansgat mandibular thicknesses are more similar to the sample of *A. robustus* at P_3 and P_4, while they are discriminated to some degree from the sample of *A. robustus* at M_1, M_2, and M_3.

Dimensions representing the height of the mandible at M_1, M_2, and M_3 could not differentiate the Makapansgat sample from specimens of either *A. africanus* or *A. robustus*. However, the samples of *A. africanus* and *A. robustus* were significantly different in lingual mandibular height at M_2 ($p = 0.04$; $N = 18$) and approached significance in buccal mandibular height at M_3 ($p = 0.07$; $N = 12$). The mandibular heights of the Makapansgat sample were more similar to those of *A. robustus* than *A. africanus*. In light of these results, it is not surprising that the Makapansgat mandibles could not be statistically distinguished from the samples of *A. africanus* or *A. robustus* in indices of mandibular robustness.

TABLE 7-5: Significance Testing of Mandibular Variables for Makapansgat versus A. africanus, *Makapansgat versus* A. robustus, *and* A. robustus *versus* A. africanus *via Non-Parametric Mann-Whitney U.*

Variable	N Mak	N *A. afric*	N *A. rob*	Exact Significance (Mak/*A. afric*)	Exact Significance (Mak/*A. rob*)	Exact Significance (*A. afric*/*A. rob*)
P_3 Corpus thickness	4	5	7	0.11	0.79	0.15
P_4 Corpus thickness	4	6	10	0.26	0.73	0.07†
M_1 Corpus thickness	7	9	12	0.47	0.05*	0.003*
M_2 Corpus thickness	6	9	9	0.22	0.07†	0.02*
M_3 Corpus thickness	5	5	5	0.95	0.31	0.01*
M_1 Corpus height (ext)	3	8	12	0.77	0.84	0.38
M_2 Corpus height (ling)	3	7	11	0.27	0.77	0.04*
M_3 Corpus height (ext)	3	4	8	0.40	1.00	0.07†
M_1 mandibular robustness (ext)	3	7	10	0.52	0.77	0.36
M_2 mandibular	3	7	8	0.83	0.50	0.69

robustness (ling)						
M_3 mandibular robustness (ext)	3	3	5	---±	0.57	0.39

*Significant at α = 0.05
†Approaching significance
± Excluded from analyses on the basis of sample sizes

Multivariate analyses were executed on mandibular variables. Both PCA and DFA were selected as ways to examine variation. Variables were selected for multivariate analysis on the basis of being biologically meaningful as well as both maximizing sample sizes and considering cross-correlation among variables (Tables 7-6 and 7-7). As PCA excludes specimens with missing data, the australopith specimens included in analyses were limited. Regardless, the larger extant primate comparative sample provides a basis for discussion of the smaller fossil sample sizes. Results of a PCA of non-size-standardized data for mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale) are available in Figure 7-12a & b. These same variables were size-standardized by the geometric mean and results of a PCA of these data are available in Figure 7-13a & b. A cross-correlation table of the raw variables for these analyses is available in Table 7-6. Pogonion height consistently exhibited the lowest cross-correlations. This is a result of the relatively unusual pogonion height values for modern humans due to the presence of a procumbent chin.

The non-size-standardized PCA (Figure 7-12) produced results where principal component (PC) 1 explains 73% of the variance, PC 2 explains 19% of the variance, PC 3 explains 5% of the variance, PC 4 explains 2% of the variance, and PC 5 explains 1% of the variance. PC 1 explains over 88% of the variance for all but one variable (97% of P_3 mandibular thickness, 97% of genion height, 95% of symphyseal thickness, and 89% of lingual distance between bilateral P_3s). A large percentage of the variance explained by PC 1 likely can be accounted for by size differences within the sample. Pogonion height, however, exhibits a value of -28% in the component matrix for PC 1. PC 2 explains 96% of the variance in pogonion height and only a small portion of the variance in other variables (18% of lingual distance between bilateral P_3s, 13% of symphyseal thickness, 3% of P_3 mandibular thickness, and - 4% of genion height). The discrepancy with pogonion height can be explained in part by the morphologically distinct human chin. PC 3 explains 23% of genion height and 4% of pogonion height, but exhibits negative values for P_3 mandibular thickness, symphyseal thickness, and lingual distance between bilateral P_3s.

Principal components 1, 2, and 3 were plotted to assess groupings of taxa. A plot of PC 1 by PC 2 produced clear groupings of most extant primates, albeit much of this appears due to size differences within PC 1. Modern humans are distinguished from other extant primates by large PC 2 values. As PC 2 values are largely driven by pogonion height, the distinction of humans relative to all other taxa is not surprising. The fossil hominins primarily group within the chimpanzee and gorilla clusters. These include all of the specimens from Makapansgat included in analyses (MLD 2, MLD 18, MLD 27), the only specimen of *A. africanus* (STS 52), one of the two specimens of *A. robustus* (SKW 5), and the only fossil member of genus *Homo* included in this analysis (SK 15). As the fossil hominins are essentially chimpanzee-sized and do not exhibit a distinct chin, they are indistinguishable from each other. One robust australopith stands out by plotting closest to modern humans (SK 23). This placement is driven by pogonion height as the SK 23 mandible exhibits a vertical symphysis. While this specimen does not exhibit a true chin, pogonion was recorded on the inferiormost portion of the vertical symphysis. Part of the distinctiveness of this mandible is related to its symphyseal morphology, while part of it is due to methodology regarding the recording of pogonion in a relatively vertical symphysis.

A plot of PC 2 by PC 3 produced nicely differentiated clusters for the extant primates. Macaques are particularly tightly clustered to the exclusion of all other taxa. Chimpanzees and gorillas overlap considerably on PC 2, but are discriminated on the basis of PC 3 (driven primarily by genion height). Humans are clearly distinguished from all other taxa. The fossil hominins included in this PCA fall essentially within the gorilla cluster, with the exception of SK 23. The latter is distinguished from all other primates on the basis of values for PCs 2 and 3, driven by a somewhat anomalous pogonion height.

A PCA of these variables size-standardized by the geometric mean (Figure 7-13) explains 72% of the variance in PC 1, 17% in PC 2, 6% in PC 3, 3% in PC 4, and 2% in PC 5. PC 1 explains a large percentage of the variance for each variable (92% of mandibular thickness at P_3, 90% of genion height, 84% of symphyseal thickness, 57% of lingual distance between bilateral P_3s, and - 96% of pogonion height. PC 2 is largely driven by lingual distance between bilateral P3s, explaining 80% of the variance of that variable (as well as 1% of the variance in genion height). PC 2 includes a number of negative results, - 40% for symphyseal thickness, - 20% for lingual distance between bilateral P3s, and - 6% for pogonion height.

The first three principal components for these size-standardized data were plotted. The plot of PC 1 by PC 2 clearly distinguishes modern humans from all other taxa, primarily on the basis of PC 1. Chimpanzees and gorillas can be distinguished from each other with little overlap, however, macaques exhibit significant overlap with both gorillas and chimps. A gorilla outlier (FMNH 18402) can be attributed to its particularly low value for pogonion height. Most of the fossil hominins plot within the gorilla-macaque cluster (MLD 2 and MLD 18 from Makapansgat, STS 52 of *A. africanus*, and SKW 5 of *A. robustus*, and SK 15 of *Homo*). SK 15 and MLD 27 plot together on the border of the gorilla and chimpanzee clusters. SK 23 is distinguished from all other specimens, in large part due to pogonion height. The plot of PC 2 by PC 3 does not cluster well for the extant primate samples, although gorillas and chimpanzees can be distinguished to some degree.

Comparison of the PCA of both raw variables and those standardized by the geometric mean indicate that modern humans can be clearly distinguished on the basis of mandibular variables, but the fossil hominins included in these PCAs cannot be differentiated from apes (and size-standardized macaques). Although SK 23 is an exception, this is likely due to the combination of both methodology and a relatively vertically oriented symphysis in a thick ape-like mandible.

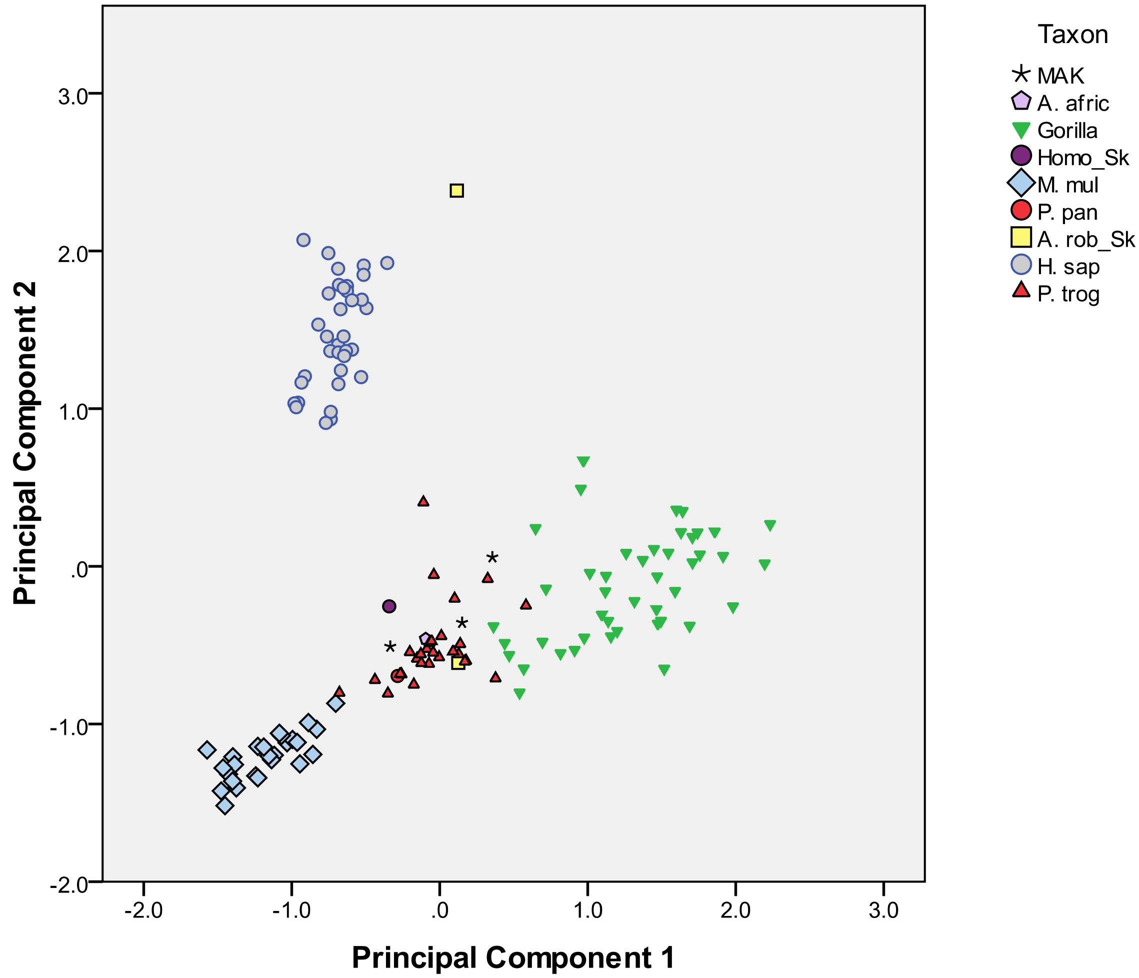
PCAs of both the raw data and data size-standardized by the geometric mean were recalculated for the same variables (mandibular symphyseal thickness, mandibular thickness at P3, lingual distance between bilateral P_3s, and genion height), with the exclusion of pogonion height to assess its impact on previous PCA results. Results of these analyses are available in Figures 7-14 and 7-15. For the PCA of the raw variables, PC 1 explains 89% of the variance, PC 2 explains 7% of the variance, PC 3 explains 3% of the variance, and PC 4 explains 1% of the variance. With the exception of modern humans, PC 1 seems largely size related and explains a minimum of 90% of the variance for each variable. PC 2 is primarily driven by lingual distance between bilateral P_3s. Plotting of PCs 1 and 2 produced a clear macaque cluster, a large gorilla cluster, and slight overlap in the modern human and chimp clusters. Several of the fossil hominins can be distinguished from the comparative sample as a small cluster, including MLD 2, MLD 18, STS 52, and SK 15. This is an interesting result, considering the fact that this small cluster includes specimens typically attributed to the species of *A. africanus* from Makapansgat and Sterkfontein, as well as attributed to *Homo* from Swartkrans [the latter being a specimen argued to be a new species of *Homo* (Curnoe, 2006)]. MLD 27 is positioned in the region of overlap of the chimp and gorilla clusters. SK 23 is again positioned separately from all other specimens, even without the inclusion of the variable pogonion height. The plot of PCs 2 and 3 did not distinguish any groups, and only accounted for a total of only 10% of the variance. The size-standardized PCA of these variables discriminates the extant primates poorly. In essence, pogonion height and size contribute a large part of the discriminatory ability of PCA of selected mandibular variables.

A Discriminant Function Analysis (DFA) of the variables utilized in the first PCAs, mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale), was calculated as DFA 1. A second DFA was analyzed for mandibular symphyseal thickness, mandibular thickness at M_1, lingual distance between bilateral P_3s, and pogonion height. While DFA and PCA are both multivariate methods, they attempt to explain variance in slightly different ways. PCA works to maximize the variance explained for each variable, while DFA seeks to maximize the variance explained for each identified group. DFA permits cases to be ungrouped and assessed on the basis of standard deviations to group centroids. MLD 2 was included in mandibular analyses as it is considered an important mandibular specimen from Makapansgat. However, a series of extant specimens at comparable developmental stages were also included in these mandibular analyses to provide a basis with which to assess MLD 2.

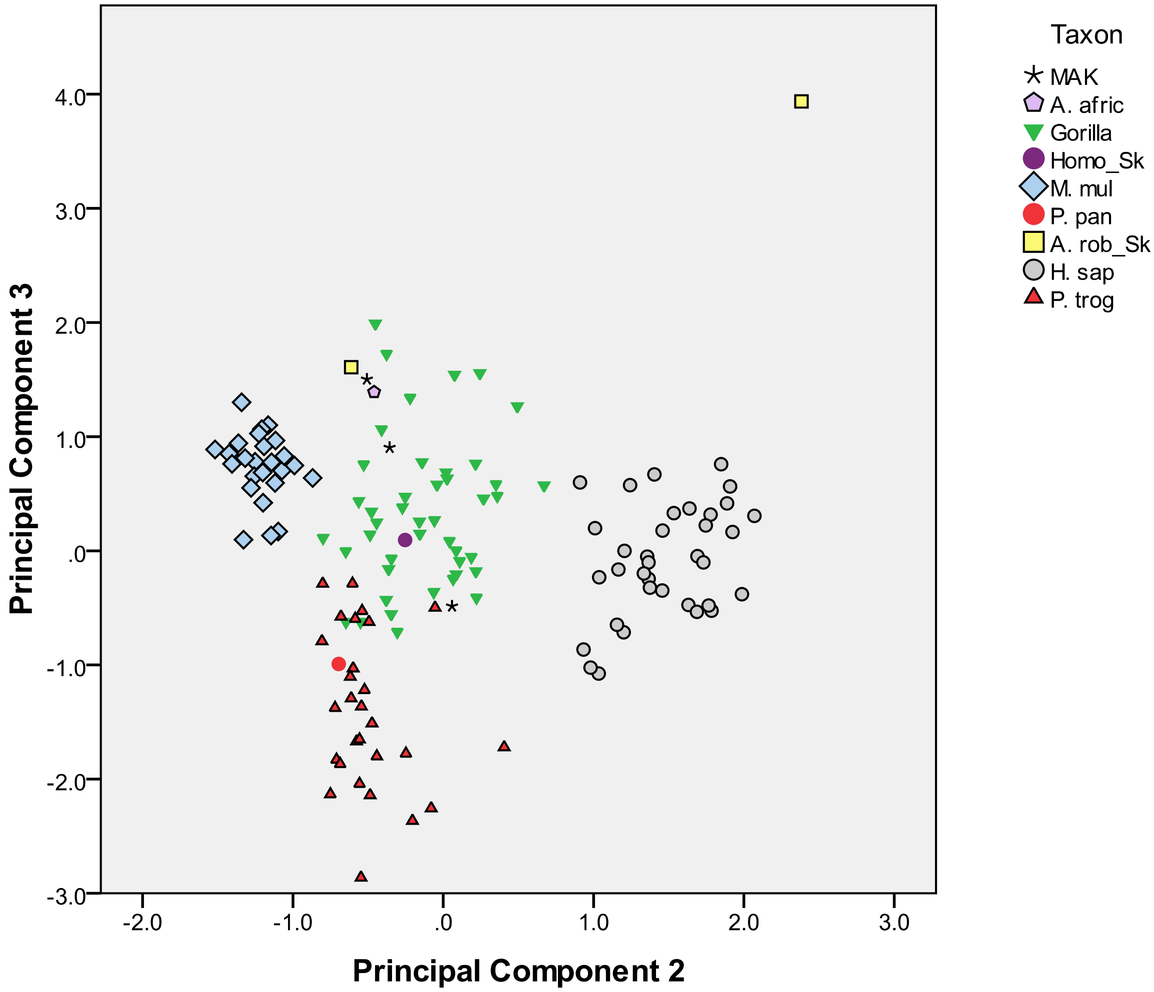
The first DFA produced excellent clusters for each of the extant primates. The centroid for robust australopiths nestled distantly between the values for SKW 5 and SK 23, the latter plotting closest to the modern human centroid. The Makapansgat hominins MLD 2 and MLD 18 were assigned to the group for the specimens of *A. africanus*, while MLD 27 was assigned to the group for the specimens of fossil *Homo*. Despite the designation, MLD 27 is closely affiliated with the groups for fossil *Homo* (based solely upon the SK 15 specimen), *A. africanus*, and *Pan*. In essence, essentially all of the fossils included in this analysis, with the exception of the human-like SK 23, cluster reasonably close together. MLD 27 and SKW 5 both sit just outside the chimpanzee cluster.

The second DFA similarly produced tight clusters for the extant primates. However, the fossil plots are better discriminated in comparison to DFA 1. The two robusts were distantly positioned with SKW 5 plotting with the gorillas and SK 23 plotting closest to the modern human cluster (but this time closer to the weak "robust" centroid). The Makapansgat hominins MLD 2 and MLD 18, *A. africanus* (STS 52), and SK 15 are again closely positioned. The predictive power of this DFA with regard to the fossils is disappointing and provides little explanatory value.

Figure 7-12a & b: PCA 1 of raw mandibular variables. Variables included in this PCA are mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale), where principal component (PC) 1 explains 73% of the variance, PC 2 explains 19% of the variance, and PC 3 explains 5% of the variance.

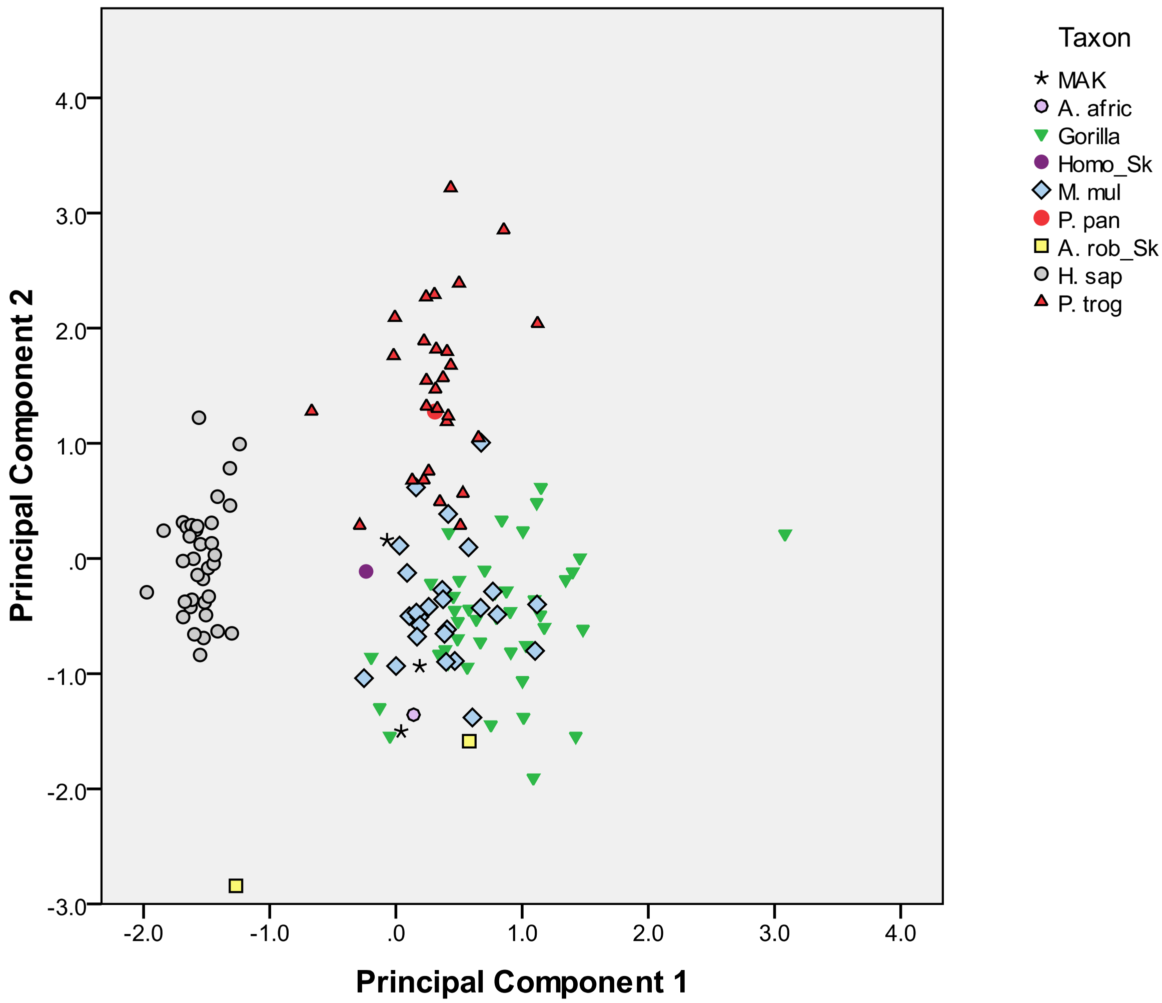


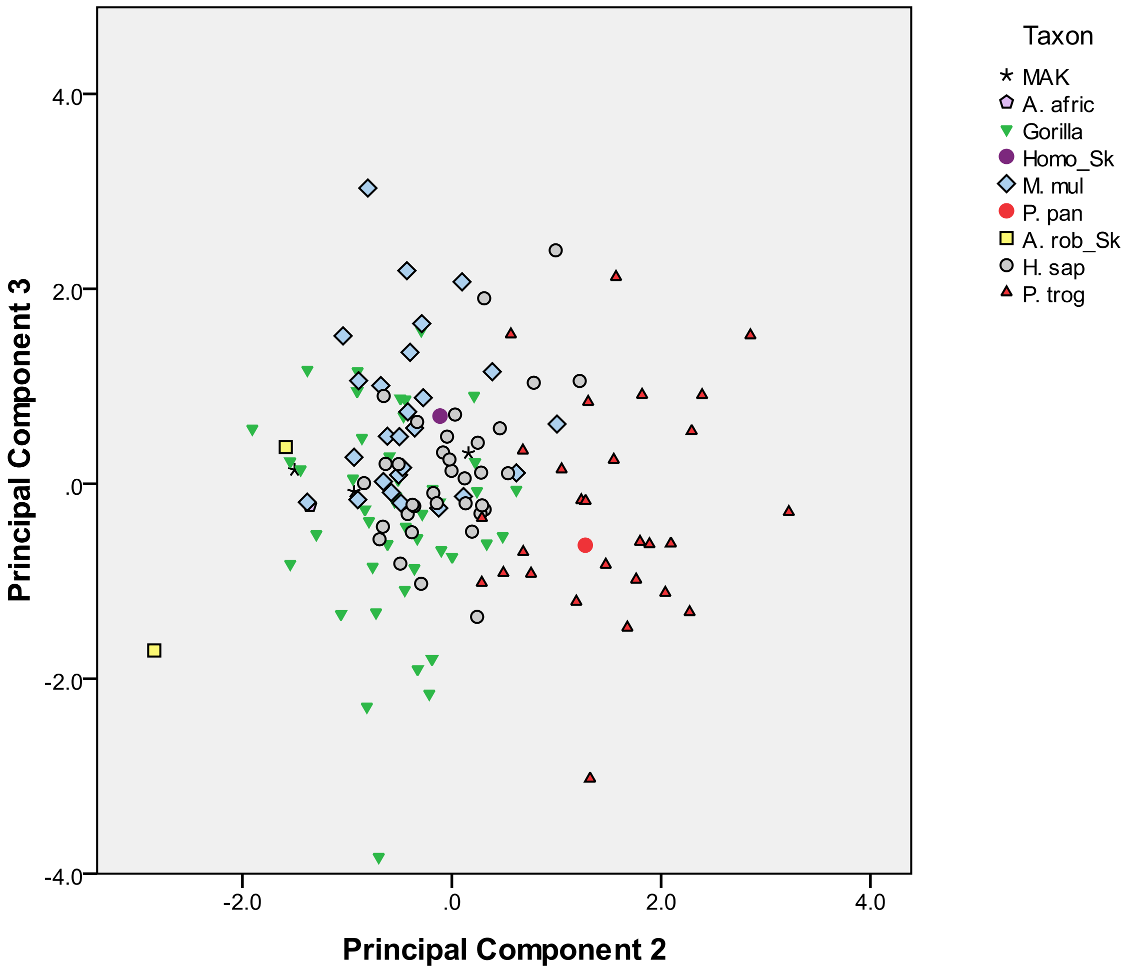
Taxon
MAK
A. afric
Gorilla
Homo_Sk
M. mul
P. pan
A. rob_Sk
H. sap
P. trog
Principal Component 2
3.0
2.0
1.0
.0
-1.0
-2.0
-2.0
-1.0
.0
1.0
2.0
3.0
Principal Component 1



Taxon
MAK
A. afric
Gorilla
Homo_Sk
M. mul
P. pan
A. rob_Sk
H. sap
P. trog
4.0
3.0
2.0
1.0
.0
-1.0
-2.0
-3.0
-2.0
-1.0
.0
1.0
2.0
3.0
Principal Component 3
Principal Component 2

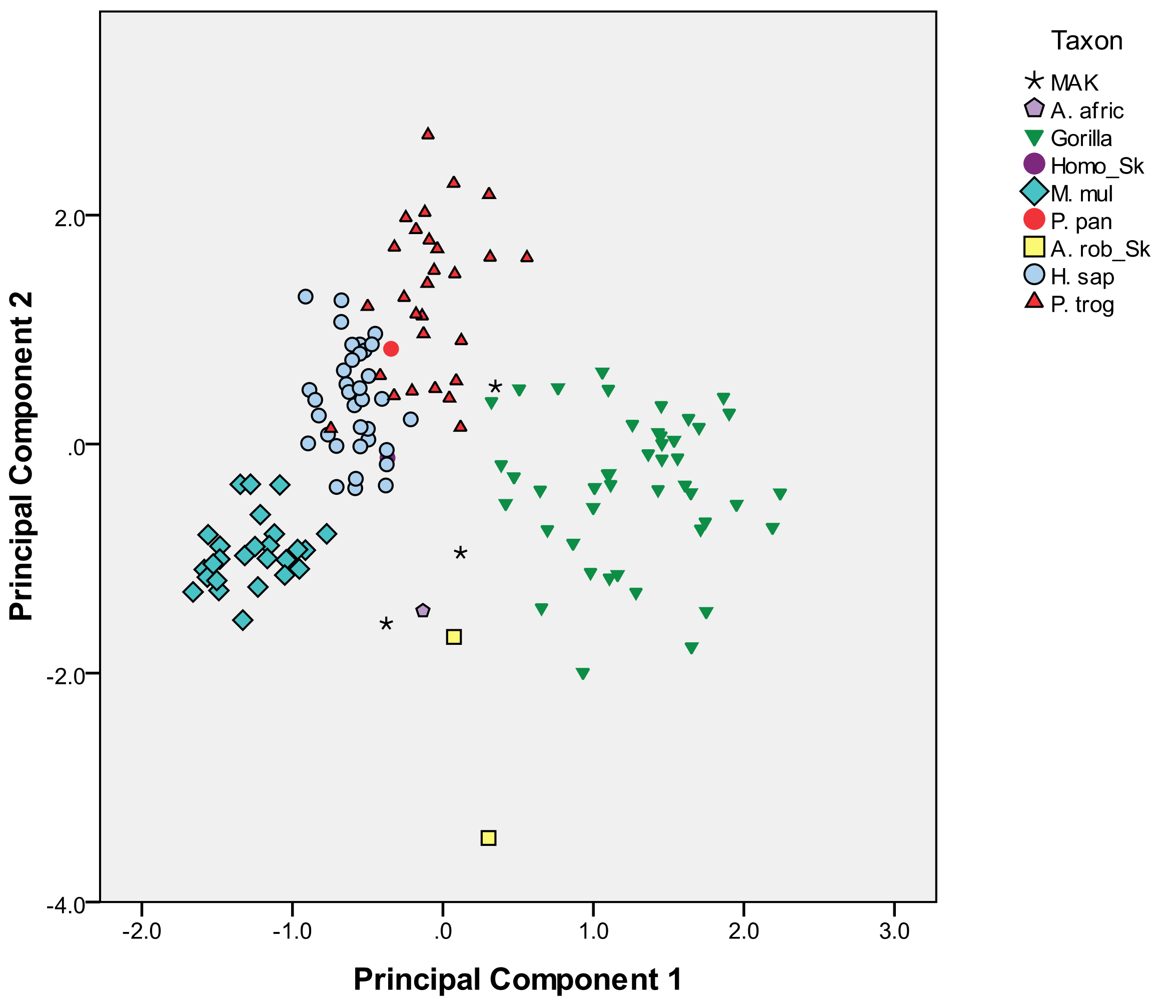
Figure 7-13a & b. PCA 1 of variables size standardized by the geometric mean. Variables included in this PCA are mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale), where PC 1 explains 72%, PC 2 explains 17%, PC 3 explains 6%, PC 4 explains 3%, and PC 5 explains 2% of the variance.





Principal Component 3
Principal Component 2
4.0
2.0
.0
-2.0
-4.0
-2.0
.0
2.0
4.0
Taxon
MAK
A. afric
Gorilla
Homo_Sk
M. mul
P. pan
A. rob_Sk
H. sap
P. trog

Figure 7-14a & b. PCA 2 of raw mandibular variables. Variables included in this PCA are mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), and genion height (genion-linguale), where PC 1 explains 89%, PC 2 explains 7%, PC 3 explains 3%, and PC 4 explains 1% of the variance for these data.



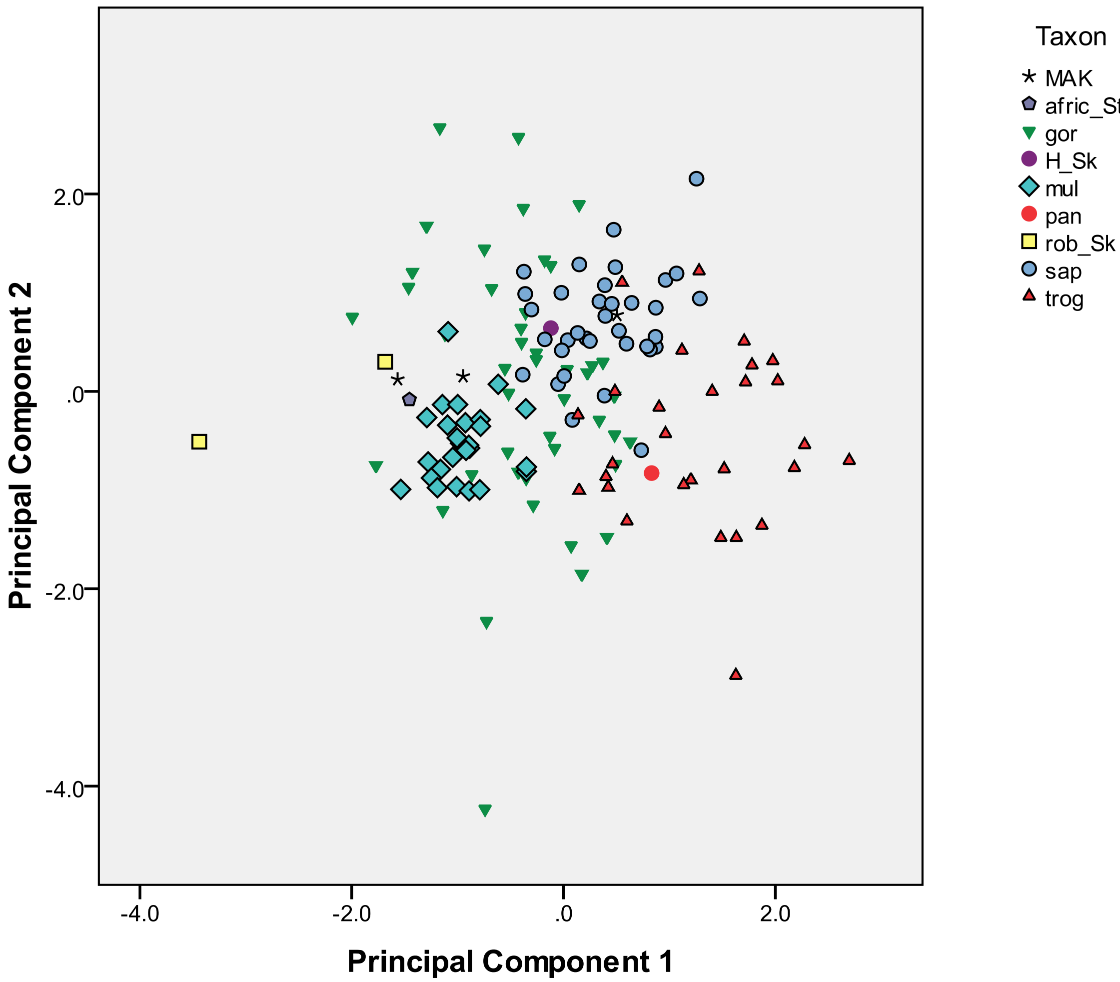
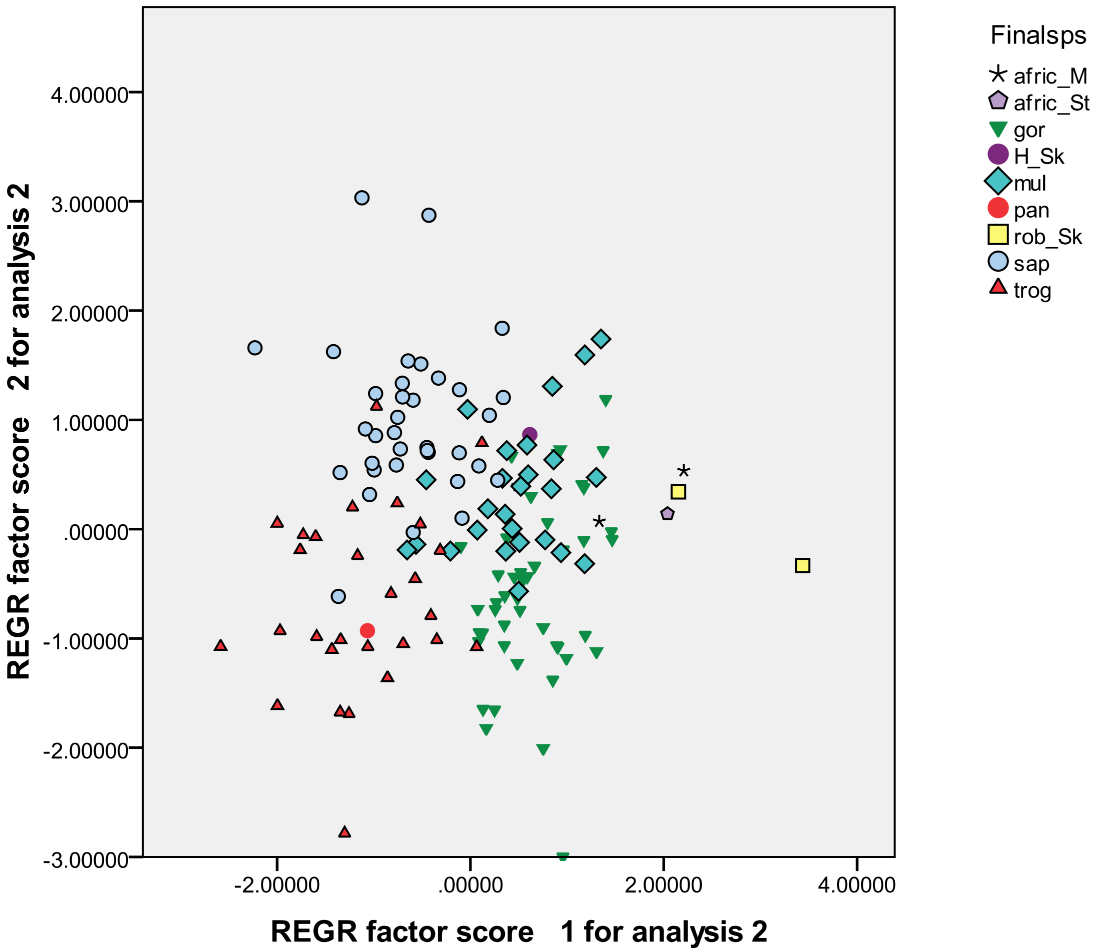
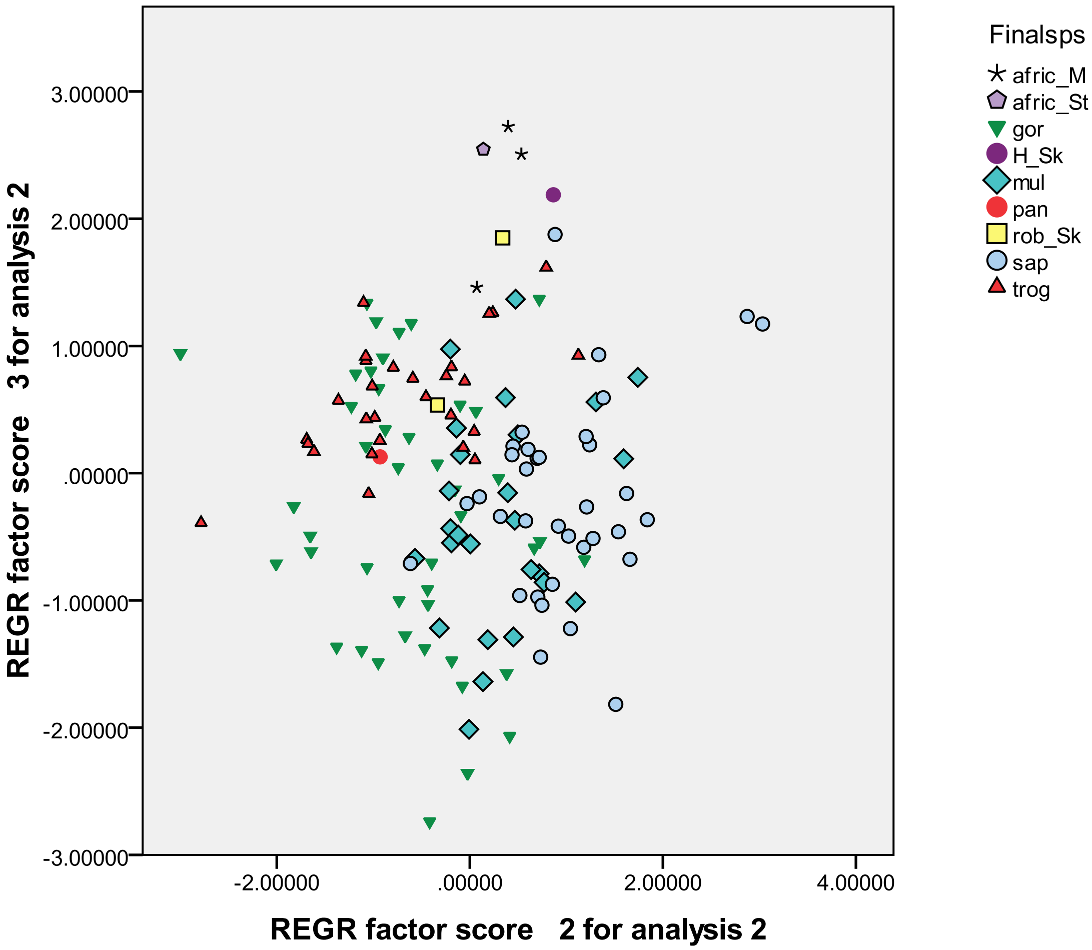

Taxon
MAK
afric_St
gor
H_Sk
mul
pan
rob_Sk
sap
trog
2.0
.0
-2.0
-4.0
Principal Component 2
-4.0
-2.0
.0
2.0
Principal Component 1

Figure 7-15a & b. PCA 2 of variables size standardized by the geometric mean. Variables included in this PCA are mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), and genion height (genion-linguale), where principal component (PC) 1 explains 44%, PC 2 explains 37%, PC 3 explains 18%, and PC 4 explains < 1% of the variance.





Finalsps
afric_M
afric_St
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H_Sk
mul
pan
rob_Sk
sap
trog
3.00000
2.00000
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-1.00000
-2.00000
-3.00000
REGR factor score 3 for analysis 2
-2.00000
.00000
2.00000
4.00000
REGR factor score 2 for analysis 2

Table 7-6: Variable Cross-Correlation. Similarity matrix of mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale; pgid), and genion height (genion-linguale; geli).

	sw__rt	P3w	biP3l	pgid	geli
sw__rt	1.000	.934	.773	-.142	.894
P3w	.934	1.000	.804	-.240	.928
biP3l	.773	.804	1.000	-.097	.825
pgid	-.142	-.240	-.097	1.000	-.298
geli	.894	.928	.825	-.298	1.000

Figure 7-16*: *DFA 1 of Mandibular Variables. Variables include symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale) where DF 1 explains 62% and DF 2 28% of the variance in data.

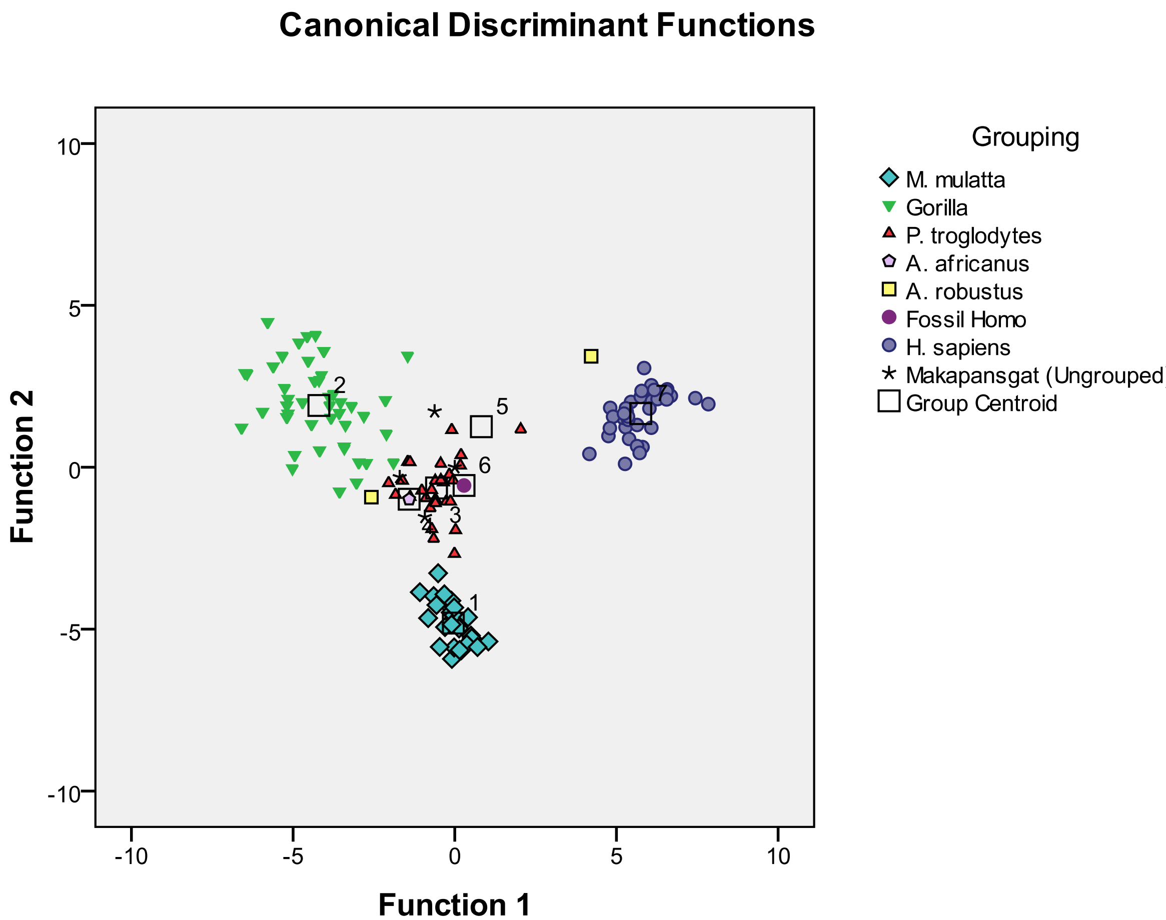


TABLE 7-7: Pooled Within Group Correlations for DFA of Mandibular Variables. Variables include mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale) where DF 1 explains 62% and DF 2 28% of the variance in data.

Variable	DF 1	DF 2
Pogonion Height	0.668	0.577
Lingual Distance between P3s	-0.329	0.740
Corpus Thickness at P3	-0.531	0.702
Symphyseal Thickness	-0.442	0.678
Genion Height	-0.448	0.505

TABLE 7-8: Classification Matrix for DFA of Mandibular Variables. Variables include mandibular symphyseal thickness (sw_rt), mandibular thickness at P3 (P3_w), lingual distance between bilateral P_3s (bi-P3l), pogonion height (pogonion-infradentale), and genion height (genion-linguale) where DF 1 explains 62% and DF 2 28% of the variance in data.

Specimen Number	# of Missing Values	Actual Group	1st Predicted Group	*p*	2nd Predicted Group	*p*
MLD 18	0	Ungrouped	*A. africanus*	0.77	Fossil *Homo*	0.15
MLD 2	0	Ungrouped	*A. africanus*	0.98	Fossil *Homo*	0.02
MLD 27	0	Ungrouped	Fossil *Homo*	0.16	*A. africanus*	0.01
Sts 52	0	*A. africanus*	*A. africanus*	1.00	Fossil *Homo*	0.01
SK 23	0	*A. robustus*	*A. robustus*	0.00	*H. sapiens*	0.00
SKW 5	0	*A. robustus*	*A. africanus*	0.87	*A. robustus*	0.00

Figure 7-17: DFA 2 of Mandibular Variables. Variables include mandibular symphyseal thickness (sw_rt), mandibular thickness at M_1 (M1w), lingual distance between bilateral P_3s (bi-P3l), and pogonion height (pogonion-infradentale), where DF 1 explains 54% and DF 2 33% of the variance in data.

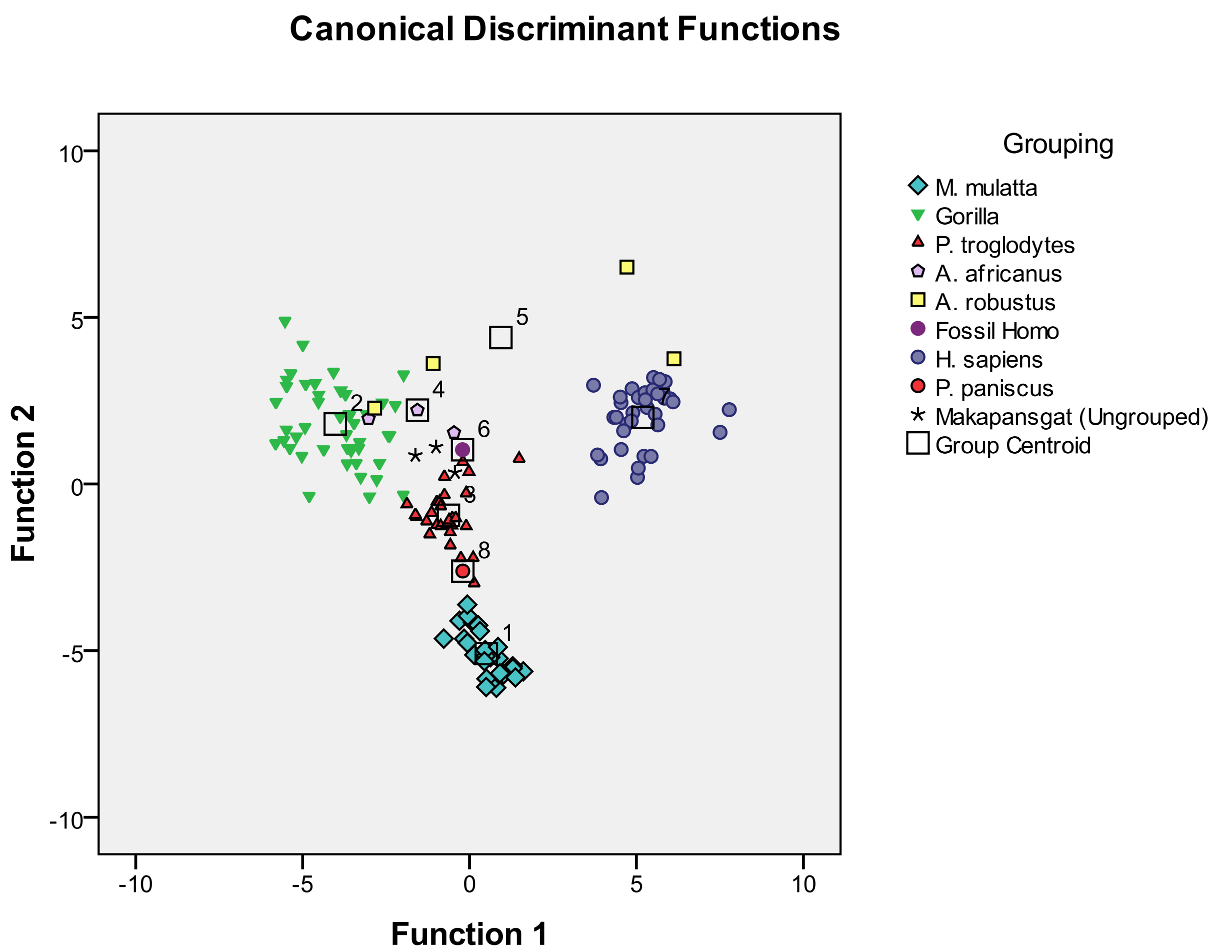


TABLE 7-9: Pooled Within Group Correlations for DFA of Mandibular Variables. Variables include mandibular symphyseal thickness (sw_rt), mandibular thickness at M_1 (M1w), lingual distance between bilateral P_3s (bi-P3l), and pogonion height (pogonion-infradentale), where DF 1 explains 54% and DF 2 33% of the variance in data.

Variable	DF 1	DF 2
Pogonion Height	0.693	0.602
Corpus Thickness at M1	-0.418	0.814
Lingual Distance of P3s	-0.396	0.603
Symphyseal Thickness	-0.504	0.584

TABLE 7-10: Classification Matrix for DFA of Mandibular Variables. Variables include symphyseal thickness (sw_rt), mandibular thickness at M_1 (M1w), lingual distance between bilateral P_3s (bi-P3l), and pogonion height (pogonion-infradentale), where DF 1 explains 54% and DF 2 33% of the variance in data.

Specimen Number	# of Missing Values	Actual Group	1st Predicted Group	*p*	2nd Predicted Group	*p*
MLD 18	0	Ungrouped	Fossil *Homo*	0.42	*A. africanus*	0.00
MLD 2	0	Ungrouped	*A. africanus*	0.63	Fossil *Homo*	0.02
MLD 27	1	Ungrouped	*P. troglodytes*	0.56	*P. paniscus*	0.04
Sts 36	1	*A. africanus*	Fossil *Homo*	0.71	*P. troglodytes*	0.00
Sts 52	0	*A. africanus*	*A. africanus*	1.00	*A. robustus*	0.00
Sts 7	2	*A. africanus*	*A. africanus*	0.13	Fossil *Homo*	0.04
SK 23	0	*A. robustus*	*A. robustus*	0.00	*A. africanus*	0.00
SK 74/74a	2	*A. robustus*	*H. sapiens*	0.25	*P. troglodytes*	0.00
SK 81	2	*A. robustus*	*A. africanus*	0.15	*A. robustus*	0.01
SKW 5	0	*A. robustus*	*A. africanus*	0.75	*A. robustus*	0.00

Morphology of the Makapansgat Mandibular Sample. The Makapansgat mandibular sample can be generalized by a few features. Features of the sample are discussed by region in the following pages, particularly where overlapping regions are preserved. There is a preservation bias resulting in a greater sample of the distal portions of the mandibular corpus at Makapansgat. Few symphyses and even fewer mandibular rami are preserved within the Makapansgat sample, making generalizations of these regions difficult to impossible.

Symphyseal Morphology. The morphology of the mandibular symphysis traditionally has been considered important for phylogenetic and functional reconstructions of fossil hominins (e.g. Weidenreich, 1941; Hylander, 1984, 1985; Daegling, 2001; Dobson and Trinkaus, 2002). One contributing factor is that symphyseal morphology among primate species is well known to be extremely variable. Extant primate mandibular symphyses range in morphology from a vertically-oriented, gracile symphysis with a classic mental trigone for members of the genus *Homo* to a sloping symphysis with large genial muscle attachments for members of the genus *Pan*. Symphyseal morphology is also highly variable among hominin taxa whereby some australopiths (e.g. *A. afarensis*) exhibit apelike and sloping symphyses with extreme genioglossal pitting and the absence of mental trigones, which stands in stark contrast to modern human symphyseal form.

Given the preceding discussion, it may seem somewhat paradoxical that the symphyseal shape of different primates sometimes overlaps considerably (Daegling and

Jungers, 2000; Sherwood *et al.*, 2005; Guy *et al.*, 2007). Adding greater complexity to the goal of classifying the Makapansgat mandibular symphyses is that the morphology of the symphysis can be enormously variable within hominin taxa. Modern humans exhibit significant variation in symphyseal morphology, primarily due to variation in the development of the chin (Guy *et al.*, 2007). Perhaps not surprisingly, the hypodigm of *A. afarensis* has been found to be the most variable hominin taxon in terms of symphyseal morphology (Guy *et al.*, 2007), while temporal, sexual, and geographic variation within the hypodigm of *A. afarensis* may contribute to this variability (see Lockwood *et al.*, 2000; Reno *et al.*, 2003; Reno *et al.*, 2005; Plavcan *et al.*, 2005; Kimbel *et al.*, 2006). Some authors (Guy *et al.*, 2007), however, indicate that while the sample of *A. afarensis* exhibits great variability in symphyseal morphology (including mandibular torus and fossa development), this does not pattern particularly well with temporal variation. Although differences in symphyseal shape are not clearly attributable to sex within most primate species (Daegling and Jungers, 2000; Sherwood *et al.*, 2005; Taylor, 2006), sex has been argued to contribute bias (Daegling and Jungers, 2000; contra Guy *et al.*, 2007).

Producing generalizations regarding the symphyseal morphology of South African hominins is plagued with difficulty due to the likelihood of overlapping morphology in closely related species, the possibility of high within-species symphyseal variation, and the small fossil sample sizes. The Makapansgat sample includes only a handful of specimens preserving the symphyseal region, specifically MLD 2, MLD 18, MLD 27, and MLD 29. On the basis of these four specimens, some preliminary generalizations can be made with the caveat that a larger sample would likely preserve a greater range of variation at Makapansgat.

The external aspect of the symphysis lacks a mental protuberance and slopes posteriorly to varying degrees in all of the preserved symphyses from Makapansgat. The lack of a mental protuberance is to be expected in early South African australopiths. An attempt to quantify the location of the mental protuberance, or lack thereof, was made by recording pogonion height (see Figure 7-18). A receding symphysis is indicated by a low value for pogonion height, as pogonion was recorded wherever the mandibular symphysis was most prognathic (even if that position was subincisal). The appearance of these data for Makapansgat and specimens of *A. africanus* from Sterkfontein is precisely that which is expected for a primitive hominin. However, the data for the sample of *A. robustus* exhibits a considerable range, partially overlapping with the other South African australopiths and partially with modern *Homo*. This lends weight to a few possibilities 1) the sample of *A. robustus* used in this study includes some specimens that should be attributed to *Homo*, 2) the hypodigm of *A. robustus* includes specimens of *Homo*, or 3) the hypodigm of *A. robustus* shares features in the symphysis that are similar to *Homo* (whether due to phylogenetic, functional, or ontogenetic reasons).

A median alveolar jugum extending from the alveolar bone inferiorly is preserved in MLD 2 and MLD 18, although the portion of this region preserved in MLD 27 exhibits a small fossa. The Makapansgat symphyseal region also may be characterized by preserving moderate to marked incisive fossae for attachment of the *levator labii inferioris* and enlarged canine jugae (MLD 2, MLD 18, and arguably MLD 40).

Internally, the symphyseal region of the Makapansgat hominins can be characterized as exhibiting a strongly proximodistally curved and transversely angled symphysis, shallow incisal subalveolar plane, and moderate superior transverse torus.

In some ways, the MLD 2 mandible stands out in its symphyseal morphology. The MLD 2 mandible does not exhibit a clear distinction between the superior and inferior mandibular tori and has little bony development for the attachment of genial musculature. Most notably, MLD 2 is the only specimen preserving the region that does not exhibit a genioglossal fossa or genial pit. All other mandibles from Makapansgat preserve genial pits, as do many specimens of *A. africanus* from Sterkfontein, and several specimens of *A. robustus*. In contrast to the rest of the Makapansgat sample, MLD 2 also fails to demonstrate a clear distinction between the superior and inferior mandibular tori. This is almost certainly related in part to the absence of a genial pit, as well as the comparatively young developmental stage for this specimen. However, it should be noted that this is in contrast to the Taung subadult mandible, which exhibits a deep genial pit and weakly distinct superior and inferior mandibular tori. The presence of a strong genioglossal fossa or genial pit is likely a primitive feature generally indicative of powerful genial musculature. Genioglossal fossae are clearly demarcated and deep in chimps, while gorillas tend to exhibit shallower genioglossal fossae.

The height of genion (the superiormost tip of the mental spine at the symphysis) was recorded for all specimens (see Figure 7-19). Unfortunately, relatively few specimens permitted this measurement. As a group, the robusts exhibited a greater genion height than the sample from Makapansgat. This is likely a reflection of the robusts exhibiting taller mandibles (see discussion below). Only a single specimen of *A. africanus* from Sterkfontein was available for measurement of this dimension.

The height of the symphysis is only available in the MLD 2 mandible at Makapansgat. The MLD 2 symphysis is shorter than any other South African australopith included in this study (see Figure 7-2 and MLD 2 discussion above). Almost certainly, the subadult status of this specimen is a contributing factor. The thickness of the symphysis is preserved in a few specimens from Makapansgat (MLD 2, MLD 18, and MLD 27) whose range encompasses the entire sample of *A. africanus* from Sterkfontein for this dimension (see Figure 7-20). In addition, all three of the Makapansgat specimens fall below the range of variation known for specimens of *A. robustus* in symphyseal thickness.

It is difficult to quantitatively compare the mandibular symphysis without geometric morphometric techniques as linear dimensions do not fully describe the complex morphology of the symphysis. In particular, the thickness of the mandibular corpus may result from expansions of either the superior or inferior tori. Indeed, the expansions of the inferior and superior mandibular tori vary among South African australopiths and even within the Makapansgat sample. Previous work by Guy and colleagues (2007) has indicated that gorillas and some australopiths (*A. afarensis* and *A. bahrelghazali*) have relatively thicker symphyses than chimps, bonobos, modern humans, and orangutans. When these authors examined the symphyseal outline, however, they found that specimens of *A. afarensis* tend to be relatively thicker because of an expansion of the superior torus, whereas gorillas were relatively thicker due to expansion of either the superior or inferior tori. In contrast, these authors found that specimens of *A. bahrelghazali* exhibited a more expanded inferior torus. It is likely that a geometric morphometric examination of the symphyseal region in South African australopiths would be enlightening in terms of patterns of mandibular torus development within and among samples.

Figure 7-18: Pogonion Height. The median (line), 1st and 3rd quartiles (box), and range (bars) of pogonion height (pogonion-infradentale) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant gorilla and chimpanzee samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 27. The fossil sample sizes for this analysis are: *A. africanus* (n = 3), Swartkrans *A. robustus* (n = 3), and Swartkrans *Homo* (n = 1).

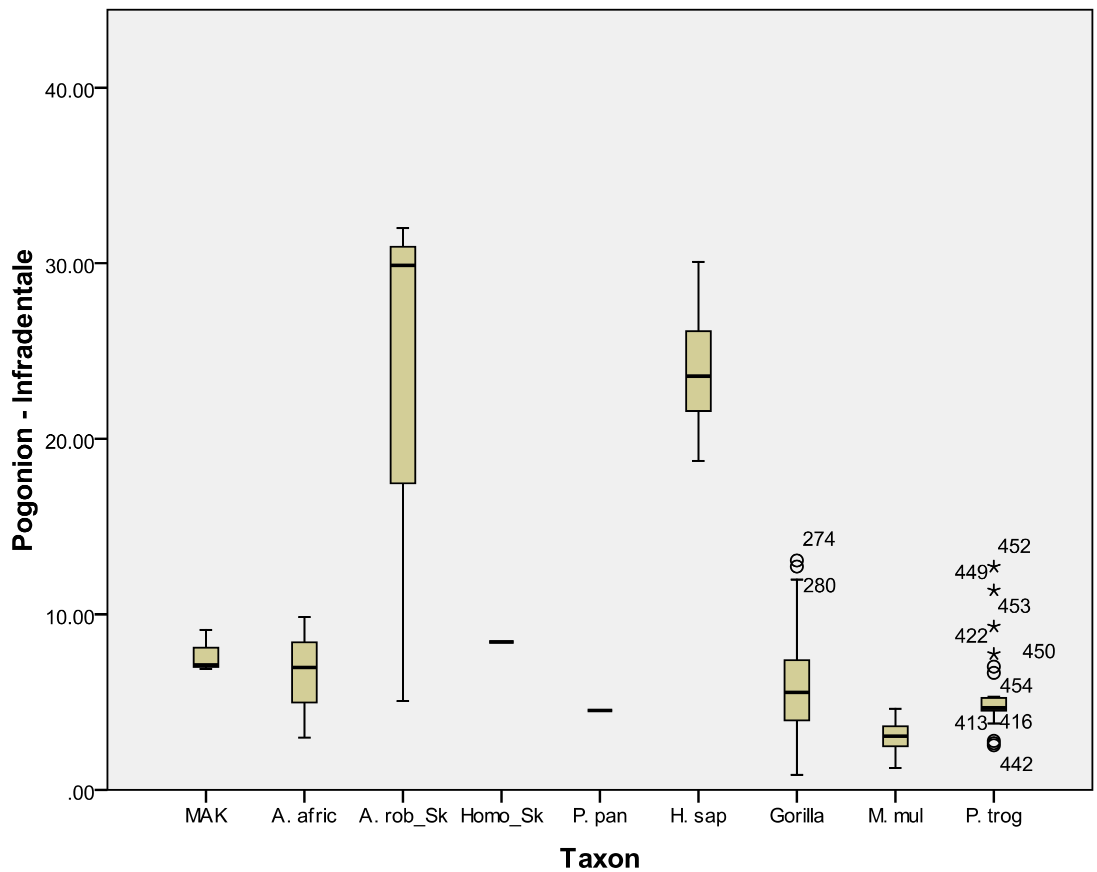


Figure 7-19: Genion Height. The median (line), 1st and 3rd quartiles (box), and range (bars) of genion – linguale (geli) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant gorilla and chimpanzee samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 18, MLD 40, and MLD 34. The fossil sample sizes for this analysis are: *A. africanus* (n = 1), Swartkrans *A. robustus* (n = 3), and Swartkrans *Homo* (n = 1).

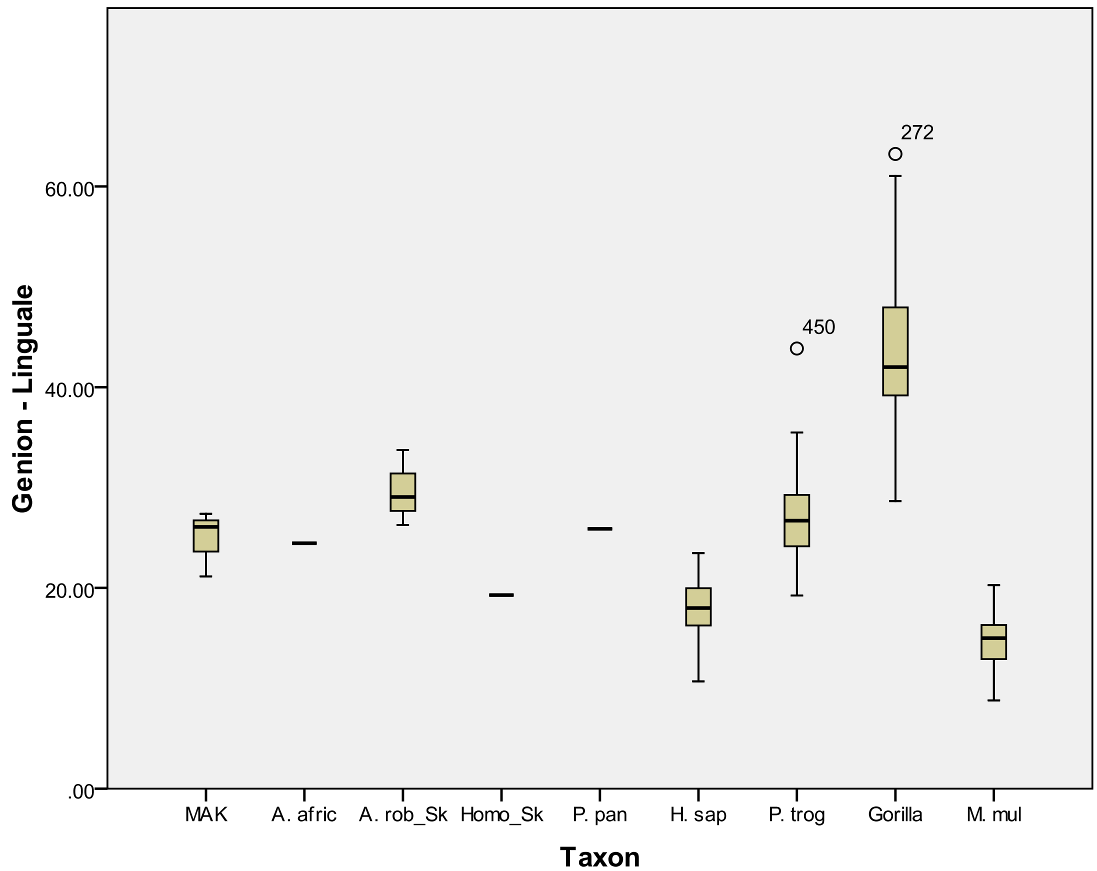
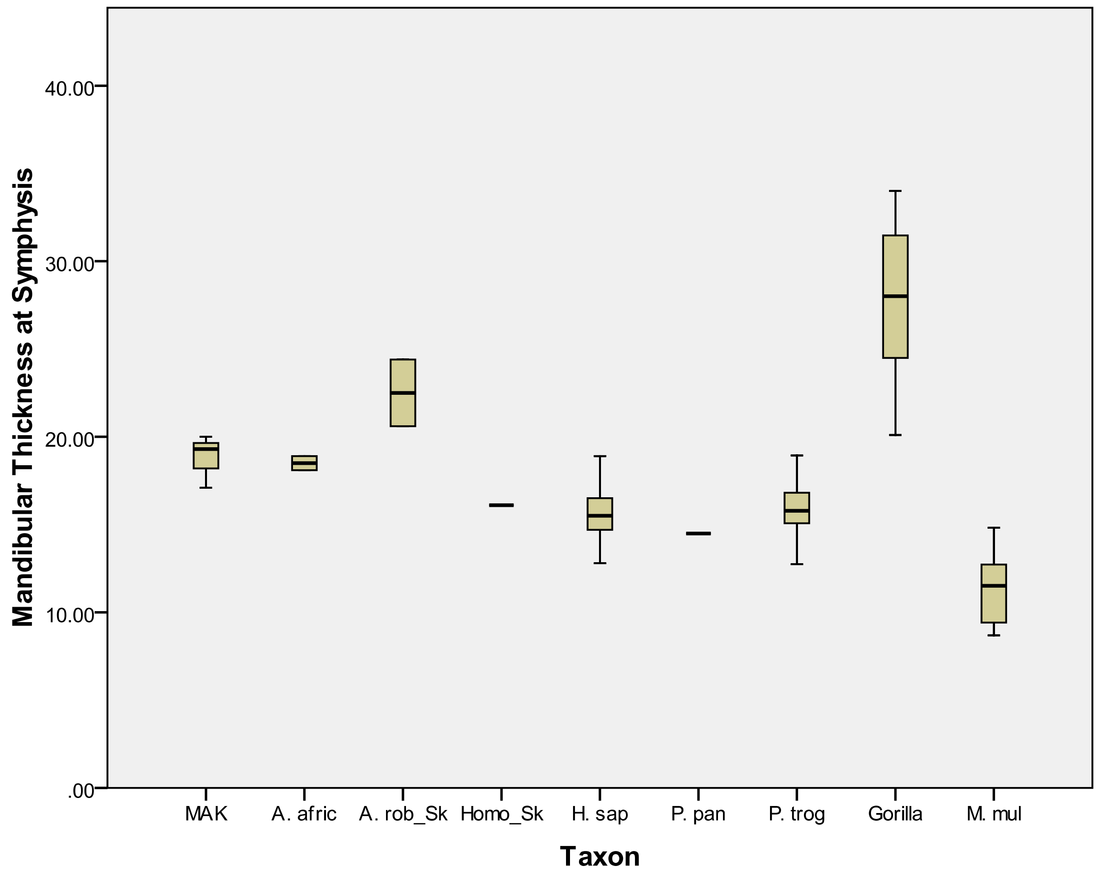


Figure 7-20: Mandibular Thickness at Symphysis. The median (line), 1st and 3rd quartiles (box), and range (bars) of mandibular thickness at the symphysis (sw_rt) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 27. The fossil sample sizes for this analysis are: *A. africanus* (n = 2), Swartkrans *A. robustus* (n = 2), and Swartkrans *Homo* (n = 1).



Corpus Morphology. The region of the mandibular corpus is preserved more frequently than the ramus or symphysis at Makapansgat. The mandibular corpora permit the most thorough evaluation of mandibular size and shape for the Makapansgat sample. Mandibular size and shape have aided reconstructions of dietary adaptations in extant and extinct primates (e.g. Du Brul, 1977; Smith, 1978, 1983; Hylander, 1979, 1985; Bouvier, 1986; Daegling and Grine, 1991; Schwartz and Conroy, 1996; Taylor, 2006). Mandibular dimensions and body mass also have been studied within primates by a variety of authors (e.g. Smith, 1983; Bouvier, 1986; Hylander, 1988; Wood and Aiello, 1998, Taylor, 2005).

The Makapansgat hominins consistently display a moderate to marked lateral prominence, thick mandibular corpus, broad (and occasionally rugose) extramolar sulcus indicating a large area of attachment for the buccinator, and visible but variably developed mylohyoid line. Most specimens from Makapansgat, with the notable exception of MLD 34, also exhibit a broad, blunt mandibular base.

The bi-P_3 lingual breadth of the mandible could not discriminate among hominin samples (Figure 7-21). The Makapansgat hominins are more similar to modern humans and to members of *A. africanus* from Sterkfontein than to other samples in the distance from the mental foramen to the alveolus (Mentale position, Figure 7-22). Even so, many of the samples overlap to some degree and do not clearly discriminate taxa.

There is a strong relationship between both mandibular corpus height and arguably mandibular thickness with body mass across primates (Smith, 1983, Hylander, 1988; Wood and Aiello, 1998). There is evidence that larger bodied taxa exhibit relatively thicker mandibles (Smith, 1983), although it has been argued that the inclusion of a large number of platyrrhines with relatively thin mandibular corpora skewed these results (Hylander, 1988). Other studies provide evidence that larger bodied catarrhine taxa have relatively tall mandibular bodies (Bouvier, 1986). These seemingly conflicting results are likely the result of differences in the taxa included and treatment of sex, whether pooled (Bouvier, 1986; Wood and Aiello, 1998) or single-sex samples (Smith, 1983; Hylander, 1988). However, these relationships are of more limited value when focused exclusively upon closely related species with comparable body mass estimates.

Mandibular thickness was evaluated by non-parametric Mann-Whitney U analyses discussed under Mandibular Landmark Data (above) and examination of boxplots representing the median, first and third quartiles, and range of mandibular thicknesses at a variety of positions (see Figure 7-23 to 7-27). The statistical testing of these data indicated that the Makapansgat sample could be distinguished to some degree from the sample of *A. robustus* in mandibular thickness at the molars but could not be distinguished from the Sterkfontein sample. The examination of boxplots contributes to the discussion as it is clear that the Makapansgat sample exhibits a partially overlapping range, but tendency towards greater mandibular thickness at P_3, P_4, M_1, M_2, and M_3 than the sample of *A. africanus*. This pattern is weakest for M_1 and M_2 mandibular thickness for which the Makapansgat and Sterkfontein samples overlap considerably. Comparison of these Makapansgat data to those of specimens of *A. robustus* illustrates a strange patterning of these data. At P_3, the robusts actually have an enormous range of mandibular thickness, which completely encompasses the range of values exhibited by both the Makapansgat and Sterkfontein samples. To emphasize this range of variation, the mandibular thickness at P_3 for the robusts overlaps partly with both the modern human and gorilla ranges. For the mandibular thickness at M_1, M_2, and M_3, the Makapansgat sample plots in an intermediate position between the samples of *A. africanus* and *A. robustus*. Whereas the mandibular thickness near the molars can be strongly impacted by the position and expansion of the lateral eminence, this does not appear to be the case at P_3. Instead, the mandibular thickness at the premolars is strongly related to the actual corpus expansion or lack thereof.

Mandibular height also was evaluated by non-parametric Mann-Whitney U analyses discussed under Mandibular Landmark Data (above) and examination of boxplots representing the median, first and third quartiles, and range of mandibular heights at a variety of positions (see Figures 7-27 to 7-29). As previously discussed, the samples of specimens attributed to *A. robustus* and *A. africanus* could be distinguished on the basis of mandibular corpus height at M_2 and approached significance at M_3 while the Makapansgat sample could not be distinguished from either taxon. An examination of the plotting of raw data indicate that the Makapansgat sample falls within the ranges of variation for samples of both *A. africanus* and *A. robustus*, although the robusts exhibit a slight tendency towards taller mandibles. The Makapansgat sample tends to exhibit somewhat intermediate mandibular heights (falling on the higher end of the range of *A. africanus* and the lower end of the range of *A. robustus*).

Mandibular robustness was evaluated for the mandible by non-parametric analysis (above) and plotting of boxplots representing raw data (see Figures 7-30 through 7-32).

As discussed above, none of the samples could be distinguished on the basis of statistical analysis. An examination of the median, first and third quartiles, and range illuminate these results. For mandibular robustness at M_1 and M_2, the samples exhibit significant overlap. The robustness of the mandible at M_3 places the Makapansgat mandibles closer to the robusts than to the sample of *A. africanus* from Sterkfontein. This result is driven by mandibular thickness at M_3, as the mandibular heights for all samples overlap considerably. Mandibular robustness at other locations is difficult to distinguish for any of the samples due to considerable overlap of both mandibular thicknesses and heights.

It would be interesting to examine mandibular robustness data for all of the South African australopiths in light of solid dates for their associated deposits. Mandibular corpus height, breath, and size at the level of M_1 were found to increase over time for specimens of *A. afarensis* (Lockwood *et al.*, 2000). These authors suggested that corpus height particularly increased over time for specimens of *A. afarensis*. On the other hand, corpus shape did not appear to change over time for specimens of *A. afarensis*, suggesting that mandibular size does not affect shape in this taxon (Kimbel and White, 1988a; Kimbel *et al.*, 1994; Lockwood *et al.*, 2000). Although a sample of *A. boisei sensu stricto* did not statistically change in size over time (Wood *et al.*, 1994; Lockwood *et al.*, 2000), a non-significant decrease in mandibular robustness was described by some authors (Lockwood *et al.*, 2000). As was the case for the sample of *A. afarensis*, corpus shape and size did not appear to covary in the sample of *A. boisei* despite particularly large differences in corpus size for *A. boisei*. Unfortunately, comparable temporal data are not currently available for the South African australopiths.

Both mandibular height and size are strongly correlated with body mass among species. That said, anthropoids exhibit taller mandibles than prosimians (Hylander, 1979), but cercopithecoids have particularly tall mandibles with regard to body mass (Smith, 1983; Bouvier, 1986; Wood and Aiello, 1998). However, increased corpus thickness has been argued to have a stronger relationship with functional requirements than mandibular height. If so, corpus bending and torsion would increase mandibular corpus thickness in primates to better resist these forces (Wood and Aiello, 1998; contra Smith, 1983). On this basis, Wood and Aiello (1998) argued that these forces are particularly great in robust australopiths and low in *Homo erectus* and *H. ergaster* among hominins. The two robusts examined (*A. boisei* and *A. robustus*) were larger in mandibular corpus size than any anthropoid, while *A. afarensis* and *A. africanus* were considered to resist corpus torsion in the range of anthropoids, *Homo habilis sensu stricto* and *H. rudolfensis* were intermediate, and *H. ergaster H. erectus* were comparable to the low levels for extant apes (Wood and Aiello, 1998). These authors warn, however, that their interpretations are based on the assumption that the mandibular extant and fossil taxa share the same internal structure.

Should Wood and Aiello (1998) be correct, the Makapansgat hominin sample could be argued to have a slightly greater tendency to resist corpus torsion than specimens attributed to *A. africanus* at Sterkfontein. Unfortunately, however, it has also been postulated that mandibular characters exposed to high strain during chewing vary more within species than other aspects of the skull and only poorly discriminate species (Wood and Lieberman, 2001).

It also remains a possibility that a skewed sample biases these interpretations. Extant apes are well known to exhibit sexual dimorphism of the mandible. Orangutan and gorilla mandibles are highly sexually dimorphic, but chimpanzees exhibit lower levels of mandibular sexual dimorphism (Taylor, 2006). Although modern human mandibles are sexually dimorphic (Giles, 1964; Wood *et al.*, 1991; Humphrey *et al.*, 1999), the degree of sexual dimorphism appears to vary with differing human populations (e.g. Humphrey *et al.*, 1999). Mandibular dimorphism in great apes is mainly related to size dimorphism rather than shape dimorphism (Taylor, 2006). Although breadth dimensions tend to be better at distinguishing between sexes within hominoids (Wood *et al.*, 1991).

Figure 7-21: Bi-P_3 Lingual Breadth. The median (line), 1st and 3rd quartiles (box), and range (bars) of bi-P3 lingual breadth (P3l-P3l) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 27. The fossil sample sizes for this analysis are: *A. africanus* (n = 1), Swartkrans *A. robustus* (n = 4), Sterkfontein *Homo* (n = 1), and Swartkrans *Homo* (n = 1).

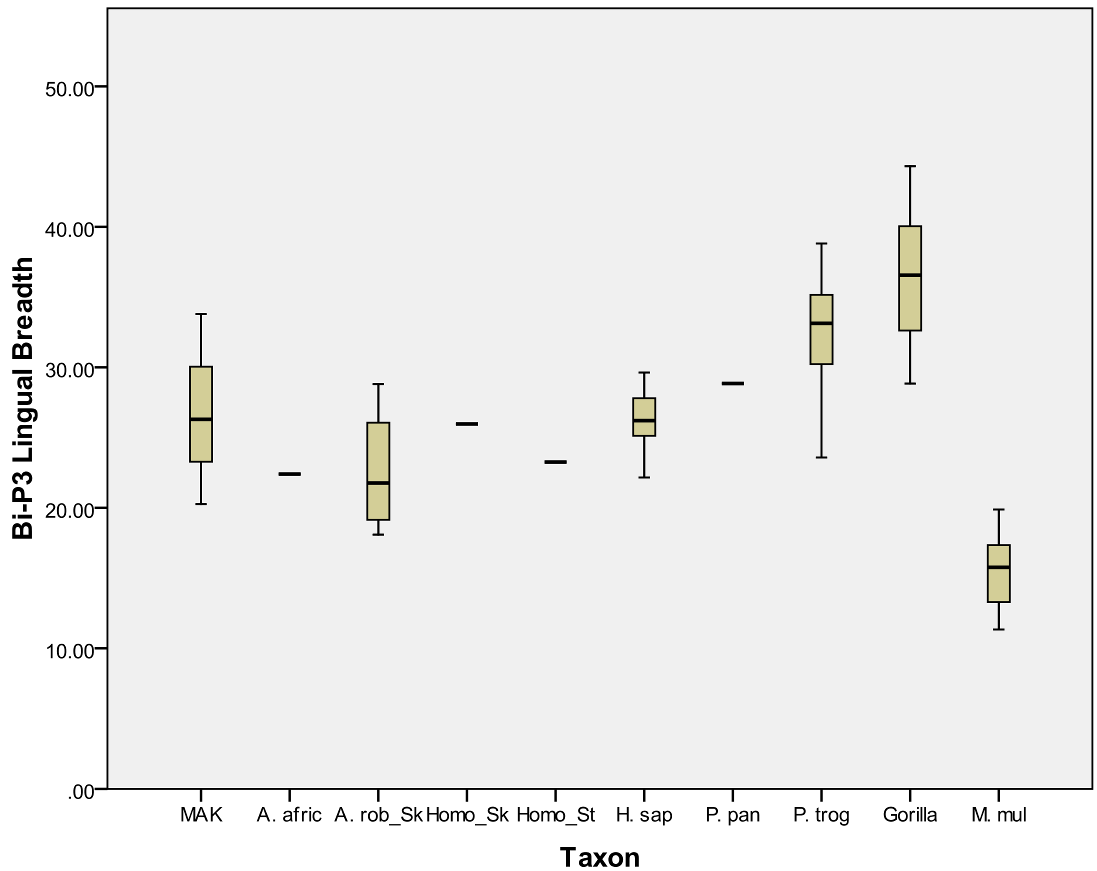


Figure 7-22: Mentale Position. The median (line), 1st and 3rd quartiles (box), and range (bars) of mental foramen height (ml-mfl) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 5), Swartkrans *A. robustus* (n = 7), Kromdraai *A. robustus* (n = 1) and Swartkrans *Homo* (n = 1).

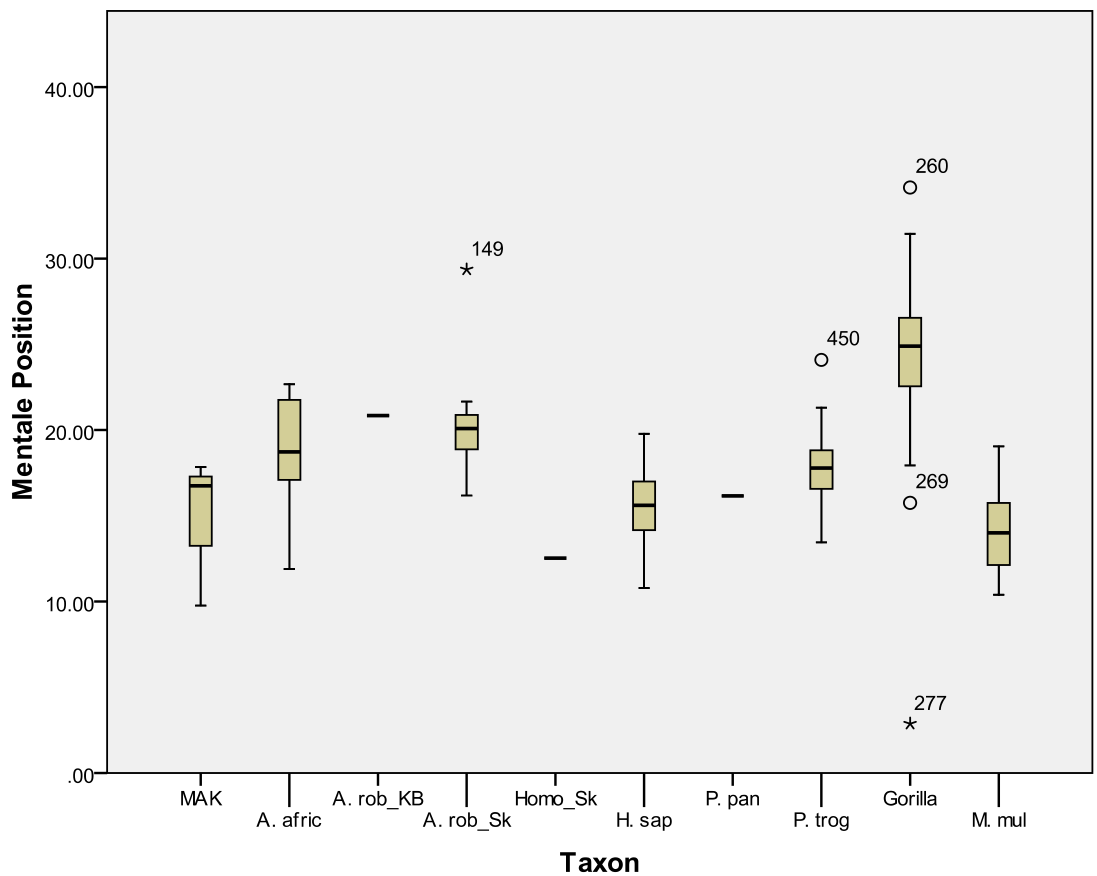


Figure 7-23: Mandibular Thickness at P_3. The median (line), 1st and 3rd quartiles (box), and range (bars) of P_3 mandibular thickness (P3w) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 27, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 5), Swartkrans *A. robustus* (n = 6), Kromdraai *A. robustus* (n = 1), Sterkfontein *Homo* (n = 1), and Swartkrans *Homo* (n = 1).

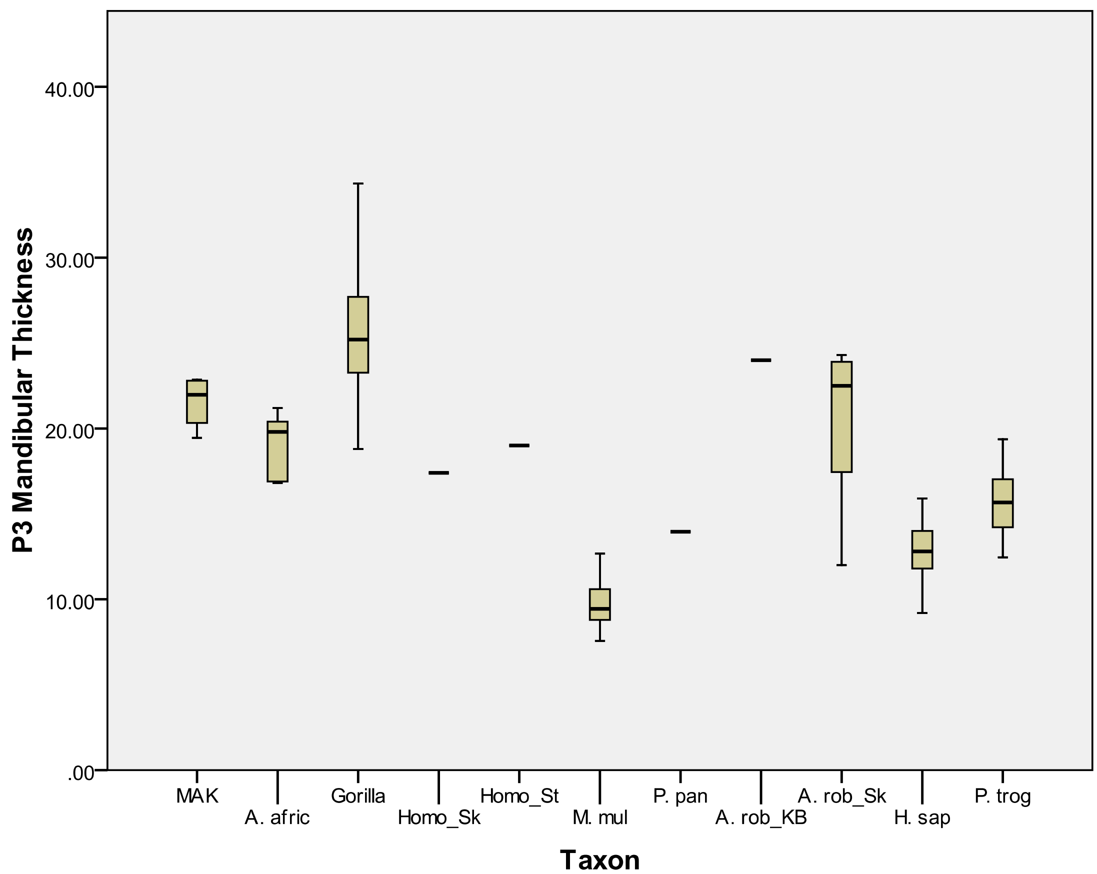


Figure 7-24: Mandibular Thickness at P_4. The median (line), 1st and 3rd quartiles (box), and range (bars) of P_4 mandibular thickness (P4w) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant gorilla and human samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 29, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 6), Swartkrans *A. robustus* (n = 9), Kromdraai *A. robustus* (n = 1), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

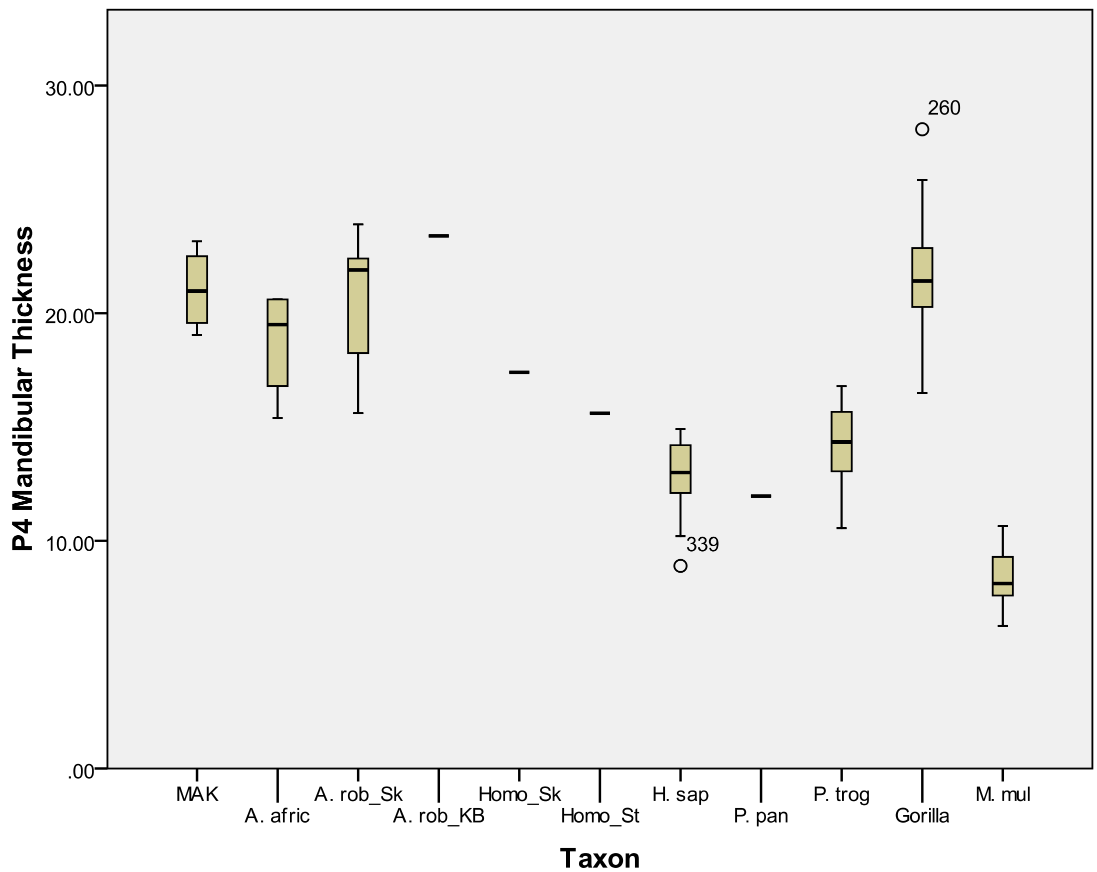


Figure 7-25: Mandibular Thickness at M_1. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_1 mandibular thickness (M1w) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant gorilla and robust australopith samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 22, MLD 29, MLD 34, MLD 40, and MLD 48. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 11), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 1).

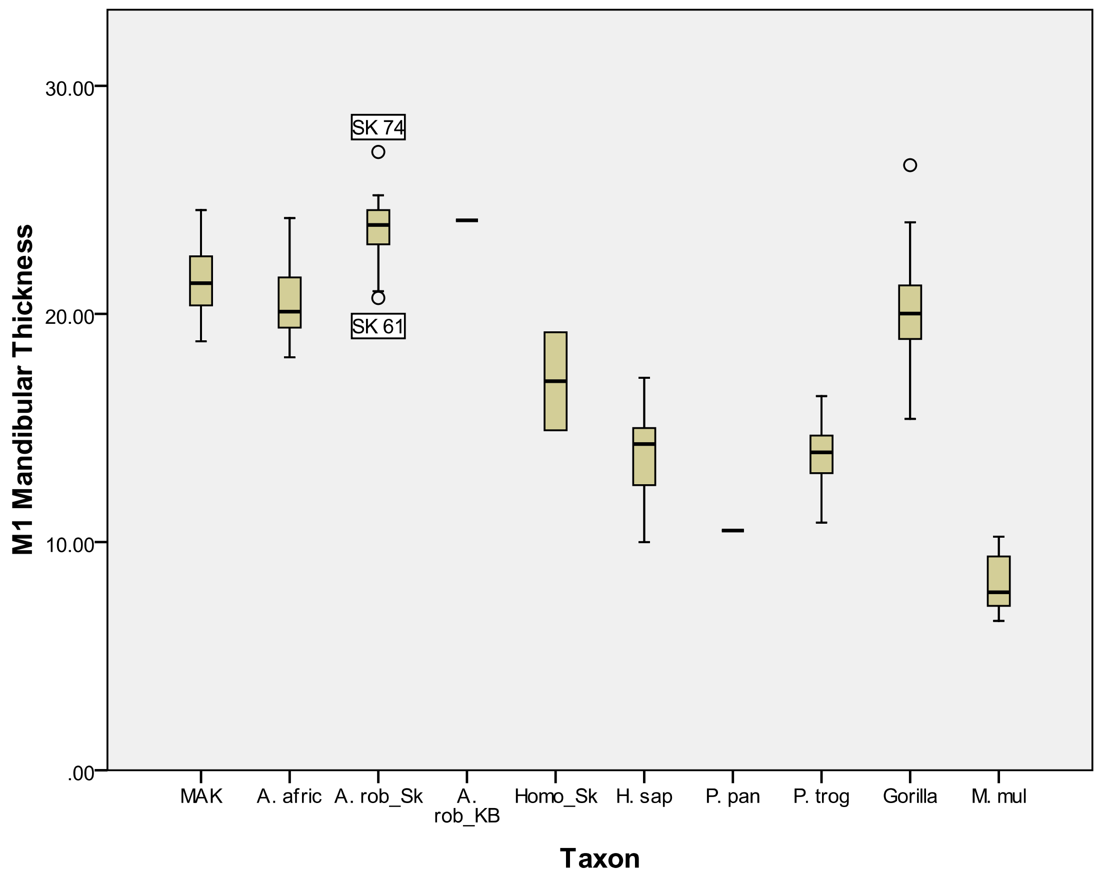


Figure 7-26: Mandibular Thickness at M_2. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_2 mandibular thickness (M2w) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant chimpanzee and Makapansgat samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 22, MLD 34, MLD 40, and MLD 48. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 9), and Swartkrans *Homo* (n = 1).

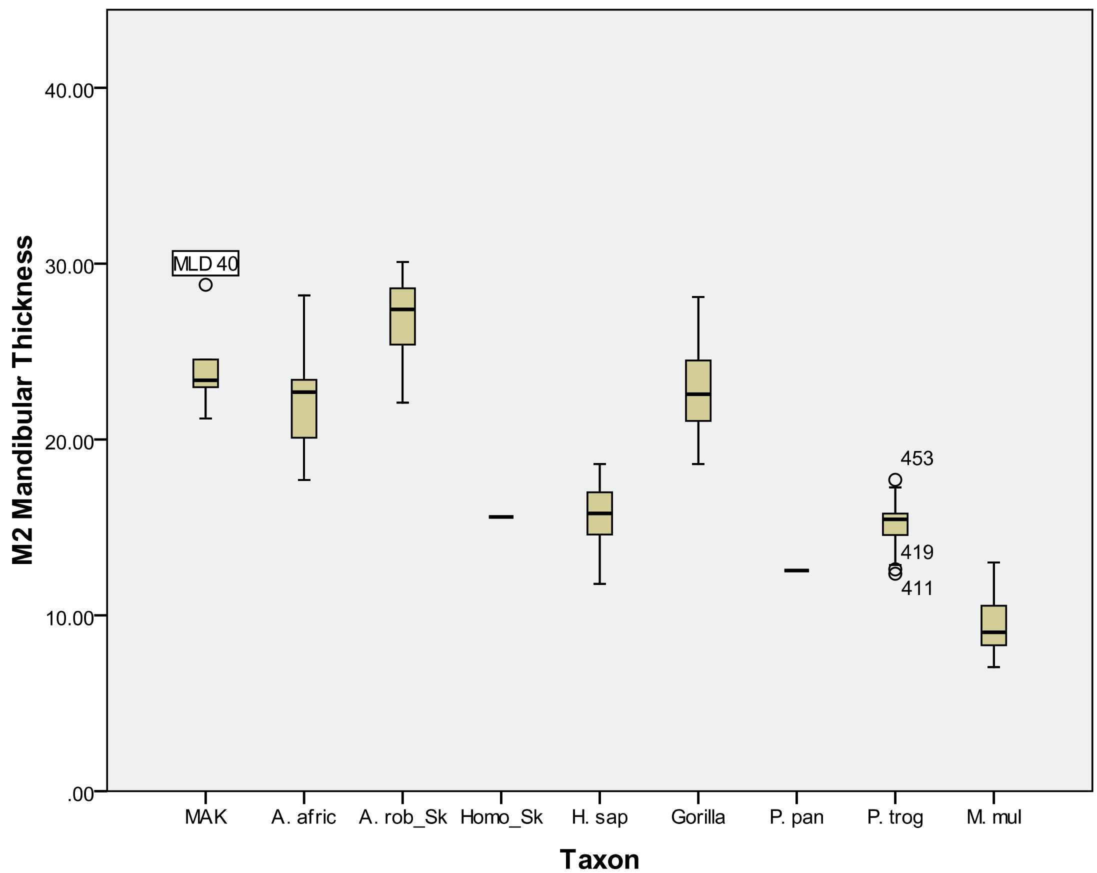


Figure 7-27: Mandibular Thickness at M_3. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_3 mandibular thickness (M3w) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant gorilla and human samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 18, MLD 19, MLD 22, MLD 40, and MLD 47. The fossil sample sizes for this analysis are: *A. africanus* (n = 5), Swartkrans *A. robustus* (n = 4), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

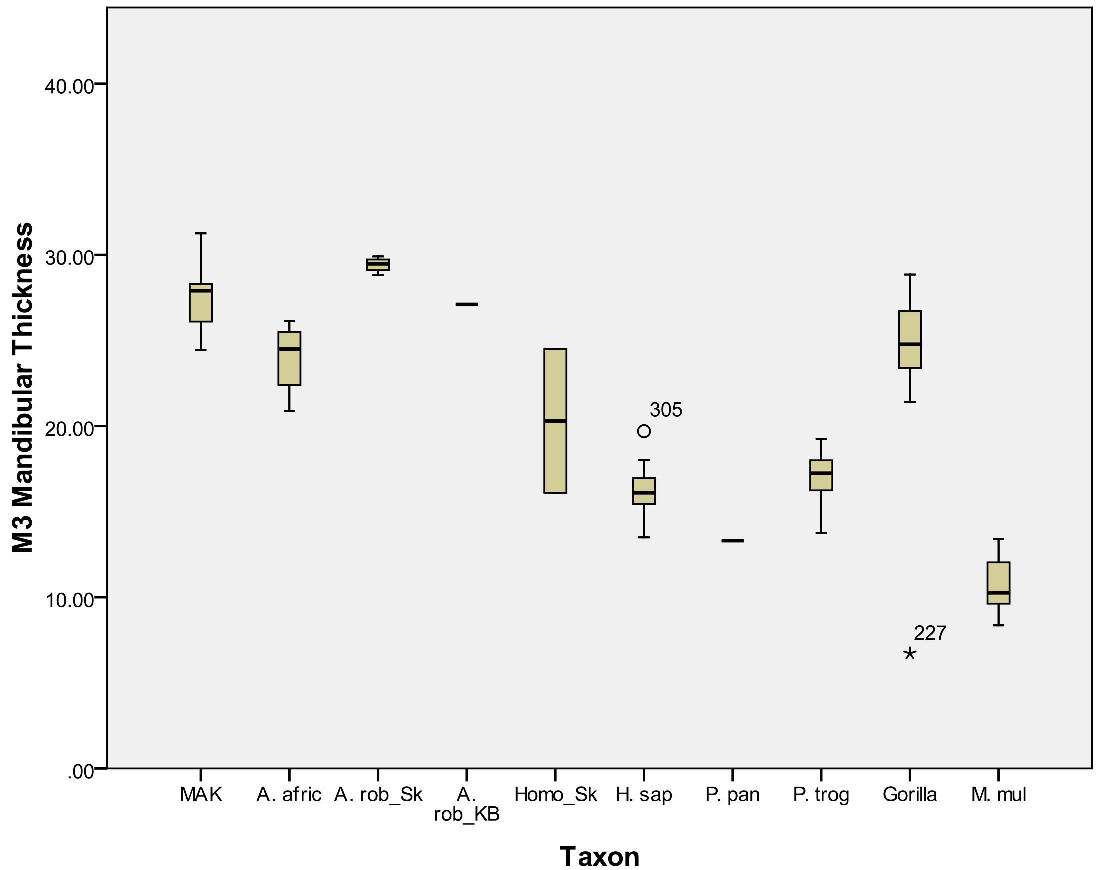


Figure 7-28: External Mandibular Height at M_1. The median (line), 1st and 3rd quartiles (box), and range (bars) of external mandibular height at M_1 (M1eM1b) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The extant chimpanzee and human and Swartkrans *A. robustus* samples display outliers (the numbers identify the specific individuals). The Makapansgat sample is represented here by MLD 18, MLD 34, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 8), Swartkrans *A. robustus* (n = 11), Kromdraai A. robustus (n = 1), and Swartkrans *Homo* (n = 2).

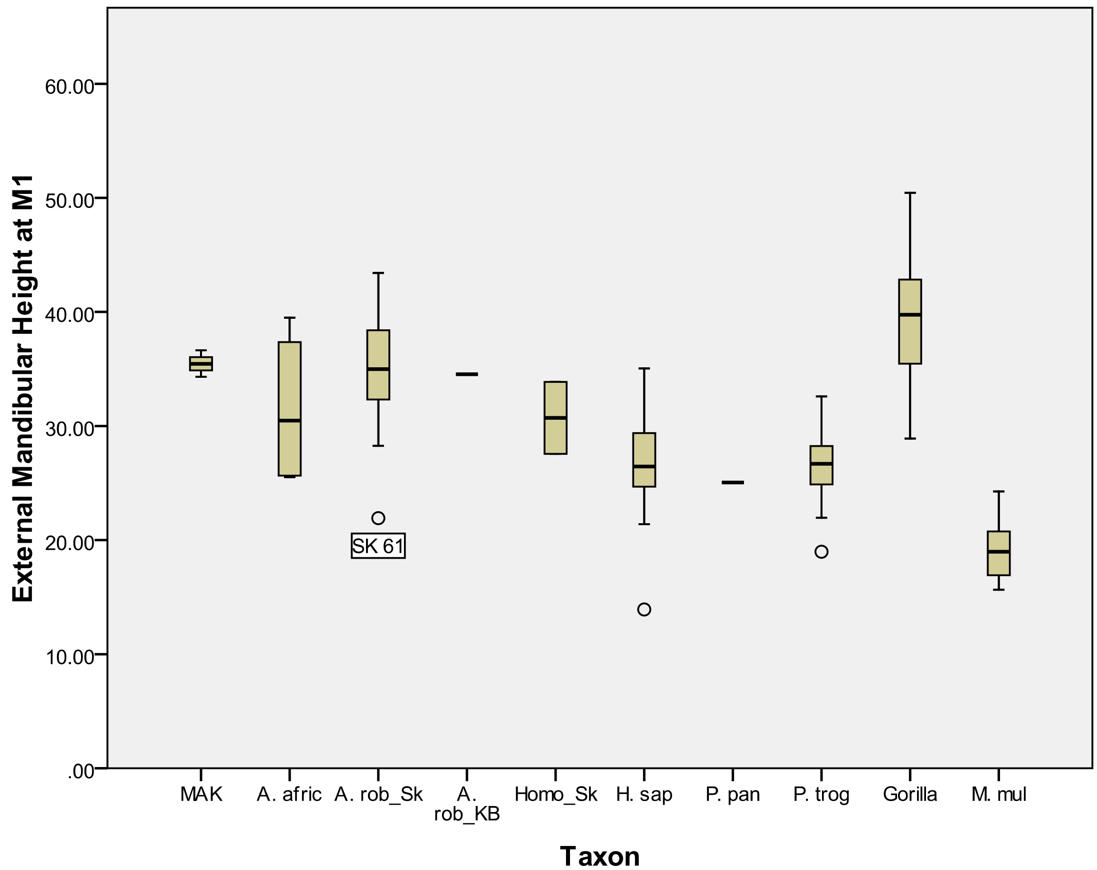


Figure 7-29: Lingual Mandibular Height at M$_2$. The median (line), 1st and 3rd quartiles (box), and range (bars) of lingual mandibular height at M$_2$ (M2lM2b) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers with associated numbers identify the specific individuals. The Makapansgat sample is represented here by MLD 18, MLD 34, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 7), Swartkrans *A. robustus* (n = 10), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

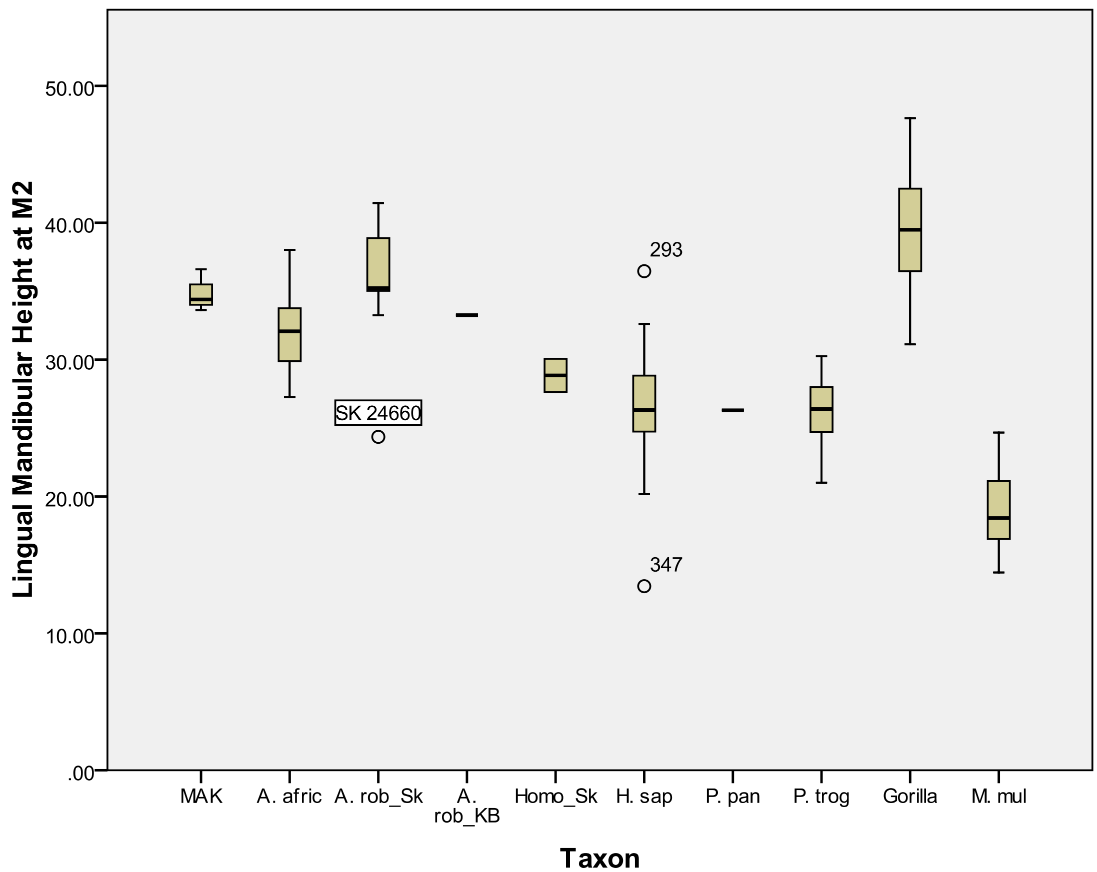


Figure 7-30: External Mandibular Height at M_3. The median (line), 1st and 3rd quartiles (box), and range (bars) of external mandibular height at M_3 (M3eM3b) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers with associated numbers identify the specific individuals. The Makapansgat sample is represented here by MLD 18, MLD 34, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 4), Swartkrans *A. robustus* (n = 7), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

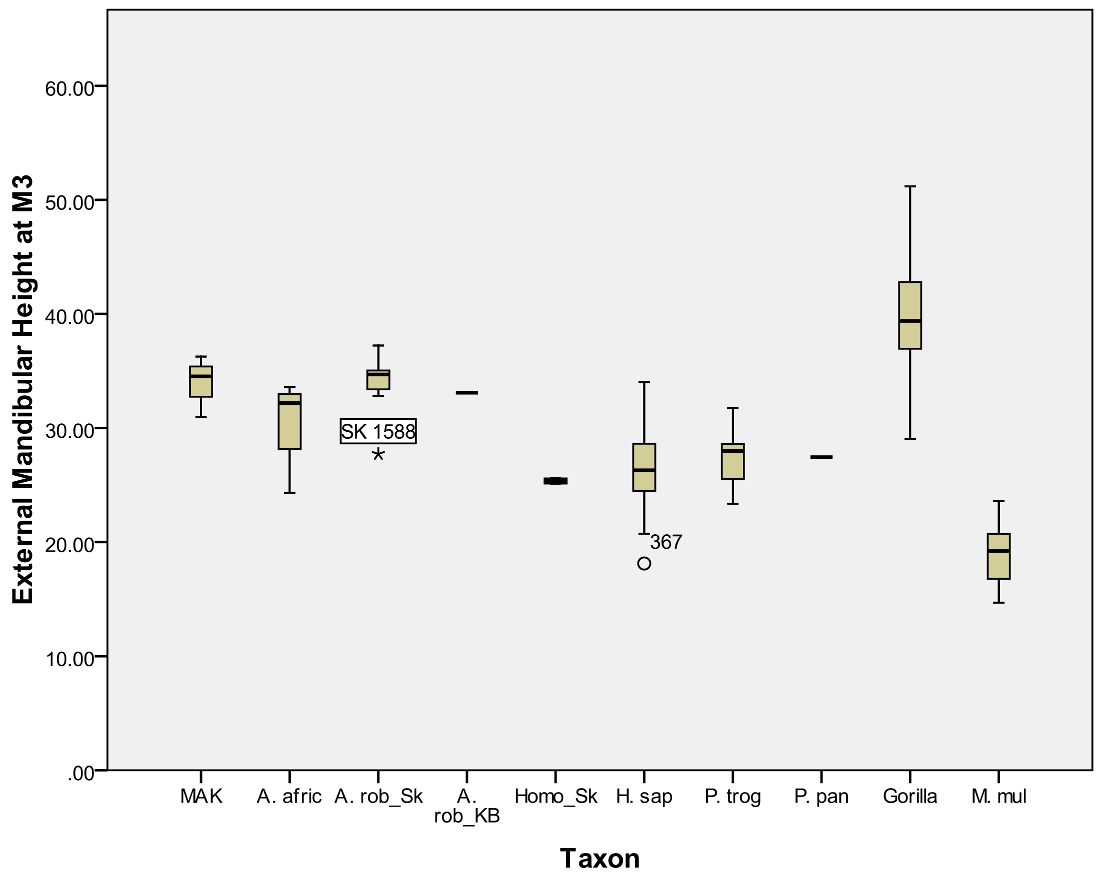


Figure 7-31: Mandibular Robustness at M_1. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_1 mandibular robustness (M1w/M1eM1b*100) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers with associated numbers identify the specific individuals. The Makapansgat sample is represented here by MLD 18, MLD 34, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 7), Swartkrans *A. robustus* (n = 9), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

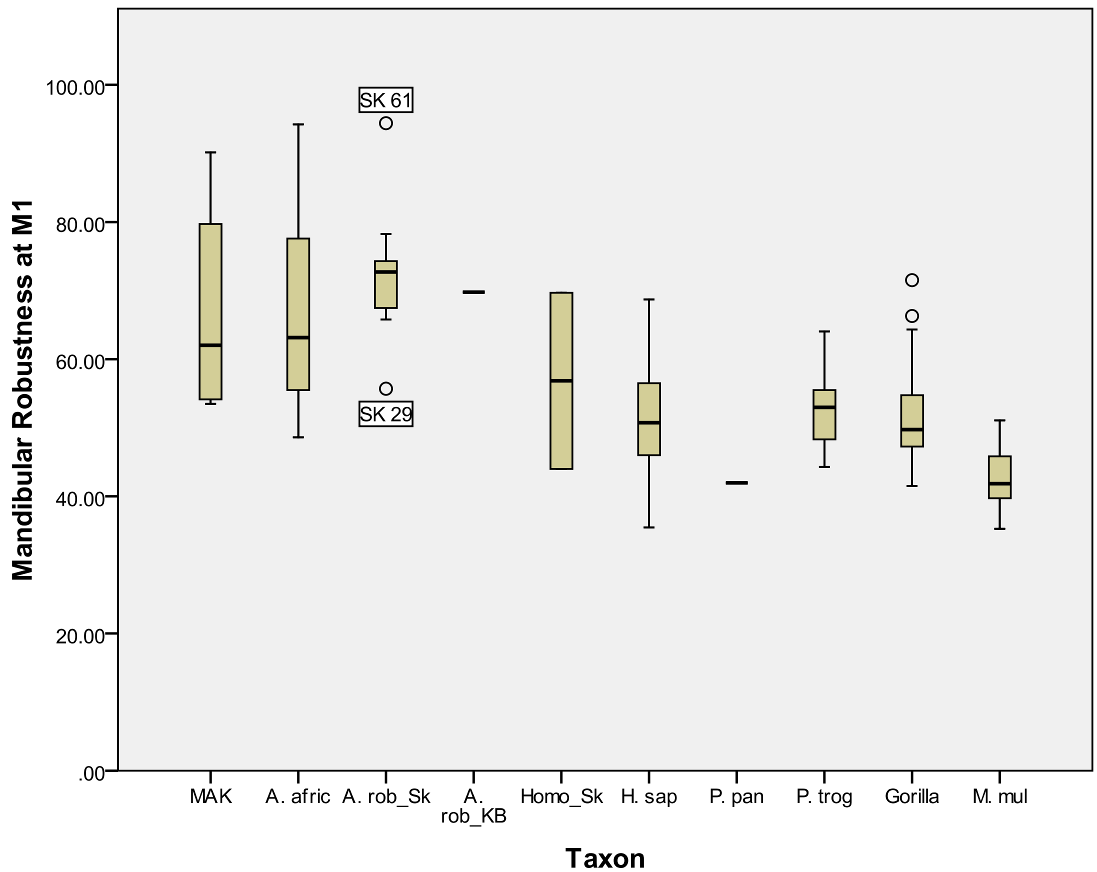


Figure 7-32: Mandibular Robustness at M_2. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_3 mandibular robustness (M2w/M2lM2b*100) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. The Makapansgat sample is represented here by MLD 18, MLD 34, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 7), Swartkrans *A. robustus* (n = 8), and Swartkrans *Homo* (n = 1).

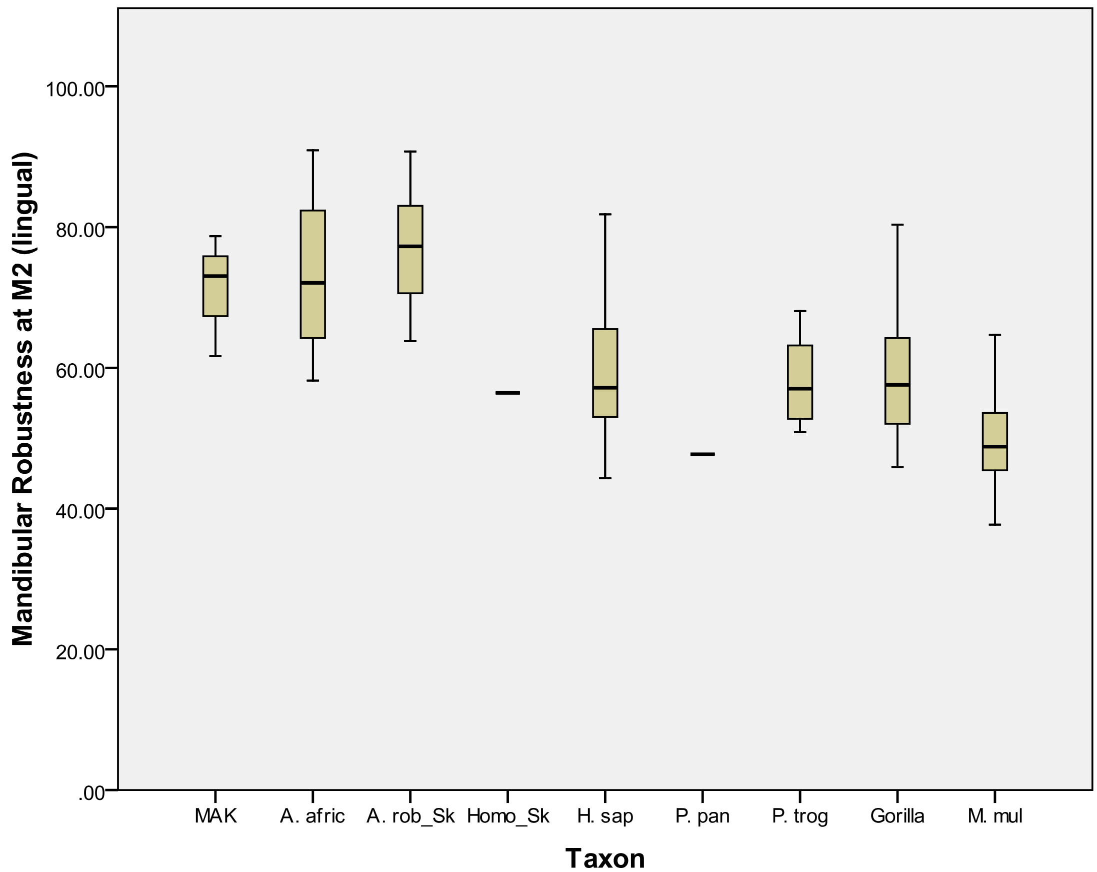
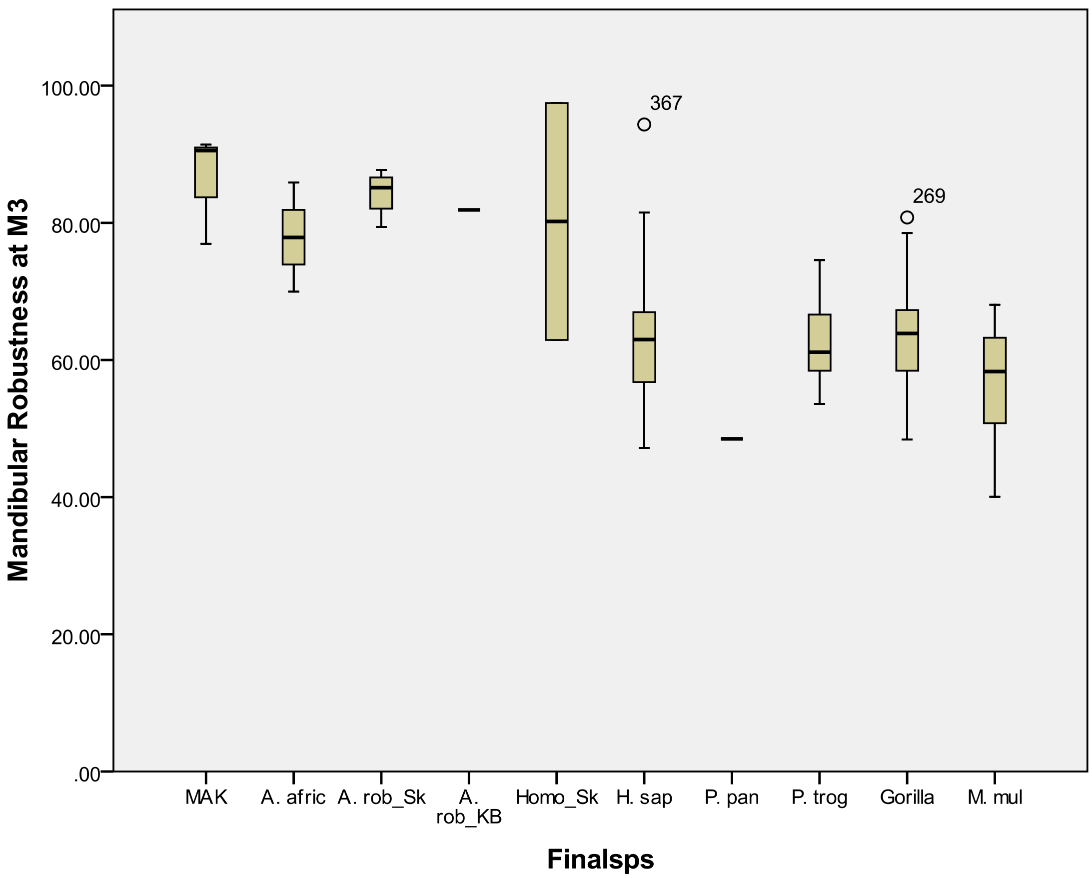


Figure 7-33: Mandibular Robustness at M_3. The median (line), 1st and 3rd quartiles (box), and range (bars) of M_3 mandibular robustness (M3w/M3eM3b*100) for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers with associated numbers identify the specific individuals. The Makapansgat sample is represented here by MLD 18, MLD 40, and MLD 47. The fossil sample sizes for this analysis are: *A. africanus* (n = 3), Swartkrans *A. robustus* (n = 4), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).



Ramus Morphology. Although analyses of the overall shape of the mandible easily distinguished specific and even subspecific variation for several apes (Schmittbuhl *et al.*, 2007), the whole lateral mandibular outline is not preserved in the Makapansgat sample. Instead, the condyle and ramus are typically damaged due to postdepositional processes (including activity by carnivores and rodents). As a result, little can be discussed regarding the ramus due to the scant number of mandibles preserving them at Makapansgat. However, the anterior root of the mandibular ramus originates at or anterior to M_2 in all of the Makapansgat specimens. The relatively anterior positioning of the root is a single salient ramal characteristic exhibited by the Makapansgat hominins. This characteristic is shared by the samples of Makapansgat and *A. robustus* and is considered to be a derived feature in hominin mandibles.

Within the Makapansgat sample, the mandibular ramus is best preserved in MLD 40. Its morphology exhibits rugose attachments for presumably powerful muscles of mastication. While mandibular condyle morphology and ramus length aid interpretations of dietary adaptations, no condyles are preserved in the Makapansgat sample. Regardless, the MLD 40 ramus permits some interpretation of condylar position. Condyle height is not preserved in many of the South African australopiths, but MLD 40 would likely be considered tall compared with modern humans, but similar to that of SK 34 and likely greater than that of STS 36. While condyle and ramal heights are strongly correlated across primates, more folivorous extant apes exhibit taller rami increasing both the adductor attachment area and potential bite force (Taylor, 2005). In comparison with chimps, the higher condylar positioning relative to the postcanine dentition and the wider condyles indicates that gorillas more evenly distribute their forces across the postcanine dentition and have greater resistance to condylar loads. The latter perhaps also being more distributed on the lateral aspect of the condyle in gorillas (Hylander and Bays, 1979). The presumably tall ramus of MLD 40 (compared with modern humans and possible STS 36) permits increased bite force. However, the condyle has been argued to be a regional growth site for the ramus, regulating mandibular growth to some degree (Enlow and Hans, 1996). It is likely that the condyle and ramal height are not easily modified independently and that modifications of other mandibular regions may result in modification of these features (Wall, 1999; Taylor, 2005). Thus it remains a possibility that any increases in condyle or ramal height in fossil australopiths are the result of modification of other aspects of the mandible, as well as other craniofacial elements, rather than direct selection.

Summary

The Makapansgat early hominin mandibular sample is represented by a relatively large sample. Morphological features align these specimens with both *A. africanus* and *A. robustus*, although there is considerable variation within these hypodigms. The Makapansgat mandibular specimens appear intermediate or distinct in some features and the MLD 2 mandible stands out.

DENTAL DESCRIPTIONS AND RESULTS

Dentition

Descriptions. The dental remains from Makapansgat are variable in morphology, although they are typically included in the hypodigm of *A. africanus*. The hominin dentition preserved at Makapansgat includes a number of specimens, including teeth at a variety of developmental stages. Some specimens exhibit notable dental wear (particularly MLD 22 and MLD 27), while others exhibit partially erupted adult (e.g. MLD 2 and MLD 11/30) or deciduous (e.g. MLD 2 and MLD 5) teeth. In addition, the mandibular dentition (14 specimens) is better represented than the maxillary dentition (10 specimens) at Makapansgat.

The dentition from Makapansgat has been included in numerous analyses of australopith dentition, yet was typically only briefly described by Dart (1948a, 1948b; 1949a; 1954b; 1959a,b; 1962a; 1962b) and in greater detail by J.T. Robinson (1954a, 1954c; 1955, 1956). The descriptions below are based on a combination of these original works by Dart and Robinson, despite differences in the use of terminology, as well as the addition of further details contributed by this author. Here, cusps are defined as enamel features with independent apices, which are partially defined by their fissures (see discussion in Methods). Alveoli are discussed in the following pages to assess root morphology, but cautiously. While alveoli may provide solid evidence of short and narrow roots, a variety of pre- and post-mortem influences can increase the breadth and length of alveoli. Age at death estimates are included in the pages below where they have not already been presented within the cranial or mandibular discussions of these specimens and are summarized in Table 9-1.

MLD 2

Overview. The MLD 2 mandible preserves the right C_1, P_3, dp_4, M_1, M_2 and left P_3, P_4, M_1, and M_2 (see Figure 8-1). The alveoli for the right and left I_1, I_2, and dc_1/C_1 are also preserved. The right C_1 is partially visible in the crypt but has not yet emerged to the level of the alveolar crest. The left P_3 is in full occlusion, while the right P_3 has erupted but is not yet in full occlusion. The left P_4 exhibits a buccal cusp tip scarcely above the buccal alveolar crest, while the right dp_4 is present and worn. Finally, the right and left M_1 and left M_2 are in full occlusion, while the right M_2 is in the final stages of eruption. The eruption sequence of the MLD 2 mandible's preserved teeth is $M_1 > M_2 > P_3 > P_4$.

Incisors. The incisor alveoli indicate short to moderate I_1 and I_2 roots, but provide no further discriminating information.

Canines. The right C_1 cusp tip is barely visible in the crypt. As a result, the morphology of the canine is obscured. However, a study examining CTs revealed that the crown is completely formed and the root formation is well underway (Conroy and Vannier, 1991).

Premolars. The MLD 2 premolars are essentially unworn and are not fully erupted. The P_3s are considerably mesiodistally shorter and buccolingually narrower, particularly on the mesial aspect, than the P_4. Regardless, the premolars display similar degrees of development of the external grooves. The occlusal morphology of the P_3s and P_4 are otherwise quite expectedly distinct.

The P_3s are somewhat large in comparison to many of the South African australopith specimens. They are essentially unworn. The right and left P_3 specimens are slightly asymmetrical. The right P_3's mesiodistal axis is oriented several degrees externally (mesial aspect is buccal and distal aspect is lingual) in comparison to the left. In addition, the right P_3, although not fully erupted, appears buccolingually narrower and mesiodistally longer than its antimere. Despite these distinctions, both teeth are buccolingually broad with a well demarcated mesial and distal fovea. The mesial fovea is a small, deep pit in contrast to the broader, shallower distal fovea.

The P_3s exhibit three cusps: a prominent somewhat mesial protoconid, mesially positioned and mesially tilting metaconid, and a distally positioned accessory cuspulid on the talonid. The metaconid is distinct in that it exhibits a concave lingual external surface. This appearance is particularly marked on the left P_3 and appears to relate to the development of the talonid. The protoconid and metaconid cusp tips are positioned in close proximity and starkly contrast the great breadth of the crown near the CEJ. The protoconid displays a slight enamel elevation mesial to its cusp tip, but not so developed as to be called an additional cuspulid. The protoconid lacks a mesial accessory ridge, but displays a marked distal accessory ridge. The metaconid similarly lacks a mesial accessory ridge, but displays a faint and indistinct distal accessory ridge. A median longitudinal fissure etches the single and prominent transverse connecting the two main cusps. The mesial marginal ridge is marked and appears to be essentially an extension of the mesial aspect of the protoconid. The talonid is well-developed with a marked distal marginal ridge extending between the main cusps. The left P_3 talonid exhibits an extra shelf or slight crest dividing the talonid basin. It appears as an enamel development extending across the talonid basin from the region of the external distobuccal groove to the lingual margin.

Grooves of the occlusal surface include a weak mesiobuccal groove, intermediate to marked distobuccal groove, prominent mesiolingual groove that divides the mesial marginal ridge, and weak to developed distolingual groove not extending to the marginal ridge. The external aspect (or faces) of the P_3s display distinct mesiobuccal grooves (although weaker and ill-defined on the left), weak to moderate distobuccal grooves, an ill-defined triangular depression instead of a true mesiolingual groove (entirely absent on the right P_3), and moderate distolingual grooves. The buccal grooves are associated with corresponding enamel pillars (with the exception of the mesiobuccal aspect of the left P_3). A faint buccal cingulid is displayed by the P_3s and appears to relate in part to the external mesiobuccal groove.

Although the left P_4 has not yet fully erupted, much of its occlusal surface is visible for assessment. The specimen displays no wear due to its developmental status. The crown appears essentially symmetrical when comparing the buccal and lingual aspects of the tooth. The P_4 displays a prominent protoconid and metaconid and three accessory distal cuspulids. The protoconid and metaconid are both mesially positioned and appear similarly sized. The metaconid is slightly more mesially positioned than the protoconid [*contra* Robinson (1956), who suggested they are situated opposite to each other]. There is a single, weakly developed transverse crest connecting the protoconid and metaconid [*contra* Dart (1948a)]. Mesial and distal to the protoconid's cusp tip and along the occlusal margin are slight enamel elevations that are not distinct enough to be considered accessory cuspulids. The protoconid exhibits related moderately developed mesial and distal accessory ridges, while the metaconid exhibits weakly developed mesial and distal accessory ridges.

The median longitudinal fissure extends between the mesial and distal fovea and moderately etches the transverse ridge, but is not quite the same depth as the mesial and distal fovea [*contra* Dart (1948a)]. Dart actually referred to the P_4 morphology as "ultra human" on the basis of its independent cusps with, what he described as, lacking in crest development between the cusps (1948a:404). The mesial fovea is moderately developed, while the posterior fovea is broad. There are two mesial marginal tubercles [referred to as "vestigial cuspules" by Dart (1948a:404)] on the mesial aspect of the crown. The grooves of the occlusal surface include a marked distobuccal groove cutting through the marginal ridge, weak mesiolingual groove, and marked distolingual groove extending to the marginal ridge without dividing it. There is essentially no mesiobuccal groove. Although the entire crown is not visible, the external aspect of the tooth appears to have a weak external mesiobuccal groove and intermediate external distobuccal groove. The external lingual grooves are not observable.

The deciduous premolar is discussed in this section despite its functional and morphological similarity to the molars. The dp_4 is extremely worn. The dentinal areas of the protoconid, hypoconid, hypoconulid, and metaconid have coalesced with an enamel peninsula partly extending from the metaconid. Although this dp_4 is mesiodistally longer than buccolingually broad, it is nevertheless relatively broad. It is similar in this sense to the Taung dp_4 and to a lesser extent StW 151; however the cusp proportions and positions are strikingly different for MLD 2. In addition, the MLD 2 dp_4 is considerably larger than the Taung and StW 151 dp_4. The MLD 2 entoconid is small, which is related to the relatively large adjacent cusps. The metaconid is very large, particularly in the mesiodistal dimension. The hypoconulid also is large and is lingually expanded, resulting in a somewhat buccolingually centered position on the basis of the crown outline. Although there does not appear to be accessory cuspulids or tubercles indicated on the distal aspect of the tooth, the extreme wear exhibited by this dp_4 prevents further assessment of their presence. In a number of features, which include the small entoconid, large centrally-situated hypoconulid, and mesiodistally long metaconid, the dp_4 resembles the molars.

Molars. The MLD 2 molars include right and left M_1s and M_2s. These molars exhibit slight wear and extensive enamel pitting in the unworn aspects of the occlusal surface, particularly near the occlusal fissures. The molars exhibit a Y-5 pattern with a generally broad contact between the metaconid and hypoconid. The mesiobuccal and lingual limbs of the Y fissure system are essentially in line with each other. The molars can be described as being relatively broad with a sloping buccal aspect, unusually small entoconids, large metaconid, large and somewhat centrally situated hypoconulids (particularly in M_1), deep furrow dividing the hypoconid and hypoconulid, mesial marginal tubercles, and well-developed protostylids. The M_2 is larger than the M_1 in both mesiodistal and buccolingual dimensions.

The M_1s exhibit slightly to moderately developed wear facets on the protoconid, hypoconid, and hypoconulid. An extremely faint point of dentine exposure is visible on the protoconid. A *tuberculum intermedium* is not present, although a short fissure branching off the lingual aspect of the occlusal surface is visible on the right M_1. A *tuberculum sextum* is not present. The distal trigonid crest connecting the cusps of the protoconid and metaconid is interrupted by the longitudinal fissure. A deflecting wrinkle is weakly indicated on the left M_1 by the distal deflection of the medial ridge; however, it does not appear to contact the entoconid. An entoconid-hypoconulid crest is present, but is etched by a longitudinal fissure. The appearance of this crest is demarcated in part by a distinct fovea situated between the hypoconulid and entoconid, just distal to the entoconid-hypoconulid crest. The mesial fovea is moderately large, but the distal fovea is indistinct. The protostylid is well developed as an enamel shelf in both M_1s. The protostylid of the right M_1 has an apex and extends from the mesiobuccal corner to just inferior to the mesial aspect of the hypoconid (referred to by Robinson as a protoconidal cingulum). The protostylid of the left M_1 exhibits vertical grooves further enhancing its development.

Overall, the M_2s exhibit similar morphological features to the M_1s. The MLD 2 M_2s are virtually unworn, displaying only faint enamel wear of the cusp tips. These molars display a Y pattern. The right M_2 exhibits 5 cusps, while the left exhibits 6 cusps. A *tuberculum intermedium* is weakly developed on the right with an independent cuspulid-like feature partially distinguished by short surrounding fissures, but is less developed on the left. The distal trigonid crest is unusual in appearance, being weakly indicated and divided by the longitudinal fissure on the right and essentially absent on the left.

A deflecting wrinkle appears on the left M_2 as an L-shaped medial ridge contacting the entoconid but divided by the longitudinal fissure. On the right the deflecting wrinkle is weaker and appears as a medial ridge deflecting distally but not contacting the entoconid. The left M_2 exhibits a small cuspid demarcated by enamel fissures on the internal occlusal surface between the metaconid and entoconid. The entoconid-hypoconulid crest is interrupted by the longitudinal fissure. The mesial fovea is distinct with two pits (more developed on the left). The mesial marginal tubercles are large and are so developed on the left tooth as to be considered an accessory cuspulid. The protostylid (or cingulid) is well developed with a clear shelf extending across the buccal aspect of the protoconid.

Discussion. The MLD 2 mandible boasts well-preserved postcanine teeth at varying developmental stages and numerous dental traits that are obscured by wear in other Makapansgat specimens. The detailed descriptions of dental morphology discussed in the preceding pages are put into a comparative context here. Although the MLD 2 P_3 has been described [Remane (1952), as cited in Dart (1954b)], the manuscript is difficult to acquire and has not been reviewed by this author.

The MLD 2 P_3 morphology is most similar to that exhibited by specimens attributed to *A. africanus*, although the MLD 2 premolars do not precisely match any

South African hominin specimen. The robust australopiths tend to exhibit broader premolars with thicker enamel, a more developed talonid, and more bulbous cusps than MLD 2. Despite differences in the shape of the talonid basins, MLD 2 seems most similar to the P_3 of StW 142 and Sts 52 in the appearance of the cusps and mesial aspect of the tooth, the latter feature displaying a discontinuous mesial marginal ridge. Its buccal cingulid and enamel pillar resembles that of Sts 52 and, to some extent, MLD 40. The MLD 2 P_3 is most like specimens of *A. robustus* or large specimens of *A. africanus* on the basis of estimated crown area.

The overall appearance of the P_4 is fairly molarized due to its mesial marginal tubercles, large talonid basin, and distal cuspulids. In these features it appears similar to the robusts, although the major cusp tips appear to be more centrally located in MLD 2 than many of the robusts. Given these comments, the crown morphology is most similar to the moderately worn SK 1587 and SK 1588 among specimens of *A. robustus*. The overall P_4 morphology of MLD 2 appears perhaps even more similar to that of Sterkfontein specimens StW 131, StW 147, and possibly a less worn StW 404. The main distinguishing feature is that MLD 2 appears somewhat more bulbous than these Sterkfontein specimens. Despite similarities with some Sterkfontein specimens, MLD 2 is quite distinct in the degree of crown symmetry from most of the Sterkfontein specimens (i.e. MLD 2 has a more mesially expanded lingual cusp). In a sense, the P_4 morphology of MLD 2 is somewhat intermediate in morphology between the South African hominin species.

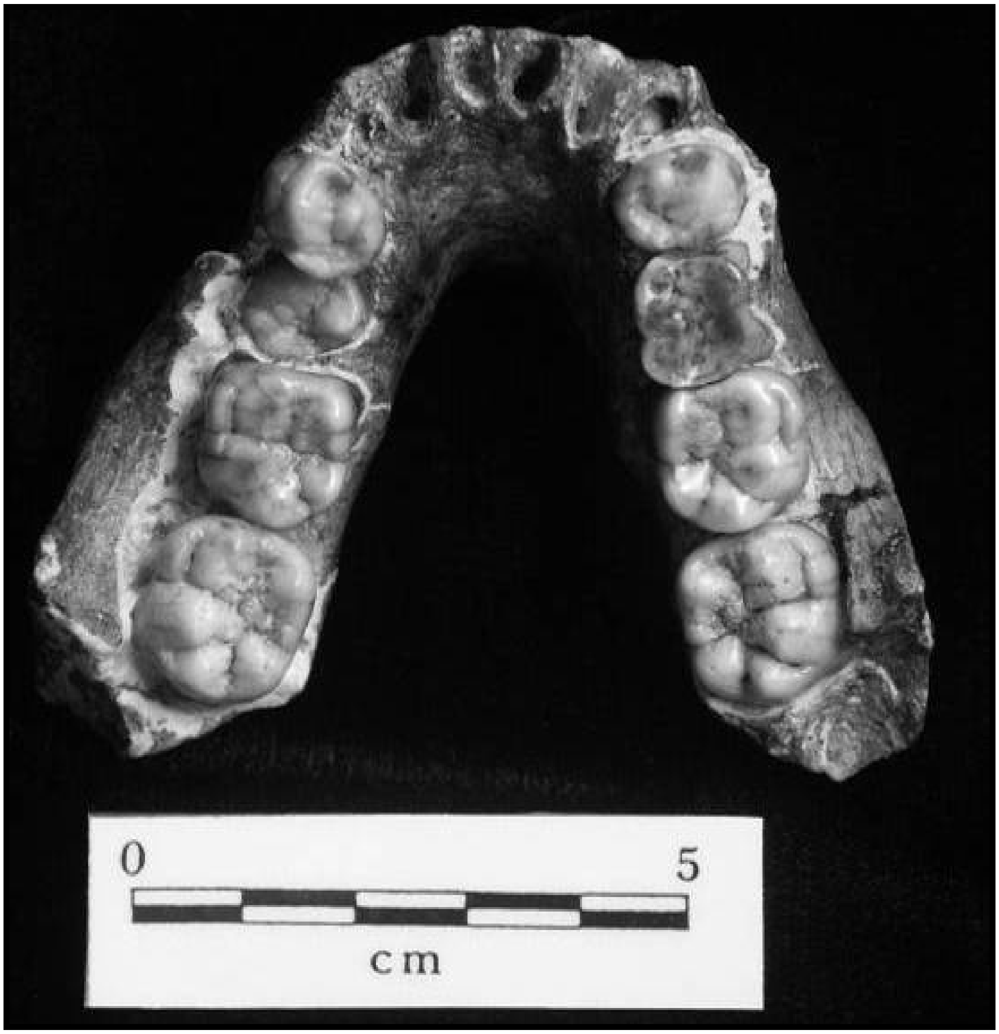
The MLD 2 molars appear more similar overall to specimens attributed to *A. africanus* than to *A. robustus*, but they are distinct from both species in some features. The MLD 2 molars are distinct in their great mesial breadth, which is partly related to their enormous protostylid. The molars also tend to exhibit broader buccal cusps, in general, when compared to specimens of *A. africanus* from Sterkfontein. The centrally positioned hypoconulid is quite distinct in MLD 2 and is most closely approached by StW 123. The M_1s are most comparable to StW 123, SK 3974, and StW 421. However, SK 3974 is perhaps more similar to StW 421 than either is to MLD 2 due to the morphology of the distal portion of the tooth. The MLD 2 molars are unlike SK 3974 in being less bulbous on the buccal aspect of the tooth, having a narrower metaconid, and fewer cuspulids. The most favorable comparison can be made between the StW 123 and MLD 2 M_1s in terms of cusp positions and overall proportions. While similar in the shape of the occlusal outline and overall cusp proportions to the SK 843 specimen of *A. robustus* and the StW 412 specimen of *A. africanus*, the MLD 2 M_2s are somewhat intermediate in their bulbous appearance and accessory enamel features. The MLD 2 molars are intermediate in many features relating to thickness and size, but are distinct in their squared corners, broad mesial aspect, and centrally positioned hypoconulid.

As the MLD 2 mandible is one of few specimens at Makapansgat preserving evidence for timing of dental eruption, it warrants some expanded discussion. The timing of dental eruption for the preserved teeth progresses as M_1, M_2, P_3, P_4, and finally C_1. This specimen was one of the first early hominins to be identified as exhibiting a distinct eruption sequence from extant humans (Dart, 1948a). The eruption of the M_2 prior to the

P_3 is unusual for modern human populations (see also Conroy and Vannier, 1991), but there is substantial variation in dental eruption sequences (e.g. Smith and Garn, 1987). The dental row also suggested early on an extended infancy in australopiths due to the extensive wear of the dp_4, which is characteristic of modern humans (Le Gros Clark, 1947; Dart, 1948a,b).

Another feature displayed by the MLD 2 dentition is the presence of extensive pitting of the occlusal surfaces of the molars (particularly apparent in the M_2s). This characteristic appearance was most frequently noted in the comparative ape sample, but was also noted in SK 3974, SK 100, SK 64, SK 63, and StW 81, among other fossil specimens. It appears these enamel pits may be the result of disruptions in amelogenesis, i.e. enamel hypoplasia, and enamel hypoplastic pits are generally indicative of poor health or general physiological stress during development (Skinner and Goodman, 1992). The extreme thickness of enamel and significant wear exhibited by most of the South African australopith teeth may suggest that this sort of enamel defect was present in a fairly large percentage of early hominins but their appearance was obscured by wear in many individuals that survived into later adulthood.

Figure 8-1**:** ***MLD 2.*** The subadult MLD 2 mandible in occlusal view.



MLD 4

Overview. The MLD 4 specimen is a young adult mandibular fragment with a fully erupted left M_3. This specimen is not included in the mandibular descriptions because it does not preserve diagnostic mandibular features. The mesial portion of the roots and mesial cervical margin of the crown are not preserved due to a somewhat oblique fracture through the specimen. The specimen was originally cited as belonging to MLD 6 (Dart, 1949a), but later was reattributed to MLD 18 (Dart, 1954b).

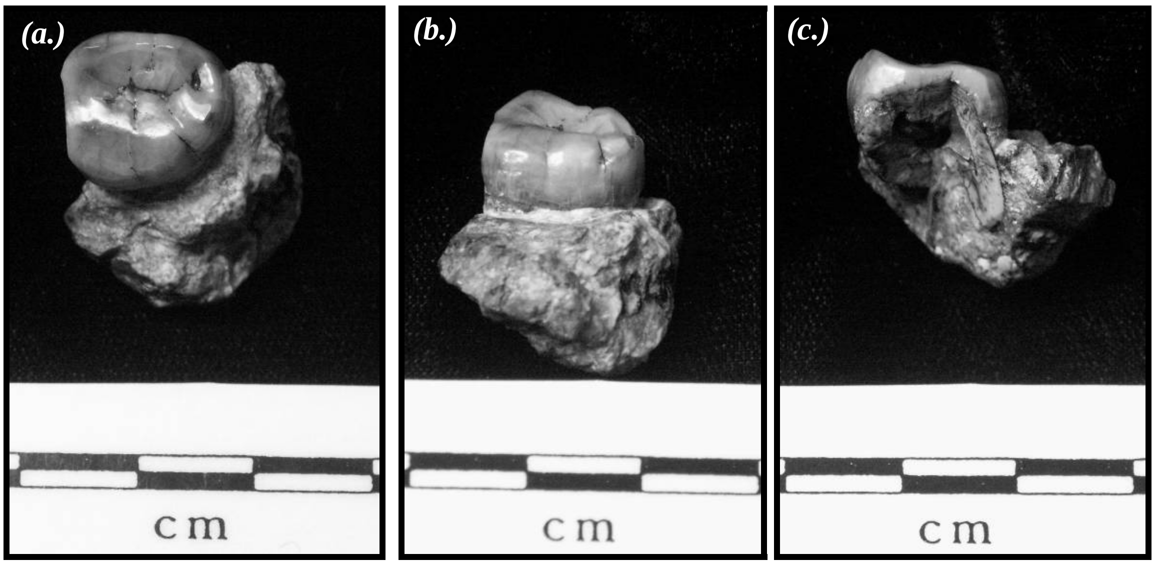
Molars. The M_3 displays moderate enamel wear but no exposed dentine. The mesial aspect of the tooth exhibits marked interproximal wear. The occlusal surface displays the typical Y-pattern. By the definition of a cusp used by this author (described in the methods), this tooth is here identified as most likely exhibiting 7 cusps (*contra* Dart and Robinson). These include the 5 major cusps, as well as a probable *tuberculum sextum* (identified on the basis of fissures) and a distinct *tuberculum intermedium* developed enough to be included in the cusp count. The *tuberculum intermedium* appears to be more closely related to the entoconid, rather than the metaconid. The protoconid and hypoconid are large, being particularly broad in the buccolingual dimension. The adjacent metaconid and entoconid are correspondingly buccolingually narrow but the metaconid is also mesiodistally short, which gives the metaconid an appearance of being unusually small.

A mesial fovea is not observable, but there is a distinct posterior fovea. An incipient distal trigonid crest is indicated, the junction of the entoconid and hypoconid appearing slightly more developed although deeply carved by the main longitudinal fissure. The entoconid-hypoconulid crest is displayed as a continuous crest that is not deeply incised by the longitudinal fissure. In addition, distal to the entoconid-hypoconulid crest there is a deep second distal fovea that is partly bounded by a distal marginal ridge extending distally between the entoconid and hypoconulid. The occlusal fissures include a barely visible transverse fissure distal to the protoconid and metaconid that deeply cuts the buccal aspect of the tooth. Externally, there is a slight mesial bend to the buccal groove but no clear indication of protostylid development. The tooth is reasonably worn and potentially obscures this feature.

Discussion. MLD 4 was discovered in Sept 1948 and was first described by Dart as an adult female on the basis of attrition (1949a). It likely represents the same individual as MLD 18 due to the similar morphology, manganese staining, and wear. This specimen is clearly a young adult on the basis of the full eruption and moderate wear of the M_3.

The morphology of the MLD 4 M_3 is tremendously similar to MLD 18 and MLD 19 in appearance of the occlusal outline, cusp proportions, and cusp shape. The development of the *tuberculum intermedium* is also a feature shared by the MLD 18 and MLD 19 lower molars and MLD 5 dp_4. The overall occlusal outline appears most similar to the SK 34 molar with a somewhat tapered distal border, although the accessory cuspulids of the robust australopith occlusal surface are unmatched in MLD 4. The specimen appears intermediate between the morphologies of *A. africanus* and *A. robustus* as it appears broader with lower-lying cusps than specimens attributed to *A. africanus* and not as cuspulated or thick as specimens attributed to *A. robustus*. A favorable comparison can be made between MLD 4, StW 133, and StW 109, although the hypoconulid appears distinct in MLD 4 with a deep and broad distal fovea that is unmatched in the comparative samples.

Figure 8-2*: *MLD 4a, b, & c. The MLD 4 mandibular fragment with left M_3 in occlusal (*a*), buccal (*b*), and mesial (*c*) view.



<u>MLD 5</u>

Overview. This infant specimen is an isolated deciduous premolar with the occlusal surface preserved and the roots embedded within breccia (technically sandstone). The occlusal surface also exhibits visible hypoplastic pitting similar to that of the unworn MLD 2 molars.

Molars. This right dp_4 (dm_2) exhibits essentially no interproximal or occlusal wear. Its general appearance is somewhat long mesiodistally, although it is considerably buccolingually broader near the CEJ. This dp_4 displays a Y-fissure pattern [*contra* Dart

(1949a)] and 6 cusps, which includes a *tuberculum intermedium* demarcated by a fissure extending from the lingual fissure into the metaconid (although see Dart 1949a). The occlusal fissures between the protoconid and hypoconid and the hypoconid and hypoconulid are particularly deep, as is the central fovea.

The protoconid is positioned slightly mesial to the metaconid. A *tuberculum sextum* is not present. Two crests extend between the protoconid and metaconid, one of these is continuous while the other is incised by a median groove. The distal trigonid crest is present and continuous and not fully incised by the main longitudinal fissure, while the accessory crest is less developed. Nestled between these crests is a deep and transversely oriented mesial fovea. On the mesial margin of the tooth is a crest extending between the protoconid and metaconid with several large mesial marginal tubercles that are so developed they are considered cuspulids by some authors (e.g. Dart, 1949a). This mesial marginal crest encloses a second transversely oriented fovea on the mesialmost aspect of the tooth.

Although a deflecting wrinkle is not present, its incipient development is indicated by a medial ridge that is constricted at its midpoint. An entoconid-hypoconulid crest is indicated but interrupted by the longitudinal fissure. A protostylid appears as small shelf and pit below a branch off of the mesiobuccal groove. The dp_4 root form appears to be two roots a mesial and a distal, but this aspect is difficult to assess.

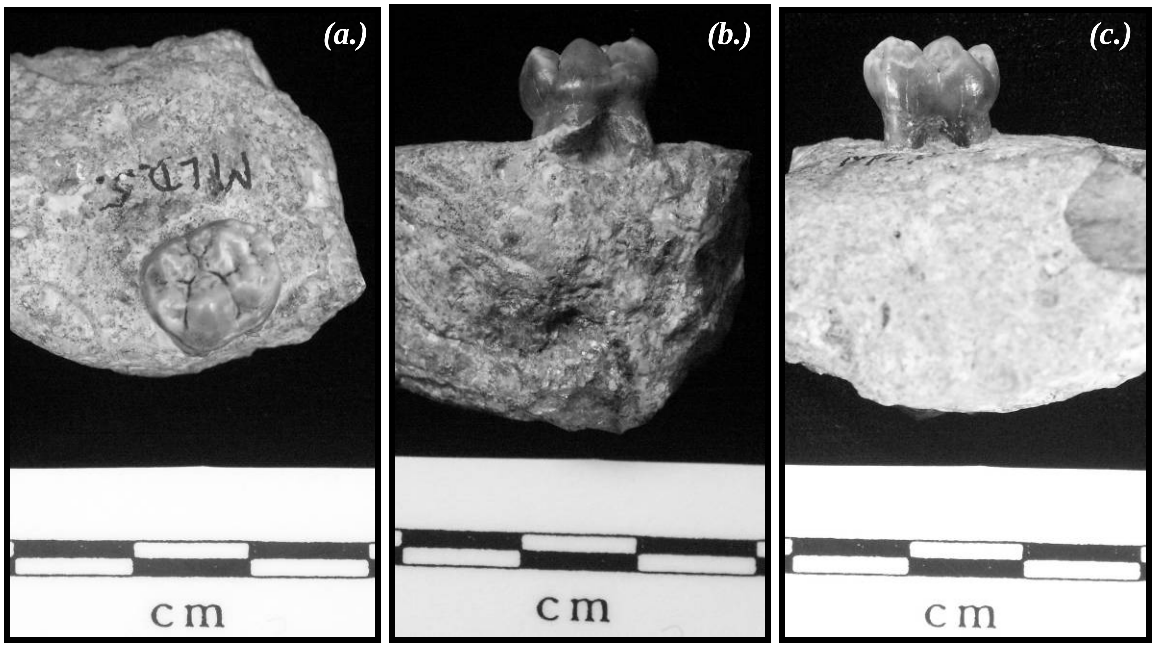
Discussion. MLD 5 was discovered in September of 1948. This specimen is considered to fit into the category of infancy due to the incomplete development of the roots and non-occlusion of the crown. It originally was described as a juvenile male

(Dart, 1949a). More likely, this individual was approximately or slightly older than 1 year on the basis of an ape model of dental development (Bromage, 1987). Please see Table 9-1 for a complete summary of age at death estimates for this specimen.

The smaller MLD 5 dp_4 is similar in its occlusal outline shape and cusp proportions to MLD 2, although the latter's advanced wear prevents further comparison. The morphology of this specimen is quite distinct from the mesially narrow Sterkfontein specimens such as StW 428. MLD 5 is most similar to the SK 64, SK 3978, and KB 5503 among robust australopith specimens in a number of features. Notably, these specimens all share a Y-fissure pattern, with strong accessory distal fovea associated with an enamel feature on the distal margin, similar mesial marginal ridge with large tubercles, two crests connecting the protoconid and metaconid, and enhancement (pit and/or shelf formation) of the mesiobuccal groove on the external aspect of the tooth. The similarities between MLD 5 and these robust australopith dp_4s are almost as striking as the differences between it and some specimens from Sterkfontein (e.g. StW 151 and StW 307). However, several specimens from Sterkfontein (in contrast to the robusts) share with MLD 5 two crests connecting the protoconid and metaconid where the distal trigonid crest is more marked than the accessory crest and a more mesially positioned protoconid relative to the metaconid (Grine, 1985).

Unfortunately, the significant wear of many of the Sterkfontein dp_4s limit the number of specimens with which solid comparisons can be made. Comparison of dimensions of the crown indicate that the Sterkfontein sample is highly variable in size and the MLD 5 specimen tends to situate itself near the low end of the robust sample and the high end of the Sterkfontein australopith sample.

Figure 8-3*: *MLD 5. The MLD 5 right dp_4 in occlusal (*a*), buccal (*b*), and lingual (*c*) views.



MLD 6

Overview. This specimen is a young adult right craniofacial fragment preserving the canine alveolus and at least portions of P^3-M^3. Almost half of the buccal aspect of the P^3 crown is missing due to a superobuccally angled fracture extending from the center of the crown's occlusal surface. In addition, no part of the crown and only the buccal portion of the M^3 roots are preserved. Moderate to advanced attrition partly obscures some details of the occlusal surface of the MLD 6 dentition. It is likely that MLD 23 and MLD 6 are associated on the basis of comparison of the P^3 lingual cusp morphology and wear, as well as examination of the attrition of the perikymata of MLD 6's P^4 and MLD 23's P^3 under 10x magnification (see expanded discussion in Chapter 5).

Canines. Although the canine alveolus is preserved, it is with great caution that its features are used to assess the missing tooth (although see Plavcan *et al.*, 2009). The alveolus indicates that the canine root was relatively small in comparison to many specimens attributed to *A. africanus*.

Premolars. Where both premolars are preserved, lingually and distally, they exhibit similar morphology. Although the P^3 is only partly preserved, it was smaller than the P^4 in overall dimensions (this is the case for the mesiodistal aspect at a minimum). Both premolars exhibit weak distolingual grooves of the occlusal surface. In addition, they both exhibit a somewhat centrally located protocone and a gently curved lingual outline, contributing to a broad and bulbous overall appearance for the lingual aspect of these teeth.

The P^3 does not preserve any part of the median longitudinal fissure. A distal accessory ridge is present as a marked crest extending distally from the protocone. Although only partly preserved, the distal aspect of this tooth exhibits development of a ridge extending along its distal periphery. The external aspect of the crown exhibits a faint, ill-defined mesiolingual groove and no external distolingual groove. External buccal grooves are considered to be present on the basis of the natural breccia cast, as originally noted by Dart (1949a). These external grooves are generally associated with corresponding stylar development. In addition, the P^3 displays what appear to be 2 distinct roots and no suggestion of a third root.

The P^4 is preserved in its entirety, although the crown exhibits moderate wear with dentine exposure on both major cusps. The paracone is positioned on the edge of the occlusal surface, particularly in comparison to the more centrally positioned protocone. A median longitudinal fissure is partly interrupted by the enamel ridges extending between the main cusps as a transverse ridge. A broad distal accessory ridge extends from the protocone.

The grooves of the occlusal surface include a marked mesiobuccal groove, a marked distobuccal groove that cuts through the tooth's margin, a marked distolingual groove, and a weak and short mesiolingual groove. The mesial fovea is small, although the posterior fovea is comparatively large. This specimen exhibits a ridge extending along the entire distal periphery of this tooth as well as distal accessory marginal tubercles. It is possible that one of these tubercles may have been identified as cuspule with an independent apex in a less worn tooth. The degree of wear also makes it unclear if accessory marginal tubercles were present mesially.

The external aspect of the P^4 exhibits weak and ill-defined external mesiobuccal and distobuccal grooves (or corresponding styles), while the lingual aspect of the tooth does not display external grooves. The perikymata are clearly visible on the external aspect of the crown, as well as a narrow linear enamel hypoplastic (LEH) defect. The latter defect accentuates an enamel swelling that is here identified as a slight cingulum. The buccal root appears to be a single root. However, it should be noted that hominin mandibular premolar and molar root number has been studied by a number of authors (e.g. Abbott, 1984; Tobias, 1995; Wood et al., 1988, others). Root number may not be a good variable with which to assess variation among phylogenetically distinct populations since assessment of numerous human populations indicates that some root variants are more common in males and the size of the postcanine primordia may impact root form, size, and number (Shields, 2005).

Molars. The crowns of M^1 and M^2 are well-preserved, but display attrition that partly obscures the occlusal surface. The molars are similar in morphology, although the M^2 is larger than the M^1 in overall dimensions.

The M^1 exhibits dentine exposure on the paracone, protocone, and hypocone. The occlusal surface displays a large distally positioned protocone and a large distally extending hypocone. The metacone and paracone appear similarly sized; however, examination of the M^2 suggests that mesial interproximal wear has significantly reduced the mesiodistal dimension of the paracone in the M^1. The relative sizes and orientations of the cusps produce a somewhat rhomboidal occlusal outline. The distal aspect of the tooth exhibits enamel development in the form of a ridge along the distal marginal aspect, but further description is obscured by attrition. The crista obliqua appears as a thick continuous crest that is weakly incised by the main longitudinal fissure.

The buccal groove extends the majority of the height of the crown and exhibits a small parastyle near the cementoenamel junction. A faint vertical groove is visible on the mesiobuccal aspect of the paracone. A similar faint vertical groove is evident on the distobuccal aspect of the metacone, producing what could be argued to be a weak metastyle. The lingual groove exhibits significant wear, but was marked nonetheless. A Carabelli's cusp is not evident on the crown; however, it is difficult to assess due to the degree of wear. A small dimple in the worn mesiolingual aspect of this tooth may indicate some Carabelli-related development. Robinson (1956a) similarly argued that the shape of the mesiolingual angle in both molar crowns indicates the presence of a Carabelli structure, although his argument is somewhat tenuous.

The M^2 is moderately worn with no dentine exposure on the cusps, strong mesial interproximal wear, and moderate distal interproximal wear. Aside from larger overall dimensions and occlusal wear taken into account, the M^2 exhibits the same approximate rhomboid-shaped occlusal outline, cusp orientation and cusp proportions as the M^1. The paracone is clearly larger than the metacone in this tooth. A distal cuspule is present and associated with both the distal aspect of the metacone and the distal marginal ridge [although see Dart's discussion of a "post-foveal enamel ridge and no cusplet crenulation upon it" (1949a:200)]. The distal marginal ridge is particularly thick nearest the hypocone and serves to distally extend the distolingual aspect of the tooth in its occlusal outline. A crista obliqua is present but is distinctly interrupted by the main longitudinal fissure.

The external aspect of the M^2 displays a number of features of interest. The buccal groove displays an ill-defined parastyle and the groove itself is more marked, but shorter than on the M^1. A weak vertical groove is displayed on the mesiobuccal aspect of the paracone. In comparison to the M^1, a similarly positioned, but more marked vertical groove and better defined metastyle are apparent on the distobuccal aspect of the metacone. The lingual groove, although moderately worn, is estimated to have been marked. The faint stylar cusps and associated grooves of the M^1 and M^2 are located in regions well associated with and thus are argued to be related to cingular development (e.g. Dahlberg, 1950). Enamel development relating to a Carabelli's cusp is not apparent, although a dimple in the worn occlusal surface indicates its presence was partly obscured by wear.

Discussion. The premolars are somewhat intermediate in morphology between the specimens attributed to the species of *A. africanus* and *A. robustus*. In the appearance of the P^3 protocone MLD 6 is squared and somewhat bulbous and moderately worn, enough so that it is difficult to compare with either hominin taxon. However, the relatively low values for crown dimensions and area establish a closer alignment with specimens of *A. africanus*.

The P^4 is morphologically intermediate in comparison to the 2 South African taxa [*contra* Robinson (1956)], although the extreme variation in upper premolar morphology within the Sterkfontein and Swartkrans samples is striking and considerable overlap of these two samples exists. The MLD 6 P^4 is more like the robust sample in being mesiodistally longer and more bulbous than most of the Sterkfontein specimens. However, its occlusal morphology and proportions are most similar to the TM 1511 specimen currently attributed to the species of *A. africanus* (although it appears to be somewhat unique within the sample). Even more, a comparison of the actual occlusal fissures and cusp positions and proportions of the MLD 6 P^4 is also quite similar to SK 13. The major distinction in the latter comparison is that the buccal face of the crown displays greater external grooves distinguishing the overall occlusal outline of the MLD 6 specimen from SK 13 (although see the robust australopith specimen TM 1517). The overall shape of the occlusal outline is relatively square in MLD 6, as it is in specimens attributed to *A. africanus* and *A. robustus*, in part due to the external buccal grooves. MLD 6, TM 1511 (attributed to *A. africanus*), and SK 13 (attributed to *A. robustus*) are more similar to each other than TM 1511 is to StW 280 (attributed to *A. africanus*).

The samples of specimens attributed to *A. africanus* and *A. robustus* have grown, along with the ranges of variation displayed by the species samples, comparisons of the MLD 6 dentition have become further confused due to its similarity to specimens attributed to both species. This is not terribly surprising when the degrees of upper premolar variation within the Swartkrans and Sterkfontein samples are examined. In fact, there are specimens at Swartkrans and Sterkfontein that are more similar to each other than they are to other specimens attributed to the corresponding species. In recognition of this difficulty, the upper premolars are considered not only intermediate, but also somewhat indeterminate in their closes affinities.

The MLD 6 molars present a similar situation as the premolars, that is, the molar morphology could be considered intermediate or the degree of morphological variation within the South African hominin samples could be considered so variable that the MLD 6 molars could be attributed to either taxon reasonably. Among the robust australopith specimens, the MLD 6 M^2 is most similar to SK 13, SK 47, SK 48, and SK 49. These specimens share a similar rhomboidal occlusal outline, similar cusp proportions, marked distal marginal ridge with a distal cuspule [*contra* Dart (1949a)], and the development of a moderate mesial marginal ridge or mesial marginal tubercles (suggested in the more worn MLD 6 and SK 48 molars). In comparison with the Sterkfontein specimens attributed to *A. africanus*, the MLD 6 M^2 is most similar to Sts 22, StW 183, StW 73, and Sts 52. These specimens generally share a shallow distal fovea, a similarly incised crista obliqua, and buccolingually truncated metacone. Sts 52 does not share all of these characters, but its distal marginal ridge, and hypocone proportions are quite similar to that of MLD 6. In consideration of all of the features of the crown, the MLD 6 molars are considered by this author to be somewhat intermediate in morphology, but slightly more similar to the robusts. Interestingly, Dart originally said this specimen was distinct (1949a) but later, on the basis of a larger Sterkfontein sample, argued that MLD 6 falls within range of variation at Sterkfontein.

Figure 8-4*: *MLD 6. The MLD 6 craniofacial fragment with right P^3-M^3 in occlusal view.

MLD 9/12

Overview. This adult specimen is composed of two right maxillary fragments with P^3-M^3. The dentition exhibits advanced wear strongly obscuring the morphology of the crowns.

Incisors. The incisors are missing, but their alveoli suggest relatively short roots.

Canines. The canine is not preserved, but the partly eroded canine alveolus generally indicates a long, broad canine root.

Premolars. The premolars exhibit significant wear. The P^3 displays extensive dentine exposure that is worn to the 2 roots both lingually and buccally, while the P^4 displays significant dentine exposure retaining an island of enamel on the distobuccal aspect of the tooth. The only aspect of the crown that is evident is that the P^4 appears relatively short mesiodistally; however, this is likely the result of extreme occlusal and interproximal wear rather than a characteristic of the unworn crown. There appears to be a faint LEH defect on the superiormost buccal aspect of the P^4 crown. The roots of the P4 exhibit only 2 roots.

Molars. The molars exhibit marked occlusal and interproximal wear. The M^2 is larger than the M^1 and M^3, although the latter two specimens are difficult to compare to each other due to wear and preservation issues. The M^1 exhibits dentine exposure on all major cusps that has coalesced and only retained a centrobuccal island of enamel and peripheral rims of enamel. The buccal groove is marked and likely extended approximately half of the height of the unworn crown. The mesiobuccal aspect of the paracone exhibits a faint, ill-defined groove that may be interpreted to indicate slight stylar cusp or weak cingular development.

The M^2 exhibits dentine exposure on all 4 cusps and coalescence of the dentine exposures of the protocone, paracone, and hypocone. The buccal aspect of this tooth preserves a great deal of enamel, while the lingual aspect retains limited enamel along the periphery. The buccal groove is moderately developed and is estimated to have extended a shorter aspect of the crown than in the M^1. The distobuccal aspect of the metacone exhibits a trace groove that may indicate either slight cingular or stylar cusp development. The M^2 displays a single, broad lingual root with a fairly deep groove and two buccal roots.

The M^3 displays dentine exposure on the protocone, paracone, and hypocone, as well as the coalescence of the dentinal areas of the protocone and paracone. A large portion of the mesiolingual aspect, small portion of the mesiobuccal corner, and a small chip of the distobuccal periphery of this tooth are not preserved. The preserved aspect of the buccal groove is moderately developed and is estimated to extend less of the height of the crown than either than M^1 or M^2.

Discussion. This MLD 9 fragment was found in November of 1948, while the MLD 12 fragment was found in November of 1949. The MLD 9/12 teeth are extremely worn, making comparison to other specimens difficult. The canine alveolus tentatively suggests a long, broad canine root was present providing subtle and debatable indications of a similarity to specimens attributed to *A. africanus*. The premolars cannot be confidently compared to other specimens as both samples exhibit oval occlusal outlines when so considerably worn (e.g. SK 46, SKW 8, and StW 9). Although significantly more worn, the M^2 is similar to the MLD 6 molars in rhomboidal outline and the M^3 is similar to the MLD 6 molars in their hypocone and metacone proportions and large distal marginal ridge extending between the hypocone and metacone.

Figure 8-5*: *MLD 9/12. The MLD 9/12 maxillary fragment with P^3-M^3 in occlusal view.

MLD 11/30

Overview. The MLD 11/30 specimen was originally composed of two right maxillary fragments with I^2, C^1, P^3, P^4, M^1 at varying stages of development; however, Robinson sacrificed the maxillary fossil fragments to extract the dentition from the crypt. Casts of both the original specimens and the extracted fossil teeth were examined. The eruption sequence is apparent on the basis of the stages of development for the preserved teeth. The M^1 was fully erupted, the I^2 had erupted to a point that its apex is just deep to the alveolar plane but had incomplete root development, the P^4 and P^3 had not yet erupted, and the C^1 is the furthest from eruption and displays a fully developed crown with little root development. The specimen is reconstructed as an individual in late childhood at death (see Table 9-1).

Incisors. The MLD 11/30 I^2 is unworn with a fully formed crown and partially developed roots that were damaged during extraction from the maxillary bone. Examination of a cast of the original specimen indicates that the I^2 had not yet erupted. This claim is in contrast to Robinson (1956), as he indicated that it was impossible to assess the stage of eruption from the fragmentary maxillary specimens. Thus, it seems likely that the maxillary specimen had already undergone some destruction prior to Robinson's first examination. The mesiolingual corner of incisal margin suffered post-depositional damage. The overall appearance of the incisor crown is small and narrow with a tapered distal aspect. The buccal face of the crown is somewhat unexceptional, with the exception of the marked linear enamel hypoplasia running transversely across the middle of the crown. This marked enamel defect suggests this individual underwent a period of physiological stress. The lingual aspect of the crown is faintly shovel-shaped. It also displays a small tubercle, moderately developed distal marginal ridge, and only a faint mesial marginal ridge. The incisal edge exhibits three mamelons and relatively rounded mesial and distal incisal margins (most marked along the distal margin). Although it is considered here to exhibit no wear, some have argued that the incisal margin exhibits some wear.

Canines. This canine specimen was originally in the maxilla and was unerupted (in the crypt) prior to removal by Robinson. The canine crown is fully developed, but there is virtually no root development for this specimen. The crown is short and asymmetrical with sloping mesial and distal incisal edges, and the former extending longer and sloping more strongly than the latter. The asymmetry in the canine is more marked than is typical for either *A. africanus* or *A. robustus*, but does not fully approach the marked asymmetry of earlier hominins. The buccal aspect of the crown is strongly transversely and vertically curved (producing a somewhat distally tilted apex) with weak buccal grooves. The lingual aspect of the crown exhibits a small lingual tubercle, 2 weak lingual grooves, and weak mesial and distal marginal ridges that converge near a moderate eminence near the CEJ and just proximal to the lingual tubercle. The mesial marginal ridge is longer and more developed than the distal and extends from the marginal eminence to the apex.

Premolars. The P^3 is unworn as it had not yet erupted. The protocone is bulbous and mesially situated in comparison to the paracone. The protocone and paracone are separated by a deep and uninterrupted median longitudinal fissure extending between the deep mesial and broad, shallow distal fovea. The grooves of the occlusal surface include marked mesiobuccal, distobuccal, and distolingual grooves and weak, virtually absent mesiolingual groove. The paracone exhibits a marked mesial accessory ridge and intermediate distal accessory ridge. The protocone does not display a mesial accessory ridge, but does exhibit a weak distal accessory ridge. The buccal essential crest bifurcates into two ridges. Clearly defined mesial and distal marginal ridges extend around the periphery of the tooth with both mesial and distal accessory marginal tubercles. The external grooves of the tooth include an ill-defined external mesiobuccal groove that appears as a triangular depression. There is no external mesiolingual nor distolingual groove and the distobuccal groove is obscured by matrix.

The MLD 11/30 P^4 is only partly preserved. It was unerupted and displays no wear of the crown. The roots were only partly developed. The lingual aspect of the crown is embedded within the remaining maxillary bone and a small portion of the buccal aspect of this tooth is exposed. The preserved and visible buccal aspect of the tooth is somewhat unremarkable. It suggests that the overall size of the P^4 is relatively small.

Molars. The M^1 exhibits minor wear and is only partly preserved. The paracone and most of the metacone are missing due to a crack extending longitudinally along the buccal aspect of the crown. The protocone is broad, bulbous, and large in contrast to its small, broad, and mesiodistally truncated hypocone. The crista obliqua is a continuous thick crest extending between the protocone and metacone that is etched by the main longitudinal fissure. A narrow marginal ridge extends between the metacone and hypocone and exhibits two small and indistinct distal cuspules with independent apices.

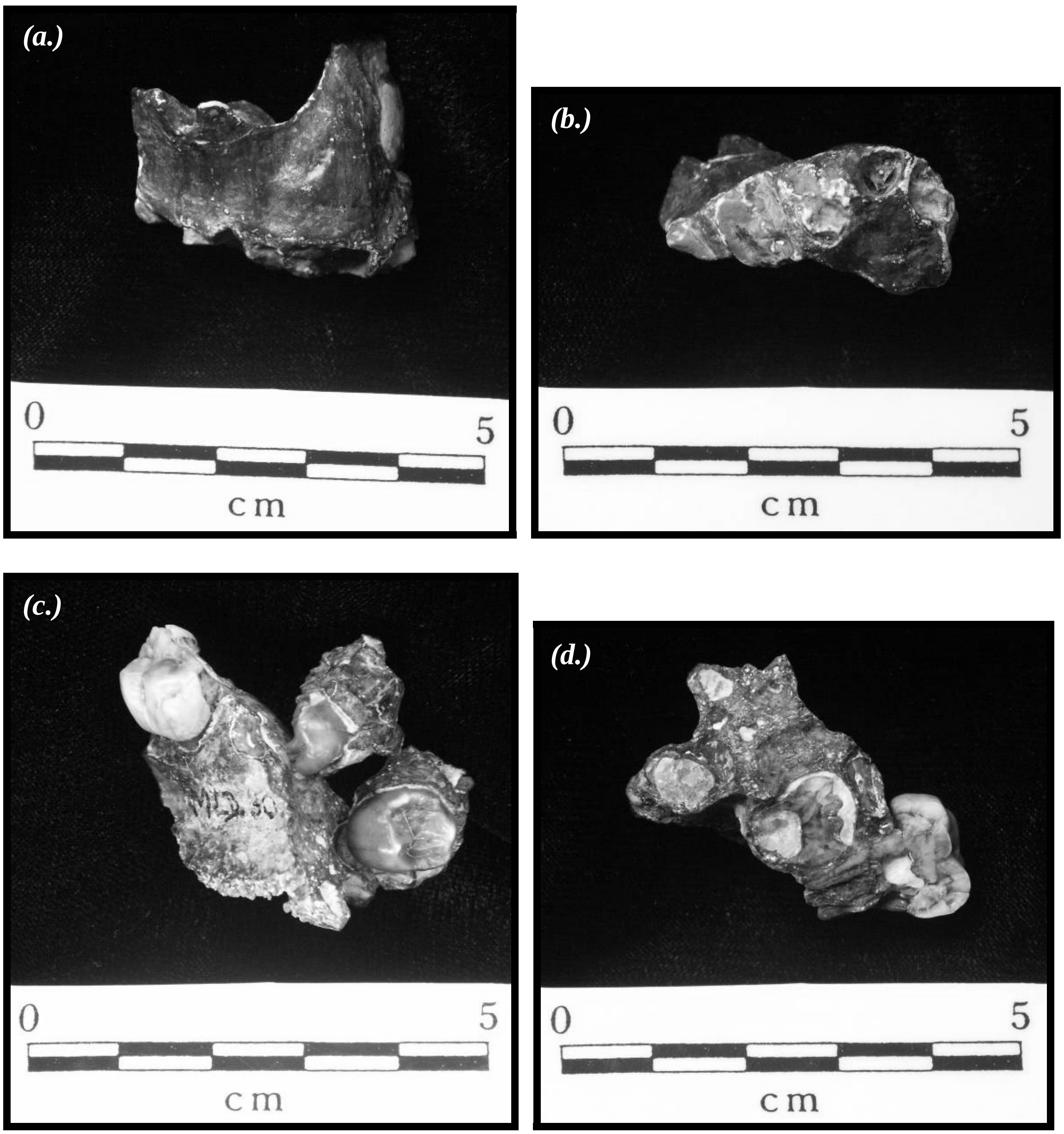
A clear Carabelli's enamel formation appears as a definite shelf of enamel related to protocone with a small apex. The lingual groove is marked and extends approximately half way up the external aspect of the crown. This molar is similar to the MLD 6 specimen in its lingual groove morphology, appearance and proportions of the protocone, metacone, and hypocone. The overall outline of this molar is somewhat distinct from that of MLD 6 due to the less developed distal marginal ridge in MLD 11/30, which does not extend the distolingual aspect of the tooth.

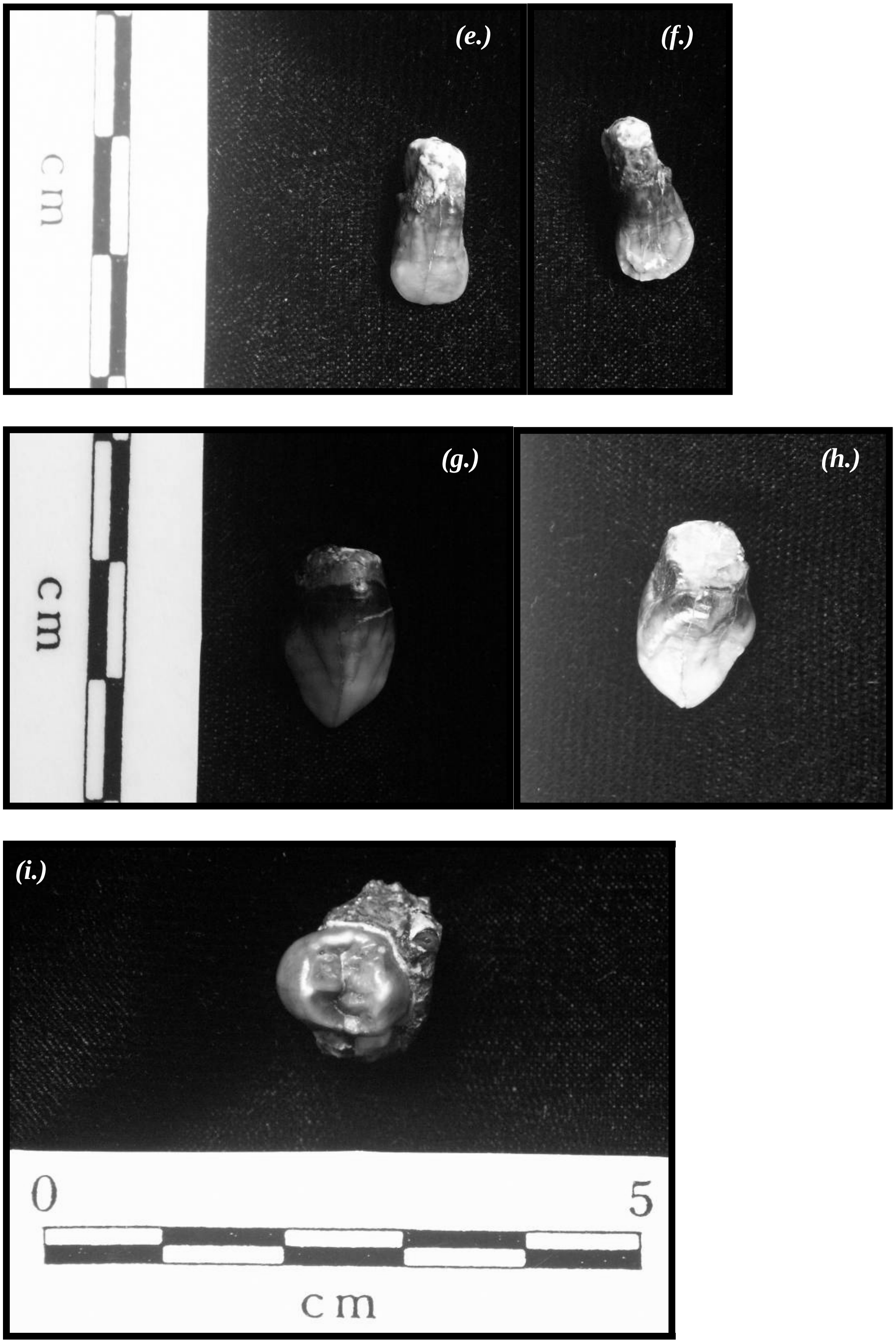
Discussion. The MLD 11/30 maxillary fragments were discovered in July of 1949. The lateral incisor is mesiodistally broader than specimens of *A. robustus* and is within the middle of the range of *A. africanus*. Its lingual tubercle is unusual among the South African early hominins. The canine appears relatively short, but is more similar to the sample of *A. africanus* on the basis of the strongly asymmetrical crown. Its overall calculated crown area is more similar to the median and mean of the sample of *A. africanus* and at the extremely high range of the sample of *A. robustus*.

The MLD 11/30 premolar is fairly long in the mesiodistal dimension and strongly resembles the worn MLD 23 P^3. It most closely resembles specimens that currently are attributed to the taxon of *A. robustus*, namely the SK 822 and SK 24 P^3s. The resemblance to SK 24 is particularly striking in virtually every feature of the crown: the cusp positions, cusp proportions, fissures, occlusal outline, essential crests, and mesial and distal marginal ridges. The more oval or rounded occlusal outline of most of the Sterkfontein specimens is unlike that of MLD 11/30 (although see StW 408). The overall dimensions more closely align this specimen with the sample of *A. africanus*. The MLD 11/30 P4, however, suggests its dimensions would have been relatively small.

The MLD 11/30 M^1 is similar to that of MLD 6 in the overall occlusal outline. Its morphology is characterized by an expanded protoconid, mesiodistally truncated hypocone, moderate Carabelli feature, and etched crista obliqua. In all of these features, MLD 11/30 M^1 strongly resembles SK 63. However, the overall dimensions of MLD 11/30 molar are relatively small. In comparison to the Taung M^1 morphology, MLD 11/30 appears slightly larger, with more externally situated cusp tips, similarly developed distal marginal ridge, contrasting Carabelli formation (or lack thereof in Taung), and broader crista obliqua. In comparison to the Sterkfontein sample, MLD 11/30 is perhaps most similar to Sts 32 as they share a mesiodistally truncated hypocone, similarly developed distal marginal ridge, broad crista obliqua, and moderate Carabelli feature. The mesiodistal dimensions of the M^1 crown to not help to discriminate the MLD 11/30 specimen from either sample.

Figure 8-6*: *MLD 11/30. The MLD 11/30 maxillary fragment with I^2-M^1 at varying stages of eruption, where a cast of the original specimen is in buccal (*a*) and occlusal (*b*) views, the actual specimen is in occlusal (*c*) and mesiolingual (*d*), the I2 is in buccal (*e*) and lingual (*f*) views, the C^1 is in buccal (*g*) and lingual (*h*) views, the P^3 is in occlusal (*i*) view, and the M^1 is in occlusal (*j*) view.




(e.)
(f.)
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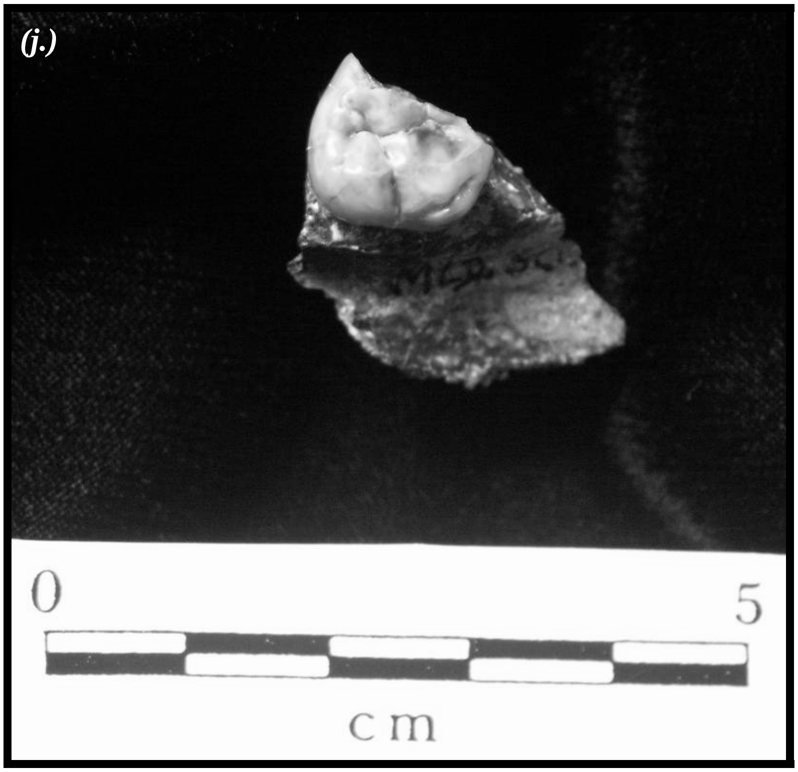


(j.)

MLD 18

Overview. MLD 18 is a relatively complete young adult mandibular fragment with right I_1-M_3 and left I_1-C_1, P_4, and a portion of the roots of P_3. The teeth exhibit a variety of cracks and chips described in more detail below. The dentition exhibits significant wear, including marked occlusal and interproximal wear on most of the premolars and molars. The enamel of the incisors appears relatively thin, particularly in consideration of the thicker enameled premolars and molars.

Incisors. The incisors are well preserved, although the left I_2 displays an obliquely running crack through the middle of the tooth along a mesiolingual to distobuccal axis. The incisors exhibit extreme wear, preserving only a small portion of the incisor crowns.

The preserved aspect suggests a relatively vertical incisor crown. Weak linear enamel hypoplasias are displayed on the buccal surfaces of the incisors, particularly the I_2s, and are only slightly more developed than standard perikymata. The roots are exposed for quite a distance from the CEJ to the alveoli and appear fairly broad.

Canines. The right canine is well preserved but displays a planar crack extending through the tooth from the centrobuccal and mesiolingual aspects of the occlusal surface to the mesial aspect of the root at the alveolus. The left canine preserves much of the lingual aspect of the tooth, but the buccal aspect suffered numerous cracks that have resulted in little preservation of the occlusal surface and virtually no preservation of the buccal face of the tooth. Both canines exhibit considerable wear of the occlusal surface as well as moderate distal interproximal wear. The overall appearance of the canine crown is large and morphologically comparable to specimens attributed to the species of *A. africanus*. The lingual aspect of the right C_1 displays a shallow mesial fovea and moderate distal fovea surrounding a worn, but marked lingual ridge. The distal fovea is highlighted by a moderate distal marginal crest. Only the distal fovea is preserved in the left C_1, but it is shallow. The right C_1 exhibits faint vertical enamel pillars on the mesial and distal margins of its buccal aspect. The left canine preserves a small fragment of a similarly developed vertical pillar on the distal margin of its external buccal aspect. The buccal aspect of the right C_1 displays marked linear enamel hypoplasias.

Premolars. The MLD 18 premolars exhibit considerable wear of the occlusal and interproximal surfaces. The premolars are generally fairly broad and bulbous, despite their advanced state of attrition. Beyond this shared feature, the P_3 and P_4 are morphologically quite distinct.

The right P_3 is missing most of its mesiobuccal aspect. The left P_3 only preserves a small portion of its roots and no part of the crown; thus, all observations were made on the right P_3. The right P_3 exhibits marked occlusal wear with the coalescence of the buccal and lingual exposures. A lingual enamel peninsula is barely continuous with a complete, but distally slender enamel rim. The overall occlusal outline indicates an asymmetrical crown with mesially situated protoconid and a mesially truncated lingual cusp. Other features of the crown are not preserved due to the advanced state of attrition. The buccal aspect of the external tooth exhibits a weakly developed linear enamel hypoplastic feature.

The right and left P_4s are preserved, the right in its entirety and the left preserving the mesial approximately two-thirds of the crown and a portion of its roots. Both P_4s display marked occlusal and interproximal (particularly distal) wear. The crown exhibits the coalescence of its buccal and lingual dentine exposures, although it maintains considerable enamel on the distolingual quadrant of the crown. The protoconid is mesially situated, but in contrast to the $P_{3,}$ the P_4 displays a more square-shaped, symmetrical crown due to a mesiodistally expanded metaconid and talonid basin. In addition, the P_4 is larger overall and exhibits greater mesiodistal and buccolingual dimensions than the P_3. The only other feature of the occlusal surface that is preserved is presumed to be a trace of a distal fovea.

Molars. The MLD 18 molars exhibit wear to varying degrees, specifically they exhibit an advanced state of attrition in M_1, a less advanced state of attrition in M_2, and a moderate state of attrition in M_3, suggesting a substantial delay between the eruption of this individual's molars. The overall appearance of the molars is bulbous and somewhat buccolingually broad. The size of the molars is greatest in M_2, then M_3, and least in M_1 (although the significant wear of M_1 makes this a reconstruction).

The M_1 is mostly preserved and is only missing a small portion of the enamel on the lingual aspect of the crown. The occlusal wear is significant, retaining only a partial enamel rim along the buccal and lingual margins of the crown and displaying dentine exposure on the rest of the occlusal surface. The extreme wear of the M_1 impedes the description of any additional features of this tooth.

The right M_2 exhibits a couple of minor fractures along the distal portion of the crown and a more significant crack that has resulted in the loss of enamel broadly across the mesiodistal corner and along a narrowing belt extending to the hypoconid. The occlusal surface is extensively worn to a point at which it exposed dentine on all cusps but coalescence of mesial dentine islands is unclear due to cracks (but likely). The mesial and distal interproximal wear is considerable. This extensive wear of the crown partially obscures its features from confident assessment. This molar preserves its five main cusps with no indication of a *tuberculum intermedium* or *tuberculum sextum*, although the crown is too worn to assess whether these features were present with any confidence. The preservation of faint fissures suggests that the protoconid and hypoconid were buccolingually broad. The hypoconulid appears to have been quite buccally situated. The considerable enamel, admittedly worn flat, sitting between the hypoconulid and entoconid suggests an enamel feature once rested in this location (potentially a distal marginal crest extending between the hypoconulid and entoconid). There is no evidence of a protostylid, although the advanced wear and the loss of enamel adjacent to the CEJ in the mesiobuccal corner of the tooth makes assessment uncertain. There is a faint buccal groove and a faint groove separating the hypoconid and hypoconulid on the external aspect of this molar.

The M_3 is completely preserved and exhibits considerably less wear than the more mesial postcanine dentition teeth. The occlusal wear involves enamel wear without any dentine exposure, which preserves the major features of the crown. The mesial interproximal wear facet is broad. This tooth is considered here to exhibit 6 cusps [*contra* Dart (1954b)], which includes a small cuspulid-like feature resting between the metaconid and entoconid on the lingual margin of the tooth. This feature displays an independent apex and is defined mesially and distally by faint fissures that suggest it is more closely related to the entoconid than the metaconid. Although a *tuberculum sextum* is not indicated, a small tubercle-like feature is displayed on the distal margin of the tooth without being clearly demarcated by fissures. A *tuberculum intermedium* does not appear to be present. This M_3 displays an X-fissure pattern with distinct contact between the protoconid and entoconid. Although a deflecting wrinkle is not present, its early development is suggested by a straight medial ridge that tapers at its midpoint. An entoconid-hypoconulid crest is quite broad, but it is deeply incised by the main longitudinal fissure. The distal aspect of the tooth displays a transversely oriented and deep fovea partially demarcated by a distal crest extending between the hypoconulid and entoconid. The external aspect of this molar exhibits branching of the mesiobuccal groove suggestive of protostylid formation, but the degree to which it had developed is partially obscured by wear. There is a distinct triangular fissure between the hypoconid and hypoconulid.

Discussion. The MLD 18 specimen is considered a young adult on the basis of the eruption of all of the dentition and their wear (for more details, see discussion in Chapter 7). Comparison of the anterior and posterior dentition results in a fairly distinct pattern for the MLD 18 dentition: the incisors and canines are more similar to specimens of *A. africanus*, while the cheek teeth are more similar to specimens of *A. robustus*. The incisors are extremely worn and do not encourage comparative assessment beyond saying that, once wear is taken into account, the I_2s probably more closely resembled the typically broader incisors of specimens of *A. africanus*. Comparison of the cervical data for the incisors (see Figures 8-8 and 8-9), however, does not support this assertion and instead suggest that the MLD 18 incisors are intermediate in size at the cervix. A boxplot of the cervical areas of I_1 place the MLD 18 specimen within the region of overlap for the samples of *A. africanus* and *A. robustus* and closer to the median of *A. robustus*. A boxplot of the cervical areas of I_2 also position the MLD 18 specimen in an intermediate position, but the MLD 18 value is closer to the median of *A. africanus* in this case.

The canines, although worn, preserve enough of the crown to make solid comparisons to other Makapansgat specimens and to South African hominin taxa in general. The canine is large, strongly asymmetrical and would have been tall on the basis of the preserved aspect of the mesial and distal borders. In these features and the strong distal marginal ridge and vertical enamel pillars on the buccal face, MLD 18 most closely resembles both MLD 42 and specimens attributed to the species of *A. africanus* (e.g. StW 351, StW 498). Comparison of the crown area and index for the C_1 (Figures 8-10 and 8-11) indicates that the MLD 18 C_1 is most like the sample of *A. africanus* in the former variable and indistinguishable from either taxon in the latter variable. The canine crown area, although more like the sample of *A. africanus*, places the MLD 18 canine at the lower limits of the range known for *A. africanus*.

The premolars appear relatively large, with regard to the M_1. The M_1 and M_2 are bulbous, but are worn enough that they could fit within the range of variation of either South African hominin taxon. The M_3 exhibits a somewhat tapered distal aspect, broad mesial aspect, broad protoconid and hypoconid, and mesiodistally compressed hypoconulid with accessory distal fovea. In these features, the MLD 18 M_3 most closely resembles the MLD 19 M_3. This combination of features is quite distinct and is not closely approximated by any of the South African hominin M_3s examined. StW 404 is the closest approximation among the specimens attributed to the species of *A. africanus*, as a result of its broad protoconid and mesiodistally truncated hypoconulid. In addition, the cingulid of StW 404 results in an expanded buccolingual breadth of the mesial tooth. However, the distal fovea and distal marginal ridge of MLD 18 is replaced with two distal cuspulids in StW 404 and the buccal cusp outlines are distinct. In many cases, the robust australopiths exhibit a broad mesial aspect of the M_3 and broad protoconid, but a more cuspulated and bulbous occlusal surface.

The linear enamel hypoplasias displayed by several of the MLD 18 teeth are of notable interest. Recent advances in dental analyses of bioarchaeological samples involve the assessment of hypoplasias for the developmental timing of the periods of stress (e.g. Goodman *et al.*, 1980; Goodman and Rose, 1990; Larsen, 1997; Guatelli-Steinberg, 2001, Guatelli-Steinberg *et al.*, 2004). While these studies in humans have recently produced disparate results depending upon the methods used (Ritzman *et al.*, 2008), the potential for the application of these methods to paleoanthropological samples is attractive and largely unexplored. The appearance of enamel defects in the associated dentition of fossil specimens that died as adults can be used to assess dental developmental sequences for those individuals. Moreover, once the variance in dental developmental sequences and timing is well established for a taxon, LEHs may be of utility in identifying the timing of those moments during which the individual was exposed to the physiological stressor. If the timing of LEHs are coordinated well enough within a taxon and by histological study, those data could even be used in estimating the timing of major developmental events such as weaning (e.g. Lacruz *et al.*, 2005). Certainly, this is an area of research that has great potential for contributing previously unaccessible or rarely accessible behavioral and developmental information.

Figure 8-7*: *MLD 18. The MLD 18 mandible with left I_1-C_1, P_4 and right I_1-M_3 in occlusal view.

Figure 8-8: I_1 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I_1 cervical area [I_1 mesiodistal length of cervix * I_1 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 7), and Sterkfontein *Homo* (n = 1).

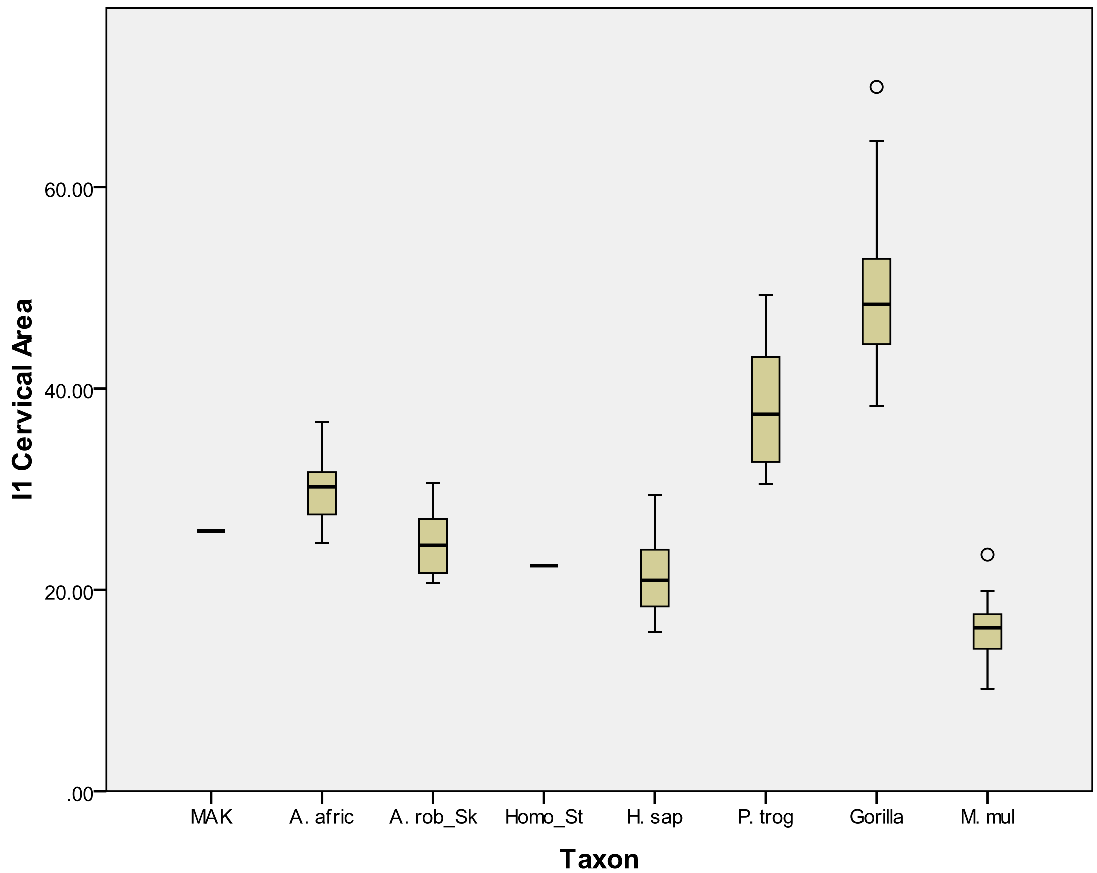


Figure 8-9: I_2 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I_2 cervical area [I_2 mesiodistal length of cervix * I_2 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18. The fossil sample sizes for this analysis are: *A. africanus* (n = 8), Swartkrans *A. robustus* (n = 7), and Sterkfontein *Homo* (n = 1).

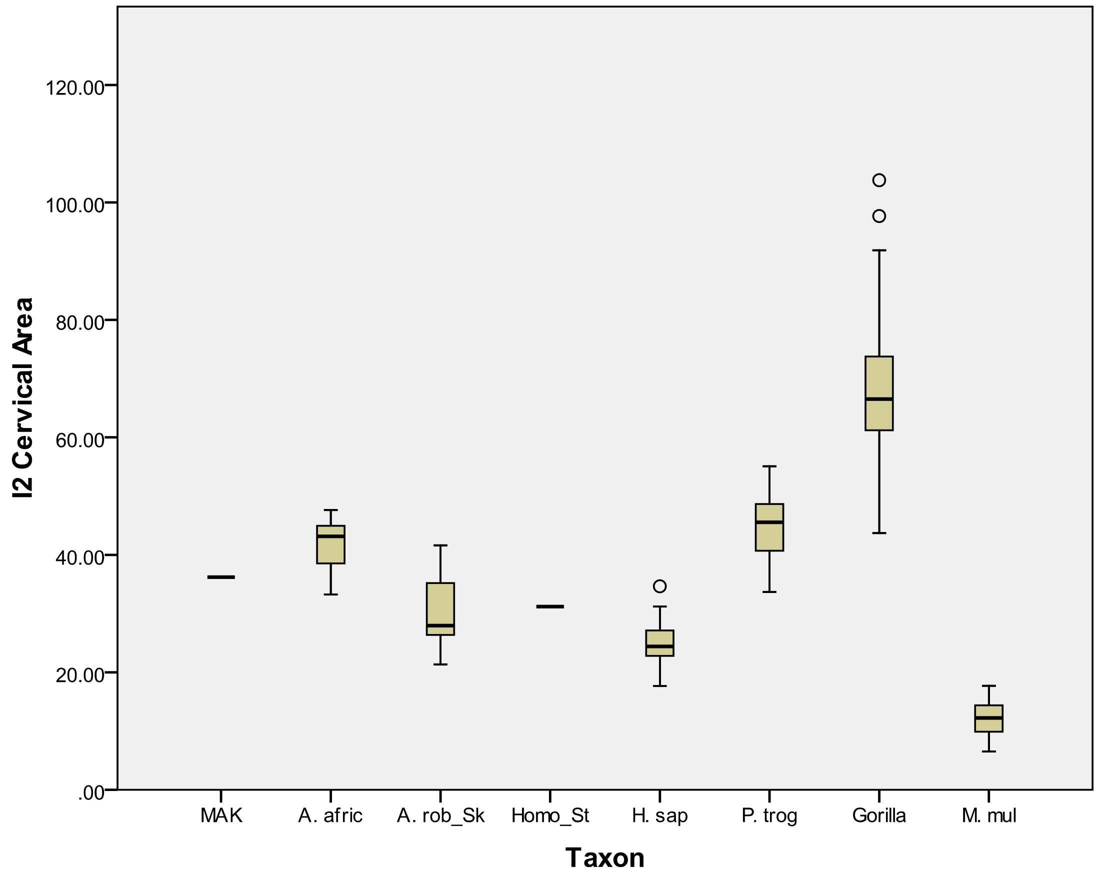


Figure 8-10: C_1 Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the C_1 crown index [(C_1 mesiodistal length of crown /C_1 buccolingual breadth of crown) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18. The fossil sample sizes for this analysis are: *A. africanus* (n = 22), Swartkrans *A. robustus* (n = 10), and Sterkfontein *Homo* (n = 1).

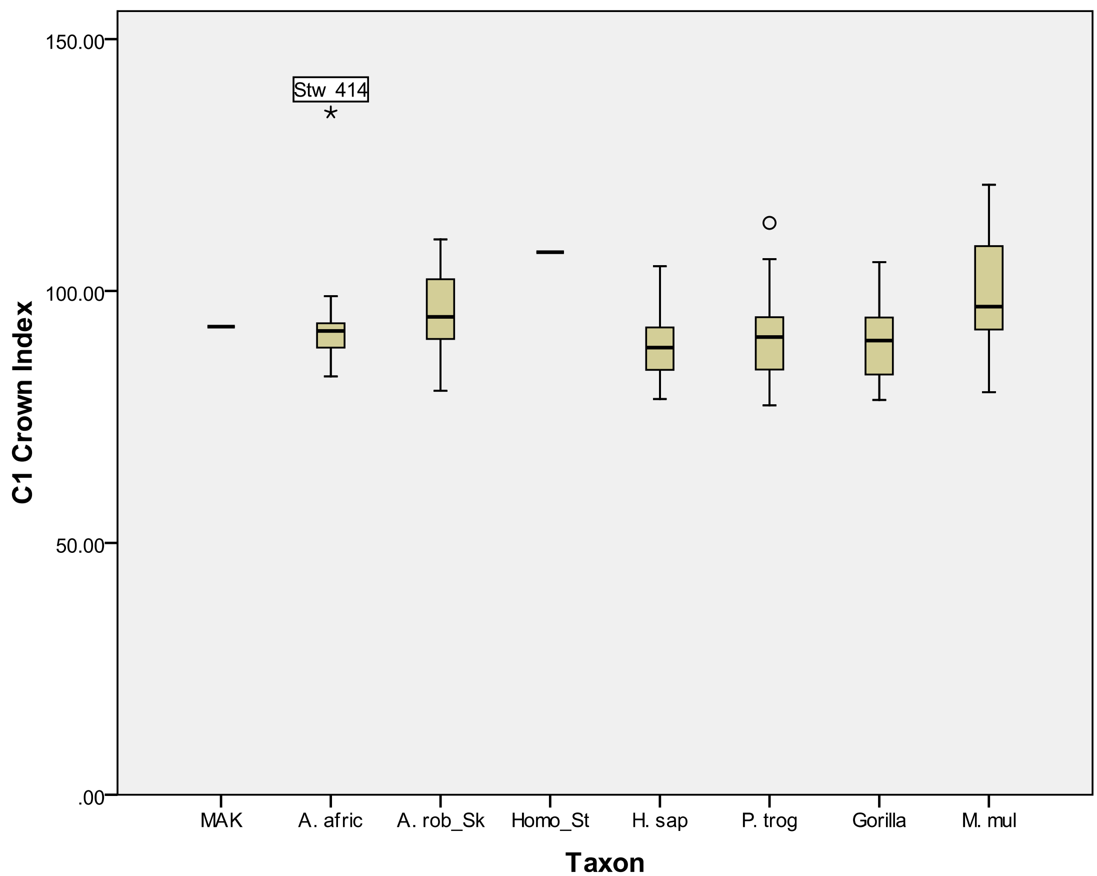
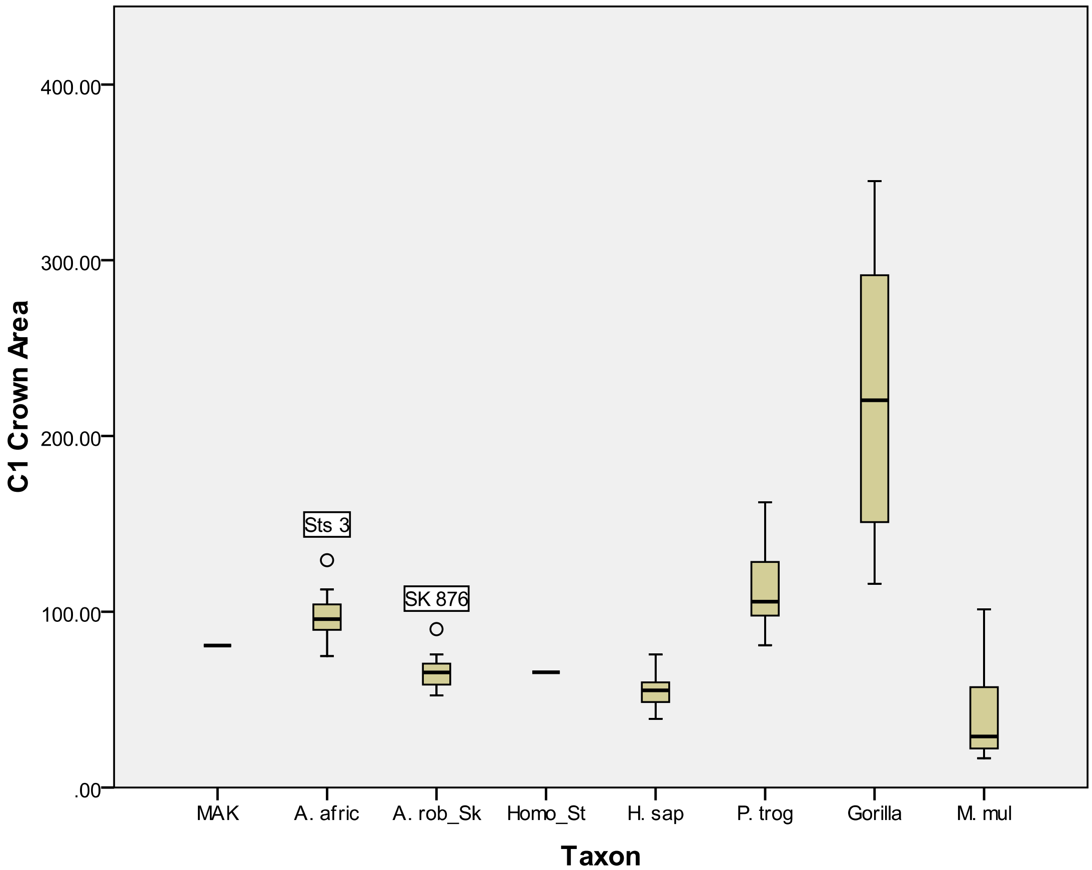


Figure 8-11: C_1 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the C_1 crown area [C_1 mesiodistal length of crown * C_1 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle and identified by specimen number. The Makapansgat sample is represented here by MLD 18. The fossil sample sizes for this analysis are: *A. africanus* (n = 22), Swartkrans *A. robustus* (n = 10), and Sterkfontein *Homo* (n = 1).



MLD 19

Overview. MLD 19 is an adult left mandibular corpus fragment with a well-preserved, but worn M_3.

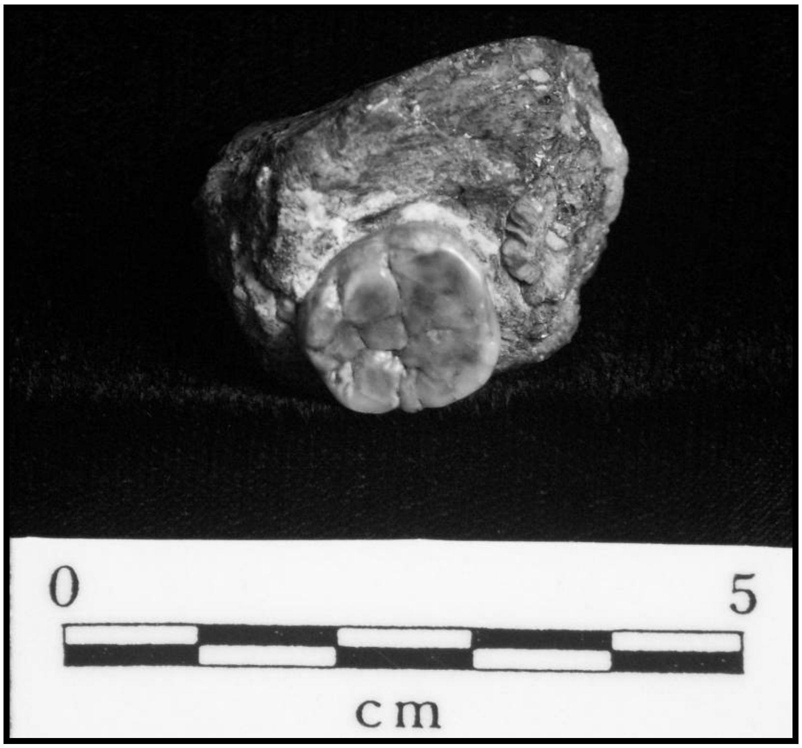
Molars. The M_3 is worn, exhibiting notably flat wear facets on the protoconid, metaconid, hypoconid, and entoconid. The mesial interproximal surface displays a moderately developed wear facet. Despite the extensive wear of this tooth, the occlusal surface does not display any exposed dentine. Overall, this M_3 exhibits a buccolingually broad hypoconid, correspondingly buccolingually narrow entoconid, and a broad and somewhat buccally situated hypoconulid. This molar displays 7 cusps, which includes a small *tuberculum intermedium* defined by fissures. A cuspulid is partially separated from the distolingual portion of the hypoconulid. There are 2 additional small cuspulid-like features on the distal aspect of this tooth, but they are only faintly demarcated by incomplete grooves. In addition, an indistinct cusp-like enamel feature is visible in the region of a *tuberculum sextum* with fissures but not developed enough to be treated as an independent cusp. A deflecting wrinkle is displayed as an L-shaped medial ridge contacting the entoconid but interrupted by the transverse fissure and partly obscured by wear. There is no entoconid-hypoconulid crest in this specimen. The buccal aspect of the external crown displays deep mesiobuccal and distobuccal grooves. In addition, some degree of protostylid development is indicated by a faint groove extending from the external mesiobuccal groove.

Discussion. MLD 19 was found on April 21, 1945. This specimen is considered to be an adult on the basis of the worn M_3 (see Table 9-1).

The shape of the molar's occlusal outline is quite similar to the MLD 18 M_3. It displays the early development of some accessory cuspulids on the lingual and distal portions of the crown. The protoconid and hypoconid are broad.

The occlusal surface exhibits deep pitting between the fissures similarly displayed by MLD 2, particularly when wear is taken into account. This feature likely indicates some form of stress during the development of the M_3. Moreover, the enamel of the preserved buccal, lingual, and distal aspects of the crown exhibits discoloration. Presumably, the mesial surface would have also displayed these features had it not displayed such interproximal wear. The affected regions of the crown display white-colored vertical enamel striations without any accompanying enamel grooves. At first glance, these features resemble vertically oriented enamel crenulations, but closer inspection reveals that these features are regions of enamel discoloration rather than topographic features. Dental opacities, or hypocalcifications, are known to result from regions of poor mineralization deep to the visible feature. Their possible presence in MLD 19, when coupled with the hypoplastic pits described above, would generally indicate some developmental insult or stress impacting both the secretion and maturation of the tooth. Opacities are frequently accompanied by enamel hypoplasias, although it is possible that these white striations may result from post-depositional staining rather than developmental events. Further assessment would be required to confidently distinguish between these two contrasting possibilities.

Figure 8-12*: *MLD 19. The MLD 19 mandible left M_3 in occlusal view.



<u>MLD 22</u>

Overview. The MLD 22 specimen is a left mandibular corpus with M_2-M_3 and some part of the alveoli for P_3-M_1. As discussed in chapter 6, this mandible is only known from a cast due to the misplacement of the original sometime before April 7, 1962. Minor shrinkage due to the casting process is expected for all measurements. Many of the detailed features of the crown are indistinct due to the poor quality of the available original cast.

Premolars. The premolar alveoli do not permit the assessment of root morphology due to the inability to discriminate where the cast represents the actual alveoli versus a breccia matrix infilling.

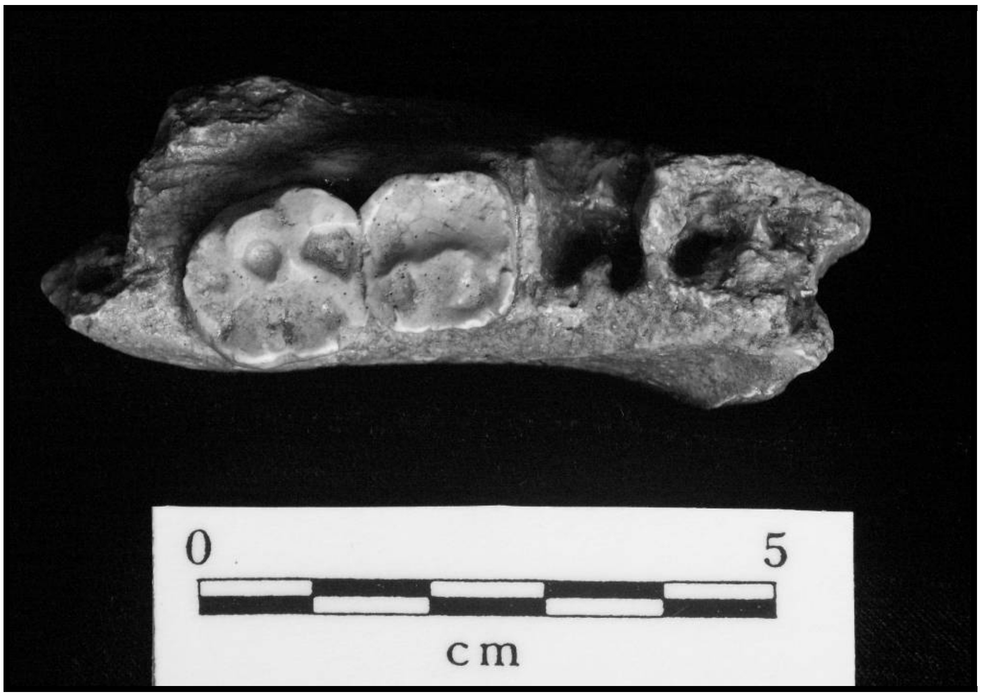
Molars. The M_1 alveolus is preserved, permitting the determination that its root form was unexceptional: two-rooted with a mesial and buccal root. The preserved molars are well worn and the M_3 is considerably larger than the M_2. Both molars are well preserved, although the mesiobuccal corner of the M_2 crown may have undergone some minor postmortem damage. The M_2 exhibits occlusal wear that can be characterized by dentine exposure on all of the major cusps, which also includes the coalescing of the three buccal dentinal exposures as a deep basin. Interproximal wear was considerable and results in the appearance of a somewhat square occlusal outline.

The M_3 occlusal surface displays dentine exposures on each of the cusps (with the exception of the entoconid), although none of the exposures coalesced. This molar appears to have displayed and indeterminate (likely 5 or 6) number of cusps due to the degree of wear and further obscuring by casting. A small indistinct cusp-like feature is evident distally, but is not treated as a true *tuberculum sextum*. There is no evidence of a *tuberculum intermedium* having been present. A distinct protostylid is not preserved. However, the formation of the mesiobuccal groove is suggestive that a large protostylid might have been present.

Discussion. The M_3 is fully erupted and well worn and, on these bases, is considered to represent an adult (see Table 9-1). The specimen is quite similar to MLD

18 on the basis of the occlusal outline. The limited detail and advanced wear make other comparisons of limited utility.

Figure 8-13*: *MLD 22. The MLD 22 mandible left M_2 - M_3 in occlusal view.



<u>MLD 23</u>

Overview. MLD 23 is a young adult left maxillary fragment with I^2, P^3, and the canine alveolus. The dentition exhibits moderate to slight wear. Perikymata are clearly visible on the external surfaces of these teeth.

Incisors. This left I^2 is moderately worn. The mesial aspect of the tooth is quite vertical, while the lateral aspect is gently tapered. This incisor exhibits minor shoveling. The mesial and distal aspects of the incisor display lingual marginal ridges. The degree of development of the mesial marginal ridge is obscured by wear, but the distal marginal ridge was strongly developed on the basis of the accompanying fissure. The tuberculum was moderately developed.

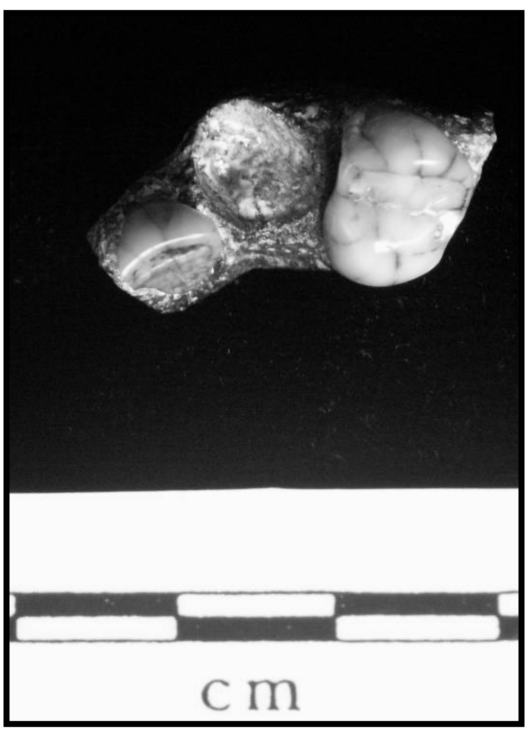
Canines. On the basis of the well-preserved alveolus, the canine root appears buccolingually and mesiodistally compressed. It also was short in comparison to many specimens attributed to *A. africanus*.

Premolars. The P^3 exhibits only minor wear of the cusps, involving the enamel exclusively. Interproximal wear of the mesial surface is minor, while wear of the distal surface produced a large wear facet. The paracone is peripherally positioned and the protocone is more centrally positioned, albeit the latter is more mesially situated than the former. The lingual outline is gently curved, producing a broad and bulbous lingual aspect very much like that of MLD 6. Dental attrition obscures some details of the occlusal surface, but it appears that weak accessory ridges may have been displayed on the paracone and a more marked accessory ridge on the distal aspect of the protocone.

Accessory marginal tubercles are displayed on the distal aspect of the tooth, while the mesial aspect of the premolar exhibits a ridge extending between the paracone and protocone. The median longitudinal fissure is a deep and uninterrupted groove dividing the two major cusps. Additional grooves of the occlusal surface include weak mesiobuccal and distobuccal grooves and a marked distolingual groove. Finally, the external grooves of this P^3 include a strong mesiobuccal and ill-defined somewhat triangular distobuccal groove. The mesiobuccal groove is associated with an enamel feature that extends along the buccal aspect of the premolar near the CEJ as a buccal cingulum and rises vertically as an enamel column on the mesiobuccal aspect of the tooth. No external grooves or accessory enamel features are visible on the lingual aspect of the crown.

Discussion. The morphology of the P^3 is very much like that of the MLD 6 and they may in fact represent the same individual. The P^3 morphology is also similar to that of MLD 11/30. Its squared outline is reminiscent of SK 24, but its dimensions are most like those of specimens attributed to *A. africanus*.

Figure 8-14*: *MLD 23. The MLD 23 left maxillary fragment with I^2 and P^3 in occlusal view.



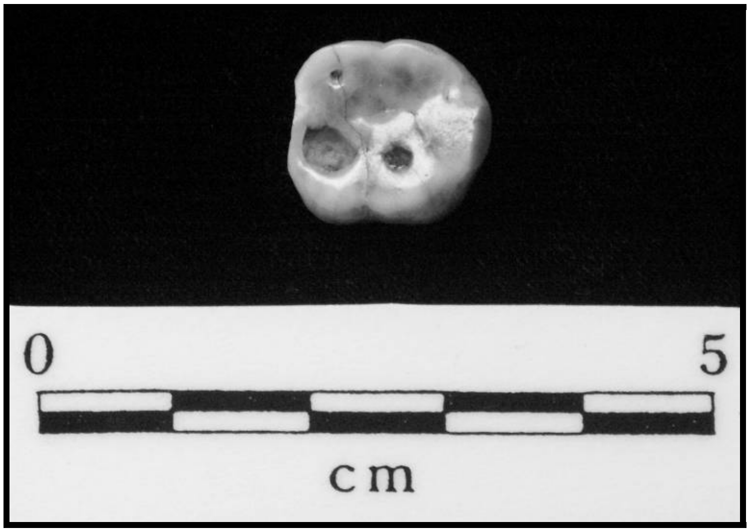
MLD 24

Overview. MLD 24 is a well-preserved, but isolated left M_2 [*contra* Mann (1975)] from a young adult individual.

Molars. The MLD 24 M_2 displays considerable occlusal wear with dentine exposed on the protoconid, metaconid, and hypoconid. The mesial interproximal facet is large, while the distal interproximal facet is moderately sized. The occlusal wear is significant enough to partially obscure the features of the crown. This molar displays the 5 major cusps as well as what appears to be either a small cusp-like feature or a distal marginal crest on the distal aspect of the tooth between the hypoconulid and entoconid although attrition makes it difficult to confidently assess this feature. A *tuberculum intermedium* is not present. The occlusal surface exhibits a + fissure pattern with contact between the metaconid, protoconid, entoconid, and hypoconid. The entoconid appears buccolingually compressed, while the hypoconulid appears buccolingually broad and buccally situated. There is no indication of protostylid development on the mesiobuccal aspect of the crown although wear could have obscured its presence.

Discussion. The MLD 24 specimen represents a young adult on the basis of the degree of M_2 wear. A precise age estimate is not discussed as the only study to produce one misidentified the tooth (Mann, 1975). This specimen is similar to the MLD 18 and MLD 40 M_2s in overall size and cusp proportions, most notably the broad protoconid.

Figure 8-15*: *MLD 24. The MLD 24 left mandibular M_2 in occlusal view.



MLD 27

Overview. MLD 27 is an adult mandibular fragment preserving the symphyseal region and at least some portion of the I_1-C_1 and right P_4 alveoli and partial roots of the right and left P_3s.

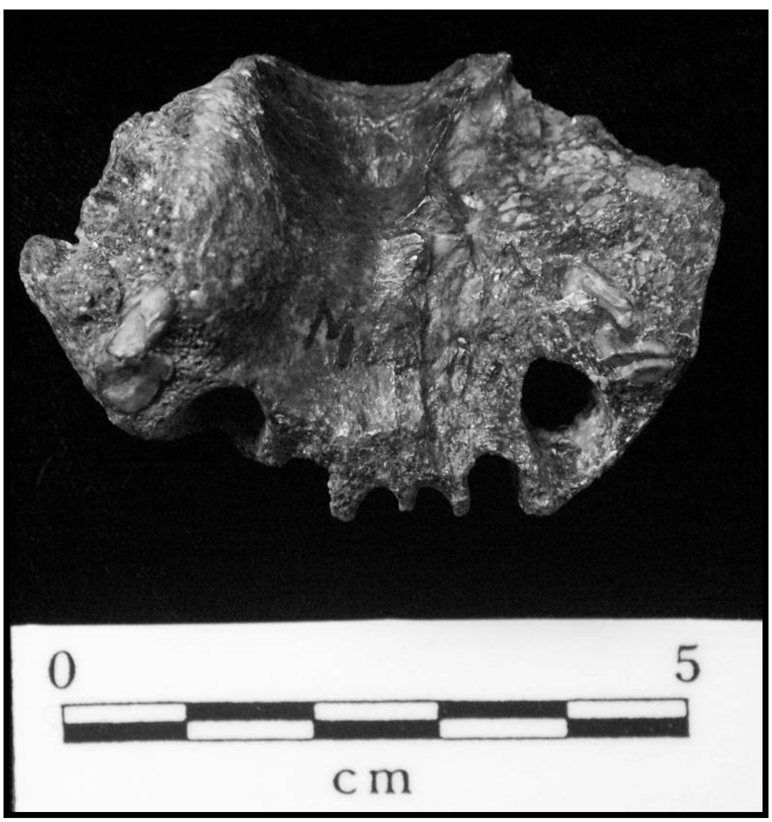
Incisors. The incisor alveoli are preserved, but the anterior bony wall has been broken away. The incisor alveoli indicate fairly short and narrow I_1 roots that are otherwise unexceptional and longer I_2 roots that were probably broad, although this latter feature is to be only cautiously considered.

Canines. The right C_1 alveolus is preserved with the exception of the proximal ~1/3rd of the anterior face. The left C_1 alveolus is preserved in the middle of the alveolus. The canine alveoli suggest long and broad canine roots for MLD 27.

Premolars. Part of the right and left P_3 roots are preserved. The right P_4 partial alveolus indicates a two-rooted form with what appears to have been a mesial and distal root.

Discussion. The MLD 27 specimen represents a probable adult on the basis of the large mandibular size and presumably permanent dentition for the I_1-P_4. The presumably large canines support a closer alignment of this specimen to specimens attributed to the species of *A. africanus*.

Figure 8-16*: *MLD 27. The MLD 27 mandibular fragment with partial alveoli for the right and left I_1-C_1 and right P_4 and partial roots of the P_3s in occlusal view.



MLD 28

Overview. This specimen is a young adult right maxillary fragment with approximately two-thirds of the M^2 and the complete M^3.

Molars. The molars are fully erupted and moderately to markedly worn. Both teeth exhibit a buccolingually broader mesial aspect of the crown. The M^2 is significantly larger and more worn than the M^3.

The M^2 is quite worn, with exposed dentine on all four cusps. The dentine exposures of the paracone and protocone have coalesced. There is no evidence that distal cuspules were present; however, the crown's features have been so obscured by wear it is impossible to assess whether this would have been the case when unworn. A crista obliqua connects the protocone and the metacone. The distal marginal ridge was probably well developed due to the appearance of the distal fovea. The overall occlusal outline of the molar is similar to that exhibited by MLD 6. However, the proportions of the metacone and hypocone stand in contrast to the MLD 6 molars in that the hypocone and metacone give the impression of being similarly sized. However, wear has masked the fissures distinguishing enamel of the distal marginal ridge from the hypocone. It is likely that the morphology of the distal marginal ridge and hypocone were similar to MLD 6 in that a well developed distal marginal ridge extends from the hypocone and serves to extend the distolingual aspect of the tooth. The buccal and lingual grooves are virtually obliterated by wear and are reconstructed to have been only weakly developed.

The M^3 occlusal wear is moderate and consists of only enamel wear. The metacone and hypocone are well preserved. The protocone is bulbous; however, its distolingual aspect is partially divided by a groove extending down the cusp surface. The resulting effect is a crista obliqua, which extends from the protocone as a distinct enamel ridge. The crista obliqua is, however, distinctly interrupted by the main longitudinal fissure. The metacone is small, particularly in the mesiodistal dimension, and mesially situated. It is notably smaller than both the paracone and the hypocone. Just distal to the metacone is a large and distinct accessory cuspule. The hypocone is mesiodistally truncated and extends a slender distal marginal ridge towards the accessory cuspule. A slight groove at the mesiolingual corner of the worn crown indicates that an enamel feature relating to Carabelli's complex was likely present in the unworn crown. The buccal and lingual grooves are faint and extend vertically a very short distance of the crown. The buccal and lingual ridges are faint in comparison to most of the Makapansgat specimens.

Discussion. The mesial aspect of the molars is broader than the distal aspect of the crown in both teeth. The distal tapering of the tooth is even more apparent in the M^3 due to the distal tapering of its hypocone. The overall appearance of the M^2 with consideration of differences in the degree of wear, resembles that of MLD 6 closely despite the buccolingually broader metacone of MLD 6. The MLD 28 M^2's mesially broad and tapering outline is similar to several specimens attributed to *A. robustus* (e.g. SK 13 and SK 48) and *A. africanus* (e.g. Sts 52 and StW 73). The lighter attrition of the MLD 28 M^3 aids more extensive comparison of it to other South African hominin specimens.

The M^3 is somewhat distinct in its suite of features. Its overall outline with strongly tapering distal aspect is prevalent in M^3s of both australopith species, but cusp proportions and other features of the crown are not. The deep and broad distal fovea with a slender distal marginal ridge and the partially divided protocone are unusual among the australopith specimens. The mesiodistally short and mesially situated metacone coupled with a large and presumably metacone derived distal accessory cuspule is unmatched. It is important to note, however that the M^3 samples for each species is extremely variable and numerous specimens display accessory fissures and crenulations on the occlusal surface. Considering these unusual features of the MLD 28 M^3, the strongest comparisons can be made among SK 48, SK 3975, Sts 53, and StW 252. However, the small M^3 crown area of 199 mm^2 is low for South African australopiths and more similar to the sample of *A. africanus*, albeit within the range of variation known for both species.

Figure 8-17*: *MLD 28. The MLD 28 right maxillary fragment with M^2 and M^3 in occlusal view.

MLD 29

Overview. The MLD 29 old adult right mandibular corpus fragment includes a considerably worn right P_4 and M_1, as well as partial roots of the P_3 and C_1.

Canine. An obliquely oriented fragment through the mandible exposed a distal section of the canine root, whose position suggests a long root for this specimen.

Premolars. The P_3 roots are partially exposed via the same oblique mandibular fracture plane and indicate a two-rooted form with mesiobuccal and distal roots. The large P_4 crown is mostly preserved, with the exception of the mesial enamel rim. The P_4 displays marked occlusal wear with extensive dentine exposure but retaining what was presumably a complete or nearly complete enamel rim. The overall shape of the occlusal surface is buccolingually broad and fairly symmetrical, with a somewhat mesially situated protoconid and a more mesiodistally expanded metaconid. The P_4 is relatively large in comparison to the M_1.

Molars. The M_1 exhibits extreme occlusal and interproximal wear. A large fragment of the distolingual crown is missing due to a fracture plane extending from the mesiolingual to the distobuccal aspect of the crown. Dentine exposure is extensive and only a small enamel rim partially surrounds the occlusal surface. Although the M_1 is heavily worn, it is reconstructed here as being fairly small. The M_1 roots must have been moderate to short in length as they are not exposed on the internal aspect of the hollowed out corpus. The M_2 crown is not preserved, but a portion of the M_2 alveolus preserves impressions of a mesial root.

Discussion. This specimen is considered an old adult on the basis of the extreme dental attrition. The state of dental wear exhibited by this specimen is one of the most advanced exhibited by any of the Makapansgat specimens.

Figure 8-18*: *MLD 29. The MLD 29 mandibular fragment with P^4 and M^1 in occlusal view.

<u>MLD 34</u>

Overview. This specimen is a right mandibular corpus fragment with the broken roots of M_1 and M_2. MLD 34 potentially belongs to the same individual as MLD 22.

Molars. The mesial and distal roots of the M_1 and M_2 are exposed above the alveolus, but no part of the tooth crown remains. The M_2 roots are mesiodistally longer than those of the M_1.

Discussion. Providing a precise age estimate is not possible on the basis of the dental remains beyond the general description of a likely age of adulthood. The proximal roots of these molars tentatively suggest that $M_2 > M_1$, at least in mesiodistal length.

Figure 8-19*: *MLD 34. The MLD 34 mandibular fragment with M_1 and M_2 in occlusal view.

MLD 37/38

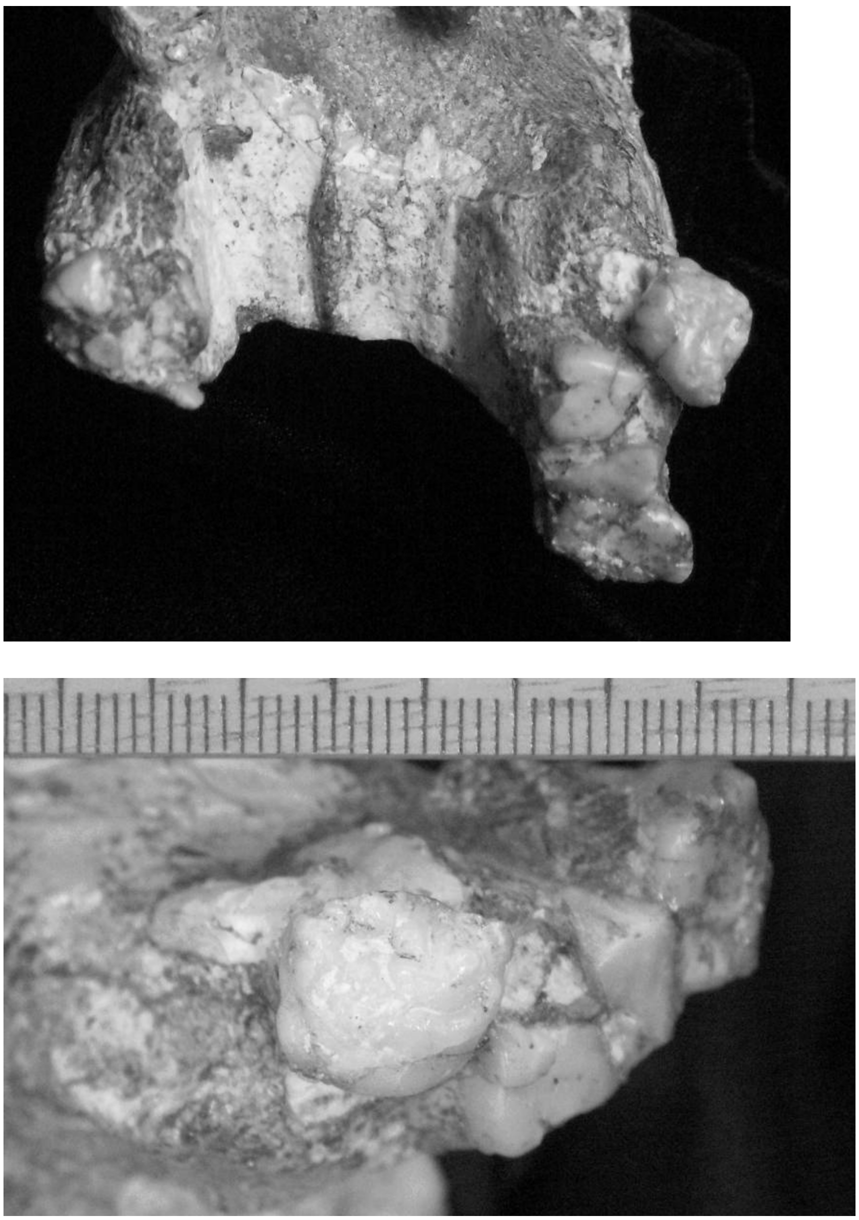
Overview. The MLD 37/38 young adult partial cranium preserves fragmented right M^1 and right and left M^2, as well as most of the right M^3 [*contra* Dart (1962b) who identified these as a right M^2, right and left M^3, and accessory right M^3]. Despite their fragmentary nature and the sedimentary matrix splaying the molar fragments apart, the M^1 and M^2 are quite visibly worn with at least some dentine exposure. In contrast, most of the M^3 crown is preserved (the lingual approximately 2/3) and it exhibits only minimal wear of the occlusal surface.

Molars. The M^1 and M^2 crowns are too obscured by wear for description. The M^3 exhibits essentially no occlusal wear and preserves all of the major features of the preserved crown. The occlusal surface exhibits extensive enamel crenulations and extra cusp-like enamel formations. The protocone is large and extends its contribution to the crista obliqua as an expanding ridge, thickest near the metacone. The crista obliqua is etched by the median longitudinal fissure, but not deeply interrupted by it, contributing to deep and distinct mesial and distal foveae. The hypocone is significantly reduced, as is commonly the case in modern human M^3s. However, the region of the hypocone could best be described as an expanded, ridge-like distolingual margin with several short cuspules, rather than a single, clear distolingual cusp. The Carabelli's complex is strongly developed as a distinct enamel shelf extending from the mesial aspect of the protocone to the distolingual occlusal surface, where it essentially blends into the poorly developed or indistinct hypocone. A slight cingulum extends around the base of the hypocone. In sum, virtually the entire external surface of the lingual crown exhibits accessory enamel features, thus giving the appearance of significantly expanded buccolingual and mesiodistal dimensions of the crown near the CEJ.

Discussion. The MLD 37/38 specimen represents a young adult on the basis of its unworn and fully erupted M^3. An age estimate of 50 years at death was produced for this specimen partly on the basis of dental wear by Dart, but this assessment involved identification of an accessory molar whereas that tooth is considered here to be an M^3. The discrepancy between these age estimates rests primarily on the identification of the unworn molar.

Only the M^3 preserves enough features of the crown to permit comparison among australopith specimens. It exhibits extensive crenulations of the occlusal surface, which is relatively common in both South African hominin taxa. Regardless, the small size and less bulbous crown features are more similar to specimens attributed to the species of *A. africanus* (e.g. StW 189).

Figure 8-20*: *MLD 37/38. The MLD 29 mandibular fragment with P^4 and M^1 in occlusal view.



MLD 40

Overview. MLD 40 includes the greater part of the left half of a thick adult mandible with parts of left C_1-M_3 and alveolus for I_2. The dentition exhibits considerable wear.

Incisors. The I_2 alveolus is preserved and appears broad, but its mesial bony boundaries are not fully preserved and the bottom of the alveolus is partly lined with sedimentary matrix making assessment unreliable.

Canines. The left canine is only partly preserved. Most of the labial and occlusal surfaces are missing. The preserved part of the occlusal surface (distally) indicates this canine was well worn. The canine's crown and root were large. The preserved mesial and lingual portions of the canine exhibit a moderate distal fovea with a distal marginal ridge. The mesial face of displays horizontal linear grooves in the enamel that are suggestive that enamel hypoplasia was exhibited by labial aspect of the canine.

Premolars. The premolars are well preserved, but markedly worn. The P_3 is missing the enamel of the external aspect of the distolingual crown, while the P_4 is missing a small enamel fragment from the mesiolingual crown. Both premolars are buccolingually broad and large overall, particularly when the M_1 size is considered. The P_4 is larger than the P_3, most notably in mesiodistal length.

The left P_3 exhibits advanced attrition with the coalescence of the main dentinal areas. An island of enamel is retained on the distolingual corner of the occlusal surface, as well as a presumably complete rim of enamel along the margins. Mesial and distal interproximal wear is moderate. The crown is asymmetrical in occlusal view with the lingual cusp mesially truncated. The external aspect of the crown displays a faint buccal cingulid extending across the buccal surface, not unlike that of the MLD 2 P_3s. The external aspect of the crown displays a mesial pillar and a small segment of a faint distobuccal enamel pillar.

The P_4 displays advanced attrition, only slightly less than that of the P_3. Dentine is exposed in the regions of the protoconid and metaconid, while the talonid basin and a slender marginal rim retains enamel. Mesial interproximal wear is moderate, while distal interproximal wear is advanced. The crown is mesiodistally symmetrical and exhibits a particularly long lingual dimension in comparison to the reduced buccal length. The mesiobuccal corner appears somewhat truncated, in stark contrast to the appearance of the P_3. While most of the crown was worn away, the buccal aspect of the crown displays a distal enamel pillar and indications that a faint buccal cingulid was present.

Molars. The molars display marked attrition. Despite preservation issues, it is clear that the $M_3 > M_2 > M_1$.

The M_1 is well preserved, but its occlusal surface displays considerable wear with dentine exposure on each of the 5 major cusps. The dentine exposures appear as deep coalesced basins extending between the metaconid, protoconid, hypoconid, and hypoconulid. Its interproximal surfaces display large flat wear facets, which mesiodistally truncate the appearance of the tooth. The entoconid is moderate in size, but buccolingually narrow. There is a hint of a fissure junction or fovea distobuccal to the entoconid, which suggests a distal enamel feature. There is no indication of protostylid development, although this molar is too worn for confidence. The lingual groove on the external aspect of the crown is only partly preserved, but suggests a moderate or marked groove had been present.

The M_2 exhibits only slight enamel damage on the mesiodistal margin of the crown. The marked occlusal wear involves three deeply basined and coalesced buccal dentinal areas as well as minor buccal dentinal areas. Large interproximal wear facets are present mesially and distally. The occlusal fissures are faintly visible in places and weakly indicate a Y-fissure pattern. The metaconid and entoconid are buccolingually narrow. The entoconid appears to be further truncated by distal enamel features indicated by occlusal fissures (possibly a deep distal fovea coupled with either a distal marginal ridge extending between the entoconid and hypoconulid or distal cuspulids). The hypoconulid appears to be centrobuccally positioned, although indications of a distal enamel feature make this reconstruction uncertain. The external aspect of the crown preserves a small segment of a marked buccal groove. There is no indication of protostylid formation on the preserved aspects of this tooth.

The M_3 crown is not preserved, although the plane of section appears to be just below the CEJ. The preserved aspect of the tooth indicates that a mesiodistally elongated crown was present. Both mesiodistal and, only barely, buccolingual dimensions of the preserved tooth exceed that of the M_2.

Discussion. The MLD 40 specimen represents an adult mandible, although see Table 9-1.

The canine, although poorly preserved, displays a moderate distal fovea and distal marginal ridge. Its morphology is more similar to the taller, more marked canines of specimens attributed to the species of *A. africanus* (e.g. StW 498).

The fragmentary premolar exhibits a faint buccal cingulid and the overall shape of the proximal crown, which resembles the comparable portion of the MLD 2 P_3. The overall shape of the occlusal outline resembles that of specimens attributed to the species of *A. africanus*, such as Sts 52 and StW 193. Although the premolar is similar in some respects to robust australopith premolars, the overall asymmetry is more like those of specimens assigned to the species of *A. africanus*. The MLD 40 P_4 exhibits heavy occlusal wear, but can be most readily compared with specimens of the species of *A. africanus* (most notably StW 193 and a worn StW 537) in its occlusal dimensions. It exhibits a distinctly short buccal aspect whose appearance was likely enhanced by the mesial interproximal wear.

The MLD 40 molars are somewhat mesiodistally longer, but are otherwise similar to MLD 2 and MLD 18. Perhaps most notable is that the MLD 40 premolars and molars, in marked contrast to the mandibular corpus, exhibit crown areas that are on the low end for both South African australopith samples.

Figure 8-21*: *MLD 40. The MLD 40 mandibular fragment with C_1 - M_3 in occlusal view.

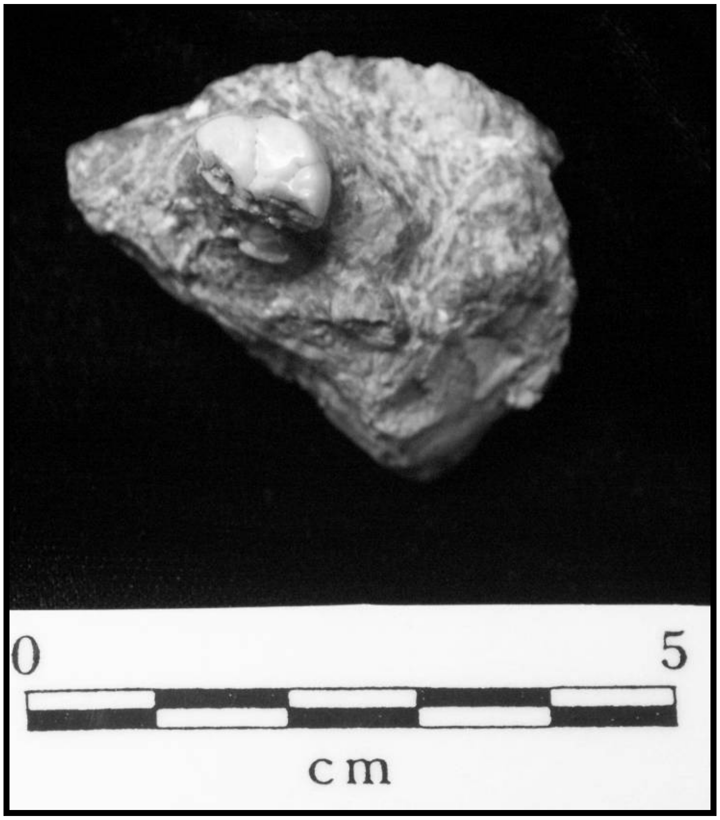
MLD 41

Overview. MLD 41 consists of a left mandibular molar preserving the lingual and distal aspects of the crown and tiny uninformative mandibular fragments. The overall size and somewhat square shape of the preserved parts of the molar are most similar to an M_1. This specimen is moderately worn and does not exhibit a distal interproximal facet, although the degree of wear does not negate the possibility that the M_2 had not yet fully erupted. On the basis of the morphology of the crown, the isolated molar is presumed here to be an M_1 [*contra* RJ Clarke, who identified this molar as a left M^3 in the University of the Witwatersrand Makapan Catalogue].

Molars. This molar displays only minor occlusal wear and no exposed dentine. The broken border of the tooth extends obliquely from the mesiolingual corner to the distobuccal corner of the tooth. The preserved portion of the crown and its features are somewhat deceptive at first glance and required extensive examination to determine whether a maxillary or mandibular tooth. They provide a misleading appearance reminiscent of a maxillary molar due to the symmetrical shape, the distal cuspulid easily mistaken as a distal accessory cuspule, and the incised hypoconid-entoconid crest resembling a broad crista obliqua. The occlusal fissures suggest this specimen is a mandibular molar as they would otherwise indicate an unmatched buccolingually broad paracone and mesiodistally long protocone (its contribution to the crista obliqua). The fissures are arguably better interpreted as demarcating a typical metaconid, entoconid, and hypoconid (although see discussion below regarding the hypoconulid).

Discussion. This specimen exhibits an unusually mesiodistally short and hypoconulid appearance (see Taung).

Figure 8-22*: *MLD 41. The MLD 41 M_1 in occlusal view.



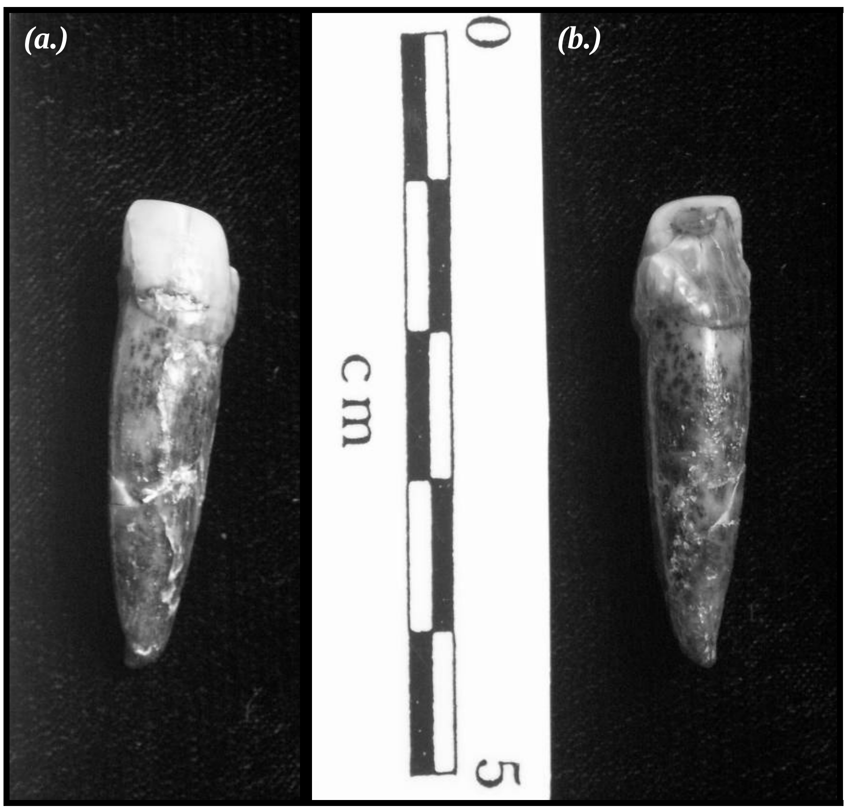
MLD 42

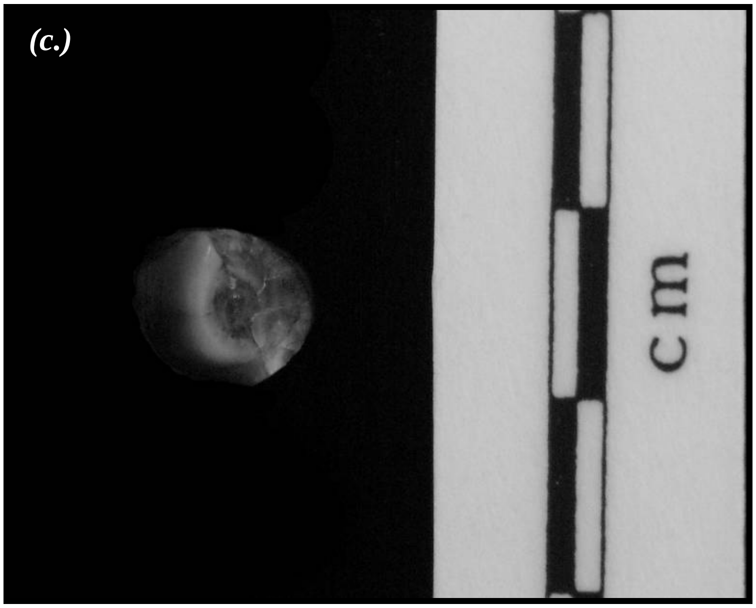
Overview. MLD 42 is a well-preserved and isolated left adult C_1.

Canines. The C_1 is preserved except for a small enamel region of the labial crown near the CEJ. The crown exhibits marked wear in the form of extensive dentine exposure and a slanted occlusal facet that slopes distolingually. The crown exhibits considerable asymmetry of the mesial and distal borders. The labial aspect of the C_1 displays a marked mesial enamel pillar with a somewhat independent apex (a stylid). The lingual aspect displays a moderate lingual ridge, a faint and partly preserved mesial marginal ridge, and a marked distal marginal ridge associated with the mesiolabial enamel feature. The root is long and broad with a slight mesial tilt to the root tip.

Discussion. This canine is large and well worn. It is most similar morphologically to specimens attributed to the species of *A. africanus* in its marked asymmetry, marked distal marginal ridge, and large size. The distal stylid is quite distinct in the MLD 42 specimen. This specimen reached middle childhood at least and probably young adulthood on the basis of wear, but a more precise age estimate is not available.

Figure 8-23*: *MLD 42. The MLD 42 C_1 in labial, lingual, and occlusal view.





MLD 43

Overview. This specimen is a well-preserved unworn and isolated left I^1.

Incisors. MLD 43 preserves the entire crown except for a miniscule chip of enamel on the distal incisal edge. The tip of the root is also missing at least partly due to postmortem events. It is possible that the root was not fully formed, but the broken distal borders make this possibility difficult to assess. The crown exhibits virtually no wear and preserves seven small mammelons. Mammelon number in the mandibular incisors has been identified as being distinct for *A. africanus*, *A. afarensis*, and *A. robustus* on the basis of limited samples (White *et al*., 1981), but variation in mammelon numbers for the maxillary and mandibular incisors of modern humans suggests intraspecific variation in this developmental feature and limited phylogenetic utility.

The overall appearance of the crown is tall, with a slightly tapered distal border, and mesiodistally broad, although not nearly as broad as is typically exhibited by specimens of *A. afarensis*. Aside from perikymata, the buccal aspect of the crown exhibits no features of interest. The lingual aspect displays a more bulbous and rounded distal margin with a weak distal marginal ridge. In addition, the lingual face is gently curved with faint vertical ridges that become more marked proximally. The root is broad and the preserved portion leans somewhat distally.

Discussion. An age within the period of late childhood is estimated for the individual represented by MLD 43 on the basis of the fully formed crown lacking incisal wear and the almost completely developed root (at a minimum). The crown and cervical areas of MLD 43 are most similar to those calculated for specimens attributed to *A. africanus*, being larger than most specimens attributed to *A. robustus* (see Figures 8-25 and 8-26). The crown index falls within the range of *A. africanus* and *A. robustus* but the cervical index falls below both taxa (Figures 8-27 and 8-28). The cervical index indicates reflects the unusually mesiodistally short and buccolingually broad cervical dimensions of this specimen. This relationship is more similar to the hypodigm of *A. robustus* than *A. africanus*.

Figure 8-24*: *MLD 43. The MLD 43 left I^1 in lingual (*a*) and labial (*b*) view.

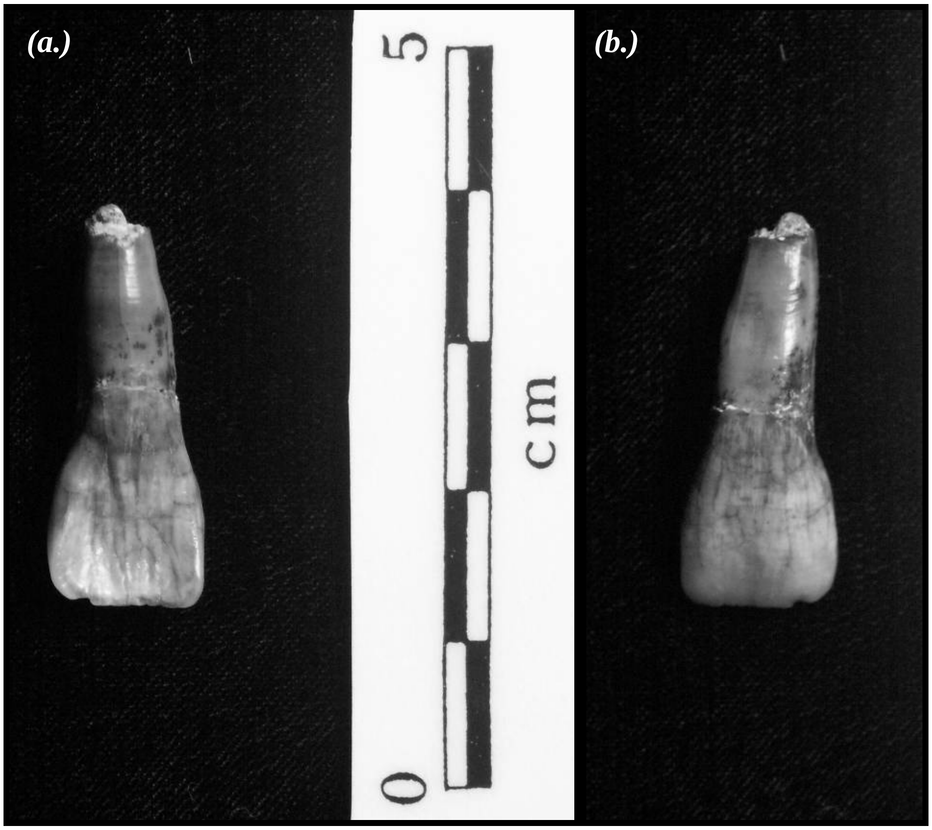

(a.)
(b.)
5
cm
0

Figure 8-25: I^1 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I^1 crown area [I^1 mesiodistal length of crown * I^1 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle and associated numbers identify the individual. The Makapansgat sample is represented here by MLD 43. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 12), Kromdraai *A. robustus* (n = 1), Sterkfontein *Homo* (n = 2), Swartkrans *Homo* (n = 1), and Swartkrans *incertae sedis* (n = 2).

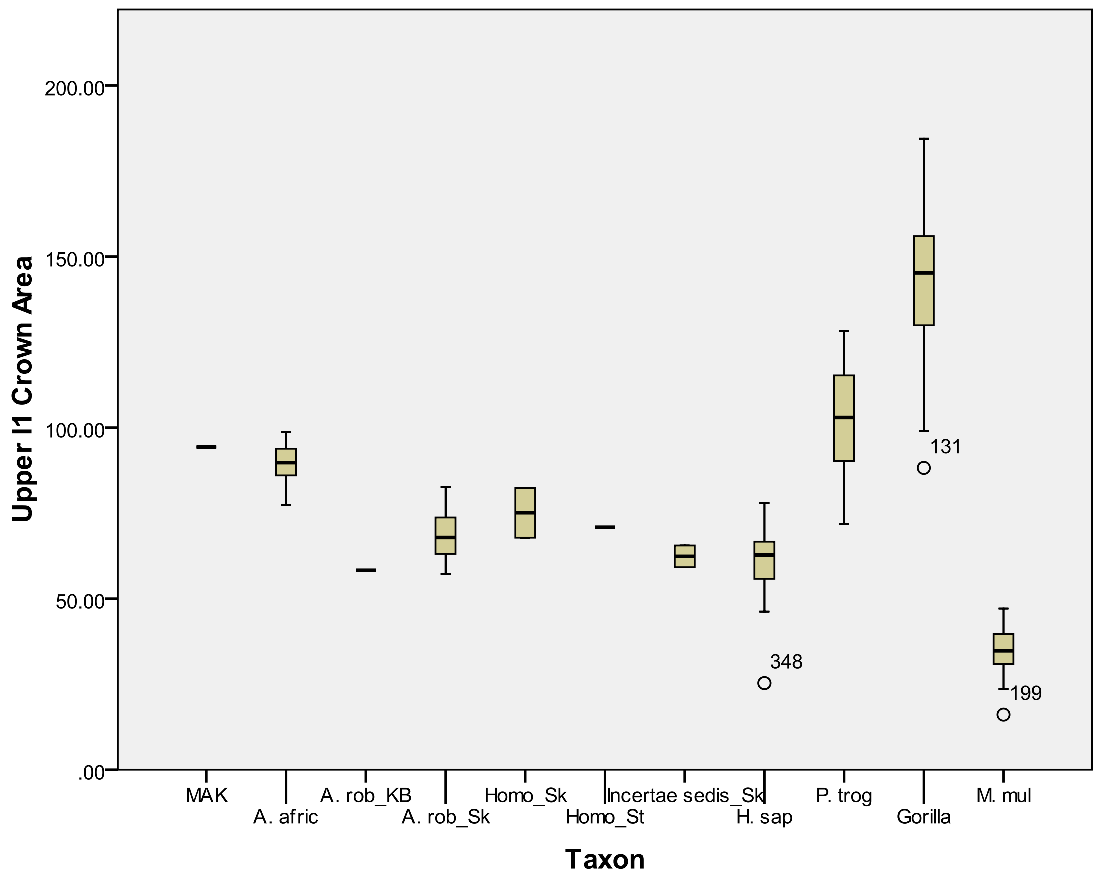


Figure 8-26: I^1 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I^1 cervical area [I^1 mesiodistal length of cervix * I^1 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 43. The fossil sample sizes for this analysis are: Cooper's A. africanus (n = 1), Sterkfontein *A. africanus* (n = 10), Swartkrans *A. robustus* (n = 12), Kromdraai *A. robustus* (n = 1), Swartkrans *Homo* (n = 2), Sterkfontein *Homo* (n = 1), and Swartkrans *incertae sedis* (n = 1).

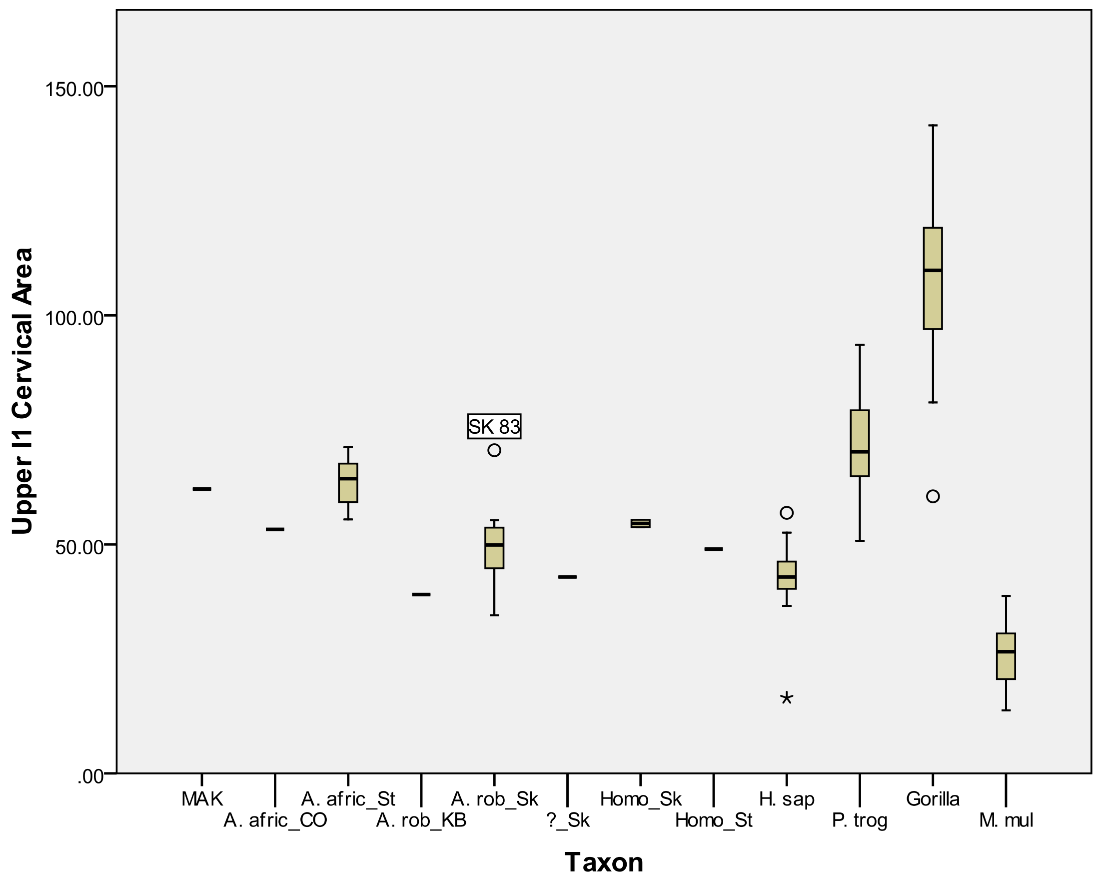


Figure 8-26: I^1 Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I^1 crown index [(I^1 mesiodistal length of crown /I^1 buccolingual breadth of crown) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 43. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 12), Kromdraai *A. robustus* (n = 1), Swartkrans *Homo* (n = 2), Sterkfontein *Homo* (n = 1), and Swartkrans *incertae sedis* (n = 2).

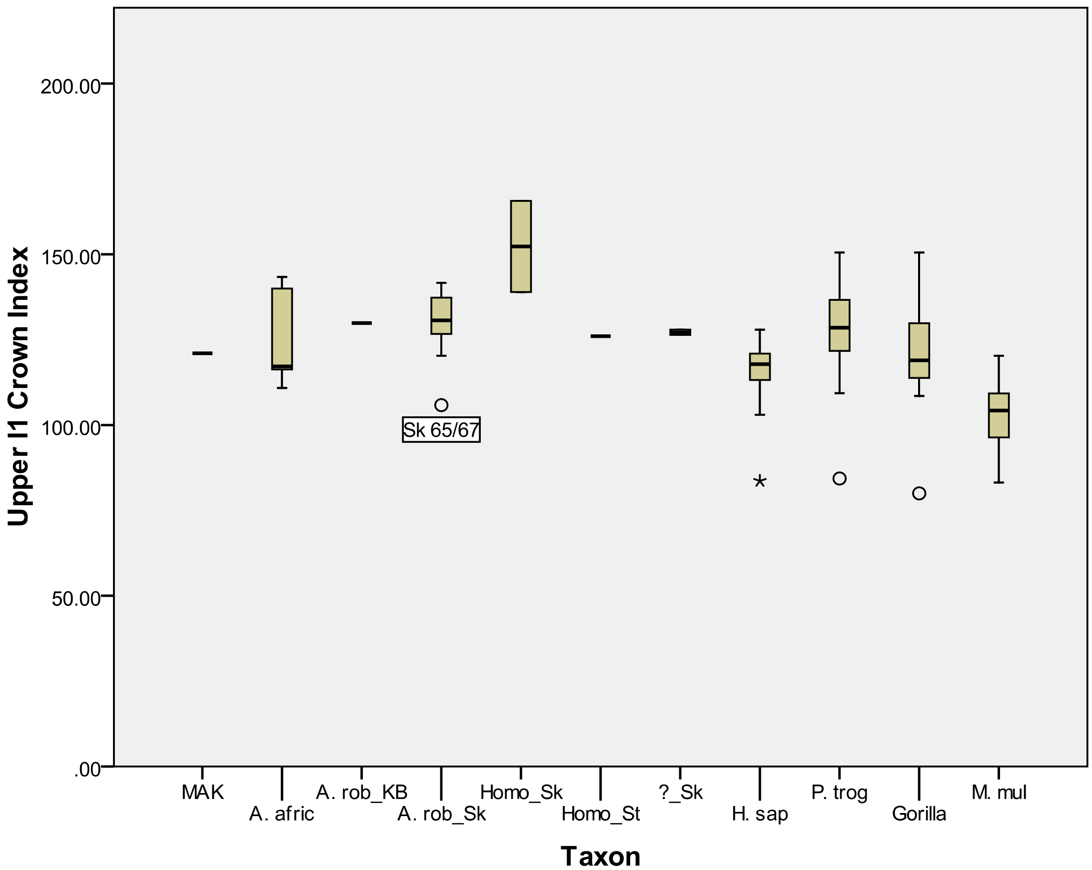
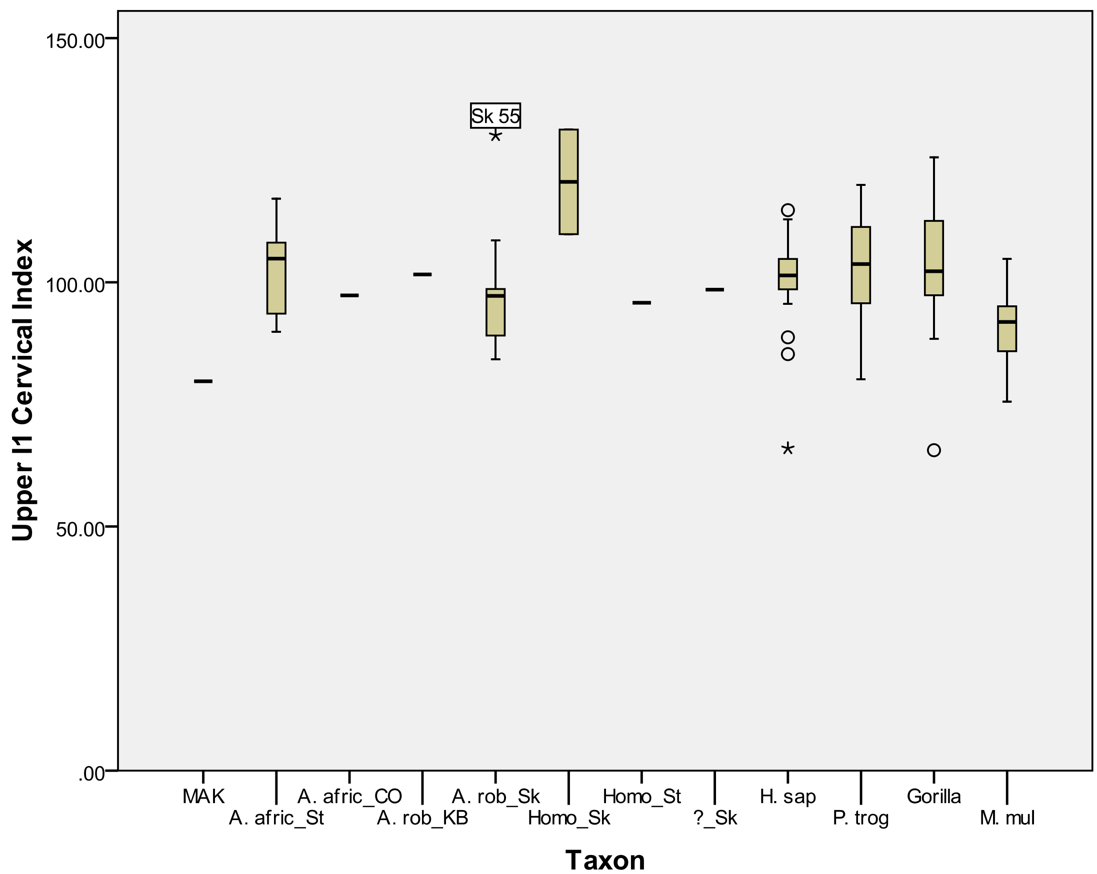


Figure 8-27: I[1] Cervical Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the I[1] cervical index [(I[1] mesiodistal length of cervix /I[1] buccolingual breadth of cervic) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 43. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 12), Swartkrans *Homo* (n = 2), Sterkfontein *Homo* (n = 1), and Swartkrans *incertae sedis* (n = 1).



MLD 44

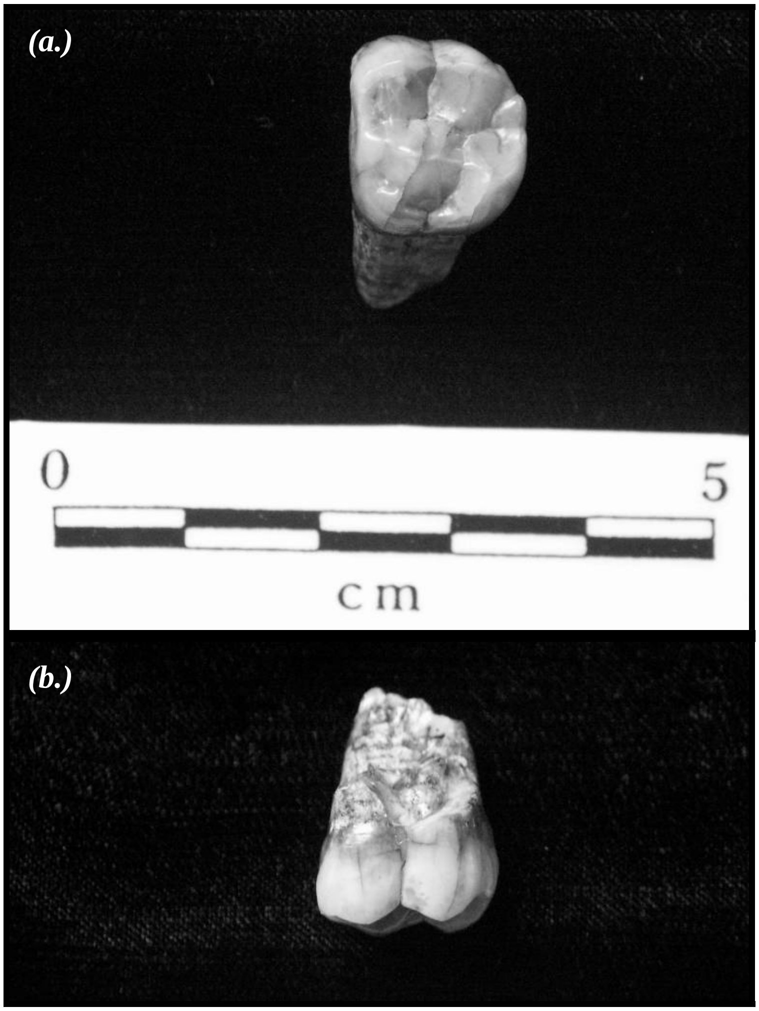
Overview. The MLD 44 specimen is an isolated left maxillary molar that preserves most of the crown, with the exception of a sliver of enamel nearest the CEJ on the buccodistal aspect and approximately three-quarters of the lingual root. The crown is well-preserved and only slightly worn. The identification of this specimen to specific molar number is somewhat problematic. This specimen was identified as a left M^3 by an unknown contributor in the Makapan Catalogue presumed to be RJ Clarke on the basis of the handwriting for this and other specimen entries. In support of Clarke's identification, the MLD 44 molar does not exhibit a distal wear facet and South African hominin *in situ* M^3s exhibit considerable variation in morphology. Regardless, the degree of wear exhibited by this tooth does not preclude the possibility that an adjacent distal molar had not yet produced wear facets due to late eruption, a large interproximal gap, or (even less likely) being congenitally absent. The overall crown shape with only minor tapering of the distal aspect is most similar to the typical South African australopith M^1 (and is an excellent match in all features but size with the StW 252 M^1) and is not known for South African australopith M^3s. Even so, the morphology of this crown is also similar in virtually all features to the MLD 6 M^2 and the only feature distinguishing the overall outlines for these teeth is the more distally extended distal cuspule on MLD 44. In addition, the buccolingual and mesiodistal dimensions of the tooth provide weak support for its M^2 status. On these somewhat tenuous bases, the MLD 44 molar is considered to be a probable left M^2 despite some evidence to the contrary.

Molars. This M^2 merely exhibits enamel wear of the occlusal surface. The mesial interproximal facet is moderately developed and extends 6 mm broad and 3.6 mm high. The distal aspect of the tooth does not exhibit a distal wear facet. The paracone and metacone are approximately equal in size. As is the case in several of the molar specimens from Makapansgat, the hypocone is somewhat mesiodistally truncated with a well developed distal marginal ridge extending between it and the metacone. The protocone is broad, bulbous, and larger and more centrally positioned than the paracone. The crista obliqua is a thick continuous crest that is only slightly etched by the main longitudinal fissure. The overall shape of the occlusal outline is consistent with australopith M^2 morphology with a buccolingually tapering distal aspect, although not as rapidly as it is in the MLD 28 M^2. This latter feature relates, in part, to enamel features of the lingual aspect described below.

The distal marginal ridge is thickest near the metacone and exhibits a distinct distal cuspule and a less developed, but vertically oriented tubercle. The mesial aspect of the occlusal surface is elaborated with at least one mesial marginal tubercle on a mesial marginal ridge. The nearby mesial fovea is small. The external aspect of the crown displays a moderate buccal groove and a short, weak lingual groove that is closely situated to a feature relating to the Carabelli's complex in MLD 44. The Carabelli's enamel feature is a definite, marked shelf of enamel extending from the mesiobuccal corner of the protocone to the buccal groove. The enamel development of the lingual aspect of this molar is interrupted by the buccal groove, but essentially continues on the hypocone as a short lingual cingulum blending into and expanding the buccolingual dimension of the hypocone.

Discussion. MLD 44 is considered to represent a young adult on the degree of dental attrition. The identification of this tooth to molar number is critical in assessing its morphology and assigning an age. If it were considered an M^3 it would be a clear morphological outlier with regard to the samples of *A. robustus* and *A. africanus*, thus its assignment as an M^2.

Figure 8-28*: *MLD 44. The MLD 44 probable M^2 in occlusal (*a*) and buccal (*b*) views.



MLD 45

Overview. The MLD 45 probably adult right maxillary fragment preserves the P^3 and a small portion of the mesial aspect of the P^4 roots. A small chip of enamel is missing from the distal portion of the crown.

Premolars. The P^3 exhibits moderate enamel wear, but no exposed dentine. The protocone is broad and bulbous and more mesially positioned than the paracone. The paracone displays intermediate mesial and distal marginal ridges. The protocone possibly hints at a moderately developed distal accessory ridge, but the cusp's morphology is too obscured by wear for any confidence. The mesial and distal marginal ridges are well developed. The median longitudinal fissure extends as a deep, uninterrupted enamel fissure from the small mesial fovea to the more marked distal fovea. Grooves of the occlusal surface include marked mesiobuccal, marked distobuccal, weak distolingual, and weak mesiolingual grooves. None of the occlusal grooves extend to the periphery of the premolar. The grooves of the external non-occlusal aspect of this P^3 include a marked mesiobuccal groove with a related vertically oriented enamel thickening and a weak and ill-defined triangular distobuccal, trace distolingual, and no mesiolingual groove. In addition, there is a slight buccal cingulum. This specimen has three roots, of which the two buccal roots are partially exposed.

Discussion. The MLD 45 P^3 is similar to that of MLD 23 in the buccal cingulum, grooves of the buccal face, occlusal fissures, and cusp proportions. Its morphology is more similar to *A. africanus* than *A. robustus*.

Figure 8-29*: *MLD 45. The MLD 45 maxillary fragment with P^3 in occlusal view.

<u>MLD 47</u>

Overview. MLD 47 is an adult right mandibular corpus with partial M_2 and M_3 roots.

Molars. This specimen preserves very little of its dentition. Only the mesial and distal roots of M_3 and a small portion of the distal roots of M_2 are preserved. As a result, little can be discussed regarding the morphology of the MLD 47 molars. However, the M_3 appears to be broader mesially than distally and, on the basis of the root chamber's shape, strongly distally tapered.

Discussion. Discovered by the Makapansgat Field School in 2000, this specimen is one of few specimens discovered in recent filtering of the *ex situ* fossiliferous breccia piles. The M_3 was fully erupted and indicates that this specimen represents an adult individual.

Figure 8-30*: *MLD 47. The MLD 47 right mandibular fragment root fragments of M_2 and M_3 in occlusal view.

MLD 48.

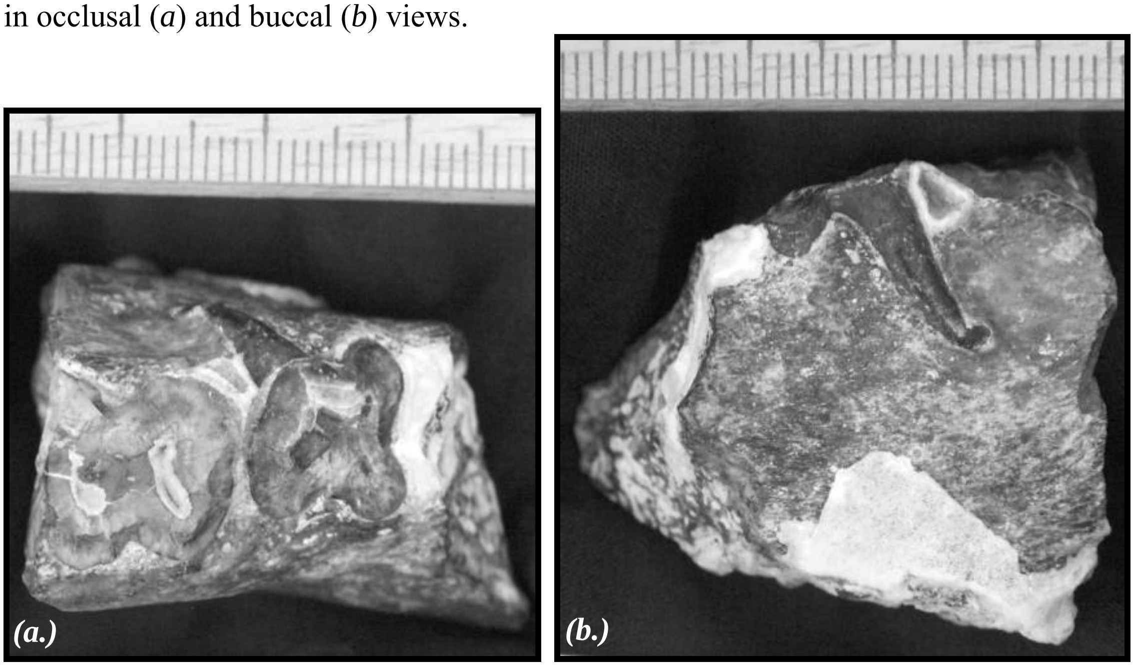
Overview. This is a left adult mandibular fragment preserving M_1 and M_2 roots and a tiny fragment of the distal P_4 roots.

Premolars. A fleck of the distalmost P_4 roots appear to be preserved, but permit no further discussion.

Molars. The molars are poorly preserved with virtually none of the crown remaining. The M_2 is larger than the M_1, but this difference is driven primarily by the mesiodistal length. The M_1 preserves the roots, CEJ, and a sliver of the distobuccal crown. The CEJ appears broader on the mesial aspect of the tooth. The buccal aspect of the distal root is exposed and the tip tilts distally. The M_2 preserves no part of the crown and all of the mesial and part of the distal roots.

Discussion. Discovered by the Makapansgat Field School in 2001, this specimen was recovered from *ex situ* fossiliferous breccia piles. Indications of a broad mesial aspect of the M_1 for this specimen is consistent with other molar specimens from Makapansgat.

Figure 8-31*: *MLD 48. The MLD 48 left mandibular fragment with fragments of P_4-M_2 in occlusal (*a*) and buccal (*b*) views.



Dental Traits. Trait data for the dentition provide further evidence (beyond the cranial and mandibular trait data previously discussed) of extensive intra-specific variation in South African australopiths (see Tables 8-1 to 8-10). The vast majority of traits were coded as variable for South African australopiths. On the basis of extensive variation in dental traits and the few Makapansgat specimens that preserve the dentition well enough for trait assessment beyond the assessment of occlusal wear, these data do little to illuminate the appropriate position of the Makapansgat hominins. Specific details regarding dental traits are discussed in the following pages, with several lengthy tables following the discussion.

Lower Dentition. The traits of the mandibular dentition exhibit extensive variation, however, variation within the Makapansgat sample cannot be assessed due to the low sample sizes. The traits exhibiting the lowest levels of variation across fossil taxa include the form of the transverse crest in the mandibular premolars and the M_{1-2} fissure pattern.

The form of the transverse crest was the only virtually monomorphic trait recorded for the fossils. Its form was identified as single in all of the fossil P_3s and all but one of the fossil P_4s (SK 7). M_{1-2} fissure pattern exhibited low levels of variation, particularly for the sample of *A. robustus*. The fissure pattern of M_1s and M_2s was most frequently identified as Y-patterned with contact between the metaconid and hypoconid. For the M_1, almost all of the fossils exhibit a Y-pattern. These include all of the specimens from Makapansgat (n = 1), attributed to *Homo* (n = 4), and attributed to *A.*

robustus (n = 22). However, 2 M_1s attributed to *A. africanus* (7% of the sample) exhibited a +-pattern and 1 M_1 attributed to *A. africanus* (~4% of the sample) exhibited an X-pattern. The M_2 fissure pattern frequencies were similar, where all of the specimens attributed to *A. robustus* (n = 18) and *Homo* (n = 1) exhibit a Y- pattern, although out of 25 specimens attributed to *A. africanus*, 80% exhibit a Y-pattern, 16% exhibit a +-pattern, and 4% exhibit an X-pattern. In addition, 1 of the 3 Makapansgat specimens exhibits a +-pattern. The higher variation in the sample of *A. africanus* and variation in the small Makapansgat sample provide some support for presuming a closer affinity with *A. africanus* in this feature and for the assumption of low levels of variation within the Makapansgat hominins in molar fissure patterns like that of *A. africanus*. Please note, however, that the larger sample size increased the likelihood of identifying variation in *A. africanus* compared to *A. robustus*.

Despite these patterns for the M_1 and M_2 in South African fossils, the M_3 exhibits increased variation in the molar fissure pattern in both of the large samples of *A. africanus* and *A. robustus* with regard to their metameres. For the M_3 samples, 1 specimen attributed to *A. robustus* exhibits a +-fissure pattern (4% of a total of 23 specimens) and over half of the specimens attributed to *A. africanus* display a non-Y-fissure pattern (37% display a + and 21% display an X fissure pattern out of a total of 26 specimens). The increased frequency of non-Y-fissure patterns in the M_3 is not surprising when the overall levels of variation in molars is considered, as M_3s are well known to be more morphologically variable than the M_1 or M_2.

Despite the low sample size, the Makapansgat sample can be distinguished from the samples of *A. africanus* and/or *A. robustus* in some features. In addition, comparisons of specimens attributed to *A. africanus* and *A. robustus* provide interesting information. The lower premolar trait that best discriminated between the South African australopith species is the symmetry or asymmetry of the P_3 crown. A vast 94% of the total number of specimens attributed to *A. africanus* (n = 16) were recorded as displaying an asymmetrical P_3, compared to 12% of those attributed to *A. robustus* (n = 17). All 3 of the specimens from Makapansgat for which this trait was recorded displayed an asymmetrical P_3, aligning the Makapansgat hominins with the hypodigm of *A. africanus* in this feature. The prominence of the P_3 talonid was long ago indicated as associating the Makapansgat specimens with *A. africanus* (Sperber, 1974). In contrast, the Makapansgat P_4s are markedly distinct from the P_3s since all of the Makapansgat P_4s are symmetrical (n = 4). Unfortunately, this feature contributes little discriminatory power even though the sample of *A. africanus* displays a higher frequency of symmetrical P_4 crowns (70%) compared to that of *A. robustus* (44%).

The frequency of traits describing the appearance of the distal accessory ridge of the premolar protoconid also distinguished the fossil samples to some degree. The distal accessory ridge of the MLD 2 P_3 protoconid was more marked than in any of the specimens attributed to *A. africanus* (n = 13), but similar in degree of development to 40% of the total sample attributed to *A. robustus* (n = 5). The distal accessory ridge of the P_4 protoconid tends to be more developed in the sample of *A. robustus*, but considerable overlap between the samples of *A. robustus* and *A. africanus* makes it impossible to distinguish the MLD 2 P_4 from either sample.

As are so many of the dental traits, the grooves of the external aspect of the premolar crown are poor discriminators among the fossil samples, albeit with one notable exception. The mesiobuccal external groove tends to be more weakly developed in the P_3 sample of *A. robustus* than *A. africanus*. A 94% majority were coded as a trace groove or more weakly developed in the sample of *A. robustus* compared with 26% of the sample of *A. africanus*. The Makapansgat specimen (MLD 2) cannot be distinguished as it exhibits a trace groove, displayed by specimens of both australopith samples. The case is reversed for the P_4 where the mesiobuccal external groove in *A. robustus* tends to be more developed than it is in *A. africanus*. Sixty-three percent of the specimens attributed to *A. robustus* display external mesiobuccal grooves of the P_4 that are more moderately or strongly developed in comparison to only 8% of the specimens attributed to *A. africanus*. In this feature, the single Makapansgat specimen for which this trait is recorded displays no mesiobuccal external groove whatsoever, and aligning it with the sample of *A. africanus*. Finally, although the appearance of the lingual essential crest did little to discriminate among australopith samples, the only P_3 specimen with no lingual essential crest whatsoever was attributed to the genus *Homo* (50% of n = 2).

The traits of the mandibular molars discriminate the samples of *A. africanus* and *A. robustus* well in some features. The molar cusp number displays considerable overlap between the samples of *A. africanus* and *A. robustus*, yet the latter sample tends to exhibit more cusps than the former. For the M_1, only 31% of the total *A. africanus* sample (n =

29) exhibit more than the 5 main cusps compared to 85% of the total *A. robustus* sample (n = 20). It is also noteworthy that all 4 of the specimens attributed to *Homo* display more than the 5 main cusps. The solitary Makapansgat specimen for which the M_1 cusp number was preserved (MLD 2) displays only 5 cusps, but cannot be discriminated from either australopith sample on this basis alone. For the M_2, the pattern is similar with only 46% of the total sample of *A. africanus* (n = 24) displaying accessory cusps and 100% of the total sample of *A. robustus* (n = 20). The Makapansgat sample (MLD 2 and MLD 18) display either 5 or 6 cusps. The Makapansgat sample is thus more similar to that of *A. africanus* in this feature although sampling bias remains possible. Finally, the M_3 samples display considerable overlap in cusp number with 100% of the total robust sample (n = 23) exhibiting accessory cusps compared to 90% of the total sample of *A. africanus* (n = 29).

The appearance of the *tuberculum intermedium* or *tuberculum sextum* is related to cusp number since these accessory cusps may be counted in the cusp number if they are sufficiently developed (see "Methods"). With this caveat, these accessory cusps are discussed here independently. A *tuberculum sextum* (or distal cusp) is absent in the solitary M_1 specimen preserving this trait at Makapansgat (MLD 2) and does not distinguish it from either South African australopith species. Even so, its absence is more common in M_1 specimens attributed to *A. africanus*. The *tuberculum sextum* is also absent in 2 of the 3 Makapansgat M_2 specimens, 50% of the 11 M_2 specimens attributed to *A. africanus*, and none of the 22 M_2 specimens attributed to *A. robustus*. This provides strong evidence linking the MLD 2, MLD 18, and MLD 24 specimens with *A. africanus* in at least this aspect of M_2 morphology. The case is quite different for the Makapansgat M_3 sample, which preserves a *tuberculum sextum* in all 4 specimens. On a related note, the appearance of the *tuberculum sextum* is more developed in the M_3s of *A. robustus* and *A. africanus* than their metameres. The M_3 *tuberculum sextum* is present in 100% of the total sample of *A. robustus* (n = 24) and 77% of the total sample of *A. africanus* (n = 31). The appearance of the *tuberculum intermedium*, or lack thereof, in some of the Makapansgat mandibular molars does not aid discrimination due to the similar frequencies of character states between the two australopith species.

While the protostylid was never included in cusp counts, its morphology provides for some interesting comparisons among fossil samples. Using a more strict and conservative definition of a protostylid than employed here, Hlusko (2004) found differences in frequencies in protostylid characters in both *A. africanus* and *A. robustus* and protostylid variants were more frequently absent in the sample of *A. africanus*. The data presented here indicate that the protostylid is quite variable in appearance in presence and appearance in both of the South African australopith taxa, as well as the small sample from Makapansgat. The M_2 protostylid is recorded as absent in a relatively large percentage of specimens from Makapansgat (75%). Although additional traits of the lower molars may discriminate the 2 australopith species to some degree (e.g. the appearance of the M_2 entoconid-hypoconulid crest, M_2 deflecting wrinkle, and M_3 distal trigonid crest), the inconsistencies between metamere ($M_{1\text{-}3}$) comparisons suggest that these results are likely related more to sample size issues than biological reality. Hlusko

(2002) also found variation in the distribution of lower mandibular morphology among metameres within the Sterkfontein Member 4 sample.

A discussion of dental traits would not be complete without commenting on the occlusal wear of the lower dentition. The premolars do not aid assessment of the occlusal wear of the Makapansgat sample. Even with consideration of the low sample sizes, the mandibular molars from Makapansgat are relatively worn in comparison to the samples of *A. africanus* and *A. robustus*. The percentage of Makapansgat specimens with three or more dentine exposures (code ≥ 5) is 90% of the M_1s, 80% of the M_2s, and 25% of the M_3s. This can be compared to 44% of the M_1s, 28% of the M_2s, and 6% of the M_3s for specimens attributed to *A. africanus* and 37% of the M_1s, 22% of the M_2s, and 4% of the M_3s for specimens attributed to *A. robustus*. These data, while interesting, may be related to a distinction in diet, population demographics, taphonomic bias, enamel thickness, or simply sample size bias (i.e. poor luck).

TABLE 8-1: P_3 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 3	N = 20	N = 19	N = 2
1	1 / 33	5.5 / 28	1 / 5	1 /50
2	0 / 0	4.5 / 23	5 / 26	1 / 50
3	0 / 0	3 / 15	9 / 47	0 / 0
4	0 / 0	2 / 10	2 / 11	0 / 0
5	2 / 67	2 / 10	2 / 11	0 / 0
6	0 / 0	2 / 10	0 / 0	0 / 0
7	0 / 0	1 / 5	0 / 0	0 / 0
8	0 / 0	0 / 0	0 / 0	0 / 0
Cusp Number	N = 1	N = 11	N = 7	N = 2
1	0 / 0	0 / 0	0 / 0	0 / 0
2	0 / 0	2 / 18	2 / 29	1 / 50
3	1 / 100	7 / 64	3 / 43	0 / 0
4	0 / 0	0 / 0	1 / 14	0 / 0
5	0 / 0	2 / 18	1 / 14	1 / 50
Med Long Fiss	N = 1	N = 14	N = 13	N = 2
0	0 / 0	6 / 43	5 / 38	0 / 0
1	0 / 0	0 / 0	2 / 15	0 / 0
2	1 / 100	6 / 43	6 / 46	2 / 100
3	0 / 0	2 / 14	0 / 0	0 / 0
Metaconid Place	N = 1	N = 11	N = 10	N = 2
0	1 / 100	7 / 63	9 / 90	1 / 50
1	0 / 0	4 / 36	1 / 10	1 / 50
2	0 / 0	0 / 0	0 / 0	0 / 0
Crown asym	N = 3	N = 16	N = 17	N = 2
0	0 / 0	1 / 6	15 / 88	0 / 0
1	3 / 100	15 / 94	2 / 12	2 / 100
Bucc Ess Crest	N = 1	N = 13	N = 7	N = 2
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	6 / 46	4 / 57	1 / 50
2	0 / 0	3 / 23	2 / 29	1 / 50
3	0 / 0	4 / 31	0 / 0	0 / 0
4	0 / 0	0 / 0	1 / 14	
Ling Ess Crest	N = 1	N = 13	N = 6	N = 2
0	0 / 0	0 / 0	0 / 0	1 / 50
1	1 / 100	8 / 62	5 / 83	1 / 50
2	0 / 0	2 / 15	1 / 17	0 / 0
3	0 / 0	3 / 23	0 / 0	0 / 0

Transv Cr – P	N = 1	N = 14	N = 8	N = 2
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	3 / 21	2 / 25	1 / 50
2	0 / 0	4 / 29	4 / 50	1 / 50
3	1 / 100	7 / 50	2 / 25	0 / 0
Transv Cr – F	N = 1	N = 14	N = 7	N = 2
1	1 / 100	14 / 100	7 / 100	2 / 100
2	0 / 0	0 / 0	0 / 0	0 / 0
Mesiobuccal Gr	N = 1	N = 13	N = 9	N = 1
0	0 / 0	4 / 31	6 / 67	0 / 0
1	1 / 100	6 / 46	2 / 22	1 / 100
2	0 / 0	3 / 23	0 / 0	0 / 0
3	0 / 0	0 / 0	1 / 11	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distobuccal Gr	N = 1	N = 13	N = 9	N = 2
0	0 / 0	1 / 8	0 / 0	0 / 0
1	0 / 0	4 / 31	4 / 44	0 / 0
2	0 / 0	4 / 31	2 / 22	1 / 50
3	1 / 100	4 / 31	1 / 11	0 / 0
4	0 / 0	0 / 0	2 / 22	1 / 50
Mesiolingual Gr	N = 1	N = 13	N = 9	N = 1
0	0 / 0	4 / 31	7 / 77	1 / 100
1	0 / 0	3 / 23	2 / 22	0 / 0
2	0 / 0	1 / 8	0 / 0	0 / 0
3	0 / 0	1 / 8	0 / 0	0 / 0
4	1 / 100	4 / 31	0 / 0	0 / 0
Distolingual Gr	N = 1	N = 13	N = 10	N = 2
0	0 / 0	3 / 23	1 / 10	1 / 50
1	0 / 0	0 / 0	3 / 30	0 / 0
2	1 / 100	2 / 15	2 / 20	0 / 0
3	0 / 0	4 / 31	4 / 40	0 / 0
4	0 / 0	2 / 15	0 / 0	1 / 50
Bucc Cusp: MAR	N = 1	N = 13	N = 6	N = 1
0	1 / 100	11 / 85	5 / 83	1 / 100
1	0 / 0	0 / 0	0 / 0	0 / 0
2	0 / 0	1 / 8	0 / 0	0 / 0
3	0 / 0	1 / 8	1 / 17	0 / 0
Bucc Cusp: DAR	N = 1	N = 13	N = 5	N = 2
0	0 / 0	3 / 23	1 / 20	1 / 50
1	0 / 0	4 / 31	1 / 20	0 / 0
2	0 / 0	6 / 46	1 / 20	1 / 50
3	1 / 100	0 / 0	2 / 40	0 / 0

Ling Cusp: MAR	N = 1	N = 11	N = 6	N = 2
0	1 / 100	10 / 91	4 / 67	2 / 100
1	0 / 0	0 / 0	2 / 33	0 / 0
2	0 / 0	1 / 9	0 / 0	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Ling Cusp: DAR	N = 1	N = 12	N = 6	N = 2
0	0 / 0	5/ 42	1 / 17	2 / 100
1	1 / 100	5 / 42	1 / 17	0 / 0
2	0 / 0	2 / 17	4 / 67	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Mesiobucc Ext Gr	N = 1	N = 16	N = 17	N = 2
0	0 / 0	2 / 13	2 / 12	0 / 0
1	0 / 0	0 / 0	4 / 24	0 / 0
2	1 / 100	2 / 13	10 / 59	2 / 100
3	0 / 0	1 / 6	1 / 6	0 / 0
4	0 / 0	11 / 69	0 / 0	0 / 0
Distobucc Ext Gr	N = 1	N = 13	N = 17	N = 2
0	0 / 0	0 / 0	2 / 12	0 / 0
1	0 / 0	4 / 31	2 / 12	0 / 0
2	0 / 0	3 / 23	9 / 53	1 / 50
3	1 / 100	3 / 23	3 / 18	1 / 50
4	0 / 0	3 / 23	1 / 6	0 / 0
Mesioling Ext Gr	N = 1	N = 13	N = 12	N = 2
0	0 / 0	5 / 38	8 / 67	1 / 50
1	1 / 100	4 / 31	3 / 25	0 / 0
2	0 / 0	4 / 31	1 / 8	1 / 50
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distoling Ext Gr	N = 1	N = 12	N = 11	N = 2
0	0 / 0	8 / 67	10 / 91	1 / 50
1	0 / 0	0 / 0	0 / 0	1 / 50
2	1 / 100	1 / 8	1 / 9	0 / 0
3	0 / 0	3 / 25	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0

TABLE 8-2: P_4 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 4	N = 24	N = 18	N = 1
1	1 / 25	3 / 13	2 / 11	1 / 100
2	0 / 0	9 / 38	9 / 50	0 / 0
3	0 / 0	2 / 8	5 / 28	0 / 0
4	0 / 0	3 / 13	1 / 6	0 / 0
5	2 / 50	5 / 21	1 / 6	0 / 0
6	1 / 25	1 / 4	0 / 0	0 / 0
7	0 / 0	1 / 4	0 / 0	0 / 0
8	0 / 0	0 / 0	0 / 0	0 / 0
Cusp Number	N = 1	N = 14	N = 11	N = 1
1	0 / 0	0 / 0	0 / 0	0 / 0
2	0 / 0	1 / 7	0 / 0	0 / 0
3	0 / 0	6 / 43	1 / 9	0 / 0
4	0 / 0	1 / 7	4 / 36	0 / 0
5	1 / 100	3 / 21	2 / 18	1 / 100
6	0 / 0	3 / 21	4 / 36	0 / 0
Med Long Fiss	N = 1	N = 15	N = 11	N = 1
0	0 / 0	0 / 0	2 / 18	0 / 0
1	0 / 0	3 / 20	3 / 27	0 / 0
2	1 / 100	10 / 67	6 / 55	1 / 100
3	0 / 0	2 / 13	0 / 0	0 / 0
Metaconid Place	N = 1	N = 12	N = 12	N = 1
0	1 / 100	9 / 75	11 / 92	0 / 0
1	0 / 0	3 / 25	1 / 8	1 / 100
2	0 / 0	0 / 0	0 / 0	0 / 0
Crown asym	N = 4	N = 20	N = 16	N = 1
0	4 / 100	14 / 70	7 / 44	1 / 100
1	0 / 0	6 / 30	9 / 56	0 / 0
Bucc Ess Crest	N = 1	N = 15	N = 11	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	12 / 80	4 / 36	1 / 100
2	0 / 0	2 / 13	6 / 55	0 / 0
3	0 / 0	1 / 7	1 / 9	0 / 0
Ling Ess Crest	N = 1	N = 15	N = 11	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	13 / 87	5 / 45	1 / 100
2	0 / 0	1 / 7	6 / 55	0 / 0
3	0 / 0	1 / 7	0 / 0	0 / 0

Transv Cr – P	N = 1	N = 15	N = 12	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	6 / 40	8 / 67	1 / 100
2	0 / 0	9 / 60	4 / 33	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Transv Cr – F	N = 1	N = 15	N = 11	N = 1
1	1 / 100	15 / 100	10 / 91	1 / 100
2	0 / 0	0 / 0	1 / 9	0 / 0
Mesiobuccal Gr	N = 1	N = 13	N = 11	N = 1
0	1 / 100	2 / 15	0 / 0	1 / 100
1	0 / 0	10 / 77	4 / 36	0 / 0
2	0 / 0	0 / 0	5 / 45	0 / 0
3	0 / 0	1 / 8	2 / 18	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distobuccal Gr	N = 1	N = 16	N = 13	N = 1
0	0 / 0	1 / 6	0 / 0	0 / 0
1	0 / 0	4 / 25	1 / 8	0 / 0
2	0 / 0	7 / 44	2 / 15	0 / 0
3	0 / 0	1 / 6	3 / 23	0 / 0
4	1 / 100	3 / 19	7 / 54	1 / 100
Mesiolingual Gr	N = 1	N = 14	N = 11	N = 1
0	0 / 0	6 / 43	6 / 55	1 / 100
1	1 / 100	5 / 36	2 / 18	0 / 0
2	0 / 0	2 / 14	1 / 9	0 / 0
3	0 / 0	0 / 0	1 / 9	0 / 0
4	0 / 0	1 / 7	1 / 9	0 / 0
Distolingual Gr	N = 1	N = 17	N = 13	N = 1
0	0 / 0	0 / 0	1 / 8	0 / 0
1	0 / 0	6 / 35	0 / 0	0 / 0
2	0 / 0	3 / 18	1 / 8	0 / 0
3	1 / 100	6 / 35	7 / 54	0 / 0
4	0 / 0	2 / 12	4 / 31	1 / 100
Bucc Cusp: MAR	N = 1	N = 8	N = 7	N = 1
0	0 / 0	5 / 63	3 / 43	1 / 100
1	0 / 0	2 / 25	3 / 43	0 / 0
2	1 / 100	1 / 13	1 / 14	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Bucc Cusp: DAR	N = 1	N = 12	N = 8	N = 1
0	0 / 0	2 / 17	0 / 0	0 / 0
1	0 / 0	4 / 33	4 / 50	1 / 100
2	1 / 100	3 / 25	3 / 38	0 / 0
3	0 / 0	3 / 25	1 / 13	0 / 0

Ling Cusp: MAR	N = 1	N = 8	N = 7	N = 1
0	0 / 0	1 / 13	2 / 29	1 / 100
1	1 / 100	3 / 38	3 / 43	0 / 0
2	0 / 0	4 / 50	1 / 14	0 / 0
3	0 / 0	0 / 0	1 / 14	0 / 0
Ling Cusp: DAR	N = 1	N = 11	N = 7	N = 1
0	0 / 0	1 / 9	1 / 14	0 / 0
1	1 / 100	4 / 36	2 / 29	0 / 0
2	0 / 0	3 / 27	2 / 29	0 / 0
3	0 / 0	3 / 27	2 / 29	1 / 100
Mesiobucc Ext Gr	N = 1	N = 15	N = 15	N = 1
0	0 / 0	3 / 20	4 / 27	0 / 0
1	0 / 0	0 / 0	5 / 33	0 / 0
2	1 / 100	4 / 27	4 / 27	0 / 0
3	0 / 0	5 / 33	2 / 13	1 / 100
4	0 / 0	3 / 20	0 / 0	0 / 0
Distobucc Ext Gr	N = 1	N = 17	N = 15	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	1 / 6	1 / 7	0 / 0
2	0 / 0	6 / 35	3 / 20	0 / 0
3	1 / 100	6 / 35	9 / 60	0 / 0
4	0 / 0	4 / 24	2 / 13	1 / 100
Mesioling Ext Gr	N = 0	N = 15	N = 15	N = 1
0	0 / 0	14 / 93	13 / 87	1 / 100
1	0 / 0	0 / 0	1 / 7	0 / 0
2	0 / 0	1 / 7	1 / 7	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distoling Ext Gr	N = 0	N = 15	N = 14	N = 1
0	0 / 0	12 / 80	6 / 43	0 / 0
1	0 / 0	2 / 13	4 / 29	0 / 0
2	0 / 0	1 / 7	2 / 14	1 / 100
3	0 / 0	0 / 0	2 / 14	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0

TABLE 8-3: M_1 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 5	N = 40	N = 24	N = 5
1	0 / 0	5 / 13	2 / 8	2 / 40
2	0 / 0	11 / 28	11 / 46	1 / 20
3	1 / 10	3.5 / 9	0 / 0	0 / 0
4	0 / 0	3.5 / 9	2 / 8	0 / 0
5	1 / 10	5 / 13	3 / 13	0 / 0
6	0 / 0	4 / 10	2 / 8	1 / 20
7	0 / 0	0 / 0	0 / 0	0 / 0
8	0 / 0	3 / 8	2 / 8	0 / 0
9	1 / 20	0 / 0	1 / 4	0 / 0
10	0 / 0	1 / 3	0 / 0	0 / 0
11	0 / 0	0 / 0	0 / 0	0 / 0
12	2 / 40	2 / 5	1 / 4	0 / 0
13	1 / 20	2 / 5	0 / 0	1 / 20
Cusp Number	N = 1	N = 29	N = 20	N = 4
5	1 / 100	20 / 69	3 / 15	0 / 0
6	0 / 0	7.5 / 26	15 / 75	4 / 100
7	0 / 0	1.5 / 5	2 / 10	0 / 0
8	0 / 0	0 / 0	0 / 0	0 / 0
Tuberculum sextum / Cusp 6	N = 1	N = 30	N = 20	N = 4
0	1 / 100	21 / 70	2 / 10	3 / 75
1	0 / 0	2 / 7	2 / 10	0 / 0
2	0 / 0	7 / 23	16 / 80	1 / 24
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Tuberculum intermedium / Cusp 7	N = 1	N = 30	N = 21	N = 4
0	0 / 0	11 / 37	8 / 38	1 / 25
1	1 / 100	15 / 50	9 / 43	0 / 0
2	0 / 0	3 / 10	4 / 19	3 / 75
3	0 / 0	1 / 3	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Protostylid	N = 2	N = 28	N = 18	N = 4
0	1 / 50	3 / 11	2 / 11	1 / 25
1	0 / 0	3 / 11	7 / 39	0 / 0
2	0 / 0	9 / 32	8 / 44	3 / 75
3	0 / 0	10 / 36	1 / 6	0 / 0
4	1 / 50	2 / 7	0 / 0	0 / 0
5	0 / 0	1 / 4	0 / 0	0 / 0
6	0 / 0	0 / 0	0 / 0	0 / 0

Distal Trigonid Crest	N = 1	N = 16	N = 15	N = 3
0	0 / 0	1 / 6	2 / 13	1 / 33
1	1 / 100	14 / 88	7 / 47	1 / 33
2	0 / 0	1 / 6	6 / 40	1 / 33
Deflecting Wrinkle	N = 1	N = 16	N = 13	N = 3
0	0 / 0	3 / 19	0 / 0	0 / 0
1	0 / 0	3 / 19	2 / 15	0 / 0
2	1 / 100	8 / 50	5 / 38	2 / 67
3	0 / 0	2 / 13	6 / 46	1 / 33
4	0 / 0	0 / 0	0 / 0	0 / 0
Entoconid-Hypoconulid Crest	N = 1	N = 19	N = 19	N = 3
0	0 / 0	3 / 16	1 / 5	0 / 0
1	1 / 100	12.5 / 66	14 / 74	0 / 0
2	0 / 0	3.5 / 18	4 / 21	3 / 100
Fissure Pattern	N = 1	N = 27	N = 22	N = 4
0	1 / 100	24 / 89	22 / 100	4 / 100
1	0 / 0	2 / 7	0 / 0	0 / 0
2	0 / 0	1 / 4	0 / 0	0 / 0

TABLE 8-4: M_2 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 5	N = 32	N = 23	N = 3
1	1 / 20	0 / 0	2 / 9	0 / 0
2	0 / 0	3 / 9	12 / 52	1 / 33
3	0 / 0	15 / 47	1 / 4	0 / 0
4	0 / 0	2.5 / 8	3 / 13	0 / 0
5	1 / 20	2 / 6	2 / 9	2 / 67
6	0.5 / 10	5 / 16	2 / 9	0 / 0
7	0.5 / 10	0 / 0	0 / 0	0 / 0
8	2 / 40	1 / 3	0 / 0	0 / 0
9	0 / 0	0 / 0	0 / 0	0 / 0
10	0 / 0	1 / 3	1 / 4	0 / 0
11	0 / 0	0 / 0	0 / 0	0 / 0
12	0 / 0	0 / 0	0 / 0	0 / 0
13	0 / 0	0 / 0	0 / 0	0 / 0
Cusp Number	N = 2	N = 24	N = 20	N = 1
5	1 / 50	12 / 50	0 / 0	0 / 0
6	1 / 50	7.5 / 31	12 / 60	1 / 100
7	0 / 0	3.5 / 15	6 / 30	0 / 0
8	0 / 0	0 / 0	2 / 10	0 / 0
		11???		
Tuberculum sextum / Cusp 6	N = 3	N = 22	N = 22	N = 2
0	2 / 67	11 / 50	0 / 0	0 / 0
1	1 / 33	4 / 18	0 / 0	0 / 0
2	0 / 0	5 / 23	17 / 77	2 / 100
3	0 / 0	1 / 5	4 / 18	0 / 0
4	0 / 0	1 / 5	1 / 5	0 / 0
Tuberculum intermedium / Cusp 7	N = 3	N = 24	N = 18	N = 2
0	2 / 67	4 / 17	3 / 17	1 / 50
1	0 / 0	12.5 / 52	11 / 61	1 / 50
2	1 / 33	4.5 / 19	4 / 22	0 / 0
3	0 / 0	1 / 4	0 / 0	0 / 0
4	0 / 0	2 / 8	0 / 0	0 / 0
Protostylid	N = 4	N = 23	N = 19	N = 1
0	3 / 75	2 / 9	1 / 5	1 / 100
1	0 / 0	4 / 17	3 / 16	0 / 0
2	0 / 0	2.5 / 11	6 / 32	0 / 0
3	1 / 25	9.5 / 41	8 / 42	0 / 0
4	0 / 0	4 / 17	0 / 0	0 / 0
5	0 / 0	0 / 0	1 / 5	0 / 0
6	0 / 0	1 / 4	0 / 0	0 / 0

Distal Trigonid Crest	N = 1	N = 19	N = 14	N = 1
0	0.5 / 50	1 / 5	4 / 29	0 / 0
1	0.5 / 50	15 / 79	9 / 64	1 / 100
2	0 / 0	3 / 16	1 / 7	0 / 0
Deflecting Wrinkle	N = 1	N = 18	N = 15	N = 0
0	0 / 0	5 / 28	0 / 0	0 / 0
1	0 / 0	2 / 11	0 / 0	0 / 0
2	0 / 0	7 / 39	14 / 93	0 / 0
3	1 / 100	4 / 22	1 / 7	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Entoconid-Hypoconulid Crest	N = 1	N = 20	N = 16	N = 0
0	0 / 0	3 / 15	12 / 75	0 / 0
1	1 / 100	14 / 70	4 / 25	0 / 0
2	0 / 0	3 / 15	0 / 0	0 / 0
Fissure Pattern	N = 3	N = 25	N = 18	N = 1
0	2 / 67	20 / 80	18 / 100	1 / 100
1	1 / 33	4 / 16	0 / 0	0 / 0
2	0 / 0	1 / 4	0 / 0	0 / 0

TABLE 8-5: M_3 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 4	N = 35	N = 24	N = 2
1	0 / 0	7 / 20	6 /25	0 / 0
2	3 / 75	20 / 57	13.5 / 56	1 / 50
3	0 / 0	4 / 11	2.5 / 10	0 / 0
4	0 / 0	2 / 6	1 / 4	0 / 0
5	0 / 0	1 / 3	1 / 4	0 / 0
6	1 / 25	0 / 0	0 / 0	0.5 / 25
7	0 / 0	0 / 0	0 / 0	0.5 / 25
8	0 / 0	0 / 0	0 / 0	0 / 0
9	0 / 0	1 / 3	0 / 0	0 / 0
10	0 / 0	0 / 0	0 / 0	0 / 0
11	0 / 0	0 / 0	0 / 0	0 / 0
12	0 / 0	0 / 0	0 / 0	0 / 0
13	0 / 0	0 / 0	0 / 0	0 / 0
Cusp Number	N = 3	N = 29	N = 23	N = 1
5	0.5 / 11	3 / 10	0 / 0	0 / 0
6	0.5 / 11	7 / 24	7 / 30	1 / 100
7	2 / 67	11.5 / 40	7 / 30	0 / 0
8	0 / 0	5.5 / 19	5 / 22	0 / 0
9	0 / 0	2 / 7	2 / 9	0 / 0
10	0 / 0	0 / 0	2 / 9	0 / 0
Tuberculum sextum / Cusp 6	N = 4	N = 31	N = 24	N = 1
0	0 / 0	7 / 23	0 / 0	0 / 0
1	3 / 75	0 / 0	0 / 0	0 / 0
2	1 / 25	13 / 42	10 / 42	1 / 100
3	0 / 0	10 / 32	12 / 50	0 / 0
4	0 / 0	1 / 3	2 / 8	0 / 0
Tuberculum intermedium / Cusp 7	N = 4	N = 32	N = 23	N = 1
0	2 / 50	2 / 6	1 / 4	0 / 0
1	0 / 0	12 / 38	12 / 52	1 / 100
2	2 / 50	12 / 38	8 / 35	0 / 0
3	0 / 0	6 / 19	1 / 4	0 / 0
4	0 / 0	0 / 0	1 / 4	0 / 0
Protostylid	N = 4	N = 29	N = 22	N = 1
0	1 / 25	4 / 14	1 / 5	1 / 100
1	3 / 75	2 / 7	6 / 27	0 / 0
2	0 / 0	8.5 / 29	9 / 41	0 / 0
3	0 / 0	9 / 31	4 / 18	0 / 0
4	0 / 0	5.5 / 19	1 / 5	0 / 0
5	0 / 0	0 / 0	1 / 5	0 / 0
6	0 / 0	0 / 0	0 / 0	0 / 0

Distal Trigonid Crest	N = 1	N = 23	N = 20	N = 1
0	0 / 0	4 / 17	14 / 70	0 / 0
1	1 / 100	15 / 65	6 / 30	0 / 0
2	0 / 0	4 / 17	0 / 0	1 / 100
Deflecting Wrinkle	N = 2	N = 23	N = 20	N = 1
0	0 / 0	5 / 22	0 / 0	0 / 0
1	1 / 50	2 / 9	1 / 5	0 / 0
2	0 / 0	9 / 39	14 / 70	0 / 0
3	1 / 50	7 / 30	5 / 4	1 / 100
4	0 / 0	0 / 0	0 / 0	0 / 0
Entoconid-Hypoconulid Crest	N = 3	N = 21	N = 22	N = 1
0	1 / 33	14 / 67	17 / 77	0 / 0
1	1 / 33	5 / 24	3 / 17	1 / 100
2	1 / 33	2 / 10	2 / 9	0 / 0
Fissure Pattern	N = 0	N = 26	N = 23	N = 1
0	0 / 0	11 / 42	22 / 96	1 / 100
1	0 / 0	9.5 / 37	1 / 4	0 / 0
2	0 / 0	5.5 / 21	0 / 0	0 / 0

Upper Dentition. The traits of the maxillary dentition exhibit, as did the mandibular dentition, extensive variation. Despite the low sample sizes, the Makapansgat specimens also exhibit considerable variation. The traits of the maxillary dentition exhibiting the lowest levels of variation among fossil samples is the form of the transverse crest in the maxillary premolars, which was single in all but one specimen (the StW 498 P^4).

The maxillary premolars of the 2 australopith species can be distinguished on the basis of the appearance of the main longitudinal fissure, which has a greater tendency to be deep and uninterrupted in the robusts. However, the low sample sizes make it difficult to discriminate the Makapansgat sample from either species. The maxillary premolars are most easily discriminated on the basis of the number of accessory marginal tubercles. The P^3 specimens attributed to *A. africanus* display accessory marginal tubercles in 69% of the total sample (n = 13) compared to 100% for *A. robustus* (n = 14). In addition, 93% of the robusts display P^3 accessory marginal tubercles both mesially and distally compared to only 23% of the sample of *A. africanus*. The Makapansgat P^3s display both mesial and distal accessory marginal tubercles in every case (n = 2), but cannot be distinguished from either sample. The P^4 accessory marginal tubercles display a similar pattern with 100% of the specimens of *A. robustus* (n = 15) having mesial and distal accessory marginal tubercles compared to only 33% of the total sample of *A. africanus* (n = 6). The single Makapansgat specimen (MLD 6) displays accessory marginal tubercles only distally, weakly supporting its alignment with specimens of *A. africanus* in this feature. While minor differences in sample frequencies were evident for the 2 South African australopiths in a number of traits (e.g. appearance of the occlusal grooves, distal accessory ridge of the protocone, and external grooves), they aid neither efforts to discriminate the Makapansgat sample nor biologically meaningful discussion. Indeed, most of these features have been identified as being quite variable across modern human populations (e.g. Burnett, 2010).

The traits recorded for the maxillary molars have little discriminatory power and exhibit extensive variation. Data recorded for Carabelli's Complex were highly variable among all of the fossil samples and did not aid discrimination of the Makapansgat hominins. The Makapansgat hominins alone displayed remarkable variation in the appearance of the Carabelli's Complex in its small sample. The presence of a distal cuspule also did surprisingly little to discriminate the fossil samples as its presence was common in all of the samples. Similar to the case of the premolars, the appearance of marginal accessory tubercles is the best trait with which to compare the fossil samples. Mesial marginal accessory tubercles were most marked in the robust samples. Nearly all of the robust molars (100% of the M^1s and M^3s and 75% of the M^2s) display mesial marginal tubercles. Although their presence is also common in specimens of *A. africanus*, they are less common and less marked. The Makapansgat hominins preserve only 1 molar (the MLD 44 M^2) for which this trait was recorded as present but weakly developed. Unfortunately, the mesial marginal accessory tubercles do not discriminate the Makapansgat hominins from either sample.

The occlusal wear of the maxillary dentition does not distinguish the South African australopiths. In addition, the Makapansgat sample is small and inconsistent in degrees of occlusal wear within differing teeth. These data also support the likelihood that the high frequency of worn mandibular molars resulted from sampling size bias.

In summary, there are some differences among the fossil samples. These differences are related to the frequency of characters rather than a clear presence or absence, however. This makes it difficult to confidently assign an isolated tooth to either taxon on the basis of traits.

TABLE 8-6: P^3 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 4	N = 25	N = 32	N = 2
1	1 / 25	4 / 16	4 / 13	1 / 50
2	2 / 50	10 / 40	14 / 44	0 / 0
3	0 / 0	6 / 24	3 / 9	0 / 0
4	0 / 0	4 / 16	9.5* / 30	0 / 0
5	0 / 0	1 / 4	1.5* / 5	1 / 50
6	1 / 25	0 / 0	0 / 0	0 / 0
Cusp Number	N = 3	N = 19	N = 20	N = 1
1	0 / 0	0 / 0	0 / 0	0 / 0
2	3 / 100	17 / 89	13 / 65	1 / 100
3	0 / 0	1 / 5	5 / 25	0 / 0
4	0 / 0	1^{+} / 5	2 / 10	0 / 0
Med Long Fiss	N = 3	N = 20	N = 21	N = 1
1	3 / 100	6 / 30	15 / 71	1 /100
2	0 / 0	14 / 70	6 / 29	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Mesiobuccal Gr	N = 3	N = 19	N = 18	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	2 / 11	2 / 11	0 / 0
2	1 / 33	12 / 63	8 / 44	1 / 100
3	2 / 67	4 / 3	6 / 33	0 / 0
4	0 / 0	1 / 5	2 / 11	0 / 0
Distobuccal Gr	N = 3	N = 19	N = 19	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	2 / 11	1 / 5	1 / 100
2	1 / 33	10 / 53	5 / 26	0 / 0
3	2 / 67	6 / 32	8 / 42	0 / 0
4	0 / 0	1 / 5	5 / 26	0 / 0
Mesiolingual Gr	N = 3	N = 18	N = 16	N = 1
0	2 / 67	8 / 44	6 / 38	1 / 100
1	0 / 0	6 / 33	5 / 31	0 / 0
2	1 / 33	2 / 11	4 / 25	0 / 0
3	0 / 0	2 / 11	1 / 6	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distolingual Gr	N = 4	N = 18	N = 16	N = 1
0	0 / 0	7 / 39	1 / 6	1 / 100
1	1 / 25	4 / 22	5 / 31	0 / 0
2	1 / 50	3 / 17	5 / 31	0 / 0
3	2 / 25	2 / 11	5 / 31	0 / 0

4	0 / 0	2 / 11	0 / 0	0 / 0
Bucc Cusp: MAR	N = 3	N = 16	N = 14	N = 1
0	0 / 0	6 / 38	3 / 21	0 / 0
1	1 / 33	2 / 13	2 / 14	0 / 0
2	1 / 33	4 / 25	4 / 29	1 / 100
3	1 / 33	4 / 25	5 / 36	0 / 0
Bucc Cusp: DAR	N = 3	N = 16	N = 14	N = 1
0	0 / 0	4 / 25	4 / 29	0 / 0
1	1 / 33	4 / 25	3 / 21	0 / 0
2	2 / 67	3 / 12	3 / 21	1 / 100
3	0 / 0	5 / 20	4 / 29	0 / 0
Ling Cusp: MAR	N = 2	N = 14	N = 13	N = 1
0	2 / 100	10 / 71	8 / 62	1 / 100
1	0 / 0	2 / 14	2 / 15	0 / 0
2	0 / 0	1 / 7	2 / 15	0 / 0
3	0 / 0	1 / 7	1 / 8	0 / 0
Ling Cusp: DAR	N = 3	N = 14	N = 15	N = 1
0	0 / 0	5 / 36	0 / 0	0 / 0
1	2 / 67	2 / 14	2 / 13	1 / 100
2	0 / 0	3 / 21	4 / 27	0 / 0
3	1 / 33	4 / 29	9 / 60	0 / 0
Bucc Ess Crest	N = 2	N = 16	N = 13	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	2 / 100	11 / 69	6 / 46	1 / 100
2	0 / 0	5 / 31	4 / 31	0 / 0
3	0 / 0	0 / 0	1 / 8	0 / 0
4	0 / 0	0 / 0	2 / 15	0 / 0
Ling Ess Crest	N = 2	N = 16	N = 14	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 50	12 / 75	8 / 57	1 / 100
2	0 / 0	4 / 25	5 / 36	0 / 0
3	1 / 50	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	1 / 7	0 / 0
Transv Cr – P	N = 3	N = 17	N = 16	N = 1
0	1 / 33	2 / 12	9 / 56	0 / 0
1	2 / 67	13 / 77	4 / 25	1 / 100
2	0 / 0	2 / 12	3 / 19	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Transv Cr – F	N = 1	N = 15	N = 7	N = 1
1	1 / 100	15 / 100	7 / 100	1 / 100
2	0 / 0	0 / 0	0 / 0	0 / 0

Acc Marg Tub	N = 2	N = 13	N = 14	N = 1
0	0 / 0	4 / 31	0 / 0	0 / 0
1	0 / 0	1 / 8	1 / 7	1 / 100
2	0 / 0	5 / 38	0 / 0	0 / 0
3	2 / 100	3 / 23	13 / 93	0 / 0
Mesiobucc Ext Gr	N = 3	N = 23	N = 17	N = 1
0	0 / 0	0 / 0	1 / 6	0 / 0
1	1 / 33	2 / 9	4/ 24	0 / 0
2	0 / 0	6 / 26	9 / 53	0 / 0
3	0 / 0	6 / 26	3 / 17	1 / 100
4	2 / 67	9 / 39	0 / 0	0 / 0
Distobucc Ext Gr	N = 2	N = 22	N = 18	N = 1
0	0 / 0	0 / 0	1 / 6	0 / 0
1	2 / 100	2 / 9	3 / 17	0 / 0
2	0 / 0	14 / 64	7 / 39	0 / 0
3	0 / 0	6 / 27	5 / 28	1 / 100
4	0 / 0	0 / 0	0 / 0	0 / 0
Mesioling Ext Gr	N = 4	N = 21	N = 18	N = 1
0	3 / 75	17 / 81	16 / 89	1 / 100
1	0 / 0	0 / 0	1 / 6	0 / 0
2	1 / 25	3 / 14	1 / 6	0 / 0
3	0 / 0	1 / 5	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distoling Ext Gr	N = 4	N = 20	N = 18	N = 1
0	3 / 75	17 / 85	11 / 61	0 / 0
1	0 / 0	1 / 5	1 / 6	1 / 100
2	1 / 25	2 / 10	6 / 33	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0

* Value recorded as 0.5 if single individual coded differently on antimeres or in the rare case of being recorded on the cusp of two character states, e.g. 0/1.

+ The number of cusps for STW 408 was recorded on the basis of independent peaks, defined in the methods.

TABLE 8-7: P^4 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 2	N = 20	N = 37	N = 2
1	0 / 0	0 / 0	7 / 19	0 / 0
2	0 / 0	10 / 50	16 / 43	0 / 0
3	0 / 0	4 / 20	1 / 3	0 / 0
4	2 / 100	4 / 20	13 / 35	1 / 50
5	0 / 0	1 / 5	0 / 0	1 / 50
6	0 / 0	0 / 0	0 / 0	0 / 0
Cusp No	N = 1	N = 10	N = 21	N = 1
1	0 / 0	0 / 0	0 / 0	0 / 0
2	1 / 100	6 / 60	2 / 10	0.5 / 50
3	0 / 0	2 / 20	6 / 29	0.5 / 50
4	0 / 0	2 / 20	6 / 29	0 / 0
5	0 / 0	0 / 0	4 / 19	0 / 0
6	0 / 0	0 / 0	2 / 10	0 / 0
7	0 / 0	0 / 0	1 / 5	0 / 0
Med Long Fiss	N = 1	N = 11	N = 23	N = 1
1	0 / 0	5 / 45	15 / 65	0 / 0
2	1 / 100	6 / 56	8 / 35	1 / 100
3	0 / 0	0 / 0	0 / 0	0 / 0
Mesiobuccal Gr	N = 1	N = 10	N = 21	N = 1
0	0 / 0	0 / 0	1 / 5	0 / 0
1	0 / 0	1 / 10	7 / 33	1 / 100
2	0 / 0	8 / 80	3 / 14	0 / 0
3	1 / 100	1 / 10	7 / 33	0 / 0
4	0 / 0	0 / 0	3 / 14	0 / 0
Distobuccal Gr	N = 1	N = 11	N = 22	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	1 / 9	0 / 0	0 / 0
2	0 / 0	4 / 36	2 / 9	1 / 100
3	0 / 0	5 / 45	9 / 41	0 / 0
4	1 / 100	1 / 9	11 / 50	0 / 0
Mesiolingual Gr	N = 1	N = 10	N = 21	N = 1
0	0 / 0	6 / 60	14 / 67	0 / 0
1	1 / 100	4 / 40	1 / 5	1 / 100
2	0 / 0	0 / 0	5 / 24	0 / 0
3	0 / 0	0 / 0	1 / 5	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distolingual Gr	N = 1	N = 10	N = 21	N = 1
0	0 / 0	1 / 10	2 / 10	0 / 0

1	0 / 0	1 / 10	1 / 5	0 / 0
2	0 / 0	5 / 50	6 / 29	1 / 100
3	1 / 100	3 / 30	9 / 43	0 / 0
4	0 / 0	0 / 0	3 / 14	0 / 0
Bucc Cusp: MAR	N = 0	N = 9	N = 16	N = 0
0	0 / 0	2 / 22	5 / 31	0 / 0
1	0 / 0	1 / 11	5 / 31	0 / 0
2	0 / 0	2 / 22	3 / 19	0 / 0
3	0 / 0	4 / 44	3 / 19	0 / 0
Bucc Cusp: DAR	N = 1	N = 7	N = 16	N = 0
0	0 / 0	1 / 14	6 / 38	0 / 0
1	0 / 0	0 / 0	7 / 44	0 / 0
2	1 / 100	3 / 43	0 / 0	0 / 0
3	0 / 0	3 / 43	3 / 19	0 / 0
Ling Cusp: MAR	N = 0	N = 6	N = 14	N = 0
0	0 / 0	2 / 33	6 / 43	0 / 0
1	0 / 0	3 / 50	7 / 50	0 / 0
2	0 / 0	0 / 0	1 / 7	0 / 0
3	0 / 0	1 / 17	0 / 0	0 / 0
Ling Cusp: DAR	N = 0	N = 9	N = 15	N = 0
0	0 / 0	2 / 22	1 / 7	0 / 0
1	0 / 0	0 / 0	3 / 20	0 / 0
2	0 / 0	1 / 11	2 / 13	0 / 0
3	0 / 0	6 / 67	9 / 60	0 / 0
Bucc Ess Crest	N = 1	N = 9	N = 16	N = 0
0	0 / 0	0.5 / 6*	0 / 0	0 / 0
1	1 / 100	7.5 / 83	7 / 44	0 / 0
2	0 / 0	1 / 11	8 / 50	0 / 0
3	0 / 0	0 / 0	1 / 6	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Ling Ess Crest	N = 1	N = 8	N = 14	N = 0
0	0 / 0	0 / 0	0 / 0	0 / 0
1	1 / 100	1 13	11 / 79	0 / 0
2	0 / 0	7 / 88	2 / 14	0 / 0
3	0 / 0	0 / 0	1 / 7	0 / 0
4	0 / 0	0 / 0	0 / 0	
Transv Cr – P	N = 1	N = 8	N = 17	N = 0
0	0 / 0	2 / 25	12 / 71	0 / 0
1	1 / 100	4 / 50	5 / 29	0 / 0
2	0 / 0	2 / 25	0 / 0	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
Transv Cr – F	N = 1	N = 7	N = 5	N = 0

1	1 / 100	6 / 86	5 / 100	0 / 0
2	0 / 0	1 / 14	0 / 0	0 / 0
Acc Marg Tub	N = 2	N = 6	N = 15	N = 0
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	0 / 0	0 / 0	0 / 0
2	1 / 100	4 / 67	0 / 0	0 / 0
3	0 / 0	2 / 33	15 / 100	0 / 0
Mesiobucc Ext Gr	N = 1	N = 12	N = 19	N = 1
0	0 / 0	0 / 0	3 / 16	0 / 0
1	0 / 0	2 / 17	5 / 26	0 / 0
2	1 / 100	5 / 42	9 / 47	1 / 100
3	0 / 0	5 / 42	2 / 11	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0
Distobucc Ext Gr	N = 1	N = 12	N = 24	N = 1
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	3 / 25	4 / 17	1 / 100
2	1 / 100	4 / 34	5 / 21	0 / 0
3	0 / 0	5 / 42	12 / 50	0 / 0
4	0 / 0	0 / 0	3 / 13	0 / 0
Mesioling Ext Gr	N = 1	N = 12	N = 18	N = 0
0	1 / 100	12 / 100	15 / 83	0 / 0
1	0 / 0	0 / 0	1 / 6	0 / 0
2	0 / 0	0 / 0	1 / 6	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	1 / 6	0 / 0
Distoling Ext Gr	N = 4	N = 10	N = 16	N = 0
0	1 / 100	7 / 70	6 / 38	0 / 0
1	0 / 0	1 / 10	3 / 19	0 / 0
2	0 / 0	2 / 20	7 / 44	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	0 / 0

*Value recorded as 0.5 if single individual coded differently on antimeres or in the rare case of being recorded on the cusp of two character states, e.g. 0/1.

TABLE 8-8: M^1 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 3	N = 25	N = 39	N = 6
1	0 / 0	3 / 12	5 / 13	2 / 33
2	1 / 33	4 / 16	10 / 26	3 / 50
3	0 / 0	3 / 12	3 / 8	0 / 0
4	0 / 0	7 / 28	6 / 15	0 / 0
5	1/ 33	1 / 4	3 / 8	0 / 0
6	0 / 0	1 / 4	2 / 5	0 / 0
7	0 / 0	3 / 12	1 / 3	0 / 0
8	0 / 0	1 / 4	1 / 3	1 / 17
9	1 / 33	1 / 4	3 / 8	0 / 0
10	0 / 0	0 / 0	1 / 3	0 / 0
11	0 / 0	1 / 4	4 / 10	0 / 0
Crista Obliqua	N = 2	N = 18	N = 28	N = 5
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	2 / 11	1 / 4	1 / 20
2	2 = 100	16 / 89	27 / 96	4 / 80
Carabelli's Complex	N = 2	N = 13	N = 19	N = 5
0	1 / 50	1 / 8	6 / 32	1 / 20
1	0 / 0	4 / 31	11 / 58	3 / 60
2	0 / 0	1 / 8	2 / 11	0 / 0
3	1 / 50	7 / 54	0 / 0	1 / 20
Distal Cuspules / Cusp 5	N = 1	N = 15	N = 27	N = 5
0	0 / 0	3 / 20	3 / 11	3 / 60
1	0 / 0	11 / 73	19 / 70	2 / 40
2	1 / 100	1 / 7	5 / 19	0 / 0
3	0 / 0	0 / 0	0 / 0	0 / 0
4	0 / 0	0 / 0	0 / 0	
Mesial Marginal Accessory Tubercles	N = 0	N = 4	N = 10	N = 4
0	0 / 0	2 / 50	0 / 0	1 / 25
1	0 / 0	1 / 25	2 / 20	1 / 25
2	0 / 0	0 / 0	3 / 30	0 / 0
3	0 / 0	1 / 25	5 / 50	2 / 50

TABLE 8-9: M^2 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 3	N = 24	N = 28	N = 4
1	0 / 0	3 / 13	1 / 4	2 / 50
2	1 / 33	13 / 54	17 / 61	0 / 0
3	0 / 0	4 / 17	0 / 0	1 / 25
4	0 / 0	1 / 4	3 / 11	0 / 0
5	0 / 0	1 / 4	2 / 7	0 / 0
6	0 / 0	0 / 0	1 / 4	0 / 0
7	1 / 33	1 / 4	1 / 4	1 / 25
8	1 / 33	0 / 0	1 / 4	0 / 0
9	0 / 0	1 / 4	0 / 0	0 / 0
10	0 / 0	0 / 0	1 / 4	0 / 0
11	0 / 0	0 / 0	1 / 4	0 / 0
Crista Obliqua	N = 2	N = 20	N = 20	N = 3
0	0 / 0	0 / 0	0 / 0	0 / 0
1	0 / 0	7.5 / 38	5 / 25	0 / 0
2	2 / 100	12.5 / 63	15 / 75	3 / 100
Carabelli's Complex	N = 2	N = 18	N = 15	N = 3
0	1 / 50	3 / 17	3 / 20	0 / 0
1	0 / 0	7 / 39	6 / 40	3 / 100
2	0 / 0	5 / 28	4 / 27	0 / 0
3	1 / 50	3 / 17	2 / 13	0 / 0
Distal Cuspules / Cusp 5	N = 1	N = 19	N = 21	N = 3
0	0 / 0	2 / 11	0 / 0	0 / 0
1	0 / 0	12 / 63	19 / 90	2 / 67
2	1 / 100	4 / 21	1 / 5	1 / 33
3	0 / 0	0 / 0	1 / 5	0 / 0
4	0 / 0	1 / 5	0 / 0	0 / 0
Mesial Marginal Accessory Tubercles	N = 1	N = 11	N = 8	N = 3
0	0 / 0	4 / 36	2 / 25	0 / 0
1	1 / 100	5 / 45	0 / 0	2 / 67
2	0 / 0	2 / 18	4 / 50	1 / 33
3	0 / 0	0 / 0	2 / 25	0 / 0

TABLE 8-10: M^3 Traits

	Makapansgat n / %	*A. africanus* n / %	*A. robustus* n / %	Fossil *Homo* n / %
Occlusal Wear	N = 4	N = 31	N = 23	N = 2
1	1 / 25	8.5 / 27	4 / 17	0 / 0
2	2 / 50	14.5 / 47	17 / 74	1 / 50
3	0 / 0	4 / 13	0 / 0	0 / 0
4	0 / 0	2 / 6	2 / 9	0 / 0
5	0 / 0	1 / 3	0 / 0	1 / 50
6	0 / 0	0 / 0	0 / 0	0 / 0
7	1 / 25	0 / 0	0 / 0	0 / 0
8	0 / 0	0 / 0	0 / 0	0 / 0
9	0 / 0	0 / 0	0 / 0	0 / 0
10	0 / 0	0 / 0	0 / 0	0 / 0
11	0 / 0	1 / 3	0 / 0	0 / 0
Crista Obliqua	N = 2	N = 20	N = 19	N = 0
0	0 / 0	4 / 20	0 / 0	0 / 0
1	1 / 50	10 / 50	12 / 63	0 / 0
2	1 / 50	6 / 30	7 / 37	0 / 0
Carabelli's Complex	N = 2	N = 21	N = 19	N = 0
0	0 / 0	3 / 14	0 / 0	0 / 0
1	1 / 50	4 / 29	8 / 42	0 / 0
2	0 / 0	9.5 / 45	2 / 11	0 / 0
3	1 / 50	4.5 / 21	9 / 47	
Distal Cuspules / Cusp 5	N = 3	N = 23	N = 20	N = 1
0	0 / 0	2 / 9	0 / 0	0 / 0
1	2 / 67	10 / 43	5 / 25	1 / 100
2	1 / 33	7 / 30	9 / 45	0 / 0
3	0 / 0	3 / 13	4 / 20	0 / 0
4	0 / 0	1 / 4	2 / 10	0 / 0
Mesial Marginal Accessory Tubercles	N = 0	N = 15	N = 14	N = 0
0	0 / 0	4 / 27	0 / 0	0 / 0
1	0 / 0	4.5 / 30	0 / 0	0 / 0
2	0 / 0	3.5 / 23	7 / 50	0 / 0
3	0 / 0	3 / 20	7 / 50	0 / 0

Dental Metrics. Non-parametric analyses were executed on areas and indices for the crown and cervix that were calculated on the basis of dental metrics. Analyses were computed as 2 tailed tests with α = 0.05. As previously discussed, the small sample sizes and obvious temporal and geographic variation encompassed within the samples make significance testing with either Bonferroni or sequential Bonferroni adjusted α-levels overly conservative. As a result, Bonferroni corrections were not employed. Results are discussed in light of p-values, statistical power, and trends within the results to avoid an excessive increase in Type II errors [see Moran (2003) and Nakagawa (2004)]. This approach has been adopted as a way of examining these data in a more biologically meaningful way rather than restricting discussions to only those variables meeting unreasonably strict α-levels. Non-parametric Mann-Whitney U analyses were executed to assess specimens 1) from Makapansgat with those attributed to *A. africanus*, 2) from Makapansgat with a pooled sample of *A. robustus*, and 3) attributed to *A. africanus* to those attributed to *A. robustus*. Results of these analyses and sample sizes are presented in Tables 8-11 and 8-12.

The mandibular incisor, canine, and premolar crown areas from Makapansgat were not analyzed due to excessively low sample sizes. Regardless, the samples of *A. robustus* and *A. africanus* were found to be statistically different in nearly all of the non-molar crown areas: I_1 crown area ($p = 0.04$), I_2 crown area ($p = 0.001$), C_1 crown area ($p < 0.001$), and P_4 crown area ($p = 0.003$). The mandibular incisor, canine, and premolar cervical areas produced similar results for the samples of *A. robustus* and *A. africanus*, where statistical significance was met by values for I_1 cervical area ($p = 0.02$), I_2 cervical area ($p = 0.004$), and C_1 cervical area ($p = 0.004$). The cervical areas for C_1 and P_3 were analyzed for the Makapansgat sample due to a slightly increased sample. In light of the inability to discriminate the samples of *A. africanus* and *A. robustus*, the P_3 cervical area for the Makapansgat sample not surprisingly was found to be indistinguishable from samples of both *A. africanus* and *A. robustus*. Unexpectedly, however, the Makapansgat sample was found to be statistically significantly distinct from the sample of *A. africanus* in C_1 cervical area ($p = 0.01$). The Makapansgat sample displays canines with cervical areas that are statistically smaller than the sample of *A. africanus* and are actually (but not statistically) larger than the sample of *A. robustus*.

The molars preserve the largest sample sizes for the mandibular dental data from Makapansgat. Analyses were calculated comparing the handful of Makapansgat specimens to the samples of *A. africanus* and *A. robustus* in molar crown and cervical areas. The samples of *A. robustus* and *A. africanus* could be distinguished from each other only in the crown and cervical areas of the M_1. These data support previous assertions by Suwa and colleagues (1994) who indicate that the molar crown and cusp areas of the M_1 for the sample of *A. africanus* are most similar to those of early *Homo* and *A. afarensis*, while the M_2 and M_3 are more similar to of specimens attributed to *A. robustus*. The Makapansgat sample could be distinguished from the sample of *A. robustus* in M_3 crown area ($p = 0.03$) and M_3 cervical area ($p = 0.004$), but were not found to be distinct from the samples of *A. africanus* in molar crown and cervical areas. These data do not lend weight to the claim that the Sterkfontein specimens exhibit larger teeth and smaller jaws than the Makapansgat specimens (Dart, 1962a).

An index comparing the crown and cervical areas of each molar was calculated [(cervical area/crown area) * 100]. These data did not discriminate between the relatively large samples of *A. africanus* and *A. robustus* in any of the lower molars, but statistically differentiated the Makapansgat sample from the samples of both *A. africanus* ($p = 0.04$) and *A. robustus* ($p = 0.01$) for the M_1. The Makapansgat sample displays a larger value than either of the South African australopith species samples indicating that the Makapansgat M_1 may be less relatively tapered near the cervix. However, this may be a result of sampling bias.

The maxillary dentition followed a similar pattern in terms of discriminating the fossil samples as did the mandibular dentition. Specifically, the incisors, canines, and premolars served to distinguish the samples of *A. africanus* from *A. robustus* better than the molars. The South African australopith species could be differentiated on the basis of I^1 crown area ($p < 0.001$), C^1 crown area ($p = 0.001$), P^3 crown area ($p < 0.001$), P^4 crown area ($p < 0.001$), I^1 cervical area ($p < 0.001$), I^2 cervical area ($p = 0.05$), C^1 cervical area ($p < 0.001$), P^3 cervical area ($p = 0.01$), and P^4 cervical area ($p < 0.001$). The samples were not found to be statistically different in only I_2 crown area ($p = 0.54$), which noticeably is one of the smallest samples for *A. robustus* ($n = 8$). The Makapansgat anterior dentition was only compared to the large South African australopith samples on the basis of P^3 crown area, for which it is statistically different from the sample of *A. robustus* ($p = 0.001$) but not *A. africanus* ($p = 0.43$). However, previous claims indicate that the Makapansgat P_4s are similar in size to those of *A. africanus*, but are broader on the buccolingual aspect of the crown (Sperber, 1974).

The crown and cervical areas of the maxillary molars were compared for the relatively large samples of *A. africanus* and *A. robustus*. The crown and cervical areas of the M^3 ($p_1 = 0.002$ and $p_2 = 0.02$, respectively) are significantly different for these species. However, the only samples from Makapansgat with large enough sample sizes to warrant comparison are significantly indistinguishable from either South African australopith species (M^2 crown and cervical area). An index comparing the crown and cervical areas of each molar was calculated [(cervical area/crown area) * 100], but did not discriminate any of the samples analyzed.

The marked differences in tooth size displayed by the upper and lower anterior dentition of the specimens attributed to *A. africanus* and *A. robustus* has long been discussed. The size differences in the anterior dentition are reflected in the crown and cervical area data presented in Tables 8-11 and 8-12 and discussed in the preceding discussion. Differences in the crown and cervical areas of the premolars also serve to discriminate the South African australopiths. The molars, in contrast, do not discriminate among fossil samples nearly as well as the incisors, canines, and premolars in crown and cervical areas.

TABLE 8-11: Significance Testing of Lower Dentition Variables, for Makapansgat versus A. africanus, *Makapansgat versus* A. robustus, *and* A. robustus *versus* A. africanus *via Non-Parametric Mann-Whitney U.*

Variable	N Mak	N *A. afric*	N *A. rob*	Exact Significance (Mak/*A. afric*)	Exact Significance (Mak/*A. rob*)	Exact Significance (*A. afric*/*A. rob*)
I_1 Crown Area	1	6	6	---±	---±	0.04*
I_2 Crown Area	1	8	7	---±	---±	0.001*
C_1 Crown Area	1	22	10	---±	---±	<0.001*
P_3 Crown Area	2	17	14	---±	---±	0.22

P_4 Crown Area	2	19	15	---±	---±	0.003*
M_1 Crown Area	3	29	23	0.67	0.21	0.02*§
M_2 Crown Area	4	26	21	0.58	0.20	0.19§
M_3 Crown Area	4	29	23	0.15	0.03*	0.38§
I_1 Cerv. Area	1	9	7	---±	---±	0.02*
I_2 Cerv. Area	1	8	7	---±	---±	0.004*
C_1 Cerv. Area	3	27	9	0.01*	0.06	<0.001*
P_3 Cerv. Area	3	16	14	0.88	0.86	0.95
P_4 Cerv. Area	2	19	15	---±	---±	0.07
M_1 Cerv. Area	4	28	21	0.64	0.26	0.03*§
M_2 Cerv. Area	4	24	20	0.68	0.35	0.40§
M_3 Cerv. Area	4	23	19	0.15	0.004*	0.47§
M_1 Cerv/Crown Index	3	26	20	0.04*	0.01*	0.09§
M_2 Cerv/Crown Index	4	24	20	0.92	0.43	0.65§
M_3 Cerv/Crown Index	3	22	19	0.15	0.16	0.14§

*Significant at $\alpha = 0.05$
± Excluded from analyses on the basis of sample sizes
§ Asymptotic significance produced instead of exact, accurate due to larger sample sizes

TABLE 8-12: Significance Testing of Upper Dentition Variables for Makapansgat versus A. africanus, *Makapansgat versus* A. robustus, *and* A. robustus *versus* A. africanus *via Non-Parametric Mann-Whitney U.*

Variable	N Mak	N *A. afric*	N *A. rob*	Exact Significance (Mak/*A. afric*)	Exact Significance (Mak/*A. rob*)	Exact Significance (*A. afric*/*A. rob*)
I^1 Crown Area	1	9	13	---±	---±	<0.001*

I^2 Crown Area	2	9	8	---±	---±	0.54
C^1 Crown Area	1	13	18	---±	---±	0.001*
P^3 Crown Area	3	14	26	0.43	0.001*	<0.001*
P^4 Crown Area	2	9	29	---±	---±	<0.001*
M^1 Crown Area	2	18	32	---±	---±	0.23§
M^2 Crown Area	3	19	22	1.00	0.45	0.19§
M^3 Crown Area	2	23	20	---±	---±	0.002*§
I^1 Cerv. Area	1	10	13	---±	---±	<0.001*
I^2 Cerv. Area	2	7	8	---±	---±	0.05*
C^1 Cerv. Area	1	14	18	---±	---±	<0.001*
P^3 Cerv. Area	2	18	24	---±	---±	0.01*§
P^4 Cerv. Area	2	13	31	---±	---±	<0.001*§
M^1 Cerv. Area	2	19	29	---±	---±	0.67§
M^2 Cerv. Area	3	18	23	0.96	0.94	0.85§
M^3 Cerv. Area	2	21	18	---±	---±	0.02*
M^1 Cerv/Crown Index	2	17	28	---±	---±	0.24
M^2 Cerv/Crown Index	3	18	22	0.89	0.40	0.40§
M^3 Cerv/Crown Index	2	20	18	---±	---±	0.63

*Significant at $\alpha = 0.05$
± Excluded from analyses on the basis of sample sizes
§ Asymptotic significance produced instead of exact, accurate due to larger sample sizes

Dental Morphometrics. Two-dimensional dental morphometric analyses of the mandibular and maxillary premolars and molars of available South African fossils were undertaken using occlusal photographs. Size and shape variation were assessed on the basis of dental landmark and semi-landmark data through Generalized Procrustes and Principal Components Analysis in Morphologika (O'Higgins and Jones, 2006). For each tooth, these analyses were repeated with 1) a sample of all available specimens that preserve the occlusal outline well enough to record a series of 50 semi-landmarks along the periphery of the tooth and 2) a smaller sample confined to only those teeth with limited wear and for which major cusp tips could be identified and added as landmarks to a series of 25 semi-landmarks representing the occlusal outline. Only the first 3 principal components are presented in the following pages to confine discussion to the principal components with the greatest explanatory power and to avoid overburdening the reader. Examination of the additional principal components was undertaken, but did not contribute to fossil taxon discrimination on the basis of these semi-landmark and landmark data. The principal components, idealized shapes along the orthogonal axes, and centroid sizes are presented in graphical form and discussed in the following pages.

Lower Dentition. A generalized Procrustes Analysis (GPA) of 50 semi-landmarks collected along the occlusal outline of the mandibular P_3s was executed, followed by a Principal Components Analysis (PCA) of these scaled coordinate data. The first 3 principal components are plotted in Figure 8-33 and explain 84% of the cumulative variance in scaled coordinate data. PC 1 explains 48%, PC 2 explains 23% and PC 3 explains 13% of the variance in these coordinate data. Examination of a plot of PC 1 by

PC 2 demonstrates considerable overlap for the specimens attributed to *A. africanus* and *A. robustus* along both axes. PC 1 demonstrates some tendencies within the samples of *A. robustus* and *A. africanus*, with most of the specimens attributed to the former producing negative values (i.e. a relatively symmetrical P_3 with a mesiolingually expanded crown) and most of the specimens attributed to the latter producing positive values (i.e. an asymmetrical P_3 with a mesiolingually truncated crown). The Makapansgat hominins (MLD 2, MLD 18, and MLD 40) are positioned in the region of greatest overlap. Specimens attributed to the genus *Homo* also plot within the region of overlap, with the exception of one specimen, which is distinguished primarily on the basis of PC 2 and can be characterized as buccolingually and mesiodistally symmetrical (circular) rather than the more typical relatively buccolingually broad crown (oval) of the other fossils.

The plot of PC 2 by PC 3 does not help to distinguish the samples. In addition, a plot of centroid size by PC 1 does little to aid discrimination of the samples. A closer examination of centroid size (calculated by the square root of the sum of squared distances of the landmarks from the centroid for each specimen) is provided in Figure 8-34. The range of centroid size values for the sample of *A. africanus* is so broad that it encompasses the centroid size values for all other fossil samples. In summary, comparison of neither size nor shape data for the P_3 occlusal outlines contribute to discrimination of the Makapansgat specimens from the other South African australopith samples.

A GPA of 25 semi-landmarks collected along the occlusal outline and 2 landmarks on the cusp tips of P_3 was executed, followed by PCA of these Procrustes transformed data. The first 3 principal components are plotted in Figure 8-35 and explain 76% of the cumulative variance in scaled coordinate data. PC 1 explains 39%, PC 2 explains 21%, and PC 3 explains 16% of the variance in data. Even in light of the smaller fossil samples, a plot of PC 1 by PC 2 demonstrates better discrimination of the fossil samples than the larger sample of occlusal outline semi-landmark data without cusp landmarks. Both PC 1 and PC2 overlap for the samples of *A. africanus* and *A. robustus*. The single Makapansgat specimen included in this analysis (MLD 2) plots within the region of overlap, but could be argued to be more similar to specimens of *A. robustus* in both axes. The only specimen attributed to the genus *Homo* is clearly distinguished from all other specimens on the basis of a more mesially positioned metaconid (lingual cusp) and a distally expanded talonid represented by PC 1 and PC 2 extreme configurations, respectively. PC 3 does not aid further discrimination of these data.

Examination of a plot of centroid size by PC 1 reaffirms the wide range of variation in centroid size represented by the sample of *A. africanus*. The largest (StW 401) and the smallest (StW 213) values for centroid size are represented by specimens of *A. africanus*. The single specimen of *Homo* is discriminated in this plot by PC 1, but also is one of the smallest values for centroid size. The Makapansgat specimen (MLD 2) plots most closely with specimens of *A. robustus* on the basis of a large centroid size, but cannot be discriminated from either South African australopith species (see Figure 8-36).

Results of the GPA and subsequent PCA of the 50 occlusal outline semi-landmarks of the P_4 are presented in Figures 8-37. The first 3 principal components explain a cumulative 81% of the variance in Procrustes-transformed coordinates. The first principal component explains 43%, second principal component explains 30%, and third principal component explains 8% of the variance in data. Neither the plot of PC 1 by PC 2 nor the plot of PC 2 by PC 3 discriminate any of the samples. SKX 4446 (attributed to *A. robustus*) is an outlier in PC 2, which likely results from the unusual truncation of the distolingual aspect of the tooth. A plot of centroid size by PC 1 does indicate some grouping of the results by taxon, although centroid size is primarily responsible. Examination of boxplots of centroid size by taxon (Figure 8-38), demonstrate that the South African australopith species overlap in P_4 centroid size considerably. Regardless, the robust sample tends to have larger centroid sizes than that of *A. africanus* for these data. As expected, the single specimen attributed to *Homo* displays one of the smallest centroid sizes. The small P_4 sample from Makapansgat (MLD 18 and MLD 40) is most similar to specimens attributed to *A. africanus* in their relatively small centroid sizes. Unfortunately, the Makapansgat P_4s are too worn to record cusp tip locations, precluding an analysis of the P_4 occlusal outline semi-landmarks and cusp tip landmarks.

Patterns of size and shape variation in the occlusal outline of the M_1 are presented in Figure 8-39. The first 3 principal components of the M_1 occlusal outline GPA explain a cumulative 94% of the variance in data, where PC 1 explains 87%, PC 2 explains 5%, and PC 3 explains 3%. The high explanatory value of this PCA with regard to occlusal outline variance is likely a reflection of the relatively high fossil sample size for the M_1 (N = 52). Although PC 1 intimates some separation of the two australopith species along its axis, considerable overlap is apparent. The Makapansgat specimens (MLD 2, MLD 18, and MLD 40) cluster closely together in the plots of PC 1 by PC 2 and PC 2 by PC3.

The Makapansgat specimens are positioned in proximity to several specimens attributed to *A. africanus*, but also near specimens attributed to *Homo* and *A. robustus*. The robust australopith outlier in PC 3 (SKX 5014), stands out along this axis and morphologically in its strongly distally tapered outline with enormous accessory distal cusp and broad mesial aspect. As in many of these GPAs and PCAs, the sample of *A. africanus* displays extreme variation in all principal components. In addition, the range of centroid size is most extreme within the sample of *A. africanus*, encompassing both the largest (StW 142) and smallest (StW 106) values (see Figure 8-40). That said, the robust australopiths also demonstrate an enormous range of variation in M_1 centroid size. Unfortunately, the plot of centroid size by PC 1 further indicates that centroid size adds little to the discriminatory power of M_1 occlusal outline variation in these analyses.

Size and shape variation in the occlusal morphology (outlines and cusp tips) are represented by the results displayed in Figures 8-41. The first 3 principal components of these analyses account for 27%, 21% and 12% of the variance in data (60% cumulatively). A plot of PC 1 by PC 2 demonstrates some discrimination between the 2 large australopith M_1 samples. The extremes along the shape configuration orthogonal axes suggest that the greatest discrimination between the samples of *A. robustus* and *A. africanus* may best be described as more internally positioned buccal cusps for the former taxon. The MLD 2 specimen plots closest to specimens attributed to *Homo* and *A. africanus* in PC 1 by PC 2. This position is driven primarily by the large positive value for PC 1. The only specimen attributed to *Homo* (StW 151) nestles within the grouping of robusts. A couple of specimens are particularly worthy of discussion with regard to their positioning in the PC 1 by PC 2 plot. A specimen of *A. robustus* (SK 61) is positioned well within the grouping of specimens attributed to *A. africanus*, having been long identified as one of the more gracile specimens from Swartkrans (e.g. Wolpoff, 1970). Two specimens attributed to *A. africanus* (StW 246 and StW 309 in the upper left and right quadrants, respectively), are within the grouping of specimens attributed to *A. robustus*. MLD 2 plots distinctly on its own, arguably a more extreme version of the pattern for *A. africanus* in M_1 occlusal outline and cusp morphology.

The plot of PC 2 by PC 3 displays a similar pattern whereby the 2 large australopith samples are separated out to some degree, but display considerable overlap in PC 3. MLD 2 plots closely to specimens of both *A. africanus* and *A. robustus*. Again, centroid size does little to discriminate between the australopith species (Figures 8-41 and 8-42). However, the robusts display a tendency towards greater centroid size values and provide the greatest range of variation in contrast to previous analyses. The MLD 2 specimen is more like the robust sample in its relatively large centroid size.

Results of the GPA and PCA for M_2 occlusal outline semi-landmark data are presented in plots of the first 3 principal components (see Figures 8-43). These 3 principal components together explain 70% of the variance in these data, 33% for PC 1, 28% for PC 2, and 10% for PC 3. The Makapansgat sample is represented by MLD 2, 18, 22, and 24. Of these specimens, MLD 18 stands out in its value for PC 2. Regardless, these data do not discriminate the samples of *A. africanus* and *A. robustus*. A boxplot of centroid size displays a wider range of size variation for *A. robustus* (Figure 8-44). The Makapansgat sample cannot be distinguished from either sample on the basis of size.

The GPA and PCA results for M_2 occlusal outline semi-landmark and cusp landmark data are presented in Figures 8-45 and 8-46. The first 3 principal components explain 60% of the variance in Procrustes-transformed data (26%, 21%, and 13%, respectively). Plots of PC 1 by PC 2 and PC 2 by PC 3 fail to discriminate the fossil samples. A plot of centroid size by PC 1 does not contribute any discriminatory power. The ranges in centroid size values for the M_2 occlusal outline and cusp sample are almost entirely overlapping for the samples of *A. robustus* and *A. africanus*. The SKX 257 specimen, attributed to *Homo*, exhibits the smallest centroid size, while StW 424 exhibits the largest. The centroid size for MLD 2 is one of the largest for any of the fossil M_2 samples. It would be interesting to compare variation between the patterning of mandibular molar variation within each species as *A. africanus* is considered to be similar to great apes and dissimilar to modern humans in have buccolingually narrower M_2s (than M_1) with more externally positioned buccal cusps. Perhaps future analyses of combined samples of M_1 and M_2 molar morphology will help to assess whether the samples of *A. africanus*, Makapansgat hominins, and *A. robustus* can be differentiated from each other on the basis of metameric patterns of variation in M_1/M_2 morphology.

The GPA and subsequent PCA of M_3 occlusal outline semi-landmarks are presented via plots of the first 3 principal components and a boxplot of centroid size (Figure 8-47). The first few principal components account for 77% of the variance in Procrustes-transformed semi-landmark data, 51% for PC 1, 15% for PC 2, and 11% for PC 3. The plot of PC 1 by PC 2 displays considerably overlap in the samples of *A. robustus* and *A. africanus*. Some trends in these data are visible, however, as numerous specimens of *A. robustus* produce more negative values in PC 2 than of *A. africanus*. Three of the Makapansgat specimens (MLD 4, MLD 18, and MLD 22) plot most closely to specimens of *A africanus*, one specimen (MLD 19) plots in the region of considerable overlap between specimens of *A. africanus* and *A. robustus*, and one specimen (MLD 40) is somewhat distinct.

The plot of PC 2 by PC 3 produces a similar pattern with some trends discernible, but considerable overlap for the South African australopiths. The Makapansgat specimens are in the regions of considerable overlap, except for MLD 40, which appears to exhibit one of the most extreme morphologies along the PC 2 axis. This morphology can be characterized as a distal truncation (lack of distal tapering) of the crown. A plot of centroid size by PC 1 does not improve discrimination of the fossil samples. Indeed, the boxplot of centroid size (Figure 8-48) indicates that both South African australopiths display considerable variation in centroid size that almost completely overlap with each other. In consideration of the small Makapansgat sample (n = 5), it also displays remarkable variation in centroid size that overlaps with the samples of both *A. robustus* and *A. africanus*.

A GPA and PCA of M_3 occlusal outline semi-landmarks and cusp tip landmarks was not executed as a result of moderate wear of the Makapansgat M_3 specimens obscuring cusp tip locations.

Upper Dentition. GPA of the P^3 occlusal outline semi-landmarks and subsequent PCA only partly discriminated the fossil taxa (see Figure 8-49). The first 3 principal components are plotted and explain 79% of the variance in these Procrustes-transformed data. These first 3 principal components account for 37%, 27%, and 15% of the variance, respectively. A plot of PC 1 by PC 2 did not discriminate fossil taxa well as the australopith species exhibit significant overlap along both axes. The SK 27 specimen, attributed to *Homo*, also failed to be discriminated. The plot of PC 2 by PC 3, however, suggested some clustering of specimens. The outlier (the SK 44 specimen, attributed to *A. robustus*) is morphologically unique in its extremely triangular and expanded occlusal outline. The Makapansgat specimens MLD 11/30 and MLD 23 are positioned most closely to *A. africanus* and MLD 45 is positioned closely to both species. SK 27 (attributed to *Homo*) plots very closely to SK 13 (attributed to *A. robustus*). A plot of centroid size by PC 1 aided separation of the australopith species and, with the boxplot of centroid size (Figure 8-50), indicate a tendency for the robusts to have larger P^3 occlusal outlines.

The size and shape variation of the P^3 occlusal outline and cusp data are presented in Figure 8-51. The first 3 principal components explain a cumulative 68% of the variance in data, where PC 1 accounts for 39%, PC 2 accounts for 18%, and PC 3 accounts for 11%. An examination of the plot of PC 1 by PC 2 demonstrates that the positioning of the specimens of *A. africanus* and *A. robustus* overlap entirely. The specimens from Makapansgat (MLD 11/30, MLD 23, and MLD 45) are positioned within the widely scattered cluster of specimens of *Australopithecus*. The single specimen attributed to the genus *Homo* plots on its own, with low values for both PC 1 and PC2.

The plot of PC 2 by PC 3 does little to discriminate among fossil samples, although the robusts exhibit a relatively tight cluster. The SK 27 specimen (*Homo*) and

MLD 11/30 are positioned somewhat distinctly in comparison to the other fossil specimens with very low values for PC 3 and moderately low values for PC 2. The orthogonal axes representing the semi-landmark and landmark extreme configurations suggest that MLD 11/30 and SK 27 stand out on the basis of a relatively broad buccal aspect with respect to the P^3. Centroid size values for these data indicate a broad range of size variation in the sample of *A. africanus* and a slightly higher median centroid size for *A. robustus*. The Makapansgat sample displays some of the smallest centroid sizes, along with SK 27. The plot of centroid size by PC 1 reveals that the Makapansgat specimens fit within the expansive realm of *A. africanus*, not *A. robustus*. Boxplots of centroid size (Figure 8-52) indicate overlap among fossil taxa, with the robusts displaying the highest values.

Analysis of the occlusal outlines of the fossil P^4 semi-landmark data explained a cumulative 80% of the variance in the first 3 principal components (see Figure 8-53). The plots of PC 1 by PC 2 and PC 2 by PC 3 serve only to discriminate the specimen attributed to SK 27 (attributed to *Homo*) and Sts 12 (attributed to *A. africanus*) from the greater fossil sample and can be morphologically accounted for by a relatively symmetrical outline. The MLD 6 specimen is positioned on the periphery in both plots. The plot of centroid size by PC 1 discriminates the fossil species despite the considerable overlap in PC 1. The Makapansgat MLD 6 specimen is positioned in close proximity to both samples, but is located most comfortably within the cluster of *A. africanus*. The centroid sizes of the specimens attributed to *A. robustus* display a tendency towards greater centroid sizes than those of *A. africanus* (see Figure 8-54). Interestingly, however, the SK 27 specimen attributed to *Homo* displays one of the greatest values for centroid size among all of the fossil samples.

The semi-landmark occlusal outline and landmark cusp tip data for the P^4s were analyzed using GPA and PCA. The first 3 principal components explain a cumulative 70% of the variance in these data and are presented in Figure 8-55. Plotting of the first 3 principal components does not discriminate the fossil samples well. The scattering of the larger sample of *A. robustus* is greater than that of the smaller sample of *A. africanus*. The MLD 6 specimen cannot be distinguished from either australopith species on the basis of these data. A plot of centroid size by PC 1 does discriminate these data, although only poorly. The Makapansgat specimen is most closely positioned to specimens of *A. africanus*, but is not easily discriminated from either australopith species. The boxplot of centroid size in Figure 8-56 demonstrates a broad range in values for *A. robustus*, including both the largest (SK 49) and one of the smallest (SK 24) values among the fossil specimens. The sample of *A. africanus* displays considerable overlap in centroid size with that of *A. robustus*, yet the 2 species are distinguishable in the tendency for the former to yield lower centroid size values compared to the latter. The MLD 6 specimen has a P^4 centroid size on the lower end of both species, yet is more similar to the median of the sample of *A. africanus*.

Size and shape variation in the occlusal outlines of the M^1 are presented in Figures 8-57. The first 3 principal components of the Procrustes-transformed semi-landmark data account for 70% of the variance in these data, 37% for PC 1, 23% for PC 2, and 10% for PC 3. Although PC 1 does little to discriminate the australopith samples (including MLD 6), the specimens attributed to *Homo* group together along the negative portion of this axis. In contrast, PC 2 displays a tendency for the specimens of *A. africanus* to position along the positive and *A. robustus* along the negative portions of this axis. PC 2 does not easily discriminate the specimens of *Homo*. MLD 6, however, is in the extensive region of overlap for the australopith samples, but is well within the cluster of *A. africanus* and along the periphery of the cluster of *A. robustus*. The plot of PC 2 by PC 3 does not discriminate the samples well. Centroid size (Figures 8-57a and 8-58) do not contribute explanatory power. Indeed, the range of centroid sizes for these semi-landmark data are broadly overlapping for the australopith samples. The sample of *Homo* has relatively low centroid sizes, but the distribution is subsumed within the range of variation for both australopith species. MLD 6 exhibits one of the lowest centroid sizes among the fossil samples.

Variation in the shape and size of the occlusal outline and cusp data for the M^1 was assessed via GPA. The first 3 principal components of the Procrustes-transformed semi-landmark and landmark data together explain 56% of the variance in data. Plots of PC 1 by PC 2 and PC 2 by PC 3 do not distinguish between the fossil samples particularly well (see Figure 8-59). A plot of centroid size by PC 1 improves discrimination (Figure 8-59a), but not clearly. The Makapansgat specimen, MLD 6, cannot be distinguished from any fossil taxon, plotting close to a specimen of each taxon. Evaluation of the boxplot for centroid size suggests that size differs surprisingly little for the M^1s of the fossil hominins (Figure 8-60).

Variation in M^2 outlines among the fossil samples supports previous indications of significant overlapping morphological variation in occlusal outlines. The first 3 principal components explain a total of 71% of the variance in these semi-landmark data (see Figure 8-61), 41% for PC 1, 17% for PC 2, and 14% for PC 3. The plot of PC 1 by PC 2 displays some ability to discriminate the fossil samples, albeit weakly. The robust australopith cluster overlaps with that for *A. africanus*, but also subsumes all of the specimens attributed to *Homo*. The Makapansgat specimens are in the extensive region of overlap between the australopith species. The plot of PC 2 by PC 3 does not aid discrimination of the fossil samples. When centroid size is plotted with PC 1, however, the separation of taxa is improved slightly, but not enough to permit meaningful discussion. Examination of the boxplot of centroid size for these M^2 data (Figure 8-62) suggests that while some trends are visible (e.g. specimens of *Homo* have small centroid size values and *A. robustus* have relatively large centroid size values), the size range within the sample of *A. africanus* is the greatest and incorporates the largest (StW 188) and smallest (StW 447) centroid size values of all fossil specimens.

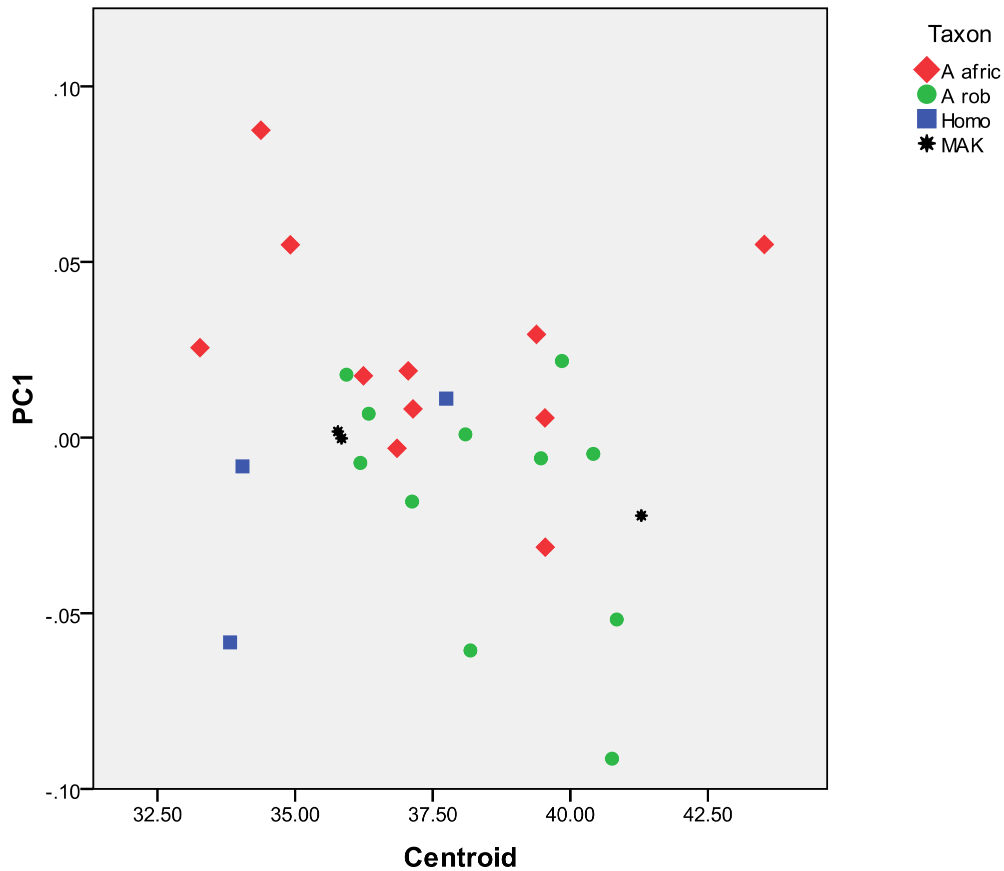
The reduced sample size for the M^2 semi-landmark outline and landmark cusp data failed to contribute much explanatory power. The first 3 principal components explain 62% of the cumulative variance in data. Plots of these principal components (Figure 8-63), however, did not permit the identification of clear groupings for any fossil group. A plot of centroid size by PC 1 failed to improve the grouping of fossil taxa. A boxplot of centroid size (Figure 8-64), displays the common pattern of greatest centroid size variation within the sample of *A. africanus*. It also displays the common pattern of broad overlap in centroid size between the 2 South African australopith species (and Makapansgat sample). The StW 151 specimen, attributed to *Homo*, exhibits a relatively small centroid size.

The M^3 occlusal outlines were also assessed using GPA and PCA. The first 3 principal components together explain 76% of the variance in data, where PC 1 accounts for 43%, PC 2 accounts for 21% and PC 3 accounts for 12%. An examination of PC 1 against PC 2 reveals that the fossil samples attributed to *A. africanus*, *A. robustus*, and *Homo* display considerable overlap, with one obvious outlier: MLD 28. The plot of PC 2 by PC 3 neither discriminates the fossil taxa nor the MLD 28 specimen. Including a graphical comparison of centroid size with PC 1 does not aid discrimination of the fossil taxa. In the contrary, the sample of *A. africanus* displays extreme variation along both axes (PC 1 representing morphological variation and centroid size representing size variation). The boxplot of centroid size for these data displays considerable variation within the sample of *A. africanus*. The MLD 28 specimen fell within the range of variation in centroid size for the sample of *A. africanus* and *Homo*, but not for *A. robustus*.

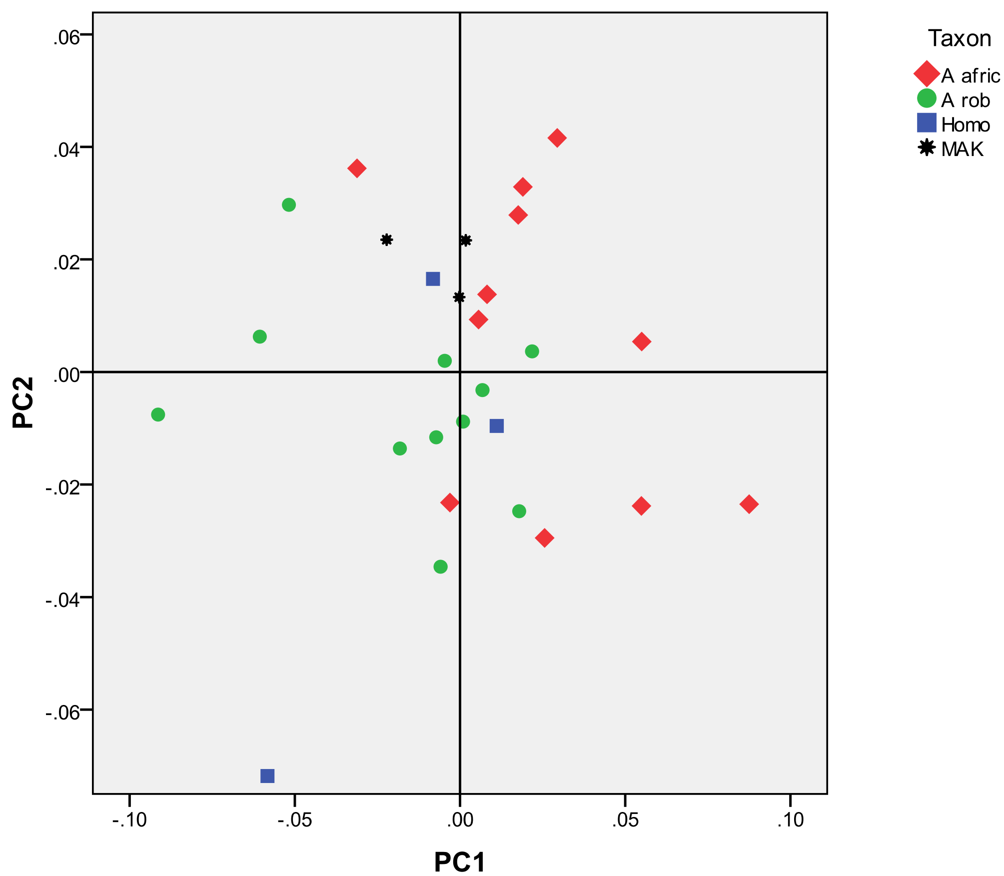
Results of the GPA and PCA of the M^3 occlusal outline and cusp semi-landmark and landmark data are presented in Figure 8-67. The first 3 principal components explain 57% of the variance cumulatively, of which PC 1 explains 23%, PC 2 explains 21%, and PC 3 explains 13%. The plot of PC 1 by PC 2 indicated that PC 2 displays some separation of the specimens attributed to *A. africanus* and *A. robustus*. MLD 28 can be distinguished from all of the fossil specimens on the basis of both PC 1 and PC 2. The extreme configurations suggest that MLD 28 is differentiated at least partly on the basis of a broad mesial aspect. The plot of PC 2 by PC 3 also discriminates *A. africanus* and *A. robustus*, but on the basis of PC 2. The plot of PC 1 by centroid size displays a tighter cluster for the robust australopiths in terms of centroid size. MLD 28 stands out with one of the smallest centroid sizes and PC 1 values. Examination of the boxplots for centroid size (available in Figure 8-68) further demonstrates the broader variation in centroid size in the sample of *A. africanus* than *A. robustus*, even despite the smaller sample size for the former. The Makapansgat MLD 28 specimen falls within the range of variation known for the hypodigm of *A. africanus*, but falls below the range of variation for *A. robustus*.

Figure 8-33*: *PCA of P_3 Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the P_3 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 48%, PC 2 explains 23%, and PC 3 explains 13% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

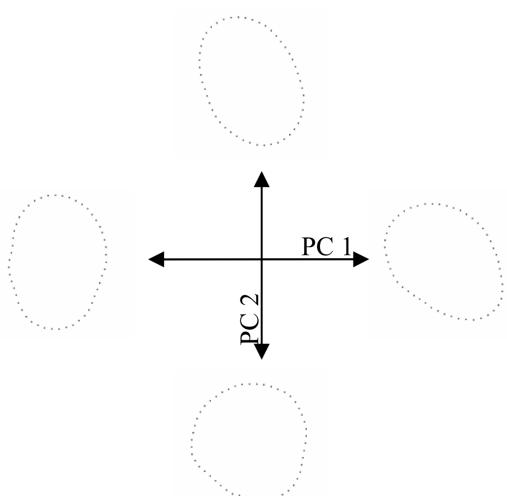


(b.)



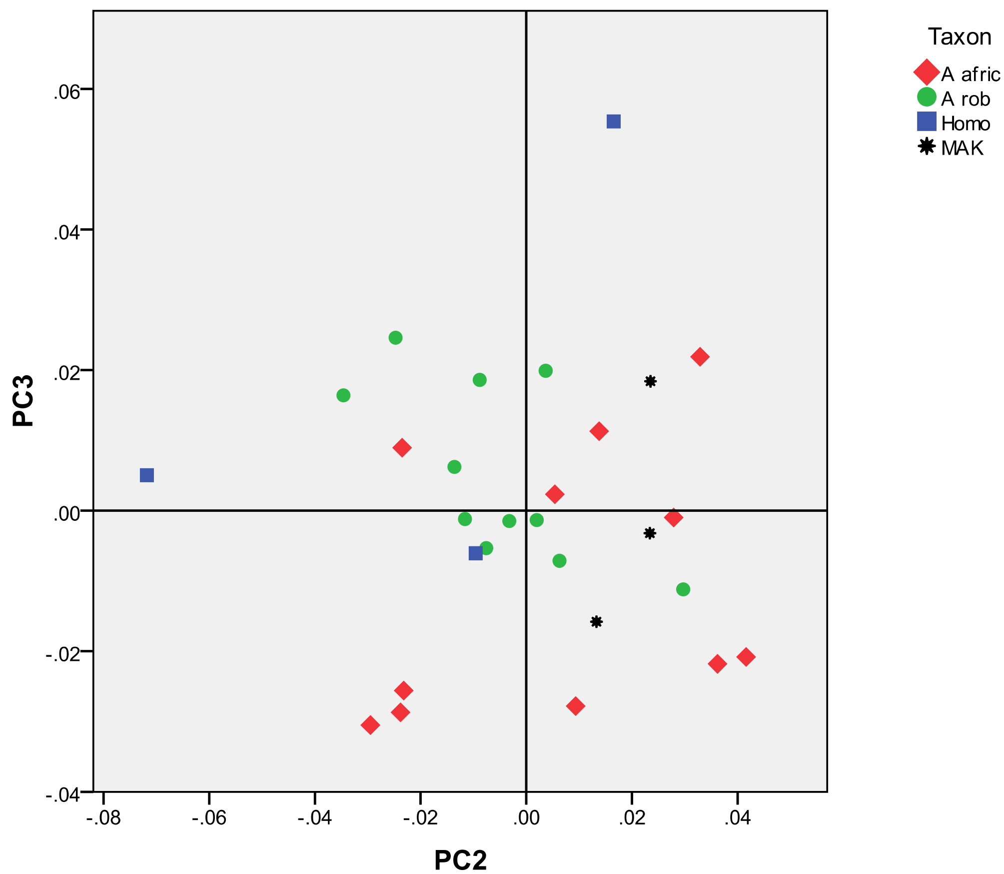
Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.06
.04
.02
.00
-.02
-.04
-.06
-.10
-.05
.00
.05
.10

(c.)



PC 1
PC 2

(d.)


Taxon
A afric
A rob
Homo
MAK
PC3
PC2
.06
.04
.02
.00
-.02
-.04
-.08
-.06
-.04
-.02
.00
.02
.04

(e.)

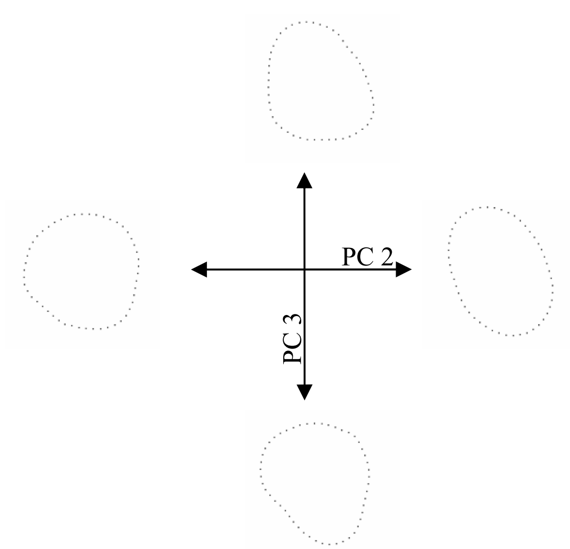

PC 2
PC 3

***Figure 8-34*: Boxplot of the Centroids for P_3 Occlusal Outline Semi-landmark Data.** The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P3 occlusal outline semi-landmark data are compared by taxon.

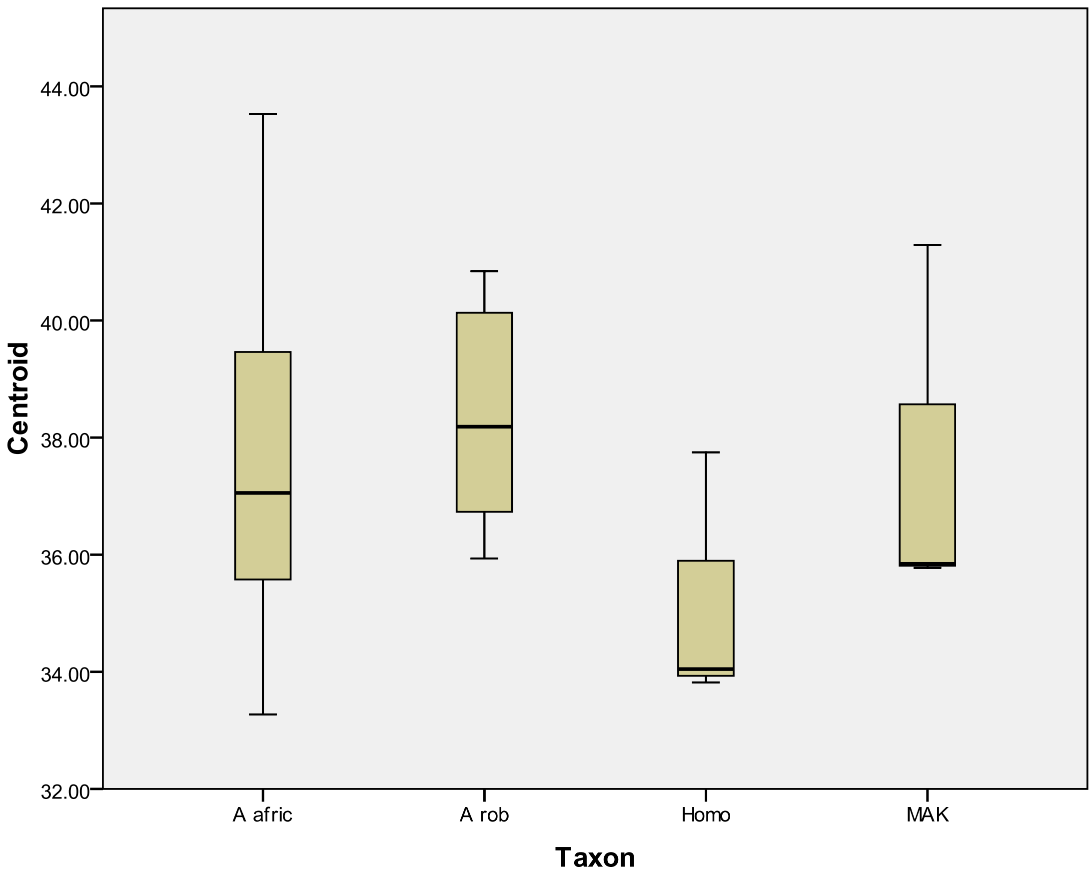
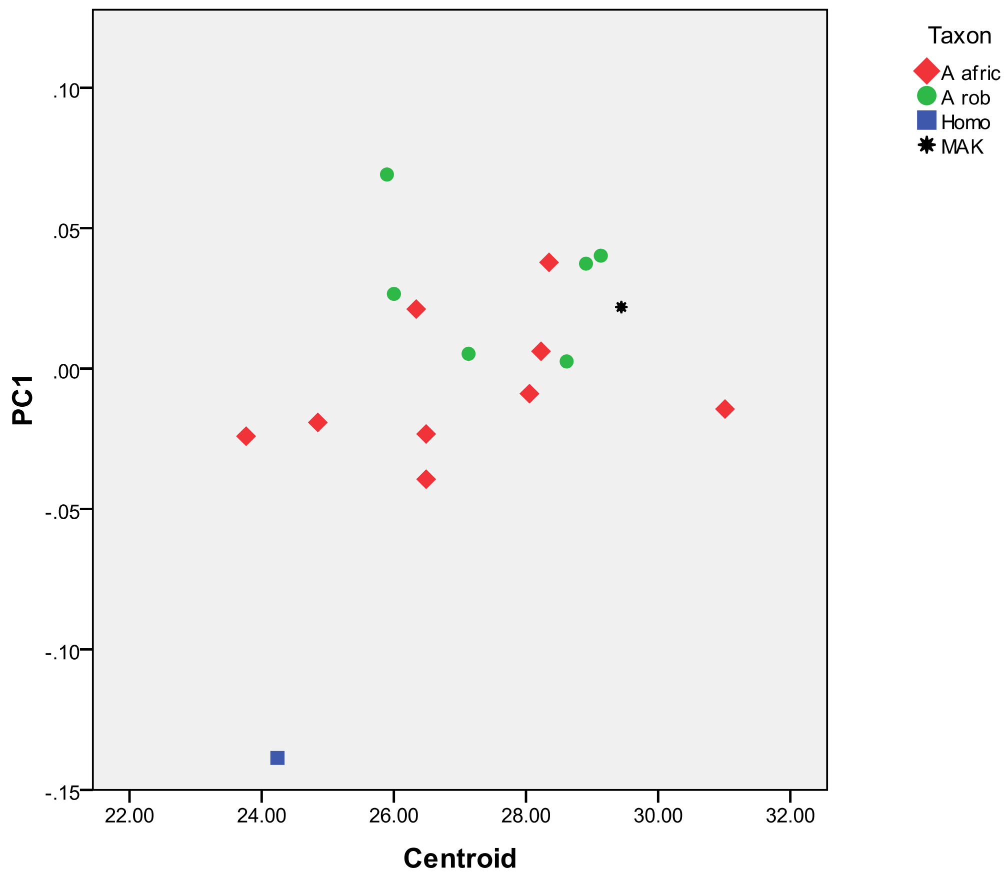
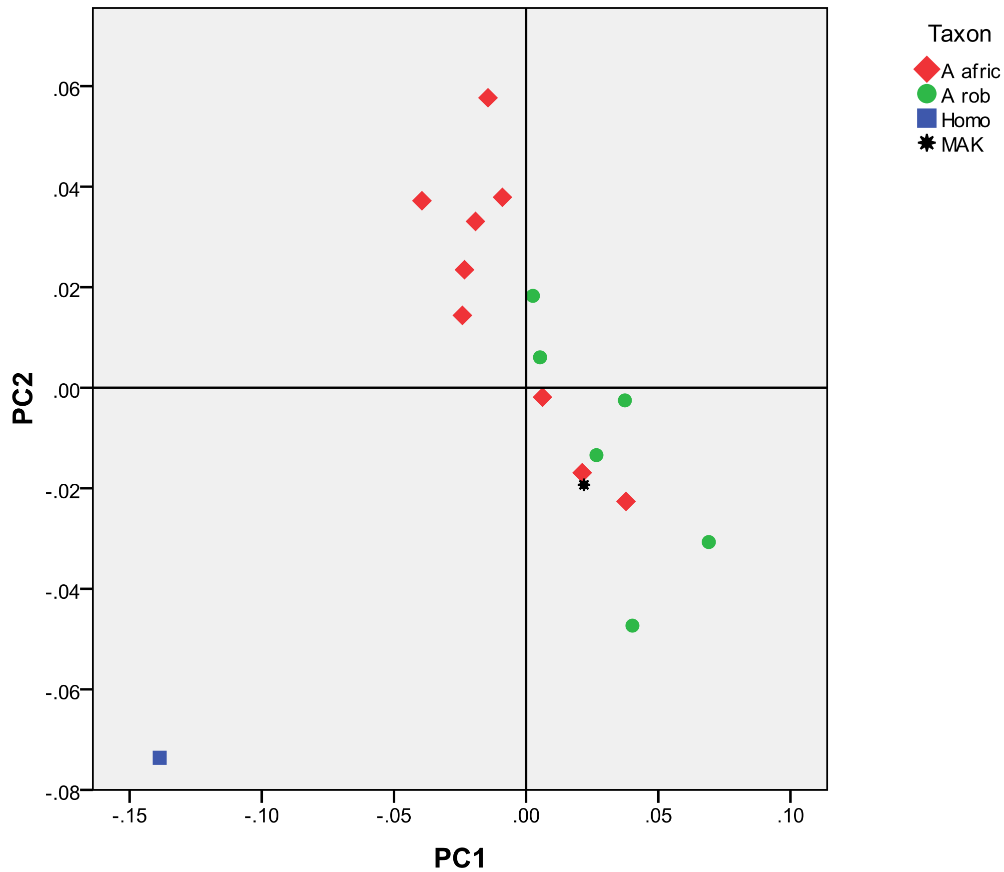


Figure 8-35*: *PCA of P_3 Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the P_3 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 39%, PC 2 explains 21%, and PC 3 explains 16% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

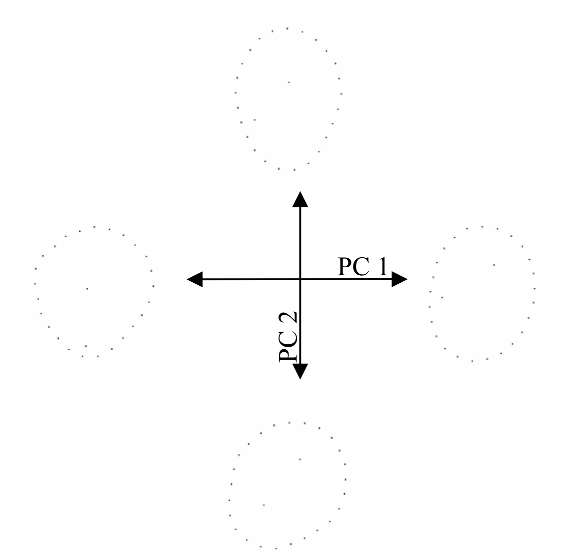
(*a*.)



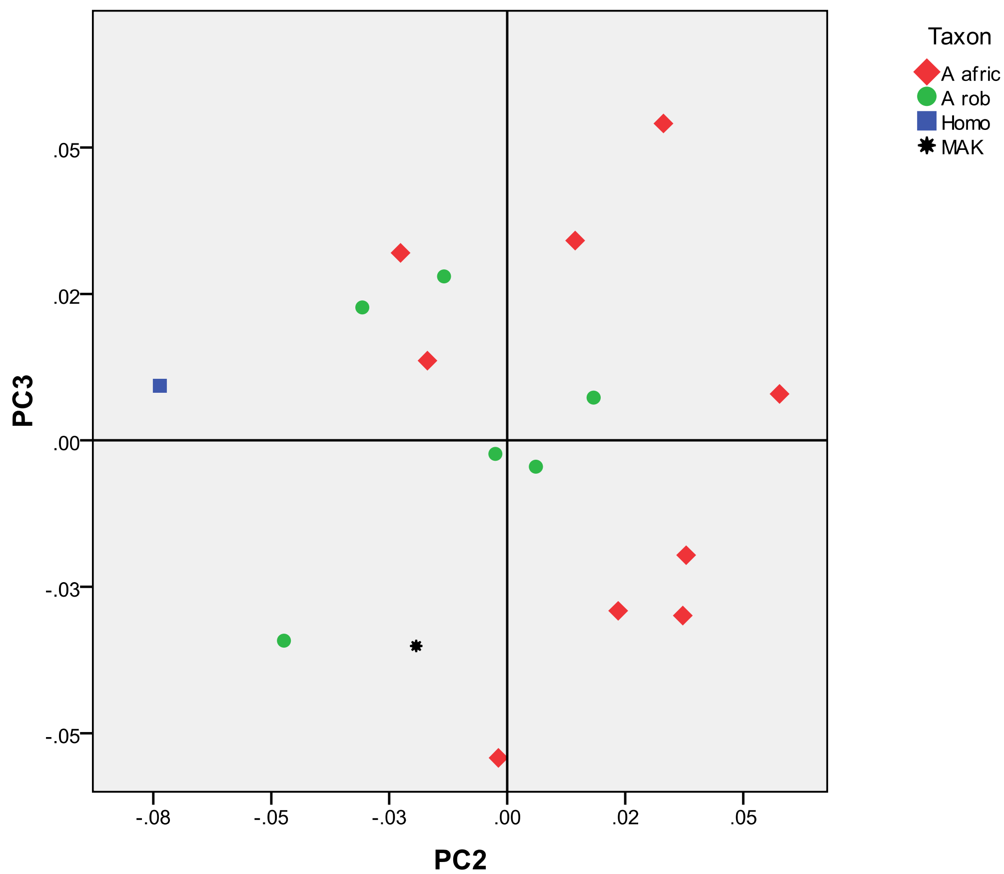
(*b*.)


Taxon
A afric
A rob
Homo
MAK
PC2
.06
.04
.02
.00
-.02
-.04
-.06
-.08
-.15
-.10
-.05
.00
.05
.10
PC1

(*c*.)

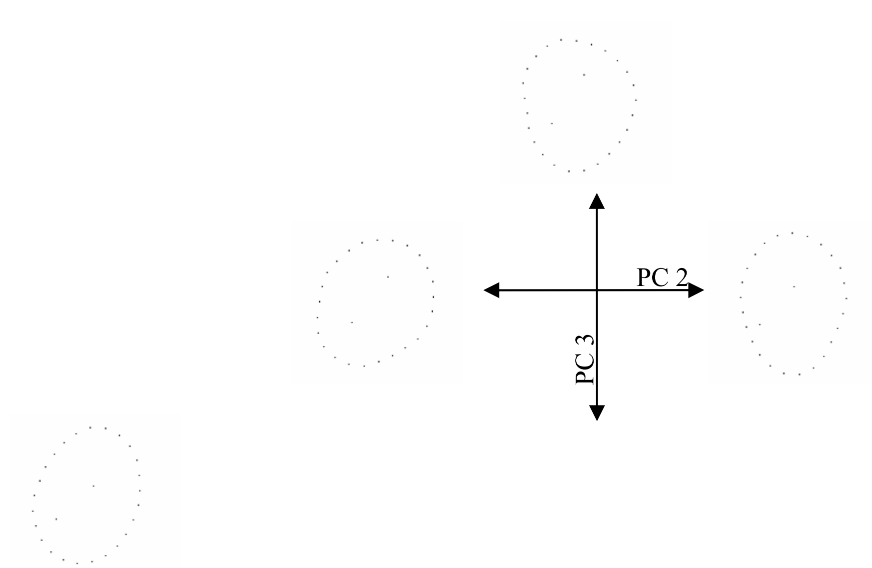

PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
.05
.02
.00
-.03
-.05
PC3
-.08
-.05
-.03
.00
.02
.05
PC2

(*e.*)



PC 2
PC 3

Figure 8-36*: *Boxplot of the Centroids for P_3 Occlusal Outline Semi-landmark and Cusp Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P3 occlusal outline semi-landmark and cusp landmark data are compared by taxon.

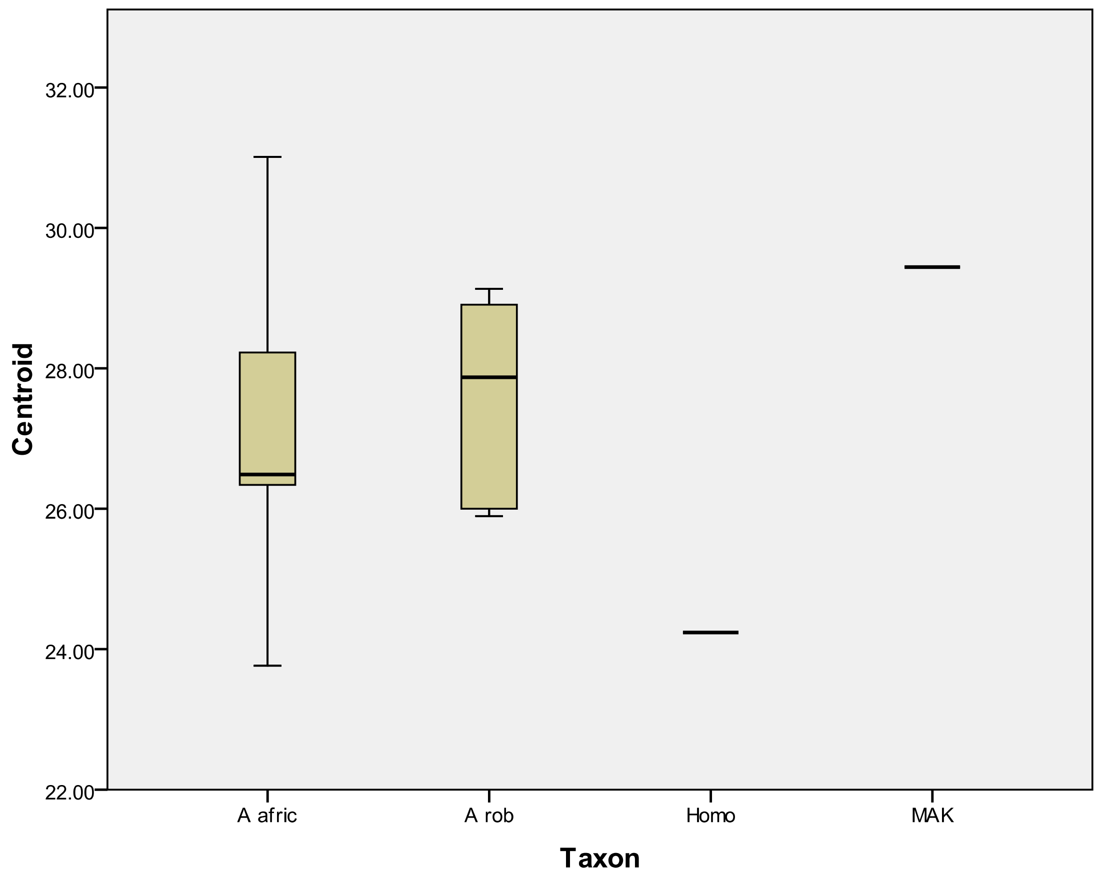
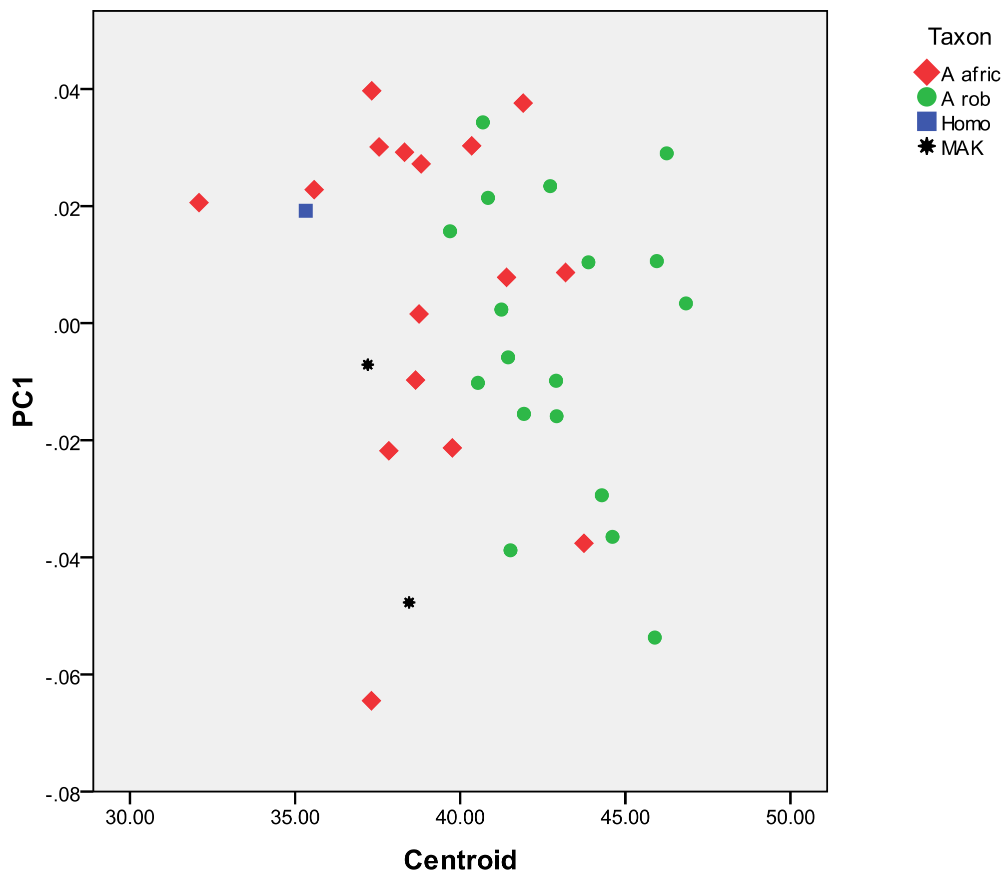
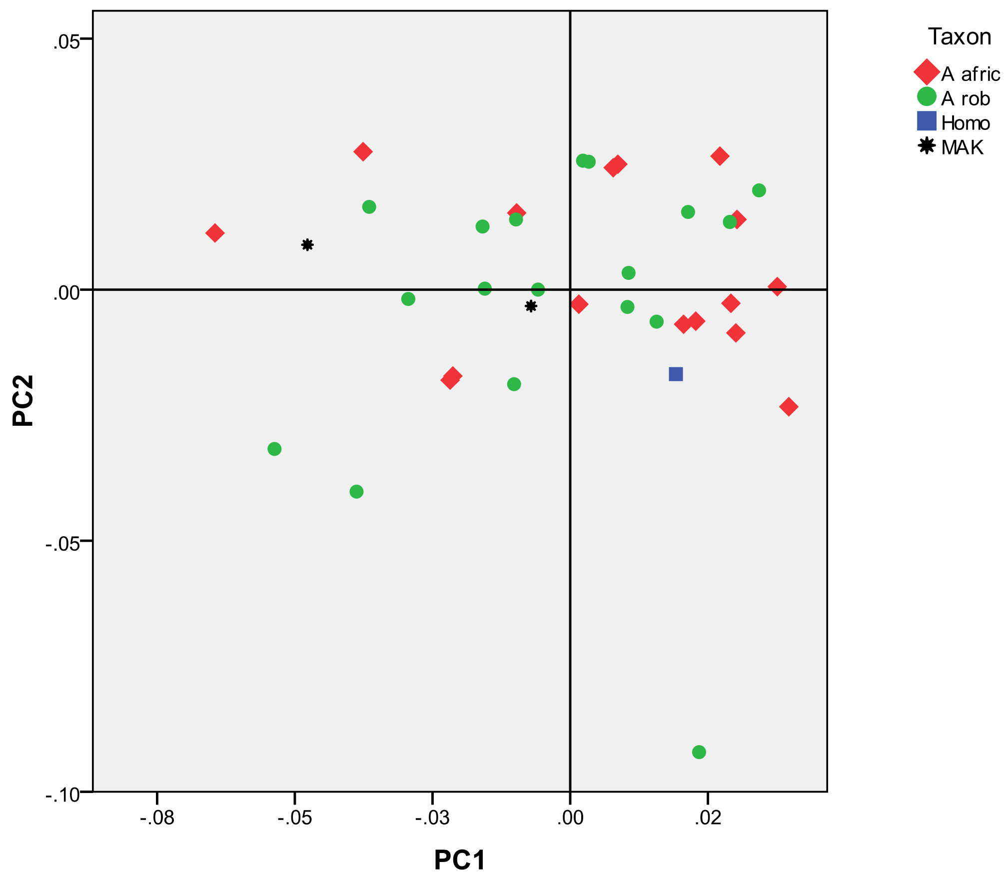


Figure 8-37*: *PCA of P_4 Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the P_4 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 43%, PC 2 explains 30%, and PC 3 explains 8% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

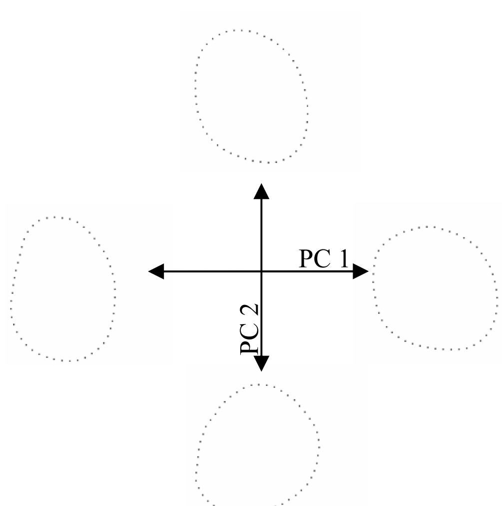


(b.)



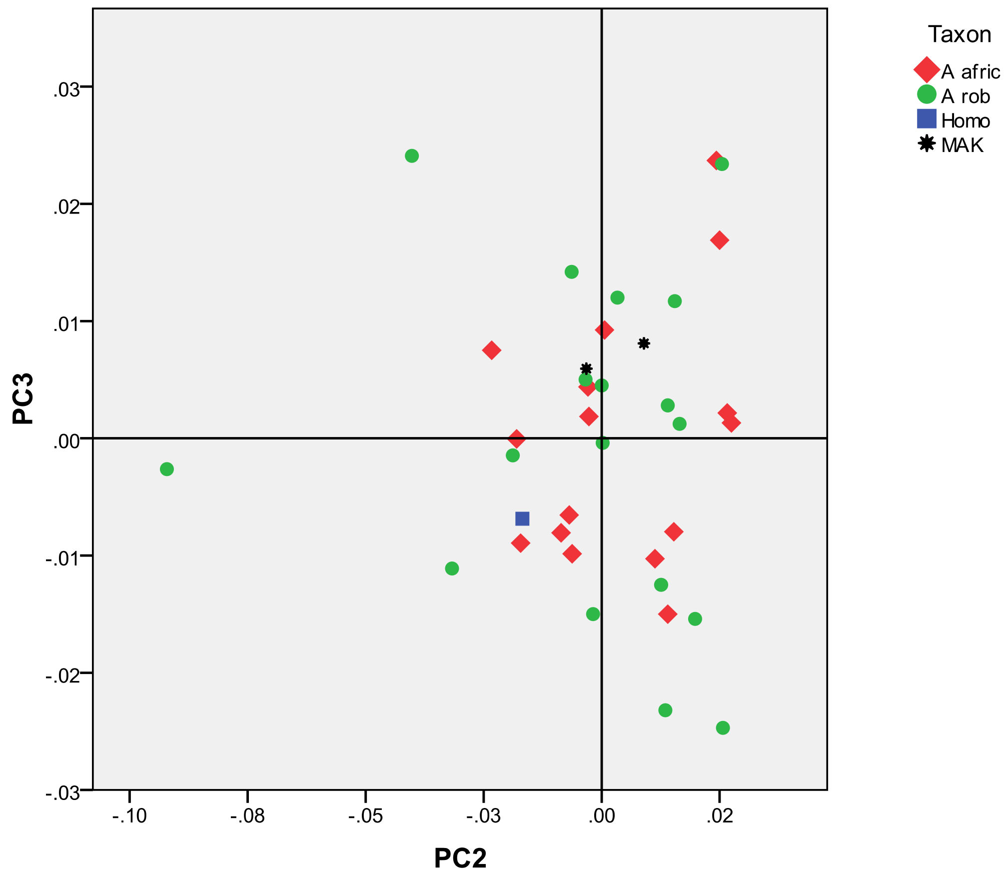
Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.05
.00
-.05
-.10
-.08
-.05
-.03
.00
.02

(c.)



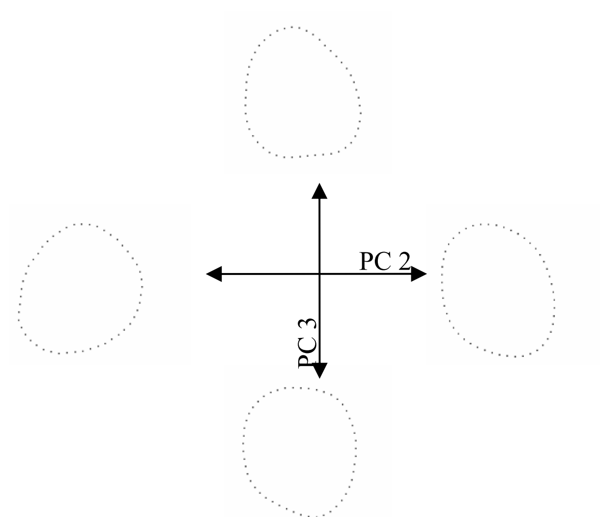
PC 1
PC 2

(d.)



Taxon
A afric
A rob
Homo
MAK
PC3
.03
.02
.01
.00
-.01
-.02
-.03
-.10
-.08
-.05
-.03
.00
.02
PC2

(e.)



PC 2
PC 3

Figure 8-38*: *Boxplot of the Centroids for P_4 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P_4 occlusal outline semi-landmark data are compared by taxon.

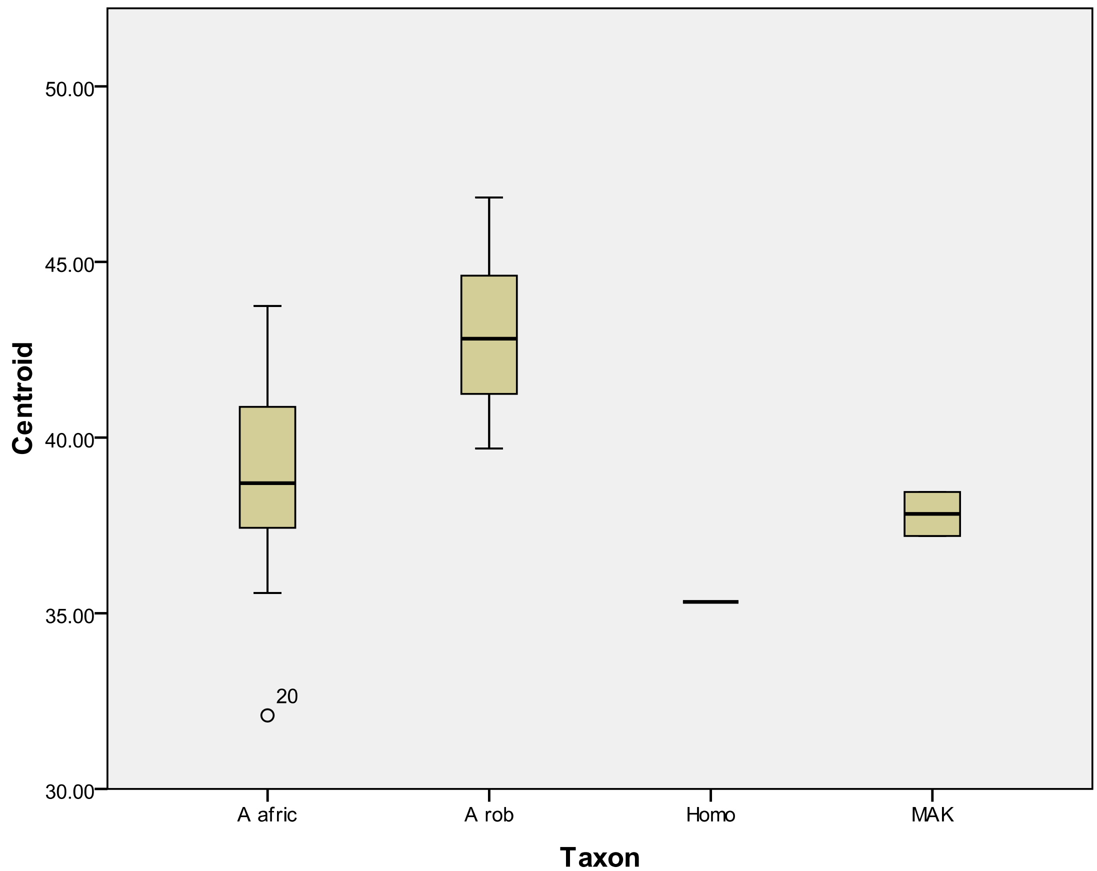
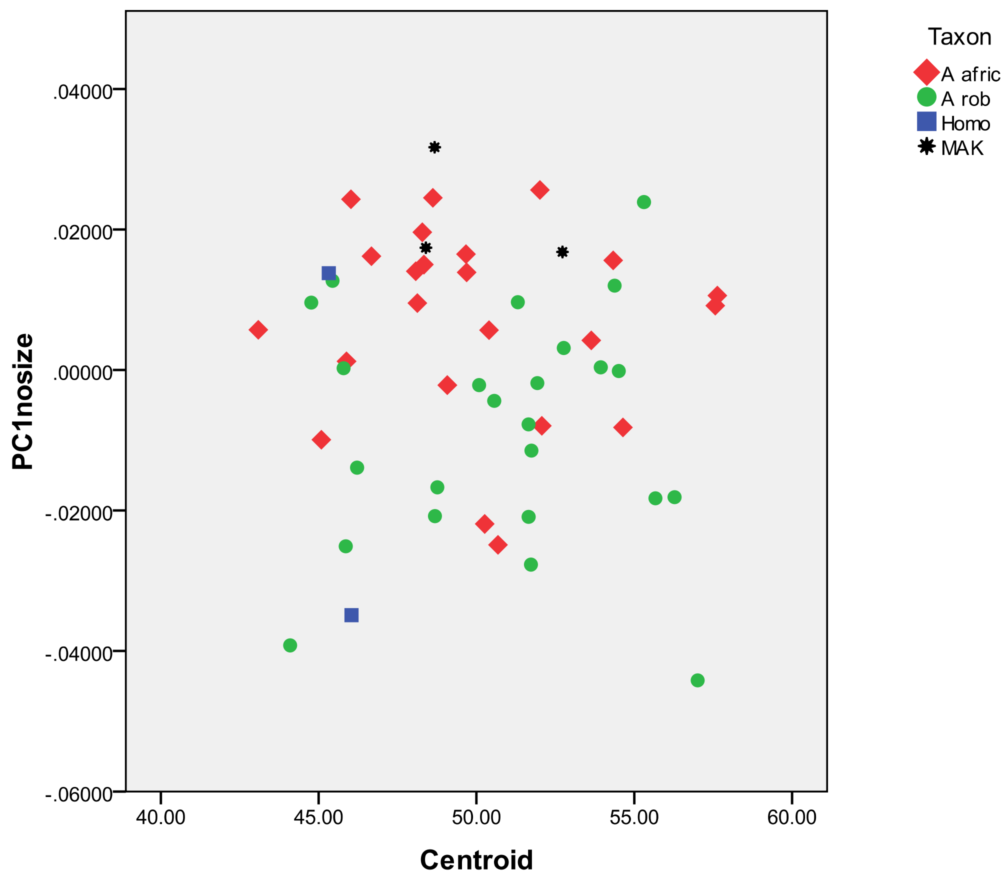
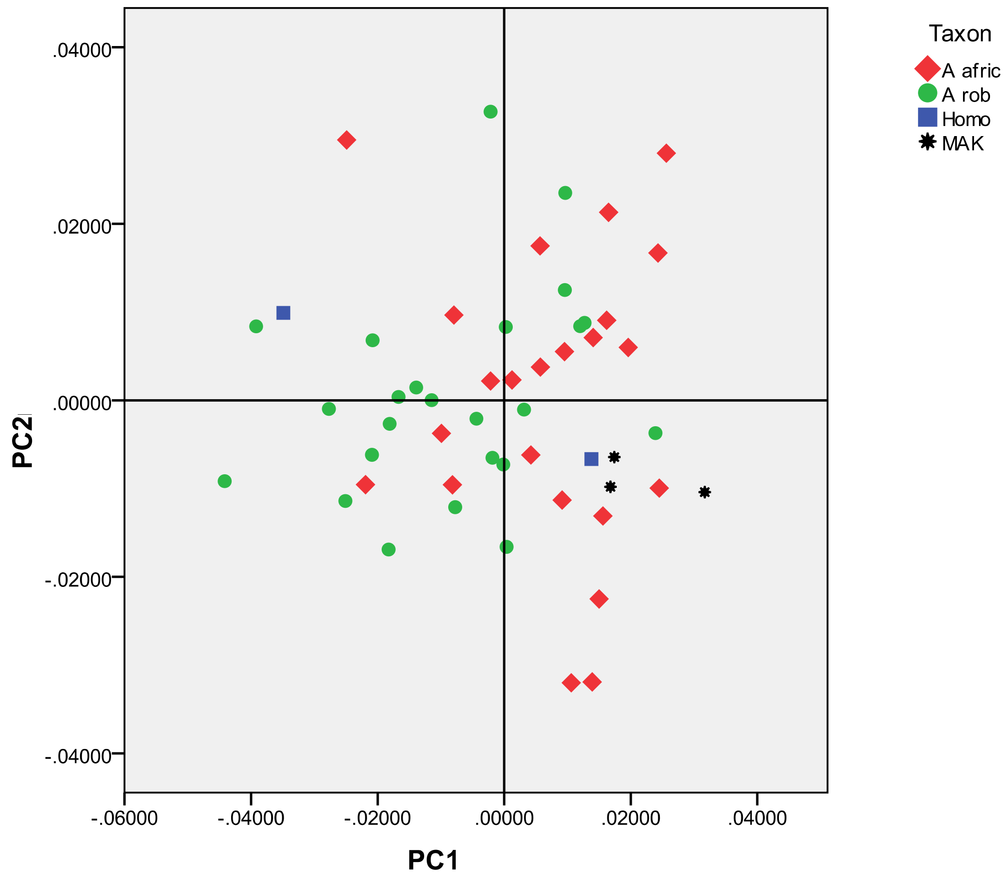


Figure 8-39*: *PCA of M₁ Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M_1 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 87%, PC 2 explains 5%, and PC 3 explains 3% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

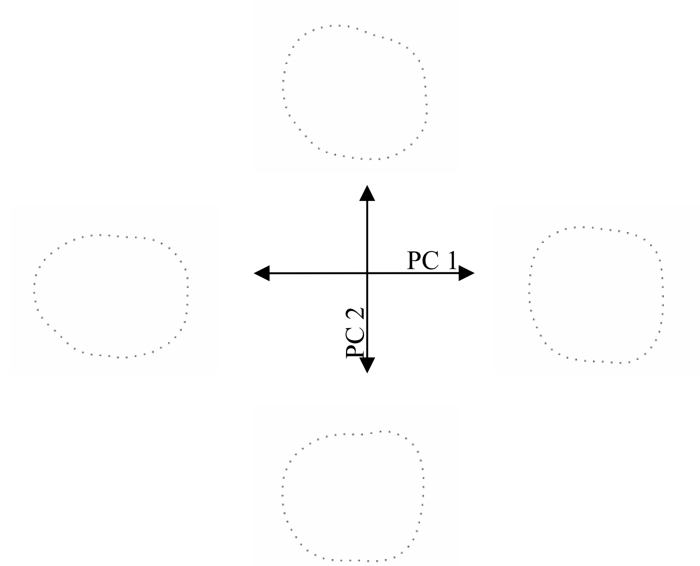


(*b.*)



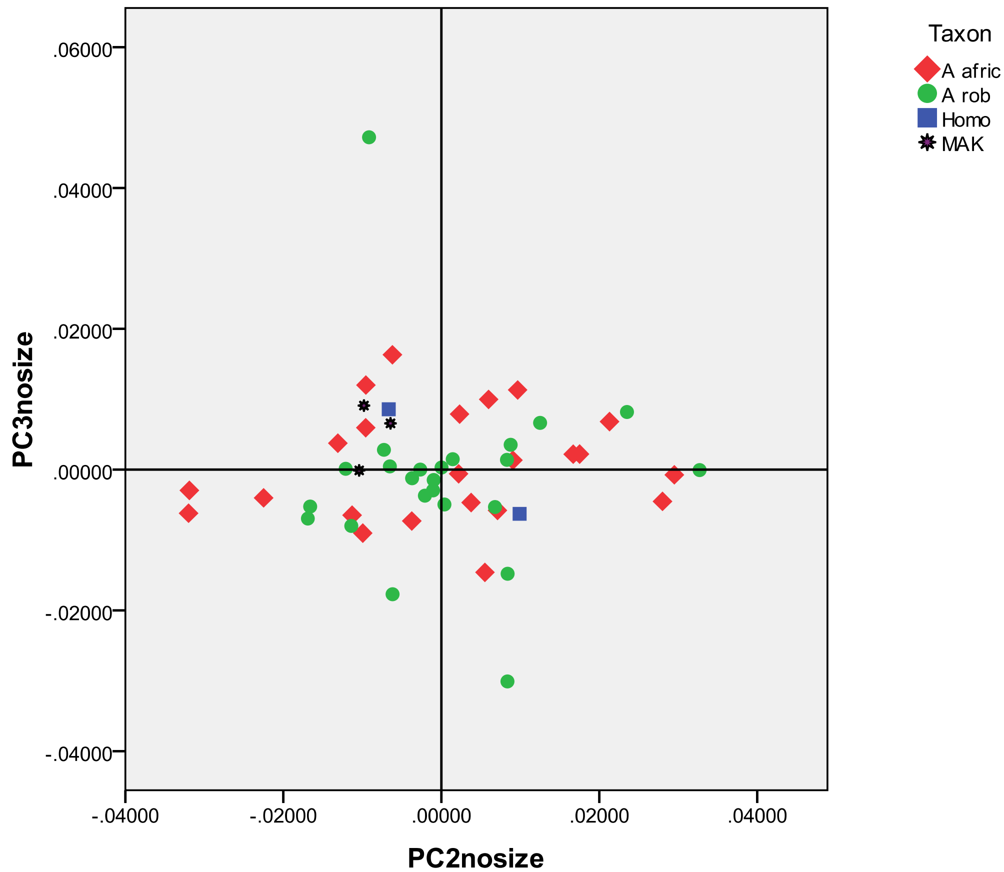
Taxon
A afric
A rob
Homo
MAK
.04000
.02000
.00000
-.02000
-.04000
PC2
-.06000
-.04000
-.02000
.00000
.02000
.04000
PC1

(*c.*)



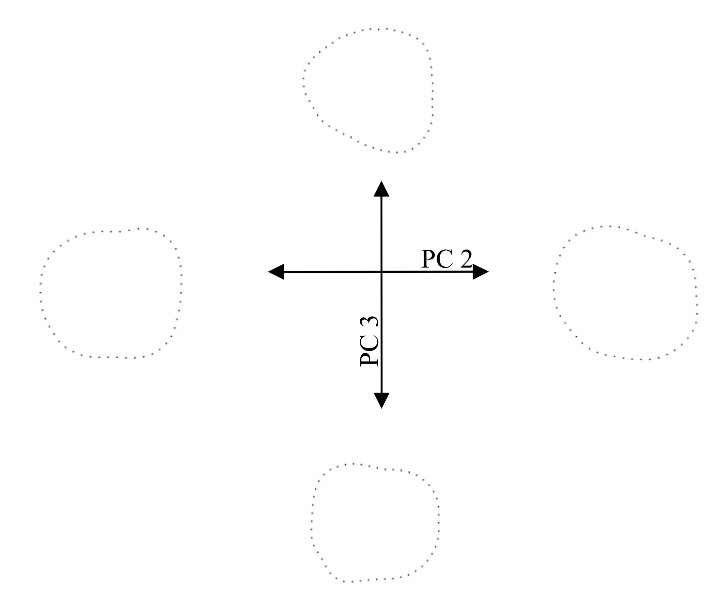
PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
.06000
.04000
.02000
.00000
-.02000
-.04000
PC3nosize
-.04000
-.02000
.00000
.02000
.04000
PC2nosize

(*e.*)



PC 2
PC 3

Figure 8-40*: *Boxplot of the Centroids for M_1 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M_1 occlusal outline semi-landmark data are compared by taxon.

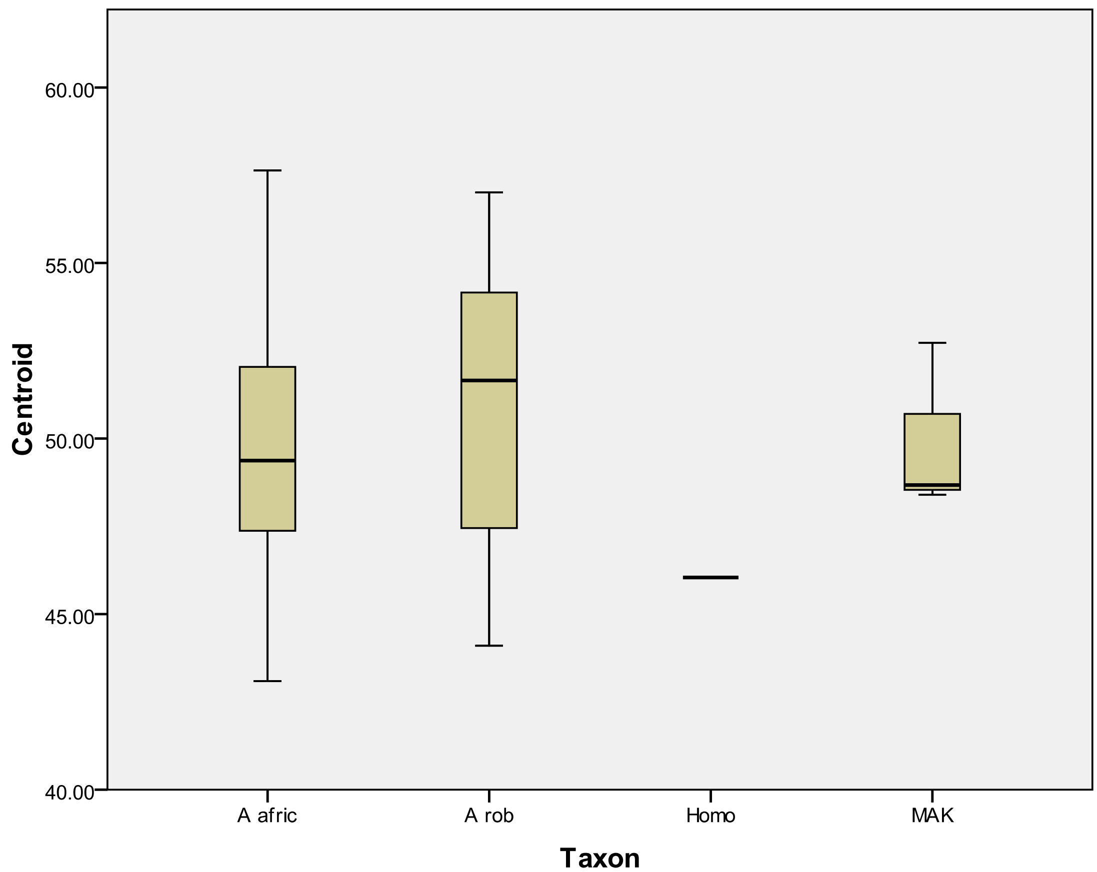
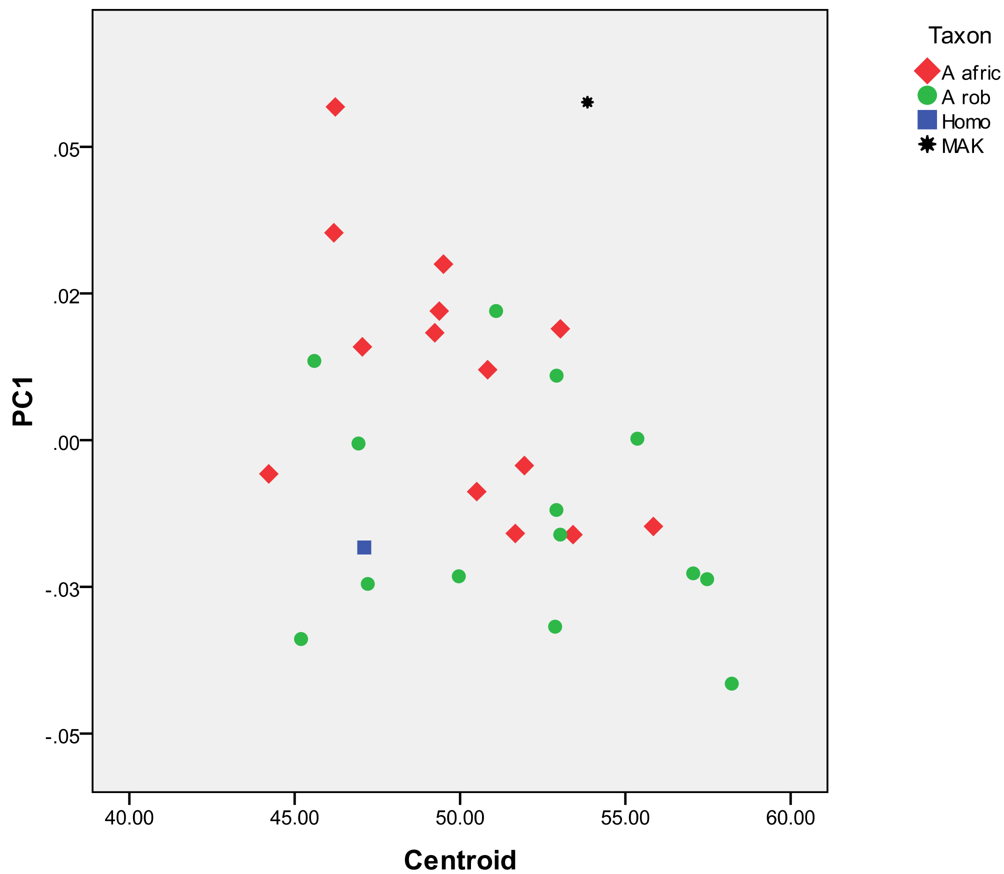
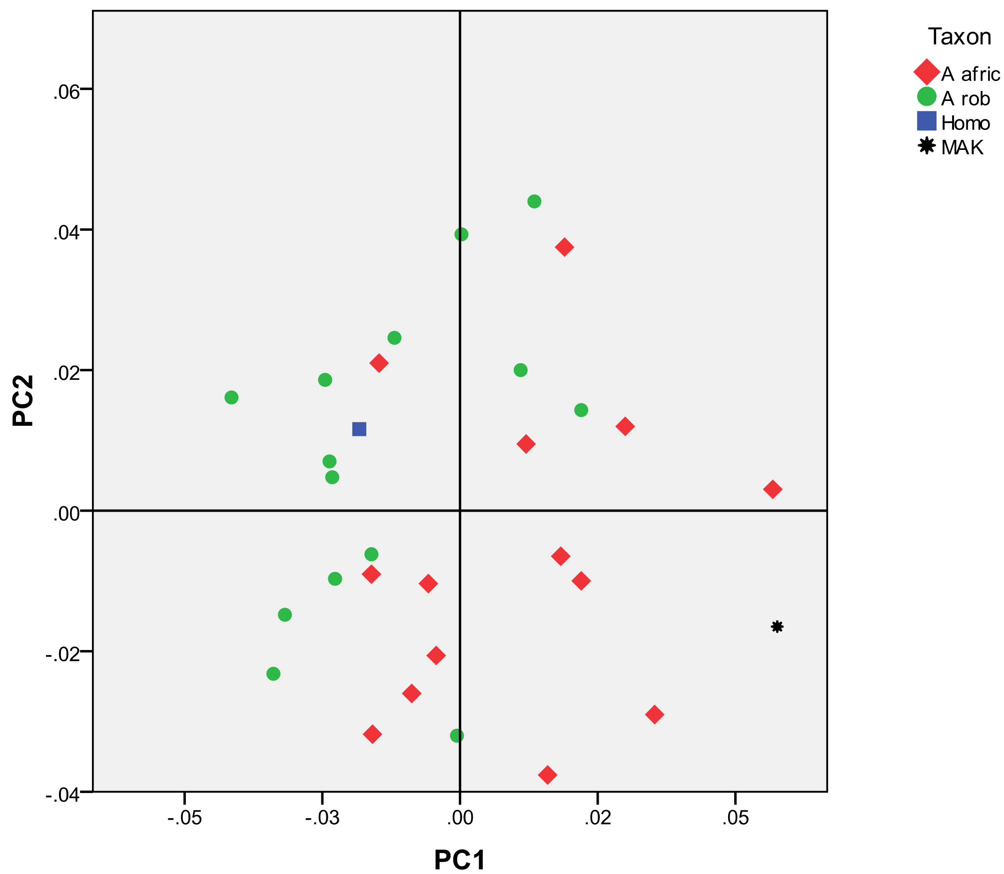


Figure 8-41*: *PCA of M_1 Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the M_1 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 27%, PC 2 explains 21%, and PC 3 explains 12% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

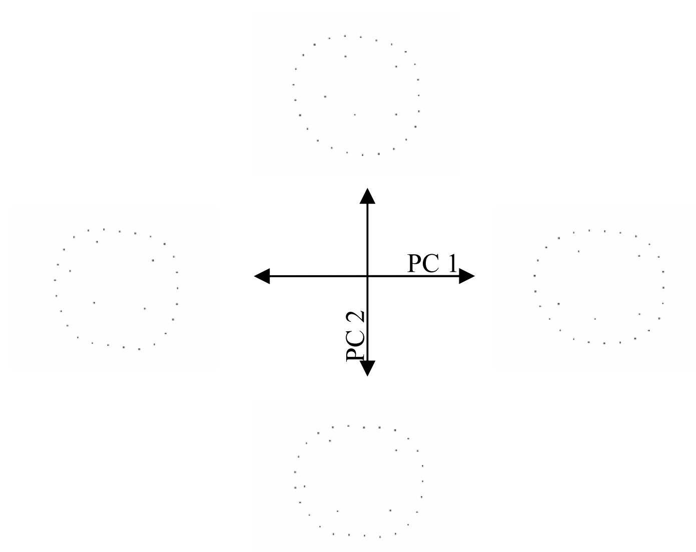
(*a*.)



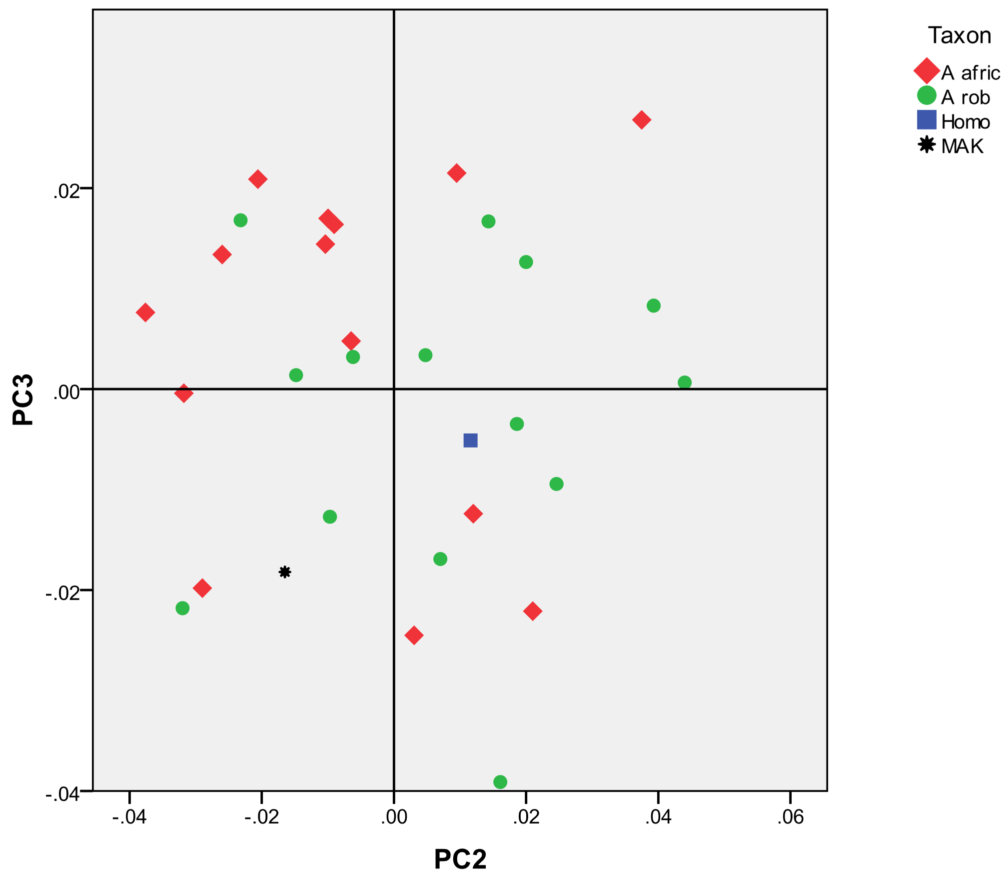
(b.)


Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.06
.04
.02
.00
-.02
-.04
-.05
-.03
.00
.02
.05

(c.)


PC 1
PC 2

(d.)


Taxon
A afric
A rob
Homo
MAK
PC3
.02
.00
-.02
-.04
-.04
-.02
.00
.02
.04
.06
PC2

(e.)

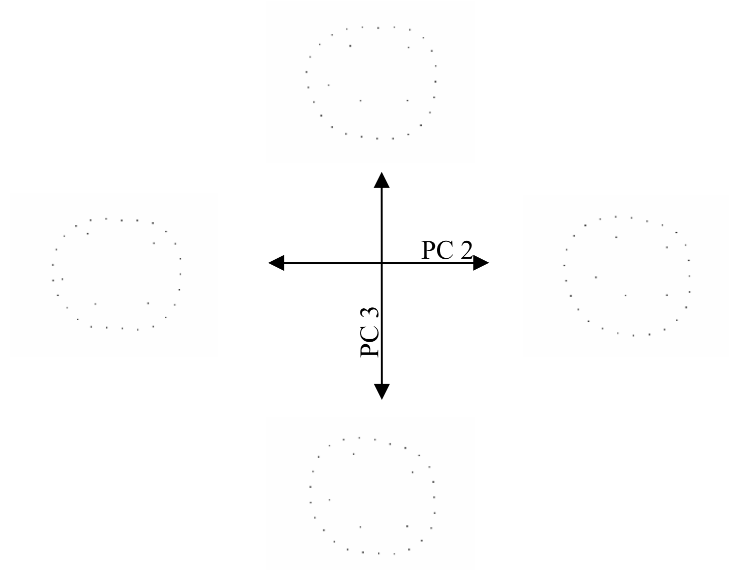

PC 2
PC 3

Figure 8-42*: *Boxplot of the Centroids for M_1 Occlusal Outline Semi-landmark and Cusp Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M_1 occlusal outline semi-landmark and cusp landmark data are compared by taxon.

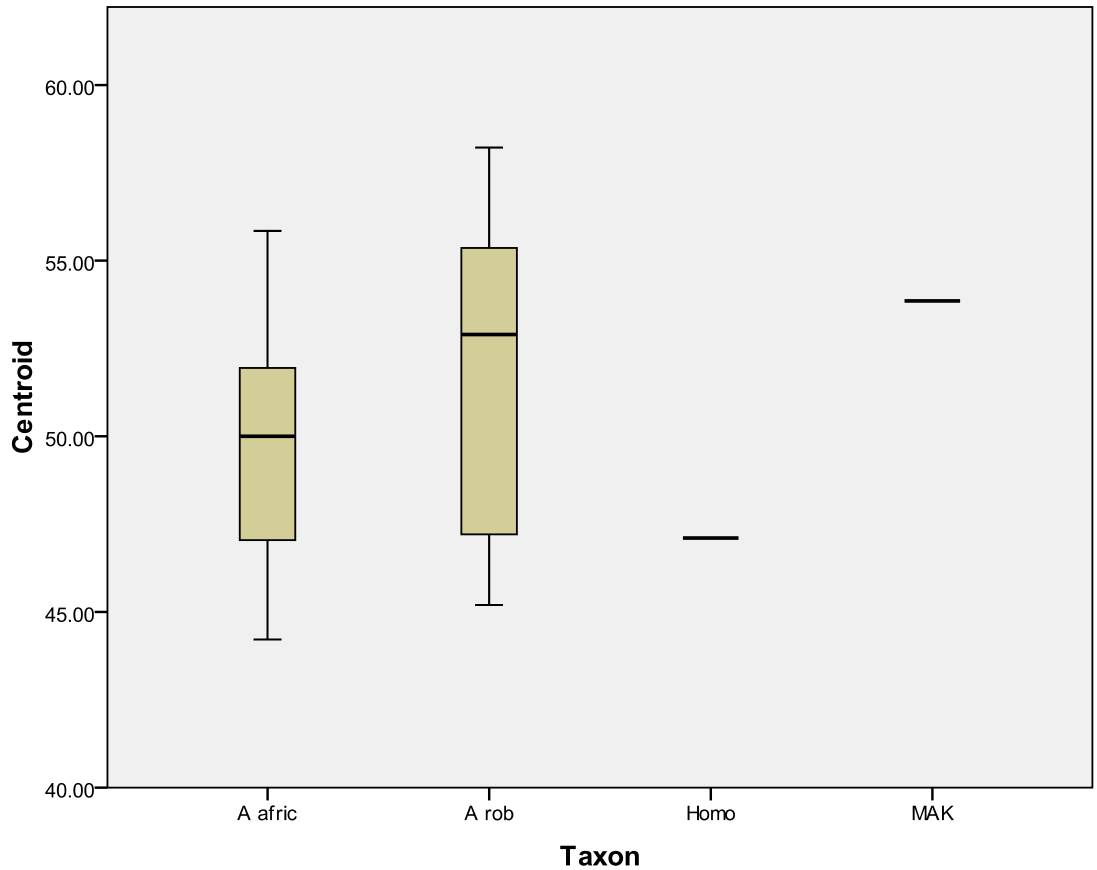
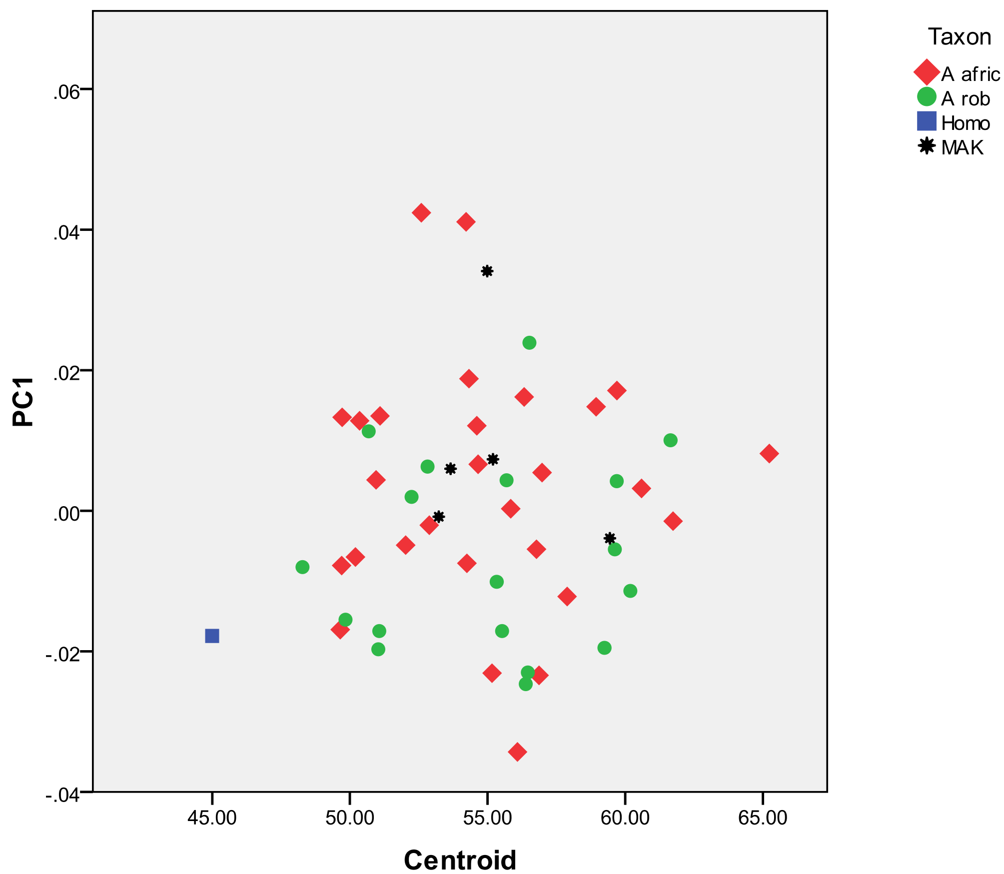
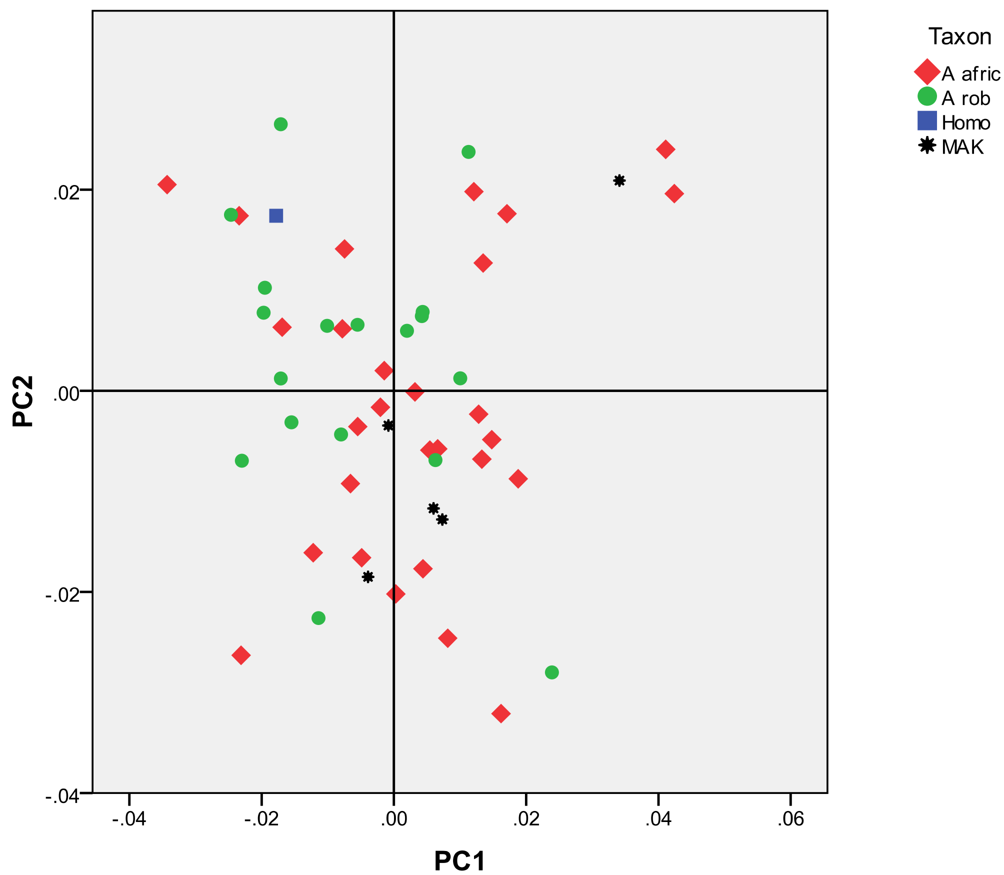


Figure 8-43*: *PCA of M_2 Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M_1 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 33%, PC 2 explains 28%, and PC 3 explains 10% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

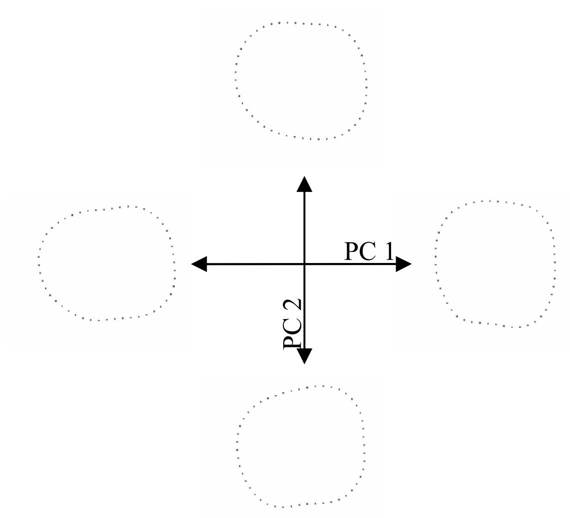
(*a*.)



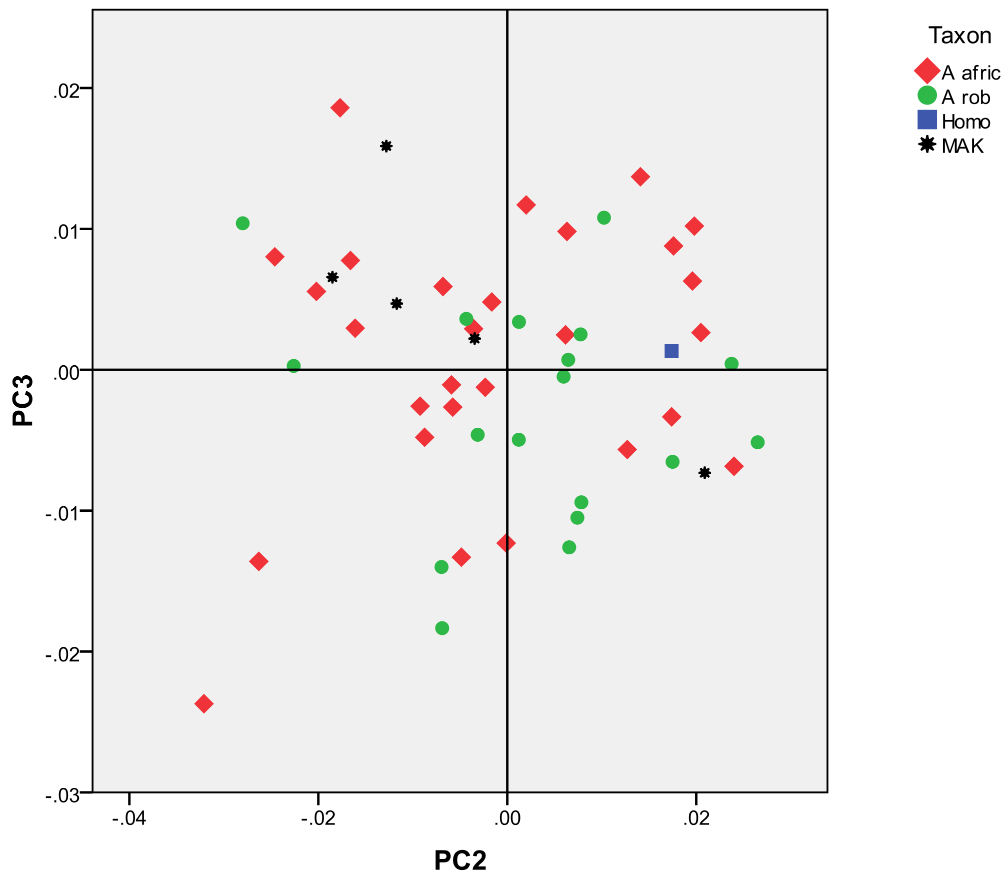
(b.)


Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.02
.00
-.02
-.04
-.04
-.02
.00
.02
.04
.06

(c.)

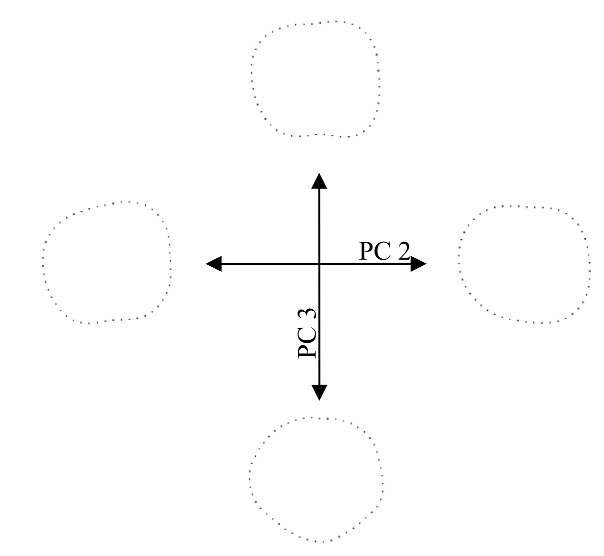

PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
.02
.01
.00
-.01
-.02
-.03
PC3
-.04
-.02
.00
.02
PC2

(*e.*)



PC 2
PC 3

Figure 8-44**: *Boxplot of the Centroids for M_2 Occlusal Outline Semi-landmark Landmark Data.*** The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M_2 occlusal outline semi-landmark data are compared by taxon.

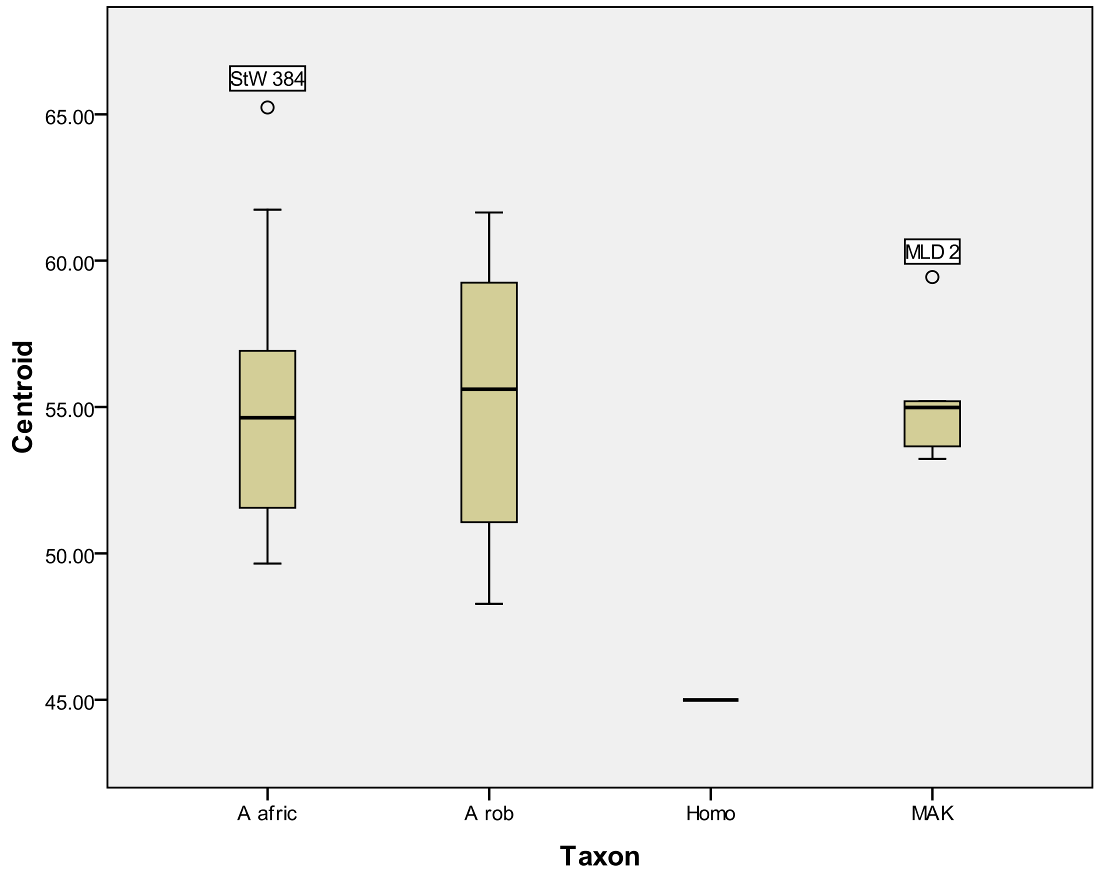
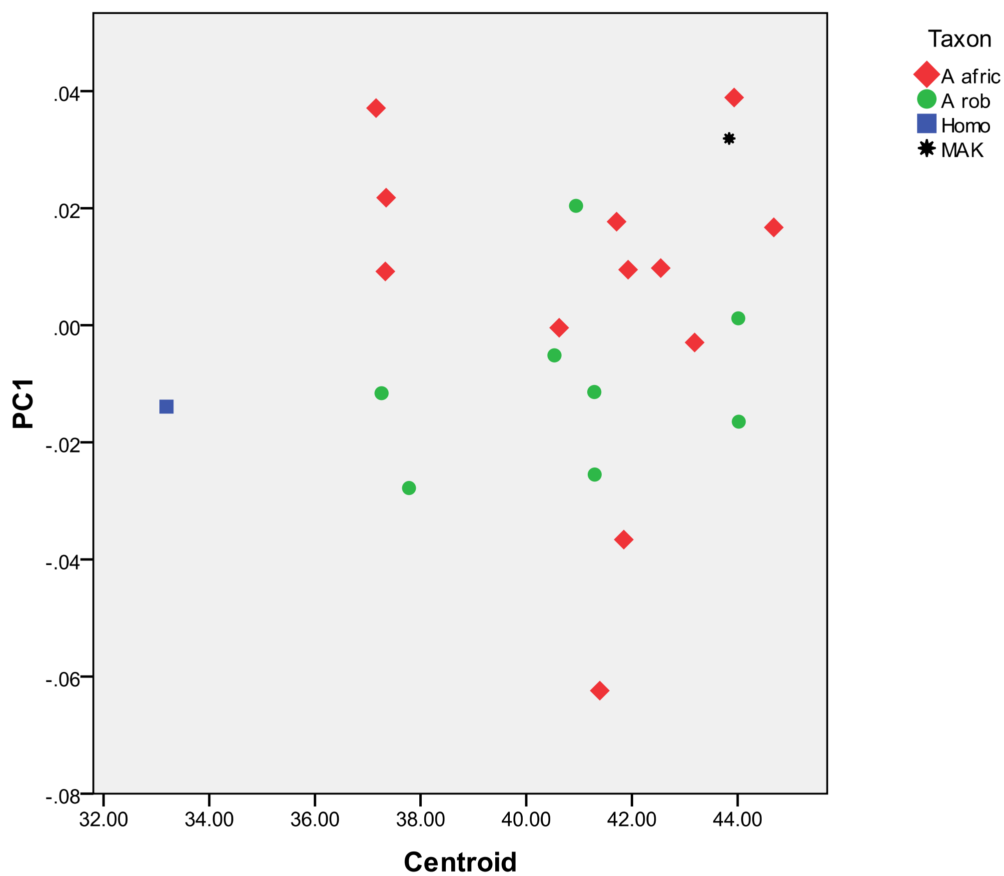
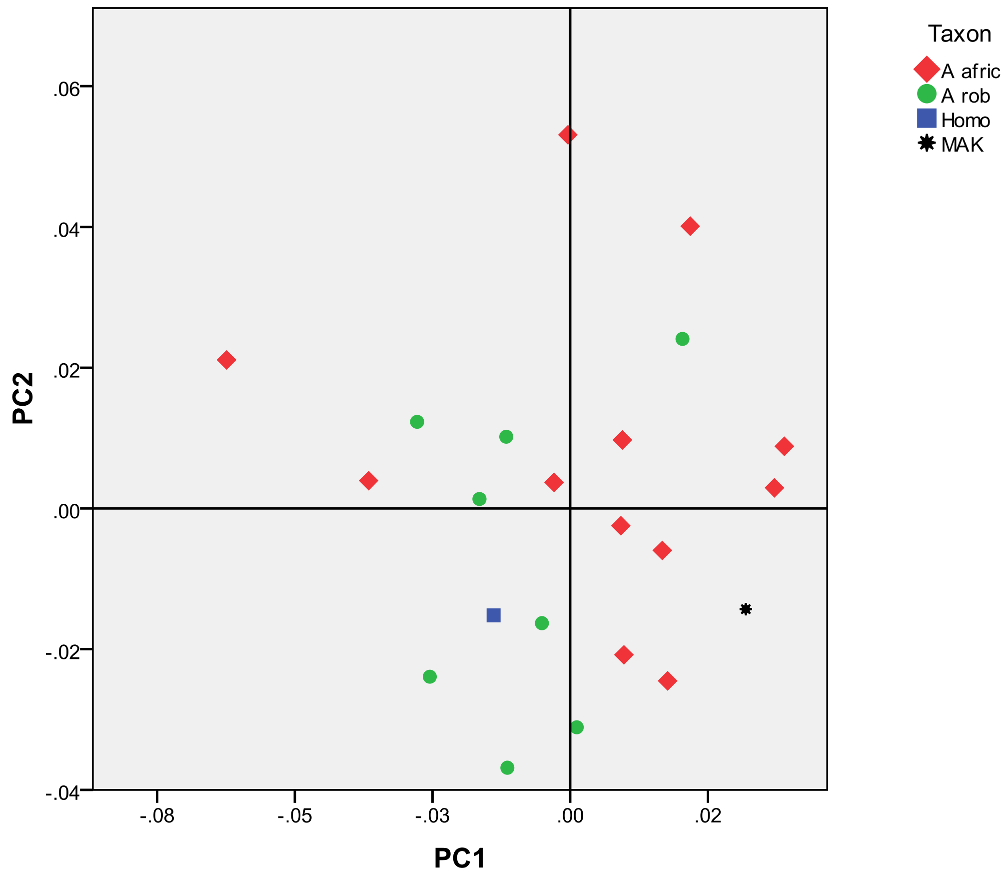


Figure 8-45*: *PCA of M_2 Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the M_2 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 26%, PC 2 explains 21%, and PC 3 explains 13% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

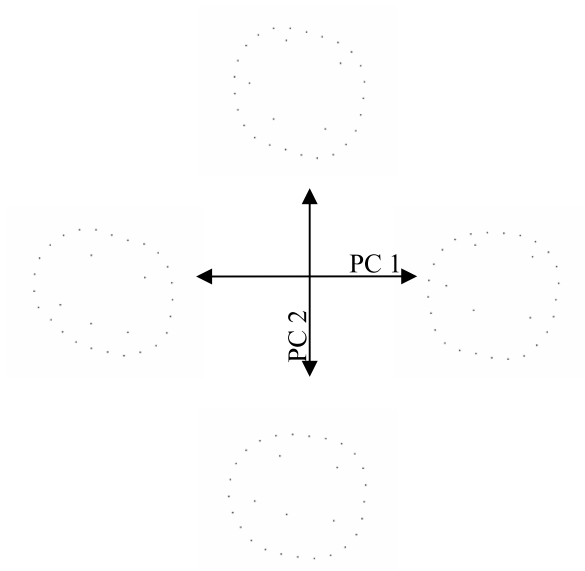
(*a*.)



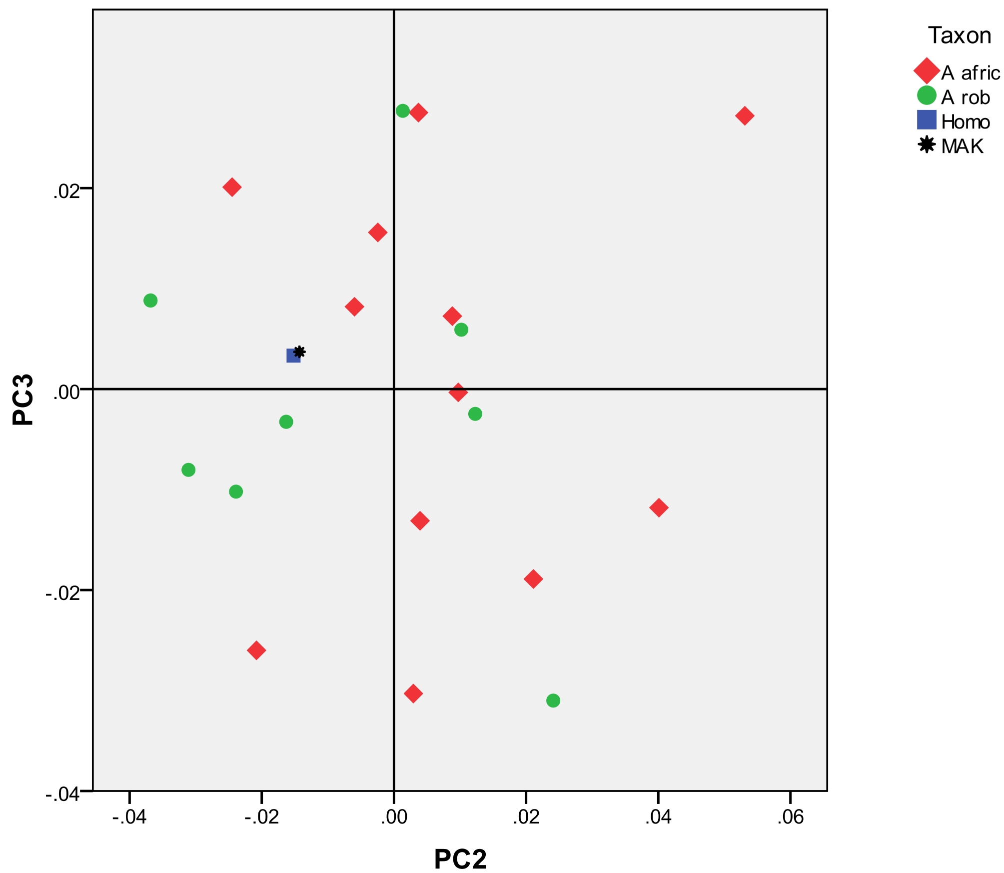
(*b.*)


Taxon
A afric
A rob
Homo
MAK
.06
.04
.02
.00
-.02
-.04
PC2
-.08
-.05
-.03
.00
.02
PC1

(*c.*)


PC 1
PC 2

(d.)


Taxon
A afric
A rob
Homo
MAK
.02
.00
-.02
-.04
PC3
-.04
-.02
.00
.02
.04
.06
PC2

(e.)

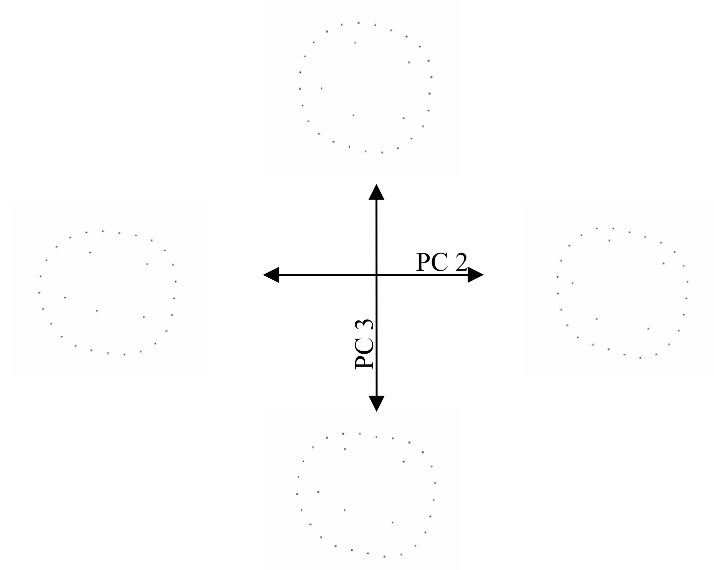

PC 2
PC 3

Figure 8-46*: *Boxplot of the Centroids for M_2 Occlusal Outline Semi-landmark and Cusp Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M_2 occlusal outline semi-landmark and cusp landmark data are compared by taxon.

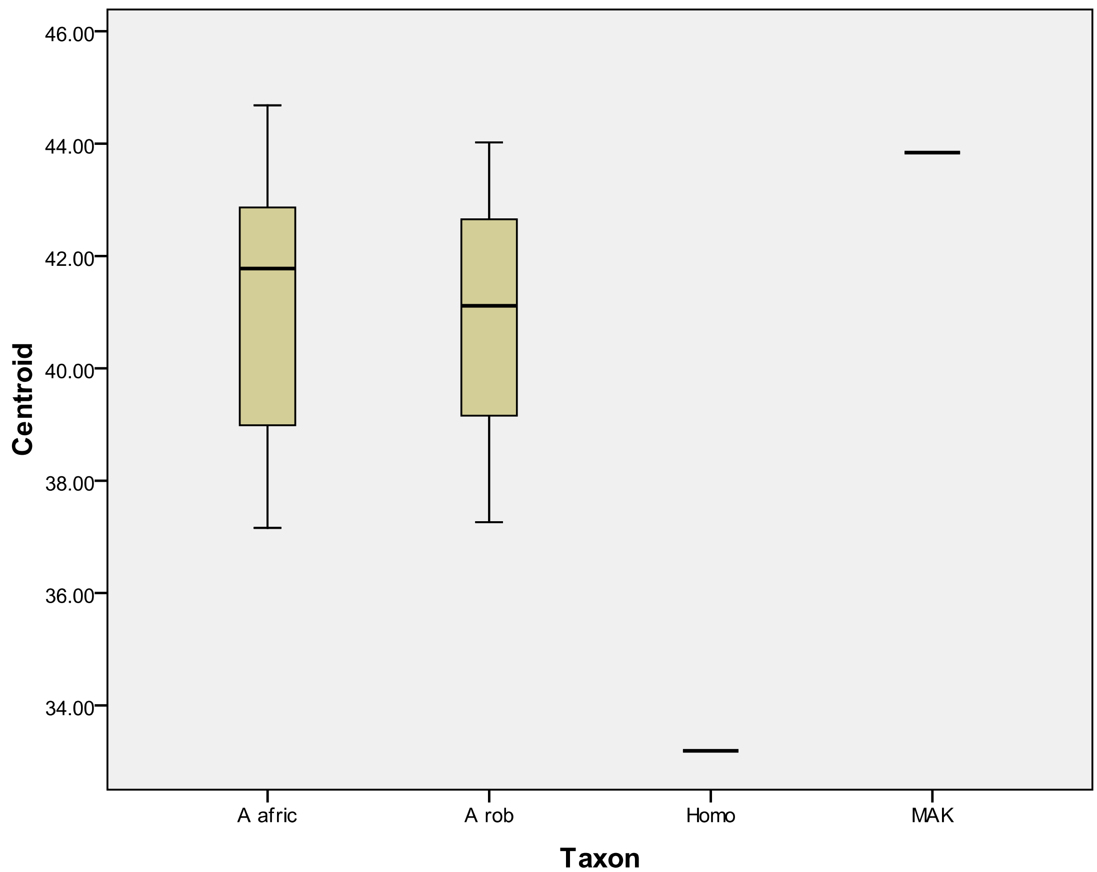
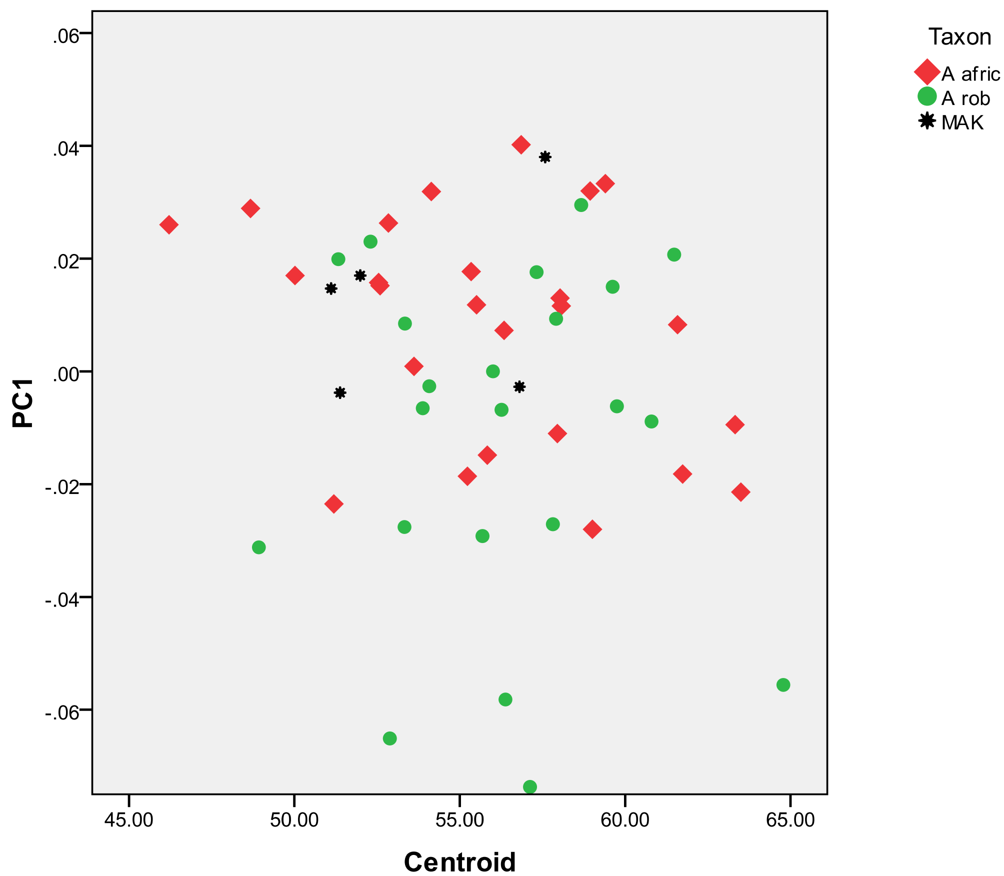
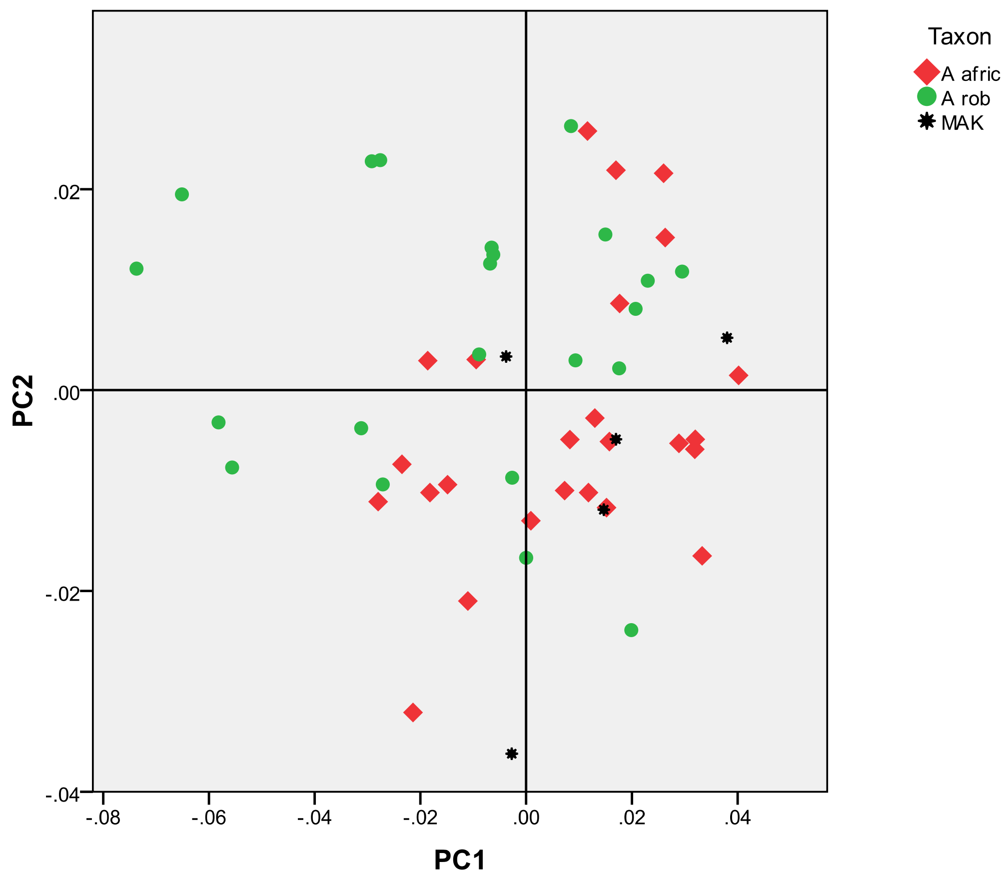


Figure 8-47*: *PCA of M_3 Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M_3 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 51%, PC 2 explains 15%, and PC 3 explains 11% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

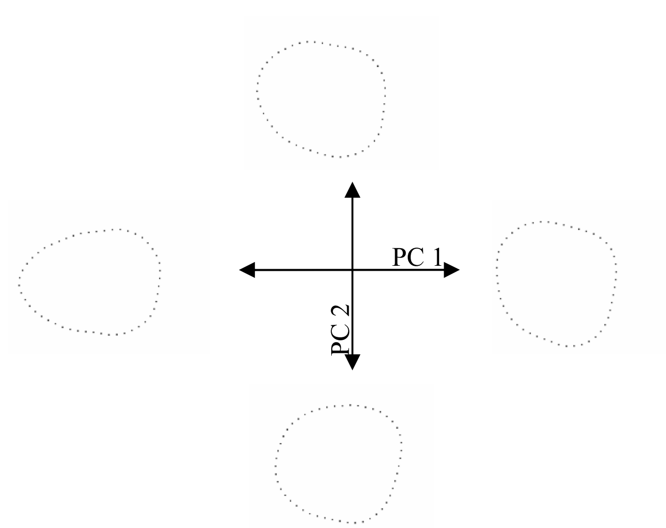
(*a*.)



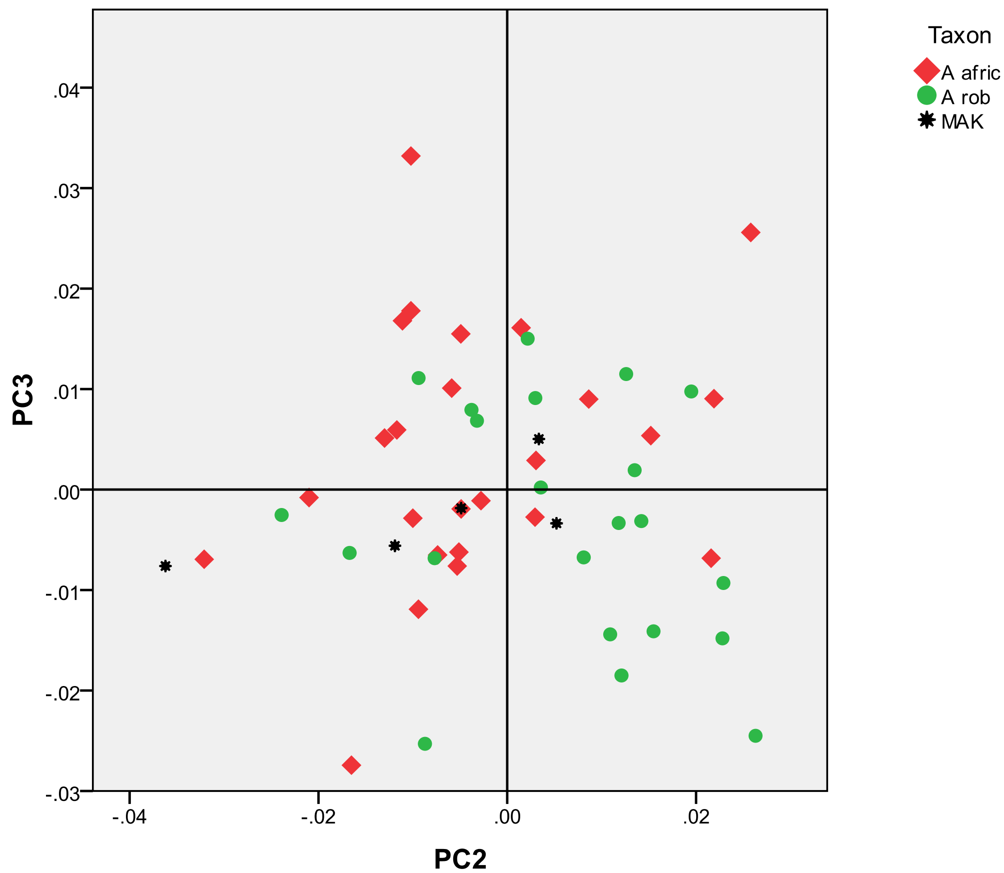
(b.)


Taxon
A afric
A rob
MAK
PC2
PC1
.02
.00
-.02
-.04
-.08
-.06
-.04
-.02
.00
.02
.04

(c.)

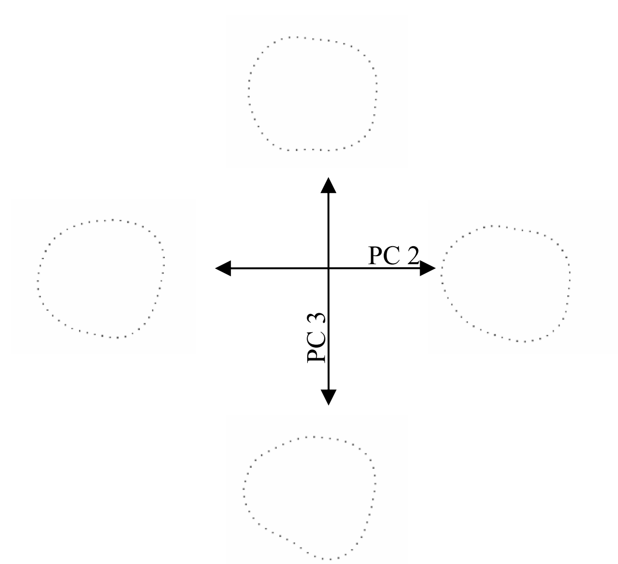

PC 1
PC 2

(d.)



Taxon
A afric
A rob
MAK
PC3
.04
.03
.02
.01
.00
-.01
-.02
-.03
-.04
-.02
.00
.02
PC2

(e.)



PC 2
PC 3

Figure 8-48*: *Boxplot of the Centroids for M_3 Occlusal Outline Semi-landmark Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M_3 occlusal outline semi-landmark data are compared by taxon.

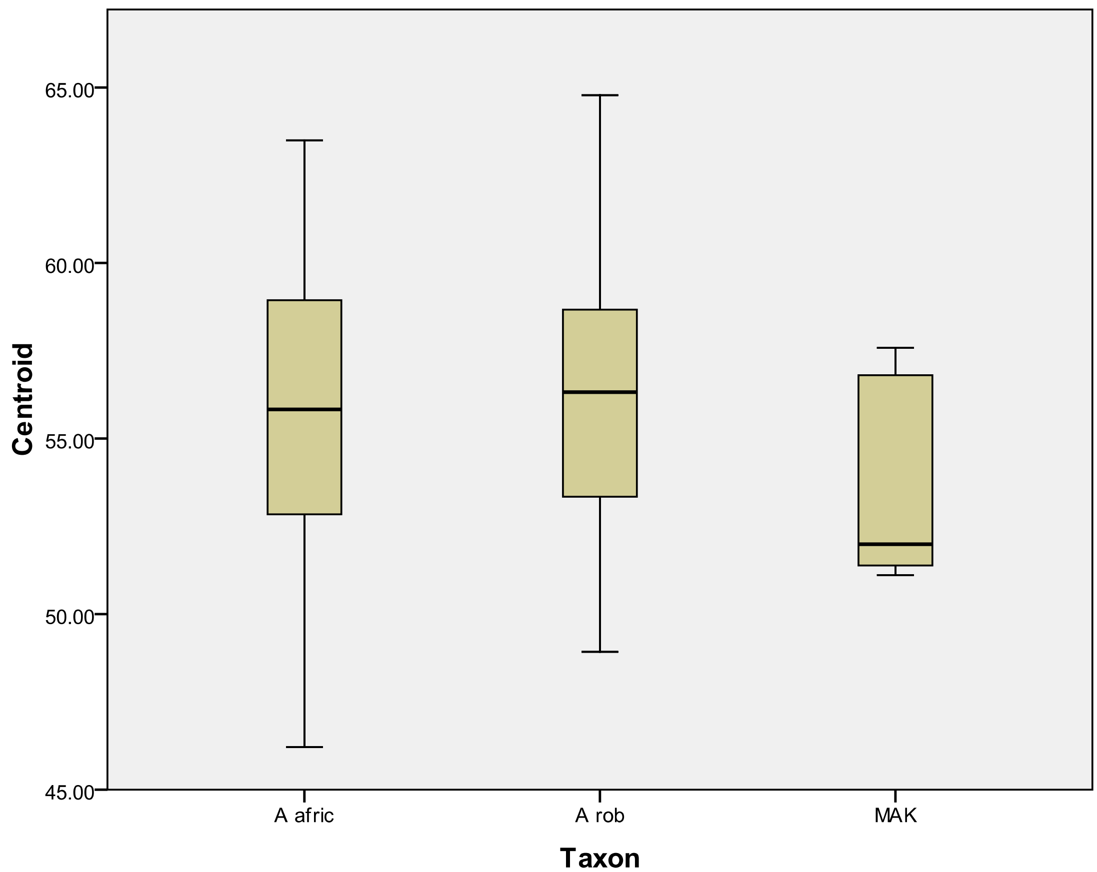
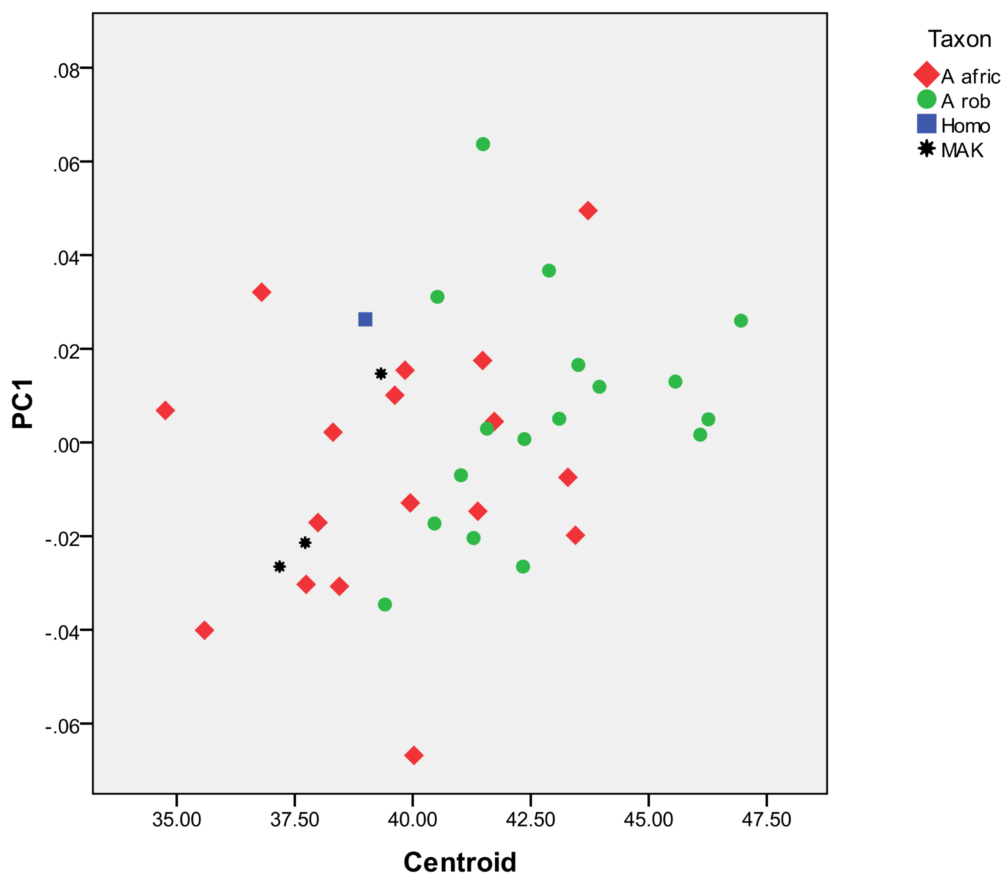
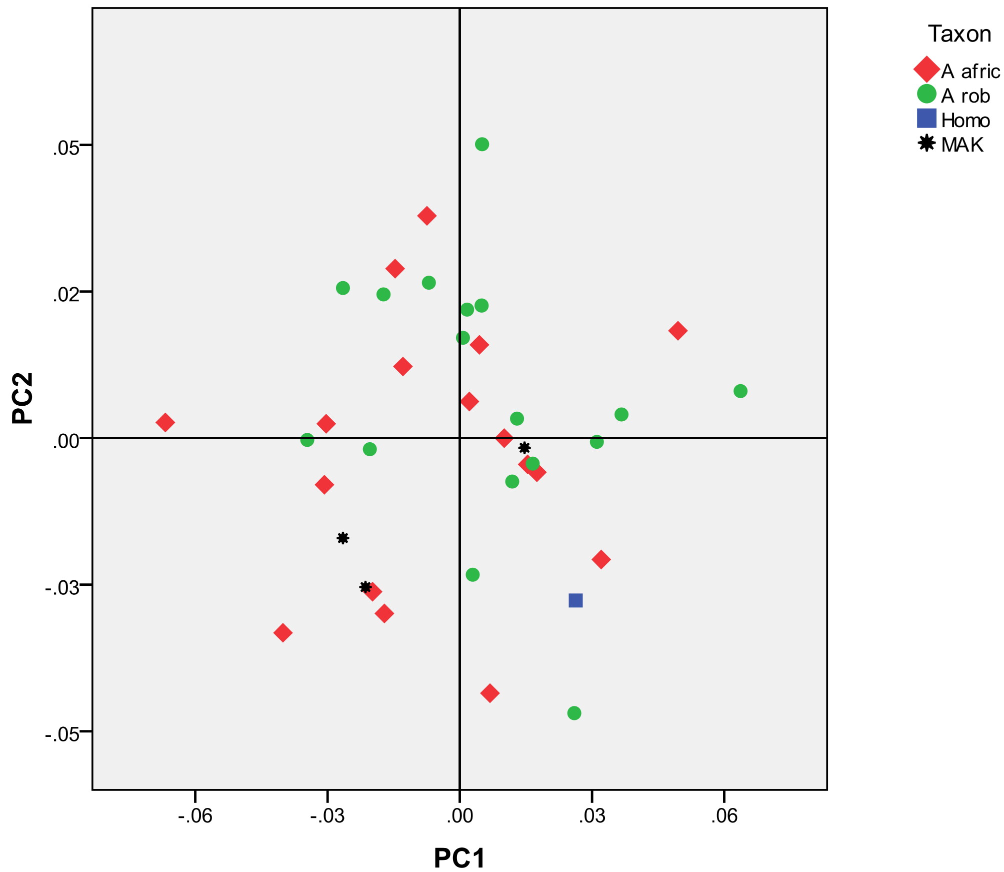


Figure 8-49*: *PCA of P³ Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the P³ semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 37%, PC 2 explains 27%, and PC 3 explains 15% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

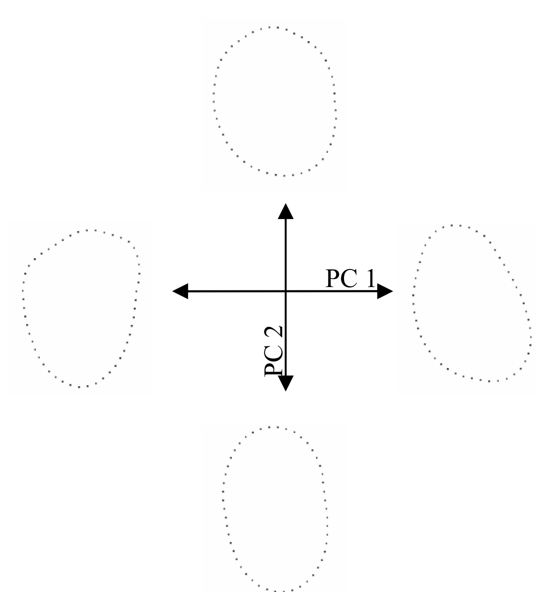


(*b.*)



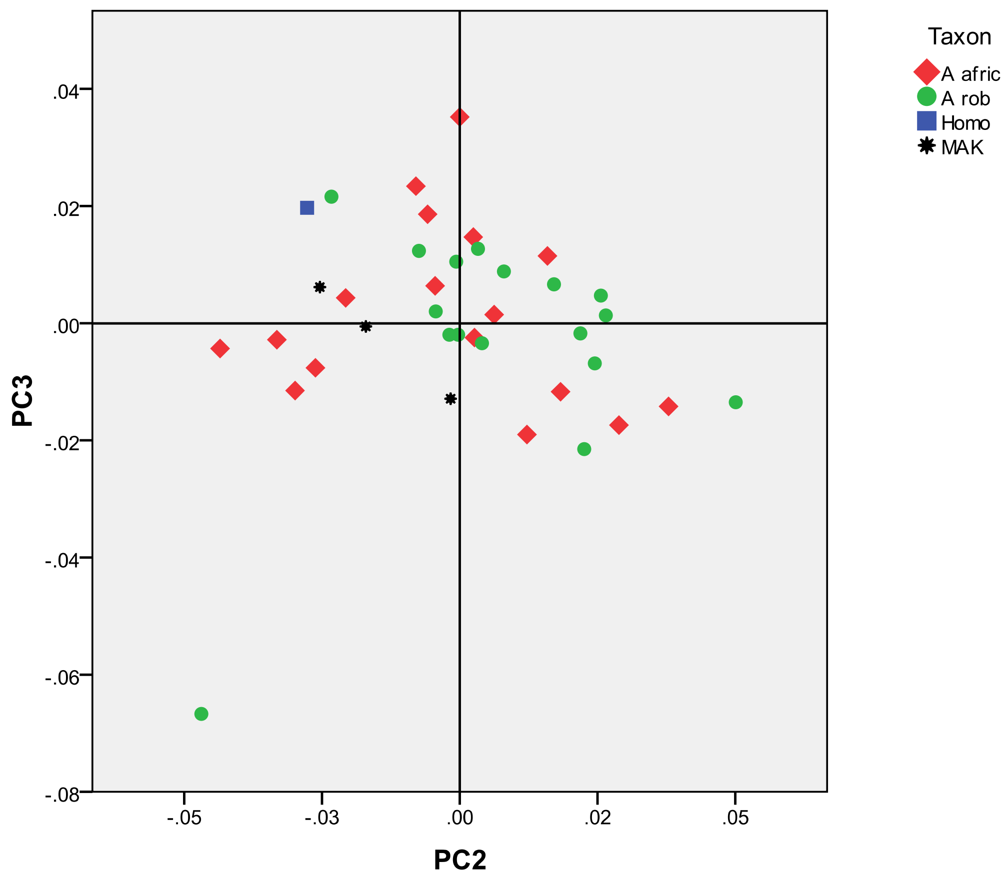
Taxon
A afric
A rob
Homo
MAK
PC2
.05
.02
.00
-.03
-.05
-.06
-.03
.00
.03
.06
PC1

(*c.*)



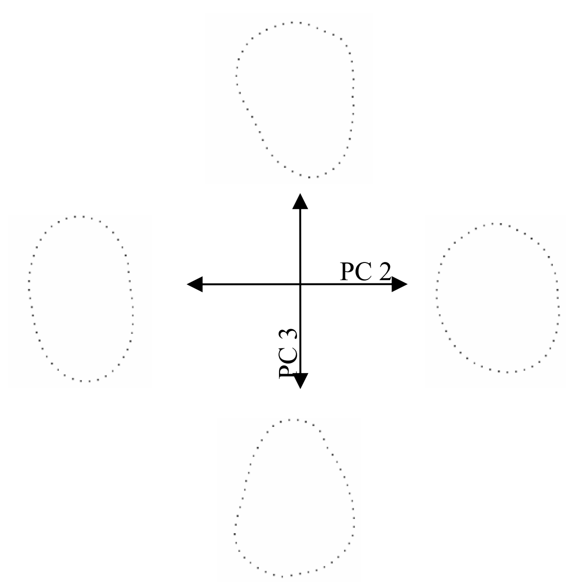
PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
.04
.02
.00
-.02
-.04
-.06
-.08
PC3
-.05
-.03
.00
.02
.05
PC2

(*e.*)



PC 2
PC 3

Figure 8-50*: *Boxplot of the Centroids for P^3 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P^3 occlusal outline semi-landmark data are compared by taxon.

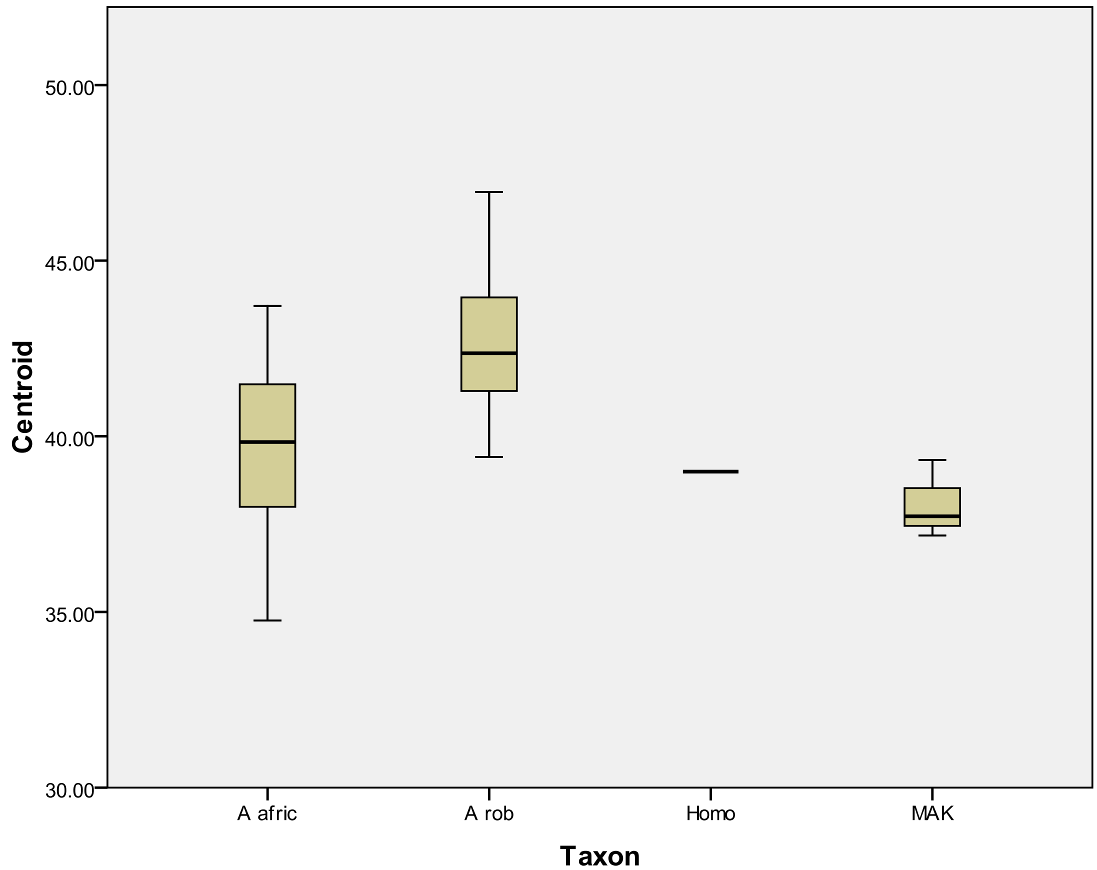
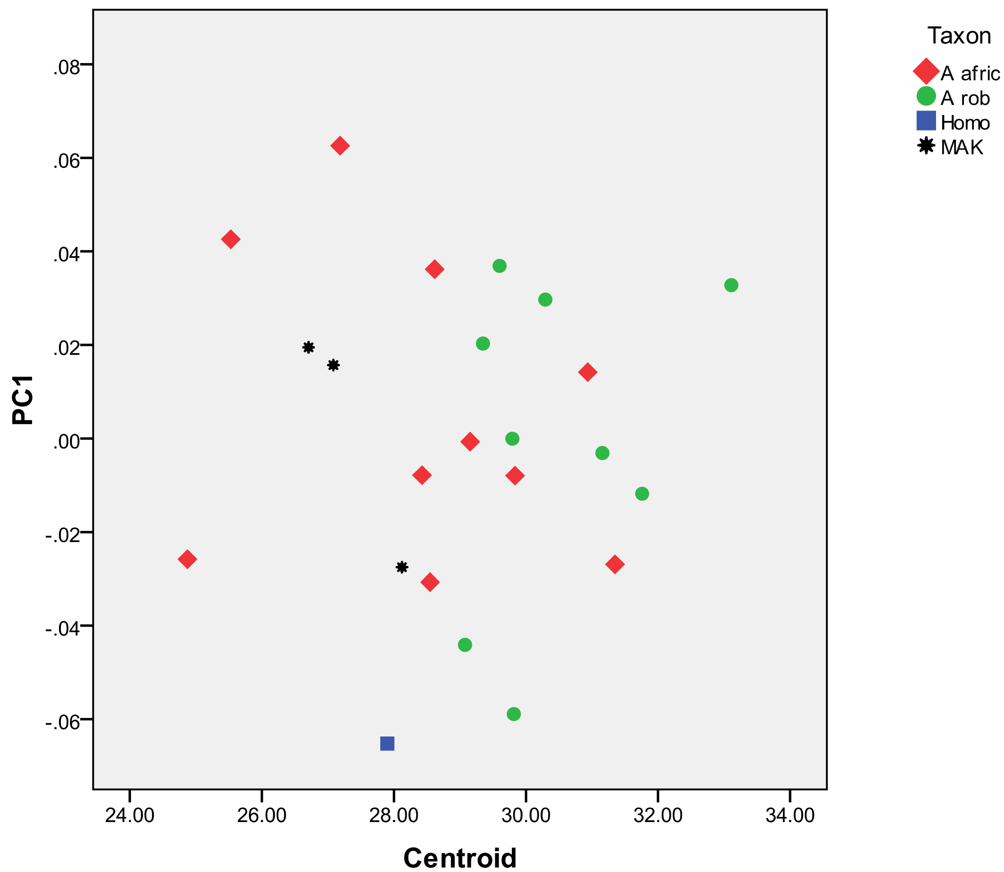
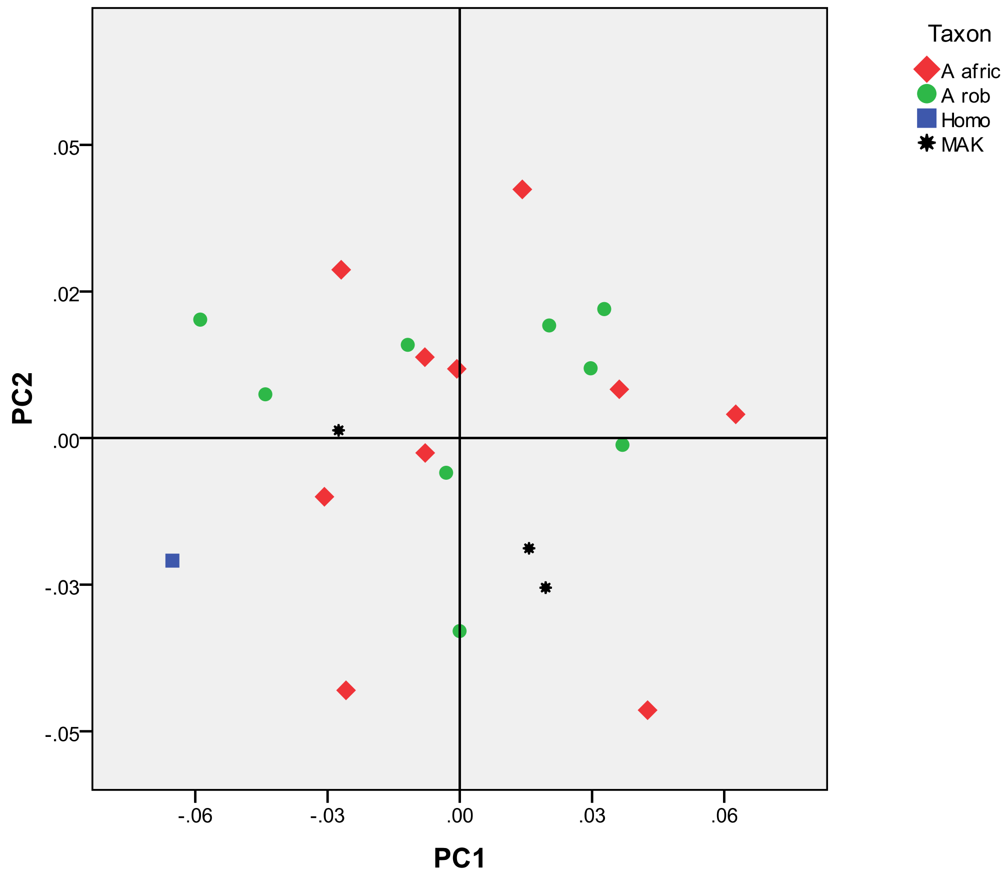


Figure 8-51*: *PCA of P³ Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the P^3 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 39%, PC 2 explains 18%, and PC 3 explains 11% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

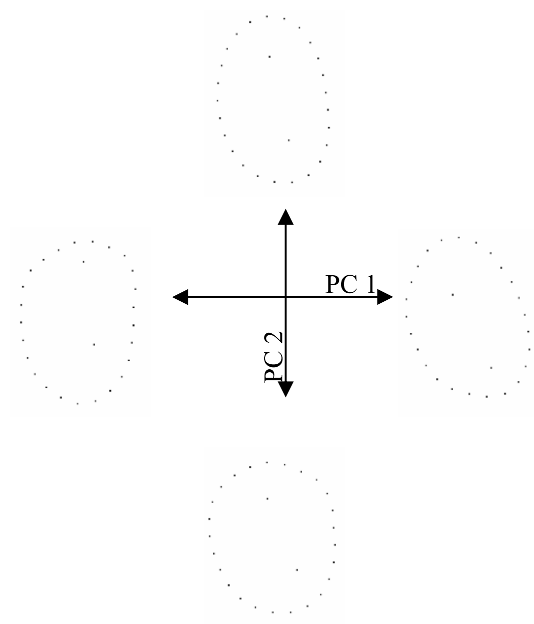


(*b.*)



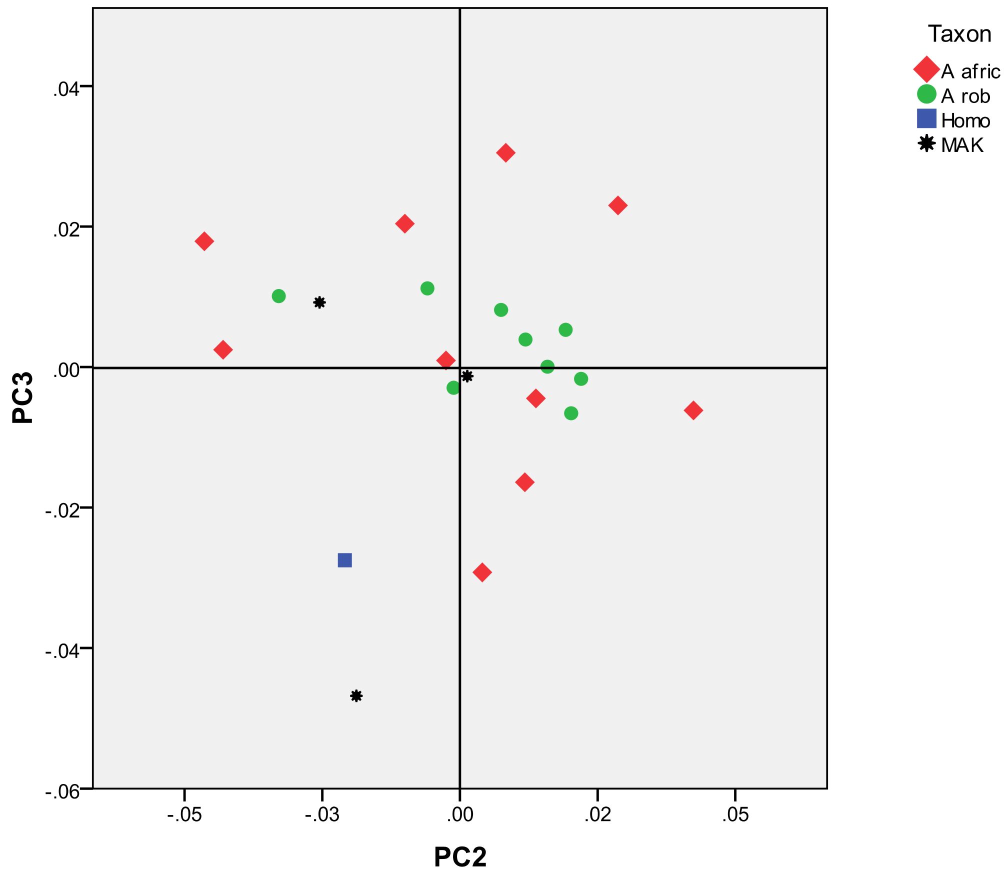
Taxon
A afric
A rob
Homo
MAK
.05
.02
.00
-.03
-.05
PC2
-.06
-.03
.00
.03
.06
PC1

(*c.*)



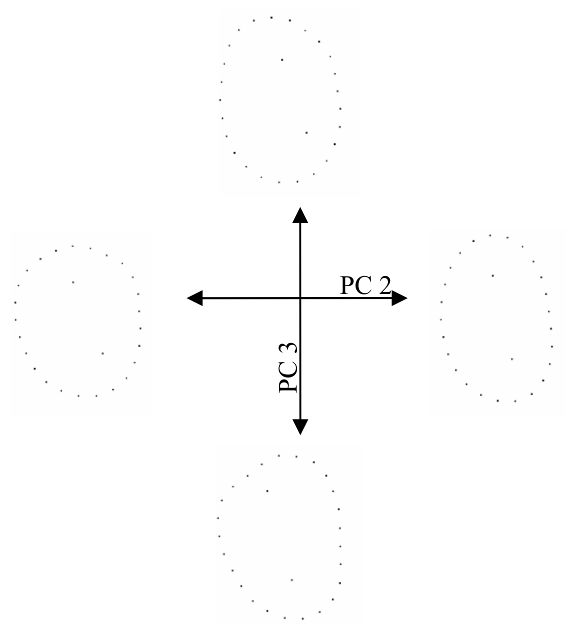
PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
PC3
.04
.02
.00
-.02
-.04
-.06
-.05
-.03
.00
.02
.05
PC2

(*e.*)



PC 2
PC 3

Figure 8-52*: *Boxplot of the Centroids for P^3^ Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P**3** occlusal outline semi-landmark data are compared by taxon.

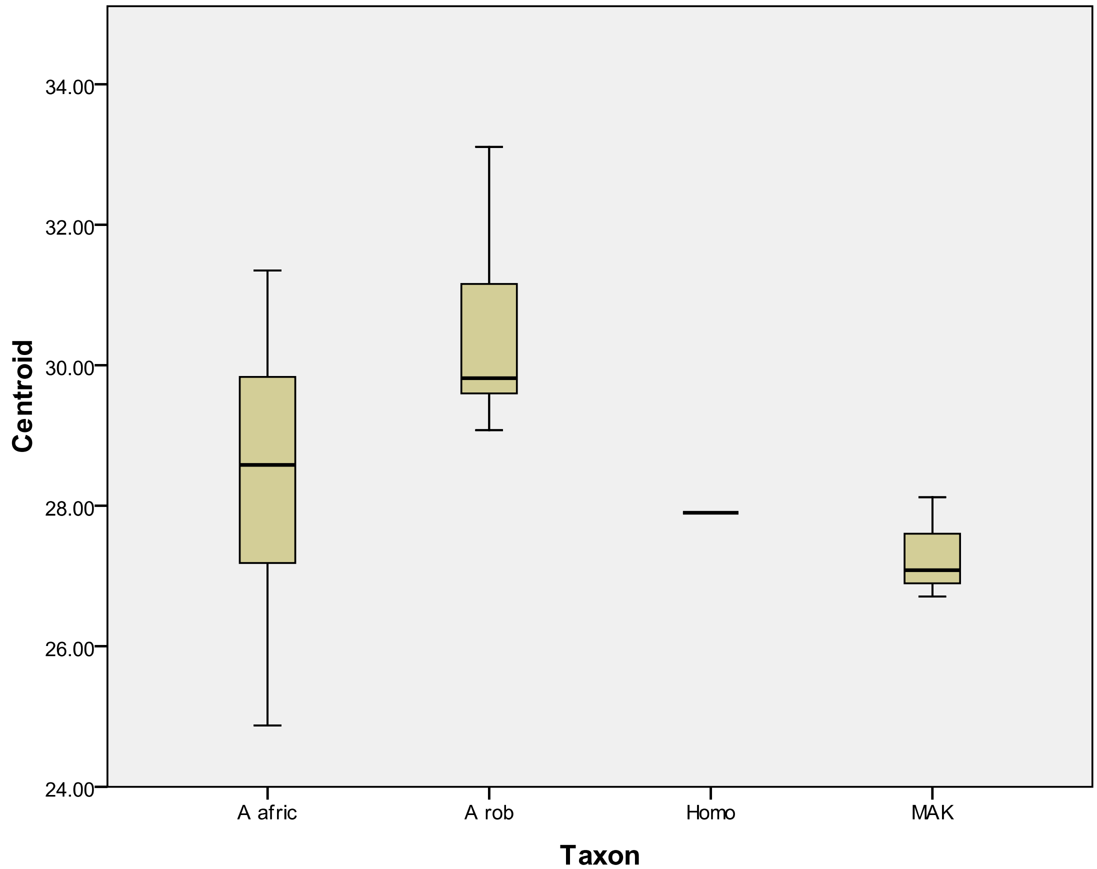
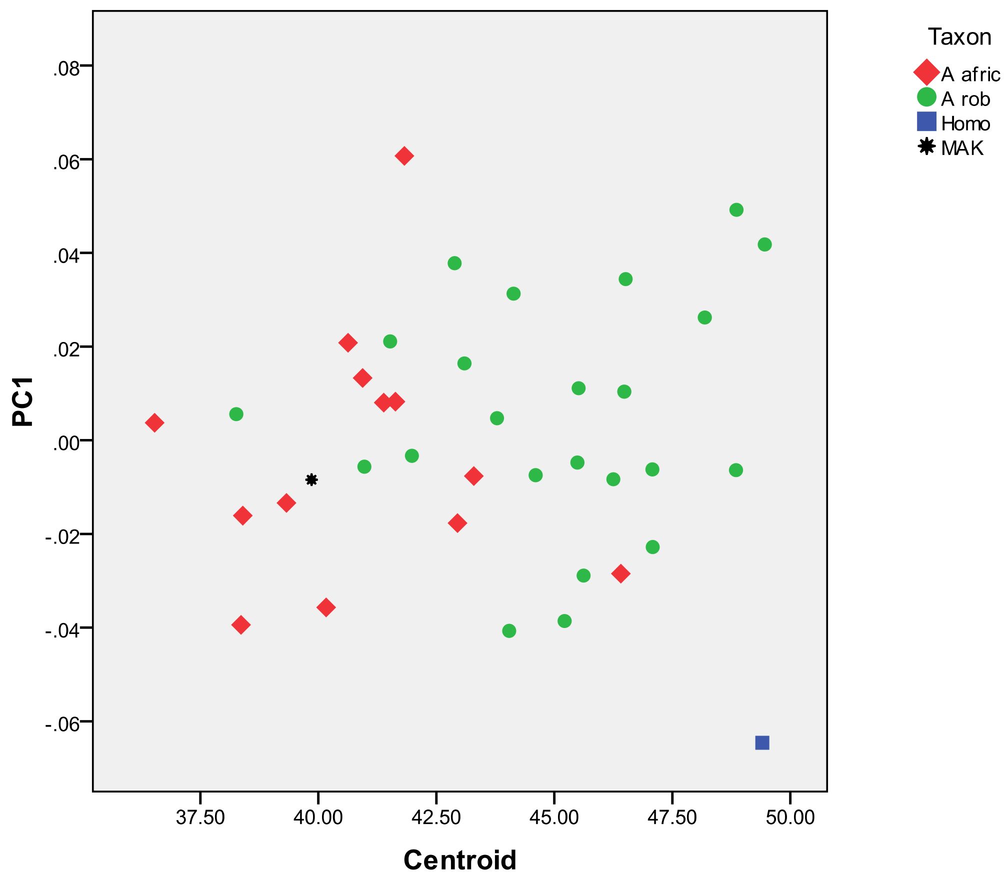
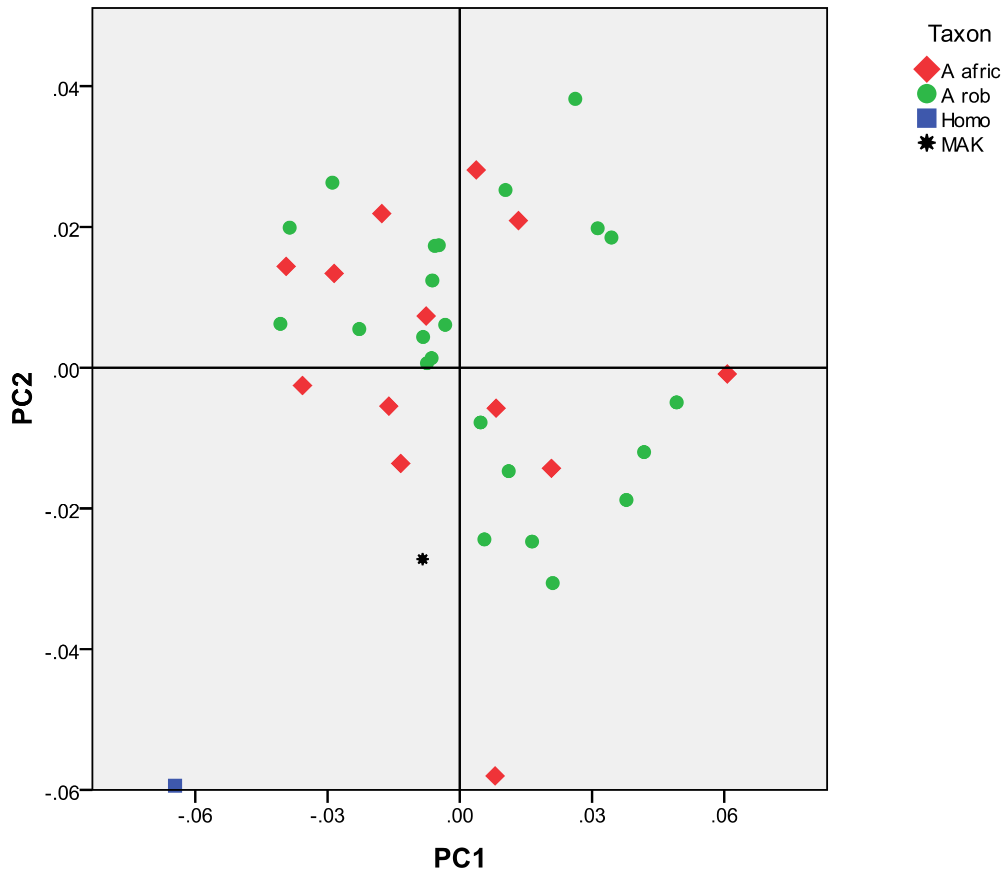


Figure 8-53*: *PCA of P^4 Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the P^4 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 42%, PC 2 explains 28%, and PC 3 explains 10% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

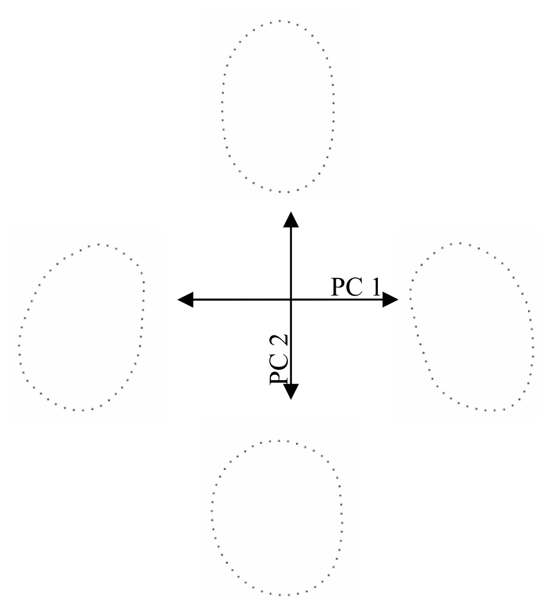
(*a*.)



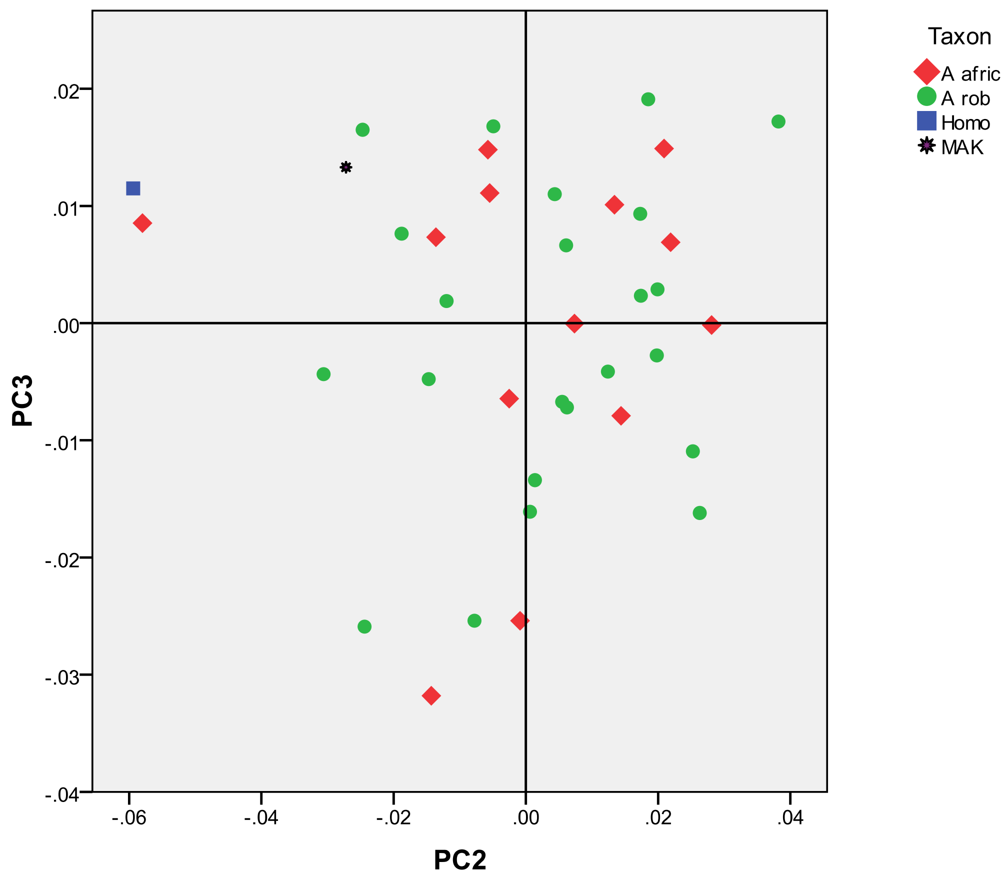
(***b.***)


Taxon
A afric
A rob
Homo
MAK
.04
.02
.00
-.02
-.04
-.06
-.06
-.03
.00
.03
.06
PC2
PC1

(***c.***)

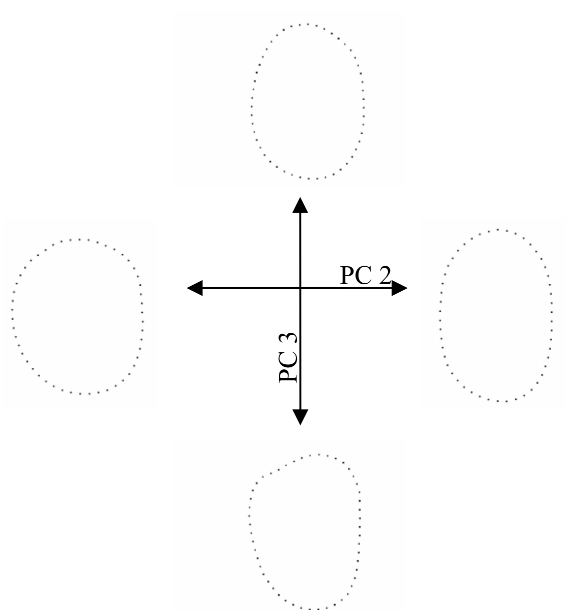

PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
Homo
MAK
PC3
.02
.01
.00
-.01
-.02
-.03
-.04
-.06
-.04
-.02
.00
.02
.04
PC2

(*e.*)



PC 2
PC 3

Figure 8-54*: *Boxplot of the Centroids for P^4 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P^4 occlusal outline semi-landmark data are compared by taxon.

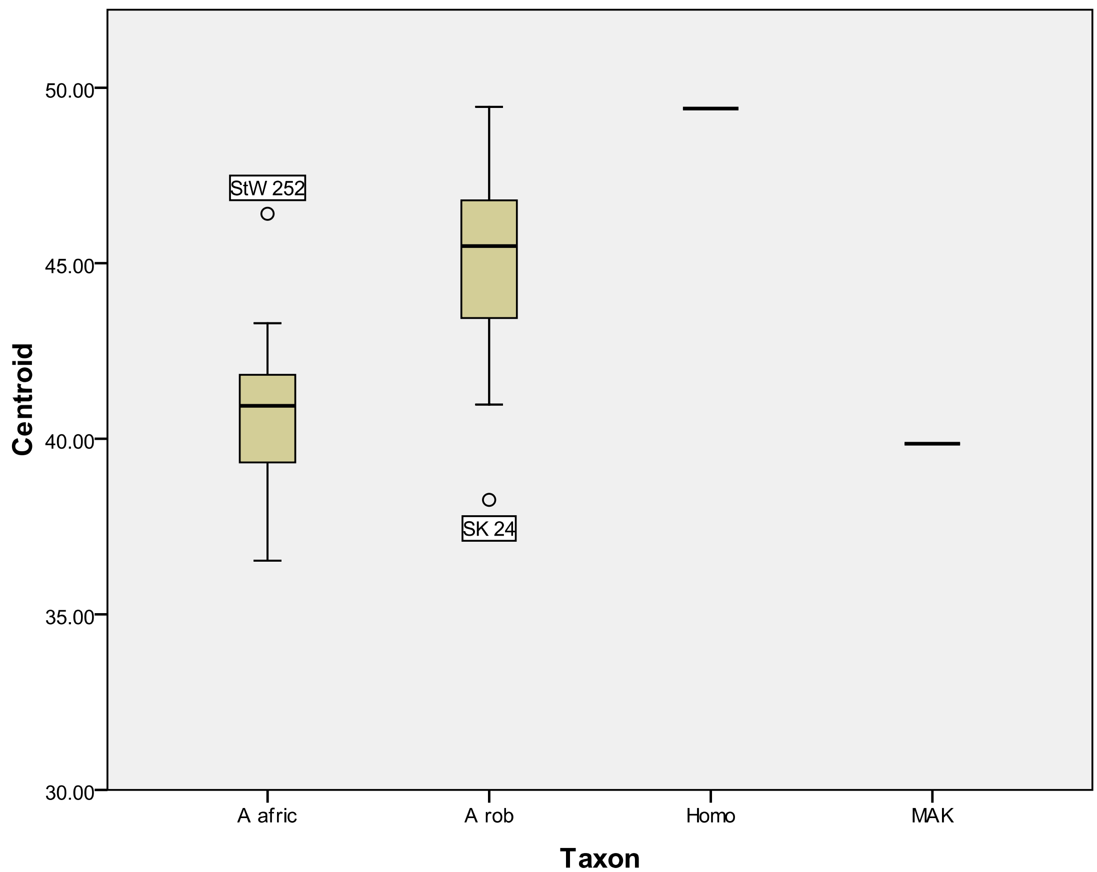
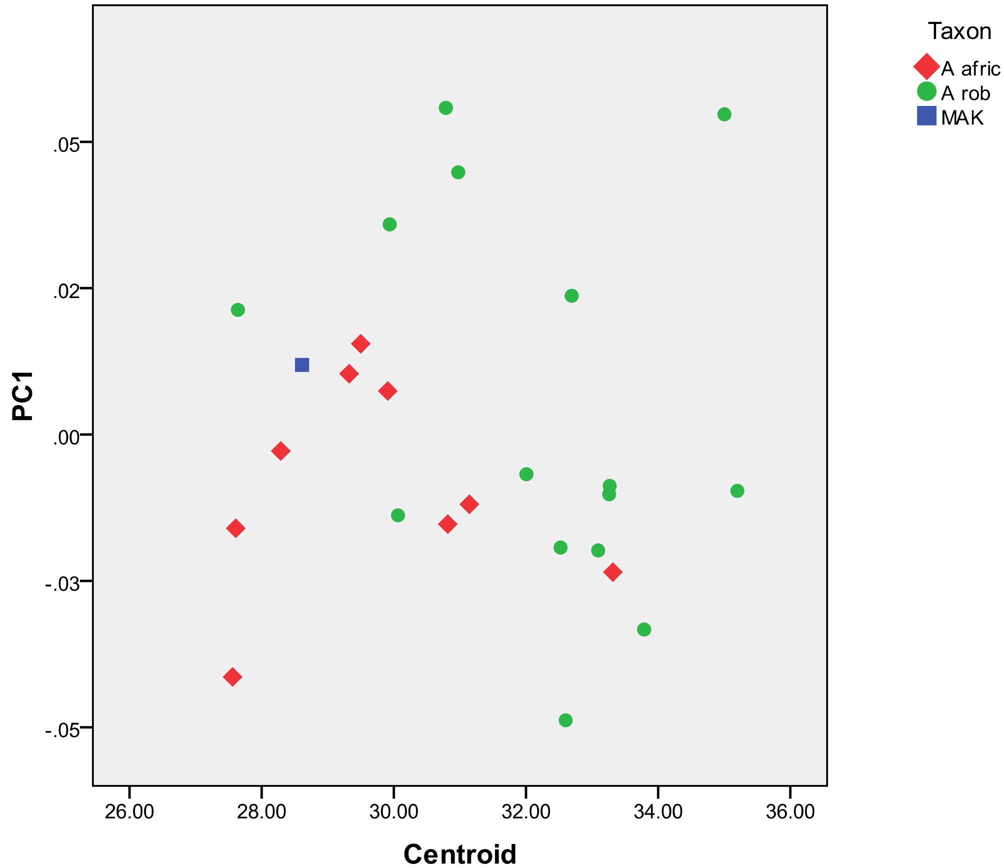
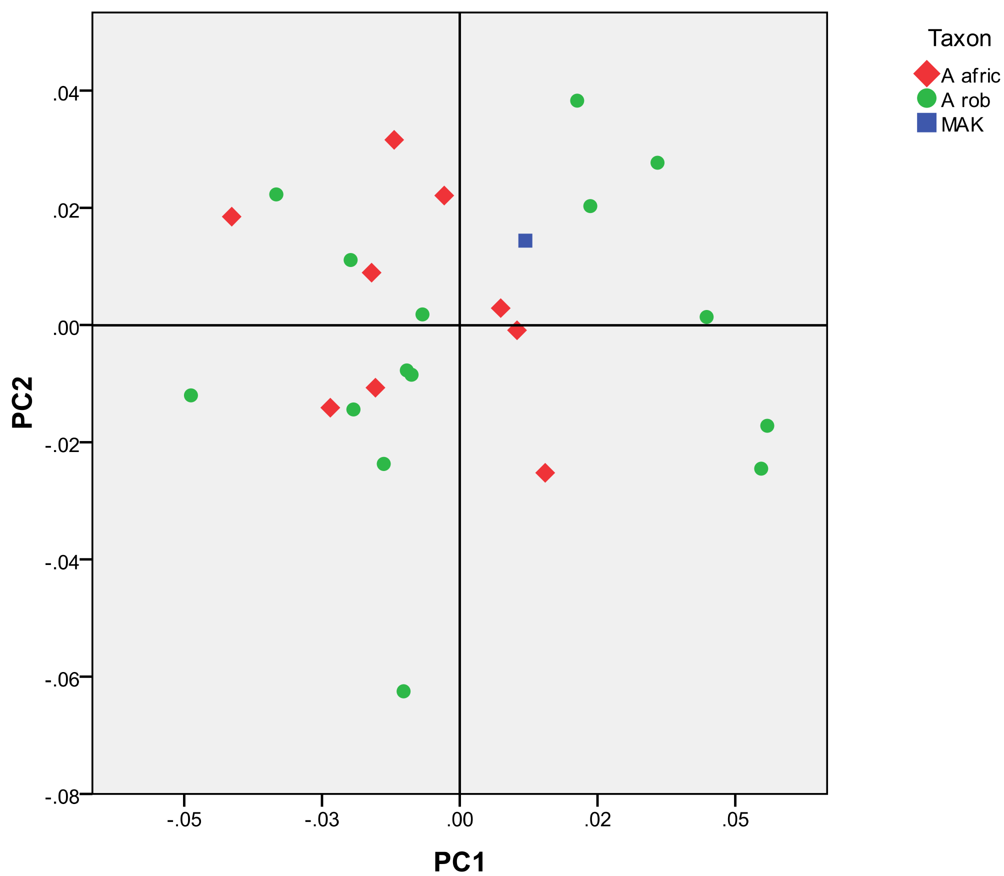


Figure 8-55*: *PCA of P⁴ Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the P^4 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 32%, PC 2 explains 21%, and PC 3 explains 17% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

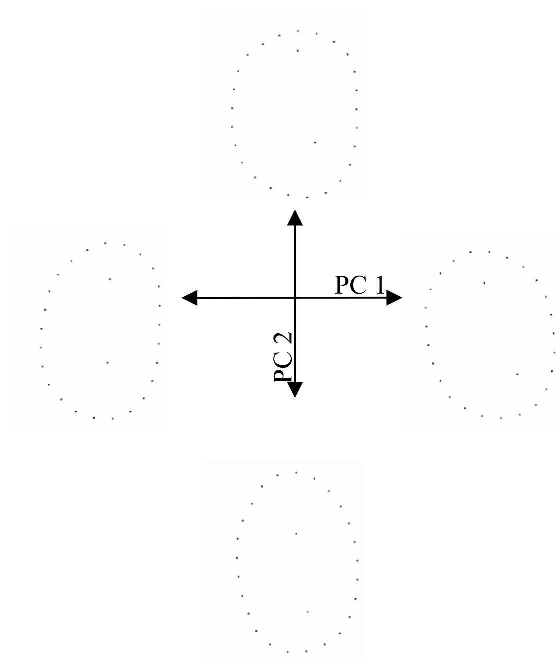
(*a*.)



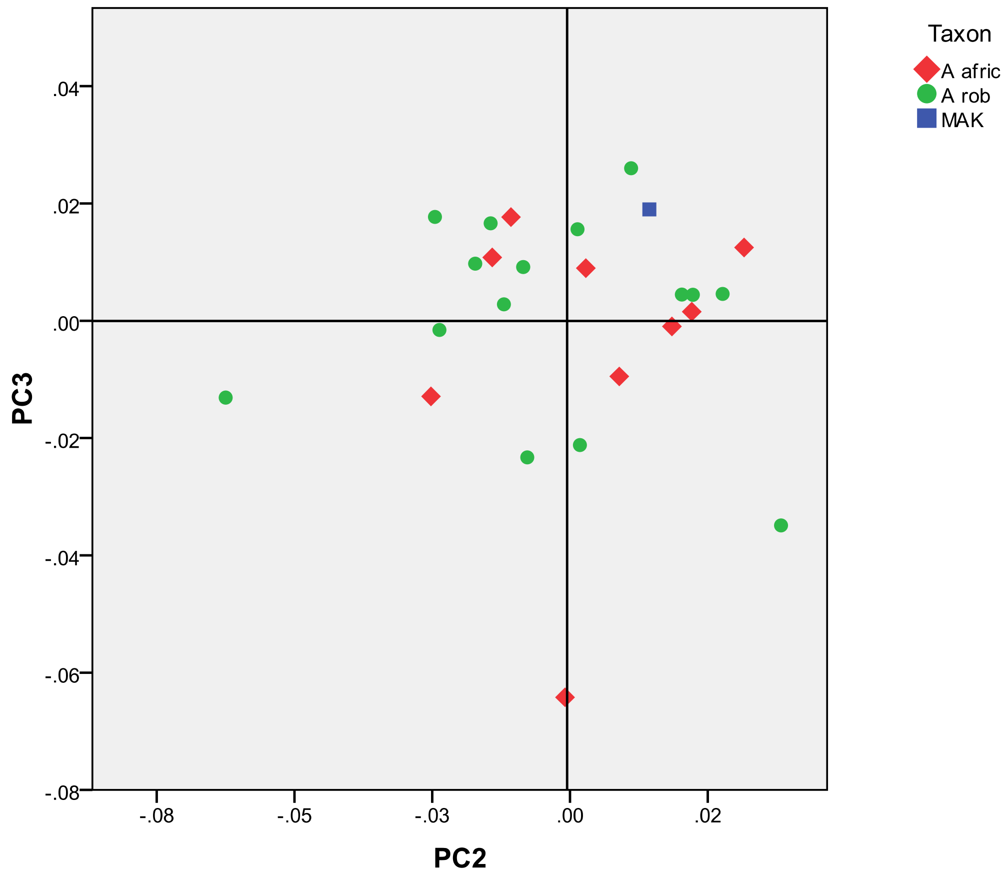
(*b.*)


Taxon
A afric
A rob
MAK
.04
.02
.00
-.02
-.04
-.06
-.08
PC2
-.05
-.03
.00
.02
.05
PC1

(*c.*)

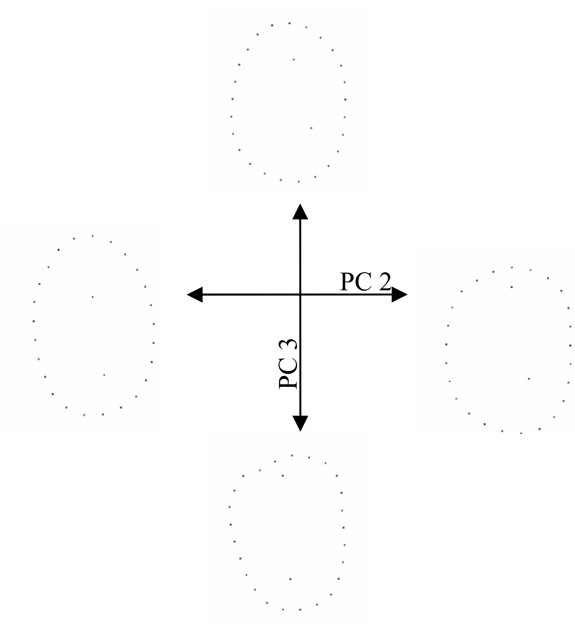

PC 1
PC 2

(*d.*)



Taxon
A afric
A rob
MAK
.04
.02
.00
-.02
-.04
-.06
-.08
PC3
-.08
-.05
-.03
.00
.02
PC2

(*e.*)



PC 2
PC 3

Figure 8-56*: *Boxplot of the Centroids for P⁴ Occlusal Outline Semi-landmark and Cusp Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P^4 occlusal outline semi-landmark and landmark data are compared by taxon.

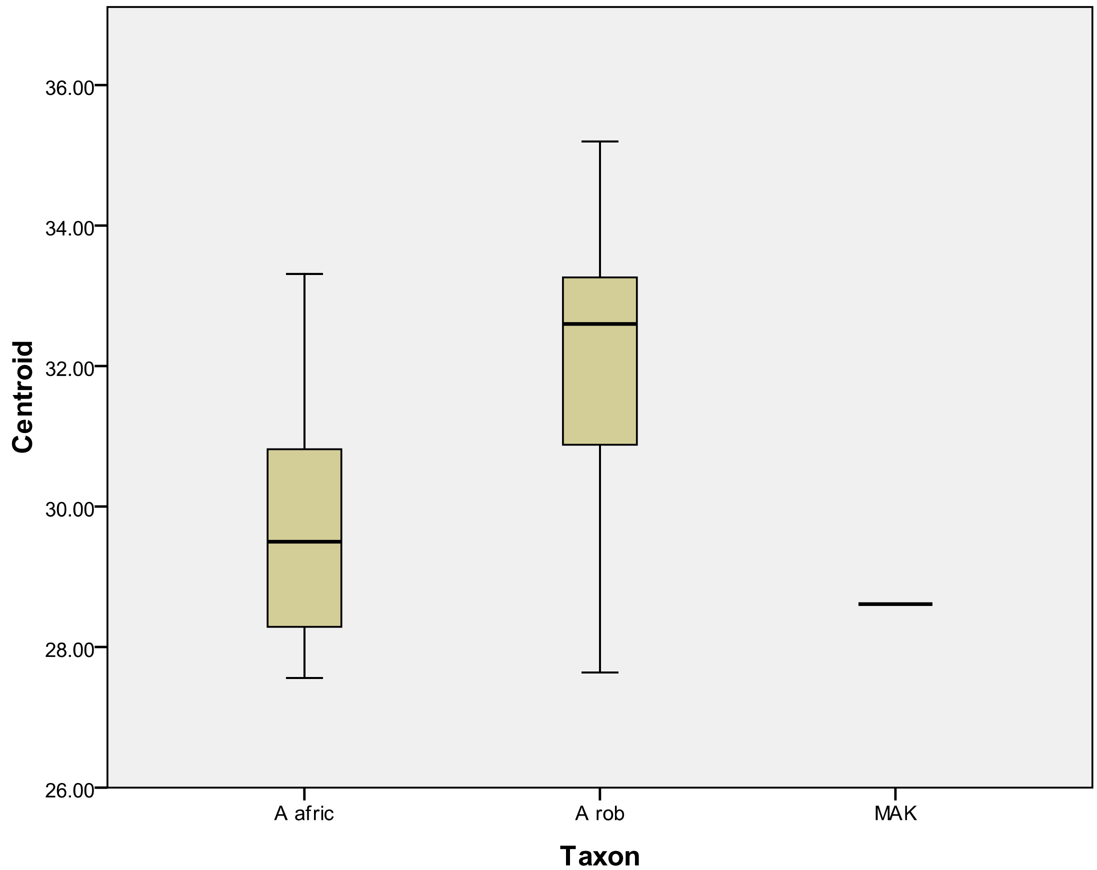
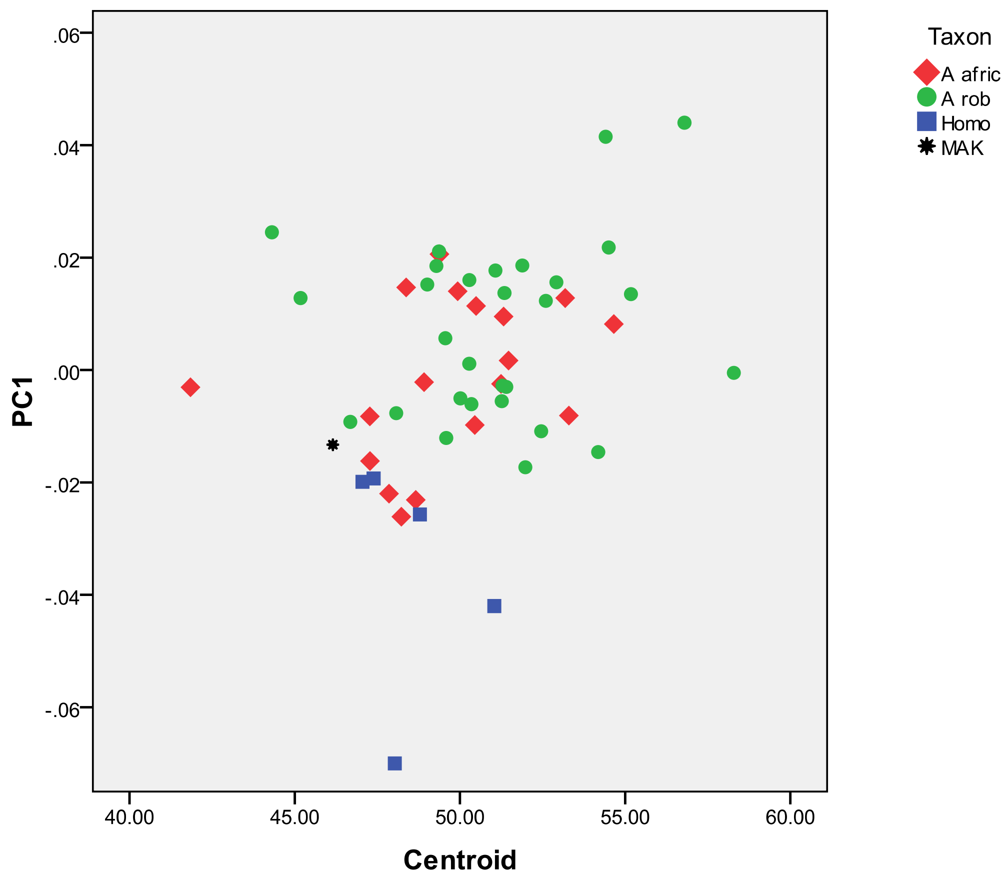
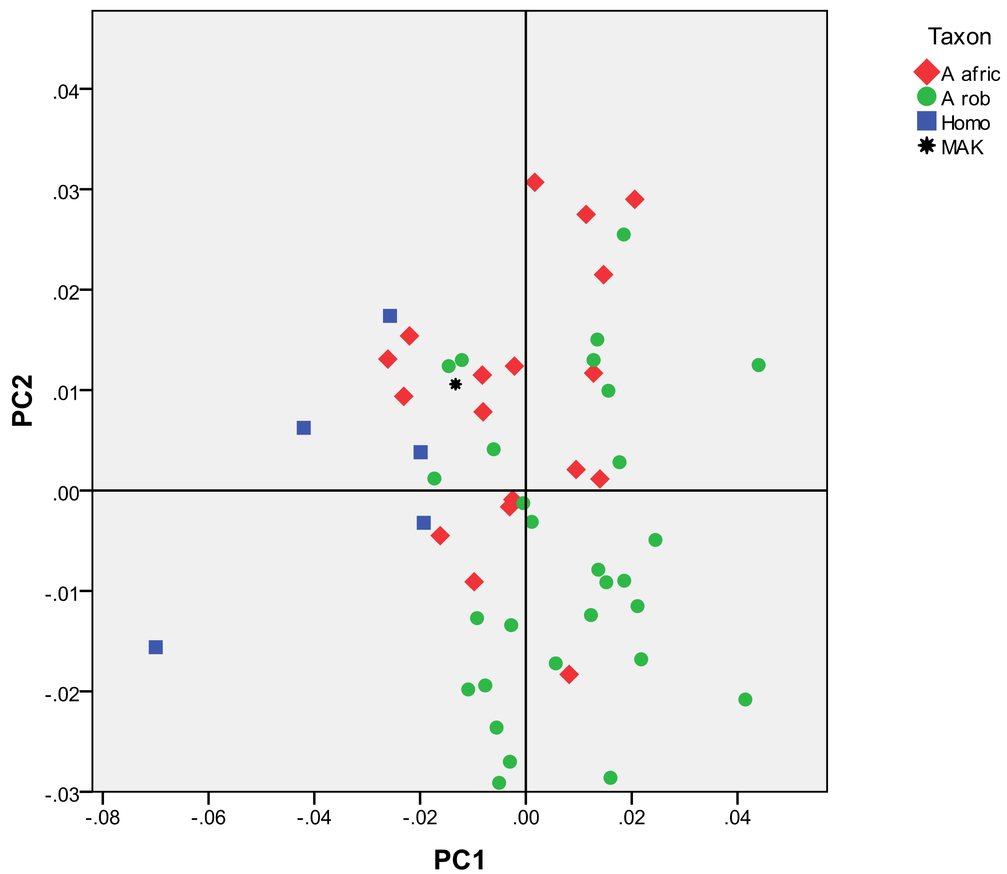


Figure 8-57*: *PCA of M[1] Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M[1] semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 37%, PC 2 explains 23%, and PC 3 explains 10% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

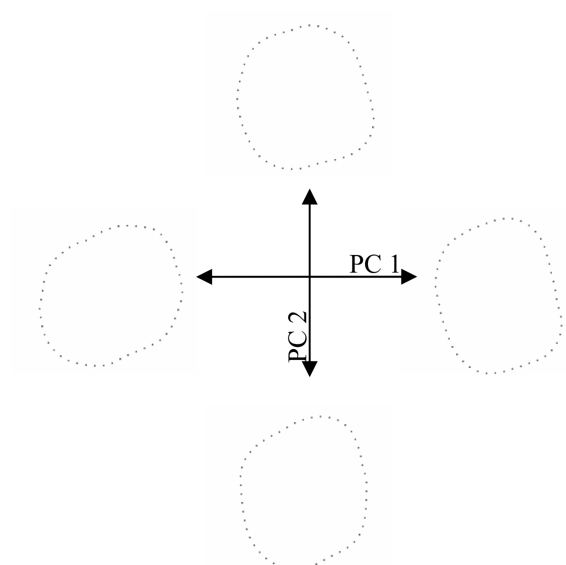
(*a*.)



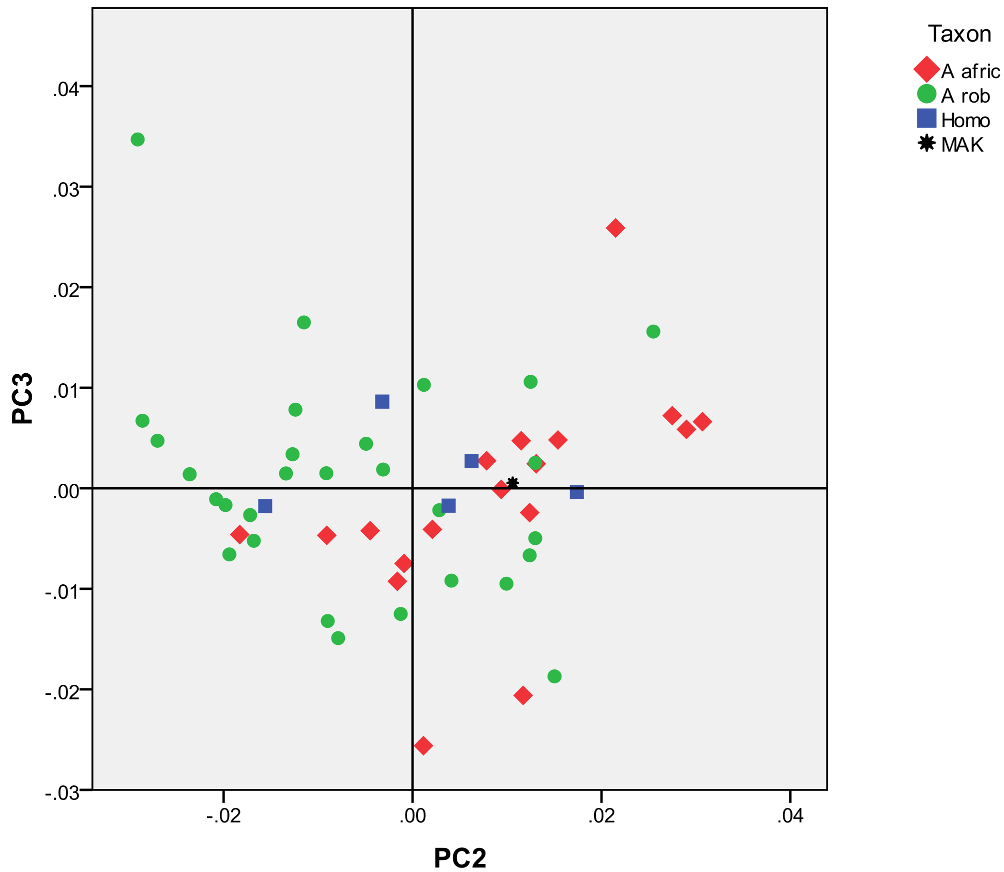
(***b.***)


Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.04
.03
.02
.01
.00
-.01
-.02
-.03
-.08
-.06
-.04
-.02
.00
.02
.04

(***c.***)

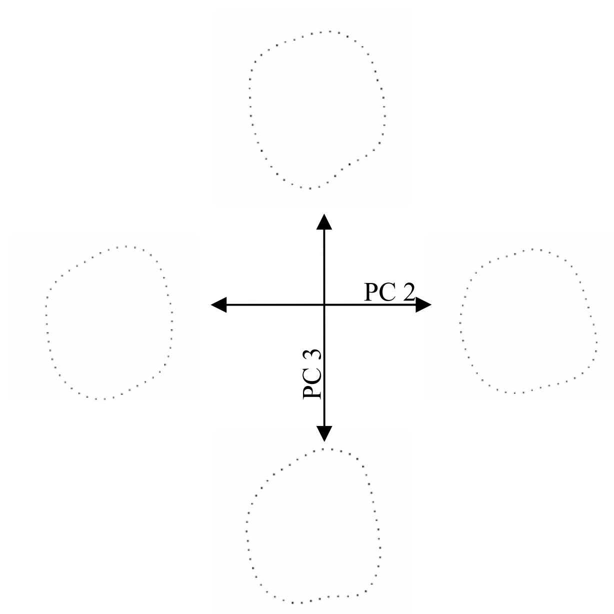

PC 1
PC 2

(d.)



Taxon
A afric
A rob
Homo
MAK
PC3
PC2
.04
.03
.02
.01
.00
-.01
-.02
-.03
-.02
.00
.02
.04

(e.)



PC 2
PC 3

Figure 8-58*: *Boxplot of the Centroids for M[1] Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M**1** occlusal outline semi-landmark data are compared by taxon.

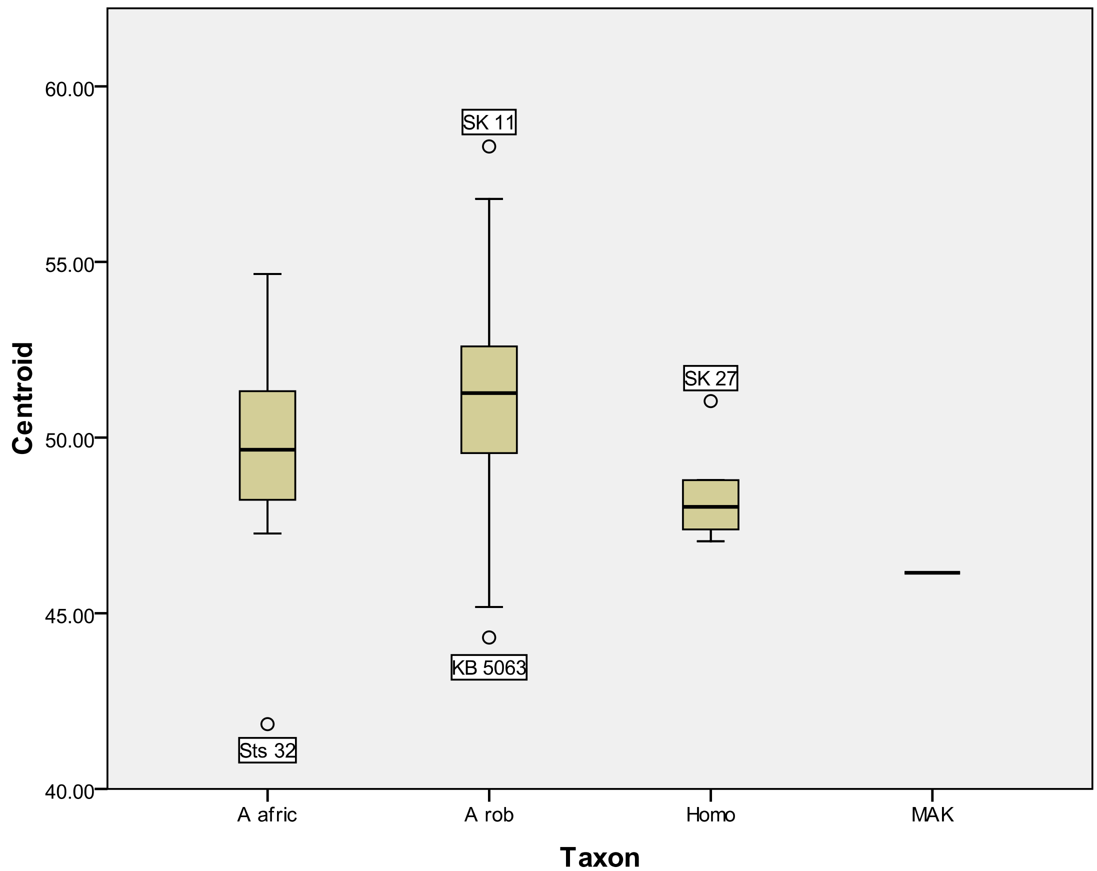
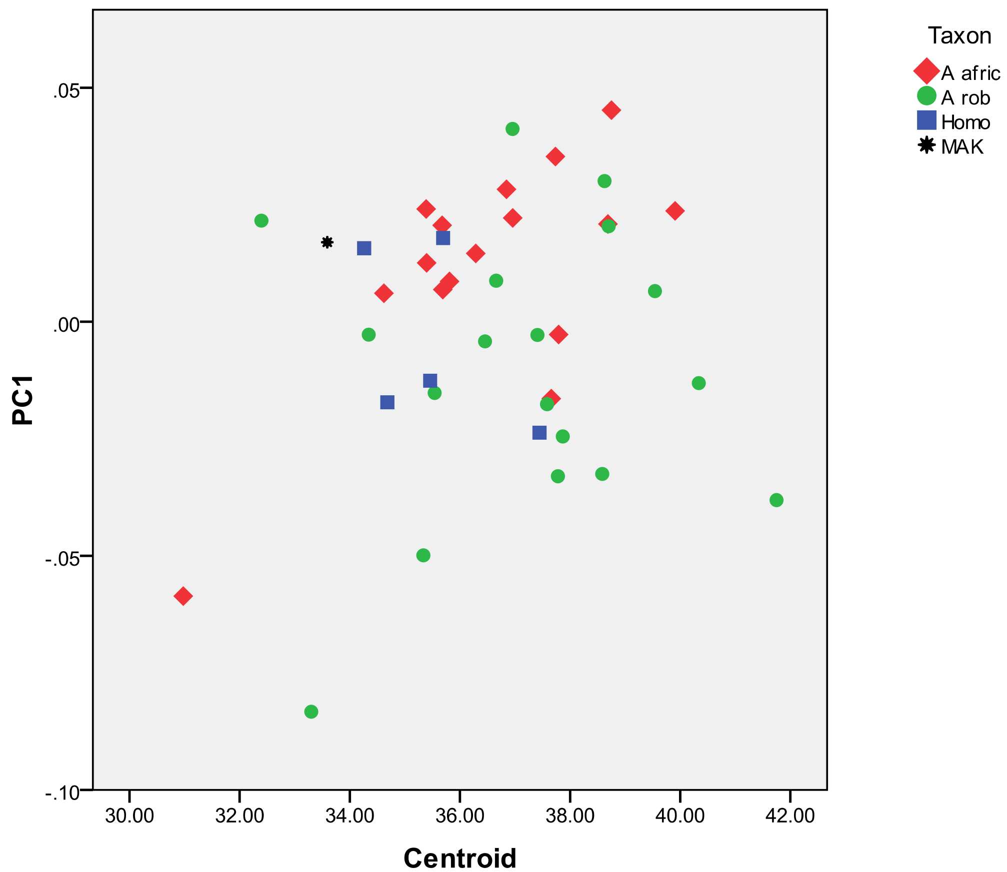
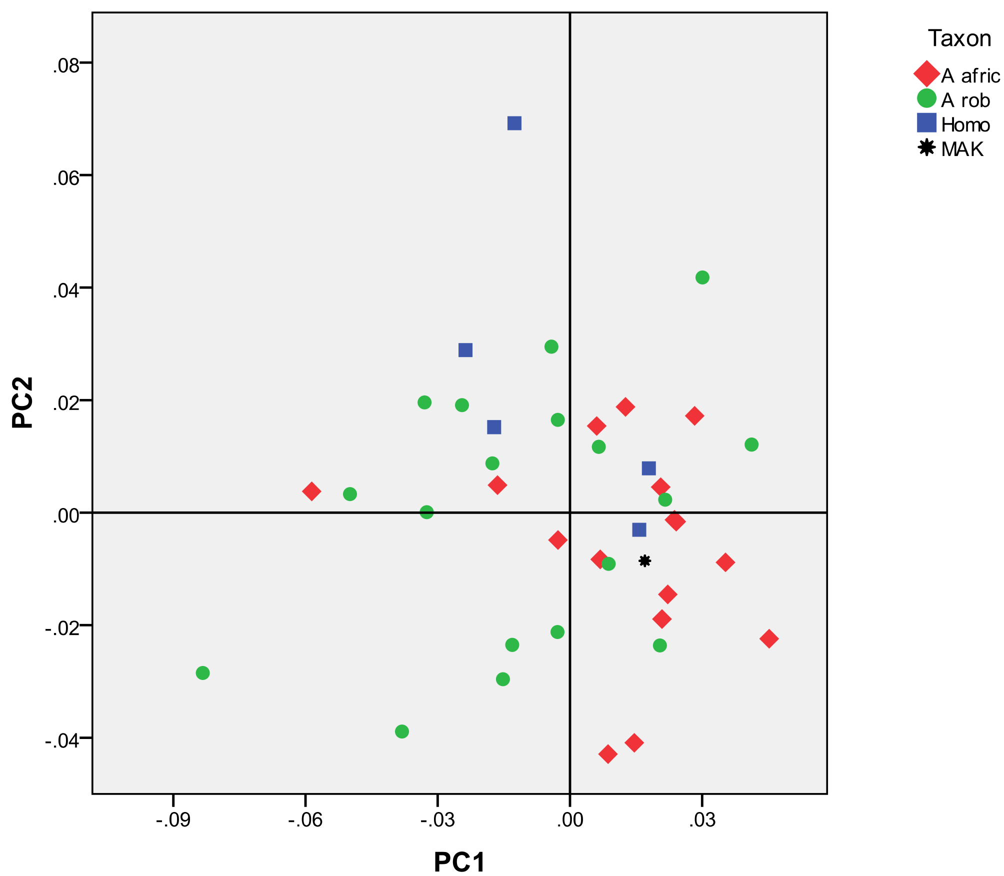


Figure 8-59*: *PCA of M¹ Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the M¹ semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 27%, PC 2 explains 18%, and PC 3 explains 12% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(a.)

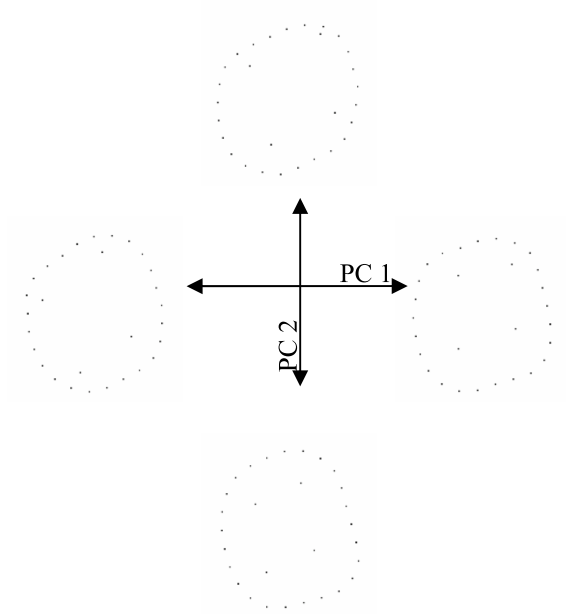


(b.)



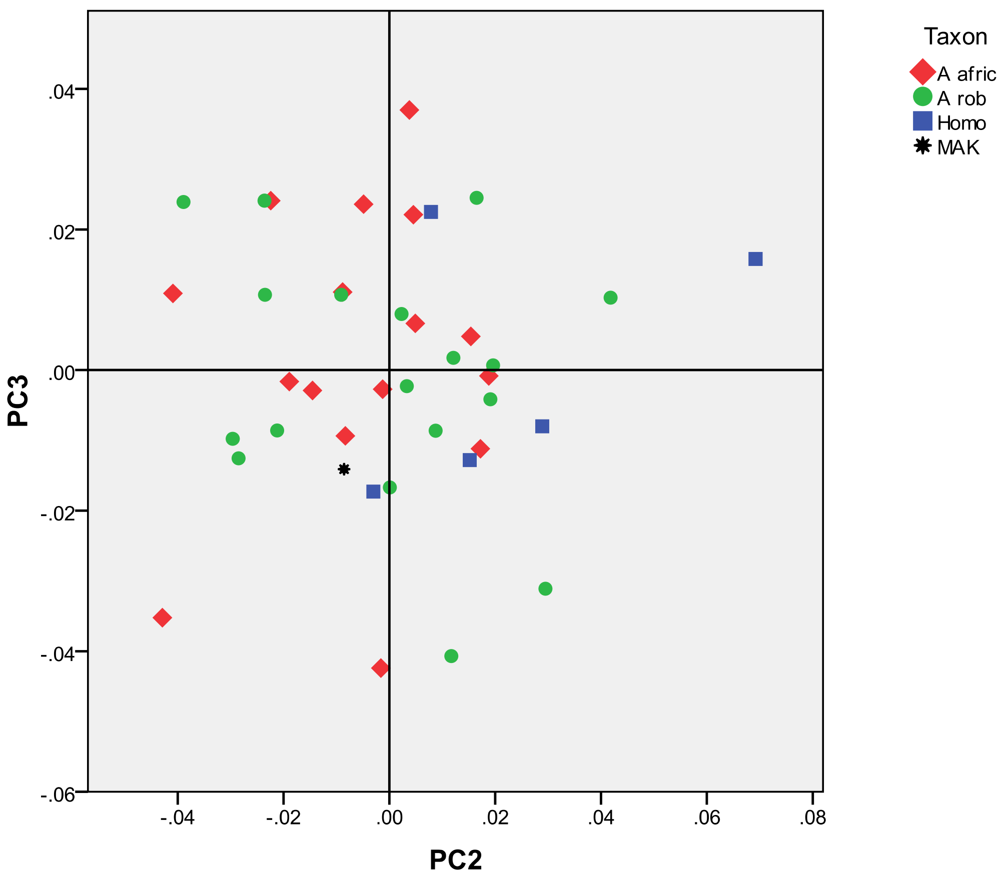
Taxon
A afric
A rob
Homo
MAK
PC2
.08
.06
.04
.02
.00
-.02
-.04
-.09
-.06
-.03
.00
.03
PC1

(c.)



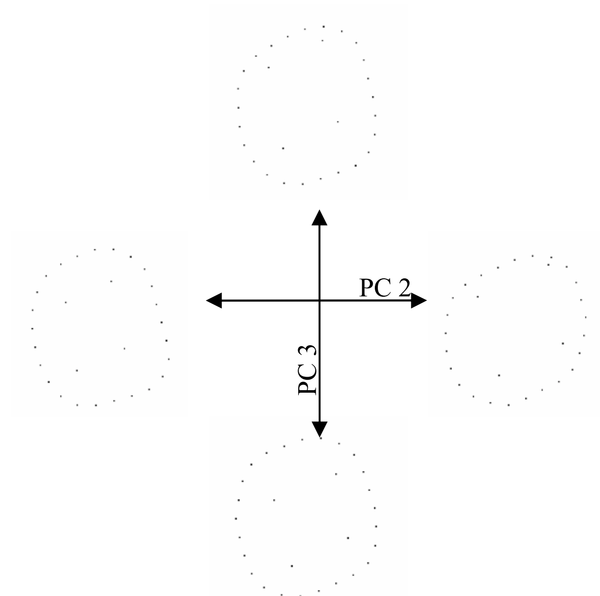
PC 1
PC 2

(d.)



Taxon
A afric
A rob
Homo
MAK
PC3
PC2
.04
.02
.00
-.02
-.04
-.06
-.04
-.02
.00
.02
.04
.06
.08

(e.



PC 2
PC 3

Figure 8-60*: *Boxplot of the Centroids for M[1] Occlusal Outline Semi-landmark and Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M**1** occlusal outline semi-landmark and landmark data are compared by taxon.

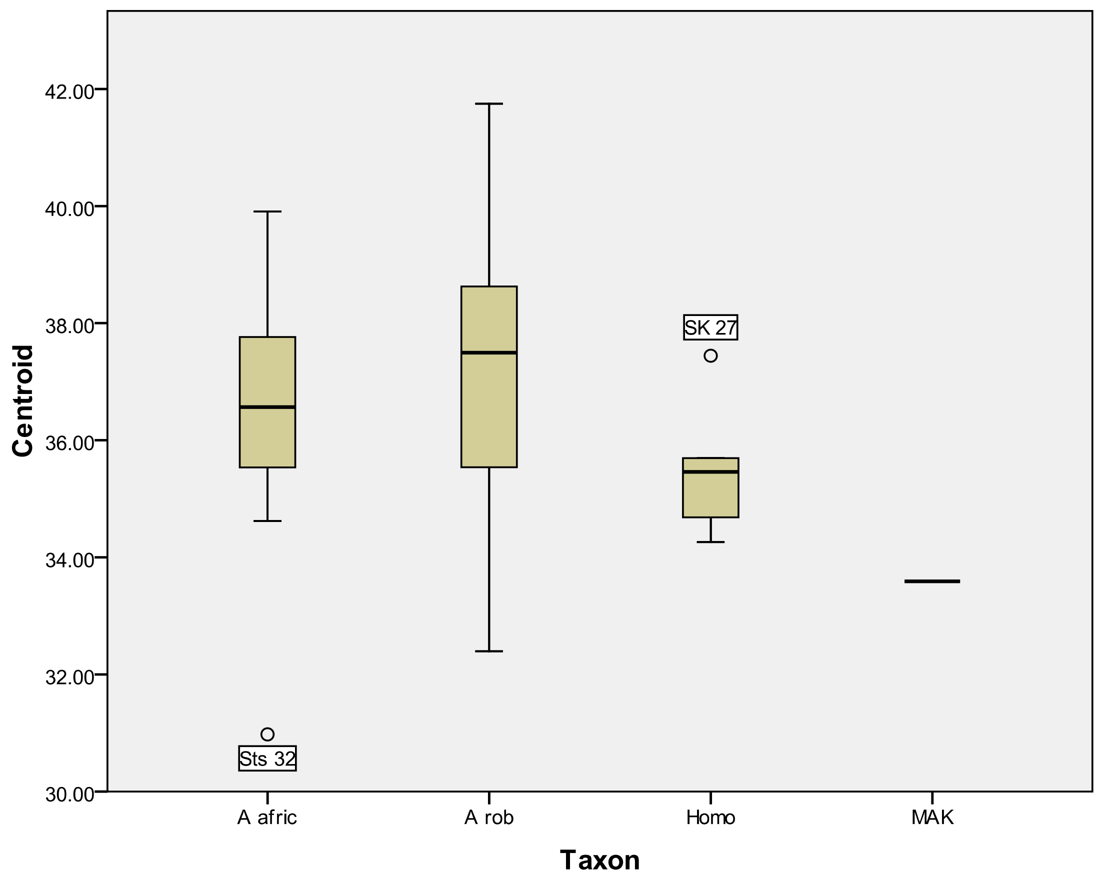
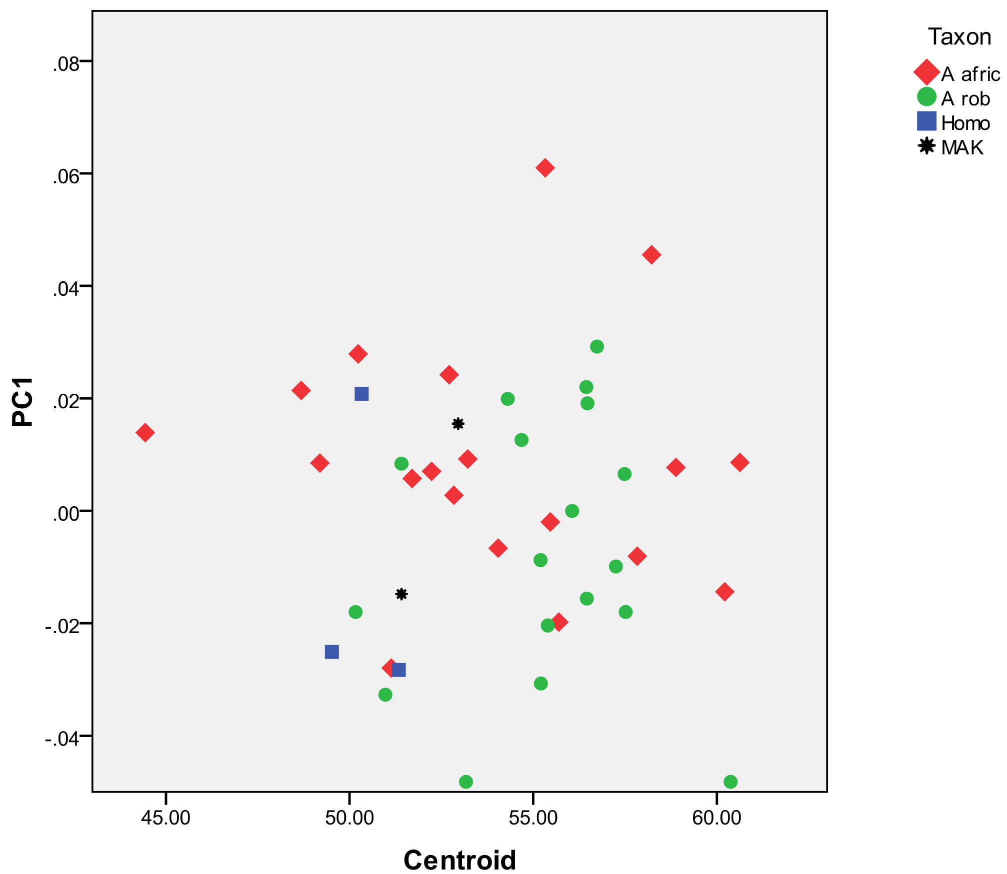
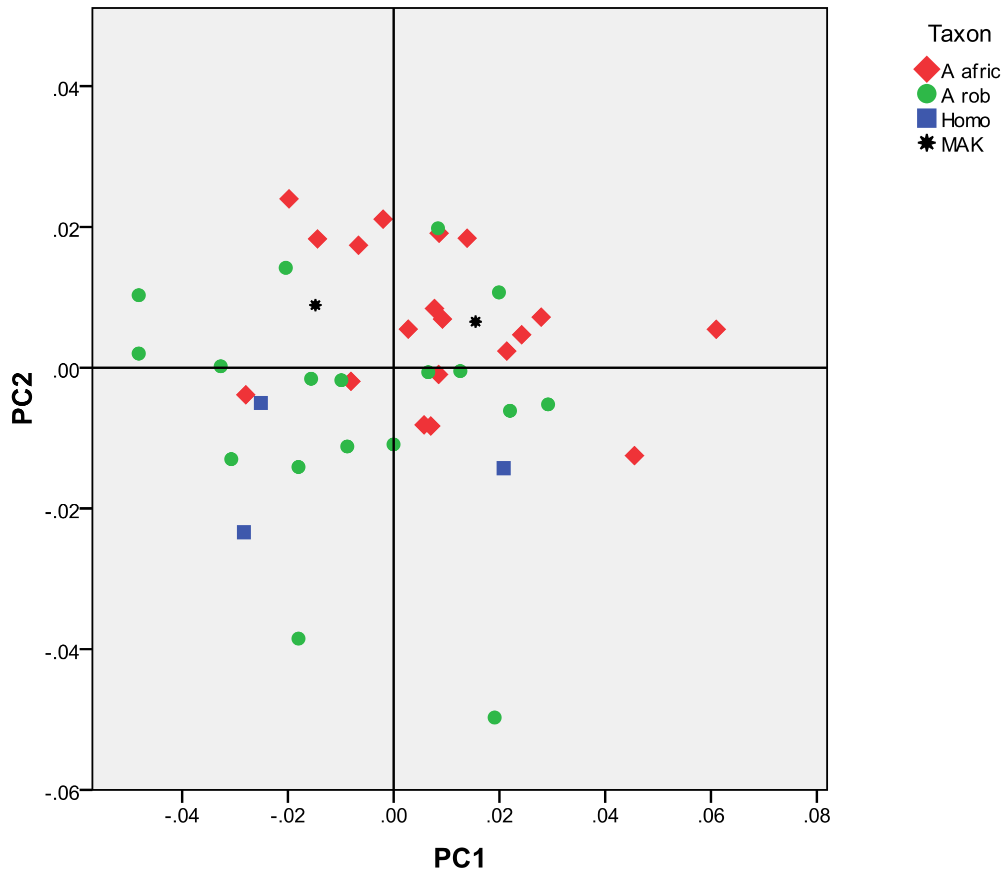


Figure 8-61*: *PCA of M² Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M^2 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 41%, PC 2 explains 17%, and PC 3 explains 14% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

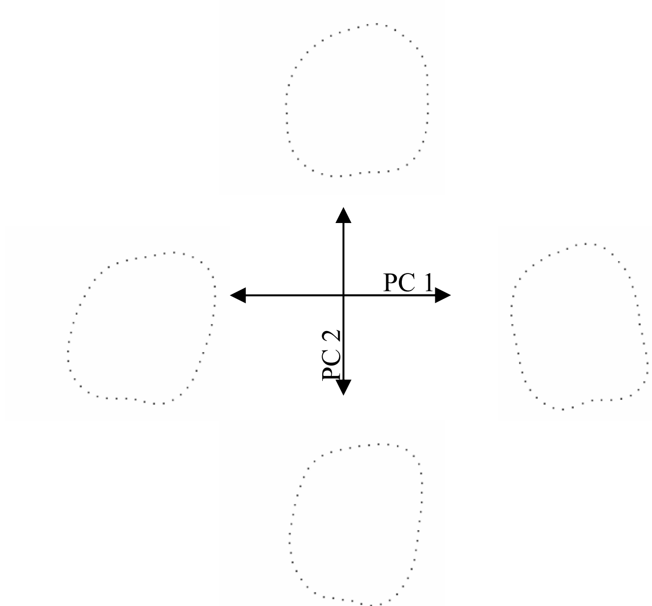
(*a*.)



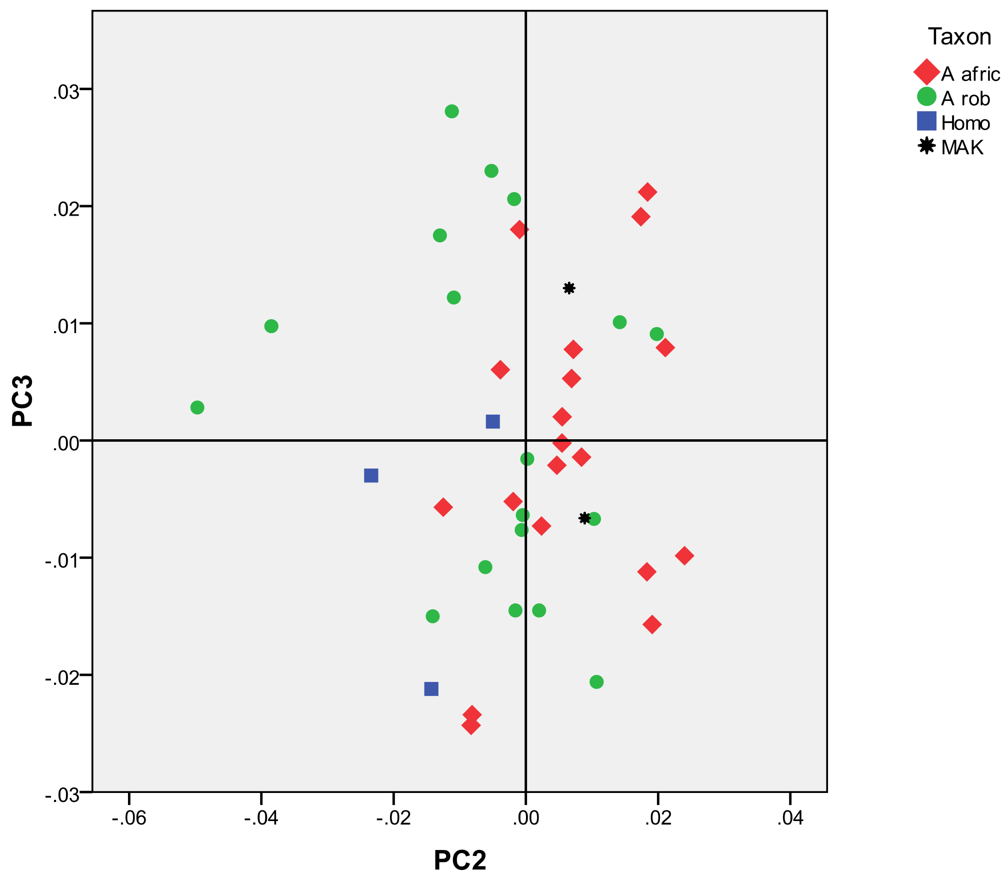
(*b*.)


Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.04
.02
.00
-.02
-.04
-.06
-.04
-.02
.00
.02
.04
.06
.08

(*c*.)

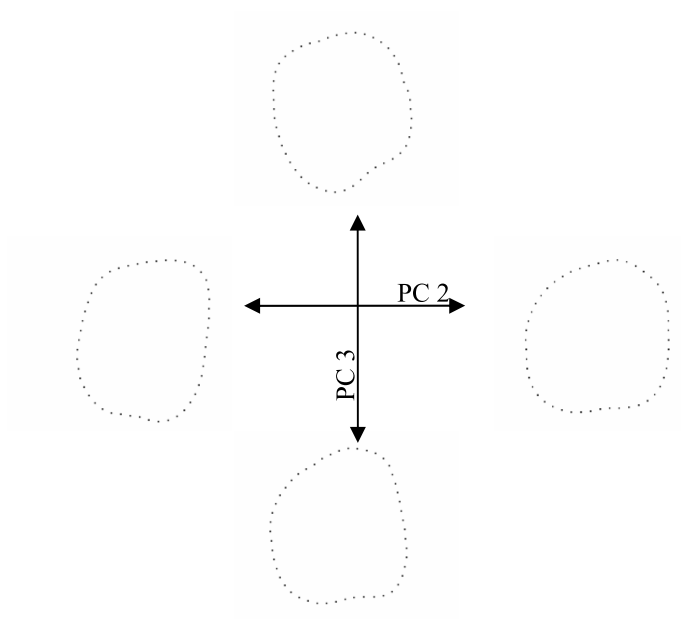

PC 1
PC 2

(d.)



Taxon
A afric
A rob
Homo
MAK
PC3
.03
.02
.01
.00
-.01
-.02
-.03
-.06
-.04
-.02
.00
.02
.04
PC2

(e.)



PC 2
PC 3

Figure 8-52*: *Boxplot of the Centroids for M^2 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M^2 occlusal outline semi-landmark data are compared by taxon.

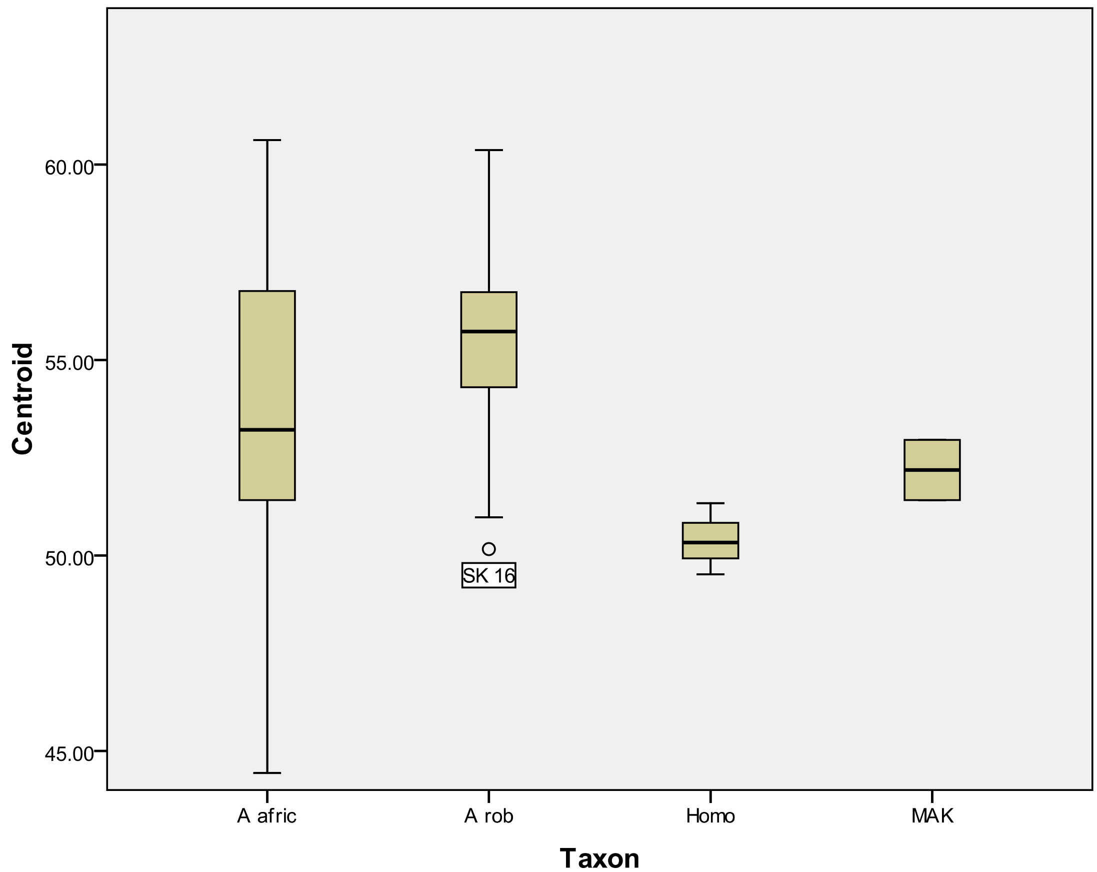
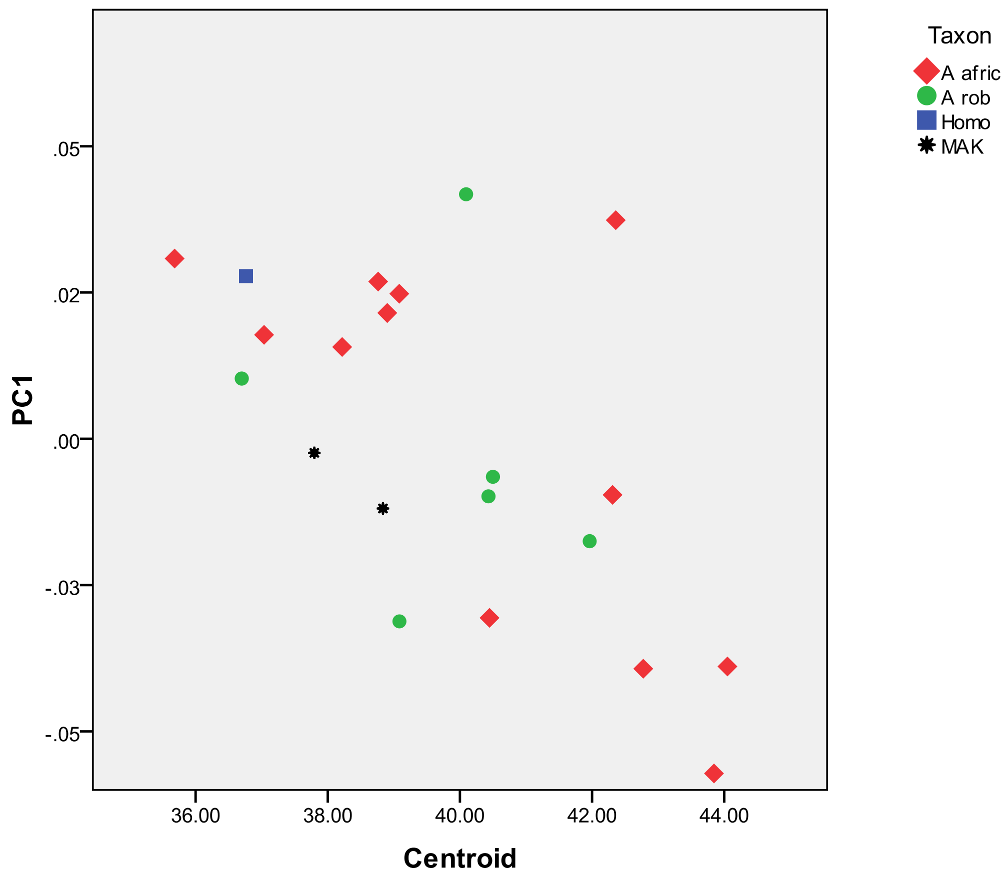
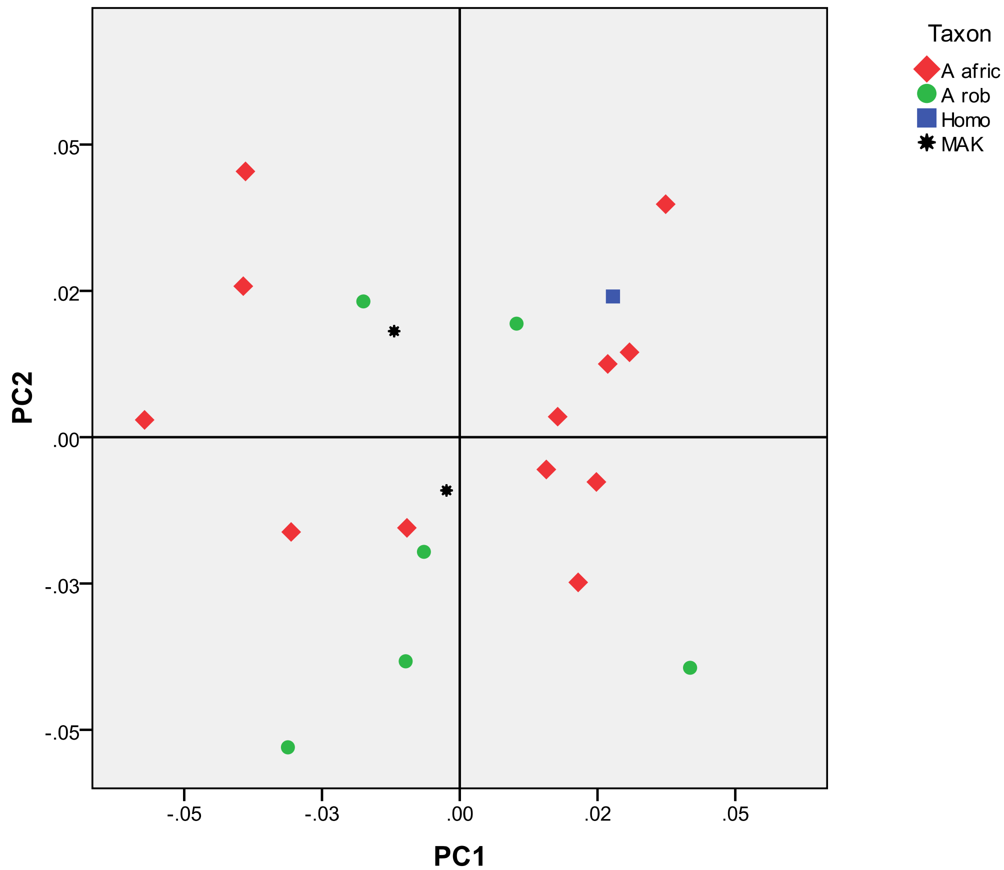


***Figure 8-53*: PCA of M^2 Occlusal Outline Semi-landmark and Cusp Landmark Data.**
The first 3 principal components and centroid for the M^2 semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 28%, PC 2 explains 24%, and PC 3 explains 10% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

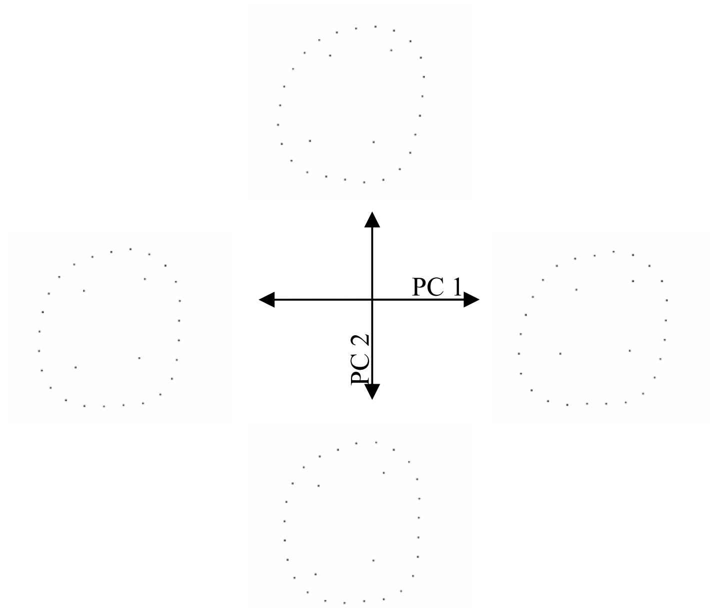
(*a*.)



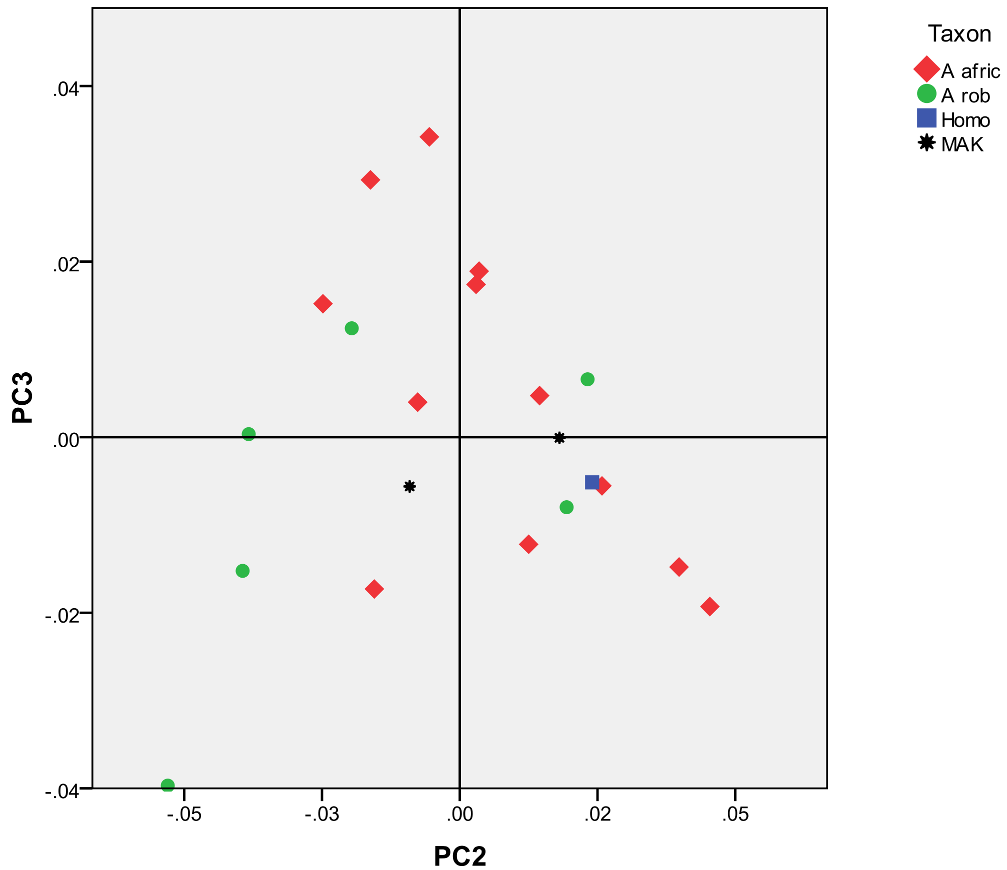
(*b.*)


Taxon
A afric
A rob
Homo
MAK
PC2
PC1
.05
.02
.00
-.03
-.05
-.05
-.03
.00
.02
.05

(*c.*)

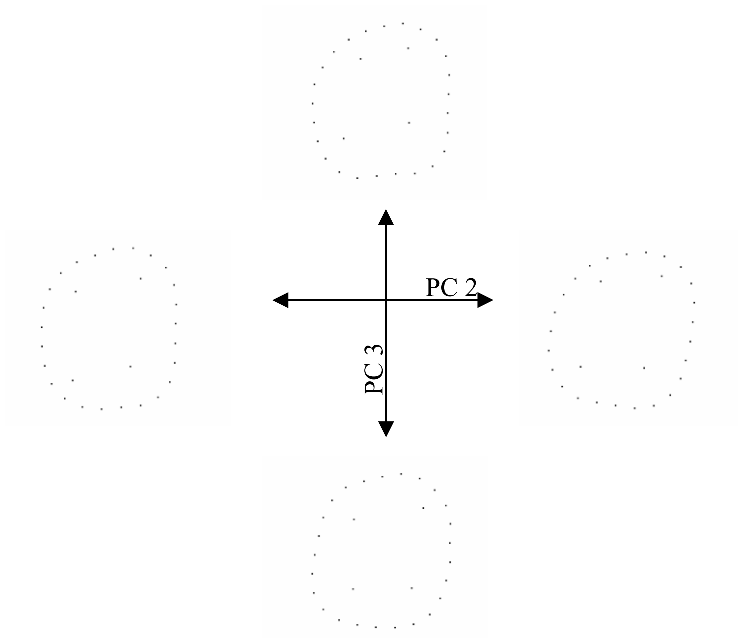

PC 1
PC 2

(***d.***)



Taxon
A afric
A rob
Homo
MAK
PC3
.04
.02
.00
-.02
-.04
-.05
-.03
.00
.02
.05
PC2

(***e.***)



PC 2
PC 3

Figure 8-54*: *Boxplot of the Centroids for M^2 Occlusal Outline Semi-landmark and Cusp Landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M^2 occlusal outline semi-landmark and landmark data are compared by taxon.

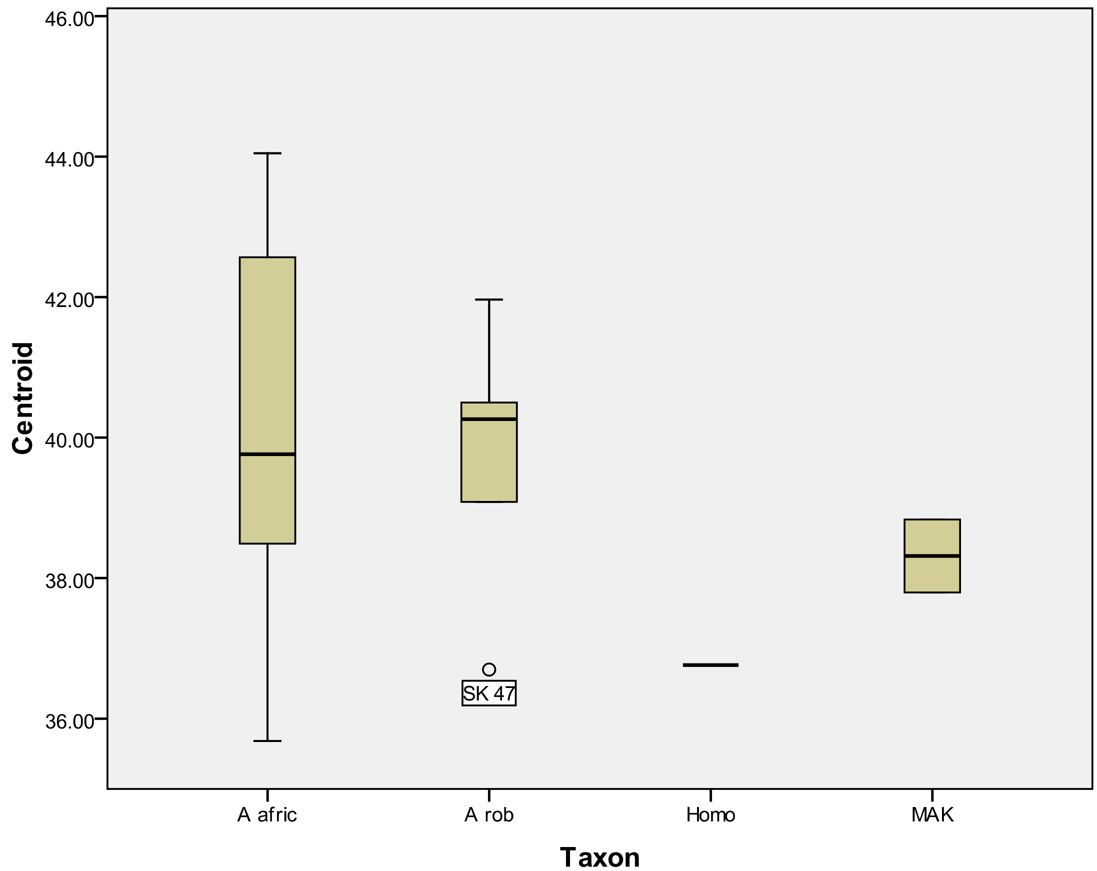
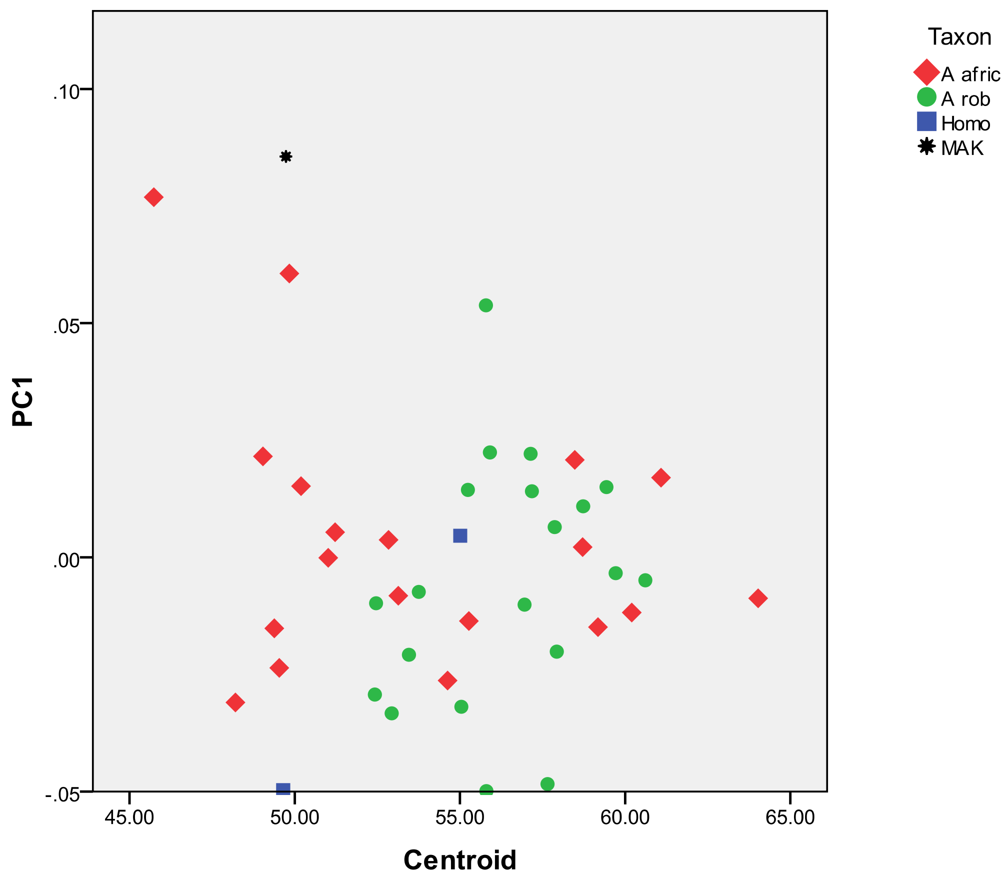
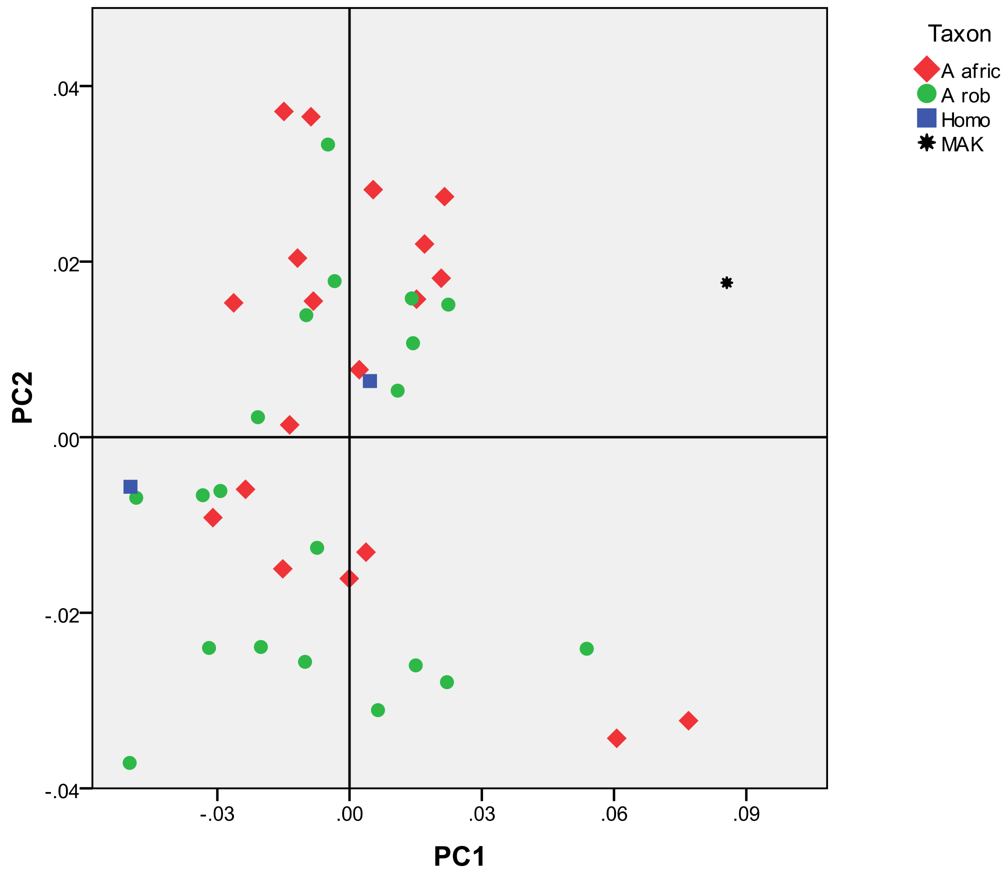


Figure 8-55*: *PCA of M³ Occlusal Outline Semi-landmark Data. The first 3 principal components and centroid for the M^3 semi-landmark occlusal outline data are plotted (*a*, *b*, and *d*), where PC 1 explains 43%, PC 2 explains 21%, and PC 3 explains 12% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

(*a*.)

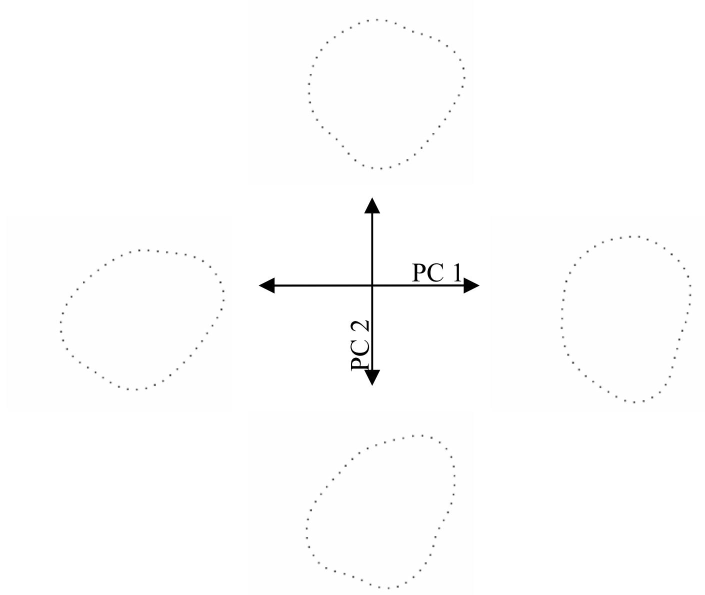


(*b.*)



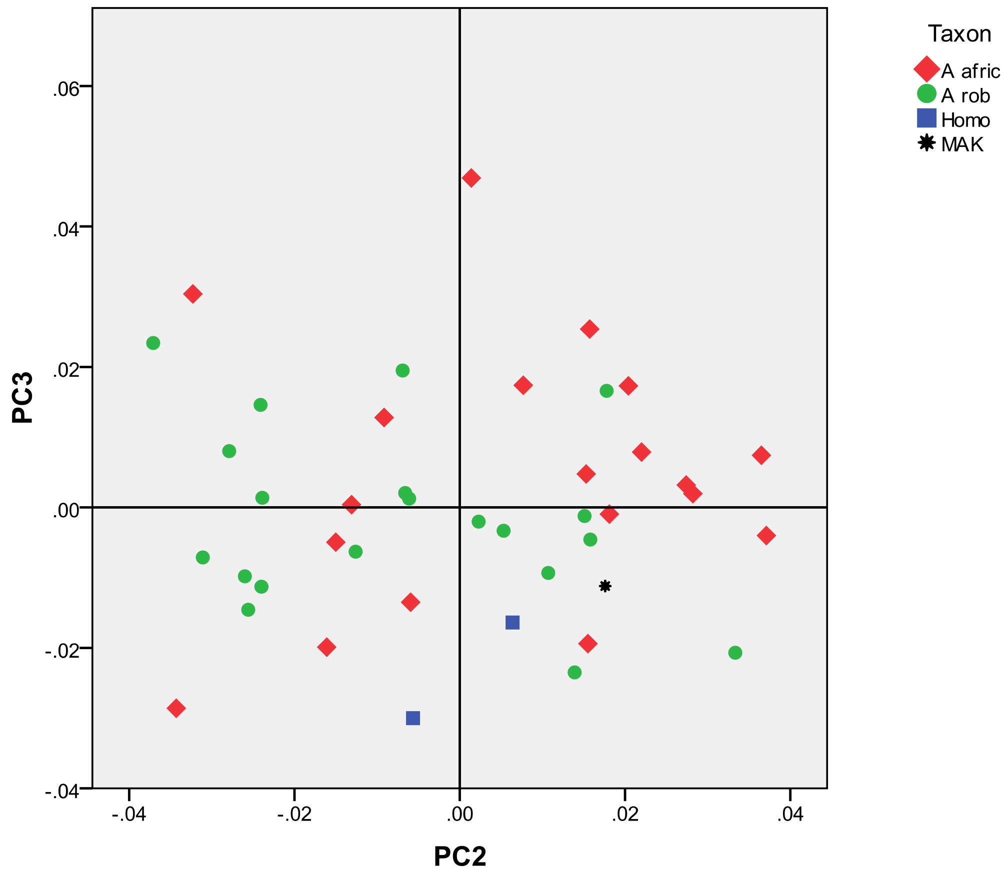
Taxon
A afric
A rob
Homo
MAK
PC2
.04
.02
.00
-.02
-.04
-.03
.00
.03
.06
.09
PC1

(*c.*)



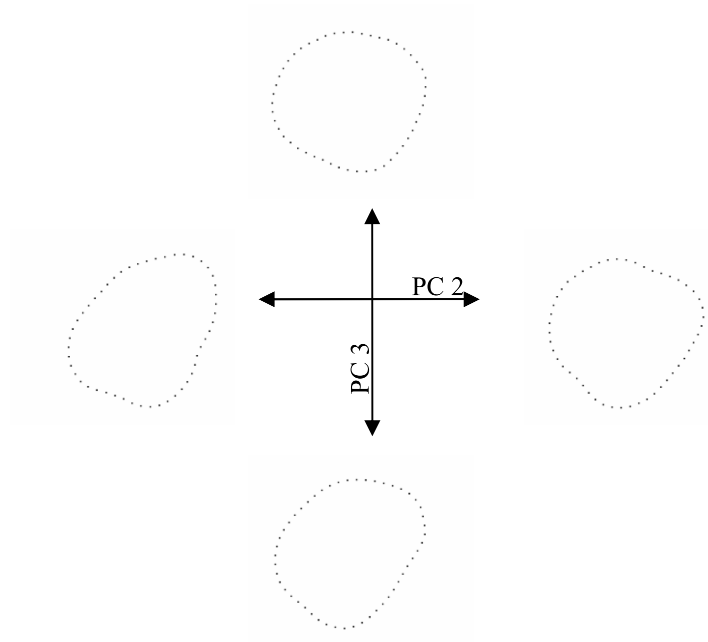
PC 1
PC 2

(d.)



Taxon
A afric
A rob
Homo
MAK
PC3
PC2
.06
.04
.02
.00
-.02
-.04
-.04
-.02
.00
.02
.04

(e.)



PC 2
PC 3

Figure 8-56*: *Boxplot of the Centroids for M^3 Occlusal Outline Semi-landmark Data. The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of M^3 occlusal outline semi-landmark data are compared by taxon.

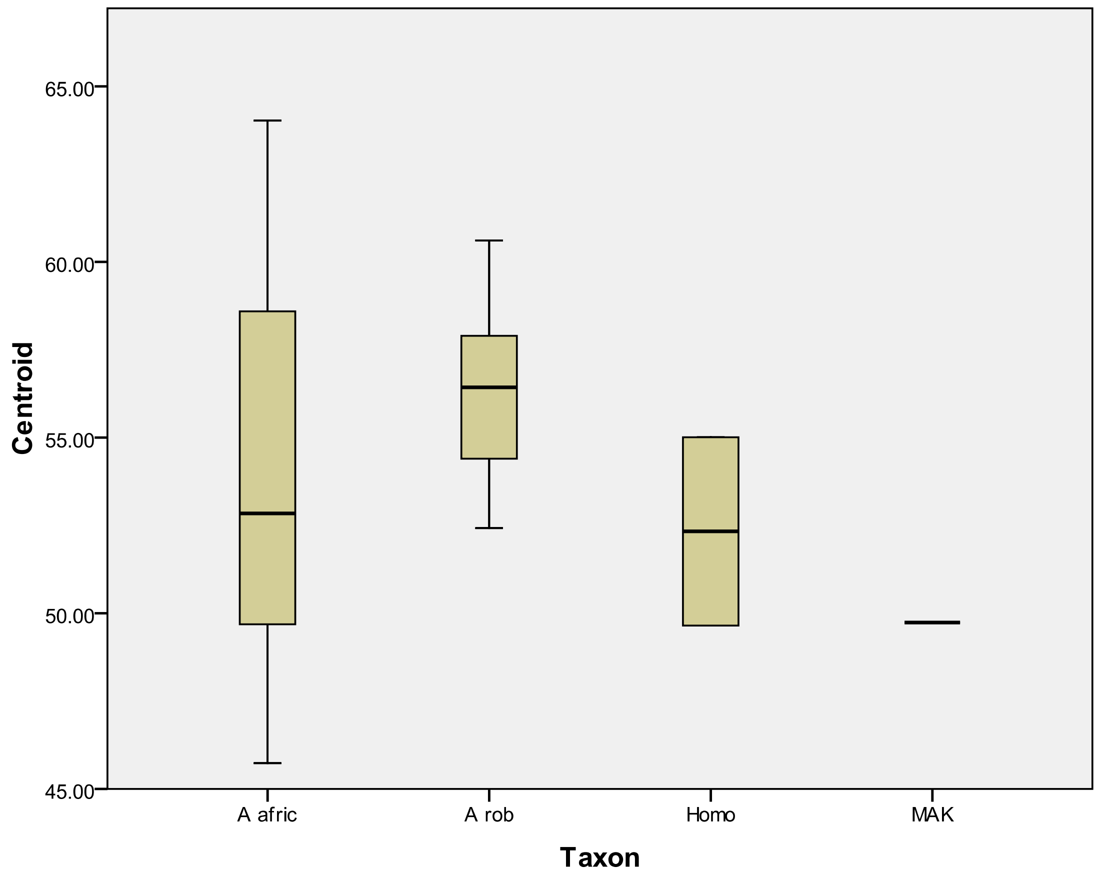
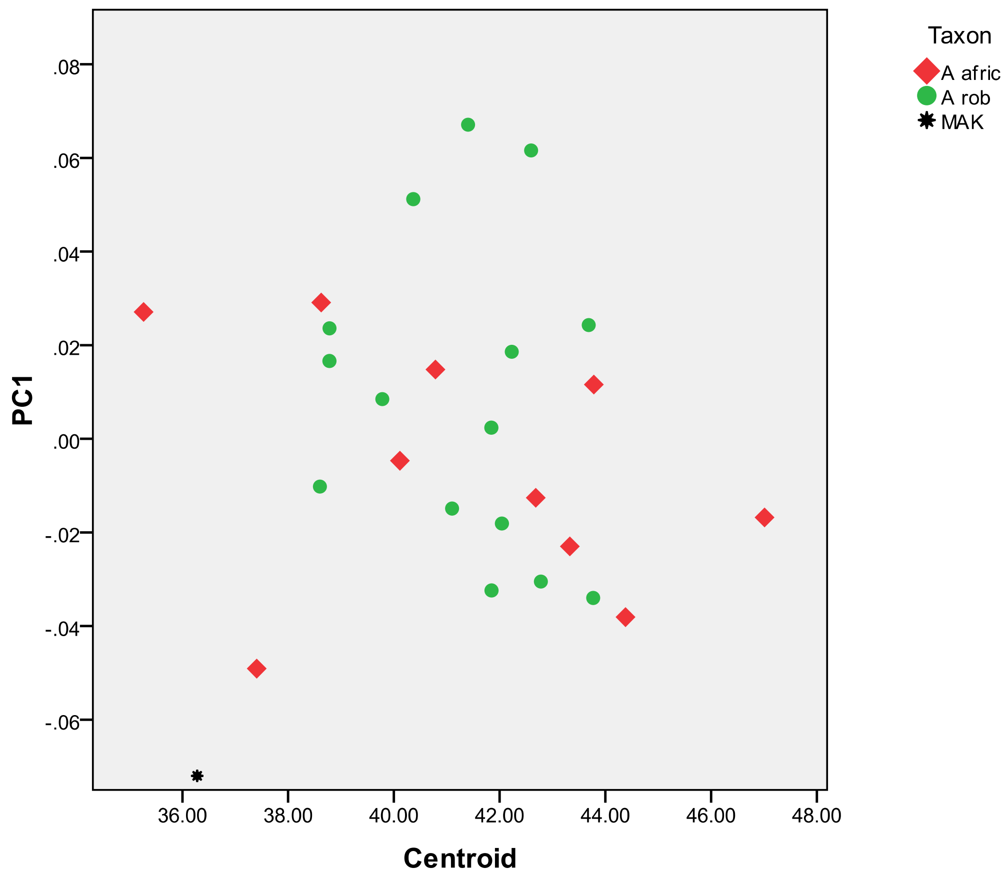
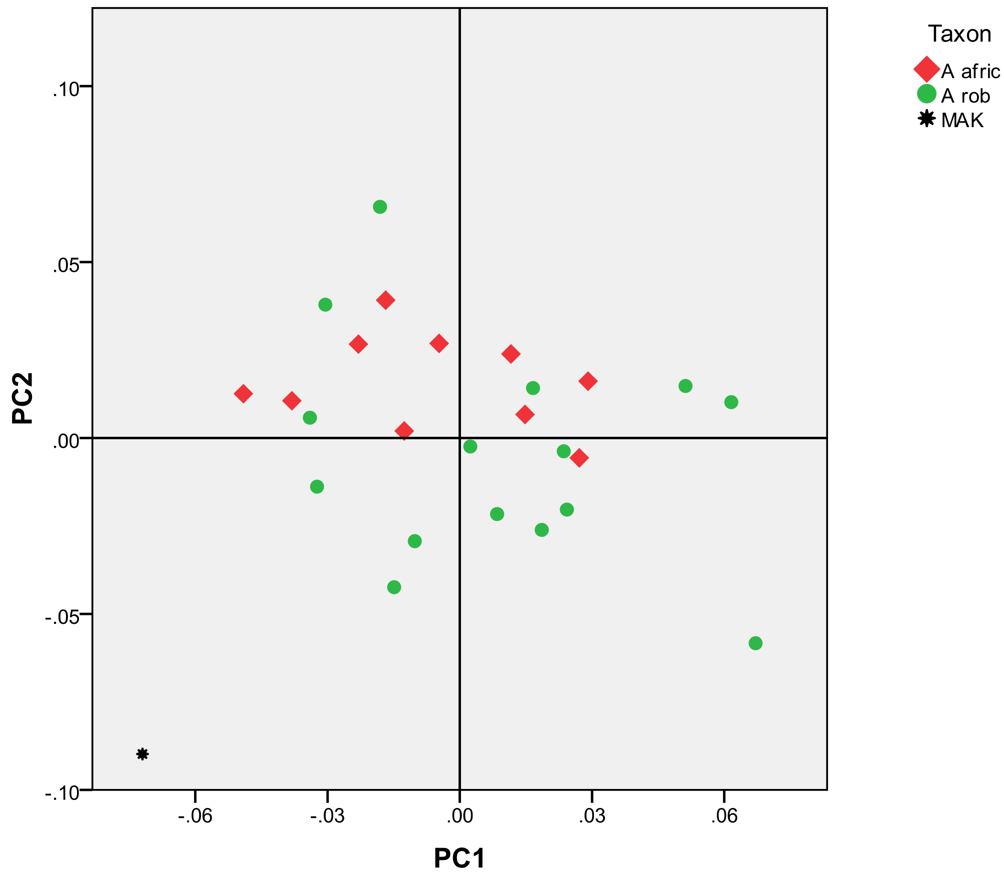


Figure 8-57*: *PCA of M³ Occlusal Outline Semi-landmark and Cusp Landmark Data. The first 3 principal components and centroid for the M³ semi-landmark occlusal outline and cusp landmark data are plotted (*a*, *b*, and *d*), where PC 1 explains 23%, PC 2 explains 21%, and PC 3 explains 13% of the variance in these data. The idealized shape configuration for the extremes of each principal component are also presented along representative axes (*c* and *e*).

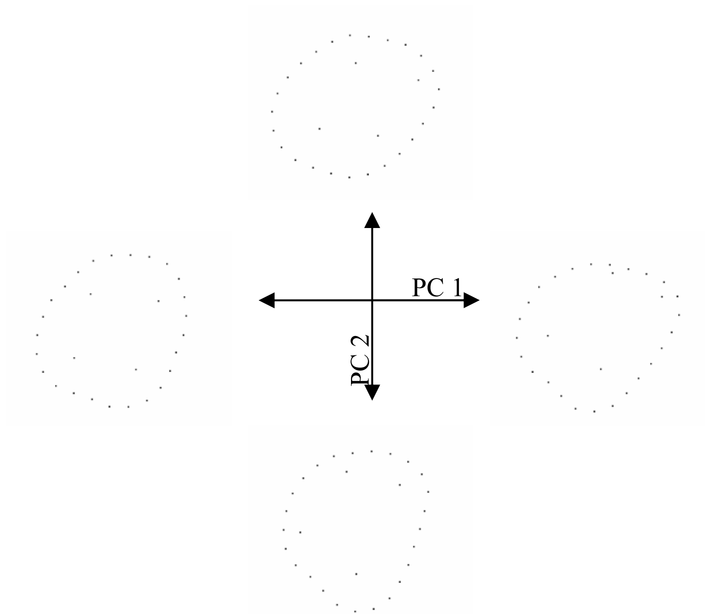
(*a*.)



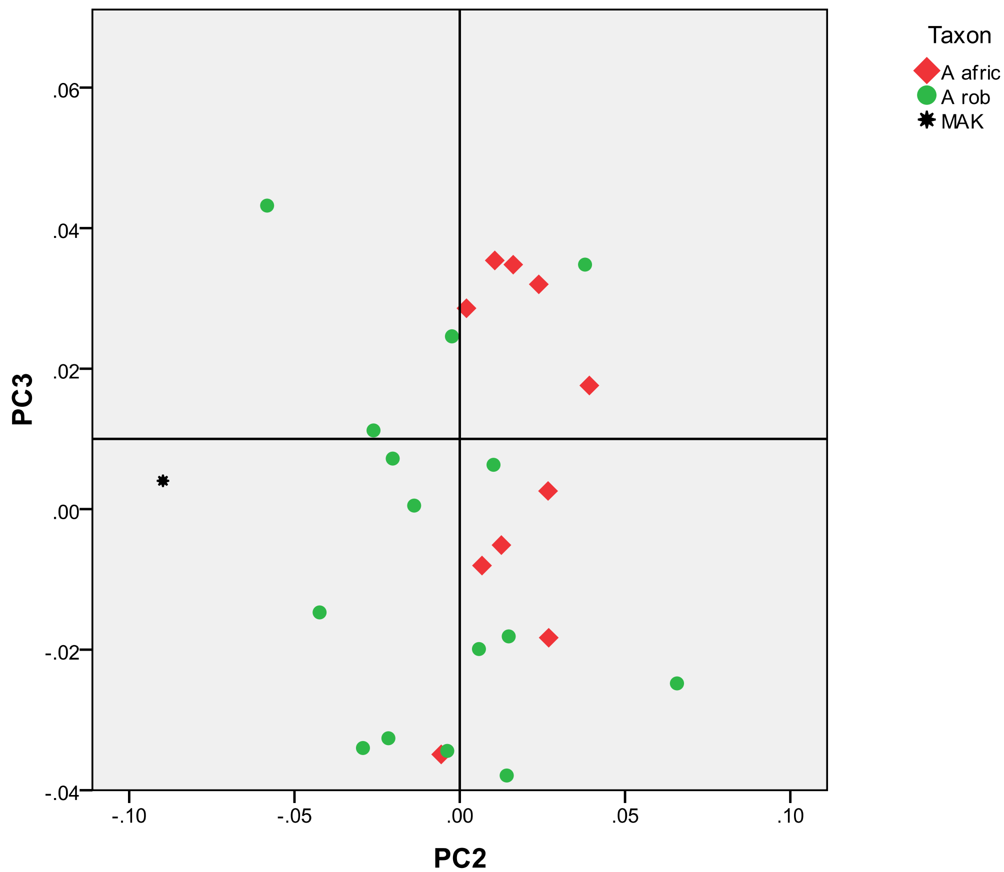
(*b.*)


Taxon
A afric
A rob
MAK
.10
.05
.00
-.05
-.10
PC2
-.06
-.03
.00
.03
.06
PC1

(*c.*)

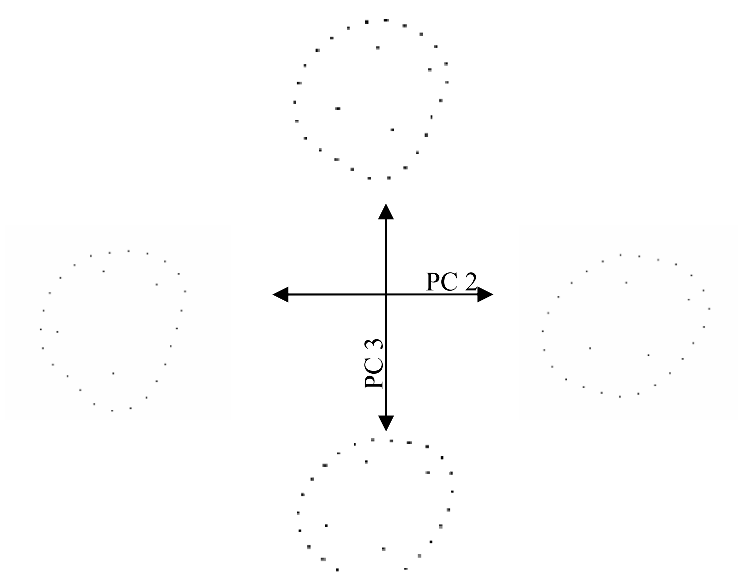

PC 1
PC 2

(d.)



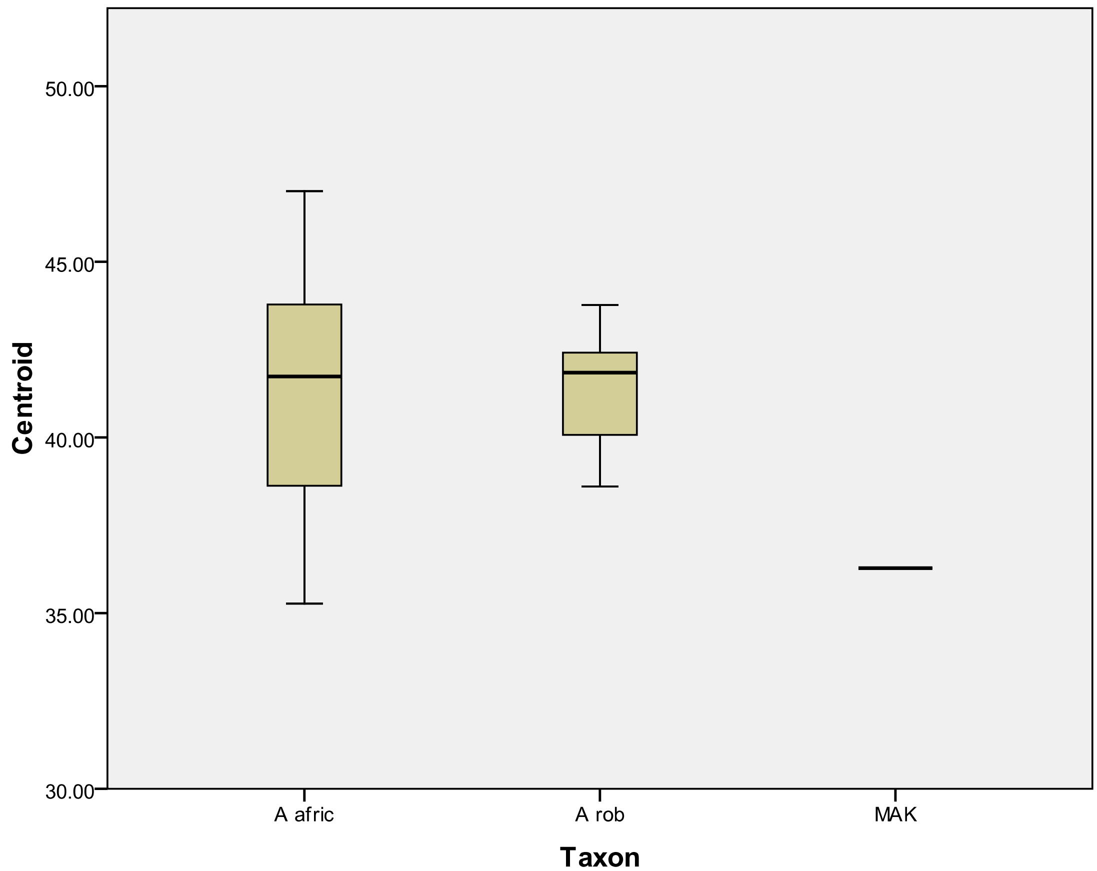
Taxon
A afric
A rob
MAK
.06
.04
.02
.00
-.02
-.04
PC3
-.10
-.05
.00
.05
.10
PC2

(e.)



PC 2
PC 3

***Figure 8-58*: Boxplot of the Centroids for P^3 Occlusal Outline Semi-landmark Data.** The median (line), 1st and 3rd quartiles (box), and range (bars) of centroid values for fossils based upon the Procrustes analysis of P^3 occlusal outline semi-landmark data are compared by taxon.



Discussion

The discussion in the following pages is focused upon characterizing the dental morphology of the Makapansgat specimens as best as possible given the limited sample sizes. Moreover, the emphasis is on trying to put these specimens into an appropriate comparative context, rather than summarizing every detail discussed in this chapter. Boxplots follow the discussion but for the sake of simplicity, only some of the more interesting boxplots are highlighted (Figures 8-59 to 8-84).

As a whole, the dentition displays considerable wear in several instances. In addition, the Makapansgat incisors and canines display linear enamel hypoplasias on a number of specimens and the unworn molars tend to exhibit fairly extensive hypoplastic pitting on the crown. Enamel hypoplasias have been identified in early hominins by a variety of authors (White, 1978; Johanson *et al.*, 1982; Tobias, 1986; Bombin, 1990; Brunet *et al.*, 2002). Guatelli-Steinberg (2003, 2004) examined these defects in light of differences in enamel development in the South and East African australopiths and found that the sample of *A. africanus* canines exhibits more defects than *A. robustus* as might be expected due to its longer crown formation period. Premolar and molar crenulation was visible in some unworn specimens of both South African australopith species, as well as the Makapansgat sample. Their prevalence is likely underestimated in South African Plio-Pleistocene hominins as a result of the moderate to heavy wear exhibited by the majority of specimens. Schwartz (2004) refers to crenulation of the postcanine dentition in South African australopiths as evidence of either an orangutan-human clade or the misidentification of South African fossil apes as hominin, while Tobias (1986) suggests that they may relate to enamel hypoplasia. Here they are considered suggestive of considerable (normal) variation in the enamel topography of unworn australopiths specimens within both of the currently recognized South African australopith species.

Incisors. Incisors have been the focus of a number of treatments that examine modern human variation in incisors between populations (e.g. Hrdlička, 1920; Mizugochi, 1985; Turner *et al.*, 1991; Scott and Turner, 1997). Moreover, the morphology of the incisors have been the focus of several arguments surrounding the phylogenetic relationships and taxonomic attribution of a variety of Miocene apes (e.g. Begun, 1992; Martin and Andrews, 1993; Andrews *et al.*, 1996; Ward *et al.*, 1999; Benefit and McCrossin, 2000). In contrast, few studies have focused exclusively on incisor variation in fossil hominins. This can be contributed, in part, to preservation issues that more heavily impact the anterior dentition of fossil hominins. Some of the best studies of early hominin incisors have focused upon dental microwear. Dental microwear analyses indicate that *A. africanus* incisors exhibit greater frequencies of microwear than *A. robustus* and, thus, suggest increased dietary variability and greater frequency of mastication of abrasives for individuals attributed to *A. africanus* (Ungar and Grine, 1991). As is the case for most early hominin samples, small sample sizes and extreme dental attrition plague the incisors known from Makapansgat. The only lower incisors preserved at Makapansgat belong to the MLD 18 mandibular fragment.

Lower Incisors. The mandibular incisors of MLD 18 are relatively vertical with broad roots and small cervical areas, but heavy wear precludes further discussion of these teeth and their morphology cannot be considered representative of the Makapansgat sample as they are merely one datum.

Upper Incisors. The maxillary incisors are better represented at Makapansgat (MLD 11/30, MLD 23, and MLD 43). The only maxillary I^1 from Makapansgat (MLD 43) is large with faint vertical ridges on the lingual face and a faint distal marginal ridge. The crown is broad and boasts a large crown area placing MLD 43 at the high end of crown area range in *A. africanus* and well above that of any specimen attributed to *A. robustus*. Its cervical area also places MLD 43 well within the range known for the samples of *A. africanus*, but above that of the hypodigm of *A. robustus* with the exception of SK 83.

The Makapansgat I^2s (MLD 23 and MLD 11/30) tend to display faint shovel-shaping and a weak to moderate distal marginal ridge, faint mesial marginal ridge, and weak to moderate lingual tubercle. The crown areas of these specimens fall within the range of the samples of both *A. africanus* and *A. robustus*, which essentially overlap. The I^2 cervical areas at Makapansgat fall within the range of both South African species, but nearest the median for the sample of *A. africanus*. The maxillary incisors more closely align the Makapansgat hominins with *A. africanus* due to their tendency to exhibit broad crowns, despite variation within the samples of *A. africanus* and *A. robustus*. A more careful study of the traits of early hominin incisors would inform these observations and the presence of particular features, such as a lingual tubercle, suggest that some of the Makapansgat specimens can be distinguished from the small Sterkfontein sample.

Examination of dental trait frequencies in extant apes clearly distinguished between species and subspecies, although these samples display considerable intra-specific and intra-subspecific variation (Pilbrow, 2006). Frequencies of mandibular and maxillary lingual incisor traits, rather than the clear presence or absence of a particular trait, discriminated the ape groups and clearly have potential for future studies of early hominins.

Canines. The morphology of the canine has been of considerable interest among researchers focused upon early hominins. Confounding these studies, however, is the potential for considerable sexual dimorphism in the early hominin canine as most anthropoids exhibit sexual dimorphism in the canines (e.g. Crook, 1972; Harvey *et al*., 1978; Plavcan, 1993, 2004, Thorén *et al*., 2006), evidence that the size and shape of the canine is not associated with diet (Plavcan, 1993), and suggestions that sexual selection on the canine is greater than body mass in haplorhines (Thorén *et al*., 2006). Even so, early hominin canine reduction has been well established for some time (e.g. Tobias, 1967; Robinson, 1972; Johanson *et al*., 1982; Greenfield, 1990; Senut *et al*., 2001; Haile-Selassie, 2001, 2004; White *et al*., 2006). Fortunately, the size and morphology of the mandibular and maxillary canines are quite disparate in the two South African australopith species. The specimens attributed to *A. robustus* are generally accepted as having smaller maxillary and mandibular canines than *A. africanus*, as well as a series of distinguishing features on the lingual aspects of these teeth (e.g. Robinson, 1954a, 1956, White *et al*., 1981).

Lower Canines. The mandibular canines represented at Makapansgat include the heavily worn MLD 18 and MLD 40 and moderately worn MLD 42 specimens. Unfortunately, having only 3 mandibular canine crowns (of which 2 are heavily worn) makes it difficult to characterize the Makapansgat specimens in terms of C_1 crown morphology. However, shared features of these C_1s include having a large crown with long and broad roots. The lingual aspects of these C_1s exhibit a variably present mesial fovea, shallow to moderate distal fovea, moderate to marked distal marginal ridge, and marked lingual ridge. The labial aspects of the C_1s display enamel pillars mesially, which is related to a stylid in one specimen (MLD 18). MLD 42, the best preserved C_1 from Makapansgat, additionally preserves a faint distal enamel pillar. This specimen also displays considerable asymmetry of the mesial and distal borders of the canine crown. The marked asymmetry in MLD 42 is likely representative of even the more worn Makapansgat C_1 specimens on the basis of the morphology of the preserved portions of the canines (i.e. slope and angle of the preserved lingual face). The C_1 area for MLD 18 is intermediate between the larger areas calculated for the samples of *A. africanus* and smaller areas for the samples of *A. robustus*. However, the C_1 area for MLD 18 likely is a slight underestimate due to the degree of attrition displayed by this tooth.

Upper Canines. The C^1 is preserved in MLD 11/30 solely, although MLD 23 preserves a maxillary canine alveolus. The single crown is asymmetrical with a longer mesial edge, weak labial grooves, small lingual tubercle, and weak mesial and distal marginal ridges. The crown and cervical areas of the C^1 are well within the range of *A. africanus*, but at the highest extreme of the sample of *A. robustus*.

The maxillary and mandibular canines provide some strong affinities to *A. africanus*, even in light of the small canine samples. The mandibular specimens are morphologically most similar to specimens attributed to *A. africanus* in their presumed large size, relatively marked asymmetry, marked distal marginal ridge, and marked lingual ridge (more obvious in the less worn specimens). The mandibular canine crowns are most similar to those of *A. africanus* by being broad with weak marginal ridges and small lingual tubercle. Although the maxillary canine at Makapansgat is somewhat asymmetrical and distinct, its overall crown morphology is more similar to the morphology that characterizes *A. africanus*. The degree of asymmetry exhibited by the maxillary canines attributed to *A. africanus* is minor in comparison to *A. afarensis*. While strongly asymmetrical canines are known within the hypodigm of *A. africanus* (White *et al*., 1981), many canines are somewhat intermediate between the degree of symmetry exhibited by robust australopiths and the earlier taxon *A. afarensis*. As a cautionary note, many of the canines available for study from Swartkrans and Sterkfontein are isolated and a more in depth treatment of canine variation in South African Plio-Pleistocene hominins is needed, particularly in light of the recent availability of new specimens from Sterkfontein and Drimolen (Moggi-Cecchi *et al*., 2006, Moggi-Cecchi, 2010).

Premolars. The premolar samples at Makapansgat permit several analyses to be undertaken, even despite the advanced dental wear of several of these specimens. LEHs are evident in some of the Makapansgat premolars (MLD 18, and MLD 6). Premolar morphology, particularly for the maxillary premolars, has been cited as distinguishing between the South African australopiths (e.g. Robinson, 1954a; Sperber, 1974).

Lower Premolars. The P_3 is preserved at Makapansgat in MLD 2, MLD 18, MLD 29, and MLD 40. Several of the P_3 specimens from Makapansgat are well worn, however, limiting the number of features that can be used to characterize the assemblage. The typical Makapansgat P_3 can be summarized as being buccolingually broad and bulbous. In addition, the P_3 crown is asymmetrical with a mesially situated protoconid and mesially truncated lingual cusp. This latter feature helps to distinguish the Makapansgat premolars (including MLD 2) from *A. robustus*. The vast majority of specimens attributed to *A. africanus* display an asymmetrical P_3 (94%), compared to a small fraction of those attributed to *A. robustus* (12%). All of the Makapansgat specimens in which this trait is visible are asymmetrical (n = 3), although this feature is least developed in the somewhat contentious MLD 2 specimen. The distal accessory ridge of the P_3 protoconid differentiates the South African australopith species as it tends to be more marked in the sample of *A. robustus* than *A. africanus*. The MLD 2 specimen is more marked in this feature than any specimen attributed to *A. africanus*, but is similar to a significant percentage of the specimens attributed to *A. robustus* (40%). This latter feature is variable across modern human populations, however (Burnett *et al.*, 2010).

Dental metrics (crown and cervical areas and indices) could statistically distinguish neither the *A. robustus* and *A. africanus* P_3 samples from each other, nor the Makapansgat sample from either of the South African australopith species samples. The ranges of these variables also failed to discriminate the samples. In his initial treatment of the South African hominin dentition, Robinson (1954a) suggested that there is more marked sexual dimorphism in the P_3 due to the great variation in size and structure displayed by the South African australopiths species. Indeed, the great variation in size and morphology within the samples supports his contention and made discrimination of the Makapansgat sample from other australopith samples difficult for the P_3. Morphometric analyses of the P_3 occlusal outline and cusps in Morphologika could not distinguish the Makapansgat sample from either South African australopith species, although it could be argued that the MLD 2 specimen shows slightly greater similarity with *A. robustus* in morphology and centroid size. The trait data provide the strongest support for a link between the samples for Makapansgat with *A. africanus*, although the MLD 2 specimen displays somewhat weaker ties to *A. africanus* in these data. Even so, considerable overlap in the morphology of the samples of *A. robustus* and *A. africanus* makes it difficult to discriminate between the South African australopith samples in terms of the presence or absence traits and, instead, requires the focus on differences in the frequency of character states.

The P_4 is preserved in MLD 2, MLD 18, MLD 29, and MLD 40. Its typical morphology can be described at Makapansgat as being relatively large (in comparison to the M_1), buccolingually broad, and having a broad, bulbous, symmetrical crown with an expanded metaconid and talonid basin. The protoconid can be characterized as being somewhat mesially situated. Many of the Makapansgat P_4s are heavily worn. The occlusal shape of the Makapansgat P_4s (of which 100% are symmetrical) align them with the sample of *A. africanus* (of which 70% are symmetrical) more so than with the sample of *A. robustus* (of which 44% are symmetrical). While P_4 crown area statistically differentiated the samples of *A. robustus* and *A. africanus* from each other ($p = 0.003$), the small Makapansgat sample size (n = 2) did not permit analysis. The mean value of crown area for *A. africanus* (128.2 mm) and *A. robustus* (150.6 mm) and actual values for MLD 2 (106.52 mm) and MLD 40 (114.21 mm) suggest a closer affinity for the Makapansgat hominins with *A. africanus*. In addition, the Makapansgat sample for P_4 area falls below the range known for *A. robustus* and within that of *A. africanus*.

Examination of the boxplots of P_4 cervical area indicate that the robusts have larger values and MLD 40 falls below the range known for specimens of *A. robustus*, but within that for specimens of *A. africanus*. Boxplots of P_4 crown index (Figure 8-66) indicate that the ratio of mesiodistal length to buccolingual breadth for the Makapansgat specimens are on the low end of both australopith species ranges. The morphometric analyses of the P_4 support many of the above conclusions as they suggest that the Makapansgat specimens are more similar to the sample of *A. africanus* morphologically and by overall size (confirming the conclusions drawn from comparison of P_4 crown and cervical area estimates).

The Makapansgat lower premolars exhibit strongest affinities to the sample of *A. africanus* on the basis of the asymmetry of the P_3 crown. The morphometric and linear metric data were inconclusive as both South African australopith species displayed considerable variation and overlap. However, the MLD 2 P_3 specimen exhibits some morphological affinities with *A. robustus*. The Makapansgat P_4s are more similar to *A. africanus* on the basis of frequency of crown symmetry, crown and cervical areas (although not statistically significant), and overall crown morphology and size.

Upper Premolars. The morphology of the P^3 is preserved in several specimens at Makapansgat, including MLD 6, MLD 11/30, MLD 23, and MLD 45. These P^3s can be characterized as being smaller than the P^4 with a bulbous lingual aspect, moderate to marked distal accessory ridge on the protocone, and accessory marginal tubercles. Accessory marginal tubercles are common in both South African species, but more so in *A. robustus* (100%) than *A. africanus* (69%). Both of the Makapansgat P^3s that preserve the region display mesial and distal accessory marginal tubercles. The presence of accessory marginal tubercles both mesially and distally occurs frequently in the *A. robustus* (93%) and less so in *A. africanus* (23%). Unfortunately, the Makapansgat sample cannot be discriminated from either sample on this basis. The number of roots is variable within the small Makapansgat sample, which fails to discriminate among the samples.

The Makapansgat sample was statistically differentiated from *A. robustus* on the basis of P^3 crown area. It falls within the middle of the range of variation in P^3 crown area for *A. africanus*, but on the lowest extreme of that for *A. robustus*. The cervical area of the P^3 falls within the range of both species. The P^3 cervical index (Figure 8-63) indicates that the ratio of P^3 mesiodistal cervical length to buccolingual breadth is high in both MLD 23 and MLD 45 in comparison to both South African australopith species. The morphometric analysis of the occlusal outline and cusps indicate that the Makapansgat P^3s are most similar to the sample of *A. africanus*, although there was some overlap with the sample of *A. robustus*. A comparison of size (via both crown areas and centroid sizes) discriminates the Makapansgat sample from that of *A. robustus*.

Only 2 specimens, MLD 6 and MLD 9/12, preserve the P^4 at Makapansgat. The Makapansgat P^4s are relatively broad buccolingually but cannot be otherwise characterized as a group due to the small sample (n = 2) and the heavy wear exhibited by one of these specimens (MLD 9/12). However, P^4 mesial and distal accessory marginal tubercles are consistently present in *A. robustus* (100%), but inconsistently in *A. africanus* (33%). MLD 6 is the only specimen for which these data were preserved at Makapansgat. Its morphology supports its alignment with the sample of *A. africanus* due to it only displaying accessory marginal tubercles distally. Despite the small sample, crown areas of the Makapansgat P^4s fell below the value of any specimen currently attributed to *A. robustus* and within the range of *A. africanus*. Their cervical areas are positioned at the lowest extreme of *A. robustus* and in the middle of the range of *A. africanus*. While statistical analysis distinguished the samples of *A. robustus* and *A. africanus* from each other in P_4 crown area, the small sample at Makapansgat (N = 2) was not statistically compared. Morphometric analysis (GPA) of the occlusal outlines and cusps do not discriminate MLD 6 from either species on the basis of size or morphology.

Unfortunately, frequency of traits do not discriminate the Makapansgat sample from either of the South African australopiths, yet the P^3 is considered to be more similar to *A. africanus* on the basis of P^3 crown area. In addition, morphometric analysis (GPA) of the overall crown outline and cusps indicates that the Makapansgat sample is more similar to *A. africanus* on the basis of morphology and size. Makapansgat P^4 trait frequencies, crown areas, and cervical areas are more similar to *A. africanus* than *A. robustus*. Morphometric analysis could not discriminate among the samples.

Molars. The morphology of hominin molars have been the focus of a number of treatments. In general, molars attributed to *A. africanus* exhibit steeper facets than those of *A. robustus*, suggesting increased shearing for the former versus grinding for the later taxon (Grine, 1981). Analyses of shearing quotients, the potential for shearing based upon measuring crest lengths along a mesiodistal axis for unworn molars (Kay, 1978, 1984), have contributed to this discussion. Specimens of both *A. robustus* and *A. africanus* exhibit lower shearing quotients than extant hominoids and, as one might expect, specimens of *A. robustus* exhibit even lower shearing quotients than those of *A. africanus* (Ungar *et al*., 1999; Teaford *et al*., 2002). In addition, dental topographic analyses were executed to analyze 3-D occlusal morphology on both worn and unworn mandibular molars in *A. africanus* and *A. robustus* and confirmed that the molars of *A. africanus* exhibit more sloped occlusal surfaces than *A. robustus* (Ungar, 2007b). This is even more extreme in unworn specimens, but the comparison is consistent regardless of the wear stage. Differences in the angle of the enamel prisms of *A. robustus* and *A. africanus* indicate that the teeth of the former are stiffer and better resist vertical tooth loads, while those of the latter are more resistant to wear and better resist lateral tooth loads (Macho and Shimizu, 2009).

Lest we assume that dental morphology reflects the foods most commonly eaten (Kay, 1975), it is critical to remember that it also reflects selection for fallback foods (e.g. Kinzey, 1978; Robinson and Wilson, 1998; Lambert *et al*., 2004; see also discussion in Ungar, 2007b). However, there are differences in microwear between *A. robustus* and *A. africanus*, indicating dietary distinctions between these species (e.g. Grine, 1986; Grine and Kay, 1988; Ungar and Grine, 1991), although there is dietary overlap in these taxa (Scott *et al*., 2005) and greater variation within *A. africanus* (Ungar *et al*., 1999). Isotope studies of four of the actual Makapansgat hominins indicate that these hominins had a variable diet and ate a diet rich in C_4 plants despite the clear availability of C_3 plants (Sponheimer and Lee-Thorp, 1999). These data suggest that the Makapansgat hominins ate either C_4 grasses and sedges or high quality animal foods, supporting a variety of morphological analyses of the dentition (e.g. Wolpoff, 1973). Isotopic data for a number of individuals attributed to *A. africanus* at Sterkfontein indicate that this species ate a diet rich in C_4 plants and was unusually varied in its dietary intake (van der Merwe *et al*., 2003); while data for *A. robustus* suggests this taxon also was a dietary generalist (Lee-Thorp *et al*., 1994; 2000).

Morphological analyses have discriminated between the South African australopiths *A. africanus* and *A. robustus*, particularly on the basis of frequencies of traits and in differences between the sample means. The variation within the sample of *A. africanus* has been considered high although Moggi-Cecchi (2003) analyzed the mesiodistal and buccolingual diameters and CVs of the Sterkfontein Member 4 dental sample, which does not support an additional species within the Sterkfontein Member 4 assemblage. Their data demonstrate that although the dental sample for *A. africanus* exhibits higher CVs for most mesiodistal and buccolingual dimensions than their sample of *A. robustus*, other taxa (*A. boisei* and *H. habilis sensu lato*) exhibit greater CVs than *A. africanus*. However, Scott and Lockwood (2004) cautioned on the basis of a study focused upon the mandibular teeth of great apes and humans, that the patterns of dental metric variation may not be useful in distinguishing mixed-species assemblages. This is particularly true for comparisons of size, but shape variation could potentially distinguish species.

Unfortunately, shape analyses are also fraught with difficulty in rejecting the assumption that a sample represents one species. Regardless, the morphology of the EDJ distinguished between the mandibular molars of *A. africanus* and *A. robustus*, although there was greater variation between metameres intraspecifically than between the same tooth interspecifically (Skinner *et al*., 2008), a pattern that holds for variation in the EDJ of extant humans maxillary and mandibular teeth but less so for chimps and Sts 52 (*A. africanus*) (Braga *et al*., 2010). Here, the Makapansgat molars were the focus of trait, linear metric, and morphometric (size and shape) analyses to assess their morphology in the context of *A. robustus* and *A. africanus*.

Lower Molars. Several specimens preserve lower molars at Makapansgat. Due to the similar morphology in M_1 and M_2 specimens at Makapansgat, these teeth are discussed as a group. The M_1 is represented by MLD 2, MLD 18, MLD 29, MLD 40, and MLD 48; while the M_2 is represented by MLD 2, MLD 18, MLD 22, MLD 24, and MLD 40. The current M_1 and M_2 samples at Makapansgat tend to exhibit a relatively small and buccolingually compressed entoconid, relatively large metaconid, highly variable protostylid, incipient to weak development of a *tuberculum intermedium*, no *tuberculum sextum*, and buccolingually broad crown (particularly mesial). The protoconid and hypoconid tend to appear buccolingually broad, although the great breadth of the former may relate to a large protostylid feature being obscured by wear in part of the sample.

Most specimens exhibit a Y fissure pattern, although a + pattern is also represented in the Makapansgat M_{1-2} sample. The M_1 is smaller than the M_2 in every case.

Although several traits discriminate the M_1 samples of *A. robustus* and *A. africanus* to some degree (i.e. frequencies of character states for the cusp number, *tuberculum sextum*, *tuberculum intermedium*, protostylid, distal trigonid crest, and fissure pattern), the small number of specimens for which traits can be confidently recorded within the Makapansgat sample severely limit the utility of these data. However, an analysis of protostylid form at the EDJ indicates differences between *A. africanus* and *A. robustus*, although the protostylid form at the EDJ does not necessarily correspond to form at the occlusal surface (Skinner *et al*., 2009).

The situation is the same for the M_2 where frequencies of characters discriminate the australopith species to some degree (i.e. cusp number, *tuberculum sextum*, distal trigonid crest, deflecting wrinkle, entoconid-hypoconulid crest, and fissure pattern). Despite overlap, cusp number most strongly discriminates between M_1 samples of *A. robustus* and *A. africanus*. However, only MLD 2 preserves the M_1 cusps. While the MLD 2 M_1 displays 5 cusps, it cannot be discriminated from either sample on this basis. In contrast, 100% of the M_2s of *A. robustus* exhibit accessory cusps compared to 46% of the M_2s of *A. africanus*. Only 1 of the 2 Makapansgat specimens preserving the cusp number exhibits an accessory cusp, aligning these specimens with *A. africanus*. Data on the presence and absence of the *tuberculum sextum* and *tuberculum intermedium* are highly suggestive of assignment to either *A. africanus* or *A. robustus*. The presence of a *tuberculum sextum* and absence of a *tuberculum intermedium* are typical in robust hominins (Wood and Abbott, 1983; Suwa *et al*., 1994). Every one of the 22 M_2s attributed to *A. robustus* exhibit a *tuberculum sextum*. As a result, the absence of a *tuberculum sextum* in 2 of the 3 Makapansgat M_2s aligns the sample with *A. africanus*.

The Makapansgat assemblage's M_1 and M_2 crown and cervical areas fall within the range of variation in both species and could not be statistically differentiated from either sample. In addition, the M_1 crown index (Figure 8-71) is relatively low at Makapansgat although it overlaps with both species. The M_1 cervical-crown index indicates that the ratio of M_1 cervical area to M_1 crown area at Makapansgat is well above the majority of South African australopiths. Only Sts 24 and SK 55 have values above the Makapansgat specimens in this variable. Morphometric analyses of the occlusal outlines and cusps did discriminate the M_1 South African australopith species on the basis of morphology and, to a lesser degree, size. The MLD 2 M_1 specimen is more like the robust sample in size but cannot be discriminated from either species on the basis of morphology, according to the morphometric analysis. The MLD 2 M_2 specimen is one of the largest of any of the australopith specimens, but otherwise could not be discriminated from either australopith species on the basis of morphometric analyses.

The M_3 is preserved in several Makapansgat specimens, MLD 4, MLD 18, MLD 19, MLD 22, MLD 40, and MLD 47. The number of cusps varies from 5 to 7. The M_3 can be characterized as having a variably developed *tuberculum sextum*, variably present *tuberculum intermedium*, variable protostylid formation, buccolingually broad protoconid and hypoconid, distally tapering occlusal outline, accessory cuspulid development (particularly distally), and buccally situated hypoconulid. The M_3 is typically larger than the M_2, with the exception of MLD 18. The ratio of *tuberculum sextum* area to hypoconulid area has been used with some success to separate *A. robustus* and *A. africanus* M_3s where the hypoconulid is larger (dividing point 0.8 - 0.9) (Suwa *et al.*, 1996). The Makapansgat sample's M_3 crown and cervical areas fall within the broad ranges of both australopith species. However, both M_3 crown and cervical area means at Makapansgat are statistically different than the sample of *A. robustus*, even though the samples of *A. robustus* and *A. africanus* are not significantly different from each other. The M_3 cervical-crown index (Figure 8-82) indicates that the ratio of M_3 cervical area to crown area is relatively low in Makapansgat sample. Morphometric analysis of the M_3 occlusal outlines and cusps suggest that the Makapansgat sample is more similar to that of *A. africanus* on the basis of morphology but there is considerable overlap in size.

The mandibular molars provide somewhat conflicting information. The M_1 and M_2 are aligned with the sample of *A. africanus* on the basis of M_2 cusp number and variable absence of an M_2 *tuberculum sextum*. The broad protoconid is relatively unique at Makapansgat, as is the extremely marked MLD 2 protostylid (although the latter is more similar to the sample of *A. robustus*). It is possible that the great protoconid breadth at Makapansgat is the result of obscured and tall protostylids that have been obscured by wear. Morphometric (GPA) analysis of the MLD 2 M_1 aligned this specimen with *A. robustus* on the basis of overall size, but could not be distinguished from either sample on the basis of morphology. Morphometric analysis of the MLD 2 M_2 could not discriminate it from either australopith taxon. The M_3 is considered to be more similar to the sample of *A. africanus* on the basis of crown and cervical areas. In addition, they are more similar to *A. africanus* in morphology and size according to morphometric analysis (GPA) of the occlusal outlines and cusps.

Upper Molars. The M^1 is represented at Makapansgat by MLD 6, MLD 9/12, and MLD 11/30, while the M^2 is represented by MLD 6, MLD 9/12, MLD 28, and MLD 44. These teeth can be characterized as having a large and broad protocone, mesiodistally short hypocone, thick crista obliqua incised by the main longitudinal fissure, variably developed distal marginal ridge, variable development of a Carabelli feature, and marked buccal groove. These teeth display a tendency towards cingular development, in general. The faint stylar cusps and associated grooves of the M^1 and M^2 are located in regions well associated with and related to cingular development. Previous analyses of cusp areas indicate that the M^1 protocone is significantly larger in *A. africanus* than *A. robustus* (Moggi-Cecchi and Boccone, 2007); however, it seems possible that the inclusion of the Makapansgat sample with broad protocones impacts these results. It has been suggested that M^1 cusp proportions change with changes in the overall size of a tooth and that the metacone reduces as crown size decreases (Quam *et al*., 2009). These authors argue that the relative size of M^1 paracone and metacone may have utility in discriminating specimens of early and late *Homo*. Perhaps the differences in the Makapansgat and Sterkfontein hominins represent a similar change in relationship over time and relating to crown size.

Carabelli's cusps had been identified previously as being highly variable but more prominent in samples of *A. africanus* than *A. robustus* while the lingual pit is more frequently absent in *A. robustus* (Sperber, 1974; Reid and van Reenen, 1995). The

Makapansgat hominins alone displayed considerable variation in the appearance of the Carabelli's Complex. Data presented in the previous pages supports that specimens of *A. africanus* exhibit greater prominence of Carabelli's cusps in M^1, but not necessarily M^2 or M^3. The size of Carabelli's cusps has been argued to increase in the more distal metameres (Reid and van Reenen, 1995). The data tables below indicate that this is the case for *A. robustus*, but the sample of *A. africanus* exhibits the most marked Carabelli's cusps in the M^1. The large Carabelli's reported in maxillary molars of *A. africanus* can be compared to molars of *A. robustus* that appear to have more enamel, in general, particularly along the lingual aspect of the protocone (e.g. Conroy, 1991; Macho and Thackeray, 1992; Schwartz *et al*., 1998). More recent analyses of these features using micro-CT support that robusts have smaller Carabelli features and thicker enamel on the lingual aspect of the protocone (Schwartz *et al*., 1998). Moreover, Carabelli's features located on the EDJ are not necessarily correlated with a cingulum or accessory cusp on the crown in SA australopiths and lack of a cingulum at the crown does not rule out the possibility that a feature is present at the EDJ.

Whenever both teeth are preserved in the Makapansgat sample, they exhibit a pattern whereby $M^2 > M^1$. The crown areas are largest in the M^2 for the sample of *A. africanus*, but for *A. robustus* they tend to increases distally, a pattern that had been identified elsewhere (Wood and Engleman, 1988; Moggi-Cecchi and Boccone, 2007).The upper M^1 and M^2 crown area ranges are almost entirely overlapping for these two species of South African australopiths. Not surprisingly, the Makapansgat M^1 and M^2 crown and cervical area samples thus fall within the ranges of both species. Neither M^1 nor M^2

crown and cervical areas statistically differentiated the South African australopith species *A. africanus* and *A. robustus*. These results support claims from a variety of earlier authors regarding similar crown areas for these taxa (e.g. Robinson, 1956; Sperber, 1973; Wood and Engleman, 1988). The Makapansgat M^1 sample was not statistically assessed due to small sample size. The M^2 crown and cervical data (for which Makapansgat had 3 specimens) did not differentiate the Makapansgat sample from either species. Morphometric analysis of the occlusal outlines and cusps for these teeth did little to discriminate the Makapansgat samples from either australopith species.

The M^3 is represented by the worn MLD 9/12 and better preserved MLD 28 and MLD 37/38 specimens (although see discussion regarding MLD 41 and MLD 44 in the preceding pages). Few features are visible in the MLD 9/12 specimen, so it is difficult to list shared traits for the Makapansgat M^3 beyond the distally tapered occlusal shape and the short height of the buccal groove. The M^2 is larger than the M^3 in each of the Makapansgat specimens preserving both teeth. The South African australopith species are distinguished on the basis of the frequency of character states for mesial marginal accessory tubercles and the distal cuspule but do not discriminate the Makapansgat sample from either taxon. The Makapansgat M^3 crown area sample falls within the middle of the range of *A. africanus* and below the range of *A. robustus*. In terms of M^3 cervical area, the Makapansgat sample falls within the ranges of both species, but closer to the median for robusts. However, GPAs and subsequent PCAs of the occlusal outlines and cusps suggest that MLD 28 is fairly unique in shape, but falls closer to the sample of *A. africanus* on the basis of its small size.

The Makapansgat M^1s and M^2s could not be discriminated from either South African australopith on the basis of traits, crown area, cervical area, or GPA. Although *A. africanus* and *A. robustus* are similar in their M^3 crown areas, they exhibit different cusp proportions (Suwa *et al*., 1994), while Boccone and Moggi-Cecchi (2006) suggest that cusp areas of *A. africanus* and *A. robustus* are only distinct without the contentious StW 252 and StW 183 specimens. The Makapansgat M^3s display closer affinities with *A. africanus* due to greater similarity in M^3 crown area. On the basis of morphometric analysis of the occlusal outline and cusps, the MLD 28 specimen is considered to be relatively distinct, but more similar to the sample of *A. africanus* by its size.

Summary

The early hominin dentition preserved at Makapansgat were assessed using qualitative and quantitative methods (trait, linear metric, and morphometric data). Results indicate a complex patterning of variation for the South African early hominin samples not aligning well with current site and taxonomic boundaries. New discoveries continue to highlight the high levels of intraspecific morphological variation, trait variation, and morphometric overlap for the dentition of South African early hominins. For instance, the recent publication of the dental remains from Drimolen (Moggi-Cecchi *et al*., 2010) suggest that these australopith teeth may be smaller and more variable than the teeth attributed to *A. robustus* from Swartkrans.

Figure 8-69: P_3 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P_3 crown area [P_3 mesiodistal length of crown * P_3 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2 and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 17), Swartkrans *A. robustus* (n = 12), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 1).

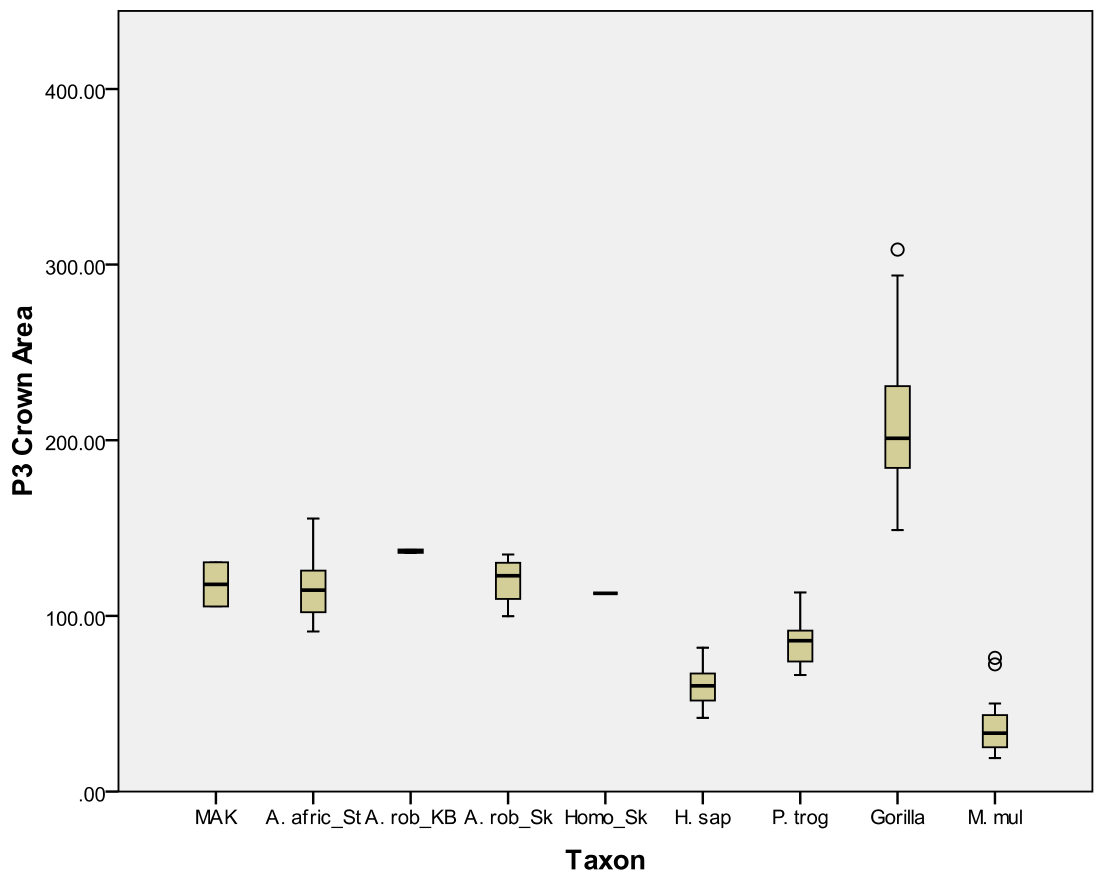


Figure 8-70: P_3 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P_3 cervical area [P_s mesiodistal length of cervix * P_4 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 16), Swartkrans *A. robustus* (n = 12), Kromdraai *A. robustus* (n = 2), and Swartkrans *Homo* (n = 1).

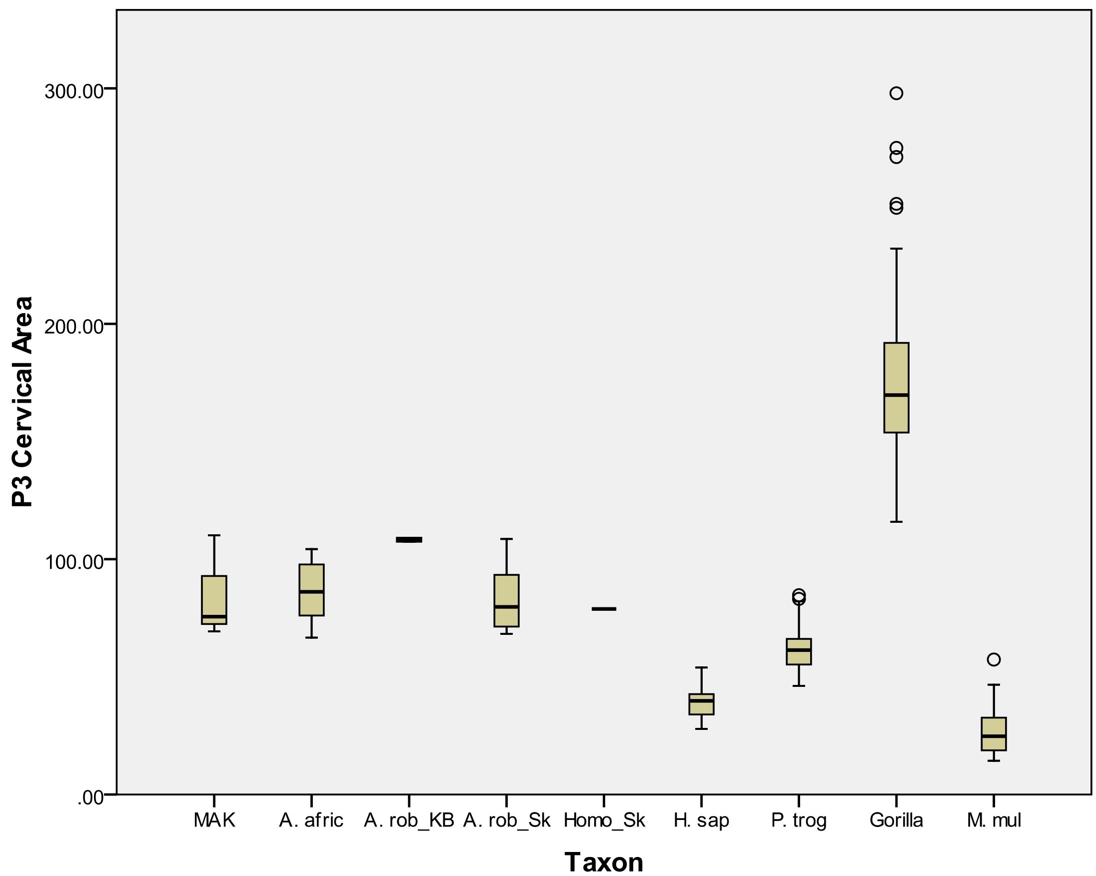


Figure 8-71: P^3 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P^3 crown area [P^3 mesiodistal length of crown * P^3 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 11/30, MLD 23, and MLD 45. The fossil sample sizes for this analysis are: *A. africanus* (n = 14), Swartkrans *A. robustus* (n = 24), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 1), Sterkfontein *Homo* (n = 1), and Sterkfontein *incertae sedis* (n = 1).

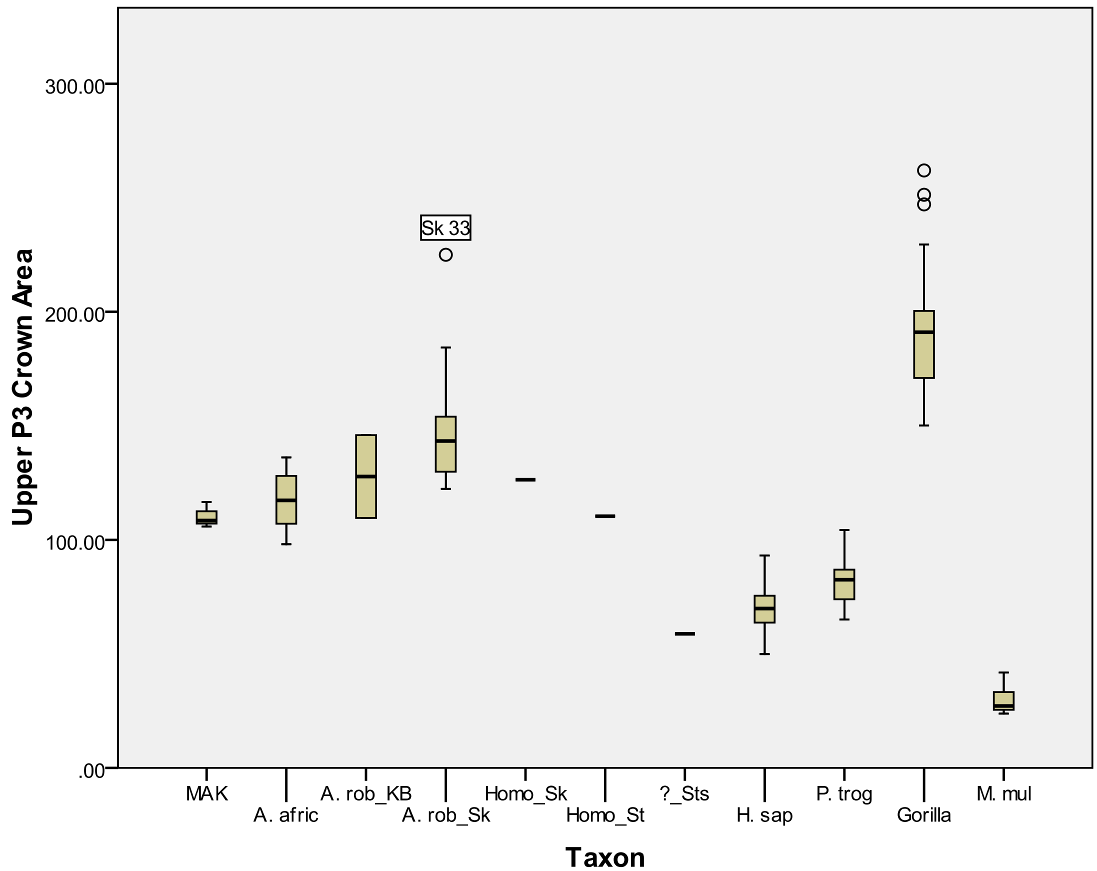


Figure 8-72: P^3 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P^3 cervical area [P^3 mesiodistal length of cervix * P^3 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 23 and MLD 45. The fossil sample sizes for this analysis are: *A. africanus* (n = 18), Swartkrans *A. robustus* (n = 22), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 2), Sterkfontein *Homo* (n = 1), Sterkfontein *incertae sedis* (n = 1).

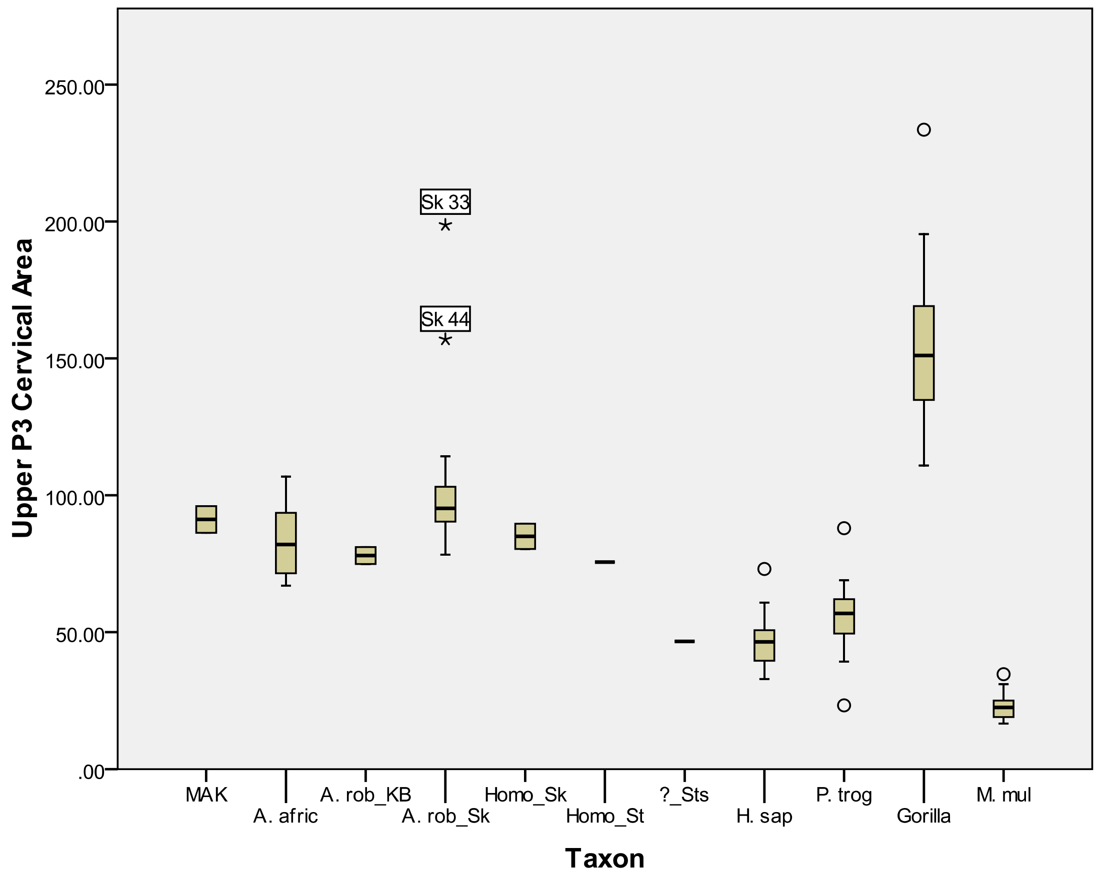


Figure 8-73: P^3 Cervical Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P^3 cervical index [(P^3 mesiodistal length of cervix /P^3 buccolingual breadth of cervic) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle or star. The Makapansgat sample is represented here by MLD 23 and MLD 45. The fossil sample sizes for this analysis are: *A. africanus* (n = 18), Swartkrans *A. robustus* (n = 22), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 2), Sterkfontein *Homo* (n = 1), and Sterkfontein *incertae sedis* (n = 1).

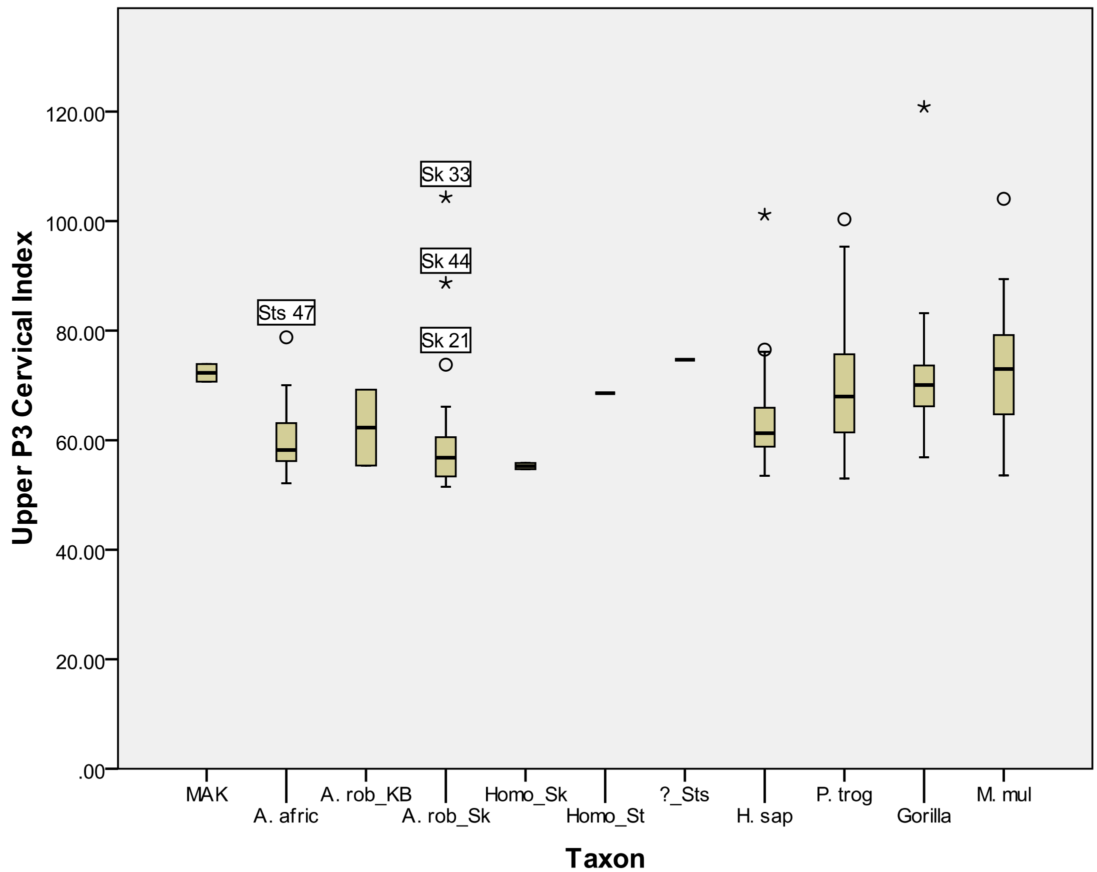


Figure 8-74: P_4 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P_4 crown area [P_4 mesiodistal length of crown * P_4 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18 and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 19), Swartkrans *A. robustus* (n = 14), Kromdraai *A. robustus* (n = 1), and Sterkfontein *Homo* (n = 1).

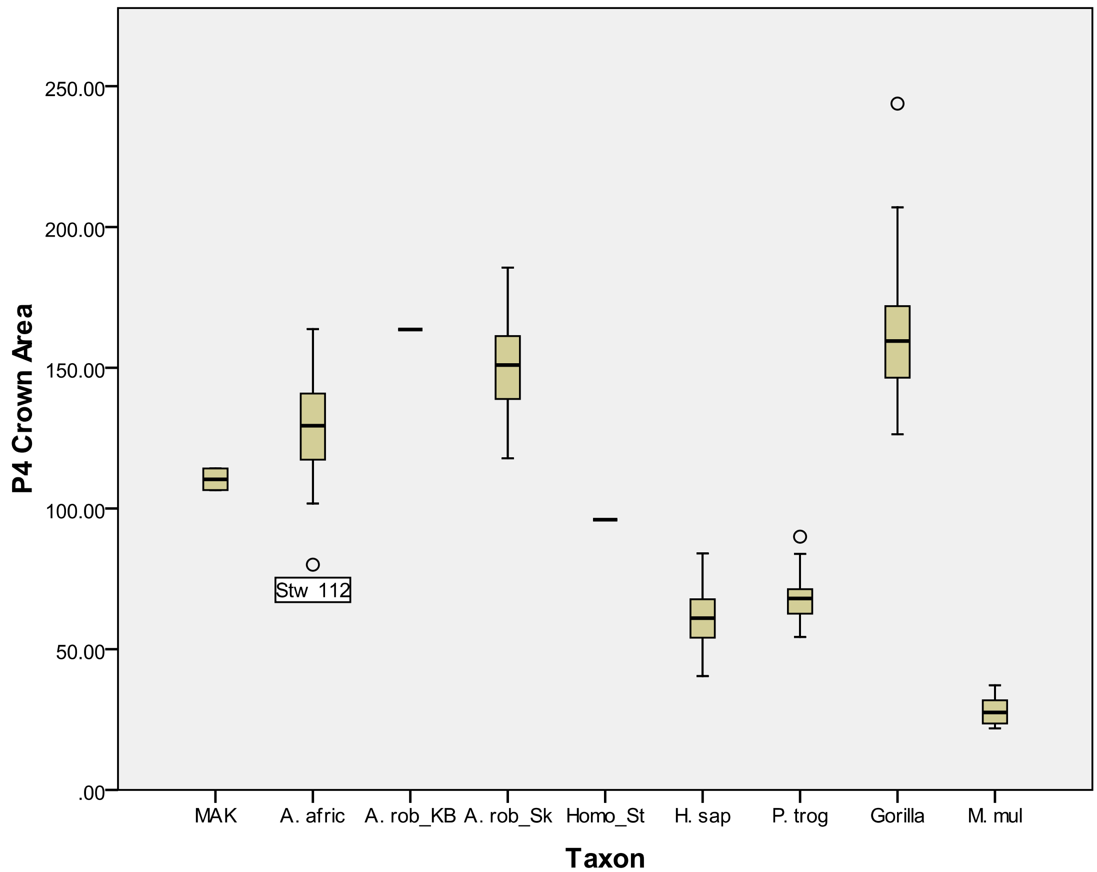


Figure 8-75: P_4 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P_4 cervical area [P_4 mesiodistal length of cervix * P_4 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18 and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 19), Swartkrans *A. robustus* (n = 14) and Kromdraai *A. robustus* (n = 1).

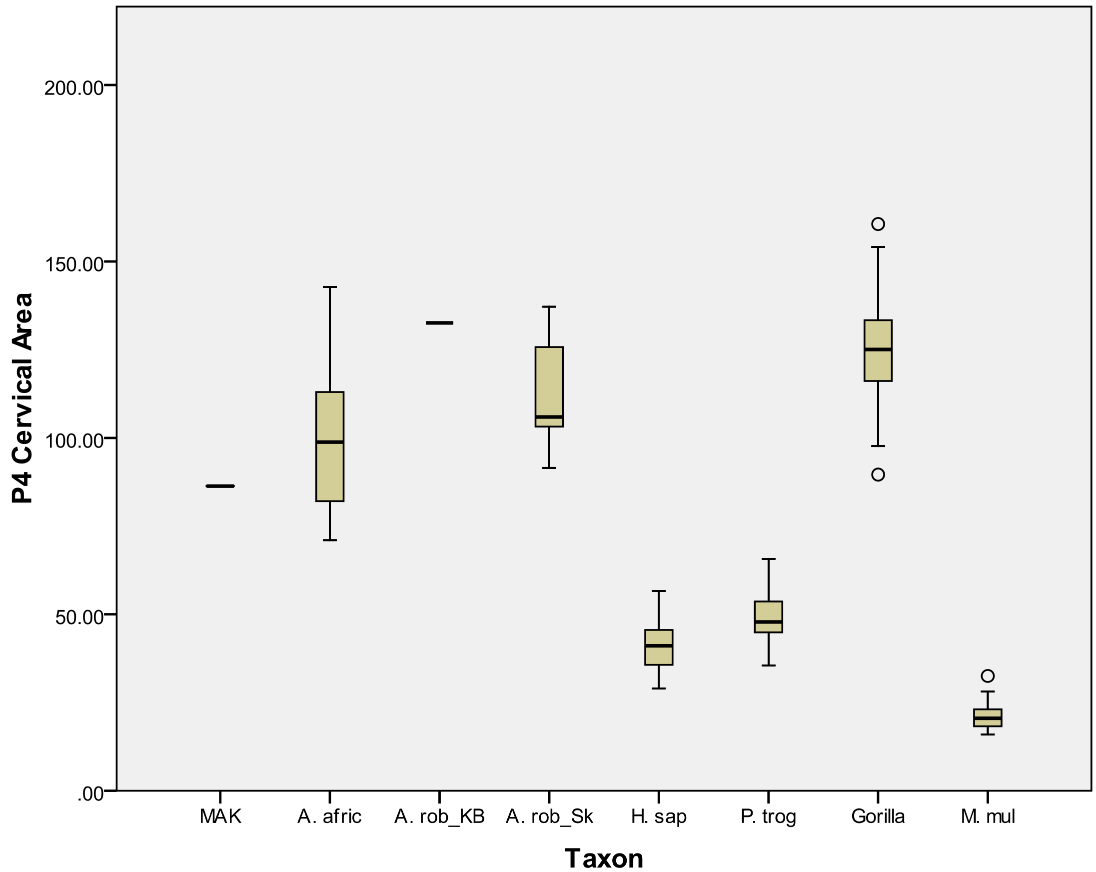


Figure 8-76: P_4 Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P_4 crown index [(P_4 mesiodistal length of crown / P_4 buccolingual breadth of crown) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18 and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 19), Swartkrans *A. robustus* (n = 14), Kromdraai *A. robustus* (n = 1), and Sterkfontein *Homo* (n = 1).

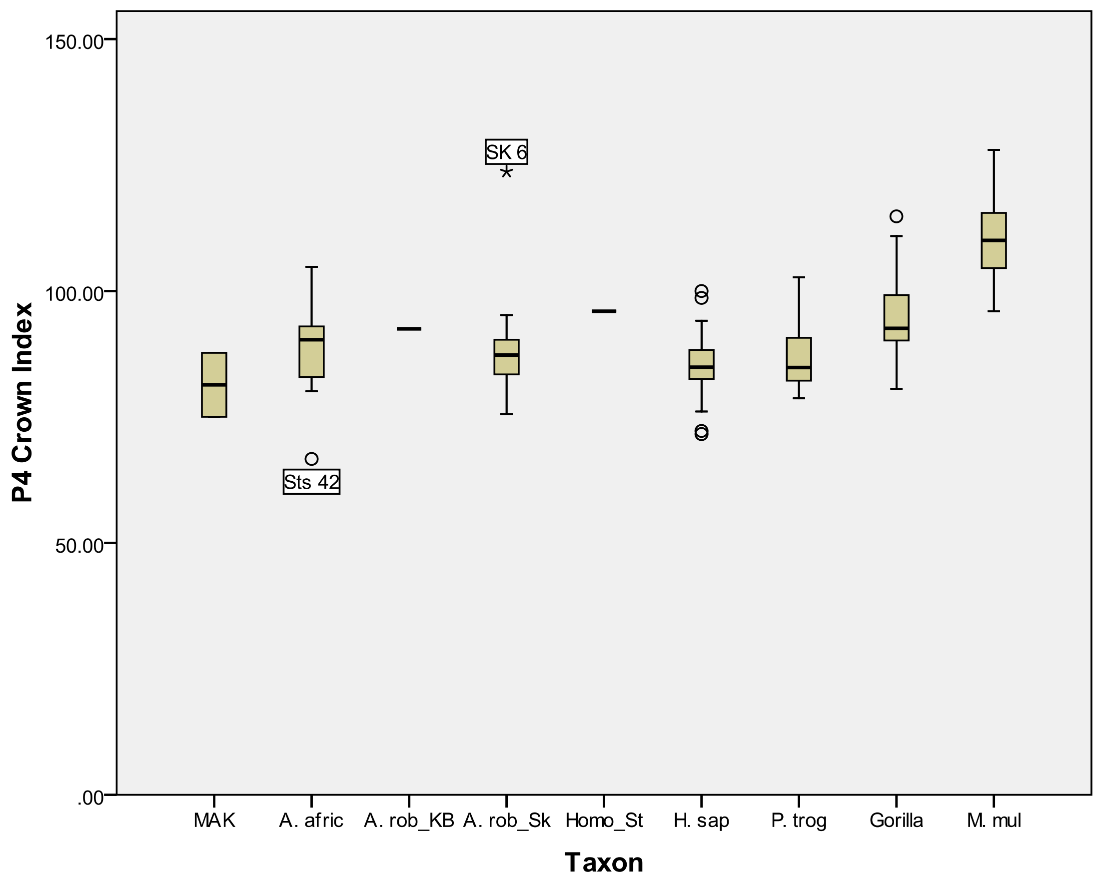


Figure 8-77: P⁴ Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P^4 crown area [P^4 mesiodistal length of crown * P^4 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6 and MLD 9/12. The fossil sample sizes for this analysis are: *A. africanus* (n = 9), Swartkrans *A. robustus* (n = 27), Kromdraai A. robustus (n = 2), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

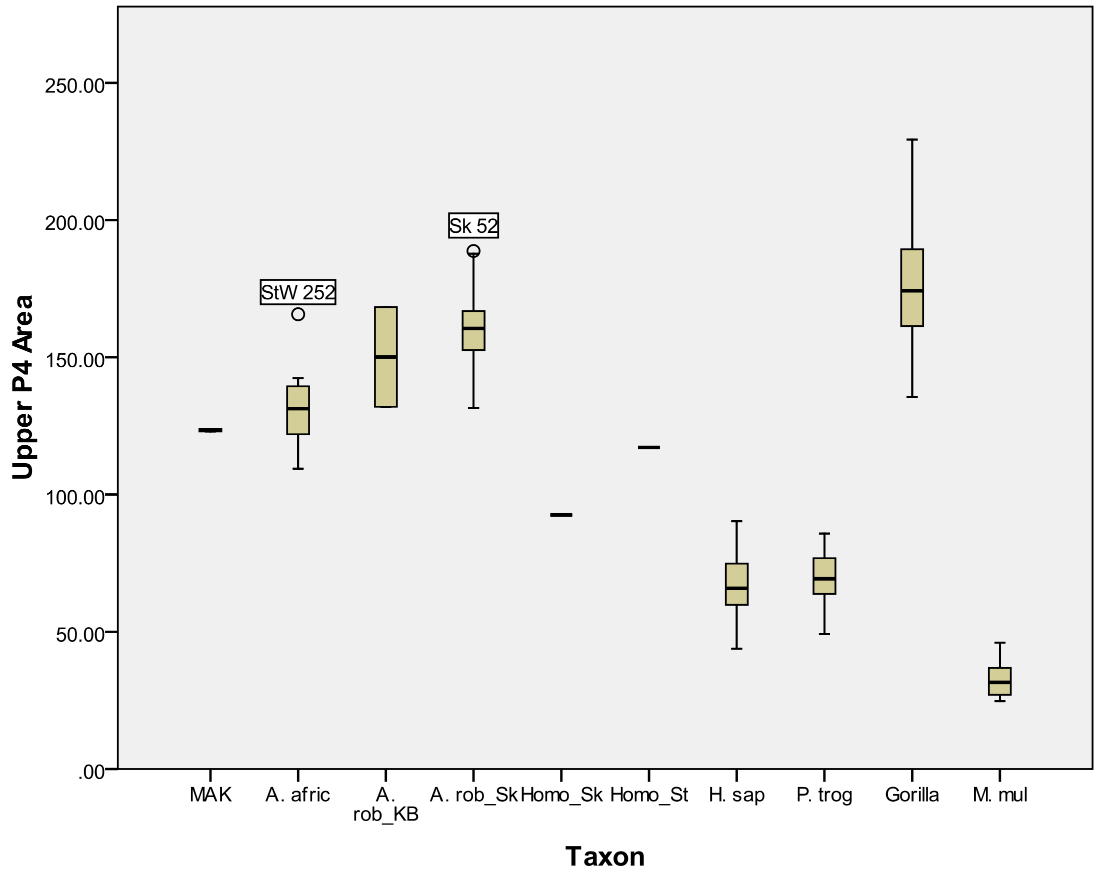


Figure 8-78: P*^{4} *Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the P^4 cervical area [P^4 mesiodistal length of cervix * P^4 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6 and MLD 9/12. The fossil sample sizes for this analysis are: *A. africanus* (n = 13), Swartkrans *A. robustus* (n = 30), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

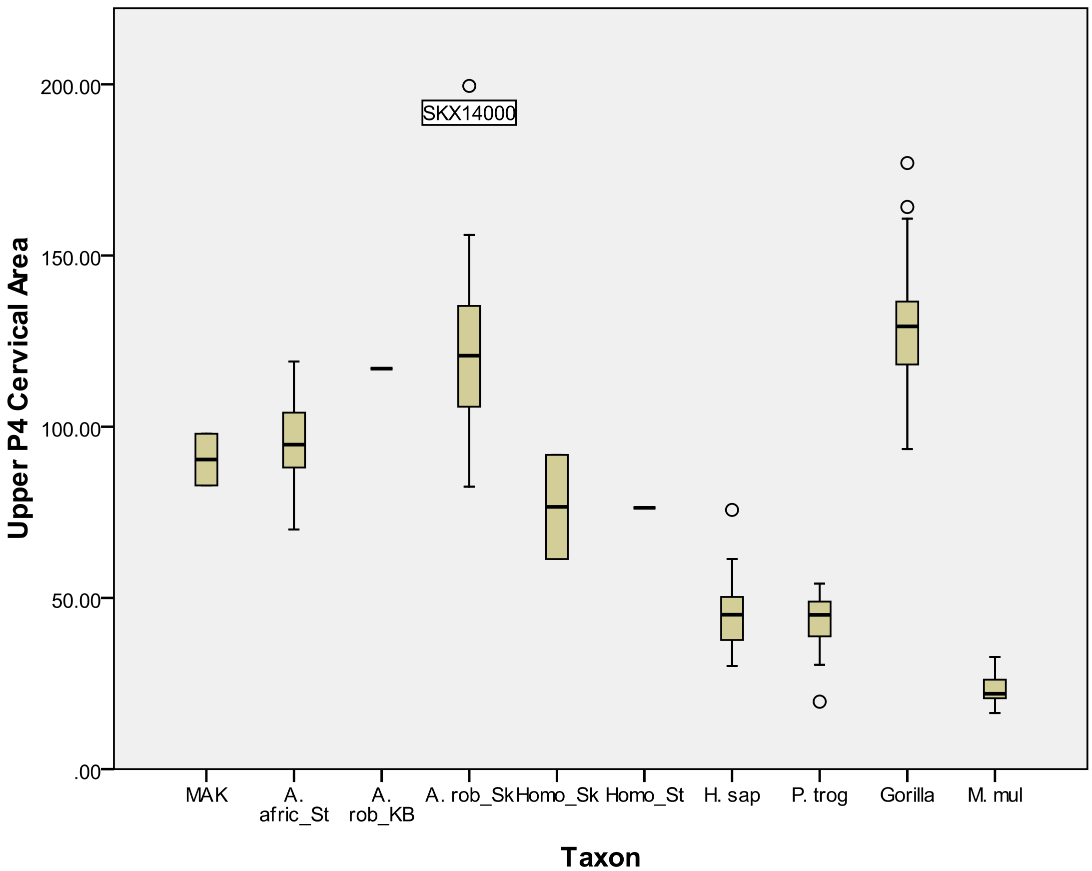


Figure 8-79: M_1 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_1 crown area [M_1 mesiodistal length of crown * M_1 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle or star. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 29), Swartkrans *A. robustus* (n = 19), Kromdraai *A. robustus* (n = 4), Swartkrans *Homo* (n = 2), and Sterkfontein *Homo* (n = 1).

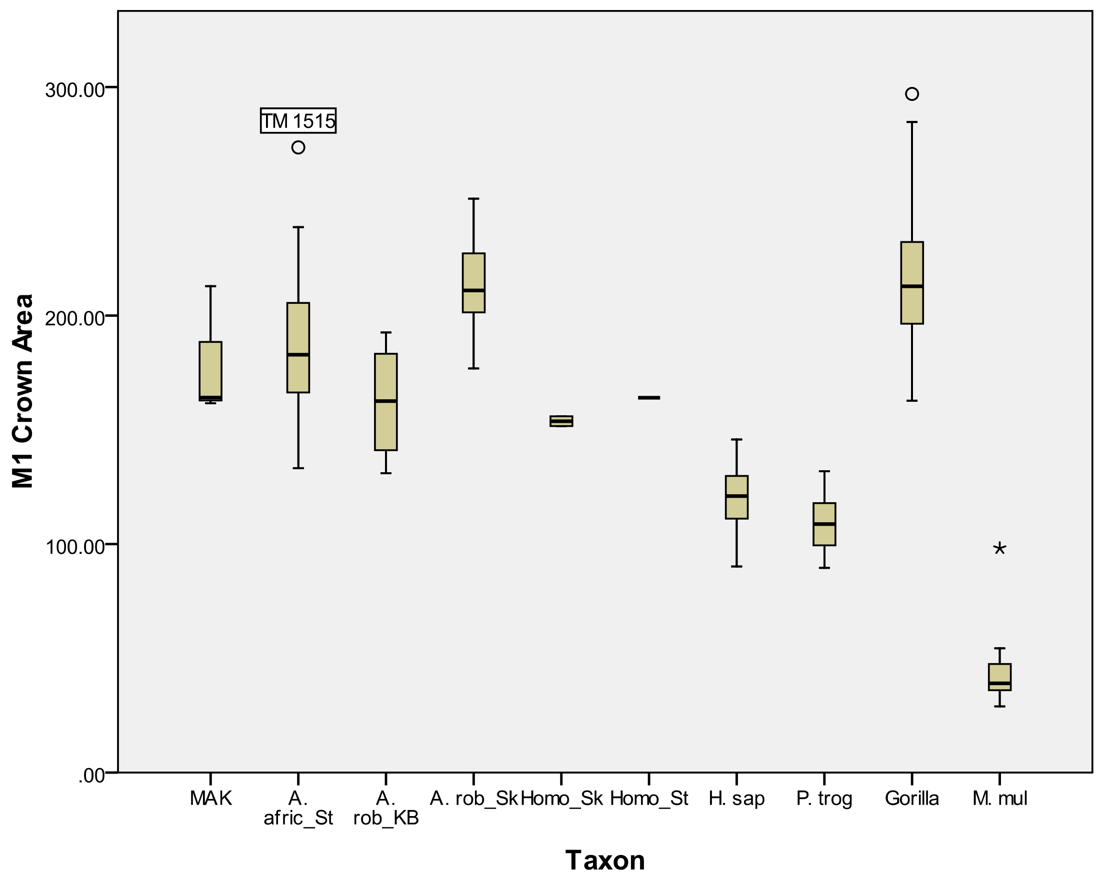


Figure 8-80: M_1 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_1 cervical area [M_1 mesiodistal length of cervix * M_1 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle or star. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 48. The fossil sample sizes for this analysis are: *A. africanus* (n = 28), Swartkrans *A. robustus* (n = 19), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 3), and Sterkfontein *Homo* (n = 1).

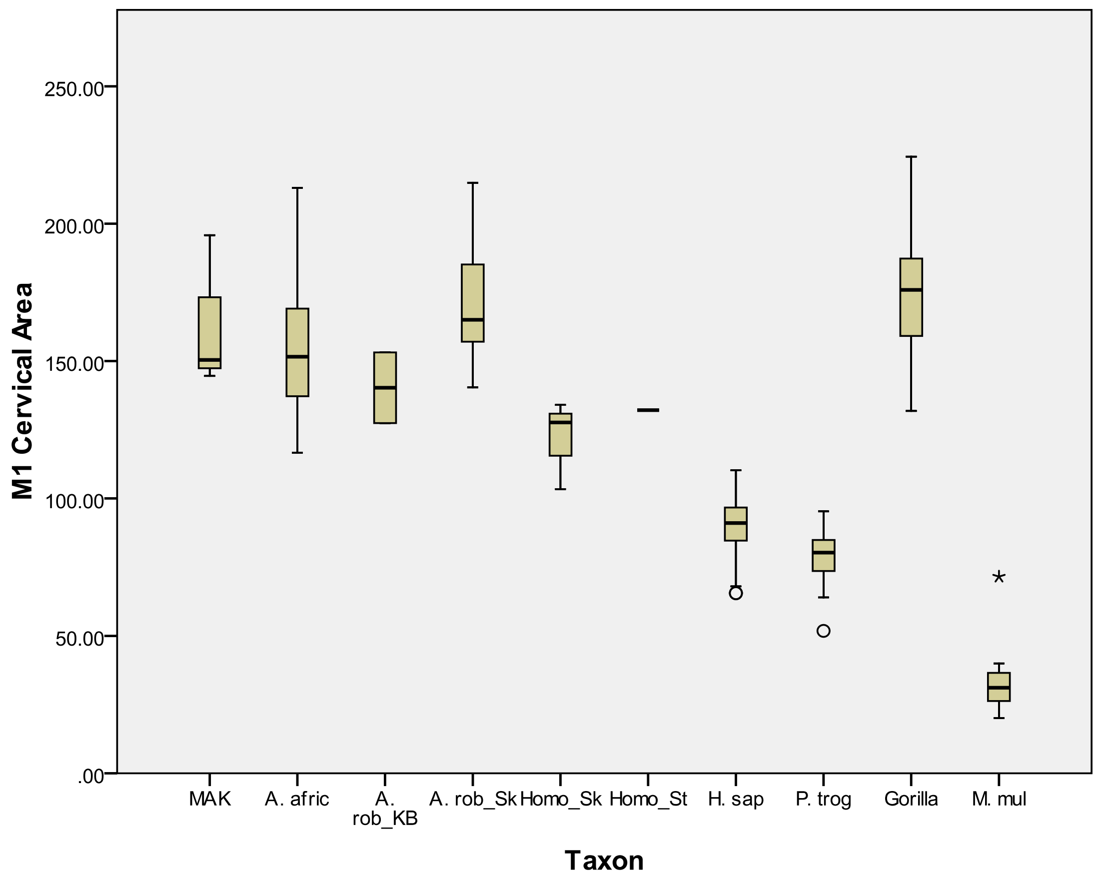


Figure 8-81: M_1 Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_1 crown index [(M_1 mesiodistal length of crown /M_1 buccolingual breadth of crown) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 29), Swartkrans *A. robustus* (n = 19), Kromdraai *A. robustus* (n = 4), Swartkrans *Homo* (n = 2), and Sterkfontein *Homo* (n = 1).

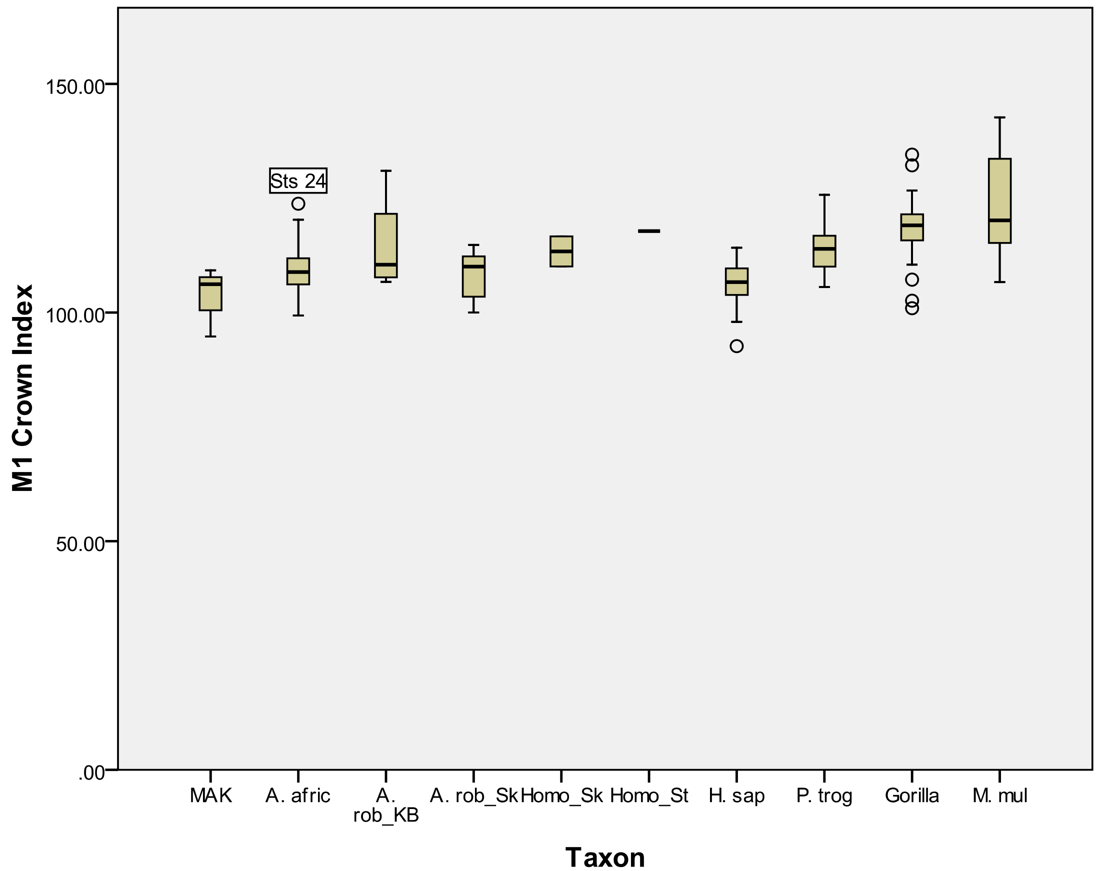


Figure 8-82: M_1 Cervical-Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_1 cervical-crown index [(M_1 cervical area /M_1 crown area) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 26), Swartkrans *A. robustus* (n = 18), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 2), and Sterkfontein *Homo* (n = 1).

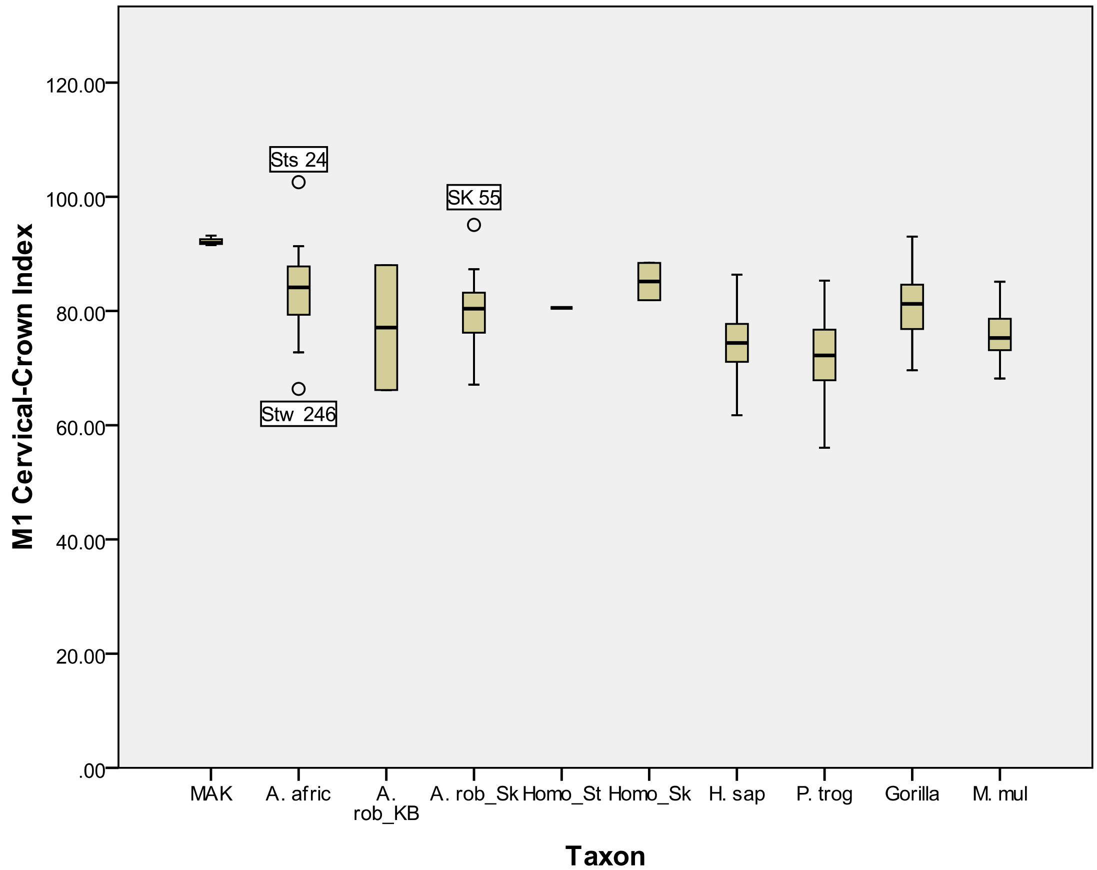


Figure 8-83: M^1 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M^1 crown area [M^1 mesiodistal length of crown * M^1 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6 and MLD 9. The fossil sample sizes for this analysis are: *A. africanus* (n = 18), Swartkrans *A. robustus* (n = 30), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 3), and Sterkfontein *Homo* (n = 1).

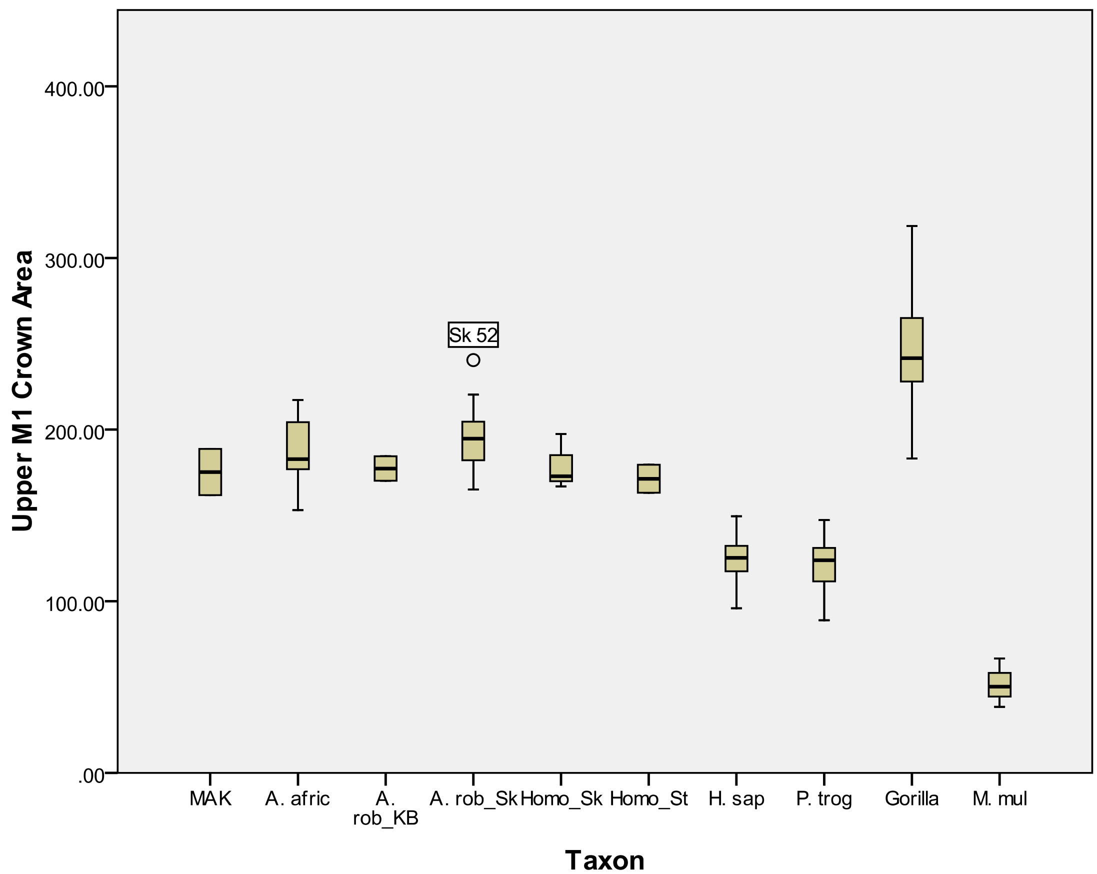


Figure 8-84: M¹ Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M¹ cervical area [M¹ mesiodistal length of cervix * M¹ buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6 and MLD 9. The fossil sample sizes for this analysis are: *A. africanus* (n = 19), Swartkrans *A. robustus* (n = 27), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 3), and Sterkfontein *Homo* (n = 2).

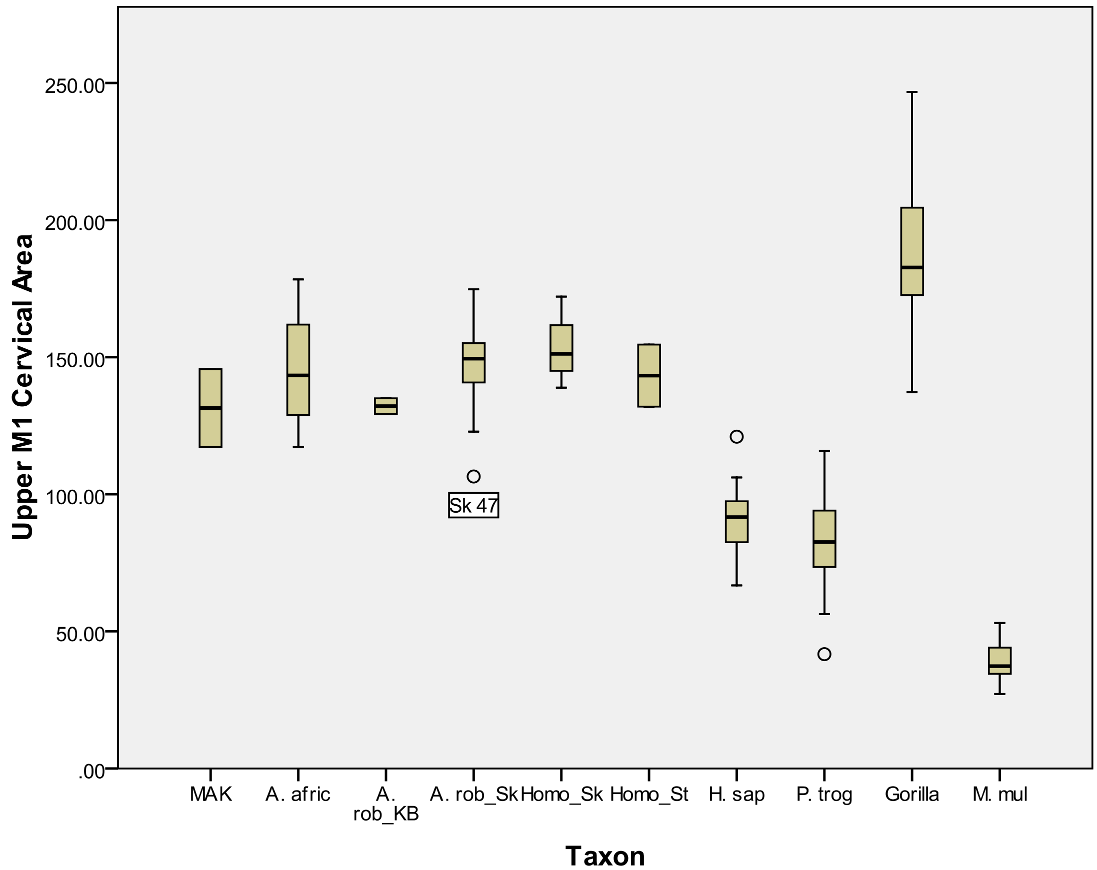


Figure 8-85: M_2 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_2 crown area [M_2 mesiodistal length of crown * M_2 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 22, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 26), Swartkrans *A. robustus* (n = 20), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

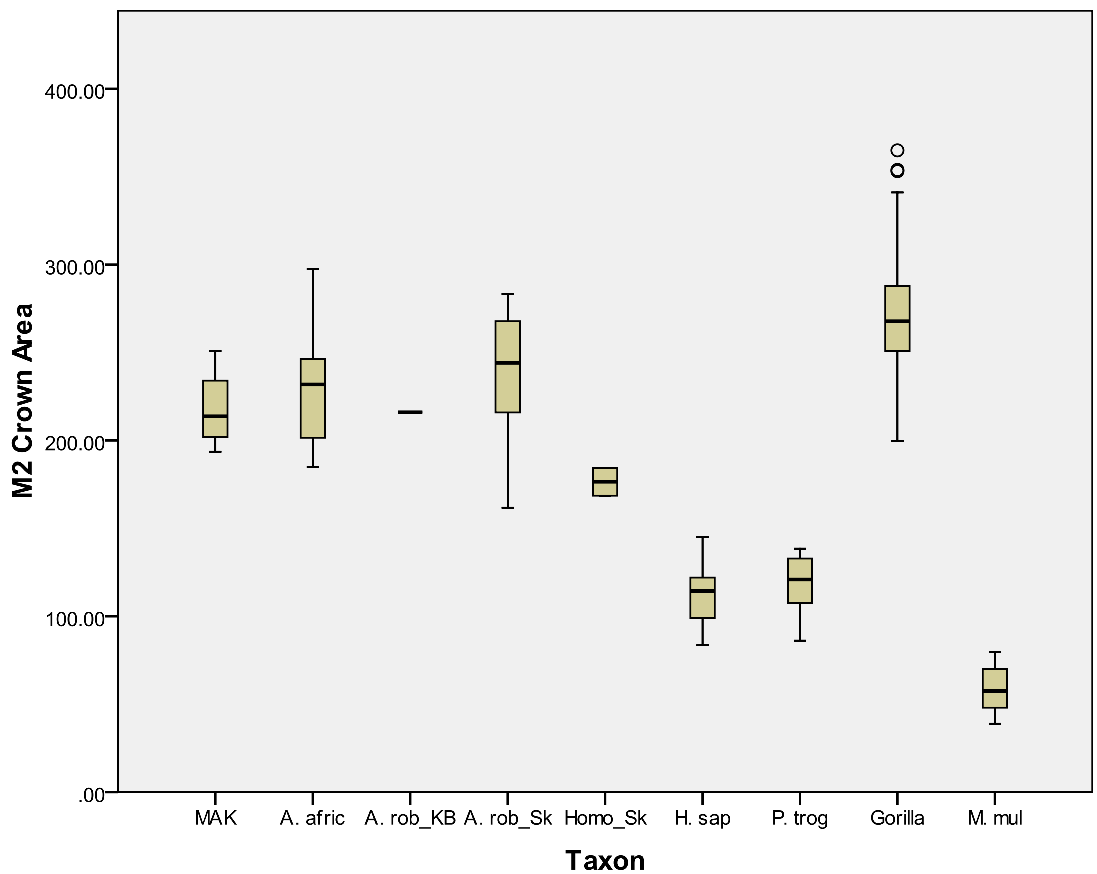


Figure 8-86: M_2 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_2 cervical area [M_2 mesiodistal length of cervix * M_2 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 22, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 24), Swartkrans *A. robustus* (n = 19), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

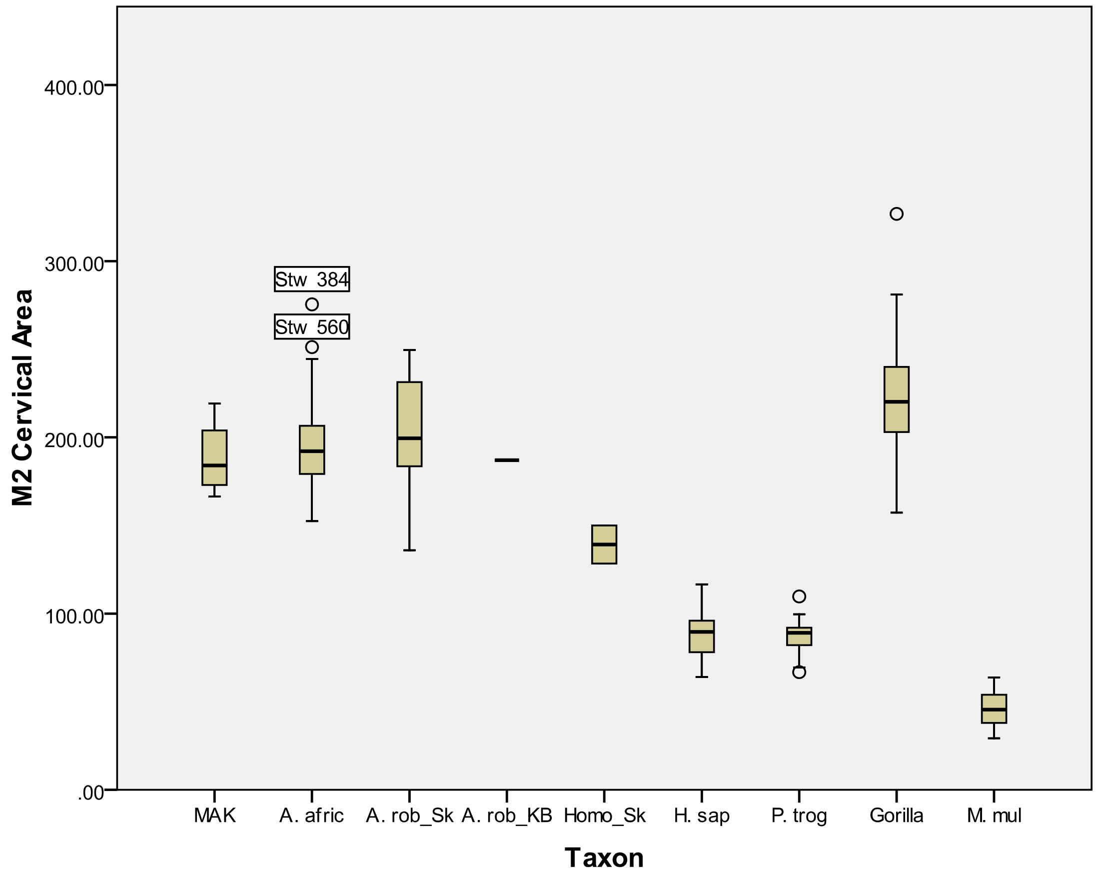


Figure 8-87: M_2 Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_2 crown index [(M_2 mesiodistal length of crown /M_2 buccolingual breadth of crown) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 2, MLD 18, MLD 22, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 26), Swartkrans *A. robustus* (n = 20), Kromdraai *A. robustus* (n = 1), and Swartkrans *Homo* (n = 2).

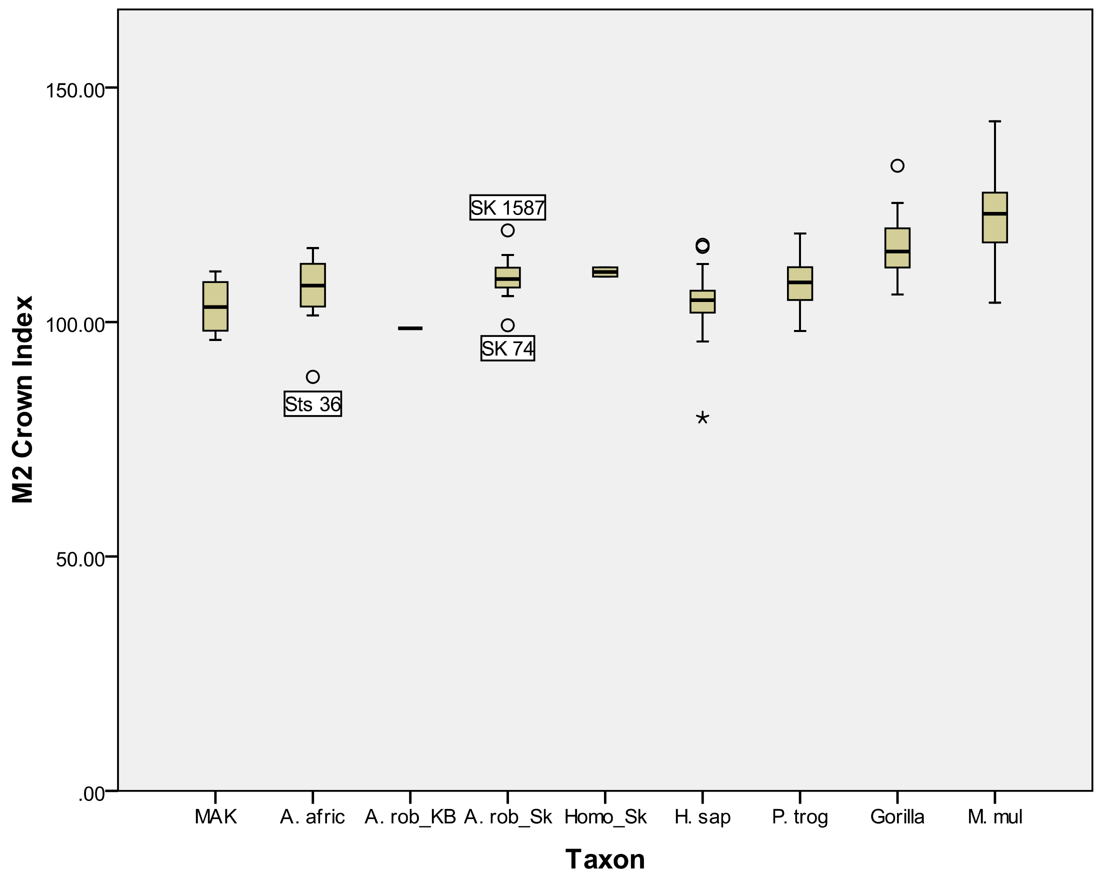


Figure 8-88: M^2 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M^2 crown area [M^2 mesiodistal length of crown * M^2 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6, MLD 9/12, and MLD 44. The fossil sample sizes for this analysis are: *A. africanus* (n = 19), Swartkrans *A. robustus* (n = 21), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 2), and Sterkfontein *Homo* (n = 3).

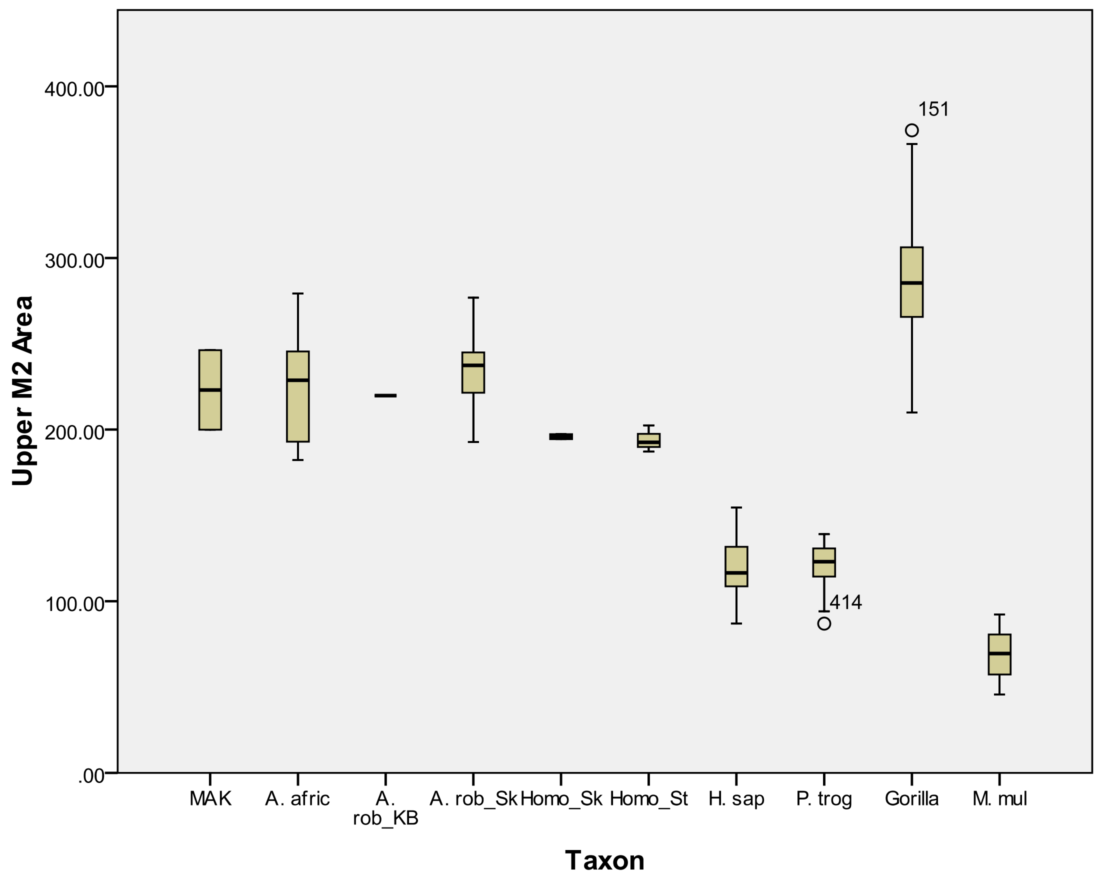


Figure 8-89: M² Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M^2 cervical area [M^2 mesiodistal length of cervix * M^2 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 6, MLD 9/12, and MLD 44. The fossil sample sizes for this analysis are: *A. africanus* (n = 18), Swartkrans *A. robustus* (n = 22), Kromdraai *A. robustus* (n = 1), and Sterkfontein *Homo* (n = 3).

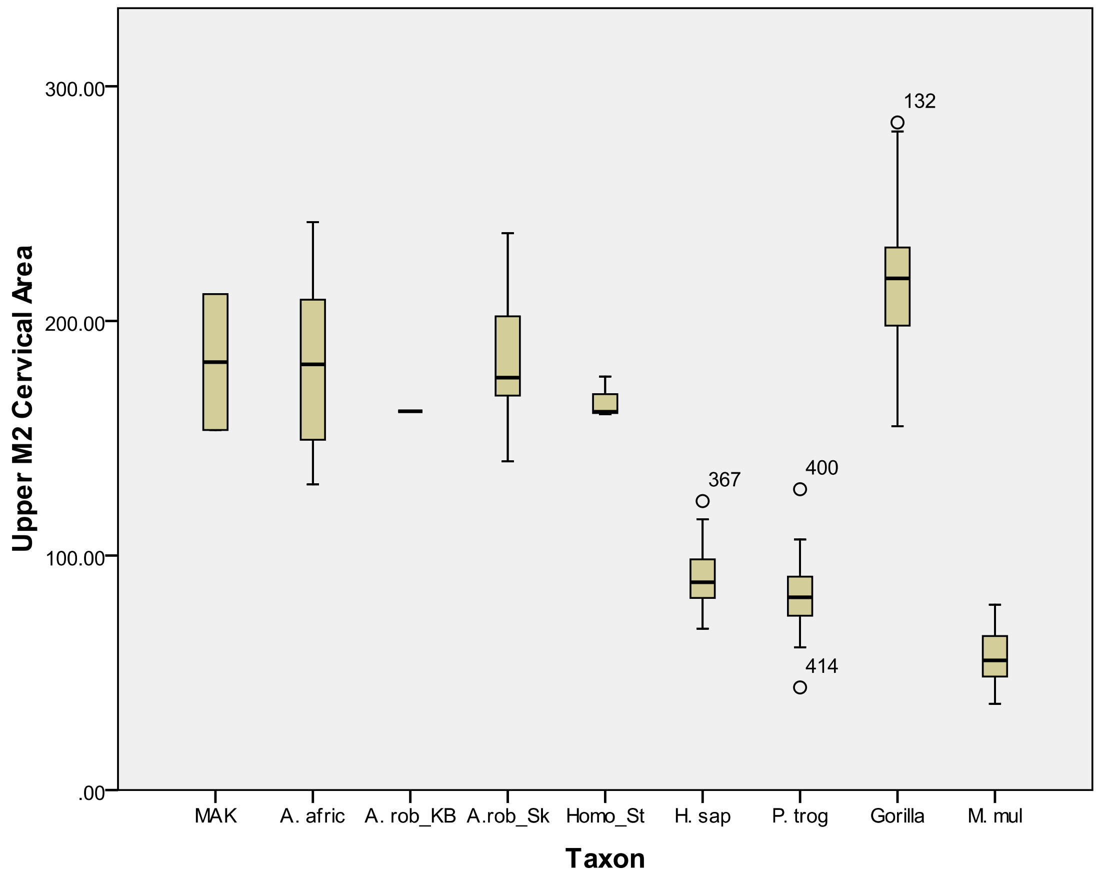


Figure 8-90: M_3 Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_3 crown area [M_3 mesiodistal length of crown * M_3 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18, MLD 19, MLD 22, and MLD 4. The fossil sample sizes for this analysis are: *A. africanus* (n = 29), Swartkrans *A. robustus* (n = 21), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

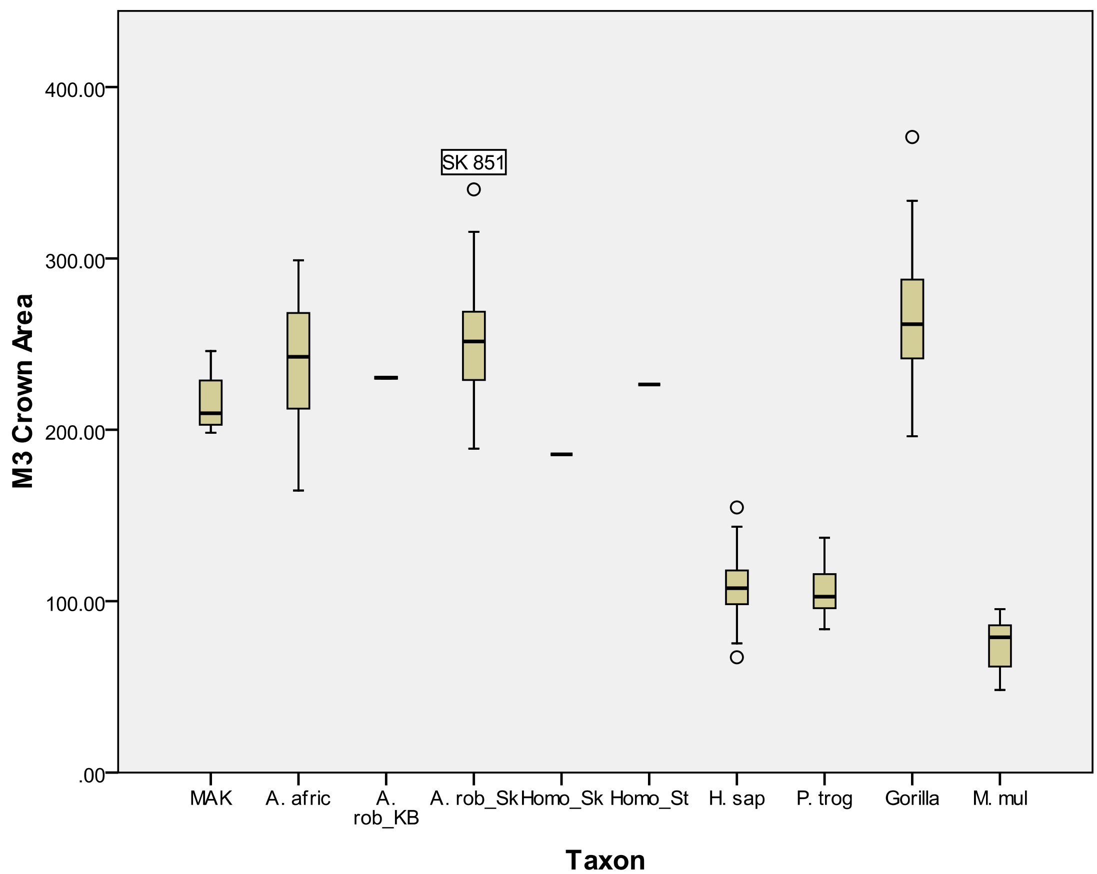


Figure 8-91: M_3 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_3 cervical area [M_3 mesiodistal length of cervix * M_3 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 18, MLD 19, MLD 4, and MLD 40. The fossil sample sizes for this analysis are: *A. africanus* (n = 23), Swartkrans *A. robustus* (n = 17), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

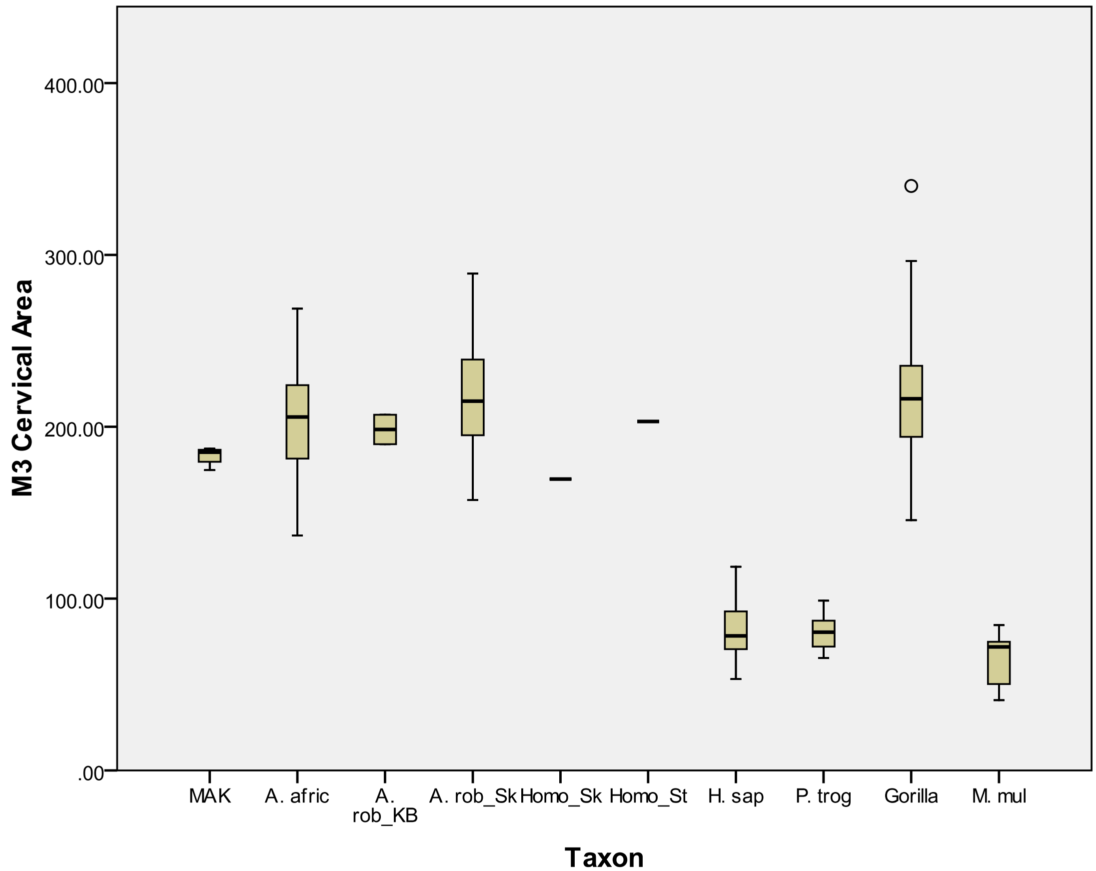


Figure 8-92: M_3 Cervical-Crown Index. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M_3 cervical-crown index [(M_3 cervical area /M_3 crown area) * 100] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 4, MLD 18, and MLD 19. The fossil sample sizes for this analysis are: *A. africanus* (n = 22), Swartkrans *A. robustus* (n = 17), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

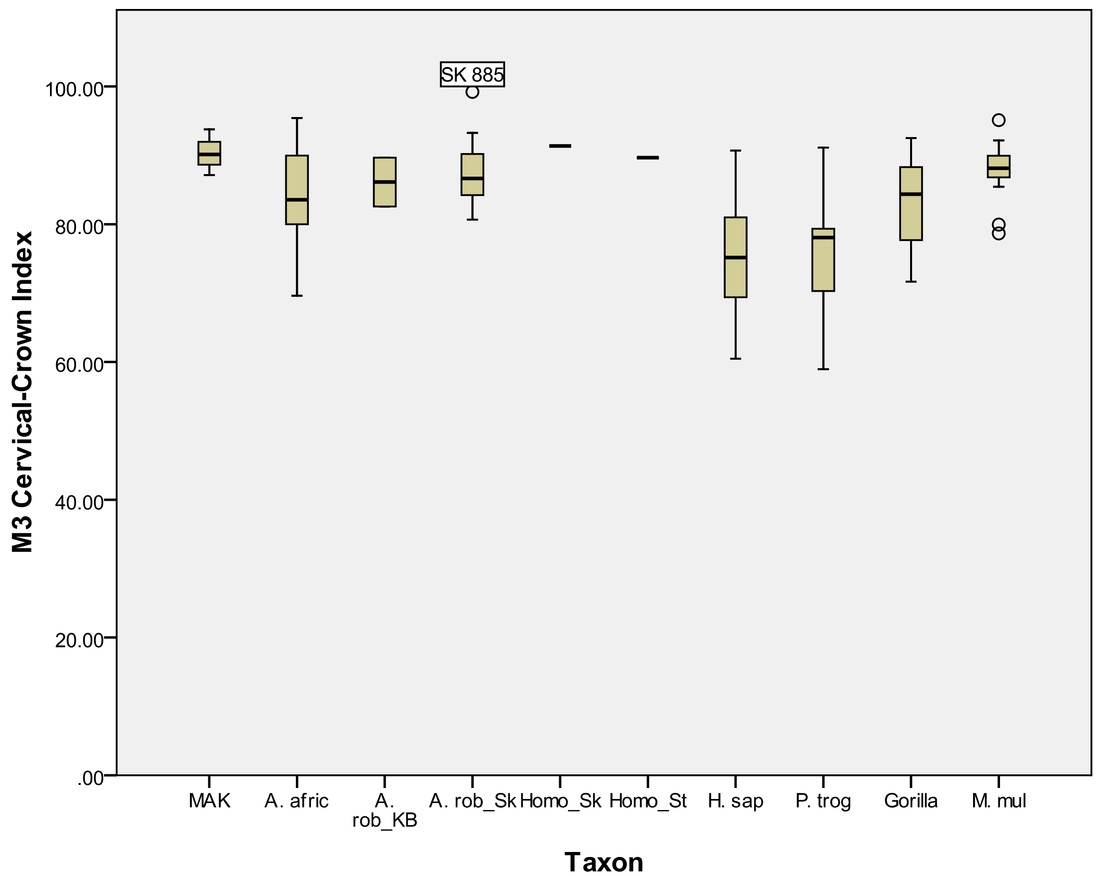


Figure 8-93: M³ Crown Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M^3 crown area [M^3 mesiodistal length of crown * M^3 buccolingual breadth of crown] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 12 and MLD 28. The fossil sample sizes for this analysis are: *A. africanus* (n = 23), Swartkrans *A. robustus* (n = 18), Kromdraai *A. robustus* (n = 2), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).

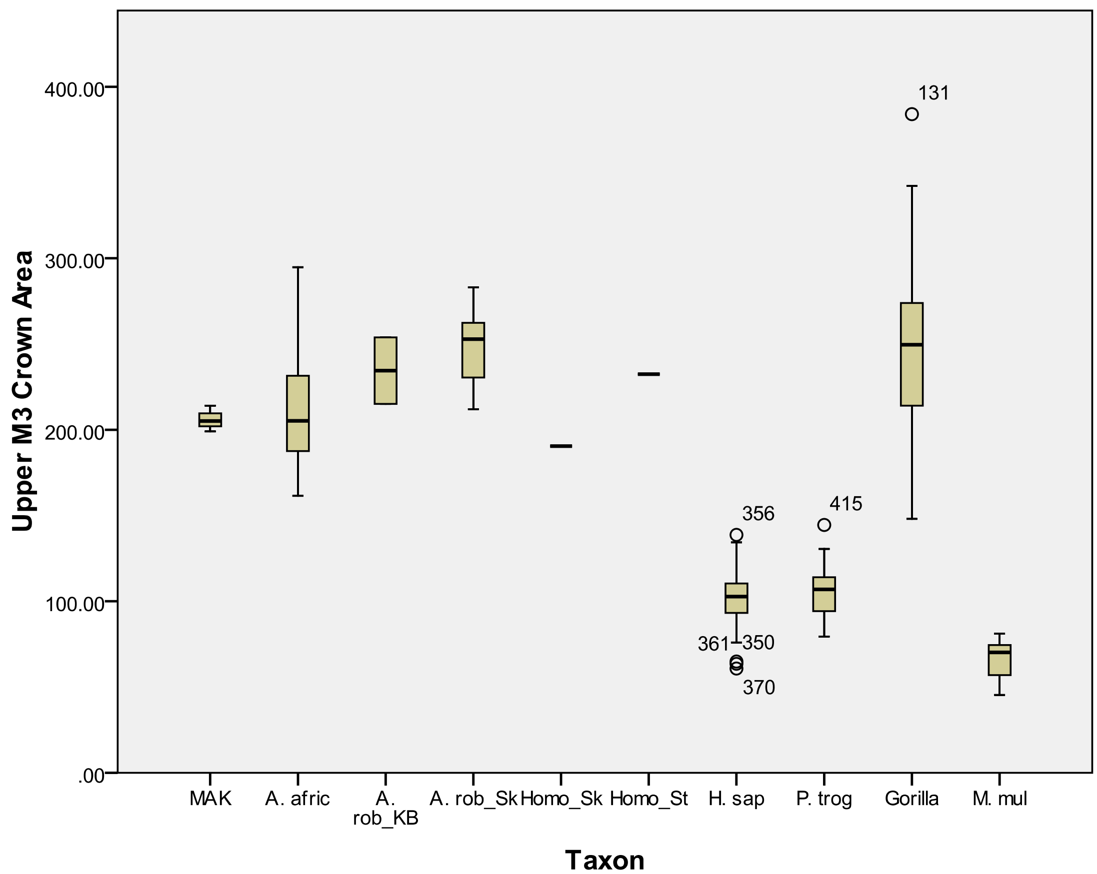
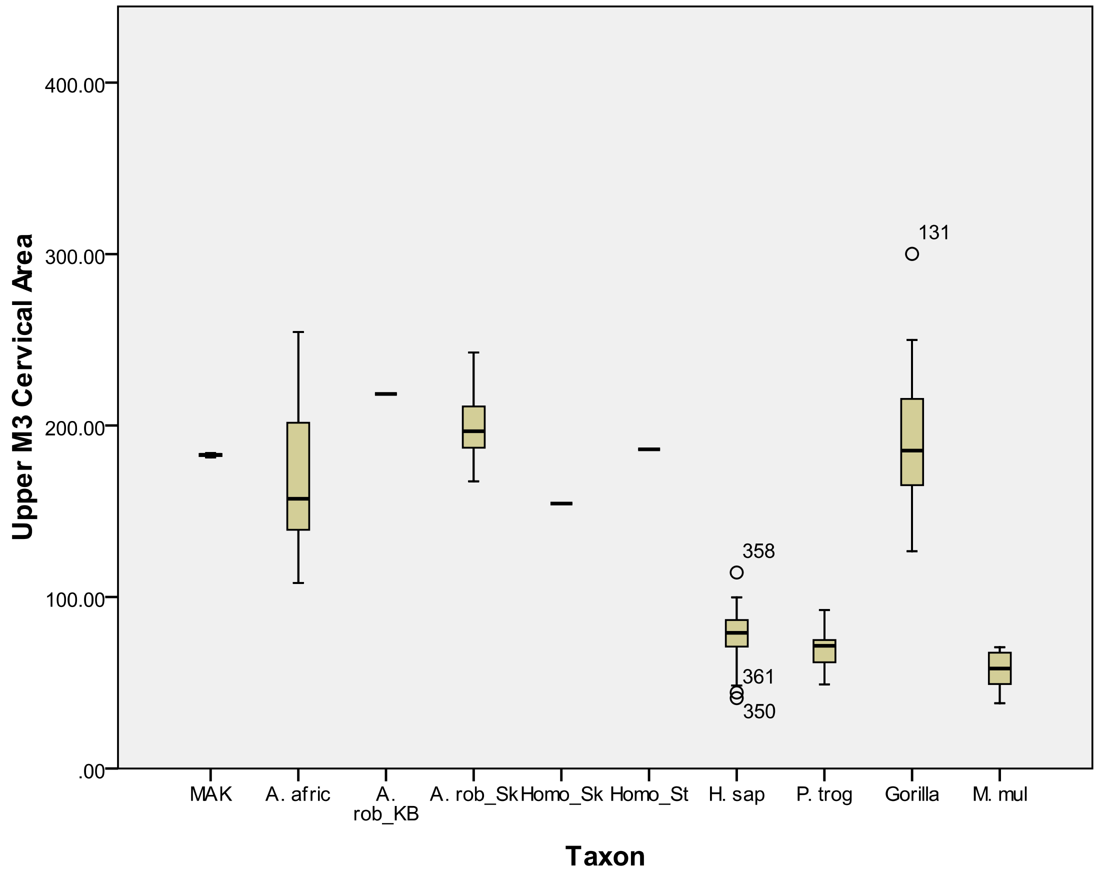


Figure 8-94: M^3 Cervical Area. The median (line), 1st and 3rd quartiles (box), and range (bars) of the M^3 cervical area [M^3 mesiodistal length of cervix * M^3 buccolingual breadth of cervix] for Makapansgat specimens in comparison to South African australopiths and a sample of extant primates. Sample outliers are identified by a circle. The Makapansgat sample is represented here by MLD 12 and MLD 28. The fossil sample sizes for this analysis are: *A. africanus* (n = 21), Swartkrans *A. robustus* (n = 17), Kromdraai *A. robustus* (n = 1), Swartkrans *Homo* (n = 1), and Sterkfontein *Homo* (n = 1).



DISCUSSION AND CONCLUSIONS

Discussion

Makapansgat Australopiths. The Makapansgat hominins have played a major role in the history of paleoanthropology and continue to be of substantial interest. Despite their general inclusion in the hypodigm of *A. africanus*, previous claims for morphological distinctions for some or all of the Makapansgat hominins, and the valuable contribution of their geographic and temporal features to studies of early hominin evolution, the assemblage has been essentially overlooked for the last few decades and its comparative analysis long overdue. Newly discovered specimens from Makapansgat and other South African Pliocene sites, as well as numerous discoveries and advances in paleoanthropology, highlight the utility of a reanalysis of the Makapansgat early hominin assemblage. The emphasis of this thesis has been to exhaustively describe the specimens from Makapansgat, incorporating previous work by Raymond Dart and J.T. Robinson with additional details, and position the Makapansgat early hominin sample in a modern comparative context.

Morphology

Crania. The 10 cranial specimens from Makapansgat represent individuals ranging in age from infancy/early childhood to old adulthood. Many of the specimens are fragmentary and few overlapping regions are preserved among the specimens. As evident from the discussions in the preceding chapters, however, the Makapansgat cranial specimens vary in size and morphology.

The facial morphology of the Makapansgat hominins exhibit a mix of features aligning them with both South African early hominin taxa. Facial prognathism has been argued to be greater in *A. africanus* than *A. robustus* (Robinson, 1956) and greater in *A. africanus* males than females (Schultz, 1962; Wood, 1976; Kimbel *et al*., 1984). Craniofacial specimens MLD 6 and MLD 9/12 exhibit a degree of prognathism most common in specimens attributed to *A. robustus*, but other features align them with *A. africanus*, such as the presence of maxillary furrows and anterior pillars (e.g. Rak, 1983; Kimbel and Rak, 1993). There is variation in the morphology of the anterior pillar and related canine fossa or maxillary furrow within the Makapansgat sample, however. In addition, the position of the zygomatic process is intermediate between the more anterior positions of specimens attributed to *A. robustus* and posterior positions of specimens attributed to *A. africanus*. As originally concluded by Lockwood (1997) in his seminal treatment of facial variation in *A. africanus*, the Makapansgat hominins exhibit some features that distinguish them craniofacially from *A. africanus* at Sterkfontein.

The neurocranial regions preserved within the Makapansgat early hominin assemblage do not contribute significantly to these discussions. Positioning of the temporal lines is variable, as it is in the other South African early hominin samples. The best evidence for sagittal cresting within the Makapansgat assemblage is represented by MLD 1 (e.g. Dart, 1962a, b; Robinson, 1954b; Wolpoff, 1974), but sagittal cresting is considered doubtful here. Assessments of whether sagittal cresting was present in MLD 1 are tied into estimates of the age of the individual at death and reconstructions for the extension of the temporal lines anteriorly.

Several studies have specifically examined the basicranial morphology of the Makapansgat MLD 37/38 cranium and have suggested that it may be distinct in some features pertaining to the glenoid and the petrous axis (e.g. Tobias, 1967, 1991; Kimbel and White, 1988; Dean and Wood, 1982). However, many of the morphological features of the cranium presented and discussed in this thesis have been demonstrated to be highly variable both within and among South African australopiths.

Mandibles. The Makapansgat mandibular assemblage includes 10 specimens that vary in age and preservation. The symphysis is characterized by a receding symphysis, moderate or marked incisive fossae, enlarged canine juga, shallow incisal subalveolar plane, and moderate superior transverse torus. The mandibular corpora provide a reasonable sample with which to make comparisons with other taxa. The Makapansgat mandibles tend to have a corpus with a relatively marked lateral prominence, thick corpus, and broad muscle attachment area for the buccinator. The ramus morphology for the Makapansgat sample is characterized by a relatively anterior positioning of the anterior root of the ramus, a feature more similar to the South African robusts.

The MLD 2 mandible is unusual in a few features, including an unclear boundary between the superior and inferior mandibular tori, small genial muscle attachment, lack of a genioglossal fossa or genial pit, and short corpus height (or great breadth). Many of these features are explained by this specimen’s subadult status (see lengthier discussion in the mandible descriptions). Most notably, the corpus height and breadth that served to align this specimen with *A. robustus* are clearly the result of this individual's developmental status. In summary, the Makapansgat mandibular sample could be distinguished in some features from both *A. robustus* and *A. africanus* and was most similar to *A. africanus* overall, but was intermediate in some features (for instance, mandibular robustness).

Dentition. The early hominin dental remains from the Makapansgat Limeworks provide the best sample with which to make extensive morphological comparisons with the samples of *A. africanus* and *A. robustus*. The dental assemblage includes teeth of a variety of developmental stages. Trait data and metric and morphometric analyses were used to comparatively assess the Makapansgat dental assemblage.

The maxillary incisors are morphologically most similar to specimens attributed to *A. africanus*, but a thorough evaluation of incisor traits in early hominins is warranted. The canines from Makapansgat clearly are most similar to specimens of *A. africanus* on the basis of size and morphology. The premolars and molars exhibit considerable variation within the sample from Makapansgat and within the samples of *A. africanus* and *A. robustus*. Although a number of features were provided in the previous chapter as characterizing the Makapansgat dentition, the incredible intraspecific variation for *A. africanus* and *A. robustus* and overlap in size and shape data among the taxonomic and site samples is confounding.

Frequencies of traits and size trends, rather than the consistent presence or absence of these features, discriminate the South African australopith samples. Considering the geographic and temporal variation of the samples and intraspecific variation in dental morphology, simply confidently assigning a small sample or isolated specimen to a taxon with confidence (and without consideration of the history of discoveries from that locality) is problematic.

Demographics

How much paleodemographic information can be extracted from the Makapansgat assemblage is highly debatable and essentially any paleodemographic interpretation is contentious. Regardless, the Makapansgat assemblage is one of eight australopith-bearing assemblages in South Africa and one of some two dozen plus *Australopithecus*-bearing sites in the world. As such, the assemblage warrants a discussion of paleodemographic attributes, however limited in scope may be the conclusions.

While prior arguments for a relatively high frequency of females at Makapansgat were interpeted as evidence that females spent more time in caves (Dart, 1962a), these sex attributions are tenuous. Numerous attempts have been made to identify the sex of early hominin specimens. With regard to the hypodigm of *A. africanus* alone, attempts have been made to identify the sex of individual specimens by prognathism (e.g. Wood, 1976; Kimbel *et al*., 1984), derived versus primitive facial characters (Rak, 1983; 1985), canine size (Broom *et al*., 1950; Wolpoff, 1975), canine eruption timing (Wallace, 1972), molar size (Kimbel and White, 1988a), and craniofacial traits and dimensions (Lockwood, 1999) with variable success. Size appears to be the most interspecifically consistent and primary difference between extant primates in sexual variation of the face

(Rak, 1983; Kimbel *et al*., 1982; Wood, 1985a) and would presumably remain true for early hominins. However, there is potential for temporal trends in the increase or decrease of the size of morphological features, as has been demonstrated for the mandibular corpus in *A. afarensis* (Lockwood *et al*., 2000). The emphasis on differences in size for both discrimination of sex and South African early hominin taxonomic affiliation (not to mention the possibility of temporal and geographic variation in size and morphology) confounds efforts to identify the probable sex of specimens within the limited Makapansgat sample. Sex attributions for the Makapansgat specimens are thus considered currently indeterminate.

Age estimates that have been recorded in the literature have been presented and discussed whenever available for each of the Makapansgat hominin specimens. Early work that attempted to calculate the age at death for early hominins produced them on the basis of a human model (e.g. Dart, 1962a; Mann, 1975), which tends to overestimate australopith ages where relative overestimation had a seemingly inverse relationship with specimen age. A variety of lines of research that primarily focus upon the formation, maturation, and eruption of early hominin dentition clearly indicate that a human model considerably overestimates age in australopiths, particularly since tooth crown formation times were shorter in early hominins than extant humans and dental developmental timing was more apelike (e.g. Bromage and Dean, 1985; Smith, 1986, 1987; Beynon and Dean, 1987; Beynon and Wood, 1987; Bromage, 1987; Conroy and Vannier, 1987; Dean, 1987a,b; Dean *et al*., 2001; Lacruz and Bromage, 2006; Lacruz and Rozzi, 2010).

In the interest of not being overly precise in estimating the ages of extinct individuals for whom there is no ideal extant analog and few solid methods for producing an age estimate with any precision or repeatability, age estimates for the Makapansgat hominins were presented on the basis of age stages rather than precise year estimates. A notable exception is that precise and repeatable age estimates have been produced by dental formation stages and dental studies focusing upon histological features of the dentition, but the latter also suffer from the assumption of a constant intraspecific appositional rate, which may be likely, and rely on an estimate of the specific rates in early hominin taxa, which requires a reasonable but somewhat greater leap. Regardless, age estimates produced on the basis of dental developmental stages and the microscopic features of the teeth were included in the current estimates as they are considered generally reliable. Current and previous age estimates are presented in summary form in Table 9-1 for each of the cranial, mandibular, and dental specimens from Makapansgat.

The Makapansgat specimens are dominated by adult specimens of varying ages. Of the 27 craniodental and mandibular specimens from Makapansgat, 22 (81%) represent an individual who reached some stage of adulthood, 3 (11%) represent individuals estimated to have died in late childhood, 1 (4%) represents an individual who died during infancy or early childhood, and 1 (4%) represents an individual who died during infancy. A minimum number of individuals (MNI) was recalculated on the basis of the new specimens and produced a MNI of 13. When the MNI estimate is taken into account, a minimum of 9 individuals (69%) died as adults, 3 individuals (23%) died in late childhood, 1 individual (8%) died on the boundary of infancy and early childhood, and 1 individual (8%) died as an infant. Before these age at death data can be used to reconstruct demographic features of the lives and deaths of the Makapansgat hominins, a discussion of the basic depositional history of the relevant deposits is warranted.

The geological features of the Makapansgat Member 3/Grey Breccia and Member 4/Pink Breccia cave deposits are quite complex and have long hindered efforts to reliably date the deposits (Latham *et al*., 1999; Crawford *et al*., 2004). However, the most thorough stratigraphic assessment (Latham *et al*., 2007) and paleomagnetic analyses of fossil-bearing breccia from Makapansgat have recently produced age estimates of ~ 2.6-2.7 Ma (Warr, 2009) that slightly predate earlier biostratigraphic and paleomagnetic age estimates for the site of 2.8 – 3.2 Ma (Vrba, 1985; McKee, 1995; McKee *et al*., 1995; Crawford *et al*., 2004; Warr *et al*., 2009). In addition, the deposition of the australopith-bearing Makapansgat deposits was quite rapid (Latham *et al*., 2007), indicating the potential for the Makapansgat hominins to reasonably approximate a biological population. Indeed, even Dart argued that the Makapansgat specimens could have been a single australopith group due to varied age estimates and the presence of what he considered to be both male and female specimens (1962a).

However, strong evidence for carnivore and rodent accumulation and gnawing of the vertebrate fossils from the most prolific australopith-bearing deposit at Makapansgat, the Member 3/ Grey Breccia (Brain, 1981; Shipman and Phillips, 1976; Shipman and Phillips-Conroy, 1977; Maguire *et al*, 1985; Reed, 1997; Latham *et al*., 1999) may suggest a taphonomic bias towards preserving older, denser skeletal remains in the Makapansgat fossil record. This argument logically would emphasize that the gnawing of bones by extinct hyenas and porcupines would more critically damage subadult specimens. Reconstructing the paleodemography of the Makapansgat hominins is further complicated by the likelihood of a pre-depositional bias involving the transport of australopith carcasses and/or elements to the cave. Even so, one might optimistically argue that the Makapansgat sample is a reasonably good proxy of a biological population on the basis of the rapid period of deposition for the australopith-bearing deposits and a potential cancelling effect of the likely taphonomic biases (one skewing towards younger specimens, the other towards older specimens).

The age at death data presented in Table 9-1 and summarized above indicate that a majority of the Makapansgat australopiths preserved in the fossil record reached adulthood. If the depositional and taphonomic context of the Makapansgat hominins is interpreted as a reasonable representation of a biological population, even if a large percentage of the population died so young that they are poorly represented in the fossil record, there may have been a critical age beyond which the chances of reaching adulthood were fairly good. There is some support for a relatively aged assemblage as the Makapansgat hominin sample exhibits relatively greater occlusal wear on the mandibular molars than either the samples of *A. robustus* or *A. africanus* (see discussion in Chapter 8).While this scenario is possible, the potential for strong taphonomic factors that may well have skewed the Makapansgat hominin assemblage leaves this author skeptical.

The general health of the Makapansgat australopiths may be explored indirectly via examination of paleopathological features displayed by the cranial, mandibular, and dental specimens, although see the cautions of Wood and colleagues (1992) and Bocquet-

Appel and Masset (1982, 1985). The primary evidence available to assess the general state of health for the Makapansgat early hominins, aside from age estimates, is disruptions in dental formation. While the MLD 46 proximal femur clearly indicates degenerative features, an extended discussion of this specimen is not repeated here [see Reed (1993)]. Linear enamel hypoplasias, hypoplastic pitting, probable opacities, and occlusal surface crenulations [argued by Tobias (1986) to relate to enamel hypoplasia in contrast to the belief adopted here that they are a “normal” variant] were identified within the Makapansgat dental sample and were described in the previous chapters. Rapid enamel deposition theoretically makes australopiths less sensitive to linear enamel disruptions with relatively minor physiological stressors compared to extant humans (Guatelli-Steinberg, 2003), so the high frequency of hypoplastic features in South African australopiths may be indicative of great stress during development or merely differences in the sensitivity of their teeth to developmental disruptions. There are indications of general physiologic stress during dental development on the basis of the frequent presence of hypoplastic features of the enamel, but the Makapansgat australopiths do not seem to stand out among the other South African hominin assemblages. More thorough analyses of the frequency of a variety of enamel defects in South African early hominin taxa are available (e.g. White, 1978; Bombin, 1990; Moggi-Cecchi, 2000; Guatelli-Steinberg, 2003, 2004).

In summary, the demographic information that can be gleaned from the Makapansgat assemblage is fairly limited, given the sample. The sample itself likely represents australopith populations living in or near the Makapansgat Valley over tens of thousands of years that were transported to the cave by hyenas and porcopupines postmortem. The Makapansgat hominin assemblage preserves a relatively high percentage of adult individuals, but this probably is partly the result of taphonomic biases. In addition, the general state of health of these individuals can be assessed to some degree by examination of paleopathological indicators. This line of reasoning suggests that linear enamel hypoplasias, hypoplastic pitting, and perhaps molar occlusal surface crenulations displayed by the Makapansgat early hominins although prevalent, are unexceptional among the South African australopith samples examined.

TABLE 9-1. Summary of Current Age Estimates for the Makapansgat Hominins.

Spec. No.	Element[3]	Thesis Estimate	Prior Estimates	Relevant Citations
MLD 1	Calvaria	Young adult	Adult	Dart, 1948d; Robinson, 1954b
MLD 2	Mandible	Late childhood, ~6.6 yrs	12-13 yrs[1] or 6.5 yrs[2]; 12 +/- 1 yrs[1]; 6.6 yrs[2]	Dart, 1948a,b; Mann, 1975; Bromage, 1987; Conroy and Vannier, 1991
MLD 3	Calvaria	Infant/Early childhood	Infant	Dart, 1949
MLD 4	M_3	Young adult	Adult	Mann, 1975
MLD 5	dp_4 (dm_2)	Infant; just > 1 yr	Juvenile; 2.5 +/- 1 yrs; Just > 1 yr	Dart, 1949a; Mann, 1975; Bromage, 1987
MLD 6	Craniodental	Young adult	Adult	Dart, 1949a
MLD 9/12	Maxilla	Adult	50 yrs[1]; > 30 yrs[1]	Dart, 1962a; Mann, 1975
MLD 10	Calvaria	Adult		Mann, 1975
MLD 11/30	Maxilla	Late childhood, ~5-6 yrs	5-6 yrs[2]; 9 +/- 1 yrs[1];	Bromage, 1987; Mann, 1975
MLD 18	Mandible	Young adult	30 yrs[1]; 24 +/- 2 yrs[1]	Dart, 1954b; Mann, 1975
MLD 19	Mandible	Adult	> 35 yrs[1]; 25 +/- 2 yrs[1]	Dart, 1962a; Mann, 1975
MLD 22	Mandible	Old adult	> 40 yrs; 32 +/- 2 yrs	Dart, 1962a; Mann, 1975
MLD 23	Maxilla	Young adult	20 +/- 1 yrs[1]	Mann, 1975
MLD 24	M_2	Young adult		
MLD 27	Mandible	Adult	"Mature"	Mann, 1975

MLD 28	Maxilla	Young adult	27 +/- 3 yrs[1]	Mann, 1975
MLD 29	Mandible	Adult	~ 35 yrs; ~ 30 yrs	Dart, 1962a; Mann, 1975
MLD 34	Mandible	Adult	26 +/- 2 yrs	Mann, 1975
MLD 37/38	Cranium	Young adult	50 yrs[1]	Dart, 1962b
MLD 40	Mandible	Adult	~ 30 yrs	Dart, 1962a
MLD 41	Probable M_1	Young adult		
MLD 42	C_1	Young adult		
MLD 43	I^1	Late childhood		
MLD 44	Probable M^2	Young adult		
MLD 45	Maxilla	Adult		
MLD 47	Mandible	Adult		
MLD 48	Mandible	Adult		

[1]Age estimates based upon a human model.
[2]Age estimates based upon an ape model.
[3]Element is a brief description of the preserved anatomical region. See text or Table 4-1 for a more detailed description of the specific bones represented.

South African Early Hominin Evolution. The announcement and description of the Taung specimen as a member of the human lineage and a newly identified ancient human genus and species, *A. africanus* (Dart, 1925a), was undeniably controversial. Yet the hypodigm of *A. africanus* has remained hotly debated virtually ever since (e.g. Robinson, 1954; Tobias, 1967, 1968, 1973; White *et al*., 1981; Kimbel and White, 1988; Clarke, 1988, 1994; Reed *et al*., 1993; Plavcan, 2003, 2006; Calcagno *et al*., 1999, Lockwood, 1999; Lockwood and Tobias, 1999, 2002; Moggi-Cecchi, 2003; Moggi-Cecchi *et al*., 1998, 2006). In the years immediately following Dart's seminal work on this first identified australopithecine, several additional australopith-bearing localities (i.e. Swartkrans, Kromdraai, Sterkfontein, and Makapansgat) were discovered in South Africa and a number of new early hominin species and genera were recognized (i.e. *A. africanus*, *A. prometheus*, *Plesianthropus transvaalensis*, *Paranthropus robustus*, and *Paranthropus crassidens*) (e.g. Dart, 1925a, b, 1948a, b, c; Broom, 1936, 1937, 1938, 1947; Broom and Robinson, 1947, 1950, 1952). Each of these new early hominin taxa was associated with the fossils from a particular site: *A. africanus* at Taung, *A. prometheus* at Makapansgat, *Australopithecus – and later Plesianthropus – transvaalensis* at Sterkfontein, *Paranthropus robustus* at Kromdraai, and *Paranthropus crassidens* at Swartkrans.

The Makapansgat hominins were first identified as a new hominin species on the basis of an *ex situ* partial calvaria (Dart, 1948d). The species-level identification for this specimen (MLD 1) was proposed due to the morphology of the occipital sutures, the large-bodied associated fauna (presumed to be their dietary remnants), and arguably the new locality. By the mid-1950's, however, Robinson had 1) subsumed the Makapansgat, Taung, and Sterktontein australopiths into the single genus and species *A. africanus* on the basis of taxonomic priority, 2) subsumed the Swartkrans and Kromdraai australopiths into the single genus and species *P. robustus*, and 3) established a dichotomous organization for South African early hominins using "gracile" and "robust" categories (Robinson, 1954a, 1961, 1962, 1963). A focus on viewing the South African australopiths as categorically disparate remained pervasive until Tobias (1967) highlighted the incredible morphological and presumed phylogenetic similarity of the two South African australopiths, *A. africanus* and *A. robustus*. Although Robinson, Tobias, and other contemporaneous paleoanthropologists continued to amend these phylogenetic scenarios and specific taxonomic attributions, most (arguably) can be considered a variation of these dominating themes [see also discussion in White and colleagues (1981)].

The Makapansgat assemblage has weighed heavily in many of these discussions and several regions have been long considered somewhat distinct from *A. africanus* at Sterkfontein. Even in some of the original descriptions, the Makapansgat specimens were argued to be distinct from the Taung holotype of *A. africanus*, but close affilations between all four of the then known South African australopith samples were recognized (Dart, 1948a). When Robinson subsumed all species of his "gracile" australopith category into the hypodigm of *A. africanus*, he concluded that "in practically every feature the variation within the Sterkfontein sample seems sufficient to include the Makapansgat specimens" (1954:194). However, Tobias (e.g. 1967, 1980) highlighted distinctions between the Sterkfontein and Makapansgat specimens attributed to *A. africanus* and suggested that morphological features of the Makapansgat specimens that are more similar to *A. robustus* are the result of a highly variable *A. africanus*. Not surprisingly, many of Tobias' early papers were used as a platform for single species arguments (e.g. Wolpoff, 1970; Brace, 1973). Tobias, himself, later even went on to controversially subsume *A. afarensis* within a single morphologically variable and geographically and temporally expansive species, *A. africanus* (Tobias, 1980).

The Makapansgat hominins have been generally accepted as belonging to the hypodigm of *A. africanus* since they (as *A. prometheus*) were first subsumed into the taxon (e.g. Robinson, 1954; Tobias, 1967; Clarke, 1977; White, 1977; Tobias 1978; White *et al.*, 1981; Rak, 1983). However, the MLD 2 mandible has been referred to *A. robustus* by some (e.g. Aguirre, 1970, 1972), the Makapansgat and Sterkfontein australopiths have been referred to different species by others (e.g. Tobias, 1968, 1973), and whether the hypodigm of *A. africanus* is actually a mixed-species assemblage has been argued at great length (e.g. Kimbel and White, 1988; Clarke, 1988, 1994, 2008;

Calcagno *et al.*, 1999, Lockwood, 1999; Lockwood and Tobias, 2002; Moggi-Cecchi, 2003; Moggi-Cecchi *et al.*, 2006).

This thesis was written to continue to detail the morphological variation of the South African australopiths and expand the descriptions of the Makapansgat hominins (both previously known and unknown specimens). A major result of this work is the additional evidence of high levels of intraspecific variation for the samples of *A. africanus* and *A. robustus* and considerable morphological overlap between these species and among the site-specific species samples.

There is considerable variation within the hypodigm of *A. africanus*, whether the current taxon is considered a temporally and geographically mixed assemblage of a continuously evolving species or a mixed species assemblage. Moreover, there is growing support for the notion that the hypodigm of *A. africanus* incorporates more than one taxon (e.g. Clarke, 1988, 1994; Kimbel and White, 1988a; Moggi-Cecchi *et al.*, 1998; Lockwood and Tobias, 2002), but discrimination of these taxa remains elusive. Contributing to this problem is that the currently recognized species of *A. africanus* appears to exhibit few autapomorphies (see also Wood, 1985b). Should the current hypodigm of *A. africanus* actually include multiple species, they would almost have to be closely related and, in many ways, morphologically alike. However, as Kimbel and White eloquently suggested with regard to the potential for multiple early hominin species in Sterkfontein Member 4, "… the inability to adequately diagnose closely related species in practice in no way diminishes their reality in nature" (1988:189). As a result, sorting out the phylogenetic relationships and taxonomic schemes of South African early hominins and the Makapansgat assemblage within this framework is riddled with difficulties and their placement within early hominin phylogenies is inconsistent. Yet, the results of this study and the recent publication of a number of relevant works permit discussion of current competing phylogenetic scenarios for *A. africanus* presented in the background chapters.

A. afarensis. It remains possible that the hypodigm of *A. afarensis* is merely a geographic variant or subspecies of a single, highly variable species, *A. africanus* (e.g. Boaz, 1979; Tobias, 1980). This phylogenetic hypothesis is difficult to falsify. Although objective methods can be employed to try to answer this question, the hypothesis hinges on an inherently subjective question: *how much morphological variation in the early hominin fossil record is enough to require a species-level distinction?* A belief in a broadly distributed and enormously inclusive South and East African *A. africanus* was not widely adopted. Nor does this scenario appear likely on the basis of enormous levels of variation within the combined samples vastly exceeding what would be a reasonable application of levels of interspecific varaiation in extant primates to the fossil record.

A more likely scenario is that *A. africanus* is a direct descendant of *A. afarensis* (e.g. Rak, 1985; Skelton et al., 1986; Skelton and McHenry, 1992; McHenry, 1992), which emphasizes the similarity in the two species while acknowledging the significant morphological differences between the more primitive and earlier *A. afarensis* and more derived and later *A. africanus*. This scenario also emphasizes the likelihood of significant (albeit unidirectional) gene flow.

A robust australopithecine monophyly (i.e. *Paranthropus*). These phylogenetic scenarios stress a close relationship between *A. africanus* and a monophyletic group of robust australopiths (e.g. Chamberlain and Wood, 1987; Skelton, 1986; Tobias, 1988; Skelton and McHenry, 1992). Numerous morphological similarities of the samples of *A. africanus* and *A. robustus* have been detailed here and elsewhere (e.g. Tobias, Wolpoff, 1970; Aguirre, 1970, 1972; Brace, 1973; Sperber, 1974; White *et al*., 1981; Kimbel *et al*., 2004). On the basis of these similarites (many of which are derived), the taxon of *A. africanus* is considered here almost certainly closely related to *A. robustus*. However, the relationship of *A. robustus* to the East African species of *A. boisei* and *A. aethiopicus* (members of the Robinsonian gracile versus robust dichotomy) seems less clear. Proponents of "*Paranthropus*" stress derived craniodental specializations relating to similar masticatory features for *A. robustus*, *A. boisei*, and *A. aethiopicus*. Opponents, in contrast, caution against treating the morphological features of the "robust" masticatory complex as independent phylogenetic variables (e.g. McCollum, 1999; Collard and Wood, 2001). The monophyly of *Paranthropus* cannot be falsified on the basis of current knowledge.

Homo. The taxon of *A. africanus* has been linked to early *Homo* by a variety of authors on the basis of primarily craniofacial features. The inclusion of *A. africanus* into the genus *Homo* or a clade with the genus *Homo* to the exclusion of *A. robustus* (e.g. Robinson, 1963, 1972; Lieberman *et al*., 1996) appears unwarranted due to morphological similarity and shared derived features for *A. africanus* with *A. robustus*. The scenario that supports a close relationship for *A. africanus* with both *A. robustus* and

Homo cannot be falsified. In fact, the recent discovery and announcement of *A. sediba* (Berger *et al*., 2010) provides some support to this hypothesis. However, the suggestion that *A. africanus* is ancestral to *Homo* (e.g. Grine, 1988; Tobias, 1991) is not supported and perhaps is even falsifiable on the basis of the morphology and closer alignment of the hypodigm of *A. sediba* with the genus *Homo*. It was argued that the specimens assigned to *Homo* in South Africa may indicate a generally primitive South African early hominin lineage on the basis of a lack of derived features shared with specimens of early *Homo* in East Africa (e.g. Smith and Grine, 2008). However, many of these specimens were incorporated recently into the contentious new species *Homo guatengensis* (Curnoe, 2010).

The extensive similarities of *A. sediba* to both *A. africanus* and *Homo* support a close affinity for these taxa. A modification of these hypotheses has been proposed where *A. africanus* is ancestral to *A. sediba*, which in turn is ancestral to *Homo* (Berger *et al*., 2010). To date, a significant shortcoming to this argument is the ~1.87 million year old dates that have been produced for the Malapa hominin-bearing deposits, post-dating early *Homo* in South and East Africa (e.g. Wood, 1991; Kimbel *et al*., 1997).

<u>A sister taxon to *Homo* and "robust" australopiths</u>. This phylogenetic scenario stresses a few derived features of the hypodigm of *A. africanus* and tends to result from theoretical concerns regarding parsimony in sorting phylogenies (e.g. Strait *et al*., 1997; Asfaw *et al*., 1999). A phylogenetic scenario with *A. africanus* as a sister taxon to *Homo* and "*Paranthropus*" remains plausible. This argument remains open to critique regarding the non-independence of features within the robust masticatory complex. Although a

logical and reasonable tool in deciding among otherwise equivalent scenarios, it must be remembered that parsimony was not a driving force in human evolution. The increasing evidence of a bushy phylogenetic history with new fossil and site discoveries (*Sahelanthropus*, *Kenyanthropus*, *A. garhi*, *A. sediba*, *H. guatengensis*, among others) and with improvements in dating estimates will likely force a revision of the specifics for this scenario.

How do the Makapansgat hominins fit into these phylogenetic scenarios? The range of variation exhibited at Makapansgat exceeds neither that expected for a single species nor that exhibited by *A. africanus* from Sterkfontein (and Taung). The Makapansgat hominins can be considered most similar to specimens of *A. africanus* at Sterkfontein, but they are similar to *A. robustus* in some features. Moreover, in other features and the combination of features displayed by the Makapansgat specimens, the sample is either morphologically intermediate or unique. This is true even with consideration of the frequent overlap in variation apparent between the samples of *A. africanus* and *A. robustus*. Whatever the answer, the inclusion of the Makapansgat hominin sample within the hypodigm of *A. africanus* has, by definition, impacted interpretations of this taxon. For instance, inclusion of the Makapansgat mandibular corpus sample within studies of *A. africanus* nearly doubles the sample size for this taxon.

The Makapansgat hominin assemblage is dated to ~2.7-2.6 million years ago (MA) by the latest combined paleomagnetic and biochronological analysis (Warr, 2009) and ~2.8 – 3.2 million years by faunal seriation and U-Pb analyses of hominin-bearing deposits (Vrba, 1985; McKee, 1995; McKee *et al.*, 1995; Crawford *et al.*, 2004; Warr *et al.*, 2009). Even the more conservative estimate of 2.6-2.7 MA is half a million years prior to the current estimates of ~ 2.2 MA for *A. africanus* elsewhere at Sterkfontein (Walker *et al*., 2006). Meanwhile, the earliest dates for *A. robustus* and *A. sediba* in South Africa are 1.0 -1.8 MA from Sterkfontein and ~ 1.87 MA from Malapa (Berger *et al*., 2010, Dirks *et al*., 2010), respectively. The Makapansgat hominins are thus the earliest fossil hominins currently known in South Africa. This makes several possibilities for their phylogenetic position apparent.

It is possible that the Makapansgat sample simply represents an early form of a temporally and geographically variable species of *A. africanus*. However, some of the derived features the Makapansgat hominins share with *A. robustus* to the exclusion of *A. africanus* may indicate that the Makapansgat hominins are representative of a closely related population that was ancestral to both *A. robustus* and *A. africanus* or a member of a sister taxon to *A. africanus* (*A. prometheus*) that may have been ancestral to *A. robustus* (depending on the monophyly or paraphyly of *Paranthropus*). It also remains possible as previously argued (Clarke, 2008) that the Makapansgat australopiths are part of a previously unidentified australopith species preserved within the Sterkfontein Member 4 deposits. Each of these hypotheses is viable and it will be difficult to falsify scenarios until additional fossils are available or until temporal variation within the hypodigms of *A. africanus* and *A. robustus* is better understood. Caution dictates that whenever the Makapansgat hominins are treated as members of *A. africanus* in analyses, that (at a minimum) the Makapansgat sample be assessed for potential temporally related morphological distinctions within the taxon as Lockwood and colleagues (2000) have done for the sample of *A. afarensis*. It might be more conservative to treat the Makapansgat hominins separately, but the small sample size will continue to limit comparative analyses until additional fossils are recovered.

Concluding Remarks

The Makapansgat assemblage provides a temporally and geographically restricted and valuable South African early hominin sample. The morphological descriptions and qualitative and quantitative comparisons of the cranial, mandibular, and dental specimens of the Makapansgat hominins presented in the previous chapters suggest: 1) the Makapansgat specimens are distinct in some ways, 2) most (if not all) of the individuals they represent share a close phylogenetic relationship with *A. africanus*, but it is currently impossible to select among several competing phylogenetic alternatives, 3) inclusion of the Makapansgat hominins in *A. africanus* impacts morphological features used to characterize the hypodigm. Whether the Makapansgat hominins are considered a single evolving population or a mixed-species assemblage, they are critical for sorting out biogeographic and phylogenetic reconstructions of early hominin evolution. More importantly, however, they provide additional evidence of the incredible complexity and morphological variability of early hominins.

Typological thinking was central to a substantial part of the history of South African paleoanthropological research. Even as most researchers have attempted to abandon Robinson’s robust and gracile dichotomy, it still permeates many studies and phylogenetic scenarios. Yet some have adopted another form of typological thinking: site typologies. In some cases (e.g. specimens of *A. sediba* from Malapa and *A. afarensis* from the Hadar 333 site), it may be appropriate to consider a fossil sample representative of a restricted population. In South Africa, however, many of the australopith-bearing deposits are known from temporally expansive cave deposits. The early hominins recovered from these sites thus represent individuals from evolving and mobile populations that lived in temporally varying habitats and many of these individuals were transported to the cave postmortem. In addition, the temporal overlap and geographical close proximity of sites preserving different australopith species is astounding. In this context, assignment of specimens to a species on the basis of the prevailing taxon at a site should be considered a tenuous practice. As a result, there are many fragmentary or isolated South African early hominin specimens whose attributions are questionable.

In this author's subjective view, many of the competing scenarios detailed above are not mutually exclusive (with obvious exceptions, such as the monophyly or paraphyly of *Paranthropus*). To think of the increasingly abundant fossil hominin species as members of discrete lineages without gene flow may be folly. Whether you adopt a splitter's or lumper's taxonomy, it is increasingly difficult to argue that contemporaneous and geographically disparate hominin fossil "species" were discrete units without inter-specific gene flow. Evidence of interbreeding by Neandertals and modern humans (e.g. Duarte *et al*., 1999; Trinkaus *et al*., 2003; Trinkaus, 2007; Green *et al.*, 2010), as well as by extant primates (e.g. Bernsteil, 1966; Dunbar and Dunbar, 1974; Sugawara, 1979; Jolly *et al*., 1979) suggest that evolution may have been either complex with rampant species- and population-level interbreeding and hybridization events, or was far more simplistic with a handful of broad-ranging and highly variable species. Although this author does not subscribe to this extreme, the latter approach is arguably the simplest of current phylogenetic scenarios. Regardless, these debates will persist and consensus almost certainly will continue to vacillate between the two extremes first championned by Robinson and Tobias. One thing is for certain: new discoveries will continue to highlight the incredible morphological diversity of our ancestors and will likely challenge our phylogenetic hypotheses and species concepts as continued morhological overlap becomes increasingly apparent between fossil species previously considered distinct.

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APPENDIX 1: FOSSIL SPECIMENS

Museum	Site	Specimen No.	Genus	Species	Code
Wits	Makapansgat	MLD 1	Australo		MAK
Wits	Makapansgat	MLD 10	Australo		MAK
Wits	Makapansgat	MLD 11/30	Australo		MAK
Wits	Makapansgat	MLD 12	Australo		MAK
Wits	Makapansgat	MLD 18	Australo		MAK
Wits	Makapansgat	MLD 19	Australo		MAK
Wits	Makapansgat	MLD 2	Australo		MAK
Wits	Makapansgat	MLD 22	Australo		MAK
Wits	Makapansgat	MLD 23	Australo		MAK
Wits	Makapansgat	MLD 24	Australo		MAK
Wits	Makapansgat	MLD 27	Australo		MAK
Wits	Makapansgat	MLD 28	Australo		MAK
Wits	Makapansgat	MLD 29	Australo		MAK
Wits	Makapansgat	MLD 3	Australo		MAK
Wits	Makapansgat	MLD 31	Australo		MAK
Wits	Makapansgat	MLD 34	Australo		MAK
Wits	Makapansgat	MLD 37/38	Australo		MAK
Wits	Makapansgat	MLD 4	Australo		MAK
Wits	Makapansgat	MLD 40	Australo		MAK
Wits	Makapansgat	MLD 41	Australo		MAK
Wits	Makapansgat	MLD 42	Australo		MAK
Wits	Makapansgat	MLD 43	Australo		MAK
Wits	Makapansgat	MLD 44	Australo		MAK
Wits	Makapansgat	MLD 45	Australo		MAK
Wits	Makapansgat	MLD 47	Australo		MAK
Wits	Makapansgat	MLD 48	Australo		MAK
Wits	Makapansgat	MLD 5	Australo		MAK
Wits	Makapansgat	MLD 6	Australo		MAK
Wits	Makapansgat	MLD 9	Australo		MAK
TM	Coopers	COA 1	Australo	africanus	afric_CO
TM	Coopers	COB 101	Australo	africanus	afric_CO
TM	Kromdraai	KB 5163	Australo	robustus	rob_KB
TM	Kromdraai	KB 5222	Australo	robustus	rob_KB
TM	Kromdraai	KB 5503	Australo	robustus	rob_Sk
TM	Kromdraai	KB5389	Australo	robustus	rob_KB
TM	Kromdraai	TM 1517	Australo	robustus	rob_KB
TM	Kromdraai	TM 1536 pool	Australo	robustus	rob_KB

TM	Kromdraai	TM 1600	Australo	robustus	rob_KB
TM	Kromdraai	TM 1601	Australo	robustus	rob_KB
TM	Kromdraai	TM 1602	Australo	robustus	rob_KB
TM	Kromdraai	TM 1604	Australo	robustus	rob_KB
TM	Kromdraai	TM 1603	Australo	robustus	rob_KB
TM	Kromdraai	TM 1601	Australo	robustus	rob_KB
TM	Sterkfontein	STS 1	Australo	africanus	afric_St
TM	Sterkfontein	STS 10	Australo	africanus	afric_St
TM	Sterkfontein	STS 12	Australo	africanus	afric_St
TM	Sterkfontein	STS 17	Australo	africanus	afric_St
TM	Sterkfontein	STS 18 pool	Australo	africanus	afric_St
TM	Sterkfontein	STS 1881	Australo	africanus	afric_St
TM	Sterkfontein	STS 19	Australo	africanus	afric_St
TM	Sterkfontein	STS 19	Australo	africanus	afric_St
TM	Sterkfontein	STS 2	Australo	africanus	afric_St
TM	Sterkfontein	STS 21	Australo	africanus	afric_St
TM	Sterkfontein	STS 22	Australo	africanus	afric_St
TM	Sterkfontein	STS 2253	Australo	africanus	afric_St
TM	Sterkfontein	STS 23	Australo	africanus	afric_St
TM	Sterkfontein	STS 24	Australo	africanus	afric_St
TM	Sterkfontein	STS 3	Australo	africanus	afric_St
TM	Sterkfontein	STS 30	Australo	africanus	afric_St
TM	Sterkfontein	STS 3009	Australo	africanus	afric_St
TM	Sterkfontein	STS 32	Australo	africanus	afric_St
TM	Sterkfontein	STS 35	Australo	africanus	afric_St
Wits	Sterkfontein	STS 36 pool	Australo	africanus	afric_St
TM	Sterkfontein	STS 4	Australo	africanus	afric_St
TM	Sterkfontein	STS 40	Australo	africanus	afric_St
TM	Sterkfontein	STS 41	Australo	africanus	afric_St
TM	Sterkfontein	STS 42	Australo	africanus	afric_St
TM	Sterkfontein	STS 44/66	Australo	africanus	afric_St
TM	Sterkfontein	STS 47	Australo	africanus	afric_St
TM	Sterkfontein	STS 48	Australo	africanus	afric_St
TM	Sterkfontein	STS 5	Australo	africanus	afric_St
TM	Sterkfontein	STS 50	Australo	africanus	afric_St
TM	Sterkfontein	STS 52	Australo	africanus	afric_St
TM	Sterkfontein	STS 53	Australo	africanus	afric_St
TM	Sterkfontein	STS 55	Australo	africanus	afric_St
TM	Sterkfontein	STS 55b	Australo	africanus	afric_St
TM	Sterkfontein	STS 56	Australo	africanus	afric_St

TM	Sterkfontein	STS 57	Australo	africanus	afric_St
TM	Sterkfontein	STS 59	Australo	africanus	afric_St
TM	Sterkfontein	STS 61	Australo	africanus	afric_St
TM	Sterkfontein	STS 67	Australo	africanus	afric_St
TM	Sterkfontein	STS 7 pool	Australo	africanus	afric_St
TM	Sterkfontein	STS 71	Australo	africanus	afric_St
TM	Sterkfontein	STS 71	Australo	africanus	afric_St
TM	Sterkfontein	STS 8	Australo	africanus	afric_St
TM	Sterkfontein	STS 9	Australo	africanus	afric_St
Wits	Sterkfontein	STW 1	Australo	africanus	afric_St
Wits	Sterkfontein	STW 104	Australo	africanus	afric_St
Wits	Sterkfontein	STW 106	Australo	africanus	afric_St
Wits	Sterkfontein	STW 107	Australo	africanus	afric_St
Wits	Sterkfontein	STW 109	Australo	africanus	afric_St
Wits	Sterkfontein	STW 110	Australo	africanus	afric_St
Wits	Sterkfontein	STW 111	Australo	africanus	afric_St
Wits	Sterkfontein	STW 112	Australo	africanus	afric_St
Wits	Sterkfontein	STW 116 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 120	Australo	africanus	afric_St
Wits	Sterkfontein	STW 123	Australo	africanus	afric_St
Wits	Sterkfontein	STW 13	Australo	africanus	afric_St
Wits	Sterkfontein	STW 13	Australo	africanus	afric_St
Wits	Sterkfontein	STW 130	Australo	africanus	afric_St
Wits	Sterkfontein	STW 131 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 132	Australo	africanus	afric_St
Wits	Sterkfontein	STW 133	Australo	africanus	afric_St
Wits	Sterkfontein	STW 134	Australo	africanus	afric_St
Wits	Sterkfontein	STW 138	Australo	africanus	afric_St
Wits	Sterkfontein	STW 14	Australo	africanus	afric_St
Wits	Sterkfontein	STW 140	Australo	africanus	afric_St
Wits	Sterkfontein	STW 142 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 143	Australo	africanus	afric_St
Wits	Sterkfontein	STW 145	Australo	africanus	afric_St
Wits	Sterkfontein	STW 146	Australo	africanus	afric_St
Wits	Sterkfontein	STW 147	Australo	africanus	afric_St
Wits	Sterkfontein	STW 148	Australo	africanus	afric_St
Wits	Sterkfontein	STW 16	Australo	africanus	afric_St
Wits	Sterkfontein	STW 17	Australo	africanus	afric_St
Wits	Sterkfontein	STW 179	Australo	africanus	afric_St
Wits	Sterkfontein	STW 18	Australo	africanus	afric_St

Wits	Sterkfontein	STW 183	Australo	africanus	afric_St
Wits	Sterkfontein	STW 183a	Australo	africanus	afric_St
Wits	Sterkfontein	STW 184	Australo	africanus	afric_St
Wits	Sterkfontein	STW 188	Australo	africanus	afric_St
Wits	Sterkfontein	STW 189	Australo	africanus	afric_St
Wits	Sterkfontein	STW 192	Australo	africanus	afric_St
Wits	Sterkfontein	STW 193 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 196	Australo	africanus	afric_St
Wits	Sterkfontein	STW 19a,b	Australo	africanus	afric_St
Wits	Sterkfontein	STW 2	Australo	africanus	afric_St
Wits	Sterkfontein	STW 20	Australo	africanus	afric_St
Wits	Sterkfontein	STW 202	Australo	africanus	afric_St
Wits	Sterkfontein	STW 204	Australo	africanus	afric_St
Wits	Sterkfontein	STW 206	Australo	africanus	afric_St
Wits	Sterkfontein	STW 208/217	Australo	africanus	afric_St
Wits	Sterkfontein	STW 209	Australo	africanus	afric_St
Wits	Sterkfontein	STW 21	Australo	africanus	afric_St
Wits	Sterkfontein	STW 212	Australo	africanus	afric_St
Wits	Sterkfontein	STW 213 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 220,221	Australo	africanus	afric_St
Wits	Sterkfontein	STW 23	Australo	africanus	afric_St
Wits	Sterkfontein	STW 234	Australo	africanus	afric_St
Wits	Sterkfontein	STW 237	Australo	africanus	afric_St
Wits	Sterkfontein	STW 246 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 247 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 252	Australo	africanus	afric_St
Wits	Sterkfontein	STW 276	Australo	africanus	afric_St
Wits	Sterkfontein	STW 280	Australo	africanus	afric_St
Wits	Sterkfontein	STW 285	Australo	africanus	afric_St
Wits	Sterkfontein	STW 286	Australo	africanus	afric_St
Wits	Sterkfontein	STW 287	Australo	africanus	afric_St
Wits	Sterkfontein	STW 288	Australo	africanus	afric_St
Wits	Sterkfontein	STW 291	Australo	africanus	afric_St
Wits	Sterkfontein	STW 295 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 296	Australo	africanus	afric_St
Wits	Sterkfontein	STW 297	Australo	africanus	afric_St
Wits	Sterkfontein	STW 3	Australo	africanus	afric_St
Wits	Sterkfontein	STW 305, 306	Australo	africanus	afric_St
Wits	Sterkfontein	STW 307	Australo	africanus	afric_St
Wits	Sterkfontein	STW 309 pool	Australo	africanus	afric_St

Wits	Sterkfontein	STW 313	Australo	africanus	afric_St
Wits	Sterkfontein	STW 317	Australo	africanus	afric_St
Wits	Sterkfontein	STW 319	Australo	africanus	afric_St
Wits	Sterkfontein	STW 32	Australo	africanus	afric_St
Wits	Sterkfontein	STW 327	Australo	africanus	afric_St
Wits	Sterkfontein	STW 33	Australo	africanus	afric_St
Wits	Sterkfontein	STW 332	Australo	africanus	afric_St
Wits	Sterkfontein	STW 333	Australo	africanus	afric_St
Wits	Sterkfontein	STW 35	Australo	africanus	afric_St
Wits	Sterkfontein	STW 351	Australo	africanus	afric_St
Wits	Sterkfontein	STW 353	Australo	africanus	afric_St
Wits	Sterkfontein	STW 364	Australo	africanus	afric_St
Wits	Sterkfontein	STW 365	Australo	africanus	afric_St
Wits	Sterkfontein	STW 369	Australo	africanus	afric_St
Wits	Sterkfontein	STW 37	Australo	africanus	afric_St
Wits	Sterkfontein	STW 379	Australo	africanus	afric_St
Wits	Sterkfontein	STW 384 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 386/385	Australo	africanus	afric_St
Wits	Sterkfontein	STW 397	Australo	africanus	afric_St
Wits	Sterkfontein	STW 401	Australo	africanus	afric_St
Wits	Sterkfontein	STW 402	Australo	africanus	afric_St
Wits	Sterkfontein	STW 404 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 406	Australo	africanus	afric_St
Wits	Sterkfontein	STW 407	Australo	africanus	afric_St
Wits	Sterkfontein	STW 408	Australo	africanus	afric_St
Wits	Sterkfontein	STW 410	Australo	africanus	afric_St
Wits	Sterkfontein	STW 412 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 413	Australo	africanus	afric_St
Wits	Sterkfontein	STW 414	Australo	africanus	afric_St
Wits	Sterkfontein	STW 415	Australo	africanus	afric_St
Wits	Sterkfontein	STW 42	Australo	africanus	afric_St
Wits	Sterkfontein	STW 420	Australo	africanus	afric_St
Wits	Sterkfontein	STW 421	Australo	africanus	afric_St
Wits	Sterkfontein	STW 423	Australo	africanus	afric_St
Wits	Sterkfontein	STW 424	Australo	africanus	afric_St
Wits	Sterkfontein	STW 425	Australo	africanus	afric_St
Wits	Sterkfontein	STW 427	Australo	africanus	afric_St
Wits	Sterkfontein	STW 428	Australo	africanus	afric_St
Wits	Sterkfontein	STW 429	Australo	africanus	afric_St
Wits	Sterkfontein	STW 43	Australo	africanus	afric_St

Wits	Sterkfontein	STW 430	Australo	africanus	afric_St
Wits	Sterkfontein	STW 446	Australo	africanus	afric_St
Wits	Sterkfontein	STW 447	Australo	africanus	afric_St
Wits	Sterkfontein	STW 45	Australo	africanus	afric_St
Wits	Sterkfontein	STW 450	Australo	africanus	afric_St
Wits	Sterkfontein	STW 47	Australo	africanus	afric_St
Wits	Sterkfontein	STW 471	Australo	africanus	afric_St
Wits	Sterkfontein	STW 472	Australo	africanus	afric_St
Wits	Sterkfontein	STW 476	Australo	africanus	afric_St
Wits	Sterkfontein	STW 480	Australo	africanus	afric_St
Wits	Sterkfontein	STW 483	Australo	africanus	afric_St
Wits	Sterkfontein	STW 487 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 488	Australo	africanus	afric_St
Wits	Sterkfontein	STW 491 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 498	Australo	africanus	afric_St
Wits	Sterkfontein	STW 5	Australo	africanus	afric_St
Wits	Sterkfontein	STW 50	Australo	africanus	afric_St
Wits	Sterkfontein	STW 502	Australo	africanus	afric_St
Wits	Sterkfontein	STW 505	Australo	africanus	afric_St
Wits	Sterkfontein	STW 513 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 52	Australo	africanus	afric_St
Wits	Sterkfontein	STW 520??	Australo	africanus	afric_St
Wits	Sterkfontein	STW 524	Australo	africanus	afric_St
Wits	Sterkfontein	STW 529	Australo	africanus	afric_St
Wits	Sterkfontein	STW 529 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 536	Australo	africanus	afric_St
Wits	Sterkfontein	STW 537 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 54	Australo	africanus	afric_St
Wits	Sterkfontein	STW 555	Australo	africanus	afric_St
Wits	Sterkfontein	STW 558	Australo	africanus	afric_St
Wits	Sterkfontein	STW 559	Australo	africanus	afric_St
Wits	Sterkfontein	STW 56	Australo	africanus	afric_St
Wits	Sterkfontein	STW 560 pool	Australo	africanus	afric_St
Wits	Sterkfontein	STW 566	Australo	africanus	afric_St
Wits	Sterkfontein	STW 569b	Australo	africanus	afric_St
Wits	Sterkfontein	STW 57	Australo	africanus	afric_St
Wits	Sterkfontein	STW 574	Australo	africanus	afric_St
Wits	Sterkfontein	STW 58	Australo	africanus	afric_St
Wits	Sterkfontein	STW 585	Australo	africanus	afric_St
Wits	Sterkfontein	STW 586	Australo	africanus	afric_St

Wits	Sterkfontein	STW 587	Australo	africanus	afric_St
Wits	Sterkfontein	STW 59	Australo	africanus	afric_St
Wits	Sterkfontein	STW 6	Australo	africanus	afric_St
Wits	Sterkfontein	STW 60	Australo	africanus	afric_St
Wits	Sterkfontein	STW 61	Australo	africanus	afric_St
Wits	Sterkfontein	STW 67	Australo	africanus	afric_St
Wits	Sterkfontein	STW 7	Australo	africanus	afric_St
Wits	Sterkfontein	STW 71	Australo	africanus	afric_St
Wits	Sterkfontein	STW 72	Australo	africanus	afric_St
Wits	Sterkfontein	STW 73	Australo	africanus	afric_St
Wits	Sterkfontein	STW 75-79	Australo	africanus	afric_St
Wits	Sterkfontein	STW 81	Australo	africanus	afric_St
Wits	Sterkfontein	STW 82	Australo	africanus	afric_St
Wits	Sterkfontein	STW 87	Australo	africanus	afric_St
Wits	Sterkfontein	STW 90	Australo	africanus	afric_St
Wits	Sterkfontein	STW 92	Australo	africanus	afric_St
Wits	Sterkfontein	STW 95	Australo	africanus	afric_St
Wits	Sterkfontein	STW 96	Australo	africanus	afric_St
Wits	Sterkfontein	STW 9a,b	Australo	africanus	afric_St
Wits	Sterkfontein	STW34/19	Australo	africanus	afric_St
TM	Sterkfontein	TM 1511	Australo	africanus	afric_St
TM	Sterkfontein	TM 1512	Australo	africanus	afric_St
TM	Sterkfontein	TM 1514	Australo	africanus	afric_St
TM	Sterkfontein	TM 1515	Australo	africanus	afric_St
TM	Sterkfontein	TM 1519	Australo	africanus	afric_St
TM	Sterkfontein	TM 1520	Australo	africanus	afric_St
TM	Sterkfontein	TM 1523	Australo	africanus	afric_St
TM	Sterkfontein	TM 1527	Australo	africanus	afric_St
TM	Sterkfontein	TM 1528	Australo	africanus	afric_St
TM	Sterkfontein	TM 1532	Australo	africanus	afric_St
Wits	Sterkfontein	STW 151	Homo	sp.	H_St
Wits	Sterkfontein	STW 53	Homo	sp.	H_St
Wits	Sterkfontein	STW 53	Homo	sp.	H_St
TM	Sterkfontein	STS 3202	Incertae	sedis	?_Sts
TM	Swartkrans	SK 851	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1	Australo	robustus	rob_Sk
TM	Swartkrans	SK 10, 1648 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 101	Australo	robustus	rob_Sk
TM	Swartkrans	SK 102	Australo	robustus	rob_Sk

TM	Swartkrans	SK 104	Australo	robustus	rob_Sk
TM	Swartkrans	SK 105	Australo	robustus	rob_Sk
TM	Swartkrans	SK 11	Australo	robustus	rob_Sk
TM	Swartkrans	SK 12 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 13,14	Australo	robustus	rob_Sk
TM	Swartkrans	SK 14000	Australo	robustus	rob_Sk
TM	Swartkrans	SK 14001	Australo	robustus	rob_Sk
TM	Swartkrans	SK 14030	Australo	robustus	rob_Sk
TM	Swartkrans	SK 14133	Australo	robustus	rob_Sk
TM	Swartkrans	SK 14246 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1512	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1586 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1587 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1588	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1590	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1593	Australo	robustus	rob_Sk
TM	Swartkrans	SK 16	Australo	robustus	rob_Sk
TM	Swartkrans	SK 1648, 10	Australo	robustus	rob_Sk
TM	Swartkrans	SK 17	Australo	robustus	rob_Sk
TM	Swartkrans	SK 19	Australo	robustus	rob_Sk
TM	Swartkrans	SK 2	Australo	robustus	rob_Sk
TM	Swartkrans	SK 20	Australo	robustus	rob_Sk
TM	Swartkrans	SK 21, 21a	Australo	robustus	rob_Sk
TM	Swartkrans	SK 23 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 24	Australo	robustus	rob_Sk
TM	Swartkrans	SK 24660	Australo	robustus	rob_Sk
TM	Swartkrans	SK 24661	Australo	robustus	rob_Sk
TM	Swartkrans	SK 25 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 28	Australo	robustus	rob_Sk
TM	Swartkrans	SK 29	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3	Australo	robustus	rob_Sk
TM	Swartkrans	SK 30	Australo	robustus	rob_Sk
TM	Swartkrans	SK 31	Australo	robustus	rob_Sk
TM	Swartkrans	SK 32	Australo	robustus	rob_Sk
TM	Swartkrans	SK 33	Australo	robustus	rob_Sk
TM	Swartkrans	SK 34 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 36	Australo	robustus	rob_Sk
TM	Swartkrans	SK 37	Australo	robustus	rob_Sk
TM	Swartkrans	SK 38	Australo	robustus	rob_Sk

TM	Swartkrans	SK 39	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3974	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3975	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3976	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3977	Australo	robustus	rob_Sk
TM	Swartkrans	SK 3978 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 4	Australo	robustus	rob_Sk
TM	Swartkrans	SK 40	Australo	robustus	rob_Sk
TM	Swartkrans	SK 42	Australo	robustus	rob_Sk
TM	Swartkrans	SK 438	Australo	robustus	rob_Sk
TM	Swartkrans	SK 44	Australo	robustus	rob_Sk
TM	Swartkrans	SK 46	Australo	robustus	rob_Sk
TM	Swartkrans	SK 47	Australo	robustus	rob_Sk
TM	Swartkrans	SK 48	Australo	robustus	rob_Sk
TM	Swartkrans	SK 49	Australo	robustus	rob_Sk
TM	Swartkrans	SK 5	Australo	robustus	rob_Sk
TM	Swartkrans	SK 52	Australo	robustus	rob_Sk
TM	Swartkrans	SK 52/SKW 18	Australo	robustus	rob_Sk
TM	Swartkrans	SK 54	Australo	robustus	rob_Sk
TM	Swartkrans	SK 55 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 57	Australo	robustus	rob_Sk
TM	Swartkrans	SK 6 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 61 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 62 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 63 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 64	Australo	robustus	rob_Sk
TM	Swartkrans	SK 65, 65a, 67	Australo	robustus	rob_Sk
TM	Swartkrans	SK 7	Australo	robustus	rob_Sk
TM	Swartkrans	SK 70	Australo	robustus	rob_Sk
TM	Swartkrans	SK 71	Australo	robustus	rob_Sk
TM	Swartkrans	SK 72	Australo	robustus	rob_Sk
TM	Swartkrans	SK 73	Australo	robustus	rob_Sk
TM	Swartkrans	SK 74/74a	Australo	robustus	rob_Sk
TM	Swartkrans	SK 740b	Australo	robustus	rob_Sk
TM	Swartkrans	SK 79	Australo	robustus	rob_Sk
TM	Swartkrans	SK 81 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 821	Australo	robustus	rob_Sk
TM	Swartkrans	SK 822	Australo	robustus	rob_Sk
TM	Swartkrans	SK 823	Australo	robustus	rob_Sk

TM	Swartkrans	SK 824	Australo	robustus	rob_Sk
TM	Swartkrans	SK 825	Australo	robustus	rob_Sk
TM	Swartkrans	SK 826, 826a	Australo	robustus	rob_Sk
TM	Swartkrans	SK 827	Australo	robustus	rob_Sk
TM	Swartkrans	SK 829	Australo	robustus	rob_Sk
TM	Swartkrans	SK 830	Australo	robustus	rob_Sk
TM	Swartkrans	SK 833	Australo	robustus	rob_Sk
TM	Swartkrans	SK 834	Australo	robustus	rob_Sk
TM	Swartkrans	SK 837	Australo	robustus	rob_Sk
TM	Swartkrans	SK 838	Australo	robustus	rob_Sk
TM	Swartkrans	SK 839/852	Australo	robustus	rob_Sk
TM	Swartkrans	SK 83a,b	Australo	robustus	rob_Sk
TM	Swartkrans	SK 841	Australo	robustus	rob_Sk
TM	Swartkrans	SK 843 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 844	Australo	robustus	rob_Sk
TM	Swartkrans	SK 845	Australo	robustus	rob_Sk
TM	Swartkrans	SK 849	Australo	robustus	rob_Sk
TM	Swartkrans	SK 852 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 857	Australo	robustus	rob_Sk
TM	Swartkrans	SK 858, 883, 861 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 86	Australo	robustus	rob_Sk
TM	Swartkrans	SK 862	Australo	robustus	rob_Sk
TM	Swartkrans	SK 867	Australo	robustus	rob_Sk
TM	Swartkrans	SK 869	Australo	robustus	rob_Sk
TM	Swartkrans	SK 87	Australo	robustus	rob_Sk
TM	Swartkrans	SK 870	Australo	robustus	rob_Sk
TM	Swartkrans	SK 871	Australo	robustus	rob_Sk
TM	Swartkrans	SK 872	Australo	robustus	rob_Sk
TM	Swartkrans	SK 873	Australo	robustus	rob_Sk
TM	Swartkrans	SK 876 pool	Australo	robustus	rob_Sk
TM	Swartkrans	SK 877	Australo	robustus	rob_Sk
TM	Swartkrans	SK 88	Australo	robustus	rob_Sk
TM	Swartkrans	SK 881,882	Australo	robustus	rob_Sk
TM	Swartkrans	SK 884	Australo	robustus	rob_Sk
TM	Swartkrans	SK 885	Australo	robustus	rob_Sk
TM	Swartkrans	SK 9	Australo	robustus	rob_Sk
TM	Swartkrans	SK 92	Australo	robustus	rob_Sk
TM	Swartkrans	SK 93	Australo	robustus	rob_Sk
TM	Swartkrans	SK 94	Australo	robustus	rob_Sk

TM	Swartkrans	SK 95	Australo	robustus	rob_Sk
TM	Swartkrans	SK 98	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 10	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 11pool	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 12	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 14	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 2581	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 29	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 30	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 3068	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 32	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 33	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 4767	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 4768	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 4772	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 5	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 5017	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 6113	Australo	robustus	rob_Sk
TM	Swartkrans	SKW 8	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 1017	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 10642	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 10643	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 1313	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 14000	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 16060	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 162	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 1788	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 19031	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 2003	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 240	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 241	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 242	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 265	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 271	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 308	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 310	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 311	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 312	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 313	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 3300	Australo	robustus	rob_Sk

TM	Swartkrans	SKX 3354	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 3559	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 4446	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5002	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5004b	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5007	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 50078	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 50081	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5013	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5014	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 5023	Australo	robustus	rob_Sk
TM	Swartkrans	SKX 6013	Australo	robustus	rob_Sk
TM	Swartkrans	SK 18a	Homo	sp.	H_Sk
TM	Swartkrans	SK 2635	Homo	sp.	H_Sk
TM	Swartkrans	SK 27	Homo	sp.	H_Sk
TM	Swartkrans	SK 68	Homo	sp.	H_Sk
TM	Swartkrans	SK 80	Homo	sp.	H_Sk
TM	Swartkrans	SKW 3114	Homo	sp.	H_Sk
TM	Swartkrans	SKX 2671	Homo	sp.	H_Sk
TM	Swartkrans	SKX 268	Homo	sp.	H_Sk
TM	Swartkrans	SKX 339	Homo	sp.	H_Sk
TM	Swartkrans	SKX 610	Homo	sp.	H_Sk
TM	Swartkrans	SK 15 pool	Homo	sp.	H_Sk
TM	Swartkrans	SK 15 pool	Homo	sp.	H_Sk
TM	Swartkrans	SK 2635	Homo	sp.	H_Sk
TM	Swartkrans	SK 27	Homo	sp.	H_Sk
TM	Swartkrans	SK 45	Homo	sp.	H_Sk
TM	Swartkrans	SK 80	Homo	sp.	H_Sk
TM	Swartkrans	SK 831	Homo	sp.	H_Sk
TM	Swartkrans	SKX 2354,5	Homo	sp.	H_Sk
TM	Swartkrans	SKX 257/258	Homo	sp.	H_Sk
TM	Swartkrans	SK 24661	Incertae	sedis	?_Sk
TM	Swartkrans	SK 42207	Incertae	sedis	?_Sk
TM	Swartkrans	SK 69	Incertae	sedis	?_Sk
TM	Swartkrans	SK 85	Incertae	sedis	?_Sk
TM	Sterk extension	SE 1508	Homo	sp.	H_St
TM	Sterk extension	SE 1579	Homo	sp.	H_St
TM	Sterk extension	SE 1937	Homo	sp.	H_St
TM	Sterk extension	SE 255	Homo	sp.	H_St

APPENDIX 2: MEASUREMENT REPEATABILITY

Cranium Measurement Repeatability

Genus	Spec No.	Value	g-i	nas-i	g-lam	g-op	pros-i	bas-br
Homo	99.1/1728	Mean	166.83	162.01	169.54	172.24	168.16	138.39
		St. Dev.	0.21	0.08	0.04	0.23	0.08	0.04
		Coeff. Var.	0.13	0.05	0.02	0.13	0.04	0.03
Homo	99.1/1738	Mean	176.31	171.78	181.90	183.10	184.79	143.25
		St. Dev.	1.06	0.64	0.19	0.16	0.38	0.22
		Coeff. Var.	0.60	0.38	0.10	0.09	0.21	0.16
Homo	VL/2921	Mean	165.28	165.17	169.84	170.76	170.28	128.52
		St. Dev.	0.05	0.12	0.04	0.39	0.18	0.07
		Coeff. Var.	0.03	0.07	0.03	0.23	0.11	0.06
Homo	VL/2923	Mean	161.09	158.70	168.22	170.63	165.27	132.16
		St. Dev.	1.22	0.33	0.10	0.46	0.62	0.08
		Coeff. Var.	0.76	0.21	0.06	0.27	0.37	0.06
Homo	VL/2928	Mean	155.61	155.65	165.70	168.35	159.66	119.87
		St. Dev.	1.49	1.44	0.04	0.05	1.99	0.11
		Coeff. Var.	0.95	0.92	0.02	0.03	1.25	0.09
Pan	174699	Mean	123.56	123.48	114.39	123.50	184.77	87.97
		St. Dev.	0.22		0.38	0.19	0.24	0.28
		Coeff. Var.	0.18		0.34	0.16	0.13	0.32
Pan	174700	Mean	128.86	125.90	119.58	128.71	176.60	82.51
		St. Dev.	0.15	0.14	8.67	0.84	0.29	0.11
		Coeff. Var.	0.11	0.11	7.25	0.65	0.16	0.13
Pan	174701	Mean	133.80	132.18	125.11	133.69	175.67	92.01
		St. Dev.	0.15	0.05	0.04	0.31	1.09	0.13
		Coeff. Var.	0.11	0.04	0.03	0.23	0.62	0.14
Pan	174702	Mean	128.24	127.90	119.34	127.92	182.89	87.76
		St. Dev.	0.17	0.32	0.20	0.30	1.91	0.46
		Coeff. Var.	0.13	0.25	0.17	0.23	1.05	0.53
Pan	174703	Mean	128.41	127.88	117.53	127.26	174.60	88.95
		St. Dev.	0.03	0.03	0.10	0.02	0.01	0.45
		Coeff. Var.	0.02	0.02	0.09	0.02	0.01	0.51
Pan	174706	Mean	122.22	121.44	111.69	121.90	164.26	85.47
		St. Dev.	0.02	0.11	1.64	0.44	0.18	0.67
		Coeff. Var.	0.01	0.09	1.47	0.36	0.11	0.79
Pan	174707	Mean	124.97	123.65	115.33	126.27	172.07	87.56
		St. Dev.	0.01	0.14	1.32	0.89	0.64	0.11
		Coeff. Var.	0.01	0.11	1.14	0.71	0.37	0.12
Pan	174710	Mean	128.66	127.23	119.83	129.78	187.72	91.20
		St. Dev.	0.22	0.14		1.26	0.15	1.21
		Coeff. Var.	0.17	0.11		0.97	0.08	1.33
Pan	220326	Mean	134.23	132.00	127.72	133.48		94.20
		St. Dev.	0.32	0.12	4.58	0.98		0.28
		Coeff. Var.	0.24	0.09	3.58	0.73		0.29

Pan	176228	Mean	122.35	120.87	117.16	125.29	182.34	92.80
		St. Dev.	0.26	0.17	0.57	0.98	0.20	0.61
		Coeff. Var.	0.21	0.14	0.48	0.78	0.11	0.66
Pan	176229	Mean	134.77	131.72	124.38	134.81	189.60	84.68
		St. Dev.	0.40	0.01	0.21	0.57	0.45	0.18
		Coeff. Var.	0.29	0.00	0.17	0.42	0.24	0.21
Pan	176235	Mean	133.62	132.19	128.49	133.47	188.86	82.28
		St. Dev.	0.10	0.12	0.95	0.51	0.56	0.70
		Coeff. Var.	0.07	0.09	0.74	0.39	0.30	0.85
Pan	176238	Mean	138.55	137.90	128.43	138.55	189.28	91.26
		St. Dev.	0.34	0.11	2.40	0.33	0.52	
		Coeff. Var.	0.25	0.08	1.87	0.23	0.28	
Pan	176240	Mean			121.54			
		St. Dev.			0.16			
		Coeff. Var.			0.13			
Pan	176241	Mean	124.85	121.00	111.49	127.83	187.69	
		St. Dev.	4.07	4.45	0.63	0.21	1.78	
		Coeff. Var.	3.26	3.68	0.56	0.16	0.95	
Pan	176242	Mean	139.70	139.37	133.23	139.57	205.99	
		St. Dev.	0.22	0.44	1.13	0.16	0.20	
		Coeff. Var.	0.16	0.31	0.85	0.11	0.10	
Pan	220062	Mean	124.03	122.86	119.23	123.76	180.08	80.72
		St. Dev.	0.11	0.10	0.51	0.62	0.28	0.16
		Coeff. Var.	0.08	0.08	0.43	0.50	0.16	0.20
Pan	220064	Mean	122.62	122.86	114.30	122.74	176.34	83.07
		St. Dev.	0.39	0.90	1.13	0.20	0.29	0.61
		Coeff. Var.	0.32	0.73	0.99	0.16	0.16	0.73
Pan	220065	Mean	128.41	125.06	118.84	128.41	179.91	91.70
		St. Dev.	0.08	0.21	0.06	0.22	0.06	0.63
		Coeff. Var.	0.07	0.16	0.05	0.17	0.03	0.69
Pan	236971	Mean	124.85	123.32	112.23	124.84	175.91	82.48
		St. Dev.	0.40	0.39	0.22	0.36	0.23	1.12
		Coeff. Var.	0.32	0.32	0.19	0.29	0.13	1.36
Pan	282763	Mean	138.40	135.02	112.65	137.62	189.57	93.82
		St. Dev.	0.16	0.08	27.25	0.13	0.88	0.59
		Coeff. Var.	0.11	0.06	24.19	0.09	0.47	0.63
Pan	297856	Mean	129.04	126.90	119.57	129.19	185.27	90.60
		St. Dev.	0.21	0.07	1.54	0.33	0.40	0.84
		Coeff. Var.	0.16	0.05	1.29	0.26	0.22	0.93
Pan	395820	Mean	143.16	140.64	134.15	142.87	198.01	100.55
		St. Dev.	0.39	0.26	2.63	0.14	0.76	0.70
		Coeff. Var.	0.27	0.19	1.96	0.10	0.38	0.70
Pan	450071	Mean	124.22	124.34	116.31	123.62	182.74	91.71
		St. Dev.	0.46	0.27	2.48	0.46	0.32	0.14
		Coeff. Var.	0.37	0.22	2.13	0.38	0.18	0.15
Pan	477333	Mean	123.12	122.32	114.31	123.10	170.46	86.75
		St. Dev.	0.23	0.16	0.37	0.21	0.80	0.89
		Coeff. Var.	0.18	0.13	0.32	0.17	0.47	1.03

Pan	481803	Mean	135.09	133.61	123.24	135.14	186.85	91.76
		St. Dev.	0.51	0.31	2.45	0.63	0.27	0.87
		Coeff. Var.	0.38	0.23	1.99	0.47	0.14	0.95
Pan	481804	Mean	132.06	129.95	121.29	132.03	182.22	88.59
		St. Dev.	0.29	0.28	0.21	0.14	0.06	0.57
		Coeff. Var.	0.22	0.21	0.17	0.11	0.04	0.64
Gorilla	174714	Mean	186.50	183.11	168.14	187.63	271.08	115.05
		St. Dev.	0.07	0.02	0.02	0.36	0.62	0.29
		Coeff. Var.	0.04	0.01	0.01	0.19	0.23	0.26
Gorilla	174716	Mean	182.79	183.01	168.70	184.27	270.98	108.97
		St. Dev.	0.16	0.24	0.11	0.11	0.09	0.33
		Coeff. Var.	0.09	0.13	0.07	0.06	0.03	0.30
MAK	MLD 37/38	Mean						94.43
		St. Dev.						0.13
		Coeff. Var.						0.14

Genus	Spec No.	Value	bas-nas	g-br	br-ptn	br-lam	ptn-ast	lam-ast
Homo	99.1/1728	Mean	102.53	109.17	94.76	106.08	99.52	78.58
		St. Dev.	0.22	0.32	0.15	0.54	0.08	0.09
		Coeff. Var.	0.21	0.29	0.16	0.51	0.09	0.12
Homo	99.1/1738	Mean	100.64	116.78	100.88	120.20	94.63	83.62
		St. Dev.	0.67	0.85	2.45	0.14	0.03	0.13
		Coeff. Var.	0.67	0.73	2.43	0.12	0.03	0.16
Homo	VL/2921	Mean	96.73	115.76	98.50	107.30	97.86	80.11
		St. Dev.	0.24	1.07	0.80	1.62	0.15	0.14
		Coeff. Var.	0.24	0.92	0.82	1.51	0.16	0.17
Homo	VL/2923	Mean	98.23	105.29	94.05	107.15	93.05	86.38
		St. Dev.	0.17	1.38	0.01	0.01	0.08	0.11
		Coeff. Var.	0.17	1.31	0.01	0.01	0.08	0.13
Homo	VL/2928	Mean	91.21	108.66	96.99	101.68	93.99	80.86
		St. Dev.	0.46	1.54	0.37	1.78	0.02	0.57
		Coeff. Var.	0.50	1.42	0.38	1.75	0.02	0.71
Pan	174699	Mean	95.97	68.81	64.30	57.15	74.46	47.60
		St. Dev.		0.36		0.03		0.10
		Coeff. Var.		0.52		0.05		0.22
Pan	174700	Mean	91.69	63.20	60.58	66.39	71.25	46.40
		St. Dev.	0.09	0.92		11.58		1.01
		Coeff. Var.	0.10	1.45		17.45		2.19
Pan	174701	Mean	93.74	71.54	66.26	70.33	75.00	48.64
		St. Dev.	0.09	0.99	0.18	0.61	0.40	0.50
		Coeff. Var.	0.09	1.38	0.27	0.86	0.53	1.03
Pan	174702	Mean	92.98	65.31		68.63		49.31
		St. Dev.	1.03	0.71		1.59		0.61
		Coeff. Var.	1.11	1.09		2.32		1.23
Pan	174703	Mean	91.65	72.04	73.64	60.91	80.37	49.00
		St. Dev.	0.08	0.29	0.36	0.16	0.14	1.89
		Coeff. Var.	0.08	0.40	0.48	0.27	0.18	3.85
Pan	174706	Mean	88.38	61.92	61.32	61.83	74.71	44.69
		St. Dev.	0.02	1.22	0.54	1.92	0.34	1.38
		Coeff. Var.	0.03	1.96	0.88	3.10	0.46	3.10
Pan	174707	Mean	94.93	61.31		65.14		43.74
		St. Dev.	0.25	0.65		1.06		0.74
		Coeff. Var.	0.26	1.07		1.62		1.68
Pan	174710	Mean	96.00	69.85	68.48	59.92	81.75	50.40
		St. Dev.	0.21	1.85	0.44		0.61	
		Coeff. Var.	0.22	2.65	0.65		0.74	
Pan	220326	Mean	98.41	71.63	65.26	71.14	82.18	47.87
		St. Dev.	0.03	0.06		6.70		1.54
		Coeff. Var.	0.03	0.08		9.42		3.21
Pan	176228	Mean	95.53	71.68	67.18	61.34	77.77	50.12
		St. Dev.	0.68	1.60	0.35	1.72	0.41	1.04

		Coeff. Var.	0.71	2.23	0.53	2.81	0.53	2.07
Pan	176229	Mean	92.61	73.49	69.20	62.54	74.34	47.20
		St. Dev.	0.01	0.01		0.19		1.72
		Coeff. Var.	0.01	0.01		0.30		3.65
Pan	176235	Mean	92.37	70.03	68.23	71.50	80.47	44.85
		St. Dev.	0.41	1.38	0.28	2.31	1.28	0.67
		Coeff. Var.	0.44	1.97	0.42	3.23	1.59	1.48
Pan	176238	Mean	101.79	75.49	70.57	66.41	86.10	56.15
		St. Dev.		0.08	0.49	2.63	1.46	2.19
		Coeff. Var.		0.10	0.69	3.97	1.70	3.91
Pan	176240	Mean		71.50	64.37	60.81	69.76	49.93
		St. Dev.		2.09	0.52	1.62	0.01	1.02
		Coeff. Var.		2.93	0.80	2.66	0.01	2.03
Pan	176241	Mean		65.08	73.20	60.07		
		St. Dev.		0.10		0.64		
		Coeff. Var.		0.16		1.06		
Pan	176242	Mean		79.20	71.32	67.95	83.38	56.43
		St. Dev.		1.18	0.97	0.19		
		Coeff. Var.		1.49	1.36	0.27		
Pan	220062	Mean	89.00	69.48		62.74		44.67
		St. Dev.	0.38	1.36		0.83		0.18
		Coeff. Var.	0.43	1.96		1.32		0.41
Pan	220064	Mean	90.50	61.96	60.76	62.10	76.10	43.55
		St. Dev.	1.27	0.77	1.70	0.42	0.77	3.43
		Coeff. Var.	1.41	1.25	2.79	0.67	1.01	7.89
Pan	220065	Mean	99.45	67.34	68.38	63.29	70.51	44.86
		St. Dev.	0.23	0.05		0.14		0.39
		Coeff. Var.	0.23	0.08		0.22		0.86
Pan	236971	Mean	90.69	67.33	60.39	56.65	70.91	48.30
		St. Dev.	0.86	0.18	1.56	0.55	0.20	0.20
		Coeff. Var.	0.95	0.27	2.59	0.97	0.28	0.41
Pan	282763	Mean	97.25	72.79	68.88	71.73	87.00	46.40
		St. Dev.	0.15	1.22		2.38		4.66
		Coeff. Var.	0.15	1.68		3.32		10.04
Pan	297856	Mean	99.80	67.54	54.72	62.68	80.10	45.49
		St. Dev.	0.04	9.51		6.80		4.31
		Coeff. Var.	0.04	14.08		10.84		9.48
Pan	395820	Mean	103.06	82.82	76.43	69.87	88.02	47.25
		St. Dev.	0.67	0.17	0.09	3.69	0.48	3.62
		Coeff. Var.	0.65	0.20	0.12	5.28	0.55	7.67
Pan	450071	Mean	94.12	67.05	65.38	61.61	68.90	45.61
		St. Dev.	0.97	0.76		3.98		2.45
		Coeff. Var.	1.03	1.13		6.46		5.37
Pan	477333	Mean	91.52	68.34	64.23	58.01	70.64	51.67
		St. Dev.	0.33	0.91		0.15		0.18
		Coeff. Var.	0.36	1.33		0.26		0.34
Pan	481803	Mean	102.83	69.67	68.82	62.62	82.43	52.85
		St. Dev.	0.86	0.81		2.94		0.96

		Coeff. Var.	0.84	1.16		4.69		1.82
Pan	481804	Mean	96.48	73.54	69.65	60.73	82.19	50.58
		St. Dev.	0.20	1.15	1.70	0.31	0.52	0.59
		Coeff. Var.	0.21	1.56	2.43	0.51	0.64	1.16
Gorilla	174714	Mean	135.30	106.10	79.80	64.67	103.31	82.29
		St. Dev.	0.36	0.86	0.25	0.80	0.35	0.54
		Coeff. Var.	0.27	0.81	0.31	1.24	0.34	0.66
Gorilla	174716	Mean	129.47	91.02	83.69	82.86	95.07	76.90
		St. Dev.	0.19	1.78	1.54	1.56	0.49	0.09
		Coeff. Var.	0.14	1.95	1.84	1.88	0.51	0.12
MAK	MLD 1	Mean						56.80
		St. Dev.						0.17
		Coeff. Var.						0.30
MAK	MLD 10	Mean						
		St. Dev.						
		Coeff. Var.						
MAK	MLD 3	Mean			45.19		73.28	
		St. Dev.			0.24		0.43	
		Coeff. Var.			0.52		0.59	
MAK	MLD 31	Mean						
		St. Dev.						
		Coeff. Var.						
MAK	MLD 37/38	Mean			65.95	77.80		54.28
		St. Dev.			0.71	0.70		0.56
		Coeff. Var.			1.07	0.89		1.02
MAK	MLD 37/38	Mean					80.59	
		St. Dev.					0.24	
		Coeff. Var.					0.29	

Genus	Spec No.	Value	br-ast	lam-i	i-opn	lam-opn	nas-pros	bas-pros
Homo	99.1/1728	Mean	131.50	59.96			67.13	95.16
		St. Dev.	0.53	0.03			0.44	0.22
		Coeff. Var.	0.40	0.04			0.65	0.23
Homo	99.1/1738	Mean	137.10	63.62	51.47	100.04	69.53	101.80
		St. Dev.	1.11	0.40	0.45	0.11	0.52	0.45
		Coeff. Var.	0.81	0.62	0.87	0.11	0.75	0.44
Homo	VL/2921	Mean	131.55	50.12	47.69	85.06	67.32	91.19
		St. Dev.	0.20	0.56	0.10	0.21	0.47	0.06
		Coeff. Var.	0.16	1.11	0.21	0.25	0.69	0.06
Homo	VL/2923	Mean	134.16	62.14	42.62	94.90	65.80	92.50
		St. Dev.	0.23	0.84	0.87	0.22	0.37	0.29
		Coeff. Var.	0.17	1.35	2.05	0.23	0.57	0.32
Homo	VL/2928	Mean	132.53	59.73	45.27	93.06	62.70	87.21
		St. Dev.	1.04	2.32	1.92	0.59	0.62	0.45
		Coeff. Var.	0.78	3.88	4.25	0.64	0.99	0.51
Pan	174699	Mean	77.86	19.45	36.40	50.78	85.53	133.12
		St. Dev.	0.83	1.13	1.40	0.07		0.49
		Coeff. Var.	1.07	5.80	3.84	0.15		0.37
Pan	174700	Mean	81.43	26.05	35.48	42.21	74.58	123.48
		St. Dev.	0.54				0.26	0.06
		Coeff. Var.	0.66				0.34	0.05
Pan	174701	Mean	89.12	25.33	31.75	50.31	71.08	119.52
		St. Dev.	0.19	0.52	0.19	0.29	2.02	0.96
		Coeff. Var.	0.21	2.05	0.59	0.58	2.84	0.80
Pan	174702	Mean	86.84	18.33			80.80	127.97
		St. Dev.	1.09	0.49			3.31	1.94
		Coeff. Var.	1.25	2.69			4.10	1.51
Pan	174703	Mean	84.85	29.93	33.00	56.69	76.08	120.13
		St. Dev.	1.53	0.89	1.09	0.13	0.17	0.75
		Coeff. Var.	1.81	2.98	3.31	0.23	0.23	0.63
Pan	174706	Mean	77.44	22.04	35.47	50.90	69.56	109.15
		St. Dev.	0.18	2.37	0.90	0.50	0.09	0.09
		Coeff. Var.	0.24	10.73	2.53	0.99	0.13	0.08
Pan	174707	Mean	82.58	18.24	39.96	52.71	71.57	121.74
		St. Dev.	0.17	0.65	0.60	0.46	0.51	0.25
		Coeff. Var.	0.20	3.55	1.51	0.87	0.71	0.21
Pan	174710	Mean	87.32	16.47	48.70	58.57	85.31	128.08
		St. Dev.	2.22		1.07		0.40	0.24
		Coeff. Var.	2.55		2.20		0.47	0.19
Pan	220326	Mean	87.13	16.50	43.13	55.29		
		St. Dev.	0.14	4.60	2.61	4.85		
		Coeff. Var.	0.16	27.86	6.06	8.78		
Pan	176228	Mean	85.62	10.16	50.79	57.53	83.38	128.96
		St. Dev.	0.63	1.22	0.34	0.66	0.53	0.21

		Coeff. Var.	0.73	12.05	0.67	1.15	0.64	0.16
Pan	176229	Mean	81.38	19.58	40.51	51.29	81.32	130.97
		St. Dev.	0.25	0.76	0.42	0.28	0.42	0.36
		Coeff. Var.	0.31	3.87	1.03	0.56	0.52	0.28
Pan	176235	Mean	82.02	13.21	36.14	45.46	93.58	128.15
		St. Dev.	1.57	2.25	1.32	0.26	0.12	0.04
		Coeff. Var.	1.91	17.04	3.65	0.58	0.13	0.03
Pan	176238	Mean	91.88	23.08	40.39	56.39	84.26	129.99
		St. Dev.	0.70	1.87	0.14	0.87	0.98	
		Coeff. Var.	0.77	8.09	0.34	1.55	1.17	
Pan	176240	Mean	84.98				86.63	
		St. Dev.	1.26				0.29	
		Coeff. Var.	1.48				0.33	
Pan	176241	Mean		21.77			86.75	
		St. Dev.		6.51			1.05	
		Coeff. Var.		29.92			1.21	
Pan	176242	Mean	91.01	13.80			90.61	
		St. Dev.		0.55			1.59	
		Coeff. Var.		3.96			1.75	
Pan	220062	Mean	80.30	10.53	39.01	46.06	81.36	124.79
		St. Dev.	1.15	0.35	0.61	0.24	0.57	0.03
		Coeff. Var.	1.43	3.31	1.56	0.52	0.70	0.03
Pan	220064	Mean	78.81	16.78	36.48	48.55	74.55	122.73
		St. Dev.	0.73	0.50	1.19	0.59	3.24	0.16
		Coeff. Var.	0.93	2.95	3.25	1.21	4.34	0.13
Pan	220065	Mean	82.59	17.83	38.35	50.95	81.57	129.93
		St. Dev.	0.69	0.44	0.30	0.00	0.27	0.11
		Coeff. Var.	0.83	2.45	0.78	0.00	0.33	0.08
Pan	236971	Mean	80.41	24.16	36.98	53.35	74.34	125.78
		St. Dev.	0.44	0.85	0.62	0.26	0.41	0.04
		Coeff. Var.	0.55	3.52	1.68	0.48	0.55	0.03
Pan	282763	Mean	87.42		36.88	63.01	81.12	131.39
		St. Dev.	0.46		2.18	12.14	0.06	0.13
		Coeff. Var.	0.52		5.90	19.27	0.08	0.10
Pan	297856	Mean	80.61	15.53	45.62	54.33	84.36	131.01
		St. Dev.	6.83	1.69	0.33	1.46	0.67	0.55
		Coeff. Var.	8.47	10.87	0.71	2.69	0.79	0.42
Pan	395820	Mean	90.80	22.63	46.12	62.77	86.12	136.80
		St. Dev.	0.39	5.21	0.94	2.12	0.40	0.98
		Coeff. Var.	0.43	23.02	2.04	3.38	0.46	0.72
Pan	450071	Mean	79.34	17.47	40.63	53.68	89.66	123.54
		St. Dev.	1.31	1.15	0.35	0.96	0.09	0.42
		Coeff. Var.	1.66	6.61	0.87	1.79	0.11	0.34
Pan	477333	Mean	80.96	23.88	37.22	55.29	71.22	119.50
		St. Dev.	0.73	0.26	0.24	0.11	1.69	0.14
		Coeff. Var.	0.91	1.09	0.65	0.20	2.38	0.12
Pan	481803	Mean	86.31	25.12	38.30	56.90	86.65	131.53
		St. Dev.	0.05	0.76	1.41	1.62	2.24	0.18

		Coeff. Var.	0.06	3.02	3.69	2.84	2.59	0.14
Pan	481804	Mean	86.20	23.33	38.07	54.81	84.61	126.80
		St. Dev.	0.73	0.61	0.30	0.05	0.22	0.33
		Coeff. Var.	0.85	2.62	0.79	0.08	0.26	0.26
Gorilla	174714	Mean	103.01	26.03	86.78	96.46	115.40	178.49
		St. Dev.	0.12	0.32	0.91	0.51	0.68	0.73
		Coeff. Var.	0.12	1.24	1.05	0.53	0.59	0.41
Gorilla	174716	Mean	100.29	19.97	84.66	89.30	126.04	173.08
		St. Dev.	0.58	0.63	0.27	0.24	0.44	0.14
		Coeff. Var.	0.58	3.17	0.32	0.27	0.35	0.08
MAK	MLD 1	Mean		25.18	38.34	56.95		
		St. Dev.		0.83	0.28	0.90		
		Coeff. Var.		3.31	0.74	1.57		
MAK	MLD 10	Mean		27.93				
		St. Dev.		0.09				
		Coeff. Var.		0.34				
MAK	MLD 3	Mean	94.40					
		St. Dev.	0.11					
		Coeff. Var.	0.12					
MAK	MLD 37/38	Mean	98.11	36.82	32.94	59.03		
		St. Dev.	0.85	0.27	0.90	0.27		
		Coeff. Var.	0.86	0.72	2.72	0.46		

Genus	Spec No.	Value	ns-pros	sn-pros	mf-ek	orb-zm	zyo-zm	nas-ns
Homo	99.1/1728	Mean	13.59	15.50	38.91	28.89	34.15	53.63
		St. Dev.	0.02	0.20	0.41	0.39	0.24	0.46
		Coeff. Var.	0.14	1.29	1.05	1.35	0.71	0.86
Homo	99.1/1738	Mean	12.41	14.68	41.35	32.31	36.72	57.32
		St. Dev.	0.54	0.62	0.43	1.35	0.10	0.02
		Coeff. Var.	4.39	4.20	1.03	4.19	0.26	0.03
Homo	VL/2921	Mean	16.85	19.70	37.99	23.66	32.04	50.64
		St. Dev.	0.21	0.30	0.09	0.15	0.19	0.27
		Coeff. Var.	1.22	1.53	0.24	0.65	0.60	0.54
Homo	VL/2923	Mean	14.85	19.39	38.31	25.93	34.21	51.01
		St. Dev.	0.25	0.16	0.84	0.92	0.11	0.12
		Coeff. Var.	1.71	0.80	2.19	3.56	0.32	0.23
Homo	VL/2928	Mean	13.56	18.42	39.60	21.17	29.30	49.18
		St. Dev.	0.55	0.42	0.09	0.33	0.20	0.06
		Coeff. Var.	4.07	2.29	0.23	1.54	0.69	0.11
Pan	174699	Mean	30.28	32.61	34.65	28.31	30.47	58.26
		St. Dev.	2.72	1.61	0.06	0.06		
		Coeff. Var.	8.99	4.92	0.16	0.20		
Pan	174700	Mean	20.85	22.54	34.93	30.38	31.44	54.80
		St. Dev.	0.38	0.00	0.71	0.70		0.18
		Coeff. Var.	1.83	0.02	2.04	2.31		0.33
Pan	174701	Mean	20.03	22.86	37.07	32.83	31.32	52.21
		St. Dev.	1.98	1.51	0.38	1.25	0.46	0.17
		Coeff. Var.	9.89	6.62	1.01	3.82	1.47	0.33
Pan	174702	Mean	30.84	31.50	36.60	29.41	29.40	52.21
		St. Dev.	3.06	2.96	0.43	0.62	0.36	0.21
		Coeff. Var.	9.92	9.40	1.18	2.12	1.23	0.41
Pan	174703	Mean	22.72	23.60	35.62	30.46	33.37	54.99
		St. Dev.	0.97	0.70	1.55	0.78	0.30	0.52
		Coeff. Var.	4.25	2.96	4.36	2.57	0.90	0.94
Pan	174706	Mean	19.04	19.96	33.39	24.10	26.16	52.00
		St. Dev.	0.05	0.88	0.15	0.46	0.52	0.12
		Coeff. Var.	0.26	4.39	0.44	1.89	1.97	0.23
Pan	174707	Mean	22.04	23.79	34.65	21.58	23.69	50.93

		St. Dev.	2.44	1.19	0.12	0.15		1.43
		Coeff. Var.	11.09	4.99	0.34	0.67		2.81
Pan	174710	Mean	23.26	23.86	36.14	32.92	33.26	63.52
		St. Dev.	1.68	1.40	0.16	1.27		0.74
		Coeff. Var.	7.22	5.85	0.45	3.86		1.17
Pan	220326	Mean			36.39	24.08	27.99	49.60
		St. Dev.			0.85	2.26		0.43
		Coeff. Var.			2.34	9.38		0.87
Pan	176228	Mean	26.48	27.34	35.23	31.14	30.42	59.14
		St. Dev.	0.35	0.26	0.93	1.87	0.25	0.12
		Coeff. Var.	1.33	0.96	2.63	6.00	0.82	0.21
Pan	176229	Mean	32.95	34.28	36.01	24.93	32.28	49.61
		St. Dev.	0.57	0.75	0.17	1.89	5.82	0.16
		Coeff. Var.	1.74	2.19	0.48	7.56	18.02	0.32
Pan	176235	Mean	27.42	29.62	41.19	27.42	29.99	67.64
		St. Dev.	0.24	0.68	0.43	0.24	0.06	0.35
		Coeff. Var.	0.86	2.29	1.03	0.87	0.19	0.52
Pan	176238	Mean	27.93	28.98	37.02	34.98	36.74	57.61
		St. Dev.	1.72	0.19	1.01	0.42	0.07	2.19
		Coeff. Var.	6.15	0.66	2.72	1.20	0.19	3.80
Pan	176240	Mean	27.88	32.03	35.56	29.81		59.69
		St. Dev.	1.94	1.08	0.80	1.63		1.56
		Coeff. Var.	6.97	3.36	2.26	5.46		2.61
Pan	176241	Mean	28.80	31.93	34.55	33.95	36.88	62.05
		St. Dev.	2.35	0.76	0.57	1.33		0.81
		Coeff. Var.	8.16	2.36	1.65	3.92		1.30
Pan	176242	Mean	29.42	29.80	37.60	56.07	54.47	63.78
		St. Dev.	0.99	2.18	0.44	37.06	34.32	1.25
		Coeff. Var.	3.37	7.31	1.16	66.10	63.01	1.96
Pan	220062	Mean	27.93	28.87	33.11	28.86	30.23	55.30
		St. Dev.	2.63	2.07	1.35	0.42	#DIV/0!	1.44
		Coeff. Var.	9.40	7.19	4.09	1.47	#DIV/0!	2.60
Pan	220064	Mean	23.80	25.01	36.08	24.57	23.26	52.63
		St. Dev.	0.83	0.56	0.69	1.58	0.42	4.12
		Coeff. Var.	3.49	2.23	1.91	6.43	1.81	7.83
Pan	220065	Mean	27.15	29.00	35.69	25.98	29.50	55.60
		St. Dev.	1.26	1.69	0.29	1.05	#DIV/0!	0.74
		Coeff. Var.	4.64	5.82	0.82	4.04	#DIV/0!	1.34

Pan	236971	Mean	26.15	27.39	32.42	24.84	28.12	50.22
		St. Dev.	2.25	3.07	0.53	1.08	0.41	1.61
		Coeff. Var.	8.60	11.20	1.63	4.36	1.46	3.20
Pan	282763	Mean	27.20	29.78	36.75	30.38	34.21	54.83
		St. Dev.	0.56	1.47	0.76	1.00	0.18	0.56
		Coeff. Var.	2.07	4.92	2.07	3.29	0.54	1.02
Pan	297856	Mean	28.09	30.13	33.86	27.24		58.01
		St. Dev.	0.29	1.41	0.20	0.98		0.69
		Coeff. Var.	1.02	4.68	0.58	3.59		1.19
Pan	395820	Mean	34.65	37.18	32.91	30.11	31.22	52.84
		St. Dev.	1.44	1.82	0.42	2.65	0.49	1.09
		Coeff. Var.	4.16	4.90	1.28	8.79	1.58	2.07
Pan	450071	Mean	28.15	30.51	35.56	31.28	35.95	61.69
		St. Dev.	0.55	0.95	0.24	1.29	0.59	0.50
		Coeff. Var.	1.94	3.11	0.67	4.11	1.64	0.82
Pan	477333	Mean	24.92	27.15	35.33	24.94		47.84
		St. Dev.	1.21	0.14	0.13	1.21		0.71
		Coeff. Var.	4.86	0.52	0.36	4.86		1.48
Pan	481803	Mean	27.21	30.75	37.17	26.31	27.34	60.89
		St. Dev.	1.98	2.96	0.97	4.04	0.05	0.78
		Coeff. Var.	7.28	9.64	2.62	15.36	0.20	1.28
Pan	481804	Mean	24.88	25.76	36.68	32.81	29.91	60.57
		St. Dev.	0.22	0.11	0.50	0.77	0.12	0.18
		Coeff. Var.	0.87	0.41	1.36	2.36	0.39	0.30
Gorilla	174714	Mean	24.14	27.11	45.74	48.84	58.22	92.51
		St. Dev.	0.99	1.25	1.62	0.56	0.98	0.39
		Coeff. Var.	4.11	4.60	3.54	1.14	1.68	0.42
Gorilla	174716	Mean	27.05	28.45	44.57	46.35	53.48	100.09
		St. Dev.	0.41	0.83	0.51	0.87	0.90	0.01
		Coeff. Var.	1.53	2.92	1.14	1.87	1.68	0.01
MAK	MLD 9	Mean	11.94	13.79				
		St. Dev.	0.83	1.25				
		Coeff. Var.	6.96	9.10				

Genus	Spec No.	Value	rhi-ns	rhi-ans	nas-rhi	ans-ns	ans-av	ans-pros
Homo	99.1/1728	Mean	322.02	322.48	311.78	1.27	15.92	12.67
		St. Dev.	0.12	0.11	0.11	0.20	0.18	0.20
		Coeff. Var.	0.04	0.03	0.03	15.88	1.10	1.60
Homo	99.1/1738	Mean	35.96	34.28	23.82	1.81	18.03	13.91
		St. Dev.	0.17	0.38	0.08	0.44	0.38	0.21
		Coeff. Var.	0.47	1.10	0.32	24.30	2.08	1.53
Homo	VL/2921	Mean	35.10	33.65	19.16	1.75	23.22	18.18
		St. Dev.	0.37	1.00	0.50	0.65	0.72	0.73
		Coeff. Var.	1.07	2.97	2.62	37.19	3.08	3.99
Homo	VL/2923	Mean	35.24	32.91	18.53	2.45	20.14	16.89
		St. Dev.	0.19	0.19	0.00	0.02	0.07	0.27
		Coeff. Var.	0.53	0.56	0.02	0.85	0.34	1.62
Homo	VL/2928	Mean	35.66	33.40	16.80	2.41	18.82	15.96
		St. Dev.	0.10	0.05	0.10	0.02	0.48	0.52
		Coeff. Var.	0.27	0.16	0.60	0.71	2.53	3.24
Pan	174699	Mean				2.30	34.91	32.28
		St. Dev.				1.54	0.53	1.11
		Coeff. Var.				66.94	1.51	3.45
Pan	174700	Mean	26.54	24.66	28.45	3.25	26.08	23.54
		St. Dev.	0.14	0.06	0.04	0.31	0.54	0.47
		Coeff. Var.	0.53	0.24	0.12	9.45	2.05	2.00
Pan	174701	Mean	27.20	24.57	26.20	3.60	25.72	23.06
		St. Dev.	0.50	0.62	0.74	0.68	0.67	2.23
		Coeff. Var.	1.86	2.54	2.81	18.84	2.59	9.69
Pan	174702	Mean	23.92	22.66	29.05	1.77	36.43	32.35
		St. Dev.	0.99	0.26	1.11	1.02	0.01	2.22
		Coeff. Var.	4.14	1.13	3.82	57.34	0.02	6.87
Pan	174703	Mean	26.11	25.38	29.96	0.95	25.69	23.54
		St. Dev.	1.04	0.41	0.47	0.80	0.63	0.28
		Coeff. Var.	3.99	1.60	1.57	84.49	2.44	1.20
Pan	174706	Mean	22.26	19.92	30.83	2.77	22.60	21.68
		St. Dev.	0.17	0.26	0.35	0.04	0.19	0.01
		Coeff. Var.	0.77	1.29	1.13	1.39	0.86	0.03
Pan	174707	Mean	22.95	22.37	28.26	1.03	25.21	22.76
		St. Dev.	1.89	0.83	0.31	1.15	0.82	1.15
		Coeff. Var.	8.22	3.70	1.08	111.40	3.25	5.05
Pan	174710	Mean	29.07	28.03	35.56	1.96	26.34	24.76
		St. Dev.	1.55	2.27	0.52	1.82	2.71	2.99
		Coeff. Var.	5.33	8.09	1.47	92.51	10.29	12.09
Pan	220326	Mean	23.19	22.59	27.84	1.10		
		St. Dev.	0.70	0.36	0.11	0.07		
		Coeff. Var.	3.03	1.62	0.40	6.67		
Pan	176228	Mean	26.00	23.30	34.04	3.12	30.92	29.43
		St. Dev.	0.45	0.07	0.67	0.38	0.27	0.13

		Coeff. Var.	1.73	0.30	1.95	12.32	0.89	0.44
Pan	176229	Mean	24.50	22.92	26.34	2.00	37.86	34.71
		St. Dev.	0.17	0.48	0.07	0.53	0.45	0.97
		Coeff. Var.	0.71	2.07	0.28	26.62	1.19	2.80
Pan	176235	Mean	28.79	27.03	39.11	3.28	32.21	30.01
		St. Dev.	0.38	0.73	0.81	0.99	0.35	0.43
		Coeff. Var.	1.31	2.72	2.08	30.11	1.09	1.42
Pan	176238	Mean	25.46	24.69	33.07	1.63	29.52	28.71
		St. Dev.	2.04	0.15	0.44	1.07	0.08	0.36
		Coeff. Var.	8.02	0.63	1.32	65.53	0.26	1.24
Pan	176240	Mean	29.31	26.84	31.06	2.97	33.73	30.62
		St. Dev.	1.23	0.32	0.38	0.76	0.48	1.09
		Coeff. Var.	4.19	1.18	1.24	25.55	1.43	3.57
Pan	176241	Mean	26.43	23.27	36.83	4.21	36.11	32.81
		St. Dev.	1.62	0.12	0.64	1.75	0.30	0.72
		Coeff. Var.	6.11	0.53	1.73	41.55	0.83	2.18
Pan	176242	Mean	27.27	26.27	36.57	1.88	32.34	31.01
		St. Dev.	0.48	0.22	1.70	0.40	0.93	0.71
		Coeff. Var.	1.75	0.84	4.65	21.18	2.88	2.28
Pan	220062	Mean	39.78	36.03	21.09	4.61	35.09	32.40
		St. Dev.	19.82	16.86	10.77	3.23	0.95	0.57
		Coeff. Var.	49.82	46.79	51.04	70.05	2.71	1.76
Pan	220064	Mean	29.26	26.28	27.81	3.93	29.22	27.21
		St. Dev.	#DIV/0!	#DIV/0!	#DIV/0!	0.60	0.28	0.14
		Coeff. Var.	#DIV/0!	#DIV/0!	#DIV/0!	15.31	0.97	0.50
Pan	220065	Mean	24.05	21.56	32.59	3.14	32.11	29.95
		St. Dev.	0.98	0.28	0.13	0.94	0.27	0.52
		Coeff. Var.	4.06	1.31	0.39	29.96	0.83	1.72
Pan	236971	Mean	25.43	24.99	25.21	0.82	29.40	26.73
		St. Dev.	1.88	1.30	0.09	0.97	1.04	1.42
		Coeff. Var.	7.39	5.19	0.37	117.73	3.54	5.30
Pan	282763	Mean	30.89	30.37	25.79	0.91	28.86	27.76
		St. Dev.	0.23	0.25	0.41	0.37	0.16	0.08
		Coeff. Var.	0.75	0.82	1.59	39.92	0.56	0.28
Pan	297856	Mean	26.70	25.03	32.11	2.28	30.44	30.14
		St. Dev.	0.50	0.50	0.28	0.52	1.02	0.58
		Coeff. Var.	1.88	2.02	0.87	22.83	3.36	1.93
Pan	395820	Mean	30.14	28.86	24.10	1.71	37.12	35.92
		St. Dev.	1.34	0.40	0.31	1.73	0.59	0.41
		Coeff. Var.	4.44	1.37	1.29	101.63	1.60	1.15
Pan	450071	Mean	31.67	30.31	30.18	1.73	32.20	29.62
		St. Dev.	0.16	0.19	0.70	0.19	0.37	0.87
		Coeff. Var.	0.51	0.62	2.32	11.18	1.15	2.92
Pan	477333	Mean	24.32	23.98	23.72	1.03	26.60	25.35
		St. Dev.	0.99	0.87	1.64	0.49	0.98	1.20
		Coeff. Var.	4.06	3.61	6.93	46.93	3.70	4.72
Pan	481803	Mean	30.39	29.73	31.12	1.51	29.82	28.00
		St. Dev.	2.20	0.71	2.84	1.13	0.57	0.21

		Coeff. Var.	7.25	2.39	9.12	74.96	1.92	0.76
Pan	481804	Mean	32.34	32.52	28.40	0.77	27.18	24.59
		St. Dev.	0.38	0.54	0.57	0.29	0.45	0.30
		Coeff. Var.	1.18	1.67	2.00	37.50	1.65	1.21
Gorilla	174714	Mean	34.62	32.55	58.30	2.63	27.45	26.62
		St. Dev.	0.08	0.12	0.28	0.53	0.21	0.62
		Coeff. Var.	0.24	0.38	0.48	20.28	0.76	2.34
Gorilla	174716	Mean	30.99	29.25	69.17	2.11	31.30	29.10
		St. Dev.	0.66	0.39	0.75	0.25	0.26	0.14
		Coeff. Var.	2.14	1.34	1.08	11.93	0.83	0.48
MAK	MLD 6	Mean			23.34			
		St. Dev.			0.57			
		Coeff. Var.			2.44			
MAK	MLD 9	Mean				3.47	20.63	15.26
		St. Dev.				0.14	0.38	0.96
		Coeff. Var.				4.09	1.85	6.31

Genus	Spec No.	Value	ba-opn	cfma-cfmp	ol-sta	po-br	g-po	nas-po
Homo	99.1/1728	Mean			42.24	124.51	110.90	106.00
		St. Dev.			1.16	0.43	0.04	0.14
		Coeff. Var.			2.74	0.35	0.03	0.14
Homo	99.1/1738	Mean	34.12	19.06	47.85	133.52	108.12	103.97
		St. Dev.	0.48	0.59	0.18	0.46	1.40	0.58
		Coeff. Var.	1.42	3.09	0.38	0.34	1.30	0.56
Homo	VL/2921	Mean	33.93	18.67	44.84	122.11	104.69	104.62
		St. Dev.	0.17	0.07	0.58	0.11	0.30	0.36
		Coeff. Var.	0.49	0.38	1.30	0.09	0.28	0.34
Homo	VL/2923	Mean	33.79	17.58	43.82	125.92	104.96	101.62
		St. Dev.	0.55	0.25	0.11	0.14	1.77	0.50
		Coeff. Var.	1.64	1.44	0.25	0.11	1.69	0.49
Homo	VL/2928	Mean	31.40	16.59	40.40	124.14	102.48	102.50
		St. Dev.	0.32	0.83	0.48	0.57	0.21	0.25
		Coeff. Var.	1.02	5.00	1.18	0.46	0.21	0.24
Pan	174699	Mean	28.66	15.77	72.24	81.62	97.51	95.29
		St. Dev.	0.02	0.31	0.18	0.69	0.71	
		Coeff. Var.	0.07	1.96	0.25	0.85	0.73	
Pan	174700	Mean	28.34	14.83	56.26	79.30	95.85	91.19
		St. Dev.		0.38	0.49	0.13	1.81	1.65
		Coeff. Var.		2.55	0.87	0.17	1.89	1.81
Pan	174701	Mean	31.50	17.72	63.49	88.47	100.06	97.37
		St. Dev.	0.13	0.02	0.62	0.01	0.57	0.08
		Coeff. Var.	0.41	0.10	0.97	0.01	0.57	0.08
Pan	174702	Mean			69.56	84.25	95.13	92.92
		St. Dev.			0.72	1.06	0.10	0.42
		Coeff. Var.			1.03	1.26	0.10	0.45
Pan	174703	Mean	31.15	14.34	61.06	88.29	95.34	93.99
		St. Dev.	0.14	0.85	0.17	0.45	0.65	0.72
		Coeff. Var.	0.44	5.93	0.28	0.51	0.68	0.77
Pan	174706	Mean	31.24	14.61	51.92	76.65	87.80	86.15
		St. Dev.	0.33	0.31	0.12	0.06	0.65	0.23
		Coeff. Var.	1.07	2.13	0.23	0.08	0.74	0.27
Pan	174707	Mean	26.67	15.82	59.46	81.25	96.18	93.19
		St. Dev.	0.30	0.05	0.35	2.20	0.75	0.82
		Coeff. Var.	1.13	0.31	0.60	2.70	0.78	0.88
Pan	174710	Mean	29.14	19.24	62.02	89.89	103.69	100.44
		St. Dev.	0.00	2.11	0.39	1.60	0.89	1.05
		Coeff. Var.	0.01	10.96	0.64	1.79	0.86	1.04
Pan	220326	Mean	29.47	17.99		86.22	101.83	98.37
		St. Dev.	0.02	0.02		0.26	0.29	0.03
		Coeff. Var.	0.08	0.11		0.30	0.29	0.03
Pan	176228	Mean	27.23	13.19	62.10	88.23	100.36	97.37
		St. Dev.	0.03	0.03	0.24	0.75	2.67	2.22

		Coeff. Var.	0.10	0.25	0.39	0.85	2.66	2.28
Pan	176229	Mean	26.53	12.90	68.54	83.21	101.63	96.42
		St. Dev.	0.02	0.56	0.88	0.18	0.57	0.09
		Coeff. Var.	0.06	4.31	1.29	0.21	0.56	0.09
Pan	176235	Mean	31.81	11.41	66.04	83.33	103.82	101.01
		St. Dev.	0.22	0.71	1.23	1.23	0.18	0.22
		Coeff. Var.	0.68	6.23	1.86	1.47	0.18	0.21
Pan	176238	Mean	30.58	13.51	66.84	91.47	105.96	104.26
		St. Dev.			1.18	0.91	0.65	0.82
		Coeff. Var.			1.76	0.99	0.62	0.78
Pan	176240	Mean			71.55	87.09	102.40	99.89
		St. Dev.			1.16	0.63	0.87	0.37
		Coeff. Var.			1.63	0.73	0.85	0.37
Pan	176241	Mean			70.25	93.60	97.98	93.17
		St. Dev.			1.35	0.69	1.15	0.04
		Coeff. Var.			1.92	0.74	1.17	0.04
Pan	176242	Mean			79.59	90.57	109.34	107.24
		St. Dev.			0.26	0.74	0.92	0.84
		Coeff. Var.			0.32	0.82	0.84	0.78
Pan	220062	Mean	28.09	14.78	66.28	83.16	98.73	95.83
		St. Dev.	0.03	0.33	0.17	0.74	1.45	1.32
		Coeff. Var.	0.11	2.24	0.26	0.88	1.47	1.37
Pan	220064	Mean	31.76	14.49	60.49	77.00	92.78	90.85
		St. Dev.	0.05	0.57	0.53	0.09	0.73	0.37
		Coeff. Var.	0.16	3.93	0.88	0.11	0.78	0.41
Pan	220065	Mean	26.22	14.25	70.97	84.13	101.31	96.14
		St. Dev.	0.03	0.95	0.56	0.98	2.01	1.52
		Coeff. Var.	0.10	6.68	0.79	1.16	1.98	1.58
Pan	236971	Mean	25.13	16.64	65.18	80.27	94.10	91.13
		St. Dev.	0.10	0.31	0.61	1.51	1.42	0.89
		Coeff. Var.	0.42	1.86	0.93	1.88	1.51	0.97
Pan	282763	Mean	30.85	17.20	67.63	90.66	104.09	99.68
		St. Dev.	0.24	0.05	1.08	0.41	0.29	0.16
		Coeff. Var.	0.79	0.31	1.60	0.46	0.28	0.16
Pan	297856	Mean	23.93	15.61	65.08	82.15	98.56	95.02
		St. Dev.	0.04	0.80	0.80	0.96	0.93	0.54
		Coeff. Var.	0.18	5.14	1.22	1.17	0.94	0.57
Pan	395820	Mean	28.07	16.55	71.92	95.85	103.50	100.02
		St. Dev.	0.34	0.85	0.57	1.06	0.81	0.87
		Coeff. Var.	1.20	5.13	0.80	1.11	0.78	0.87
Pan	450071	Mean	32.05	17.03	65.14	86.55	97.00	94.43
		St. Dev.	0.54	1.55	0.68	2.30	2.00	1.92
		Coeff. Var.	1.70	9.12	1.04	2.65	2.06	2.04
Pan	477333	Mean	25.83	15.21	61.75	83.78	93.41	90.76
		St. Dev.	0.50	0.10	0.43	1.15	0.10	0.09
		Coeff. Var.	1.93	0.65	0.70	1.37	0.11	0.10
Pan	481803	Mean	28.75	14.14	67.52	87.99	105.04	100.96
		St. Dev.	0.21	0.17	0.65	0.46	0.68	0.06

		Coeff. Var.	0.72	1.17	0.96	0.53	0.64	0.06
Pan	481804	Mean	27.80	15.22	63.77	92.51	102.50	98.93
		St. Dev.	0.09	1.19	0.51	1.11	0.43	0.52
		Coeff. Var.	0.32	7.83	0.80	1.20	0.41	0.52
Gorilla	174714	Mean	33.62	19.78	93.30	105.19	139.23	132.17
		St. Dev.	0.09	1.01	0.33	0.11	0.32	0.25
		Coeff. Var.	0.26	5.09	0.36	0.10	0.23	0.19
Gorilla	174716	Mean	28.63	16.93	90.36	103.43	130.59	128.37
		St. Dev.	0.19	0.27	0.12	0.14	0.23	0.19
		Coeff. Var.	0.67	1.61	0.13	0.13	0.17	0.15
MAK	MLD 37/38	Mean	26.79	13.34		92.23		
		St. Dev.	0.19	1.03		0.88		
		Coeff. Var.	0.70	7.76		0.96		

Genus	Spec No.	Value	rhi-po	sn-po	av-po	ek-po	zyo-po	op-po
Homo	99.1/1728	Mean	342.00	103.13	115.56	73.29	84.66	104.69
		St. Dev.	0.01	0.45	0.13	0.79	0.13	0.51
		Coeff. Var.	0.00	0.43	0.12	1.08	0.16	0.49
Homo	99.1/1738	Mean	110.38	106.31	119.89	73.82	86.88	117.84
		St. Dev.	0.02	0.30	0.04	0.17	0.03	2.44
		Coeff. Var.	0.01	0.28	0.03	0.23	0.03	2.07
Homo	VL/2921	Mean	108.61	98.76	111.97	71.58	82.65	104.86
		St. Dev.	0.13	0.07	0.11	0.28	0.61	0.38
		Coeff. Var.	0.12	0.07	0.09	0.39	0.74	0.36
Homo	VL/2923	Mean	105.75	93.95	107.94	66.16	79.18	112.78
		St. Dev.	0.22	0.69	0.50	0.41	0.91	0.52
		Coeff. Var.	0.21	0.74	0.46	0.62	1.15	0.46
Homo	VL/2928	Mean	105.79	91.85	104.53	66.83	78.40	106.14
		St. Dev.	0.12	0.10	0.20	1.11	0.32	0.64
		Coeff. Var.	0.11	0.11	0.19	1.66	0.41	0.60
Pan	174699	Mean		110.26	139.03	69.45	80.60	73.86
		St. Dev.		1.53	0.52	1.61		1.29
		Coeff. Var.		1.39	0.37	2.32		1.74
Pan	174700	Mean	96.94	108.96	130.09	70.47	77.56	72.69
		St. Dev.	1.65	1.85	2.19	1.46		2.61
		Coeff. Var.	1.70	1.70	1.68	2.07		3.60
Pan	174701	Mean	98.66	109.61	131.07	66.96	78.16	74.86
		St. Dev.	0.14	0.22	0.23	0.04	0.10	1.15
		Coeff. Var.	0.14	0.20	0.18	0.06	0.13	1.54
Pan	174702	Mean	94.92	106.51	136.95	68.06	78.24	74.67
		St. Dev.	0.49	1.28	1.02	0.24	0.58	0.72
		Coeff. Var.	0.52	1.20	0.74	0.36	0.74	0.97
Pan	174703	Mean	94.53	107.86	128.72	66.74	78.59	70.10
		St. Dev.	0.60	0.42	1.44	1.03	0.88	1.70
		Coeff. Var.	0.64	0.39	1.12	1.54	1.12	2.42
Pan	174706	Mean	88.62	100.96	118.58	62.85	73.20	70.47
		St. Dev.	0.31	1.10	0.09	0.59	0.42	1.04
		Coeff. Var.	0.35	1.09	0.08	0.94	0.57	1.47
Pan	174707	Mean	97.19	106.07	125.65	68.90	77.21	67.52
		St. Dev.	0.63	0.79	2.27	0.10		6.10
		Coeff. Var.	0.65	0.74	1.81	0.15		9.04
Pan	174710	Mean	103.14	119.10	140.28	71.12	83.53	79.45
		St. Dev.	1.54	2.54	1.45	0.84		1.76
		Coeff. Var.	1.49	2.13	1.03	1.19		2.22
Pan	220326	Mean	99.07	110.41		72.18	82.37	76.00
		St. Dev.	0.16	0.03		0.60		0.73
		Coeff. Var.	0.16	0.03		0.83		0.96
Pan	176228	Mean	101.16	114.43	140.04	77.21	83.46	77.17
		St. Dev.	2.49	2.51	2.25	3.23	1.32	1.71

		Coeff. Var.	2.46	2.19	1.61	4.18	1.58	2.21
Pan	176229	Mean	98.41	110.50	141.87	72.55	82.01	77.14
		St. Dev.	0.18	1.20	0.61	0.97	1.58	1.50
		Coeff. Var.	0.18	1.09	0.43	1.34	1.93	1.94
Pan	176235	Mean	106.96	118.75	146.45	70.16	86.99	75.83
		St. Dev.	0.49	0.88	0.44	0.59	0.10	0.71
		Coeff. Var.	0.45	0.74	0.30	0.84	0.11	0.94
Pan	176238	Mean	104.68	115.15	139.30	77.50	85.29	81.31
		St. Dev.	1.21	0.43	1.10	0.30	0.94	0.69
		Coeff. Var.	1.16	0.38	0.79	0.39	1.11	0.85
Pan	176240	Mean	104.79	116.32	146.03	71.19		
		St. Dev.	0.10	0.77	0.11	0.36		
		Coeff. Var.	0.09	0.66	0.07	0.50		
Pan	176241	Mean	95.88	108.04	141.04	68.64	78.21	78.94
		St. Dev.	1.02	1.19	2.30	0.35		0.94
		Coeff. Var.	1.07	1.10	1.63	0.51		1.19
Pan	176242	Mean	116.68	129.44	156.70	78.80	91.07	83.14
		St. Dev.	1.00	2.47	0.43	1.50	0.93	0.54
		Coeff. Var.	0.85	1.91	0.28	1.91	1.03	0.65
Pan	220062	Mean	91.48	111.30	138.63	70.21	81.41	73.75
		St. Dev.	8.86	4.03	2.52	1.28		0.29
		Coeff. Var.	9.68	3.62	1.82	1.83		0.39
Pan	220064	Mean	91.99	110.47	131.81	66.26	75.97	73.23
		St. Dev.		3.87	0.12	1.15	0.03	0.35
		Coeff. Var.		3.51	0.09	1.73	0.04	0.48
Pan	220065	Mean	100.61	112.60	139.23	70.12	80.81	71.50
		St. Dev.	2.20	3.64	2.48	2.38		0.71
		Coeff. Var.	2.18	3.23	1.78	3.39		0.99
Pan	236971	Mean	95.37	106.75	133.11	65.91	77.13	72.14
		St. Dev.	1.05	3.28	1.19	0.37	0.35	1.56
		Coeff. Var.	1.10	3.07	0.89	0.55	0.46	2.17
Pan	282763	Mean	99.28	113.54	139.71	74.18	83.66	83.66
		St. Dev.	0.36	1.19	0.35	1.90	0.14	0.69
		Coeff. Var.	0.36	1.05	0.25	2.56	0.17	0.82
Pan	297856	Mean	97.29	109.39	135.72	70.06		75.13
		St. Dev.	0.43	1.51	0.56	1.25		5.29
		Coeff. Var.	0.44	1.38	0.42	1.78		7.04
Pan	395820	Mean	98.44	109.98	141.54	75.56	83.44	85.13
		St. Dev.	0.42	1.80	0.53	1.23	1.57	0.85
		Coeff. Var.	0.43	1.64	0.37	1.63	1.88	1.00
Pan	450071	Mean	100.38	112.74	138.49	67.47	80.70	76.02
		St. Dev.	1.50	1.91	1.17	1.81	1.87	1.20
		Coeff. Var.	1.50	1.69	0.85	2.68	2.32	1.58
Pan	477333	Mean	92.67	100.46	124.31	63.24		75.99
		St. Dev.	0.28	1.11	0.21	0.04		0.74
		Coeff. Var.	0.30	1.11	0.17	0.07		0.97
Pan	481803	Mean	101.84	111.75	138.77	69.47	81.30	76.89
		St. Dev.	0.52	3.28	0.07	1.90	0.76	3.08

		Coeff. Var.	0.51	2.93	0.05	2.73	0.94	4.00
Pan	481804	Mean	100.76	112.75	135.18	68.72	79.42	80.23
		St. Dev.	0.73	0.53	0.45	0.11	0.68	1.90
		Coeff. Var.	0.72	0.47	0.34	0.17	0.86	2.37
Gorilla	174714	Mean	153.89	165.39	191.20	96.87	110.32	112.66
		St. Dev.	0.03	0.51	0.30	0.10	1.28	0.04
		Coeff. Var.	0.02	0.31	0.16	0.10	1.16	0.04
Gorilla	174716	Mean	147.50	161.28	188.01	92.01	109.59	114.94
		St. Dev.	0.47	0.40	0.29	0.21	0.30	0.45
		Coeff. Var.	0.32	0.25	0.16	0.22	0.28	0.39
MAK	MLD 37/38	Mean						73.26
		St. Dev.						1.11
		Coeff. Var.						1.51

Genus	Spec No.	Value	zm-po	api-aps	crt-aps	pros-I1L	pros-I2L	pros-CL
Homo	99.1/1728	Mean	68.38	10.84	0.15	7.00	10.49	15.85
		St. Dev.	0.23	0.64	0.02	0.10	0.01	0.05
		Coeff. Var.	0.34	5.88	15.97	1.39	0.12	0.34
Homo	99.1/1738	Mean	74.14	14.67	0.03	7.36	11.81	17.01
		St. Dev.	0.01	1.32	0.05	0.24	0.26	0.43
		Coeff. Var.	0.02	9.02	141.42	3.24	2.22	2.55
Homo	VL/2921	Mean	64.24	16.53	0.09	8.05	12.59	17.85
		St. Dev.	0.22	0.48	0.12	0.79	0.52	0.89
		Coeff. Var.	0.34	2.91	141.42	9.85	4.10	4.97
Homo	VL/2923	Mean	62.17	14.27	0.21	7.28	11.58	16.82
		St. Dev.	0.65	3.32	0.08	0.20	0.13	0.16
		Coeff. Var.	1.05	23.27	35.98	2.80	1.14	0.92
Homo	VL/2928	Mean	61.73	14.80	0.15	6.95	11.46	16.79
		St. Dev.	0.27	0.28	0.04	0.25	0.31	0.31
		Coeff. Var.	0.44	1.87	27.11	3.54	2.71	1.86
Pan	174699	Mean	76.16	31.04	12.16	9.61	17.53	30.25
		St. Dev.	1.57	12.51	9.73	0.07	0.09	0.80
		Coeff. Var.	2.06	40.30	79.97	0.69	0.50	2.64
Pan	174700	Mean	73.46	29.58	8.27	9.28	16.39	25.74
		St. Dev.	2.51	3.40	0.05	0.10	0.13	0.00
		Coeff. Var.	3.41	11.49	0.58	1.06	0.82	0.00
Pan	174701	Mean	71.43	25.31	6.65	9.89	19.15	29.24
		St. Dev.	0.61	3.96	2.43	0.08	0.02	0.37
		Coeff. Var.	0.85	15.64	36.51	0.83	0.11	1.28
Pan	174702	Mean	72.33	33.49	12.28	9.53	16.92	28.39
		St. Dev.	1.16	0.26	0.75	0.54	0.77	0.91
		Coeff. Var.	1.60	0.77	6.12	5.69	4.53	3.22
Pan	174703	Mean	70.72	29.83	14.15	9.95	17.18	25.04
		St. Dev.	1.16	6.58	0.15	0.35	0.05	0.33
		Coeff. Var.	1.64	22.06	1.03	3.53	0.32	1.31
Pan	174706	Mean	65.58	21.99	7.69	8.58	13.94	21.85
		St. Dev.	0.10	9.23	0.39	0.06	0.13	0.63
		Coeff. Var.	0.16	41.97	5.09	0.69	0.91	2.91
Pan	174707	Mean	70.11	28.51	11.34	8.26	16.05	24.76
		St. Dev.	1.41	1.36	0.51	0.08	0.57	0.25
		Coeff. Var.	2.02	4.78	4.52	0.95	3.58	1.00
Pan	174710	Mean	79.99	28.21	8.40	9.05	15.55	24.41
		St. Dev.	1.59	0.86	2.29	0.09	0.44	0.19
		Coeff. Var.	1.99	3.05	27.24	1.04	2.84	0.76
Pan	220326	Mean	74.94	28.48	10.91			
		St. Dev.	0.42	7.62	3.05			
		Coeff. Var.	0.55	26.76	27.99			

Pan	176228	Mean	77.52	33.76	7.65	9.63	16.24	25.42
		St. Dev.	0.92	7.48	1.12	0.18	0.03	0.02
		Coeff. Var.	1.18	22.16	14.60	1.91	0.15	0.08
Pan	176229	Mean	76.53	34.65	12.92	9.35	15.73	27.24
		St. Dev.	1.60	0.50	2.09	0.78	1.00	0.96
		Coeff. Var.	2.09	1.45	16.19	8.34	6.37	3.54
Pan	176235	Mean	79.88	34.09	8.24	8.66	16.46	25.67
		St. Dev.	0.13	3.72	3.79	0.03	1.26	0.19
		Coeff. Var.	0.16	10.92	45.99	0.34	7.63	0.73
Pan	176238	Mean	73.57	33.55	11.42	10.37	16.46	26.91
		St. Dev.	1.12	1.39	0.87	0.10	0.06	0.34
		Coeff. Var.	1.53	4.14	7.65	0.92	0.36	1.25
Pan	176240	Mean	74.10	35.02	21.01	10.31	17.86	30.34
		St. Dev.	4.90	5.19	16.54	0.20	0.18	0.23
		Coeff. Var.	6.62	14.82	78.72	1.98	1.01	0.75
Pan	176241	Mean	75.85	37.05	8.95	9.93	16.88	30.50
		St. Dev.	1.30	2.97	0.20	0.19	0.38	0.33
		Coeff. Var.	1.71	8.03	2.25	1.89	2.25	1.08
Pan	176242	Mean	108.80	27.41	9.66	9.31	16.24	29.19
		St. Dev.	33.92	6.07	5.91	0.21	0.09	0.30
		Coeff. Var.	31.18	22.13	61.21	2.30	0.57	1.03
Pan	220062	Mean	74.09	28.24	7.90	9.06	16.91	27.64
		St. Dev.	3.47	8.68	0.36	0.24	0.17	1.38
		Coeff. Var.	4.68	30.74	4.50	2.66	1.00	5.00
Pan	220064	Mean	73.57	22.08	2.90	8.95	16.39	24.58
		St. Dev.	0.85	3.57	1.11	0.39	0.24	0.43
		Coeff. Var.	1.16	16.15	38.24	4.31	1.49	1.75
Pan	220065	Mean	75.66	28.25	11.92	7.91	16.59	30.49
		St. Dev.	2.27	#DIV/0!	#DIV/0!	0.97	0.61	0.54
		Coeff. Var.	2.99	#DIV/0!	#DIV/0!	12.26	3.68	1.76
Pan	236971	Mean	71.90	31.00	9.51	8.93	16.23	27.66
		St. Dev.	0.71	8.99	0.25	0.18	0.25	0.39
		Coeff. Var.	0.98	29.01	2.68	2.04	1.56	1.41
Pan	282763	Mean	74.74	37.80	9.70	9.34	17.74	26.81
		St. Dev.	0.02	9.45	0.10	0.10	0.56	1.90
		Coeff. Var.	0.03	24.99	1.00	1.12	3.16	7.09
Pan	297856	Mean	72.75	31.07	12.88	9.23	16.82	25.12
		St. Dev.	1.03	7.13	2.31	0.45	1.01	0.36
		Coeff. Var.	1.42	22.94	17.94	4.84	6.01	1.43
Pan	395820	Mean	71.51	37.65	9.73	9.64	17.26	28.60
		St. Dev.	0.14	5.76	1.75	0.01	0.25	0.27
		Coeff. Var.	0.19	15.30	18.01	0.13	1.47	0.94
Pan	450071	Mean	71.46	38.29	13.48	8.90	17.21	26.16
		St. Dev.	1.01	4.35	1.76	0.71	0.86	0.01
		Coeff. Var.	1.42	11.37	13.07	8.03	4.98	0.04
Pan	477333	Mean	65.91	34.58	12.16	9.01	15.62	25.01
		St. Dev.	0.94	9.82	0.37	0.22	0.41	0.47
		Coeff. Var.	1.43	28.40	3.02	2.45	2.61	1.87

Pan	481803	Mean	72.99	34.33	7.34	11.00	18.01	29.74
		St. Dev.	0.78	2.79	2.63	1.39	0.62	0.81
		Coeff. Var.	1.07	8.11	35.80	12.67	3.43	2.72
Pan	481804	Mean	70.90	34.26	9.50	8.59	15.72	25.65
		St. Dev.	0.21	8.74	0.87	0.09	0.01	0.32
		Coeff. Var.	0.29	25.51	9.14	1.01	0.04	1.24
Gorilla	174714	Mean	108.87	35.55	13.43	9.48	16.89	27.93
		St. Dev.	0.46	2.17	0.79	0.06	0.18	0.69
		Coeff. Var.	0.42	6.10	5.88	0.63	1.07	2.46
Gorilla	174716	Mean	105.61	34.57	14.45	9.46	16.84	27.25
		St. Dev.	0.12	1.12	1.65	0.07	0.56	1.22
		Coeff. Var.	0.12	3.25	11.38	0.72	3.33	4.49
MAK	MLD 31	Mean	329.37					
		St. Dev.	0.29					
		Coeff. Var.	0.09					
MAK	MLD 45	Mean			13.50			
		St. Dev.			0.78			
		Coeff. Var.			5.75			

Genus	Spec No.	Value	pros-P3L	pros-P4L	pros-M1L	pros-M2L	pros-M3L	pros-I1E
Homo	99.1/1728	Mean	20.55	26.01	33.67	42.89	327.08	4.20
		St. Dev.	0.05	0.08	0.17	0.29	0.13	0.24
		Coeff. Var.	0.22	0.32	0.52	0.68	0.04	5.84
Homo	99.1/1738	Mean	21.76	27.46	35.65	45.45	320.32	4.76
		St. Dev.	0.01	0.10	0.28	0.73	0.18	0.09
		Coeff. Var.	0.03	0.35	0.79	1.61	0.06	1.98
Homo	VL/2921	Mean	21.32	27.09	37.07	44.85		4.65
		St. Dev.	0.16	0.16	0.10	0.49		0.55
		Coeff. Var.	0.77	0.57	0.28	1.10		11.76
Homo	VL/2923	Mean	21.63	28.28	36.11	44.11		4.61
		St. Dev.	0.31	0.25	1.34	0.96		0.01
		Coeff. Var.	1.41	0.89	3.71	2.17		0.14
Homo	VL/2928	Mean	22.18	29.67	37.73	46.93		4.54
		St. Dev.	0.23	0.03	0.19	0.24		0.38
		Coeff. Var.	1.05	0.09	0.51	0.52		8.33
Pan	174699	Mean	35.76	41.01	47.52	54.73	63.79	7.99
		St. Dev.	0.45	0.40	0.61	0.68	0.52	0.35
		Coeff. Var.	1.25	0.98	1.29	1.24	0.82	4.32
Pan	174700	Mean	31.85	37.24	44.60	51.65	59.02	7.03
		St. Dev.	0.07	0.27	0.05	0.28	0.69	0.19
		Coeff. Var.	0.23	0.72	0.11	0.53	1.17	2.68
Pan	174701	Mean	34.07	39.38	45.70	53.87	62.08	7.68
		St. Dev.	0.72	0.41	0.32	0.47	0.87	0.88
		Coeff. Var.	2.11	1.05	0.71	0.88	1.40	11.43
Pan	174702	Mean	35.15	40.60	46.90	54.17	62.81	9.48
		St. Dev.	0.15	1.20	1.35	1.63	1.20	0.47
		Coeff. Var.	0.44	2.95	2.89	3.01	1.91	4.99
Pan	174703	Mean	31.60	36.66	43.78	52.79	61.85	8.73
		St. Dev.	0.13	0.13	0.69	0.99	0.02	0.71
		Coeff. Var.	0.42	0.34	1.58	1.87	0.04	8.13
Pan	174706	Mean	27.84	32.09	38.42	47.19	55.76	6.71
		St. Dev.	0.12	0.03	0.64	0.02	0.15	0.04
		Coeff. Var.	0.42	0.10	1.68	0.04	0.27	0.66
Pan	174707	Mean	31.08	36.64	43.17	50.80	58.70	6.20
		St. Dev.	0.27	0.19	0.34	0.17	0.13	0.72
		Coeff. Var.	0.86	0.53	0.79	0.34	0.21	11.57
Pan	174710	Mean	30.15	37.81	43.59	51.09	59.04	5.57
		St. Dev.	0.06	0.40	0.06	0.28	0.18	0.35
		Coeff. Var.	0.20	1.06	0.15	0.55	0.31	6.36
Pan	220326	Mean						
		St. Dev.						
		Coeff. Var.						
Pan	176228	Mean	32.13	37.55	44.06	52.67	61.57	7.64
		St. Dev.	0.27	0.03	0.42	0.24	0.31	0.71

		Coeff. Var.	0.84	0.07	0.96	0.46	0.51	9.30
Pan	176229	Mean	33.19	38.34	45.70	54.25	61.92	7.00
		St. Dev.	0.43	0.91	0.39	0.08	0.14	0.63
		Coeff. Var.	1.31	2.37	0.86	0.15	0.23	9.01
Pan	176235	Mean	32.32	37.81	45.99	55.11	63.27	8.43
		St. Dev.	0.13	0.11	0.42	0.25	0.50	0.88
		Coeff. Var.	0.39	0.28	0.91	0.46	0.79	10.39
Pan	176238	Mean	33.20	38.13	45.14	53.58	62.94	7.44
		St. Dev.	0.06	0.13	0.10	0.36	0.33	0.09
		Coeff. Var.	0.17	0.34	0.21	0.67	0.53	1.19
Pan	176240	Mean	38.85	42.68	50.43	60.09	67.45	7.40
		St. Dev.	0.17	0.05	0.45	0.32	0.65	0.82
		Coeff. Var.	0.44	0.12	0.89	0.53	0.96	11.04
Pan	176241	Mean	36.51	41.92	48.14	57.00	64.04	7.40
		St. Dev.	0.29	0.23	0.12	0.07	0.29	0.97
		Coeff. Var.	0.79	0.55	0.26	0.12	0.46	13.14
Pan	176242	Mean	35.22	41.18	47.33	57.25	66.64	6.67
		St. Dev.	0.29	0.34	0.26	0.07	0.24	0.26
		Coeff. Var.	0.83	0.84	0.55	0.13	0.36	3.86
Pan	220062	Mean	33.79	39.69	46.18	53.67	60.86	6.66
		St. Dev.	0.55	0.84	1.17	0.85	0.02	0.28
		Coeff. Var.	1.63	2.11	2.54	1.58	0.04	4.25
Pan	220064	Mean	31.84	37.12	43.63	51.64	59.21	5.96
		St. Dev.	0.00	0.25	0.14	0.78	0.12	0.41
		Coeff. Var.	0.01	0.68	0.32	1.52	0.20	6.85
Pan	220065	Mean	36.58	40.93	46.92	54.21	61.63	7.24
		St. Dev.	0.92	0.40	0.33	0.17	0.02	0.07
		Coeff. Var.	2.52	0.99	0.71	0.32	0.03	1.02
Pan	236971	Mean	34.87	39.75	47.08	54.94	63.92	7.45
		St. Dev.	0.10	0.54	0.72	0.64		0.08
		Coeff. Var.	0.29	1.35	1.52	1.16		1.08
Pan	282763	Mean	36.60	42.21	50.05	59.51	68.62	9.14
		St. Dev.	0.03	0.07	0.23	0.43	0.46	0.16
		Coeff. Var.	0.07	0.16	0.46	0.72	0.67	1.78
Pan	297856	Mean	31.09	39.22	48.25	57.22	63.34	8.07
		St. Dev.	0.23	0.97	0.57	1.33	1.52	0.25
		Coeff. Var.	0.75	2.48	1.17	2.32	2.40	3.07
Pan	395820	Mean	36.08	41.98	50.60	60.03	69.06	8.90
		St. Dev.	0.03	0.02	0.32	0.11	0.05	0.36
		Coeff. Var.	0.09	0.05	0.63	0.19	0.08	3.99
Pan	450071	Mean	31.55	37.29	44.71	53.86	63.45	8.20
		St. Dev.	0.22	1.21	0.80	0.20	0.35	0.31
		Coeff. Var.	0.69	3.25	1.78	0.37	0.55	3.79
Pan	477333	Mean	29.82	36.20	44.20	52.63	62.47	6.20
		St. Dev.	0.85	0.27	0.48	0.03	0.16	0.26
		Coeff. Var.	2.87	0.75	1.09	0.05	0.26	4.23
Pan	481803	Mean	34.78	40.15	48.92	59.06	67.78	8.49
		St. Dev.	0.05	0.37	0.02	0.28	0.39	0.34

		Coeff. Var.	0.13	0.92	0.04	0.48	0.57	4.03
Pan	481804	Mean	31.67	36.68	45.22	54.12	62.94	6.60
		St. Dev.	0.21	0.20	0.69	0.31	0.21	0.30
		Coeff. Var.	0.66	0.54	1.52	0.58	0.33	4.56
Gorilla	174714	Mean	41.36	49.16	61.24	74.38	88.83	7.84
		St. Dev.	0.27	0.19	0.03	0.47	0.19	0.38
		Coeff. Var.	0.66	0.38	0.06	0.63	0.22	4.88
Gorilla	174716	Mean	38.15	44.84	57.80	71.62	85.64	8.12
		St. Dev.	0.46	1.33	0.18	0.35	0.09	0.77
		Coeff. Var.	1.22	2.96	0.31	0.48	0.10	9.44

Genus	Spec No.	Value	pros-I2E	pros-CE	pros-P3E	pros-P4E	pros-M1E	pros-M2E
Homo	99.1/1728	Mean	11.61	18.96	25.07	30.81	38.56	46.42
		St. Dev.	0.39	0.02	0.44	0.12	0.02	0.05
		Coeff. Var.	3.38	0.12	1.74	0.39	0.05	0.11
Homo	99.1/1738	Mean	12.69	19.94	26.83	33.31	41.55	49.15
		St. Dev.	0.21	0.13	0.13	0.03	0.60	0.09
		Coeff. Var.	1.66	0.67	0.49	0.09	1.44	0.19
Homo	VL/2921	Mean	12.65	19.69	25.44	31.50	39.04	46.71
		St. Dev.	0.16	0.27	0.38	0.27	0.70	0.05
		Coeff. Var.	1.24	1.37	1.50	0.86	1.79	0.10
Homo	VL/2923	Mean	12.79	19.70	26.63	32.67	39.56	47.46
		St. Dev.	0.09	0.20	0.00	0.30	0.22	0.02
		Coeff. Var.	0.73	1.03	0.01	0.93	0.55	0.04
Homo	VL/2928	Mean	11.33	18.89	25.58	31.98	40.17	48.81
		St. Dev.	0.03	0.01	0.20	0.04	0.01	0.21
		Coeff. Var.	0.27	0.04	0.79	0.14	0.01	0.44
Pan	174699	Mean	18.39	33.01	41.94	48.49	54.33	62.30
		St. Dev.	0.50	0.49	0.23	0.51	0.10	0.13
		Coeff. Var.	2.69	1.48	0.55	1.04	0.18	0.22
Pan	174700	Mean	16.95	28.13	36.22	41.38	49.55	55.86
		St. Dev.	0.26	0.40	0.16	0.13	0.07	0.08
		Coeff. Var.	1.52	1.42	0.45	0.31	0.14	0.15
Pan	174701	Mean	18.34	31.19	39.95	44.67	51.16	58.68
		St. Dev.	0.32	1.39	0.73	0.19	0.60	0.78
		Coeff. Var.	1.76	4.46	1.83	0.42	1.17	1.33
Pan	174702	Mean	19.49	31.88	39.03	44.42	51.88	59.93
		St. Dev.	0.42	0.12	0.79	0.23	0.51	0.13
		Coeff. Var.	2.15	0.36	2.01	0.52	0.98	0.21
Pan	174703	Mean	17.35	28.40	36.81	42.43	48.78	57.31
		St. Dev.	0.35	0.11	0.24	0.05	0.03	0.26
		Coeff. Var.	2.03	0.39	0.64	0.12	0.06	0.45
Pan	174706	Mean	14.79	25.24	31.89	36.58	42.78	49.74
		St. Dev.	0.16	0.46	0.35	0.17	0.32	0.32
		Coeff. Var.	1.08	1.82	1.09	0.48	0.76	0.65
Pan	174707	Mean	15.06	28.23	35.37	40.96	46.69	54.53
		St. Dev.	0.32	1.05	0.09	0.36	0.10	0.63
		Coeff. Var.	2.13	3.71	0.26	0.87	0.21	1.16
Pan	174710	Mean	15.22	28.38	35.15	41.77	47.22	55.28
		St. Dev.	0.53	0.17	1.01	0.20	0.24	0.22
		Coeff. Var.	3.46	0.60	2.88	0.48	0.52	0.39
Pan	176228	Mean	17.31	31.33	38.79	42.80	48.89	57.25
		St. Dev.	0.79	1.89	0.05	0.09	0.16	0.19
		Coeff. Var.	4.56	6.04	0.12	0.22	0.34	0.33
Pan	176229	Mean	16.56	30.20	38.51	44.14	49.94	57.48
		St. Dev.	1.23	0.61	0.91	0.57	0.50	0.34

		Coeff. Var.	7.42	2.01	2.36	1.30	1.00	0.59
Pan	176235	Mean	17.19	27.70	38.44	42.43	49.21	57.51
		St. Dev.	0.49	1.20	0.53	0.52	0.51	0.16
		Coeff. Var.	2.85	4.34	1.39	1.23	1.04	0.28
Pan	176238	Mean	17.46	29.99	37.35	43.72	49.81	57.40
		St. Dev.	0.23	0.83	0.50	0.16	0.24	0.32
		Coeff. Var.	1.31	2.78	1.34	0.37	0.48	0.56
Pan	176240	Mean	18.61	33.01	42.08	48.26	55.29	64.06
		St. Dev.	0.54	0.05	0.09	0.66	0.02	0.14
		Coeff. Var.	2.92	0.16	0.20	1.38	0.04	0.22
Pan	176241	Mean	18.51	33.56	40.55	46.18	52.61	60.92
		St. Dev.	0.60	0.37	0.43	0.09	0.58	0.68
		Coeff. Var.	3.23	1.10	1.06	0.19	1.10	1.12
Pan	176242	Mean	18.24	33.82	41.89	46.90	53.15	59.49
		St. Dev.	0.22	0.07	0.36	0.09	0.10	0.08
		Coeff. Var.	1.21	0.20	0.85	0.20	0.19	0.13
Pan	220062	Mean	17.70	30.86	39.13	44.27	51.10	58.30
		St. Dev.	0.30	0.95	0.18	0.11	0.20	0.01
		Coeff. Var.	1.72	3.07	0.46	0.26	0.39	0.02
Pan	220064	Mean	16.75	27.88	34.99	39.96	47.92	54.92
		St. Dev.	0.01	0.03	0.11	0.37	0.32	0.15
		Coeff. Var.	0.09	0.12	0.31	0.94	0.67	0.28
Pan	220065	Mean	18.32	35.55	40.95	46.64	52.69	59.24
		St. Dev.	0.86	0.54	0.84	0.35	0.61	0.64
		Coeff. Var.	4.68	1.53	2.05	0.74	1.15	1.09
Pan	236971	Mean	17.59	30.57	38.90	44.04	51.92	59.13
		St. Dev.	0.40	1.18	0.38	0.26	0.43	0.27
		Coeff. Var.	2.26	3.86	0.98	0.59	0.83	0.45
Pan	282763	Mean	19.29	31.00	41.35	47.85	54.69	64.01
		St. Dev.	0.05	0.04	0.34	0.53	0.29	0.30
		Coeff. Var.	0.27	0.12	0.81	1.10	0.53	0.47
Pan	297856	Mean	17.22	30.62	37.57	42.64	49.21	55.55
		St. Dev.	0.72	0.66	0.52	0.06	1.09	0.08
		Coeff. Var.	4.15	2.15	1.38	0.15	2.21	0.15
Pan	395820	Mean	19.00	32.42	41.71	47.81	55.52	64.66
		St. Dev.	0.31	0.07	0.07	0.35	0.09	0.10
		Coeff. Var.	1.64	0.22	0.17	0.72	0.16	0.15
Pan	450071	Mean	18.53	28.92	37.36	44.03	51.27	60.11
		St. Dev.	2.30	2.67	1.80	1.57	1.66	1.69
		Coeff. Var.	12.41	9.22	4.82	3.56	3.23	2.81
Pan	477333	Mean	15.69	28.66	37.13	41.90	47.97	55.41
		St. Dev.	0.13	0.16	0.21	0.29	0.17	0.18
		Coeff. Var.	0.84	0.57	0.57	0.69	0.35	0.32
Pan	481803	Mean	18.36	32.19	40.58	46.16	54.29	64.73
		St. Dev.	0.35	0.94	0.53	0.05		0.37
		Coeff. Var.	1.88	2.91	1.30	0.11		0.57
Pan	481804	Mean	16.64	30.06	37.72	41.91	48.11	58.72
		St. Dev.	0.59	0.28	0.02	0.24	0.31	0.43

		Coeff. Var.	3.54	0.93	0.06	0.58	0.65	0.73
Gorilla	174714	Mean	16.66	35.71	48.46	56.32	66.06	77.56
		St. Dev.	0.41	0.70	0.05	0.20	0.28	0.46
		Coeff. Var.	2.46	1.97	0.10	0.35	0.43	0.60
Gorilla	174716	Mean	16.33	34.30	45.56	53.01	63.34	74.59
		St. Dev.	0.68	0.89	0.17	0.00	0.15	0.40
		Coeff. Var.	4.14	2.60	0.38	0.00	0.24	0.54

Genus	Spec No.	Value	pros-M3E	pros-M3po
Homo	99.1/1728	Mean	327.08	327.08
		St. Dev.	0.13	0.13
		Coeff. Var.	0.04	0.04
Homo	99.1/1738	Mean	320.32	320.32
		St. Dev.	0.18	0.18
		Coeff. Var.	0.06	0.06
Pan	174699	Mean	68.32	68.68
		St. Dev.	0.41	0.75
		Coeff. Var.	0.60	1.09
Pan	174700	Mean	62.09	62.61
		St. Dev.	0.23	0.42
		Coeff. Var.	0.37	0.67
Pan	174701	Mean	65.84	64.27
		St. Dev.	0.32	1.19
		Coeff. Var.	0.48	1.85
Pan	174702	Mean	66.61	66.49
		St. Dev.	0.78	1.16
		Coeff. Var.	1.18	1.74
Pan	174703	Mean	64.43	67.01
		St. Dev.	0.18	0.87
		Coeff. Var.	0.27	1.29
Pan	174706	Mean	55.87	57.95
		St. Dev.	0.13	0.02
		Coeff. Var.	0.22	0.03
Pan	174707	Mean	61.52	61.28
		St. Dev.	0.12	0.05
		Coeff. Var.	0.19	0.08
Pan	174710	Mean	61.30	61.07
		St. Dev.	0.03	0.29
		Coeff. Var.	0.05	0.48
Pan	176228	Mean	65.37	65.20
		St. Dev.	0.28	0.47
		Coeff. Var.	0.43	0.73
Pan	176229	Mean	65.07	64.96
		St. Dev.	0.40	0.84
		Coeff. Var.	0.61	1.30
Pan	176235	Mean	66.12	66.18
		St. Dev.	0.29	0.10
		Coeff. Var.	0.44	0.15
Pan	176238	Mean	65.47	65.73
		St. Dev.	0.20	0.36
		Coeff. Var.	0.30	0.55
Pan	176240	Mean	71.84	71.47
		St. Dev.	0.66	0.92

		Coeff. Var.	0.92	1.28
Pan	176241	Mean	67.81	68.47
		St. Dev.	0.65	0.02
		Coeff. Var.	0.97	0.02
Pan	176242	Mean	69.24	69.27
		St. Dev.	0.05	0.36
		Coeff. Var.	0.07	0.52
Pan	220062	Mean	65.35	64.49
		St. Dev.	0.06	0.37
		Coeff. Var.	0.09	0.58
Pan	220064	Mean	60.96	62.69
		St. Dev.	0.40	0.21
		Coeff. Var.	0.66	0.33
Pan	220065	Mean	65.20	65.41
		St. Dev.	0.23	0.36
		Coeff. Var.	0.36	0.56
Pan	236971	Mean	65.71	
		St. Dev.		
		Coeff. Var.		
Pan	282763	Mean	71.48	72.95
		St. Dev.	0.40	0.92
		Coeff. Var.	0.56	1.26
Pan	297856	Mean	63.55	66.49
		St. Dev.	0.48	1.09
		Coeff. Var.	0.75	1.64
Pan	395820	Mean	71.64	72.28
		St. Dev.	0.02	0.62
		Coeff. Var.	0.02	0.85
Pan	450071	Mean	67.20	67.27
		St. Dev.	1.76	1.15
		Coeff. Var.	2.61	1.71
Pan	477333	Mean	62.90	65.28
		St. Dev.	0.10	0.47
		Coeff. Var.	0.16	0.72
Pan	481803	Mean	70.82	70.78
		St. Dev.	0.78	0.32
		Coeff. Var.	1.11	0.46
Pan	481804	Mean	65.98	65.99
		St. Dev.	0.38	0.40
		Coeff. Var.	0.57	0.61
Gorilla	174714	Mean	89.56	91.42
		St. Dev.	0.51	0.52
		Coeff. Var.	0.57	0.57
Gorilla	174716	Mean	86.92	89.56
		St. Dev.	0.30	0.32
		Coeff. Var.	0.35	0.36

Mandible Measurement Repeatability

NOTES:

MLD 2 is not same pooled number, this is repeatability based on right side

MLD 19 repeatability not available for digitized data

MLD 18 repeatability not available for rtml-rtmfl

Genus	Spec No.	Value	sw - rt	I1w	I2w	Cw	P3w	P4w
Homo	VL/3016	Mean	13.70	13.45	13.00	12.95	11.60	10.20
		St. Dev.	0.00	0.21	0.00	0.07	0.42	0.42
		Coeff. Var.	0.00	1.58	0.00	0.55	3.66	4.16
Homo	99.1/1727	Mean	14.75	13.60	12.95	12.95	12.90	13.55
		St. Dev.	0.07	0.00	0.07	0.21	0.14	0.07
		Coeff. Var.	0.48	0.00	0.55	1.64	1.10	0.52
Homo	99.1/1171	Mean	16.75	16.55	14.70	14.20	14.75	14.35
		St. Dev.	0.07	0.49	0.00	0.28	0.07	0.07
		Coeff. Var.	0.42	2.99	0.00	1.99	0.48	0.49
Pan	174703	Mean	15.51	15.83	17.35	18.22	16.18	14.73
		St. Dev.	1.03	1.07	1.02	2.37	1.02	0.25
		Coeff. Var.	6.61	6.79	5.87	13.00	6.29	1.68
Gorilla	176216	Mean	28.25	29.50	30.50	31.90	27.10	22.80
		St. Dev.	0.07	0.28	0.42	0.57	0.85	0.14
		Coeff. Var.	0.25	0.96	1.39	1.77	3.13	0.62
Macaca	35489	Mean	12.57	12.80	13.08	13.14	11.04	9.36
		St. Dev.	0.10	0.37	0.18	0.13	0.76	0.23
		Coeff. Var.	0.79	2.87	1.41	0.97	6.86	2.49
Macaca	240704	Mean	10.26	10.40	9.88	9.78	8.24	7.54
		St. Dev.	0.34	0.11	0.15	0.16	0.11	0.32
		Coeff. Var.	3.31	1.09	1.50	1.59	1.29	4.22
Macaca	253780	Mean	11.51	11.96	11.48	11.90	10.53	9.32
		St. Dev.	0.42	0.40	0.27	0.10	0.33	0.35
		Coeff. Var.	3.69	3.37	2.34	0.83	3.16	3.72
MAK	MLD 2	Mean	17.10	17.30	18.60	20.20	20.10	19.10
		St. Dev.	0.00	0.28	0.00	0.14	0.42	0.00
		Coeff. Var.	0.00	1.63	0.00	0.70	2.11	0.00
MAK	MLD 18	Mean	20.00	20.60	20.80	21.70	21.20	20.10
		St. Dev.	0.14	0.14	0.14	0.14	0.28	0.28
		Coeff. Var.	0.71	0.69	0.68	0.65	1.33	1.41
MAK	MLD 27	Mean	19.30	19.55	20.30	21.90	22.75	
		St. Dev.	0.28	0.35	0.00	0.14	0.21	
		Coeff. Var.	1.47	1.81	0.00	0.65	0.93	
MAK	MLD 29	Mean						21.85
		St. Dev.						0.07
		Coeff. Var.						0.32
MAK	MLD 40	Mean				22.90	22.85	23.15
		St. Dev.				0.00	0.21	0.07

Coeff. Var.	0.00	0.93	0.31

Genus	Spec No.	Value	M1w	M2w	M3w	mfoML	lt	mfoSI
Homo	VL/3026	Mean						
		St. Dev.						
		Coeff. Var.						
Homo	VL/3016	Mean	10.05	11.80	15.50	5.40	4.65	3.00
		St. Dev.	0.07	0.28	0.42	0.00	0.21	0.14
		Coeff. Var.	0.70	2.40	2.74	0.00	4.56	4.71
Homo	VL/1179	Mean						
		St. Dev.						
		Coeff. Var.						
Homo	VL/1175	Mean						
		St. Dev.						
		Coeff. Var.						
Homo	99.1/1728	Mean						
		St. Dev.						
		Coeff. Var.						
Homo	99.1/1727	Mean	14.70	16.05	17.45	3.85	4.45	3.20
		St. Dev.	0.14	0.07	0.07	0.49	0.35	0.14
		Coeff. Var.	0.96	0.44	0.41	12.86	7.95	4.42
Homo	99.1/1171	Mean	14.15	16.95	17.55	5.30	4.30	4.40
		St. Dev.	0.35	0.35	0.07	0.28	0.14	0.14
		Coeff. Var.	2.50	2.09	0.40	5.34	3.29	3.21
Pan	174701	Mean						
		St. Dev.						
		Coeff. Var.						
Pan	174703	Mean	13.93	15.47	17.38	3.41	3.46	2.34
		St. Dev.	0.40	0.27	0.16	0.08	0.01	0.04
		Coeff. Var.	2.89	1.74	0.90	2.49	0.41	1.81
Gorilla	176216	Mean	20.35	22.55	25.60	6.00	4.85	3.15
		St. Dev.	0.21	1.06	0.00	0.14	0.07	0.64
		Coeff. Var.	1.04	4.70	0.00	2.36	1.46	20.20
Gorilla	252579	Mean						
		St. Dev.						
		Coeff. Var.						
Macaca	35489	Mean	9.48	11.36	12.39	2.80	2.76	1.90
		St. Dev.	0.11	0.04	0.13	0.01	0.04	0.06
		Coeff. Var.	1.12	0.37	1.03	0.51	1.54	2.98
Macaca	240704	Mean	7.21	8.71	10.52	1.66	1.47	1.58
		St. Dev.	0.01	0.30	0.03	0.09	0.06	0.04
		Coeff. Var.	0.20	3.49	0.27	5.55	4.34	2.24

Macaca	253780	Mean	8.25	9.17	10.43	2.24	2.67	1.78
		St. Dev.	0.06	0.08	0.20	0.11	0.10	0.08
		Coeff. Var.	0.69	0.93	1.90	4.75	3.71	4.77
MAK	MLD 2	Mean	21.30	23.55		2.70	1.80	1.95
		St. Dev.	0.14	0.21		0.00	0.14	0.07
		Coeff. Var.	0.66	0.90		0.00	7.86	3.63
MAK	MLD 18	Mean	19.60	24.55	28.30	5.10		3.50
		St. Dev.	0.00	0.49	0.42	0.28		0.14
		Coeff. Var.	0.00	2.02	1.50	5.55		4.04
MAK	MLD 19	Mean			24.45			
		St. Dev.			0.21			
		Coeff. Var.			0.87			
MAK	MLD 22	Mean	21.15	23.70	26.10			
		St. Dev.	0.21	0.57	0.42			
		Coeff. Var.	1.00	2.39	1.63			
MAK	MLD 29	Mean	23.35				3.90	
		St. Dev.	0.21				0.00	
		Coeff. Var.	0.91				0.00	
MAK	MLD 34	Mean	18.80	21.20				
		St. Dev.	0.00	0.28				
		Coeff. Var.	0.00	1.33				
MAK	MLD 40	Mean	24.55	28.80	31.25		4.05	
		St. Dev.	0.35	0.28	1.06		0.21	
		Coeff. Var.	1.44	0.98	3.39		5.24	
MAK	MLD 47	Mean			27.90			
		St. Dev.			0.14			
		Coeff. Var.			0.51			
MAK	MLD 48	Mean	21.35	23.05				
		St. Dev.	0.21	0.21				
		Coeff. Var.	0.99	0.92				

Genus	Spec No.	Value	lt	rtmf area	ltmf area	li-gn	rtI1l-rtI1b	rtI2l-rtI2b
Homo	VL/3026	Mean				25.57	26.88	27.50
		St. Dev.				0.05	0.00	0.12
		Coeff. Var.				0.20	0.02	0.43
Homo	VL/3016	Mean	2.91	16.20	13.49	34.24	34.51	33.94
		St. Dev.	0.01	0.76	0.62	0.08	0.26	0.10
		Coeff. Var.	0.24	4.71	4.56	0.25	0.77	0.30
Homo	VL/1179	Mean				28.99	29.07	28.69
		St. Dev.				0.22	0.13	0.05
		Coeff. Var.				0.75	0.45	0.17
Homo	VL/1175	Mean				30.24	31.48	31.59
		St. Dev.				0.57	0.09	0.04
		Coeff. Var.				1.89	0.30	0.12
Homo	99.1/1728	Mean				27.94	27.98	28.85
		St. Dev.				0.16	0.15	0.05
		Coeff. Var.				0.58	0.54	0.18
Homo	99.1/1727	Mean	3.75	12.29	16.65	31.15	31.45	32.05
		St. Dev.	0.21	1.04	0.38	0.00	0.35	0.13
		Coeff. Var.	5.66	8.46	2.29	0.01	1.11	0.41
Homo	99.1/1171	Mean	3.85	23.34	16.54	35.99	36.82	36.25
		St. Dev.	0.21	1.99	0.37	0.20	0.34	0.15
		Coeff. Var.	5.51	8.54	2.22	0.55	0.91	0.40
Pan	174701	Mean				33.44	33.32	32.70
		St. Dev.				1.28	0.09	0.03
		Coeff. Var.				3.82	0.28	0.10
Pan	174703	Mean		7.98				
		St. Dev.		0.05				
		Coeff. Var.		0.68				
Gorilla	176216	Mean	3.70	18.95	17.94	62.28	60.15	58.39
		St. Dev.	0.14	4.26	0.42	0.40	3.18	3.31
		Coeff. Var.	3.82	22.51	2.36	0.64	5.28	5.67
Gorilla	252579	Mean				52.26	52.35	51.22
		St. Dev.				0.30	0.27	0.39
		Coeff. Var.				0.57	0.51	0.77
Macaca	35489	Mean	2.15	5.32	5.92	25.91	26.07	26.66
		St. Dev.	0.06	0.19	0.08	0.52	0.61	0.45
		Coeff. Var.	2.97	3.48	1.43	2.01	2.34	1.67
Macaca	240704	Mean	1.82	2.61	2.66	18.30	18.69	18.84
		St. Dev.	0.02	0.20	0.08	0.56	0.44	0.38
		Coeff. Var.	1.17	7.79	3.18	3.04	2.36	2.04

Macaca	253780	Mean	2.08	3.98	5.54	25.57	26.94	26.40
		St. Dev.	0.01	0.38	0.19	0.80	0.46	0.58
		Coeff. Var.	0.34	9.50	3.37	3.15	1.70	2.19
MAK	MLD 2	Mean	1.35	5.27	2.44	29.56	28.87	28.36
		St. Dev.	0.07	0.19	0.32	0.24	0.40	0.43
		Coeff. Var.	5.24	3.63	13.07	0.80	1.37	1.50
MAK	MLD 18	Mean		17.87				
		St. Dev.		1.71				
		Coeff. Var.		9.58				
MAK	MLD 29	Mean	3.35		13.07			
		St. Dev.	0.07		0.28			
		Coeff. Var.	2.11		2.11			
MAK	MLD 40	Mean	3.05		12.36			
		St. Dev.	0.07		0.93			
		Coeff. Var.	2.32		7.55			

Genus	Spec No.	Value	rtCl-rtCb	rtP3l-rtP3b	rtP4l-rtP4b	rtM1l-rtM1b	rtM2l-rtM2b	rtM3l-rtM3b
Homo	VL/3026	Mean	27.16	27.07	25.70	25.28	25.16	23.48
		St. Dev.	0.00	0.10	0.08	0.07	0.04	0.16
		Coeff. Var.	0.00	0.37	0.30	0.27	0.14	0.70
Homo	VL/3016	Mean	33.94	33.82	32.81	30.53	27.67	26.25
		St. Dev.	0.02	0.20	0.26	0.28	0.13	0.10
		Coeff. Var.	0.06	0.58	0.79	0.93	0.48	0.38
Homo	VL/1179	Mean	28.37	28.97	29.23	27.67	26.39	
		St. Dev.	0.22	0.08	0.20	0.16	0.13	
		Coeff. Var.	0.76	0.29	0.68	0.59	0.49	
Homo	VL/1175	Mean	32.05	31.63	31.11	29.54	26.47	25.41
		St. Dev.	0.05	0.16	0.34	0.04	0.12	0.40
		Coeff. Var.	0.16	0.50	1.08	0.12	0.44	1.55
Homo	99.1/1728	Mean	28.98	29.43	27.58	26.70	26.76	
		St. Dev.	0.10	0.20	0.15	0.02	0.17	
		Coeff. Var.	0.33	0.69	0.53	0.07	0.62	
Homo	99.1/1727	Mean	32.94	34.01	33.74	32.65	31.92	32.23
		St. Dev.	0.24	0.03	0.14	0.18	0.10	0.03
		Coeff. Var.	0.73	0.10	0.42	0.56	0.30	0.09
Homo	99.1/1171	Mean	36.52	37.69	37.62	38.27	35.62	34.87
		St. Dev.	0.22	0.18	0.01	0.13	0.10	0.42
		Coeff. Var.	0.60	0.48	0.02	0.34	0.28	1.20
Pan	174701	Mean	31.91	31.71	29.63	28.53	27.82	27.34
		St. Dev.	0.25	0.42	0.51	0.04	0.04	0.08
		Coeff. Var.	0.79	1.33	1.72	0.13	0.15	0.28
Gorilla	176216	Mean	53.09	52.96	45.51	44.55	46.31	47.71
		St. Dev.	2.17	0.61	0.35	0.63	0.70	0.45
		Coeff. Var.	4.09	1.16	0.77	1.42	1.52	0.93
Gorilla	252579	Mean	48.69	46.29	42.36	41.23	38.90	38.68
		St. Dev.	0.15	0.51	0.16	0.11	0.15	0.14
		Coeff. Var.	0.30	1.10	0.38	0.26	0.38	0.37
Macaca	35489	Mean	24.48	24.20	23.51	25.28	23.94	24.26
		St. Dev.	0.65	0.77	0.07	0.06	0.29	0.51
		Coeff. Var.	2.64	3.19	0.28	0.25	1.22	2.09
Macaca	240704	Mean	18.39	18.36	17.05	17.18	16.64	16.86
		St. Dev.	0.10	0.29	0.17	0.12	0.42	0.24
		Coeff. Var.	0.54	1.57	1.03	0.72	2.54	1.41
Macaca	253780	Mean	25.07	23.89	21.82	23.26	23.45	23.21
		St. Dev.	0.43	0.08	0.19	0.14	0.15	0.27
		Coeff. Var.	1.73	0.34	0.89	0.58	0.62	1.18
MAK	MLD 2	Mean	29.44	29.02	28.73	26.08	23.14	
		St. Dev.	0.01	0.20	0.35	0.18	0.37	
		Coeff. Var.	0.03	0.70	1.20	0.68	1.61	

MAK	MLD 18	Mean	35.34	33.62	31.73
		St. Dev.	0.59	0.07	0.51
		Coeff. Var.	1.67	0.22	1.60
MAK	MLD 34	Mean	34.40	34.39	
		St. Dev.	0.16	0.02	
		Coeff. Var.	0.47	0.05	
MAK	MLD 47	Mean			37.18
		St. Dev.			0.02
		Coeff. Var.			0.06

Genus	Spec No.	Value	rtM3po-rtM3b	id-gn	rtmfl-rtmfb	rtI1e-rtI1b	rtI2e-rtI2b	rtCe-rtCb
Homo	VL/3026	Mean	26.06	25.81	24.39	24.03	23.51	22.36
		St. Dev.	0.62	0.33	0.40	0.59	0.13	0.14
		Coeff. Var.	2.37	1.30	1.66	2.45	0.56	0.64
Homo	VL/3016	Mean	26.85	33.72	29.87	32.14	30.82	29.43
		St. Dev.	0.36	2.08	0.13	0.01	0.04	0.48
		Coeff. Var.	1.34	6.17	0.44	0.02	0.12	1.62
Homo	VL/1179	Mean		30.73	27.58	29.23	28.85	26.96
		St. Dev.		0.23	0.22	0.18	0.44	0.04
		Coeff. Var.		0.73	0.79	0.61	1.52	0.16
Homo	VL/1175	Mean	25.51	29.64	29.53	28.92	27.27	26.58
		St. Dev.	0.21	1.95	0.18	0.26	1.62	0.85
		Coeff. Var.	0.84	6.59	0.60	0.90	5.92	3.20
Homo	99.1/1728	Mean		29.41	27.11	27.41	27.56	25.43
		St. Dev.		0.56	0.39	0.15	0.24	1.13
		Coeff. Var.		1.92	1.45	0.55	0.88	4.44
Homo	99.1/1727	Mean	33.73	31.33	32.39	29.35	29.75	29.31
		St. Dev.	0.07	0.40	0.38	0.29	0.15	0.30
		Coeff. Var.	0.20	1.29	1.18	1.00	0.49	1.02
Homo	99.1/1171	Mean	35.75	33.26	34.52	34.03	33.58	30.54
		St. Dev.	0.01	0.27	0.48	0.46	0.39	0.59
		Coeff. Var.	0.02	0.82	1.40	1.35	1.15	1.93
Pan	174701	Mean	28.64	37.02	29.56	33.08	33.34	32.12
		St. Dev.	0.20	1.10	0.07	0.15	0.02	0.51
		Coeff. Var.	0.71	2.97	0.24	0.47	0.07	1.57
Gorilla	176216	Mean	50.64	67.03	45.48	60.18	57.65	50.26
		St. Dev.	0.47	0.57	0.73	3.36	3.94	2.71
		Coeff. Var.	0.94	0.85	1.62	5.58	6.83	5.40
Gorilla	252579	Mean	38.94	56.55	39.44	54.39	52.61	47.94
		St. Dev.	0.18	0.39	0.93	0.38	0.45	0.40
		Coeff. Var.	0.46	0.70	2.35	0.70	0.85	0.84
Macaca	35489	Mean	24.99	27.53	21.11	24.51	25.92	23.46
		St. Dev.	0.12	0.89	0.18	0.85	0.72	0.96
		Coeff. Var.	0.49	3.24	0.85	3.47	2.79	4.08
Macaca	240704	Mean	18.74	19.63	17.06	17.03	19.12	17.52
		St. Dev.	0.46	0.01	0.46	0.50	0.34	0.19
		Coeff. Var.	2.48	0.04	2.69	2.91	1.78	1.10
Macaca	253780	Mean	23.55	26.43	22.46	26.25	26.91	24.91
		St. Dev.	0.17	0.81	0.79	0.23	0.44	0.38
		Coeff. Var.	0.71	3.07	3.51	0.86	1.65	1.51
MAK	MLD 2	Mean		31.22	30.28	27.95	27.78	29.10
		St. Dev.		0.27	0.49	0.38	0.09	0.65
		Coeff. Var.		0.86	1.62	1.35	0.33	2.22

Genus	Spec No.	Value	rtP3e-rtP3b	rtP4e-rtP4b	rtM1e-rtM1b	rtM2e-rtM2b	rtM3e-rtM3b	ltI1l-ltI1b
Homo	VL/3026	Mean	24.42	24.19	23.99	22.87	24.80	26.73
		St. Dev.	0.36	0.69	0.05	0.19	0.63	0.19
		Coeff. Var.	1.47	2.85	0.20	0.82	2.54	0.71
Homo	VL/3016	Mean	31.09	30.61	28.49	25.17	25.02	34.57
		St. Dev.	0.01	0.66	0.51	0.92	0.36	0.09
		Coeff. Var.	0.04	2.16	1.79	3.66	1.45	0.27
Homo	VL/1179	Mean	26.62	27.13	25.10	24.61		31.17
		St. Dev.	0.26	0.37	0.17	0.21		0.49
		Coeff. Var.	0.99	1.36	0.66	0.86		1.58
Homo	VL/1175	Mean	27.46	28.95	27.07	25.05	24.83	29.79
		St. Dev.	1.00	0.77	0.18	0.36	0.03	0.25
		Coeff. Var.	3.66	2.66	0.67	1.43	0.12	0.84
Homo	99.1/1728	Mean	26.34	27.00	24.29	24.03		29.50
		St. Dev.	0.11	0.04	0.07	0.10		0.10
		Coeff. Var.	0.42	0.16	0.29	0.41		0.35
Homo	99.1/1727	Mean	30.16	32.16	29.98	26.59	28.47	31.95
		St. Dev.	0.03	0.29	0.06	0.03	0.01	0.10
		Coeff. Var.	0.11	0.91	0.19	0.10	0.05	0.31
Homo	99.1/1171	Mean	33.26	35.22	33.65	31.02	31.98	34.17
		St. Dev.	0.20	0.22	0.55	0.11	0.23	0.89
		Coeff. Var.	0.60	0.64	1.65	0.36	0.73	2.60
Pan	174701	Mean	31.87	30.65	28.44	27.14	28.24	31.66
		St. Dev.	0.57	1.16	0.31	0.19	0.05	0.26
		Coeff. Var.	1.78	3.77	1.08	0.71	0.18	0.83
Gorilla	176216	Mean	51.43	45.88	41.55	40.33	45.18	59.00
		St. Dev.	0.73	0.36	0.61	0.12	0.15	0.55
		Coeff. Var.	1.42	0.78	1.47	0.30	0.32	0.94
Gorilla	252579	Mean	44.39	39.79	38.55	33.42	35.65	50.31
		St. Dev.	0.89	0.49	0.42	0.09	0.04	0.34
		Coeff. Var.	2.01	1.23	1.08	0.26	0.12	0.67
Macaca	35489	Mean	23.06	22.01	23.61	21.80	22.33	21.78
		St. Dev.	0.70	0.21	0.17	0.37	0.34	0.64
		Coeff. Var.	3.03	0.97	0.70	1.71	1.54	2.93
Macaca	240704	Mean	18.12	15.84	16.33	15.07	15.88	14.92
		St. Dev.	0.35	0.39	0.09	0.17	0.30	0.00
		Coeff. Var.	1.94	2.45	0.53	1.16	1.88	0.01
Macaca	253780	Mean	23.75	22.24	22.75	22.60	21.98	23.13
		St. Dev.	0.07	0.08	0.44	0.32	0.04	0.65
		Coeff. Var.	0.30	0.36	1.93	1.43	0.19	2.82
MAK	MLD 2	Mean	26.98	28.53	24.07	24.73		29.84
		St. Dev.	1.23	0.31	0.19	0.25		0.12
		Coeff. Var.	4.57	1.08	0.79	1.00		0.39
MAK	MLD 18	Mean			36.64	33.14	30.96	
		St. Dev.			1.06	0.05	0.90	

		Coeff. Var.	2.90	0.16	2.92
MAK	MLD 34	Mean	34.32	35.20	
		St. Dev.	1.17	0.79	
		Coeff. Var.	3.41	2.25	
MAK	MLD 40	Mean			
		St. Dev.			
		Coeff. Var.			
MAK	MLD 47	Mean			36.26
		St. Dev.			0.17
		Coeff. Var.			0.46

Genus	Spec No.	Value	ltI2l-ltI2b	ltCl-ltCb	ltP3l-ltP3b	ltP4l-ltP4b	ltM1l-ltM1b	ltM2l-ltM2b
Homo	VL/3026	Mean	27.15	26.21	23.83	25.73	25.48	24.08
		St. Dev.	0.28	0.47	0.13	0.35	0.29	0.09
		Coeff. Var.	1.02	1.81	0.53	1.36	1.12	0.39
Homo	VL/3016	Mean	32.97	32.66	31.51	31.25	29.24	25.60
		St. Dev.	0.51	0.09	0.63	0.18	0.34	0.17
		Coeff. Var.	1.54	0.27	2.00	0.58	1.17	0.68
Homo	VL/1179	Mean	31.11	29.18	28.22	27.15	25.89	23.45
		St. Dev.	0.23	0.21	0.49	0.55	0.09	0.04
		Coeff. Var.	0.73	0.73	1.74	2.02	0.33	0.18
Homo	VL/1175	Mean	30.53	30.65	30.75	30.45	28.87	24.41
		St. Dev.	0.04	0.73	0.13	0.21	0.40	0.46
		Coeff. Var.	0.13	2.38	0.42	0.70	1.37	1.87
Homo	99.1/1728	Mean	29.08	27.53	28.19	28.32	25.08	24.01
		St. Dev.	0.21	0.32	0.11	0.60	0.63	0.19
		Coeff. Var.	0.72	1.17	0.40	2.11	2.51	0.80
Homo	99.1/1727	Mean	32.21	32.55	30.78	32.07	31.44	28.63
		St. Dev.	0.51	0.03	0.35	0.12	1.05	1.16
		Coeff. Var.	1.59	0.08	1.14	0.38	3.33	4.05
Homo	99.1/1171	Mean	34.30	34.77	35.11	37.92	37.95	37.30
		St. Dev.	0.44	0.15	0.38	0.05	0.03	0.72
		Coeff. Var.	1.27	0.43	1.09	0.13	0.08	1.94
Pan	174701	Mean	31.53	30.65	31.37	30.94	29.57	26.82
		St. Dev.	0.10	0.14	0.36	0.01	0.18	0.32
		Coeff. Var.	0.32	0.45	1.13	0.04	0.62	1.20
Gorilla	176216	Mean	54.24	43.67	48.25	44.20	41.75	40.59
		St. Dev.	0.51	1.76	0.16	0.10	0.13	0.64
		Coeff. Var.	0.93	4.04	0.33	0.23	0.30	1.58
Gorilla	252579	Mean	46.88	43.04	43.73	38.95	38.26	33.67
		St. Dev.	0.34	0.15	0.37	0.79	0.30	0.04
		Coeff. Var.	0.72	0.34	0.85	2.02	0.77	0.13
Macaca	35489	Mean	22.64	19.41	21.94	22.45	23.10	22.55
		St. Dev.	0.43	1.26	0.80	0.01	0.22	0.41
		Coeff. Var.	1.91	6.47	3.67	0.04	0.97	1.82
Macaca	240704	Mean	17.03	17.22	17.86	15.71	16.76	14.36
		St. Dev.	0.45	0.28	0.80	0.16	0.14	0.75
		Coeff. Var.	2.63	1.60	4.49	1.02	0.83	5.21
Macaca	253780	Mean	23.67	21.54	22.88	20.86	20.80	20.39
		St. Dev.	0.14	1.31	0.62	0.13	0.13	0.02
		Coeff. Var.	0.61	6.08	2.70	0.64	0.64	0.11
MAK	MLD 2	Mean	27.26	31.62	28.38	29.25	28.21	30.94
		St. Dev.	0.07	0.18	0.27	0.21	0.58	0.78
		Coeff. Var.	0.25	0.57	0.96	0.73	2.04	2.53
MAK	MLD 29	Mean				32.01		
		St. Dev.				0.47		

		Coeff. Var.			1.47		
MAK	MLD 40	Mean	33.40	34.68	35.98	34.57	36.60
		St. Dev.	1.64	2.17	0.54	1.76	1.49
		Coeff. Var.	4.92	6.26	1.51	5.08	4.06

Genus	Spec No.	Value	ltM3l-ltM3b	ltmfl-ltmfb	ltI1e-ltI1b	ltI2e-ltI2b	ltCe-ltCb	ltP3e-ltP3b
Homo	VL/3026	Mean	25.37	24.40	23.97	24.21	22.68	21.25
		St. Dev.	0.99	0.19	0.06	0.34	0.48	0.01
		Coeff. Var.	3.91	0.77	0.24	1.39	2.14	0.07
Homo	VL/3016	Mean	25.89	27.84	32.00	30.19	29.85	29.13
		St. Dev.	0.26	0.99	0.13	0.54	0.16	0.84
		Coeff. Var.	1.01	3.55	0.41	1.80	0.55	2.88
Homo	VL/1179	Mean		25.17	28.85	28.71	25.94	25.94
		St. Dev.		0.68	0.61	0.42	0.26	0.65
		Coeff. Var.		2.69	2.11	1.46	1.01	2.49
Homo	VL/1175	Mean	26.10	28.71	26.97	27.08	27.28	28.73
		St. Dev.	0.11	0.07	0.20	0.03	0.79	0.52
		Coeff. Var.	0.43	0.25	0.74	0.10	2.89	1.81
Homo	99.1/1728	Mean		27.14	27.21	26.60	24.77	26.18
		St. Dev.		0.68	0.18	0.44	0.34	0.14
		Coeff. Var.		2.52	0.64	1.66	1.39	0.55
Homo	99.1/1727	Mean	28.75	30.33	29.69	29.95	30.17	28.64
		St. Dev.	0.40	1.55	0.30	0.63	0.04	0.55
		Coeff. Var.	1.41	5.11	1.01	2.10	0.13	1.92
Homo	99.1/1171	Mean	36.60	37.46	32.44	32.29	32.47	33.65
		St. Dev.	0.83	0.24	1.12	0.38	0.23	0.35
		Coeff. Var.	2.26	0.64	3.44	1.17	0.71	1.05
Pan	174701	Mean	28.44	29.51	34.47	34.06	31.72	31.30
		St. Dev.	0.41	1.18	0.11	0.03	0.62	0.30
		Coeff. Var.	1.44	3.98	0.33	0.10	1.95	0.95
Gorilla	176216	Mean	45.27	40.60	62.92	58.98	51.88	49.14
		St. Dev.	0.57	1.72	0.68	0.62	2.51	0.45
		Coeff. Var.	1.26	4.24	1.09	1.05	4.83	0.91
Gorilla	252579	Mean	36.95	37.68	53.50	50.55	46.99	44.04
		St. Dev.	0.31	0.68	0.32	0.41	0.08	0.16
		Coeff. Var.	0.84	1.80	0.60	0.80	0.18	0.36
Macaca	35489	Mean	22.36	21.74	24.13	24.77	21.67	21.95
		St. Dev.	0.13	0.74	0.68	0.44	1.61	0.60
		Coeff. Var.	0.57	3.42	2.80	1.79	7.44	2.74
Macaca	240704	Mean	15.09	17.30	17.21	19.09	19.00	18.21
		St. Dev.	0.93	1.06	0.19	0.38	0.09	0.96
		Coeff. Var.	6.19	6.15	1.12	1.98	0.49	5.29
Macaca	253780	Mean	19.07	21.75	25.91	25.89	23.58	23.00
		St. Dev.	0.18	0.21	0.67	0.14	1.50	0.44
		Coeff. Var.	0.92	0.95	2.58	0.53	6.35	1.92
MAK	MLD 2	Mean		26.91	29.53	27.18	31.43	27.20
		St. Dev.		0.52	0.06	0.20	0.35	0.09
		Coeff. Var.		1.95	0.20	0.73	1.12	0.33
MAK	MLD 40	Mean	37.59	35.68			34.28	35.42
		St. Dev.	3.04	0.26			1.25	2.09

Coeff. Var.	8.08	0.71			3.64	5.89

Genus	Spec No.	Value	ltP4e-ltP4b	ltM1e-ltM1b	ltM2e-ltM2b	ltM3e-ltM3b	bi-I1l	bi-I2l
Homo	VL/3026	Mean	23.82	23.43	22.46	24.19	4.09	13.91
		St. Dev.	0.19	0.38	0.18	1.07	0.22	0.09
		Coeff. Var.	0.81	1.63	0.79	4.41	5.38	0.66
Homo	VL/3016	Mean	29.60	27.90	24.62	25.07	3.57	10.86
		St. Dev.	0.47	0.20	0.02	0.10	0.12	0.04
		Coeff. Var.	1.60	0.72	0.07	0.42	3.26	0.37
Homo	VL/1179	Mean	25.51	24.28	22.53		2.89	10.35
		St. Dev.	0.47	0.03	0.12		0.01	0.27
		Coeff. Var.	1.84	0.13	0.55		0.47	2.64
Homo	VL/1175	Mean	28.38	26.78	23.08	24.76	3.31	10.83
		St. Dev.	0.12	0.27	0.31	0.03	0.22	0.60
		Coeff. Var.	0.41	1.00	1.33	0.11	6.54	5.58
Homo	99.1/1728	Mean	26.90	24.74	23.71		3.60	13.73
		St. Dev.	0.35	0.48	0.14		0.57	0.48
		Coeff. Var.	1.29	1.95	0.59		15.79	3.48
Homo	99.1/1727	Mean	30.53	30.34	27.97	28.78	5.90	14.11
		St. Dev.	0.06	1.33	0.42	0.37	0.30	0.33
		Coeff. Var.	0.20	4.37	1.51	1.29	5.08	2.36
Homo	99.1/1171	Mean	36.34	36.44	35.88	36.08	4.04	10.80
		St. Dev.	0.17	0.04	0.73	0.78	0.09	0.90
		Coeff. Var.	0.47	0.10	2.03	2.16	2.20	8.30
Pan	174701	Mean	30.82	29.49	26.70	28.40	7.76	21.04
		St. Dev.	0.05	0.20	0.38	0.45	0.03	0.57
		Coeff. Var.	0.15	0.69	1.41	1.59	0.44	2.69
Pan	174703	Mean						
		St. Dev.						
		Coeff. Var.						
Gorilla	176216	Mean	44.64	41.61	40.38	44.60	7.25	17.79
		St. Dev.	0.24	0.26	0.87	0.54	0.42	0.30
		Coeff. Var.	0.53	0.63	2.15	1.22	5.73	1.70
Gorilla	252579	Mean	39.10	37.80	32.60	35.97	6.12	17.86
		St. Dev.	0.82	0.31	0.04	0.18	0.16	0.38
		Coeff. Var.	2.09	0.83	0.13	0.50	2.66	2.13
Macaca	35489	Mean	22.44	22.96	22.48	22.30	3.21	7.71
		St. Dev.	0.00	0.29	0.34	0.21	0.25	0.11
		Coeff. Var.	0.00	1.28	1.53	0.95	7.70	1.41
Macaca	240704	Mean	15.84	16.79	14.35	15.04	2.70	6.86
		St. Dev.	0.23	0.15	0.76	0.93	0.26	0.24
		Coeff. Var.	1.46	0.89	5.31	6.16	9.54	3.52
Macaca	253780	Mean	20.98	20.87	20.36	19.09	2.78	7.15
		St. Dev.	0.11	0.29	0.12	0.13	0.14	0.22
		Coeff. Var.	0.50	1.39	0.58	0.66	5.14	3.10
MAK	MLD 2	Mean	25.92	24.14	26.30		3.81	13.33
		St. Dev.	0.25	0.96	0.38		0.32	0.05

		Coeff. Var.	0.95	3.97	1.43		8.42	0.35
MAK	MLD 18	Mean					3.49	11.52
		St. Dev.					0.16	0.05
		Coeff. Var.					4.49	0.44
MAK	MLD 27	Mean					3.54	12.68
		St. Dev.					0.06	0.32
		Coeff. Var.					1.57	2.55
MAK	MLD 29	Mean	37.43					
		St. Dev.	0.85					
		Coeff. Var.	2.28					
MAK	MLD 40	Mean	36.15	35.45	34.95	34.52		
		St. Dev.	0.17	0.55	0.35	0.39		
		Coeff. Var.	0.47	1.54	1.01	1.14		

Genus	Spec No.	Value	bi-CI	bi-P3l	bi-P4l	bi-M1l	bi-M2l	bi-M3l
Homo	VL/3026	Mean	19.86	25.76	32.51	37.19	41.26	46.63
		St. Dev.	0.34	0.54	0.12	0.18	0.18	0.14
		Coeff. Var.	1.69	2.09	0.38	0.48	0.43	0.30
Homo	VL/3016	Mean	19.01	26.65	32.73	37.39	42.80	46.14
		St. Dev.	0.07	0.32	0.19	0.11	0.31	0.05
		Coeff. Var.	0.37	1.21	0.59	0.29	0.71	0.12
Homo	VL/1179	Mean	17.54	26.74	32.56	40.42	47.44	
		St. Dev.	0.14	0.17	0.20	0.04	0.64	
		Coeff. Var.	0.82	0.62	0.60	0.11	1.34	
Homo	VL/1175	Mean	17.22	23.64	28.38	33.29	40.53	46.21
		St. Dev.	0.21	1.18	0.35	0.09	0.24	0.12
		Coeff. Var.	1.23	5.01	1.22	0.26	0.60	0.25
Homo	99.1/1728	Mean	21.43	28.53	34.50	39.60	44.69	
		St. Dev.	0.29	0.89	0.20	0.44	0.40	
		Coeff. Var.	1.36	3.13	0.59	1.12	0.89	
Homo	99.1/1727	Mean	21.38	27.83	34.30	41.16	46.36	51.11
		St. Dev.	0.06	0.14	0.43	0.02	0.19	0.10
		Coeff. Var.	0.29	0.51	1.27	0.05	0.42	0.20
Homo	99.1/1171	Mean	18.01	25.85	31.02	38.01	46.75	49.53
		St. Dev.	0.18	0.53	0.67	0.04	0.00	0.31
		Coeff. Var.	1.00	2.04	2.15	0.11	0.00	0.63
Pan	174701	Mean	28.99	35.48	36.04	36.65	37.86	39.32
		St. Dev.	0.17	0.23	0.43	0.27	0.01	0.16
		Coeff. Var.	0.57	0.66	1.19	0.73	0.02	0.40
Gorilla	176216	Mean	25.44	39.80	35.73	38.88	39.71	41.17
		St. Dev.	0.26	0.57	1.18	0.28	0.45	0.49
		Coeff. Var.	1.02	1.43	3.32	0.72	1.13	1.20
Gorilla	252579	Mean	27.37	36.03	33.65	31.82	32.05	30.68
		St. Dev.	0.06	0.41	0.08	0.78	0.27	0.29
		Coeff. Var.	0.22	1.14	0.24	2.44	0.84	0.94
Macaca	35489	Mean	8.26	16.67	19.37	20.55	20.39	21.54
		St. Dev.	0.29	0.16	0.35	0.10	0.15	0.18
		Coeff. Var.	3.56	0.97	1.81	0.47	0.74	0.85
Macaca	240704	Mean	9.77	13.63	15.58	18.41	18.24	19.38
		St. Dev.	0.12	0.23	0.08	0.14	0.43	0.03
		Coeff. Var.	1.26	1.66	0.50	0.76	2.36	0.16
Macaca	253780	Mean	10.95	14.43	15.77	18.78	20.14	22.23
		St. Dev.	0.43	0.48	0.19	0.11	0.07	0.26
		Coeff. Var.	3.97	3.35	1.23	0.57	0.34	1.19
MAK	MLD 2	Mean	22.04	20.53	25.23	29.33	36.06	
		St. Dev.	0.60	0.29	0.06	0.42	1.63	
		Coeff. Var.	2.71	1.44	0.24	1.43	4.53	
MAK	MLD 18	Mean	19.77	26.30	31.36			
		St. Dev.	0.05	0.08	0.27			

		Coeff. Var.	0.26	0.30	0.86
MAK	MLD 27	Mean	22.64	33.79	
		St. Dev.	0.24	0.04	
		Coeff. Var.	1.07	0.11	

Genus	Spec No.	Value	bi-M3po	bi-I1e	bi-I2e	bi-Ce	bi-P3e	bi-P4e
Homo	VL/3026	Mean	54.09	5.78	15.38	25.35	35.99	42.71
		St. Dev.	0.07	0.32	0.05	0.11	0.11	0.00
		Coeff. Var.	0.12	5.62	0.33	0.42	0.30	0.00
Homo	VL/3016	Mean	51.61	4.76	13.66	27.46	36.82	45.12
		St. Dev.	0.21	0.24	0.21	0.12	0.16	0.18
		Coeff. Var.	0.41	4.99	1.57	0.45	0.44	0.41
Homo	VL/1179	Mean		4.54	14.17	28.55	37.11	46.25
		St. Dev.		0.20	0.19	0.21	0.11	0.11
		Coeff. Var.		4.47	1.36	0.72	0.30	0.24
Homo	VL/1175	Mean	50.40	5.47	14.37	27.03	36.03	42.11
		St. Dev.	0.47	0.08	0.67	0.06	0.06	0.03
		Coeff. Var.	0.93	1.44	4.66	0.24	0.18	0.06
Homo	99.1/1728	Mean		5.58	16.46	30.26	41.75	47.68
		St. Dev.		0.53	0.22	0.18	0.20	0.04
		Coeff. Var.		9.50	1.33	0.61	0.47	0.07
Homo	99.1/1727	Mean	56.01	4.38	16.06	30.86	39.14	48.02
		St. Dev.	0.24	0.11	0.01	0.07	0.02	0.04
		Coeff. Var.	0.43	2.50	0.07	0.23	0.05	0.08
Homo	99.1/1171	Mean	51.30	6.10	16.13	27.73	39.83	46.11
		St. Dev.	0.01	0.39	0.43	0.97	0.22	0.14
		Coeff. Var.	0.01	6.43	2.67	3.48	0.56	0.30
Pan	174701	Mean	43.46	7.61	25.69	43.42	45.48	50.35
		St. Dev.	0.21	0.44	0.00	0.43	0.17	0.33
		Coeff. Var.	0.48	5.74	0.00	1.00	0.37	0.65
Pan	174703	Mean						
		St. Dev.						
		Coeff. Var.						
Gorilla	176216	Mean	48.62	6.23	21.35	48.64	57.53	56.67
		St. Dev.	0.01	0.03	0.65	1.84	0.40	0.15
		Coeff. Var.	0.02	0.48	3.04	3.77	0.69	0.26
Gorilla	252579	Mean	36.81	6.89	21.54	42.74	49.62	50.71
		St. Dev.	0.64	0.90	0.66	0.18	0.39	0.25
		Coeff. Var.	1.75	13.01	3.06	0.42	0.78	0.50
Macaca	35489	Mean	25.62	4.09	10.34	18.72	24.85	27.98
		St. Dev.	1.03	0.40	0.36	0.03	0.19	0.14
		Coeff. Var.	4.03	9.82	3.50	0.18	0.77	0.49
Macaca	240704	Mean	23.65	4.24	10.66	15.16	18.66	22.22
		St. Dev.	0.31	0.37	0.37	0.01	0.08	0.01
		Coeff. Var.	1.33	8.72	3.47	0.06	0.40	0.07
Macaca	253780	Mean	25.45	3.95	9.80	15.16	20.20	23.16
		St. Dev.	0.54	0.27	0.10	0.16	0.06	0.03
		Coeff. Var.	2.13	6.86	1.00	1.06	0.30	0.13
MAK	MLD 2	Mean		6.32	18.62	32.34	43.81	46.77
		St. Dev.		0.45	0.45	0.15	0.89	0.56

		Coeff. Var.	7.12	2.41	0.45	2.02	1.19
MAK	MLD 18	Mean	4.98	16.44	31.50		
		St. Dev.	0.19	0.09	0.13		
		Coeff. Var.	3.78	0.57	0.41		
MAK	MLD 27	Mean	4.74	14.56	31.79	45.21	
		St. Dev.	0.18	0.91	0.44	0.18	
		Coeff. Var.	3.87	6.28	1.38	0.40	

Genus	Spec No.	Value	bi-M1e	bi-M2e	bi-M3e	bi-I1b	bi-I2b	bi-Cb
Homo	VL/3026	Mean	53.06	57.60	62.76	3.49	12.13	23.02
		St. Dev.	0.24	0.04	0.54	0.57	0.13	1.69
		Coeff. Var.	0.46	0.08	0.85	16.23	1.06	7.32
Homo	VL/3016	Mean	50.97	57.23	60.63	3.41	11.24	22.34
		St. Dev.	0.08	0.26	0.55	0.22	0.78	0.23
		Coeff. Var.	0.16	0.46	0.90	6.34	6.97	1.04
Homo	VL/1179	Mean	55.21	62.55		3.22	11.26	23.42
		St. Dev.	0.37	0.31		1.06	0.44	0.41
		Coeff. Var.	0.67	0.50		33.03	3.88	1.76
Homo	VL/1175	Mean	49.81	57.18	61.93	3.76	12.13	23.22
		St. Dev.	0.24	0.08	0.04	1.07	1.60	0.76
		Coeff. Var.	0.49	0.15	0.07	28.43	13.15	3.27
Homo	99.1/1728	Mean	56.52	62.08		3.55	14.03	27.59
		St. Dev.	0.14	0.04		0.11	0.17	0.79
		Coeff. Var.	0.26	0.06		3.01	1.22	2.87
Homo	99.1/1727	Mean	55.80	62.72	67.22	3.97	13.91	27.00
		St. Dev.	0.02	0.19	0.07	0.07	1.05	0.33
		Coeff. Var.	0.04	0.30	0.10	1.66	7.52	1.21
Homo	99.1/1171	Mean	54.09	63.10	66.38	3.43	13.45	25.58
		St. Dev.	0.42	0.18	0.05	0.94	0.63	0.88
		Coeff. Var.	0.77	0.28	0.08	27.28	4.72	3.44
Pan	174701	Mean	54.68	55.92	56.48	4.87	13.29	20.54
		St. Dev.	0.34	0.08	0.34	0.80	1.18	1.81
		Coeff. Var.	0.62	0.15	0.60	16.37	8.86	8.83
Gorilla	176216	Mean	61.75	66.54	69.91	4.61	9.13	8.05
		St. Dev.	0.06	0.24	0.27	3.08	3.43	3.24
		Coeff. Var.	0.10	0.36	0.38	66.86	37.55	40.22
Gorilla	252579	Mean	52.69	53.11	57.07	4.01	9.83	10.91
		St. Dev.	0.09	0.36	0.54	1.23	0.93	1.46
		Coeff. Var.	0.17	0.67	0.95	30.77	9.45	13.39
Macaca	35489	Mean	30.81	33.50	34.64	2.50	5.84	6.84
		St. Dev.	0.06	0.09	0.19	0.60	0.30	1.28
		Coeff. Var.	0.19	0.26	0.54	24.19	5.18	18.75
Macaca	240704	Mean	25.76	29.03	31.91	1.22	3.78	5.82
		St. Dev.	0.15	0.01	0.20	0.27	0.94	0.34
		Coeff. Var.	0.60	0.05	0.63	22.26	24.97	5.79
Macaca	253780	Mean	26.75	31.54	33.72	1.20	3.77	6.39
		St. Dev.	0.04	0.12	0.34	0.15	0.69	0.69
		Coeff. Var.	0.16	0.38	1.00	12.86	18.21	10.76
MAK	MLD 2	Mean	53.34	62.87		3.39	11.33	20.80
		St. Dev.	0.47	0.30		0.14	1.08	2.03
		Coeff. Var.	0.89	0.48		4.20	9.52	9.77

Genus	Spec No.	Value	bi-P3b	bi-P4b	bi-M1b	bi-M2b	bi-M3b	pg-id
Homo	VL/3026	Mean	33.64	43.44	56.58	68.47	75.59	21.81
		St. Dev.	1.66	0.70	0.35	0.54	0.31	1.01
		Coeff. Var.	4.94	1.60	0.61	0.79	0.41	4.64
Homo	VL/3016	Mean	33.96	44.27	55.17	69.09	77.47	28.75
		St. Dev.	0.74	1.99	2.36	1.73	0.41	0.75
		Coeff. Var.	2.18	4.48	4.27	2.50	0.53	2.60
Homo	VL/1179	Mean	38.39	48.15	60.31	74.12		23.71
		St. Dev.	0.43	1.37	0.08	0.84		0.59
		Coeff. Var.	1.12	2.86	0.13	1.13		2.49
Homo	VL/1175	Mean	35.19	47.16	60.52	72.44	77.48	24.95
		St. Dev.	0.04	1.44	0.02	0.35	0.46	2.71
		Coeff. Var.	0.10	3.05	0.04	0.48	0.59	10.87
Homo	99.1/1728	Mean	38.88	51.01	61.61	72.86		21.11
		St. Dev.	0.25	0.59	0.34	0.22		1.18
		Coeff. Var.	0.63	1.16	0.55	0.30		5.59
Homo	99.1/1727	Mean	37.17	48.24	60.12	73.25	87.38	25.06
		St. Dev.	1.03	0.17	1.15	1.59	1.61	1.09
		Coeff. Var.	2.77	0.36	1.91	2.17	1.84	4.34
Homo	99.1/1171	Mean	39.43	49.29	60.95	76.03	86.28	25.23
		St. Dev.	0.73	0.24	0.98	1.19	0.69	0.47
		Coeff. Var.	1.86	0.48	1.61	1.56	0.80	1.86
Pan	174701	Mean	24.64	32.29	42.23	57.50	63.11	4.90
		St. Dev.	0.62	2.57	0.71	0.76	0.35	0.41
		Coeff. Var.	2.53	7.95	1.69	1.33	0.55	8.41
Gorilla	176216	Mean	8.88	22.30	38.15	68.34	84.06	3.25
		St. Dev.	3.35	1.00	0.10	2.16	1.53	0.12
		Coeff. Var.	37.67	4.46	0.26	3.16	1.82	3.73
Gorilla	252579	Mean	17.56	30.23	41.43	59.43	68.46	3.23
		St. Dev.	1.92	3.95	2.17	0.07	0.25	0.01
		Coeff. Var.	10.94	13.08	5.24	0.11	0.36	0.43
Macaca	35489	Mean	10.63	14.24	20.23	27.27	36.42	2.25
		St. Dev.	1.12	0.94	2.29	0.69	0.37	0.02
		Coeff. Var.	10.54	6.60	11.32	2.53	1.03	0.78
Macaca	240704	Mean	8.04	12.28	16.95	24.80	30.32	1.79
		St. Dev.	1.51	0.90	0.17	1.25	0.72	0.23
		Coeff. Var.	18.73	7.37	1.01	5.05	2.39	12.57
Macaca	253780	Mean	8.38	11.92	16.79	23.42	31.25	3.04
		St. Dev.	0.78	0.33	0.67	1.05	1.38	0.06
		Coeff. Var.	9.34	2.75	4.00	4.50	4.41	1.99
MAK	MLD 2	Mean	29.05	42.27	51.80	60.54		7.24
		St. Dev.	0.50	1.59	0.83	0.47		0.71
		Coeff. Var.	1.73	3.75	1.60	0.78		9.84
MAK	MLD 18	Mean						6.89
		St. Dev.						0.45
		Coeff. Var.						6.49

MAK	MLD 27	Mean	9.10
		St. Dev.	0.47
		Coeff. Var.	5.16

Genus	Spec No.	Value	ge-li	rax-rpx	ran-rpn	rtml-rtmfl	ltml-ltmfl	rtml-id/gn
Homo	VL/3026	Mean	15.22	38.04	29.14	14.40	13.76	24.26
		St. Dev.	0.01	0.67	0.14	0.11	0.21	0.17
		Coeff. Var.	0.09	1.75	0.46	0.80	1.55	0.72
Homo	VL/3016	Mean	22.72	38.40	29.38	18.08	15.51	28.91
		St. Dev.	0.12	0.12	0.17	0.08	0.08	0.01
		Coeff. Var.	0.51	0.31	0.58	0.47	0.53	0.03
Homo	VL/1179	Mean	15.89	35.40	30.15	16.14	14.64	27.24
		St. Dev.	0.87	0.18	0.05	0.28	0.16	0.32
		Coeff. Var.	5.50	0.52	0.15	1.75	1.09	1.18
Homo	VL/1175	Mean	18.60	37.35	31.06	18.07	17.22	25.54
		St. Dev.	0.44	0.29	0.26	0.63	0.18	0.26
		Coeff. Var.	2.34	0.77	0.83	3.48	1.02	1.00
Homo	99.1/1728	Mean	16.45	43.04	33.17	14.37	13.95	29.94
		St. Dev.	0.60	0.28	0.68	0.12	0.21	0.38
		Coeff. Var.	3.65	0.65	2.06	0.86	1.49	1.28
Homo	99.1/1727	Mean	19.12	41.08	30.87	17.27	15.32	28.22
		St. Dev.	0.11	0.04	0.48	0.18	0.80	0.46
		Coeff. Var.	0.59	0.09	1.54	1.02	5.22	1.64
Homo	99.1/1171	Mean	23.12	44.82	38.92	18.46	21.10	33.14
		St. Dev.	0.07	0.43	0.02	0.33	0.08	0.31
		Coeff. Var.	0.31	0.97	0.04	1.78	0.39	0.94
Pan	174701	Mean	24.40	43.72	40.92	18.02	18.30	27.14
		St. Dev.	0.76	0.12	0.03	0.23	0.55	0.86
		Coeff. Var.	3.10	0.26	0.07	1.28	3.01	3.16
Gorilla	176216	Mean	45.29	71.26	66.28	23.93	22.06	27.28
		St. Dev.	0.22	0.05	0.10	0.11	0.08	0.56
		Coeff. Var.	0.49	0.07	0.15	0.46	0.38	2.06
Gorilla	252579	Mean	38.07	64.62	59.89	24.29	22.73	27.00
		St. Dev.	0.04	0.09	0.60	0.25	0.06	0.09
		Coeff. Var.	0.09	0.13	1.01	1.01	0.28	0.34
Macaca	35489	Mean	19.18	29.39	27.90	17.11	17.75	11.46
		St. Dev.	0.03	0.33	0.53	0.06	0.72	0.37
		Coeff. Var.	0.14	1.11	1.90	0.33	4.04	3.25
Macaca	240704	Mean	12.20	22.96	22.25	11.82	11.04	7.71
		St. Dev.	0.14	0.58	0.04	0.14	0.06	0.25
		Coeff. Var.	1.14	2.52	0.18	1.16	0.56	3.28
Macaca	253780	Mean	16.36	25.22	23.00	15.64	16.13	10.39
		St. Dev.	0.38	0.40	0.00	0.28	0.23	0.08
		Coeff. Var.	2.34	1.59	0.01	1.79	1.43	0.74
MAK	MLD 2	Mean	21.92			18.24	15.06	22.00
		St. Dev.	1.09			0.73	0.50	0.23
		Coeff. Var.	4.96			4.01	3.30	1.05
MAK	MLD 18	Mean	27.38			19.14		
		St. Dev.	0.97					
		Coeff. Var.	3.54					

MAK	MLD 27	Mean	26.08	
		St. Dev.	0.39	
		Coeff. Var.	1.50	
MAK	MLD 40	Mean		17.84
		St. Dev.		0.17
		Coeff. Var.		0.96

Genus	Spec No.	Value	ltml-id/gn	id-cdc/cdc	id-go/go	bi-cdl	bi-cdm	bi-cdc
Homo	VL/3026	Mean	23.80	83.85	59.99		72.92	90.03
		St. Dev.	0.25	0.23	0.13		0.31	0.08
		Coeff. Var.	1.07	0.28	0.21		0.42	0.09
Homo	VL/3016	Mean	27.77	90.65	67.67	114.62	78.63	97.45
		St. Dev.	0.24	0.54	0.90	0.10	0.07	0.38
		Coeff. Var.	0.87	0.59	1.34	0.09	0.08	0.39
Homo	VL/1179	Mean	25.79	83.20	59.72	109.11	75.03	92.16
		St. Dev.	0.02	0.45	0.06	0.20	0.15	0.43
		Coeff. Var.	0.06	0.54	0.09	0.18	0.20	0.47
Homo	VL/1175	Mean	26.67	90.16	62.62	106.63	69.83	88.62
		St. Dev.	0.27	1.42	0.13	0.27	0.30	0.06
		Coeff. Var.	1.03	1.57	0.20	0.26	0.44	0.07
Homo	99.1/1728	Mean	29.79	96.45	65.17	102.04	73.65	87.12
		St. Dev.	0.15	0.12	0.16	0.47	0.01	0.40
		Coeff. Var.	0.51	0.13	0.24	0.46	0.02	0.46
Homo	99.1/1727	Mean	28.23	99.19	71.63	120.53	79.31	99.74
		St. Dev.	0.40	0.51	0.30	0.19	0.17	0.52
		Coeff. Var.	1.43	0.52	0.42	0.16	0.21	0.52
Homo	99.1/1171	Mean	31.79		82.40		84.33	
		St. Dev.	0.17		0.45		0.47	
		Coeff. Var.	0.52		0.54		0.56	
Pan	174701	Mean	28.02	115.34	98.47	103.56	55.55	79.59
		St. Dev.	0.19	0.53	0.47	0.14	0.08	1.20
		Coeff. Var.	0.66	0.46	0.47	0.13	0.14	1.51
Gorilla	176216	Mean	27.18	170.26	157.16	140.89	64.94	101.09
		St. Dev.	0.48	0.75	0.56	0.03	0.09	0.29
		Coeff. Var.	1.77	0.44	0.36	0.02	0.13	0.28
Gorilla	252579	Mean	24.03	151.32	136.25	128.44	64.57	96.33
		St. Dev.	0.41	0.29	0.45	0.17	0.06	0.64
		Coeff. Var.	1.72	0.19	0.33	0.13	0.09	0.67
Macaca	35489	Mean	10.73	82.77	77.71	75.72	44.61	60.38
		St. Dev.	0.00	0.02	0.10	0.11	0.15	0.12
		Coeff. Var.	0.04	0.02	0.13	0.14	0.34	0.21
Macaca	240704	Mean	6.91	65.70	60.09	63.07	40.31	51.93
		St. Dev.	0.43	0.10	0.70	0.15	0.13	0.04
		Coeff. Var.	6.16	0.15	1.16	0.24	0.32	0.08
Macaca	253780	Mean	10.60	72.28	66.68	71.92	43.87	57.83
		St. Dev.	0.23	0.14	0.01	0.02	0.05	0.55
		Coeff. Var.	2.17	0.19	0.02	0.03	0.11	0.96
MAK	MLD 2	Mean	22.54					
		St. Dev.	0.43					
		Coeff. Var.	1.92					

Genus	Spec No.	Value	rtcdm-rtcdl	ltcdm-ltcdl	bi-cr	bi-go	id-biM3po	rtgo-rtcdc
Homo	VL/3026	Mean		18.00	85.65	88.61	48.60	54.10
		St. Dev.		0.02	0.12	0.07	0.03	0.11
		Coeff. Var.		0.10	0.13	0.08	0.06	0.20
Homo	VL/3016	Mean	18.05	19.20	94.44	92.37	50.03	54.14
		St. Dev.	0.18	0.06	0.46	0.17	0.21	0.38
		Coeff. Var.	0.97	0.29	0.49	0.19	0.41	0.70
Homo	VL/1179	Mean	17.41	17.26	91.40	97.94		54.53
		St. Dev.	0.00	0.01	0.02	0.08		0.12
		Coeff. Var.	0.00	0.08	0.03	0.08		0.23
Homo	VL/1175	Mean	17.42	19.68	88.54	88.06	48.69	53.82
		St. Dev.	0.21	0.04	0.25	0.12	0.86	0.02
		Coeff. Var.	1.20	0.18	0.28	0.14	1.76	0.03
Homo	99.1/1728	Mean	16.04	15.73	85.74	94.90		54.59
		St. Dev.	0.19	0.10	0.11	0.04		0.39
		Coeff. Var.	1.20	0.64	0.12	0.04		0.72
Homo	99.1/1727	Mean	21.60	20.30	92.07	105.32	52.90	67.86
		St. Dev.	0.41	0.04	0.07	0.23	0.32	0.49
		Coeff. Var.	1.89	0.22	0.07	0.22	0.60	0.73
Homo	99.1/1171	Mean		22.82		106.71	54.14	
		St. Dev.		0.21		0.09	0.52	
		Coeff. Var.		0.91		0.09	0.96	
Pan	174701	Mean	24.43	24.49	88.83	82.87	67.81	53.12
		St. Dev.	0.11	0.12	0.00	0.23	0.04	2.14
		Coeff. Var.	0.47	0.50	0.00	0.27	0.06	4.03
Pan	174703	Mean						
		St. Dev.						
		Coeff. Var.						
Gorilla	176216	Mean	39.66	39.36	122.10	134.04	100.15	91.69
		St. Dev.	0.00	0.16	0.16	0.83	0.36	1.26
		Coeff. Var.	0.00	0.40	0.13	0.62	0.36	1.37
Gorilla	252579	Mean	32.53	32.16	100.90	101.40	87.78	62.99
		St. Dev.	0.15	0.10	0.57	0.29	0.70	0.75
		Coeff. Var.	0.46	0.30	0.57	0.29	0.80	1.19
Macaca	35489	Mean	15.70	15.77	63.12	58.00	52.07	29.10
		St. Dev.	0.12	0.03	0.68	0.11	0.49	0.24
		Coeff. Var.	0.76	0.20	1.08	0.19	0.95	0.83
Macaca	240704	Mean	11.33	11.90	57.30	49.81	42.32	21.65
		St. Dev.	0.12	0.07	0.02	0.10	0.08	0.45
		Coeff. Var.	1.08	0.63	0.03	0.20	0.19	2.08
Macaca	253780	Mean	14.69	13.86	64.53	57.75	41.89	30.57
		St. Dev.	0.10	0.06	0.42	0.01	0.00	0.55
		Coeff. Var.	0.71	0.43	0.65	0.02	0.01	1.80

Genus	Spec No.	Value	ltgo-ltcdc	rtcdc-rM1b/rM3b	ltcdc-ltM1b/ltM3b	rtcdc-rtM3b	ltcdc-ltM3b	rtcdc-rtM2e/rtM3e
Homo	VL/3026	Mean	51.29	50.98	50.67	64.88	66.69	13.43
		St. Dev.	0.21	1.56	2.00	1.64	0.33	0.25
		Coeff. Var.	0.40	3.07	3.95	2.53	0.49	1.85
Homo	VL/3016	Mean	52.52	46.01	43.93	68.13	67.55	26.15
		St. Dev.	0.19	0.69	0.34	0.89	1.09	1.80
		Coeff. Var.	0.36	1.49	0.78	1.30	1.62	6.90
Homo	VL/1179	Mean	52.27					
		St. Dev.	1.19					
		Coeff. Var.	2.27					
Homo	VL/1175	Mean	53.48	46.56	47.09	65.56	67.64	23.06
		St. Dev.	0.30	0.01	0.24	1.03	0.01	1.02
		Coeff. Var.	0.56	0.01	0.51	1.57	0.02	4.44
Homo	99.1/1728	Mean	57.45					
		St. Dev.	0.35					
		Coeff. Var.	0.61					
Homo	99.1/1727	Mean	65.39	64.15	65.05	83.18	79.94	31.41
		St. Dev.	0.10	0.04	1.68	0.08	0.82	0.92
		Coeff. Var.	0.15	0.07	2.58	0.10	1.02	2.94
Homo	99.1/1171	Mean	67.33		77.57		99.00	
		St. Dev.	0.17		1.72		1.58	
		Coeff. Var.	0.25		2.22		1.60	
Pan	174701	Mean	53.08	55.78	57.15	77.96	75.99	22.87
		St. Dev.	1.39	0.03	0.88	0.40	0.75	1.00
		Coeff. Var.	2.61	0.06	1.55	0.52	0.98	4.36
Pan	174703	Mean						
		St. Dev.						
		Coeff. Var.						
Gorilla	176216	Mean	81.88	126.43	126.11	136.62	137.13	62.50
		St. Dev.	1.99	2.29	0.76	2.39	1.13	0.72
		Coeff. Var.	2.43	1.81	0.60	1.75	0.82	1.14
Gorilla	252579	Mean	61.00	87.28	90.61	110.93	111.38	46.27
		St. Dev.	0.11	0.33	0.47	0.57	0.41	0.17
		Coeff. Var.	0.18	0.38	0.52	0.51	0.37	0.36
Macaca	35489	Mean	29.46	47.36	47.97	56.62	57.77	25.82
		St. Dev.	1.08	0.18	0.99	0.22	2.88	1.15
		Coeff. Var.	3.66	0.38	2.06	0.40	4.99	4.47
Macaca	240704	Mean	22.90	33.69	31.82	43.81	43.24	15.93
		St. Dev.	0.51	0.18	2.60	0.43	0.56	1.33
		Coeff. Var.	2.21	0.55	8.19	0.99	1.29	8.37
Macaca	253780	Mean	28.58	41.53	45.78	52.97	56.14	21.66
		St. Dev.	0.11	0.22	0.52	0.60	1.05	0.38
		Coeff. Var.	0.39	0.54	1.14	1.13	1.86	1.76

Genus	Spec No.	Value	ltcdc-ltM2e/ltM3e	rtcr-rtlg	ltcr-ltlg
Homo	VL/3026	Mean	18.97	32.87	30.92
		St. Dev.	1.13	0.28	0.46
		Coeff. Var.	5.96	0.86	1.47
Homo	VL/3016	Mean	25.34	31.50	32.84
		St. Dev.	1.38	0.09	0.28
		Coeff. Var.	5.45	0.29	0.84
Homo	VL/1179	Mean		34.13	34.44
		St. Dev.		0.07	0.06
		Coeff. Var.		0.19	0.19
Homo	VL/1175	Mean	13.20	31.97	33.06
		St. Dev.	0.58	0.02	0.62
		Coeff. Var.	4.37	0.07	1.86
Homo	99.1/1728	Mean		37.35	36.72
		St. Dev.		0.17	0.24
		Coeff. Var.		0.45	0.65
Homo	99.1/1727	Mean	30.82	32.69	32.97
		St. Dev.	0.66	0.16	0.04
		Coeff. Var.	2.15	0.49	0.11
Homo	99.1/1171	Mean	46.10		32.27
		St. Dev.	0.42		0.09
		Coeff. Var.	0.91		0.28
Pan	174701	Mean	23.07	31.37	31.53
		St. Dev.	0.31	0.33	0.45
		Coeff. Var.	1.34	1.04	1.44
Pan	174703	Mean			
		St. Dev.			
		Coeff. Var.			
Gorilla	176216	Mean	60.09	58.81	53.25
		St. Dev.	1.00	0.04	0.28
		Coeff. Var.	1.67	0.08	0.53
Gorilla	252579	Mean	47.22	40.81	39.08
		St. Dev.	1.28	0.68	0.21
		Coeff. Var.	2.71	1.66	0.53
Macaca	35489	Mean	25.77	24.88	25.37
		St. Dev.	0.92	0.45	0.79
		Coeff. Var.	3.56	1.80	3.11
Macaca	240704	Mean	15.50	19.41	21.01
		St. Dev.	0.21	0.27	0.23
		Coeff. Var.	1.36	1.41	1.12
Macaca	253780	Mean	30.43	24.45	25.32
		St. Dev.	0.46	1.59	0.27
		Coeff. Var.	1.50	6.52	1.07

Upper Dentition Measurement Repeatability

Genus	Spec No.	Value	MD_up_I1	MD_up_ I1C	MD_up_I2
Pan	176228	Mean	12.30	8.55	9.21
		St. Dev.	0.13	0.22	0.19
		Coeff. Var.	1.03	2.57	2.07
Pan	176227	Mean	12.06	9.41	10.51
		St. Dev.	0.18	0.22	0.13
		Coeff. Var.	1.52	2.33	1.28
Pan	176241	Mean	11.31	8.94	8.35
		St. Dev.	0.04	0.14	0.20
		Coeff. Var.	0.31	1.58	2.37
Gorilla	545032	Mean	14.12	10.53	11.02
		St. Dev.	0.07	0.09	0.04
		Coeff. Var.	0.50	0.87	0.32
Gorilla	545034	Mean	12.81	10.24	10.80
		St. Dev.	0.01	0.06	0.13
		Coeff. Var.	0.06	0.62	1.18
Gorilla	545036	Mean			10.53
		St. Dev.			0.01
		Coeff. Var.			0.07
Gorilla	18399	Mean	12.35	9.95	8.85
		St. Dev.	0.07	0.07	0.07
		Coeff. Var.	0.57	0.71	0.80
Gorilla	27551	Mean	12.80	11.10	10.10
		St. Dev.	0.14	0.14	0.00
		Coeff. Var.	1.10	1.27	0.00
Gorilla	16344	Mean	11.55	11.25	
		St. Dev.	0.07	0.07	
		Coeff. Var.	0.61	0.63	
Macaca	240704	Mean	5.28	4.39	4.31
		St. Dev.	0.06	0.04	0.21
		Coeff. Var.	1.07	0.97	4.76
Macaca	241160	Mean	6.69	5.20	5.44
		St. Dev.	0.08	0.04	0.04
		Coeff. Var.	1.27	0.68	0.65
Macaca	35489	Mean	6.58	5.66	6.02
		St. Dev.	0.08	0.13	0.30
		Coeff. Var.	1.18	2.25	5.05
Macaca	353187	Mean	6.16	5.00	5.23
		St. Dev.	0.11	0.03	0.13
		Coeff. Var.	1.84	0.57	2.57
Homo	VL/3045	Mean	9.80	7.90	7.50
		St. Dev.	0.00	0.14	0.00
		Coeff. Var.	0.00	1.79	0.00

Homo	VL/3105	Mean	8.00	6.40	
		St. Dev.	0.00	0.00	
		Coeff. Var.	0.00	0.00	
Homo	99.1/1717	Mean			6.55
		St. Dev.			0.07
		Coeff. Var.			1.08
Australo	MLD 11/30	Mean			7.03
		St. Dev.			0.04
		Coeff. Var.			0.50
Australo	MLD 23	Mean			7.03
		St. Dev.			0.04
		Coeff. Var.			0.60

Genus	Spec No.	Value	MD_up_I2_C	MD_up_C	MD_up_CC	MD_up_P3
Pan	176228	Mean	5.91	13.90	13.38	7.45
		St. Dev.	0.01	0.25	0.06	0.16
		Coeff. Var.	0.12	1.83	0.42	2.18
Pan	176227	Mean	6.84	12.23	11.41	8.70
		St. Dev.	0.08	0.01	0.33	0.01
		Coeff. Var.	1.14	0.06	2.85	0.08
Pan	176238	Mean				8.20
		St. Dev.				0.14
		Coeff. Var.				1.72
Pan	176241	Mean	6.19	10.47	9.75	7.76
		St. Dev.	0.11	0.32	0.01	0.16
		Coeff. Var.	1.83	3.04	0.15	2.00
Gorilla	545032	Mean	8.59	22.18	21.21	12.08
		St. Dev.	0.04	0.15	0.47	0.32
		Coeff. Var.	0.49	0.67	2.20	2.64
Gorilla	545034	Mean	7.90	22.00	19.82	12.31
		St. Dev.	0.11	0.08	0.79	0.18
		Coeff. Var.	1.43	0.39	4.00	1.44
Gorilla	545036	Mean	8.96	23.35	21.93	14.37
		St. Dev.	0.09	0.14	0.26	0.06
		Coeff. Var.	1.03	0.61	1.19	0.44
Gorilla	18399	Mean	6.75	20.45	19.80	11.30
		St. Dev.	0.07	0.07	0.00	0.28
		Coeff. Var.	1.05	0.35	0.00	2.50
Gorilla	27551	Mean	8.20	19.30	18.65	12.70
		St. Dev.	0.14	0.00	0.07	0.14
		Coeff. Var.	1.72	0.00	0.38	1.11
Gorilla	16344	Mean	7.45	22.55	21.15	12.20
		St. Dev.	0.07	0.07	0.21	0.14
		Coeff. Var.	0.95	0.31	1.00	1.16
Macaca	240704	Mean	3.53	5.58	4.77	4.57
		St. Dev.	0.16	0.14	0.28	0.13
		Coeff. Var.	4.61	2.53	5.79	2.94
Macaca	241160	Mean	4.38	7.09	6.34	5.74
		St. Dev.	0.08	0.11	0.01	0.01
		Coeff. Var.	1.94	1.60	0.22	0.25
Macaca	35489	Mean	5.03	9.56		6.05
		St. Dev.	0.20	0.02		0.31
		Coeff. Var.	3.94	0.22		5.14
Macaca	353187	Mean	4.54	6.72	6.13	5.91
		St. Dev.	0.14	0.34	0.08	0.23
		Coeff. Var.	3.12	5.05	1.27	3.83
Homo	VL/3045	Mean	5.50	8.40	6.20	7.40
		St. Dev.	0.00	0.14	0.14	0.00
		Coeff. Var.	0.00	1.68	2.28	0.00

Homo	VL/3105	Mean		7.35	5.35	6.35
		St. Dev.		0.07	0.07	0.21
		Coeff. Var.		0.96	1.32	3.34
Homo	99.1/1719	Mean		8.50	6.35	7.30
		St. Dev.		0.00	0.07	0.14
		Coeff. Var.		0.00	1.11	1.94
Homo	99.1/1717	Mean	5.25	8.55	5.80	7.90
		St. Dev.	0.07	0.35	0.14	0.00
		Coeff. Var.	1.35	4.14	2.44	0.00
Australo	MLD 6	Mean				8.69
		St. Dev.				0.02
		Coeff. Var.				0.24
Australo	MLD 11/30	Mean	5.18	10.02	8.00	9.35
		St. Dev.	0.25	0.03	0.28	0.22
		Coeff. Var.	4.91	0.28	3.54	2.35
Australo	MLD 23	Mean	5.18			8.92
		St. Dev.	0.03			0.02
		Coeff. Var.	0.55			0.24

Genus	Spec No.	Value	MD_up_P3C	MD_up_P4	MD_up_P4C
Pan	176228	Mean	5.87	7.26	5.36
		St. Dev.	0.03	0.37	0.07
		Coeff. Var.	0.48	5.17	1.32
Pan	176227	Mean	6.41	7.48	4.89
		St. Dev.	0.22	0.04	0.02
		Coeff. Var.	3.42	0.57	0.43
Pan	176238	Mean	6.44	7.61	5.13
		St. Dev.	0.00	0.18	0.22
		Coeff. Var.	0.00	2.42	4.28
Pan	176241	Mean	5.62	6.73	4.79
		St. Dev.	0.18	0.07	0.22
		Coeff. Var.	3.15	1.05	4.58
Gorilla	545032	Mean	10.18	11.12	7.75
		St. Dev.	0.30	0.04	0.14
		Coeff. Var.	2.99	0.38	1.82
Gorilla	545034	Mean	10.51	11.29	9.30
		St. Dev.	0.13	0.17	0.18
		Coeff. Var.	1.28	1.50	1.98
Gorilla	545036	Mean	11.75	11.56	10.83
		St. Dev.	0.49	0.23	0.28
		Coeff. Var.	4.21	1.96	2.55
Gorilla	18399	Mean	10.10	12.00	8.80
		St. Dev.	0.42	0.28	0.14
		Coeff. Var.	4.20	2.36	1.61
Gorilla	27551	Mean	11.20	11.65	9.05
		St. Dev.	0.14	0.07	0.35
		Coeff. Var.	1.26	0.61	3.91
Gorilla	16344	Mean	11.25	10.20	9.00
		St. Dev.	0.07	0.14	0.28
		Coeff. Var.	0.63	1.39	3.14
Macaca	240704	Mean	3.52	4.82	3.35
		St. Dev.	0.74	0.01	0.00
		Coeff. Var.	21.12	0.29	0.00
Macaca	241160	Mean	4.78	5.44	4.45
		St. Dev.	0.00	0.06	0.07
		Coeff. Var.	0.00	1.17	1.59
Macaca	35489	Mean	4.69	5.68	4.35
		St. Dev.	0.08	0.20	0.11
		Coeff. Var.	1.81	3.49	2.60
Macaca	353187	Mean	5.29	5.41	4.16
		St. Dev.	0.08	0.15	0.08
		Coeff. Var.	1.47	2.75	2.04
Homo	VL/3045	Mean	5.60	6.55	4.85
		St. Dev.	0.28	0.35	0.07
		Coeff. Var.	5.05	5.40	1.46

Homo	VL/3105	Mean	4.25	5.90	4.00
		St. Dev.	0.21	0.14	0.28
		Coeff. Var.	4.99	2.40	7.07
Homo	99.1/1719	Mean	5.65	7.90	5.15
		St. Dev.	0.07	0.14	0.21
		Coeff. Var.	1.25	1.79	4.12
Homo	99.1/1717	Mean	5.55	7.20	5.35
		St. Dev.	0.49	0.00	0.49
		Coeff. Var.	8.92	0.00	9.25
Australo	MLD 6	Mean	6.95	9.79	7.18
		St. Dev.	0.21	0.02	0.11
		Coeff. Var.	3.05	0.22	1.48
Australo	MLD 9	Mean		8.85	7.55
		St. Dev.		0.07	0.21
		Coeff. Var.		0.80	2.81
Australo	MLD 11/30	Mean	8.30		
		St. Dev.	0.14		
		Coeff. Var.	1.70		
Australo	MLD 23	Mean	7.81		
		St. Dev.	0.41		
		Coeff. Var.	5.25		

Genus	Spec No.	Value	MD_up_M1	MD_up_M1C	MD_up_M2
Pan	176228	Mean	11.26	8.62	10.97
		St. Dev.	0.37	0.35	0.06
		Coeff. Var.	3.33	4.10	0.58
Pan	176227	Mean	11.49	9.21	10.87
		St. Dev.	0.21	0.25	0.08
		Coeff. Var.	1.85	2.76	0.78
Pan	176238	Mean	10.90	8.21	10.47
		St. Dev.	0.04	0.39	0.15
		Coeff. Var.	0.32	4.74	1.42
Pan	176241	Mean	10.11	6.80	10.17
		St. Dev.	0.18	0.23	0.30
		Coeff. Var.	1.82	3.43	2.92
Gorilla	545032	Mean	16.88	13.13	18.61
		St. Dev.	0.13	0.30	0.16
		Coeff. Var.	0.75	2.26	0.84
Gorilla	545034	Mean	15.36	11.25	17.26
		St. Dev.	0.07	0.13	0.28
		Coeff. Var.	0.46	1.19	1.64
Gorilla	545036	Mean	17.05	13.84	18.63
		St. Dev.	0.08	0.50	0.11
		Coeff. Var.	0.46	3.63	0.57
Gorilla	18399	Mean	15.45	12.10	15.85
		St. Dev.	0.07	0.28	0.49
		Coeff. Var.	0.46	2.34	3.12
Gorilla	27551	Mean	15.80	13.30	16.70
		St. Dev.	0.28	0.42	0.14
		Coeff. Var.	1.79	3.19	0.85
Gorilla	16344	Mean	14.30	12.80	15.15
		St. Dev.	0.14	0.57	0.07
		Coeff. Var.	0.99	4.42	0.47
Macaca	240704	Mean	6.82	5.31	8.09
		St. Dev.	0.21	0.04	0.01
		Coeff. Var.	3.11	0.80	0.17
Macaca	241160	Mean	7.75	6.75	9.14
		St. Dev.	0.10	0.11	0.01
		Coeff. Var.	1.28	1.68	0.15
Macaca	35489	Mean	8.11	6.28	9.55
		St. Dev.	0.19	0.23	0.11
		Coeff. Var.	2.36	3.60	1.18
Macaca	353187	Mean	7.76	6.21	9.28
		St. Dev.	0.09	0.00	0.05
		Coeff. Var.	1.19	0.00	0.53
Homo	VL/3045	Mean	11.05	8.00	10.50
		St. Dev.	0.07	0.28	0.42
		Coeff. Var.	0.64	3.54	4.04

Homo	VL/3105	Mean	9.55	7.25	9.05
		St. Dev.	0.07	0.07	0.07
		Coeff. Var.	0.74	0.98	0.78
Homo	99.1/1719	Mean	10.95	8.20	10.75
		St. Dev.	0.07	0.14	0.21
		Coeff. Var.	0.65	1.72	1.97
Homo	99.1/1717	Mean	11.35	8.25	10.65
		St. Dev.	0.07	0.21	0.07
		Coeff. Var.	0.62	2.57	0.66
Australo	MLD 6	Mean	12.30	9.63	13.85
		St. Dev.	0.14	0.11	0.06
		Coeff. Var.	1.15	1.10	0.46
Australo	MLD 9	Mean	12.25	11.10	13.15
		St. Dev.	0.07	0.00	0.07
		Coeff. Var.	0.58	0.00	0.54
Australo	MLD 11/30	Mean		11.05	
		St. Dev.		0.07	
		Coeff. Var.		0.64	

Genus	Spec No.	Value	MD_up_M2C	MD_up_M3	MD_up_M3C
Pan	176228	Mean	8.86	10.97	7.08
		St. Dev.	0.45	0.03	0.30
		Coeff. Var.	5.03	0.26	4.19
Pan	176227	Mean	8.09	10.74	7.15
		St. Dev.	0.42	0.18	0.01
		Coeff. Var.	5.16	1.71	0.10
Pan	176238	Mean	7.88	10.16	7.59
		St. Dev.	0.19	0.23	0.02
		Coeff. Var.	2.42	2.23	0.28
Pan	176241	Mean	7.52	9.47	7.55
		St. Dev.	0.11	0.20	0.24
		Coeff. Var.	1.50	2.09	3.18
Gorilla	545032	Mean	13.76	18.74	14.25
		St. Dev.	0.34	0.16	0.07
		Coeff. Var.	2.47	0.87	0.50
Gorilla	545034	Mean	13.67	15.35	12.92
		St. Dev.	0.33	0.02	0.05
		Coeff. Var.	2.38	0.14	0.38
Gorilla	545036	Mean	13.32	16.82	12.56
		St. Dev.	0.08	0.18	0.23
		Coeff. Var.	0.58	1.05	1.86
Gorilla	18399	Mean	12.75	15.15	12.45
		St. Dev.	0.35	0.21	0.49
		Coeff. Var.	2.77	1.40	3.98
Gorilla	27551	Mean	14.55	17.05	13.30
		St. Dev.	0.21	0.78	0.14
		Coeff. Var.	1.46	4.56	1.06
Gorilla	16344	Mean	13.30	14.95	12.15
		St. Dev.	0.28	0.35	0.07
		Coeff. Var.	2.13	2.36	0.58
Macaca	240704	Mean	7.12		
		St. Dev.	0.18		
		Coeff. Var.	2.48		
Macaca	241160	Mean	7.84	8.65	7.94
		St. Dev.	0.03	0.12	0.04
		Coeff. Var.	0.36	1.39	0.53
Macaca	35489	Mean	8.19	8.33	7.40
		St. Dev.	0.13	0.35	0.18
		Coeff. Var.	1.64	4.16	2.39
Macaca	353187	Mean	7.95	9.17	8.04
		St. Dev.	0.19	0.15	0.21
		Coeff. Var.	2.40	1.62	2.55
Homo	VL/3045	Mean	9.15	8.60	7.10
		St. Dev.	0.07	0.14	0.00
		Coeff. Var.	0.77	1.64	0.00

Homo	VL/3105	Mean	6.95	7.10	5.15
		St. Dev.	0.07	0.14	0.07
		Coeff. Var.	1.02	1.99	1.37
Homo	99.1/1719	Mean	8.30	8.65	6.60
		St. Dev.	0.14	0.07	0.14
		Coeff. Var.	1.70	0.82	2.14
Homo	99.1/1717	Mean	8.00	8.40	6.35
		St. Dev.	0.42	0.14	0.07
		Coeff. Var.	5.30	1.68	1.11
Australo	MLD 6	Mean	11.23		
		St. Dev.	0.04		
		Coeff. Var.	0.31		
Australo	MLD 9	Mean	12.78		
		St. Dev.	0.04		
		Coeff. Var.	0.28		
Australo	MLD 12	Mean		12.90	12.10
		St. Dev.		0.14	0.14
		Coeff. Var.		1.10	1.17
Australo	MLD 28	Mean		12.44	12.30
		St. Dev.		0.23	0.28
		Coeff. Var.		1.82	2.30
Australo	MLD 41	Mean		11.40	
		St. Dev.		0.28	
		Coeff. Var.		2.48	
Australo	MLD 44	Mean		13.79	12.18
		St. Dev.		0.12	0.25
		Coeff. Var.		0.87	2.09

Genus	Spec No.	Value	BL_up_I1	BL_up_I1 C	BL_up_I2	BL_up_I2C
Pan	176228	Mean	9.57	9.05	8.39	7.76
		St. Dev.	0.14	0.31	0.03	0.06
		Coeff. Var.	1.48	3.44	0.34	0.73
Pan	176227	Mean	9.56	9.02	8.66	8.06
		St. Dev.	0.16	0.14	0.22	0.16
		Coeff. Var.	1.70	1.57	2.53	2.02
Pan	176238	Mean				
		St. Dev.				
		Coeff. Var.				
Pan	176241	Mean	9.51	9.22	8.78	8.31
		St. Dev.	0.09	0.15	0.07	0.26
		Coeff. Var.	0.97	1.61	0.81	3.15
Gorilla	545032	Mean	12.42	11.91	10.94	10.62
		St. Dev.	0.06	0.02	0.03	0.06
		Coeff. Var.	0.51	0.18	0.26	0.60
Gorilla	545034	Mean	11.25	10.73	11.44	10.93
		St. Dev.	0.07	0.04	0.15	0.01
		Coeff. Var.	0.63	0.40	1.30	0.13
Gorilla	545036	Mean			12.60	11.95
		St. Dev.			0.30	0.08
		Coeff. Var.			2.36	0.65
Gorilla	18399	Mean	10.15	9.75	8.65	8.55
		St. Dev.	0.07	0.07	0.07	0.07
		Coeff. Var.	0.70	0.73	0.82	0.83
Gorilla	27551	Mean	10.45	9.90	10.45	9.85
		St. Dev.	0.07	0.14	0.07	0.07
		Coeff. Var.	0.68	1.43	0.68	0.72
Gorilla	16344	Mean	10.25	9.90		9.10
		St. Dev.	0.07	0.00		0.14
		Coeff. Var.	0.69	0.00		1.55
Macaca	240704	Mean	5.91	5.81	4.84	4.83
		St. Dev.	0.08	0.18	0.08	0.04
		Coeff. Var.	1.32	3.16	1.75	0.73
Macaca	241160	Mean	6.25	5.90	5.57	5.07
		St. Dev.	0.03	0.28	0.05	0.10
		Coeff. Var.	0.45	4.68	0.89	1.95
Macaca	35489	Mean	6.64	6.26	5.46	5.12
		St. Dev.	0.35	0.05	0.07	0.28
		Coeff. Var.	5.22	0.79	1.30	5.52
Macaca	353187	Mean	5.72	5.36	5.11	4.77
		St. Dev.	0.10	0.06	0.00	0.14
		Coeff. Var.	1.73	1.06	0.00	2.96
Homo	VL/3045	Mean	7.95	7.20	7.65	7.25
		St. Dev.	0.07	0.42	0.07	0.07
		Coeff. Var.	0.89	5.89	0.92	0.98

Homo	VL/3105	Mean	6.75	6.40	5.45	5.40
		St. Dev.	0.07	0.42	0.07	0.00
		Coeff. Var.	1.05	6.63	1.30	0.00
Homo	99.1/1719	Mean				
		St. Dev.				
		Coeff. Var.				
Homo	99.1/1717	Mean			6.90	6.15
		St. Dev.			0.14	0.35
		Coeff. Var.			2.05	5.75
Australo	MLD 11/30	Mean			7.03	6.96
		St. Dev.			0.10	0.06
		Coeff. Var.			1.41	0.92
Australo	MLD 12	Mean				
		St. Dev.				
		Coeff. Var.				
Australo	MLD 23	Mean			6.65	6.60
		St. Dev.			0.07	0.14
		Coeff. Var.			1.06	2.14

Genus	Spec No.	Value	BL_up_C	BL_up_CC	BL_up_P3
Pan	176228	Mean	11.93	12.06	11.04
		St. Dev.	0.15	0.25	0.18
		Coeff. Var.	1.25	2.05	1.67
Pan	176227	Mean	9.64	9.02	9.61
		St. Dev.	0.11	0.47	0.11
		Coeff. Var.	1.10	5.26	1.10
Pan	176238	Mean			10.33
		St. Dev.			0.15
		Coeff. Var.			1.44
Pan	176241	Mean	8.87	8.41	9.53
		St. Dev.	0.36	0.04	0.16
		Coeff. Var.	4.07	0.42	1.63
Gorilla	545032	Mean	17.06	16.87	17.57
		St. Dev.	0.21	0.30	0.13
		Coeff. Var.	1.24	1.80	0.76
Gorilla	545034	Mean	17.60	17.36	15.97
		St. Dev.	0.09	0.08	0.04
		Coeff. Var.	0.52	0.49	0.27
Gorilla	545036	Mean	18.93	18.87	17.20
		St. Dev.	0.02	0.11	0.13
		Coeff. Var.	0.11	0.60	0.74
Gorilla	18399	Mean	14.95	14.85	13.90
		St. Dev.	0.07	0.07	0.28
		Coeff. Var.	0.47	0.48	2.03
Gorilla	27551	Mean	15.50	15.30	16.35
		St. Dev.	0.14	0.42	0.07
		Coeff. Var.	0.91	2.77	0.43
Gorilla	16344	Mean		16.95	15.95
		St. Dev.		0.07	0.49
		Coeff. Var.		0.42	3.10
Macaca	240704	Mean	5.32	5.21	5.89
		St. Dev.	0.01	0.22	0.06
		Coeff. Var.	0.13	4.21	1.08
Macaca	241160	Mean	6.02	5.69	7.12
		St. Dev.	0.09	0.13	0.01
		Coeff. Var.	1.53	2.36	0.10
Macaca	35489	Mean	6.36		6.91
		St. Dev.	0.65		0.06
		Coeff. Var.	10.23		0.82
Macaca	353187	Mean	5.55	5.56	6.69
		St. Dev.	0.08	0.12	0.04
		Coeff. Var.	1.40	2.16	0.53
Homo	VL/3045	Mean	9.80	9.55	10.00
		St. Dev.	0.14	0.21	0.00
		Coeff. Var.	1.44	2.22	0.00

Homo	VL/3105	Mean	7.55	7.15	8.50
		St. Dev.	0.07	0.07	0.00
		Coeff. Var.	0.94	0.99	0.00
Homo	99.1/1719	Mean	8.60	8.15	10.70
		St. Dev.	0.00	0.07	0.00
		Coeff. Var.	0.00	0.87	0.00
Homo	99.1/1717	Mean	9.10	8.05	10.05
		St. Dev.	0.14	0.07	0.07
		Coeff. Var.	1.55	0.88	0.70
Australo	MLD 11/30	Mean	10.02	9.25	11.61
		St. Dev.	0.17	0.07	0.29
		Coeff. Var.	1.69	0.76	2.50
Australo	MLD 23	Mean			11.87
		St. Dev.			0.09
		Coeff. Var.			0.77

Genus	Spec No.	Value	BL_up_P3C	BL_up_P4	BL_up_P4C
Pan	176228	Mean	10.51	9.94	9.35
		St. Dev.	0.05	0.12	0.42
		Coeff. Var.	0.47	1.21	4.54
Pan	176227	Mean	9.43	9.76	9.10
		St. Dev.	0.06	0.01	0.23
		Coeff. Var.	0.68	0.07	2.57
Pan	176238	Mean	9.42	10.44	9.70
		St. Dev.	0.22	0.13	0.16
		Coeff. Var.	2.33	1.22	1.60
Pan	176241	Mean	9.27	9.75	9.39
		St. Dev.	0.03	0.08	0.13
		Coeff. Var.	0.31	0.80	1.36
Gorilla	545032	Mean	16.54	17.52	16.18
		St. Dev.	0.10	0.13	0.06
		Coeff. Var.	0.60	0.73	0.35
Gorilla	545034	Mean	14.80	15.59	14.21
		St. Dev.	0.25	0.09	0.01
		Coeff. Var.	1.67	0.59	0.05
Gorilla	545036	Mean	16.16	17.54	16.35
		St. Dev.	0.08	0.12	0.18
		Coeff. Var.	0.48	0.69	1.12
Gorilla	18399	Mean	13.50	14.45	13.75
		St. Dev.	0.00	0.07	0.07
		Coeff. Var.	0.00	0.49	0.51
Gorilla	27551	Mean	14.80	17.50	16.90
		St. Dev.	0.28	0.00	0.00
		Coeff. Var.	1.91	0.00	0.00
Gorilla	16344	Mean	15.10	15.80	15.10
		St. Dev.	0.28	0.14	0.14
		Coeff. Var.	1.87	0.90	0.94
Macaca	240704	Mean	5.73	6.47	6.32
		St. Dev.	0.10	0.01	0.10
		Coeff. Var.	1.73	0.22	1.57
Macaca	241160	Mean	6.49	7.34	7.07
		St. Dev.	0.13	0.06	0.05
		Coeff. Var.	2.07	0.77	0.70
Macaca	35489	Mean	6.49	7.67	7.53
		St. Dev.	0.06	0.11	0.00
		Coeff. Var.	0.87	1.48	0.00
Macaca	353187	Mean	6.56	7.31	7.08
		St. Dev.	0.06	0.05	0.04
		Coeff. Var.	0.86	0.68	0.60
Homo	VL/3045	Mean	9.55	9.95	9.30
		St. Dev.	0.07	0.07	0.14
		Coeff. Var.	0.74	0.71	1.52

Homo	VL/3105	Mean	7.75	8.35	7.95
		St. Dev.	0.35	0.07	0.07
		Coeff. Var.	4.56	0.85	0.89
Homo	99.1/1719	Mean	9.60	10.60	9.80
		St. Dev.	0.14	0.00	0.14
		Coeff. Var.	1.47	0.00	1.44
Homo	99.1/1717	Mean	8.95	10.25	9.40
		St. Dev.	0.07	0.07	0.00
		Coeff. Var.	0.79	0.69	0.00
Australo	MLD 6	Mean		12.43	11.55
		St. Dev.		0.11	0.21
		Coeff. Var.		0.85	1.84
Australo	MLD 9	Mean	13.13	13.05	12.98
		St. Dev.	0.11	0.07	0.39
		Coeff. Var.	0.81	0.54	3.00
Australo	MLD 23	Mean	11.05		
		St. Dev.	0.07		
		Coeff. Var.	0.64		

Genus	Spec No.	Value	BL_up_M1	BL_up_M1C	BLup M2
Pan	176228	Mean	11.66	10.79	11.23
		St. Dev.	0.22	0.12	0.15
		Coeff. Var.	1.88	1.11	1.32
Pan	176227	Mean	11.21	10.74	11.78
		St. Dev.	0.11	0.14	0.02
		Coeff. Var.	0.95	1.32	0.18
Pan	176238	Mean	11.58	11.19	11.28
		St. Dev.	0.19	0.13	0.10
		Coeff. Var.	1.65	1.20	0.88
Pan	176241	Mean	11.24	10.59	11.00
		St. Dev.	0.00	0.04	0.21
		Coeff. Var.	0.00	0.40	1.93
Gorilla	545032	Mean	16.86	16.56	19.00
		St. Dev.	0.20	0.04	0.18
		Coeff. Var.	1.17	0.26	0.97
Gorilla	545034	Mean	15.64	15.40	17.68
		St. Dev.	0.07	0.08	0.07
		Coeff. Var.	0.45	0.51	0.40
Gorilla	545036	Mean	17.27	16.68	19.12
		St. Dev.	0.08	0.02	0.30
		Coeff. Var.	0.45	0.13	1.55
Gorilla	18399	Mean	14.90	14.25	16.10
		St. Dev.	0.14	0.07	0.28
		Coeff. Var.	0.95	0.50	1.76
Gorilla	27551	Mean	17.40	16.80	18.45
		St. Dev.	0.00	0.00	0.35
		Coeff. Var.	0.00	0.00	1.92
Gorilla	16344	Mean	16.25	16.05	16.90
		St. Dev.	0.07	0.07	0.14
		Coeff. Var.	0.44	0.44	0.84
Macaca	240704	Mean	6.47	6.39	7.87
		St. Dev.	0.04	0.15	0.01
		Coeff. Var.	0.66	2.33	0.09
Macaca	241160	Mean	7.99	7.86	9.04
		St. Dev.	0.01	0.03	0.03
		Coeff. Var.	0.09	0.36	0.31
Macaca	35489	Mean	8.20	8.18	9.66
		St. Dev.	0.00	0.01	0.16
		Coeff. Var.	0.00	0.17	1.61
Macaca	353187	Mean	7.75	7.55	9.58
		St. Dev.	0.11	0.01	0.06
		Coeff. Var.	1.46	0.09	0.59
Homo	VL/3045	Mean	11.65	11.15	12.65
		St. Dev.	0.07	0.07	0.07
		Coeff. Var.	0.61	0.63	0.56

Homo	VL/3105	Mean	10.85	10.45	10.45
		St. Dev.	0.21	0.07	0.07
		Coeff. Var.	1.96	0.68	0.68
Homo	99.1/1719	Mean	12.10	11.60	12.60
		St. Dev.	0.00	0.00	0.00
		Coeff. Var.	0.00	0.00	0.00
Homo	99.1/1717	Mean	12.85		12.65
		St. Dev.	0.07		0.07
		Coeff. Var.	0.55		0.56
Australo	MLD 6	Mean	12.79	12.18	14.35
		St. Dev.	0.13	0.18	0.21
		Coeff. Var.	1.00	1.45	1.48
Australo	MLD 9	Mean		13.13	
		St. Dev.		0.25	
		Coeff. Var.		1.89	
Australo	MLD 28	Mean			15.75
		St. Dev.			0.07
		Coeff. Var.			0.45

Genus	Spec No.	Value	BL_up_M2C	BL_up_M3	BL_up_M3C
Pan	176228	Mean	10.82	10.97	10.53
		St. Dev.	0.37	0.08	0.03
		Coeff. Var.	3.40	0.71	0.27
Pan	176227	Mean	11.25	11.18	9.92
		St. Dev.	0.08	0.04	0.06
		Coeff. Var.	0.75	0.38	0.57
Pan	176238	Mean	10.62	10.89	10.03
		St. Dev.	0.04	0.01	0.07
		Coeff. Var.	0.40	0.06	0.70
Pan	176241	Mean	10.35	10.48	9.89
		St. Dev.	0.16	0.17	0.18
		Coeff. Var.	1.57	1.62	1.86
Gorilla	545032	Mean	17.86	18.09	17.53
		St. Dev.	0.14	0.17	0.04
		Coeff. Var.	0.79	0.94	0.20
Gorilla	545034	Mean	16.99	16.44	14.90
		St. Dev.	0.09	0.16	0.18
		Coeff. Var.	0.54	0.95	1.19
Gorilla	545036	Mean	18.34	17.90	17.14
		St. Dev.	0.04	0.21	0.01
		Coeff. Var.	0.23	1.15	0.08
Gorilla	18399	Mean	15.05	15.30	13.90
		St. Dev.	0.21	0.00	0.14
		Coeff. Var.	1.41	0.00	1.02
Gorilla	27551	Mean	17.70	18.10	16.85
		St. Dev.	0.00	0.00	0.07
		Coeff. Var.	0.00	0.00	0.42
Gorilla	16344	Mean	16.05	16.50	15.75
		St. Dev.	0.07	0.00	0.07
		Coeff. Var.	0.44	0.00	0.45
Macaca	240704	Mean	7.77		
		St. Dev.	0.00		
		Coeff. Var.	0.00		
Macaca	241160	Mean	8.93	8.62	8.51
		St. Dev.	0.00	0.04	0.02
		Coeff. Var.	0.00	0.49	0.25
Macaca	35489	Mean	9.66	9.10	9.14
		St. Dev.	0.06	0.14	0.07
		Coeff. Var.	0.66	1.55	0.77
Macaca	353187	Mean	9.39	8.83	8.80
		St. Dev.	0.17	0.02	0.01
		Coeff. Var.	1.81	0.24	0.16
Homo	VL/3045	Mean	12.30	11.20	11.25
		St. Dev.	0.14	0.14	0.35
		Coeff. Var.	1.15	1.26	3.14

Homo	VL/3105	Mean	10.10	8.95	8.60
		St. Dev.	0.00	0.07	0.00
		Coeff. Var.	0.00	0.79	0.00
Homo	99.1/1719	Mean	12.20	13.35	12.90
		St. Dev.	0.00	0.07	0.00
		Coeff. Var.	0.00	0.53	0.00
Homo	99.1/1717	Mean	12.15	12.90	11.80
		St. Dev.	0.07	0.28	0.14
		Coeff. Var.	0.58	2.19	1.20
Australo	MLD 6	Mean	13.68		
		St. Dev.	0.11		
		Coeff. Var.	0.78		
Australo	MLD 9	Mean	16.55		
		St. Dev.	0.07		
		Coeff. Var.	0.43		
Australo	MLD 12	Mean		15.08	15.00
		St. Dev.		0.03	0.00
		Coeff. Var.		0.19	0.00
Australo	MLD 28	Mean	15.45	15.47	14.95
		St. Dev.	0.07	0.05	0.07
		Coeff. Var.	0.46	0.32	0.47

Lower Dentition Measurement Repeatability

Museum	Spec No.	Genus	Value	MD_ low_I1	MD_ low_I1C	MD_low_I2
FMNH	16344	Gorilla	Mean	7.1	5.9	7.3
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	2.0	1.2	1.0
FMNH	18397	Gorilla	Mean	9.0	5.4	10.2
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	0.8	2.6	0.0
FMNH	18402	Gorilla	Mean		6.1	10.5
			St. Dev		0.1	0.3
			Coeff. Var.		1.2	2.7
NMNH	220324	Gorilla	Mean	7.9	5.9	8.5
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	0.9	1.2	0.8
NMNH	545034	Gorilla	Mean	7.7	5.6	8.8
			St. Dev	0.0	0.2	0.1
			Coeff. Var.	0.3	2.9	1.5
NMNH	545036	Gorilla	Mean	8.4	6.0	9.7
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.1	1.4	1.1
AMNH	VL/3036	Homo	Mean	5.1	3.2	6.2
			St. Dev	0.0	0.3	0.0
			Coeff. Var.	0.0	8.8	0.0
AMNH	VL/3039	Homo	Mean	6.0	4.6	6.6
			St. Dev	0.1	0.0	0.2
			Coeff. Var.	1.2	0.0	3.2
AMNH	VL/3045	Homo	Mean	6.0	4.4	6.2
			St. Dev	0.1	0.1	0.2
			Coeff. Var.	1.2	3.2	3.4
NMNH	35489	Macaca	Mean	4.3	3.4	4.6
			St. Dev	0.1	0.0	0.0
			Coeff. Var.	3.1	0.6	0.6
NMNH	240704	Macaca	Mean	4.2	3.1	3.9
			St. Dev	0.1	0.1	0.2
			Coeff. Var.	2.0	2.9	4.4
NMNH	241160	Macaca	Mean	4.4	3.2	4.3
			St. Dev	0.0	0.0	0.1
			Coeff. Var.	0.8	0.9	2.5
NMNH	353187	Macaca	Mean	4.3	3.2	3.9
			St. Dev	0.1	0.0	0.1

			Coeff. Var.	2.3	1.1	2.2
NMNH	176228	Pan	Mean	7.8	5.4	
			St. Dev	0.0	0.1	
			Coeff. Var.	0.3	1.3	
NMNH	220327	Pan	Mean	8.2	5.2	8.9
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.2	1.9	1.4
Wits	MLD 18	Australo	Mean	4.7	4.2	6.0
			St. Dev	0.3	0.0	0.1
			Coeff. Var.	5.7	0.8	2.1
Wits	MLD 18	Australo	Mean	4.4	4.2	5.6
			St. Dev	0.0	0.1	0.5
			Coeff. Var.	1.0	3.4	8.1
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	MD_low_I2C	MD_low_C	MD_low_CC
FMNH	16344	Gorilla	Mean	6.5	15.8	15.7
			St. Dev	0.0	0.3	0.4
			Coeff. Var.	0.0	1.8	2.3
FMNH	18397	Gorilla	Mean	7.0	13.5	12.2
			St. Dev	0.0	0.4	0.9
			Coeff. Var.	0.0	3.1	7.6
FMNH	18402	Gorilla	Mean	7.4	16.4	16.1
			St. Dev	0.3	0.1	0.1
			Coeff. Var.	3.8	0.4	0.9
NMNH	220324	Gorilla	Mean	6.8	13.1	12.6
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	1.0	1.1	1.1
NMNH	545034	Gorilla	Mean	6.6	15.3	14.8
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.1	0.7	0.7
NMNH	545036	Gorilla	Mean	7.4	18.1	17.1
			St. Dev	0.0	0.3	0.1
			Coeff. Var.	0.7	1.5	0.3
AMNH	VL/3036	Homo	Mean	4.3	6.1	5.4
			St. Dev	0.3	0.1	0.1
			Coeff. Var.	6.6	1.2	1.3
AMNH	VL/3039	Homo	Mean	4.6	7.8	5.9
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	3.1	1.8	1.2
AMNH	VL/3045	Homo	Mean	4.2	7.6	6.5
			St. Dev	0.2	0.0	0.1
			Coeff. Var.	5.1	0.0	1.1
NMNH	35489	Macaca	Mean	3.2	10.3	
			St. Dev	0.2		
			Coeff. Var.	6.0		
NMNH	240704	Macaca	Mean	2.3	4.7	3.4
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	5.8	3.0	3.5
NMNH	241160	Macaca	Mean	2.5	5.0	4.8
			St. Dev	0.3	0.1	0.2
			Coeff. Var.	10.7	1.6	4.2
NMNH	353187	Macaca	Mean	2.9	5.8	5.2
			St. Dev	0.1	0.1	0.3
			Coeff. Var.	2.7	2.1	5.7
NMNH	176228	Pan	Mean	5.4	11.7	11.6

			St. Dev	0.1	0.1	0.1
			Coeff. Var.	1.4	1.0	0.7
NMNH	220327	Pan	Mean	5.5	12.4	11.7
			St. Dev	0.0	0.2	0.0
			Coeff. Var.	0.8	1.4	0.3
Wits	MLD 18	Australo	Mean	4.8	8.7	6.9
			St. Dev	0.1	0.0	0.2
			Coeff. Var.	2.2	0.6	3.6
Wits	MLD 18	Australo	Mean	4.9		6.9
			St. Dev	0.2		0.1
			Coeff. Var.	4.4		1.5
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	MD_low_P3	MD_low_P3C	MD_low_P4
FMNH	16344	Gorilla	Mean	16.3	15.1	11.3
			St. Dev	0.5	0.6	0.1
			Coeff. Var.	3.0	4.2	0.6
FMNH	18397	Gorilla	Mean	15.0	12.2	13.7
			St. Dev	0.3	0.1	0.0
			Coeff. Var.	1.9	1.2	0.0
FMNH	18402	Gorilla	Mean	18.2	16.6	12.4
			St. Dev	0.1	0.4	0.2
			Coeff. Var.	0.4	2.1	1.7
NMNH	220324	Gorilla	Mean	16.6	15.3	11.4
			St. Dev	0.3	0.5	0.0
			Coeff. Var.	1.7	3.2	0.0
NMNH	545034	Gorilla	Mean	15.6	14.4	12.3
			St. Dev	0.0	0.1	0.3
			Coeff. Var.	0.3	0.5	2.2
NMNH	545036	Gorilla	Mean	17.2	15.9	14.3
			St. Dev	0.3	0.1	0.1
			Coeff. Var.	1.6	0.5	0.7
AMNH	VL/3036	Homo	Mean	7.0	5.6	7.4
			St. Dev	0.0	0.2	0.2
			Coeff. Var.	0.0	3.8	2.9
AMNH	VL/3039	Homo	Mean	8.8	6.0	8.2
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	1.6	2.4	0.0
AMNH	VL/3045	Homo	Mean	7.3	5.4	7.6
			St. Dev	0.3	0.5	0.0
			Coeff. Var.	3.9	9.3	0.0
NMNH	35489	Macaca	Mean	10.2	9.3	6.4
			St. Dev	0.6	0.1	0.0
			Coeff. Var.	5.9	1.4	0.8
NMNH	240704	Macaca	Mean	6.0	5.2	5.2
			St. Dev	0.1	0.2	0.3
			Coeff. Var.	1.6	3.6	5.5
NMNH	241160	Macaca	Mean	8.1	6.6	5.9
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	1.5	2.1	0.7
NMNH	353187	Macaca	Mean	8.2	7.4	6.3
			St. Dev	0.0	0.3	0.1
			Coeff. Var.	0.0	3.9	1.9
NMNH	176228	Pan	Mean	10.4	8.3	7.1

			St. Dev	0.1	0.1	0.1
			Coeff. Var.	0.7	0.7	1.9
NMNH	220327	Pan	Mean	8.6	6.8	7.7
			St. Dev	0.1	0.2	0.1
			Coeff. Var.	0.9	3.4	1.0
Wits	MLD 18	Australo	Mean		6.7	8.4
			St. Dev		0.1	0.1
			Coeff. Var.		2.1	1.4
Wits	MLD 18	Australo	Mean			8.9
			St. Dev			0.0
			Coeff. Var.			0.5
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean	9.6	8.8	
			St. Dev	0.2	0.4	
			Coeff. Var.	1.9	4.0	
Wits	MLD 2	Australo	Mean	11.1	8.7	
			St. Dev	0.2	0.1	
			Coeff. Var.	1.7	1.6	
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	MD_low_P4C	MD_low_M1	MD_low_M1C
FMNH	16344	Gorilla	Mean	9.6	14.9	13.8
			St. Dev	0.6	0.1	0.5
			Coeff. Var.	5.9	0.9	3.6
FMNH	18397	Gorilla	Mean	11.9	17.5	14.4
			St. Dev	0.1	0.1	0.3
			Coeff. Var.	0.6	0.4	2.0
FMNH	18402	Gorilla	Mean	10.5	16.4	14.6
			St. Dev	0.0	0.4	0.1
			Coeff. Var.	0.0	2.2	1.0
NMNH	220324	Gorilla	Mean	10.3	15.3	13.9
			St. Dev	0.0	0.1	0.6
			Coeff. Var.	0.0	0.9	4.6
NMNH	545034	Gorilla	Mean	10.1	15.7	13.3
			St. Dev	0.1	0.1	0.3
			Coeff. Var.	0.6	0.9	2.4
NMNH	545036	Gorilla	Mean	9.7	18.1	15.0
			St. Dev	0.5	0.2	0.1
			Coeff. Var.	5.0	1.4	0.7
AMNH	VL/3036	Homo	Mean	5.6	12.2	9.3
			St. Dev	0.2	0.1	0.2
			Coeff. Var.	3.8	0.6	2.3
AMNH	VL/3039	Homo	Mean	6.2	11.8	9.5
			St. Dev	0.2	0.1	0.1
			Coeff. Var.	3.4	0.6	0.7
AMNH	VL/3045	Homo	Mean	5.6	11.7	9.6
			St. Dev	0.0	0.4	0.0
			Coeff. Var.	0.0	3.0	0.0
NMNH	35489	Macaca	Mean	5.6	7.6	6.2
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	1.3	1.9	0.1
NMNH	240704	Macaca	Mean	4.2	6.6	5.3
			St. Dev	0.1	0.0	0.2
			Coeff. Var.	1.3	0.3	3.0
NMNH	241160	Macaca	Mean	5.2	7.4	6.3
			St. Dev	0.1	0.2	0.1
			Coeff. Var.	1.6	2.6	1.1
NMNH	353187	Macaca	Mean	5.8	7.6	5.9
			St. Dev	0.0	0.2	0.4
			Coeff. Var.	0.2	2.3	6.4
NMNH	176228	Pan	Mean	6.0	11.3	9.1

			St. Dev	0.0	0.1	0.0
			Coeff. Var.	0.4	1.0	0.5
NMNH	220327	Pan	Mean	6.5	11.4	8.9
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.1	0.9	0.8
Wits	MLD 18	Australo	Mean	7.7	11.7	12.0
			St. Dev	0.3	0.2	0.3
			Coeff. Var.	3.7	1.9	2.6
Wits	MLD 18	Australo	Mean	8.5		
			St. Dev	0.1		
			Coeff. Var.	1.3		
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean		15.1	14.2
			St. Dev		0.1	0.4
			Coeff. Var.		0.4	2.7
Wits	MLD 2	Australo	Mean		14.7	14.0
			St. Dev		0.0	0.0
			Coeff. Var.		0.3	0.3
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	MD_low_M2	MD_low_M2C	MD_low_M3
FMNH	16344	Gorilla	Mean	16.5	15.3	17.4
			St. Dev	0.3	0.3	0.5
			Coeff. Var.	1.7	1.8	2.9
FMNH	18397	Gorilla	Mean	19.0	17.4	17.7
			St. Dev	0.1	0.4	0.4
			Coeff. Var.	0.7	2.4	2.0
FMNH	18402	Gorilla	Mean	19.0	17.0	19.3
			St. Dev	0.4	0.3	0.1
			Coeff. Var.	1.9	1.7	0.4
NMNH	220324	Gorilla	Mean	16.8	15.1	17.2
			St. Dev	0.3	0.1	0.2
			Coeff. Var.	1.7	0.9	1.2
NMNH	545034	Gorilla	Mean	18.1	15.6	18.1
			St. Dev	0.0	0.3	0.1
			Coeff. Var.	0.0	1.7	0.4
NMNH	545036	Gorilla	Mean	19.9	16.8	18.4
			St. Dev	0.1	0.0	0.2
			Coeff. Var.	0.3	0.0	1.3
AMNH	VL/3036	Homo	Mean	11.4	9.2	
			St. Dev	0.1	0.2	
			Coeff. Var.	0.6	2.3	
AMNH	VL/3039	Homo	Mean	12.2	10.9	
			St. Dev	0.0	0.1	
			Coeff. Var.	0.0	1.3	
AMNH	VL/3045	Homo	Mean	11.0	10.1	11.5
			St. Dev	0.4	0.1	0.1
			Coeff. Var.	3.2	1.4	0.6
NMNH	35489	Macaca	Mean	9.1	7.9	11.7
			St. Dev	0.3	0.0	0.2
			Coeff. Var.	3.6	0.2	2.0
NMNH	240704	Macaca	Mean	8.0	6.9	9.7
			St. Dev	0.2	0.1	0.2
			Coeff. Var.	2.5	1.9	1.6
NMNH	241160	Macaca	Mean	9.1	7.5	10.6
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	0.7	0.4	0.7
NMNH	353187	Macaca	Mean	9.1	7.7	10.9
			St. Dev	0.0	0.0	0.1
			Coeff. Var.	0.5	0.1	0.7
NMNH	176228	Pan	Mean	12.0	9.3	11.6

			St. Dev	0.0	0.2	0.1
			Coeff. Var.	0.1	1.8	1.0
NMNH	220327	Pan	Mean	12.2	9.4	11.8
			St. Dev	0.3	0.2	0.0
			Coeff. Var.	2.3	2.3	0.2
Wits	MLD 18	Australo	Mean	14.1	13.5	13.9
			St. Dev	0.0	0.6	0.0
			Coeff. Var.	0.3	4.4	0.3
Wits	MLD 18	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 19	Australo	Mean			14.9
			St. Dev			0.0
			Coeff. Var.			0.1
Wits	MLD 2	Australo	Mean	16.5	15.0	
			St. Dev	0.3	0.1	
			Coeff. Var.	1.8	0.5	
Wits	MLD 2	Australo	Mean	16.8	15.2	
			St. Dev	0.2	0.1	
			Coeff. Var.	1.3	0.9	
Wits	MLD 4	Australo	Mean			14.4
			St. Dev			0.2
			Coeff. Var.			1.4

Museum	Spec No.	Genus	Value	MD_low_M3C	BL_low_I1	BL_low_I1C
FMNH	16344	Gorilla	Mean	16.4	9.0	8.6
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	0.9	0.8	0.0
FMNH	18397	Gorilla	Mean	16.5	8.5	7.6
			St. Dev	0.4	0.1	0.0
			Coeff. Var.	2.1	0.8	0.0
FMNH	18402	Gorilla	Mean	17.3	9.7	9.2
			St. Dev	0.2	0.0	0.1
			Coeff. Var.	1.2	0.0	0.8
NMNH	220324	Gorilla	Mean	15.7	8.2	8.1
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	0.5	0.0	0.9
NMNH	545034	Gorilla	Mean	15.7	9.6	9.3
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	0.8	0.6	0.2
NMNH	545036	Gorilla	Mean	16.9	11.0	10.8
			St. Dev	0.5	0.0	0.0
			Coeff. Var.	2.8	0.1	0.3
AMNH	VL/3036	Homo	Mean		5.4	5.2
			St. Dev		0.2	0.1
			Coeff. Var.		4.0	2.7
AMNH	VL/3039	Homo	Mean		6.8	6.4
			St. Dev		0.0	0.4
			Coeff. Var.		0.0	6.6
AMNH	VL/3045	Homo	Mean	10.4	6.4	6.2
			St. Dev	0.0	0.0	0.0
			Coeff. Var.	0.0	0.0	0.0
NMNH	35489	Macaca	Mean	11.2	5.7	5.3
			St. Dev	0.3	0.4	0.2
			Coeff. Var.	2.6	6.6	2.9
NMNH	240704	Macaca	Mean	8.6	5.3	5.2
			St. Dev	0.3	0.0	0.1
			Coeff. Var.	3.4	0.8	1.6
NMNH	241160	Macaca	Mean	9.6	5.5	5.4
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	0.7	0.0	1.0
NMNH	353187	Macaca	Mean	9.7	5.5	5.3
			St. Dev	0.1	0.0	0.0
			Coeff. Var.	1.1	0.3	0.3
NMNH	176228	Pan	Mean	8.9	8.6	7.8

			St. Dev	0.2	0.1	0.1
			Coeff. Var.	2.7	0.7	1.9
NMNH	220327	Pan	Mean	8.6	9.3	8.4
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	1.2	0.2	1.5
Wits	MLD 18	Australo	Mean	13.9	6.2	6.1
			St. Dev	0.5	0.1	0.1
			Coeff. Var.	3.6	1.7	1.2
Wits	MLD 18	Australo	Mean		6.2	6.3
			St. Dev		0.0	0.3
			Coeff. Var.		0.2	4.5
Wits	MLD 19	Australo	Mean	14.4		
			St. Dev	0.1		
			Coeff. Var.	1.0		
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	BL_low_I2	BL_low_I2C	BL_low_C
FMNH	16344	Gorilla	Mean	9.9	9.6	18.5
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	0.7	0.7	0.4
FMNH	18397	Gorilla	Mean	10.1	9.6	14.3
			St. Dev	0.0	0.1	0.2
			Coeff. Var.	0.0	0.7	1.5
FMNH	18402	Gorilla	Mean	58.3	10.2	19.6
			St. Dev	67.5	0.0	0.1
			Coeff. Var.	115.7	0.0	0.7
NMNH	220324	Gorilla	Mean	9.9	9.8	14.5
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	1.4	1.4	0.5
NMNH	545034	Gorilla	Mean	11.4	11.1	19.3
			St. Dev	0.0	0.0	0.0
			Coeff. Var.	0.2	0.4	0.1
NMNH	545036	Gorilla	Mean	13.3	13.2	18.8
			St. Dev	0.0	0.0	0.2
			Coeff. Var.	0.3	0.4	0.9
AMNH	VL/3036	Homo	Mean	5.4	5.3	7.4
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	2.6	0.0	1.0
AMNH	VL/3039	Homo	Mean	6.6	6.8	8.5
			St. Dev	0.4	0.5	0.1
			Coeff. Var.	5.4	7.3	0.8
AMNH	VL/3045	Homo	Mean	6.8	6.4	9.3
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	1.0	0.0	0.8
NMNH	35489	Macaca	Mean	5.5	4.8	9.9
			St. Dev	0.2	0.0	
			Coeff. Var.	3.1	0.9	
NMNH	240704	Macaca	Mean	4.6	4.3	4.7
			St. Dev	0.1	0.2	0.1
			Coeff. Var.	2.1	4.5	2.4
NMNH	241160	Macaca	Mean	5.2	5.0	6.3
			St. Dev	0.0	0.0	0.2
			Coeff. Var.	0.8	0.3	3.5
NMNH	353187	Macaca	Mean	4.8	4.4	5.6
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	2.8	1.8	0.8
NMNH	176228	Pan	Mean	8.9	8.4	12.7

			St. Dev	0.0	0.3	0.0
			Coeff. Var.	0.3	4.1	0.2
NMNH	220327	Pan	Mean	9.7	8.7	13.1
			St. Dev	0.0	0.0	0.0
			Coeff. Var.	0.4	0.1	0.1
Wits	MLD 18	Australo	Mean	7.9	7.6	9.3
			St. Dev	0.2	0.0	0.1
			Coeff. Var.	2.8	0.5	1.1
Wits	MLD 18	Australo	Mean	7.6	7.5	
			St. Dev	0.1	0.2	
			Coeff. Var.	1.0	2.4	
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	BL_low_CC	BL_low_P3	BL_low_P3C
FMNH	16344	Gorilla	Mean	18.5	13.7	12.8
			St. Dev	0.0	0.2	0.1
			Coeff. Var.	0.0	1.6	0.6
FMNH	18397	Gorilla	Mean	13.0	13.4	12.6
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	0.5	1.1	0.0
FMNH	18402	Gorilla	Mean	19.2	17.0	16.6
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.0	0.8	0.9
NMNH	220324	Gorilla	Mean	14.3	11.9	11.1
			St. Dev	0.0	0.2	0.3
			Coeff. Var.	0.0	1.8	2.5
NMNH	545034	Gorilla	Mean	19.2	14.0	11.7
			St. Dev	0.1	0.0	0.3
			Coeff. Var.	0.3	0.1	2.5
NMNH	545036	Gorilla	Mean	18.7	15.4	14.6
			St. Dev	0.0	0.4	0.1
			Coeff. Var.	0.1	2.9	0.8
AMNH	VL/3036	Homo	Mean	7.2	8.1	7.5
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	2.0	0.9	0.9
AMNH	VL/3039	Homo	Mean	8.2	9.3	8.5
			St. Dev	0.0	0.1	0.0
			Coeff. Var.	0.0	1.5	0.0
AMNH	VL/3045	Homo	Mean	8.9	8.4	8.1
			St. Dev	0.3	0.0	0.1
			Coeff. Var.	3.2	0.0	1.7
NMNH	35489	Macaca	Mean		7.1	6.2
			St. Dev		0.6	0.4
			Coeff. Var.		8.2	7.1
NMNH	240704	Macaca	Mean	4.3	4.0	3.8
			St. Dev	0.1	0.2	0.0
			Coeff. Var.	2.0	4.6	0.7
NMNH	241160	Macaca	Mean	5.8	5.5	5.0
			St. Dev	0.2	0.2	0.1
			Coeff. Var.	4.3	4.1	2.0
NMNH	353187	Macaca	Mean	5.2	5.3	5.0
			St. Dev	0.2	0.1	0.1
			Coeff. Var.	3.2	2.1	2.1
NMNH	176228	Pan	Mean	12.5	8.9	8.2

			St. Dev	0.1	0.2	0.3
			Coeff. Var.	0.9	2.2	3.7
NMNH	220327	Pan	Mean	12.6	10.0	9.2
			St. Dev	0.2	0.0	0.2
			Coeff. Var.	1.2	0.5	2.1
Wits	MLD 18	Australo	Mean	9.6	11.3	10.4
			St. Dev	0.4	0.2	0.4
			Coeff. Var.	4.1	1.4	3.4
Wits	MLD 18	Australo	Mean	9.3		
			St. Dev	0.2		
			Coeff. Var.	2.3		
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean		12.6	12.8
			St. Dev		0.2	0.1
			Coeff. Var.		1.7	1.1
Wits	MLD 2	Australo	Mean		12.7	12.5
			St. Dev		0.1	0.2
			Coeff. Var.		0.7	1.7
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	BL_low_P4	BL_low_P4C	BL_low_M1
FMNH	16344	Gorilla	Mean	13.5	13.3	13.9
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	0.5	0.5	1.0
FMNH	18397	Gorilla	Mean	13.0	10.3	14.6
			St. Dev	0.5	0.2	0.0
			Coeff. Var.	3.8	2.1	0.0
FMNH	18402	Gorilla	Mean	15.2	14.4	14.5
			St. Dev	0.3	0.1	0.0
			Coeff. Var.	1.9	0.5	0.0
NMNH	220324	Gorilla	Mean	12.9	12.1	13.3
			St. Dev	0.1	0.1	0.4
			Coeff. Var.	0.6	0.6	3.2
NMNH	545034	Gorilla	Mean	13.5	12.1	13.8
			St. Dev	0.1	0.3	0.0
			Coeff. Var.	0.6	2.7	0.4
NMNH	545036	Gorilla	Mean	14.4	13.5	15.1
			St. Dev	0.2	0.0	0.0
			Coeff. Var.	1.6	0.3	0.3
AMNH	VL/3036	Homo	Mean	8.2	7.5	10.9
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	1.7	1.9	0.7
AMNH	VL/3039	Homo	Mean	9.7	9.2	11.7
			St. Dev	0.1	0.3	0.1
			Coeff. Var.	0.7	3.1	0.6
AMNH	VL/3045	Homo	Mean	9.2	8.2	10.6
			St. Dev	0.0	0.4	0.2
			Coeff. Var.	0.0	5.2	2.0
NMNH	35489	Macaca	Mean	5.8	5.8	6.6
			St. Dev	0.1	0.9	0.2
			Coeff. Var.	1.2	14.9	2.4
NMNH	240704	Macaca	Mean	4.9	4.7	5.4
			St. Dev	0.1	0.1	0.0
			Coeff. Var.	2.0	2.7	0.1
NMNH	241160	Macaca	Mean	6.1	5.4	6.6
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.3	1.4	1.4
NMNH	353187	Macaca	Mean	5.5	4.7	6.4
			St. Dev	0.1	0.0	0.2
			Coeff. Var.	1.6	0.5	2.9
NMNH	176228	Pan	Mean	8.7	7.4	9.9

			St. Dev	0.0	0.1	0.0
			Coeff. Var.	0.5	1.5	0.3
NMNH	220327	Pan	Mean	9.2	8.6	9.8
			St. Dev	0.2	0.6	0.2
			Coeff. Var.	1.8	6.9	1.6
Wits	MLD 18	Australo	Mean	11.9	10.7	13.1
			St. Dev	0.2	0.0	0.1
			Coeff. Var.	1.4	0.3	0.6
Wits	MLD 18	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean			14.1
			St. Dev			0.1
			Coeff. Var.			0.9
Wits	MLD 2	Australo	Mean			13.8
			St. Dev			0.1
			Coeff. Var.			0.7
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	BL_low_M1C	BL_low_M2	BL_low_M2C
FMNH	16344	Gorilla	Mean	13.3	14.9	14.4
			St. Dev	0.0	0.1	0.0
			Coeff. Var.	0.0	0.9	0.0
FMNH	18397	Gorilla	Mean	13.3	15.2	14.3
			St. Dev	0.1	0.1	0.4
			Coeff. Var.	1.1	0.5	2.5
FMNH	18402	Gorilla	Mean	14.2	16.4	15.5
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	1.0	0.9	0.5
NMNH	220324	Gorilla	Mean	12.4	15.1	14.2
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.0	0.5	0.5
NMNH	545034	Gorilla	Mean	12.8	15.9	15.0
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	0.6	0.2	0.4
NMNH	545036	Gorilla	Mean	14.3	17.7	16.8
			St. Dev	0.3	0.0	0.1
			Coeff. Var.	1.9	0.1	0.5
AMNH	VL/3036	Homo	Mean	9.8	10.3	9.8
			St. Dev	0.1	0.0	0.1
			Coeff. Var.	0.7	0.0	1.4
AMNH	VL/3039	Homo	Mean	10.8	11.5	10.7
			St. Dev	0.1	0.1	0.1
			Coeff. Var.	0.7	0.6	1.3
AMNH	VL/3045	Homo	Mean	9.8	10.7	9.9
			St. Dev	0.2	0.2	0.0
			Coeff. Var.	2.2	2.0	0.0
NMNH	35489	Macaca	Mean	6.4	8.8	8.1
			St. Dev	0.2	0.3	0.1
			Coeff. Var.	2.5	3.4	0.9
NMNH	240704	Macaca	Mean	5.2	6.5	5.7
			St. Dev	0.0	0.1	0.1
			Coeff. Var.	0.8	1.0	1.6
NMNH	241160	Macaca	Mean	6.0	7.7	7.4
			St. Dev	0.1	0.2	0.1
			Coeff. Var.	1.5	2.1	1.1
NMNH	353187	Macaca	Mean	6.1	7.7	7.3
			St. Dev	0.0	0.0	0.4
			Coeff. Var.	0.6	0.4	4.9
NMNH	176228	Pan	Mean	9.3	10.5	9.7

			St. Dev	0.2	0.0	0.1
			Coeff. Var.	2.4	0.1	0.9
NMNH	220327	Pan	Mean	8.9	11.2	10.2
			St. Dev	0.0	0.0	0.1
			Coeff. Var.	0.5	0.2	1.5
Wits	MLD 18	Australo	Mean	12.5	14.7	14.0
			St. Dev	0.3	0.2	0.1
			Coeff. Var.	2.5	1.2	0.5
Wits	MLD 18	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 19	Australo	Mean			
			St. Dev			
			Coeff. Var.			
Wits	MLD 2	Australo	Mean	13.9	15.1	14.8
			St. Dev	0.1	0.2	0.1
			Coeff. Var.	0.5	1.3	0.7
Wits	MLD 2	Australo	Mean	13.8	15.0	14.3
			St. Dev	0.0	0.1	0.4
			Coeff. Var.	0.3	0.4	2.5
Wits	MLD 4	Australo	Mean			
			St. Dev			
			Coeff. Var.			

Museum	Spec No.	Genus	Value	BL_low_M3	BL_low_M3C
FMNH	16344	Gorilla	Mean	15.2	14.3
			St. Dev	0.2	0.2
			Coeff. Var.	1.4	1.5
FMNH	18397	Gorilla	Mean	15.1	13.9
			St. Dev	0.1	0.1
			Coeff. Var.	0.9	0.5
FMNH	18402	Gorilla	Mean	16.7	15.6
			St. Dev	0.1	0.1
			Coeff. Var.	0.4	0.9
NMNH	220324	Gorilla	Mean	15.2	14.3
			St. Dev	0.0	0.1
			Coeff. Var.	0.0	1.0
NMNH	545034	Gorilla	Mean	15.9	13.7
			St. Dev	0.0	0.1
			Coeff. Var.	0.0	1.0
NMNH	545036	Gorilla	Mean	16.3	15.3
			St. Dev	0.1	0.0
			Coeff. Var.	0.9	0.3
AMNH	VL/3036	Homo	Mean		
			St. Dev		
			Coeff. Var.		
AMNH	VL/3039	Homo	Mean		
			St. Dev		
			Coeff. Var.		
AMNH	VL/3045	Homo	Mean	10.5	10.0
			St. Dev	0.1	0.1
			Coeff. Var.	1.3	1.4
NMNH	35489	Macaca	Mean	8.1	7.6
			St. Dev	0.1	0.0
			Coeff. Var.	1.1	0.3
NMNH	240704	Macaca	Mean	6.4	5.7
			St. Dev	0.2	0.2
			Coeff. Var.	3.8	3.8
NMNH	241160	Macaca	Mean	7.8	7.5
			St. Dev	0.2	0.0
			Coeff. Var.	2.4	0.7
NMNH	353187	Macaca	Mean	8.0	7.7
			St. Dev	0.0	0.1
			Coeff. Var.	0.5	1.7
NMNH	176228	Pan	Mean	10.8	9.5

			St. Dev	0.0	0.2
			Coeff. Var.	0.3	2.2
NMNH	220327	Pan	Mean	11.6	10.2
			St. Dev	0.0	0.2
			Coeff. Var.	0.1	1.9
Wits	MLD 18	Australo	Mean	13.9	13.4
			St. Dev	0.1	0.0
			Coeff. Var.	0.8	0.3
Wits	MLD 18	Australo	Mean		
			St. Dev		
			Coeff. Var.		
Wits	MLD 19	Australo	Mean	13.6	13.0
			St. Dev	0.0	0.1
			Coeff. Var.	0.1	1.1
Wits	MLD 2	Australo	Mean		
			St. Dev		
			Coeff. Var.		
Wits	MLD 2	Australo	Mean		
			St. Dev		
			Coeff. Var.		
Wits	MLD 4	Australo	Mean	14.0	13.2
			St. Dev	0.1	0.3
			Coeff. Var.	0.8	2.4

APPENDIX 3: MEASUREMENT CROSS-CORRELATION

Cranial Variables Cross-Correlation Similarity Matrix

	gi	nasi	glam	gop	prosi	basbr	basnas	gbr
gi	1.000	.997	.954	.985	.646	.841	.753	.824
nasi	.997	1.000	.943	.979	.683	.822	.784	.799
glam	.954	.943	1.000	.983	.437	.926	.572	.925
gop	.985	.979	.983	1.000	.552	.892	.682	.879
prosi	.646	.683	.437	.552	1.000	.231	.961	.187
basbr	.841	.822	.926	.892	.231	1.000	.401	.942
basnas	.753	.784	.572	.682	.961	.401	1.000	.347
gbr	.824	.799	.925	.879	.187	.942	.347	1.000
brptn	.811	.796	.898	.863	.235	.952	.391	.946
brlam	.713	.688	.868	.788	.000	.894	.149	.851
ptnast	.885	.896	.835	.864	.648	.770	.752	.703
lamast	.861	.851	.908	.904	.307	.928	.473	.899
brast	.745	.719	.867	.812	.043	.955	.221	.900
lami	.381	.339	.570	.488	-.416	.731	-.226	.736
iopn	.697	.731	.505	.611	.939	.334	.911	.294
lamopn	.914	.907	.940	.944	.420	.942	.563	.915
naspros	.420	.461	.208	.324	.934	.019	.860	-.024
baspros	.396	.441	.164	.292	.950	-.037	.882	-.084
nspros	.121	.158	-.072	.035	.726	-.194	.629	-.271
snpros	.194	.225	.008	.108	.717	-.095	.647	-.177
mfek	.856	.862	.772	.827	.720	.660	.811	.629
orbzm	.503	.535	.303	.409	.881	.127	.845	.093
zyozm	.633	.666	.449	.555	.915	.280	.892	.247
nasns	.508	.547	.302	.416	.943	.100	.887	.070
rhins	.801	.813	.763	.796	.608	.707	.708	.659
rhians	.790	.797	.780	.804	.555	.723	.666	.690
nasrhi	.328	.367	.112	.228	.864	-.094	.772	-.112
ansns	.136	.162	.105	.119	.178	.091	.161	.059
ansav	.212	.252	.007	.117	.772	-.111	.689	-.211
anspros	.152	.191	-.056	.054	.750	-.180	.653	-.264
baopn	.671	.660	.733	.717	.231	.802	.386	.689
cfmacfmp	.787	.784	.777	.796	.442	.754	.597	.692
olsta	.371	.419	.139	.266	.935	-.063	.864	-.109
pobr	.846	.828	.929	.894	.250	.986	.416	.943
gpo	.857	.876	.704	.796	.908	.553	.969	.514

naspo	.834	.860	.685	.775	.918	.524	.974	.488
rhipo	.784	.813	.634	.723	.928	.462	.959	.431
snpo	.519	.563	.303	.423	.976	.094	.927	.060
avpo	.461	.505	.235	.359	.969	.036	.908	-.010
ekpo	.707	.739	.517	.626	.964	.345	.976	.294
zyopo	.726	.761	.549	.650	.967	.373	.975	.328
oppo	.948	.951	.945	.961	.586	.883	.704	.840
zmpo	.558	.599	.356	.470	.971	.167	.940	.114
apiaps	.060	.095	-.177	-.056	.734	-.341	.627	-.385
crtaps	.008	.054	-.224	-.095	.684	-.373	.592	-.444
poop_pFH	.699	.690	.775	.750	.229	.847	.375	.780
prosI1L	.340	.381	.119	.238	.823	-.029	.776	-.120
prosI2L	.175	.218	-.060	.064	.783	-.205	.692	-.279
prosCL	.168	.212	-.073	.054	.815	-.253	.709	-.325
prosP3L	.236	.281	-.012	.126	.867	-.188	.770	-.249
prosP4L	.326	.370	.079	.216	.909	-.104	.829	-.164
prosM1L	.401	.444	.160	.292	.940	-.031	.871	-.089
prosM2L	.433	.477	.196	.326	.952	.001	.888	-.056
prosM3L	.444	.487	.208	.337	.956	.012	.893	-.042
prosI1E	.027	.065	-.177	-.075	.655	-.338	.537	-.376
prosI2E	.079	.125	-.144	-.030	.723	-.273	.623	-.360
prosCE	.248	.293	.002	.137	.867	-.169	.780	-.240
prosP3E	.284	.328	.037	.171	.894	-.148	.805	-.208
prosP4E	.328	.373	.083	.218	.914	-.102	.836	-.159
prosM1E	.408	.450	.167	.299	.941	-.020	.875	-.084
prosM2E	.426	.469	.188	.319	.948	-.003	.885	-.061
prosM3E	.442	.486	.206	.336	.954	.011	.892	-.042
prosM3po	.440	.484	.202	.333	.954	.005	.890	-.048

	brptn	brlam	ptnast	lamast	brast	lami	iopn	lamopn
gi	.811	.713	.885	.861	.745	.381	.697	.914
nasi	.796	.688	.896	.851	.719	.339	.731	.907
glam	.898	.868	.835	.908	.867	.570	.505	.940
gop	.863	.788	.864	.904	.812	.488	.611	.944
prosi	.235	.000	.648	.307	.043	-.416	.939	.420
basbr	.952	.894	.770	.928	.955	.731	.334	.942
basnas	.391	.149	.752	.473	.221	-.226	.911	.563
gbr	.946	.851	.703	.899	.900	.736	.294	.915
brptn	1.000	.835	.758	.887	.903	.712	.296	.905
brlam	.835	1.000	.608	.804	.931	.781	.094	.786
ptnast	.758	.608	1.000	.781	.699	.297	.647	.817
lamast	.887	.804	.781	1.000	.914	.701	.420	.964
brast	.903	.931	.699	.914	1.000	.844	.141	.870
lami	.712	.781	.297	.701	.844	1.000	-.315	.610
iopn	.296	.094	.647	.420	.141	-.315	1.000	.546
lamopn	.905	.786	.817	.964	.870	.610	.546	1.000
naspros	.048	-.211	.466	.079	-.170	-.572	.813	.187
baspros	-.014	-.272	.455	.050	-.220	-.622	.835	.154
nspros	-.158	-.385	.212	-.197	-.347	-.668	.565	-.096
snpros	-.062	-.306	.282	-.111	-.244	-.557	.545	-.018
mfek	.649	.454	.790	.694	.536	.188	.691	.741
orbzm	.107	-.103	.492	.187	-.036	-.453	.821	.280
zyozm	.260	.039	.602	.359	.114	-.324	.895	.454
nasns	.113	-.124	.529	.188	-.085	-.492	.863	.289
rhins	.722	.521	.766	.736	.608	.288	.595	.768
rhians	.724	.565	.747	.736	.630	.320	.560	.773
nasrhi	-.087	-.287	.354	-.009	-.273	-.631	.784	.095
ansns	.127	.049	.134	.171	.090	.008	.154	.130
ansav	-.077	-.320	.295	-.087	-.260	-.597	.618	.000
anspros	-.139	-.383	.236	-.169	-.333	-.654	.588	-.073
baopn	.745	.717	.684	.728	.795	.587	.205	.707
cfmacfmp	.689	.628	.725	.742	.692	.414	.462	.753
olsta	-.034	-.287	.444	.036	-.237	-.636	.822	.132
pobr	.958	.882	.780	.926	.949	.724	.331	.934
gpo	.545	.305	.826	.616	.395	-.044	.876	.689
naspo	.527	.287	.825	.593	.369	-.080	.878	.666
rhipo	.462	.233	.780	.534	.296	-.146	.879	.612
snpo	.116	-.140	.561	.189	-.087	-.517	.885	.288

avpo	.058	-.203	.514	.121	-.146	-.570	.862	.222
ekpo	.341	.096	.724	.417	.178	-.285	.909	.506
zyopo	.389	.132	.748	.445	.204	-.257	.900	.532
oppo	.834	.732	.879	.907	.787	.443	.660	.952
zmpo	.176	-.069	.615	.246	-.008	-.456	.880	.340
apiaps	-.323	-.536	.123	-.303	-.493	-.794	.587	-.213
crtaps	-.354	-.540	.125	-.275	-.489	-.753	.554	-.215
poop_pFH	.746	.710	.665	.844	.802	.609	.355	.845
prosI1L	-.027	-.253	.419	.070	-.171	-.517	.720	.132
prosI2L	-.158	-.428	.263	-.144	-.360	-.667	.632	-.063
prosCL	-.230	-.444	.259	-.172	-.396	-.736	.679	-.086
prosP3L	-.163	-.418	.297	-.104	-.356	-.709	.748	-.006
prosP4L	-.083	-.342	.381	-.016	-.278	-.656	.799	.082
prosM1L	-.019	-.268	.449	.059	-.210	-.610	.835	.155
prosM2L	.010	-.233	.477	.092	-.178	-.586	.847	.189
prosM3L	.023	-.224	.492	.108	-.165	-.577	.854	.203
prosI1E	-.283	-.490	.123	-.302	-.460	-.724	.477	-.228
prosI2E	-.226	-.474	.212	-.225	-.408	-.703	.549	-.156
prosCE	-.148	-.398	.320	-.091	-.335	-.699	.748	.006
prosP3E	-.128	-.377	.341	-.066	-.322	-.693	.777	.035
prosP4E	-.079	-.342	.387	-.014	-.279	-.658	.801	.085
prosM1E	-.007	-.259	.456	.065	-.199	-.599	.831	.161
prosM2E	.011	-.241	.473	.083	-.182	-.587	.839	.181
prosM3E	.025	-.226	.491	.107	-.165	-.576	.852	.202
prosM3po	.017	-.228	.481	.105	-.172	-.580	.856	.201

	naspro s	baspros	nspros	snpros	mfek	orbzm	zyozm	nasns
gi	.420	.396	.121	.194	.856	.503	.633	.508
nasi	.461	.441	.158	.225	.862	.535	.666	.547
glam	.208	.164	-.072	.008	.772	.303	.449	.302
gop	.324	.292	.035	.108	.827	.409	.555	.416
prosi	.934	.950	.726	.717	.720	.881	.915	.943
basbr	.019	-.037	-.194	-.095	.660	.127	.280	.100
basnas	.860	.882	.629	.647	.811	.845	.892	.887
gbr	-.024	-.084	-.271	-.177	.629	.093	.247	.070
brptn	.048	-.014	-.158	-.062	.649	.107	.260	.113
brlam	-.211	-.272	-.385	-.306	.454	-.103	.039	-.124
ptnast	.466	.455	.212	.282	.790	.492	.602	.529
lamast	.079	.050	-.197	-.111	.694	.187	.359	.188
brast	-.170	-.220	-.347	-.244	.536	-.036	.114	-.085
lami	-.572	-.622	-.668	-.557	.188	-.453	-.324	-.492
iopn	.813	.835	.565	.545	.691	.821	.895	.863
lamopn	.187	.154	-.096	-.018	.741	.280	.454	.289
naspros	1.000	.949	.839	.817	.589	.855	.846	.973
baspros	.949	1.000	.830	.798	.554	.862	.845	.921
nspros	.839	.830	1.000	.973	.310	.648	.591	.697
snpros	.817	.798	.973	1.000	.398	.641	.583	.674
mfek	.589	.554	.310	.398	1.000	.639	.708	.650
orbzm	.855	.862	.648	.641	.639	1.000	.934	.874
zyozm	.846	.845	.591	.583	.708	.934	1.000	.885
nasns	.973	.921	.697	.674	.650	.874	.885	1.000
rhins	.467	.445	.210	.272	.809	.488	.591	.524
rhians	.418	.380	.160	.206	.770	.451	.554	.484
nasrhi	.940	.884	.711	.667	.481	.833	.808	.955
ansns	.122	.174	.095	.105	.158	.079	.130	.117
ansav	.847	.857	.957	.953	.416	.674	.641	.726
anspros	.845	.850	.978	.966	.356	.666	.613	.713
baopn	.105	.039	-.039	.068	.664	.156	.261	.152
cfmacfmp	.273	.248	.029	.117	.699	.417	.482	.353
olsta	.933	.993	.817	.781	.507	.834	.825	.906
pobr	.040	-.009	-.166	-.062	.693	.168	.302	.116
gpo	.771	.780	.510	.557	.900	.805	.871	.815
naspo	.797	.799	.530	.567	.880	.813	.879	.841
rhipo	.842	.822	.524	.550	.846	.833	.902	.896
snpo	.950	.977	.737	.709	.652	.889	.901	.959

avpo	.965	.993	.813	.790	.616	.881	.879	.948
ekpo	.866	.904	.657	.668	.783	.872	.914	.885
zyopo	.888	.893	.650	.664	.808	.862	.915	.911
oppo	.371	.342	.090	.165	.837	.445	.588	.458
zmpo	.935	.962	.741	.726	.702	.876	.898	.940
apiaps	.825	.866	.873	.834	.303	.767	.665	.741
crtaps	.750	.836	.780	.729	.184	.666	.620	.687
poop_pFH	.039	.008	-.129	-.035	.592	.137	.270	.111
prosI1L	.786	.881	.762	.768	.492	.745	.714	.746
prosI2L	.812	.891	.844	.834	.386	.740	.660	.735
prosCL	.855	.922	.874	.840	.340	.752	.693	.786
prosP3L	.893	.955	.873	.835	.424	.812	.764	.836
prosP4L	.912	.974	.858	.828	.496	.840	.800	.868
prosM1L	.928	.985	.829	.807	.545	.856	.836	.897
prosM2L	.932	.986	.811	.790	.564	.861	.851	.909
prosM3L	.935	.986	.799	.775	.566	.862	.858	.917
prosI1E	.747	.783	.820	.795	.224	.669	.576	.653
prosI2E	.787	.855	.857	.842	.288	.690	.608	.693
prosCE	.883	.956	.868	.834	.428	.808	.758	.824
prosP3E	.911	.972	.863	.831	.457	.832	.788	.862
prosP4E	.919	.980	.853	.824	.498	.845	.814	.877
prosM1E	.926	.984	.828	.808	.551	.857	.837	.895
prosM2E	.931	.985	.822	.802	.562	.862	.844	.903
prosM3E	.930	.986	.803	.781	.568	.862	.855	.910
prosM3po	.930	.985	.796	.770	.562	.859	.856	.913

	rhins	rhians	nasrhi	ansns	ansav	anspros	baopn	cfmacfmp
gi	.801	.790	.328	.136	.212	.152	.671	.787
nasi	.813	.797	.367	.162	.252	.191	.660	.784
glam	.763	.780	.112	.105	.007	-.056	.733	.777
gop	.796	.804	.228	.119	.117	.054	.717	.796
prosi	.608	.555	.864	.178	.772	.750	.231	.442
basbr	.707	.723	-.094	.091	-.111	-.180	.802	.754
basnas	.708	.666	.772	.161	.689	.653	.386	.597
gbr	.659	.690	-.112	.059	-.211	-.264	.689	.692
brptn	.722	.724	-.087	.127	-.077	-.139	.745	.689
brlam	.521	.565	-.287	.049	-.320	-.383	.717	.628
ptnast	.766	.747	.354	.134	.295	.236	.684	.725
lamast	.736	.736	-.009	.171	-.087	-.169	.728	.742
brast	.608	.630	-.273	.090	-.260	-.333	.795	.692
lami	.288	.320	-.631	.008	-.597	-.654	.587	.414
iopn	.595	.560	.784	.154	.618	.588	.205	.462
lamopn	.768	.773	.095	.130	.000	-.073	.707	.753
naspros	.467	.418	.940	.122	.847	.845	.105	.273
baspros	.445	.380	.884	.174	.857	.850	.039	.248
nspros	.210	.160	.711	.095	.957	.978	-.039	.029
snpros	.272	.206	.667	.105	.953	.966	.068	.117
mfek	.809	.770	.481	.158	.416	.356	.664	.699
orbzm	.488	.451	.833	.079	.674	.666	.156	.417
zyozm	.591	.554	.808	.130	.641	.613	.261	.482
nasns	.524	.484	.955	.117	.726	.713	.152	.353
rhins	1.000	.961	.262	.296	.333	.255	.672	.677
rhians	.961	1.000	.230	.087	.223	.152	.683	.692
nasrhi	.262	.230	1.000	.048	.702	.712	-.034	.195
ansns	.296	.087	.048	1.000	.274	.225	.099	.023
ansav	.333	.223	.702	.274	1.000	.987	.042	.088
anspros	.255	.152	.712	.225	.987	1.000	-.028	.046
baopn	.672	.683	-.034	.099	.042	-.028	1.000	.741
cfmacfmp	.677	.692	.195	.023	.088	.046	.741	1.000
olsta	.421	.356	.874	.190	.845	.835	.008	.226
pobr	.747	.758	-.092	.116	-.076	-.147	.812	.757
gpo	.787	.744	.669	.186	.592	.544	.510	.687
naspo	.785	.744	.698	.193	.607	.561	.502	.683
rhipo	.749	.701	.776	.225	.601	.557	.429	.619
snpo	.545	.484	.900	.202	.781	.764	.140	.361

avpo	.498	.433	.901	.192	.849	.835	.109	.308
ekpo	.668	.613	.779	.195	.720	.687	.348	.546
zyopo	.720	.659	.794	.232	.721	.685	.384	.563
oppo	.814	.819	.268	.156	.183	.108	.722	.767
zmpo	.568	.506	.871	.212	.793	.767	.240	.410
apiaps	.156	.117	.767	-.004	.842	.866	-.169	-.011
crtaps	.096	.039	.723	.081	.774	.781	-.182	-.069
poop_pFH	.635	.677	-.068	.076	-.053	-.137	.698	.615
prosI1L	.401	.314	.698	.220	.820	.800	.112	.216
prosI2L	.283	.191	.723	.230	.866	.874	-.047	.083
prosCL	.246	.176	.792	.175	.889	.888	-.117	.044
prosP3L	.301	.237	.836	.176	.884	.885	-.063	.104
prosP4L	.379	.314	.847	.190	.877	.875	-.004	.195
prosM1L	.434	.370	.862	.195	.852	.848	.043	.258
prosM2L	.465	.400	.866	.204	.838	.832	.068	.287
prosM3L	.469	.406	.873	.194	.827	.820	.071	.294
prosI1E	.076	.032	.693	.054	.768	.810	-.186	-.071
prosI2E	.232	.142	.688	.227	.867	.881	-.087	.016
prosCE	.316	.247	.817	.195	.884	.884	-.065	.132
prosP3E	.337	.273	.853	.180	.878	.878	-.044	.155
prosP4E	.383	.318	.854	.180	.872	.870	-.007	.203
prosM1E	.438	.374	.859	.193	.853	.847	.060	.270
prosM2E	.458	.396	.861	.186	.844	.839	.068	.289
prosM3E	.466	.402	.865	.192	.829	.824	.071	.300
prosM3po	.464	.400	.869	.195	.824	.818	.063	.294

	olsta	pobr	gpo	naspo	rhipo	snpo	avpo	ekpo
gi	.371	.846	.857	.834	.784	.519	.461	.707
nasi	.419	.828	.876	.860	.813	.563	.505	.739
glam	.139	.929	.704	.685	.634	.303	.235	.517
gop	.266	.894	.796	.775	.723	.423	.359	.626
prosi	.935	.250	.908	.918	.928	.976	.969	.964
basbr	-.063	.986	.553	.524	.462	.094	.036	.345
basnas	.864	.416	.969	.974	.959	.927	.908	.976
gbr	-.109	.943	.514	.488	.431	.060	-.010	.294
brptn	-.034	.958	.545	.527	.462	.116	.058	.341
brlam	-.287	.882	.305	.287	.233	-.140	-.203	.096
ptnast	.444	.780	.826	.825	.780	.561	.514	.724
lamast	.036	.926	.616	.593	.534	.189	.121	.417
brast	-.237	.949	.395	.369	.296	-.087	-.146	.178
lami	-.636	.724	-.044	-.080	-.146	-.517	-.570	-.285
iopn	.822	.331	.876	.878	.879	.885	.862	.909
lamopn	.132	.934	.689	.666	.612	.288	.222	.506
naspros	.933	.040	.771	.797	.842	.950	.965	.866
baspros	.993	-.009	.780	.799	.822	.977	.993	.904
nspros	.817	-.166	.510	.530	.524	.737	.813	.657
snpros	.781	-.062	.557	.567	.550	.709	.790	.668
mfek	.507	.693	.900	.880	.846	.652	.616	.783
orbzm	.834	.168	.805	.813	.833	.889	.881	.872
zyozm	.825	.302	.871	.879	.902	.901	.879	.914
nasns	.906	.116	.815	.841	.896	.959	.948	.885
rhins	.421	.747	.787	.785	.749	.545	.498	.668
rhians	.356	.758	.744	.744	.701	.484	.433	.613
nasrhi	.874	-.092	.669	.698	.776	.900	.901	.779
ansns	.190	.116	.186	.193	.225	.202	.192	.195
ansav	.845	-.076	.592	.607	.601	.781	.849	.720
anspros	.835	-.147	.544	.561	.557	.764	.835	.687
baopn	.008	.812	.510	.502	.429	.140	.109	.348
cfmacfmp	.226	.757	.687	.683	.619	.361	.308	.546
olsta	1.000	-.038	.756	.780	.805	.970	.984	.885
pobr	-.038	1.000	.579	.554	.480	.119	.063	.374
gpo	.756	.579	1.000	.992	.962	.854	.825	.954
naspo	.780	.554	.992	1.000	.973	.877	.845	.961
rhipo	.805	.480	.962	.973	1.000	.907	.870	.946
snpo	.970	.119	.854	.877	.907	1.000	.991	.942

avpo	.984	.063	.825	.845	.870	.991	1.000	.930
ekpo	.885	.374	.954	.961	.946	.942	.930	1.000
zyopo	.877	.406	.959	.975	.973	.948	.929	.982
oppo	.315	.892	.808	.791	.745	.462	.407	.655
zmpo	.949	.194	.880	.900	.916	.984	.980	.961
apiaps	.852	-.298	.509	.521	.527	.785	.839	.681
crtaps	.856	-.344	.447	.471	.490	.753	.798	.631
poop_pFH	-.020	.849	.495	.468	.405	.100	.063	.321
prosI1L	.876	.019	.696	.704	.666	.828	.861	.803
prosI2L	.888	-.158	.590	.599	.587	.816	.864	.725
prosCL	.929	-.218	.584	.602	.608	.849	.897	.740
prosP3L	.953	-.157	.655	.669	.677	.899	.937	.801
prosP4L	.968	-.072	.725	.738	.741	.931	.961	.853
prosM1L	.980	-.004	.776	.788	.800	.956	.977	.891
prosM2L	.982	.025	.796	.810	.827	.967	.981	.907
prosM3L	.984	.034	.801	.816	.836	.972	.983	.911
prosI1E	.782	-.304	.421	.436	.448	.699	.753	.582
prosI2E	.858	-.225	.509	.529	.526	.773	.827	.669
prosCE	.955	-.139	.666	.678	.684	.899	.936	.811
prosP3E	.970	-.118	.694	.708	.721	.923	.956	.833
prosP4E	.977	-.071	.731	.746	.754	.940	.968	.861
prosM1E	.979	.007	.781	.793	.803	.956	.977	.896
prosM2E	.980	.024	.792	.805	.817	.962	.979	.903
prosM3E	.984	.036	.802	.818	.832	.970	.983	.912
prosM3po	.983	.028	.797	.812	.831	.970	.981	.909

	zyopo	oppo	zmpo	apiaps	crtaps	poop_pFH	prosI1L	prosI2L
gi	.726	.948	.558	.060	.008	.699	.340	.175
nasi	.761	.951	.599	.095	.054	.690	.381	.218
glam	.549	.945	.356	-.177	-.224	.775	.119	-.060
gop	.650	.961	.470	-.056	-.095	.750	.238	.064
prosi	.967	.586	.971	.734	.684	.229	.823	.783
basbr	.373	.883	.167	-.341	-.373	.847	-.029	-.205
basnas	.975	.704	.940	.627	.592	.375	.776	.692
gbr	.328	.840	.114	-.385	-.444	.780	-.120	-.279
brptn	.389	.834	.176	-.323	-.354	.746	-.027	-.158
brlam	.132	.732	-.069	-.536	-.540	.710	-.253	-.428
ptnast	.748	.879	.615	.123	.125	.665	.419	.263
lamast	.445	.907	.246	-.303	-.275	.844	.070	-.144
brast	.204	.787	-.008	-.493	-.489	.802	-.171	-.360
lami	-.257	.443	-.456	-.794	-.753	.609	-.517	-.667
iopn	.900	.660	.880	.587	.554	.355	.720	.632
lamopn	.532	.952	.340	-.213	-.215	.845	.132	-.063
naspros	.888	.371	.935	.825	.750	.039	.786	.812
baspros	.893	.342	.962	.866	.836	.008	.881	.891
nspros	.650	.090	.741	.873	.780	-.129	.762	.844
snpros	.664	.165	.726	.834	.729	-.035	.768	.834
mfek	.808	.837	.702	.303	.184	.592	.492	.386
orbzm	.862	.445	.876	.767	.666	.137	.745	.740
zyozm	.915	.588	.898	.665	.620	.270	.714	.660
nasns	.911	.458	.940	.741	.687	.111	.746	.735
rhins	.720	.814	.568	.156	.096	.635	.401	.283
rhians	.659	.819	.506	.117	.039	.677	.314	.191
nasrhi	.794	.268	.871	.767	.723	-.068	.698	.723
ansns	.232	.156	.212	-.004	.081	.076	.220	.230
ansav	.721	.183	.793	.842	.774	-.053	.820	.866
anspros	.685	.108	.767	.866	.781	-.137	.800	.874
baopn	.384	.722	.240	-.169	-.182	.698	.112	-.047
cfmacfmp	.563	.767	.410	-.011	-.069	.615	.216	.083
olsta	.877	.315	.949	.852	.856	-.020	.876	.888
pobr	.406	.892	.194	-.298	-.344	.849	.019	-.158
gpo	.959	.808	.880	.509	.447	.495	.696	.590
naspo	.975	.791	.900	.521	.471	.468	.704	.599
rhipo	.973	.745	.916	.527	.490	.405	.666	.587
snpo	.948	.462	.984	.785	.753	.100	.828	.816

avpo	.929	.407	.980	.839	.798	.063	.861	.864
ekpo	.982	.655	.961	.681	.631	.321	.803	.725
zyopo	1.000	.681	.963	.642	.601	.328	.773	.705
oppo	.681	1.000	.520	-.011	-.038	.861	.326	.129
zmpo	.963	.520	1.000	.756	.738	.176	.830	.795
apiaps	.642	-.011	.756	1.000	.866	-.245	.814	.891
crtaps	.601	-.038	.738	.866	1.000	-.271	.822	.856
poop_pFH	.328	.861	.176	-.245	-.271	1.000	.106	-.116
prosI1L	.773	.326	.830	.814	.822	.106	1.000	.927
prosI2L	.705	.129	.795	.891	.856	-.116	.927	1.000
prosCL	.721	.117	.824	.909	.880	-.147	.894	.947
prosP3L	.779	.187	.877	.918	.873	-.095	.899	.952
prosP4L	.834	.274	.912	.898	.854	-.026	.913	.946
prosM1L	.875	.347	.938	.874	.836	.033	.914	.922
prosM2L	.894	.376	.948	.856	.823	.050	.900	.899
prosM3L	.899	.384	.951	.844	.816	.053	.889	.885
prosI1E	.558	-.037	.666	.900	.803	-.268	.768	.883
prosI2E	.654	.044	.748	.903	.854	-.174	.878	.968
prosCE	.786	.197	.877	.913	.868	-.083	.894	.948
prosP3E	.812	.230	.899	.915	.866	-.064	.904	.947
prosP4E	.844	.276	.920	.903	.863	-.027	.912	.941
prosM1E	.878	.351	.939	.875	.835	.035	.913	.925
prosM2E	.887	.368	.943	.865	.825	.046	.905	.913
prosM3E	.899	.383	.951	.847	.820	.052	.895	.894
prosM3po	.896	.379	.950	.842	.820	.045	.890	.886

	prosCL	prosP3L	prosP4L	prosM1L	prosM2L	prosM3L	prosI1E	prosI2E
gi	.168	.236	.326	.401	.433	.444	.027	.079
nasi	.212	.281	.370	.444	.477	.487	.065	.125
glam	-.073	-.012	.079	.160	.196	.208	-.177	-.144
gop	.054	.126	.216	.292	.326	.337	-.075	-.030
prosi	.815	.867	.909	.940	.952	.956	.655	.723
basbr	-.253	-.188	-.104	-.031	.001	.012	-.338	-.273
basnas	.709	.770	.829	.871	.888	.893	.537	.623
gbr	-.325	-.249	-.164	-.089	-.056	-.042	-.376	-.360
brptn	-.230	-.163	-.083	-.019	.010	.023	-.283	-.226
brlam	-.444	-.418	-.342	-.268	-.233	-.224	-.490	-.474
ptnast	.259	.297	.381	.449	.477	.492	.123	.212
lamast	-.172	-.104	-.016	.059	.092	.108	-.302	-.225
brast	-.396	-.356	-.278	-.210	-.178	-.165	-.460	-.408
lami	-.736	-.709	-.656	-.610	-.586	-.577	-.724	-.703
iopn	.679	.748	.799	.835	.847	.854	.477	.549
lamopn	-.086	-.006	.082	.155	.189	.203	-.228	-.156
naspros	.855	.893	.912	.928	.932	.935	.747	.787
baspros	.922	.955	.974	.985	.986	.986	.783	.855
nspros	.874	.873	.858	.829	.811	.799	.820	.857
snpros	.840	.835	.828	.807	.790	.775	.795	.842
mfek	.340	.424	.496	.545	.564	.566	.224	.288
orbzm	.752	.812	.840	.856	.861	.862	.669	.690
zyozm	.693	.764	.800	.836	.851	.858	.576	.608
nasns	.786	.836	.868	.897	.909	.917	.653	.693
rhins	.246	.301	.379	.434	.465	.469	.076	.232
rhians	.176	.237	.314	.370	.400	.406	.032	.142
nasrhi	.792	.836	.847	.862	.866	.873	.693	.688
ansns	.175	.176	.190	.195	.204	.194	.054	.227
ansav	.889	.884	.877	.852	.838	.827	.768	.867
anspros	.888	.885	.875	.848	.832	.820	.810	.881
baopn	-.117	-.063	-.004	.043	.068	.071	-.186	-.087
cfmacfmp	.044	.104	.195	.258	.287	.294	-.071	.016
olsta	.929	.953	.968	.980	.982	.984	.782	.858
pobr	-.218	-.157	-.072	-.004	.025	.034	-.304	-.225
gpo	.584	.655	.725	.776	.796	.801	.421	.509
naspo	.602	.669	.738	.788	.810	.816	.436	.529
rhipo	.608	.677	.741	.800	.827	.836	.448	.526
snpo	.849	.899	.931	.956	.967	.972	.699	.773

avpo	.897	.937	.961	.977	.981	.983	.753	.827
ekpo	.740	.801	.853	.891	.907	.911	.582	.669
zyopo	.721	.779	.834	.875	.894	.899	.558	.654
oppo	.117	.187	.274	.347	.376	.384	-.037	.044
zmpo	.824	.877	.912	.938	.948	.951	.666	.748
apiaps	.909	.918	.898	.874	.856	.844	.900	.903
crtaps	.880	.873	.854	.836	.823	.816	.803	.854
poop_pFH	-.147	-.095	-.026	.033	.050	.053	-.268	-.174
prosI1L	.894	.899	.913	.914	.900	.889	.768	.878
prosI2L	.947	.952	.946	.922	.899	.885	.883	.968
prosCL	1.000	.977	.963	.936	.918	.909	.874	.943
prosP3L	.977	1.000	.992	.970	.954	.945	.867	.931
prosP4L	.963	.992	1.000	.988	.976	.969	.838	.913
prosM1L	.936	.970	.988	1.000	.996	.992	.820	.887
prosM2L	.918	.954	.976	.996	1.000	.998	.801	.865
prosM3L	.909	.945	.969	.992	.998	1.000	.791	.849
prosI1E	.874	.867	.838	.820	.801	.791	1.000	.917
prosI2E	.943	.931	.913	.887	.865	.849	.917	1.000
prosCE	.980	.991	.988	.970	.957	.948	.865	.935
prosP3E	.974	.993	.994	.984	.974	.967	.862	.923
prosP4E	.962	.989	.997	.992	.983	.978	.846	.914
prosM1E	.939	.972	.989	.998	.995	.991	.823	.891
prosM2E	.926	.961	.982	.997	.997	.996	.812	.875
prosM3E	.912	.948	.972	.993	.997	.998	.793	.855
prosM3po	.906	.944	.968	.991	.997	.999	.787	.847

	prosCE	prosP3E	prosP4E	prosM1E	prosM2E	prosM3E	prosM3po
gi	.248	.284	.328	.408	.426	.442	.440
nasi	.293	.328	.373	.450	.469	.486	.484
glam	.002	.037	.083	.167	.188	.206	.202
gop	.137	.171	.218	.299	.319	.336	.333
prosi	.867	.894	.914	.941	.948	.954	.954
basbr	-.169	-.148	-.102	-.020	-.003	.011	.005
basnas	.780	.805	.836	.875	.885	.892	.890
gbr	-.240	-.208	-.159	-.084	-.061	-.042	-.048
brptn	-.148	-.128	-.079	-.007	.011	.025	.017
brlam	-.398	-.377	-.342	-.259	-.241	-.226	-.228
ptnast	.320	.341	.387	.456	.473	.491	.481
lamast	-.091	-.066	-.014	.065	.083	.107	.105
brast	-.335	-.322	-.279	-.199	-.182	-.165	-.172
lami	-.699	-.693	-.658	-.599	-.587	-.576	-.580
iopn	.748	.777	.801	.831	.839	.852	.856
lamopn	.006	.035	.085	.161	.181	.202	.201
naspros	.883	.911	.919	.926	.931	.930	.930
baspros	.956	.972	.980	.984	.985	.986	.985
nspros	.868	.863	.853	.828	.822	.803	.796
snpros	.834	.831	.824	.808	.802	.781	.770
mfek	.428	.457	.498	.551	.562	.568	.562
orbzm	.808	.832	.845	.857	.862	.862	.859
zyozm	.758	.788	.814	.837	.844	.855	.856
nasns	.824	.862	.877	.895	.903	.910	.913
rhins	.316	.337	.383	.438	.458	.466	.464
rhians	.247	.273	.318	.374	.396	.402	.400
nasrhi	.817	.853	.854	.859	.861	.865	.869
ansns	.195	.180	.180	.193	.186	.192	.195
ansav	.884	.878	.872	.853	.844	.829	.824
anspros	.884	.878	.870	.847	.839	.824	.818
baopn	-.065	-.044	-.007	.060	.068	.071	.063
cfmacfmp	.132	.155	.203	.270	.289	.300	.294
olsta	.955	.970	.977	.979	.980	.984	.983
pobr	-.139	-.118	-.071	.007	.024	.036	.028
gpo	.666	.694	.731	.781	.792	.802	.797
naspo	.678	.708	.746	.793	.805	.818	.812
rhipo	.684	.721	.754	.803	.817	.832	.831
snpo	.899	.923	.940	.956	.962	.970	.970

avpo	.936	.956	.968	.977	.979	.983	.981
ekpo	.811	.833	.861	.896	.903	.912	.909
zyopo	.786	.812	.844	.878	.887	.899	.896
oppo	.197	.230	.276	.351	.368	.383	.379
zmpo	.877	.899	.920	.939	.943	.951	.950
apiaps	.913	.915	.903	.875	.865	.847	.842
crtaps	.868	.866	.863	.835	.825	.820	.820
poop_pFH	-.083	-.064	-.027	.035	.046	.052	.045
prosI1L	.894	.904	.912	.913	.905	.895	.890
prosI2L	.948	.947	.941	.925	.913	.894	.886
prosCL	.980	.974	.962	.939	.926	.912	.906
prosP3L	.991	.993	.989	.972	.961	.948	.944
prosP4L	.988	.994	.997	.989	.982	.972	.968
prosM1L	.970	.984	.992	.998	.997	.993	.991
prosM2L	.957	.974	.983	.995	.997	.997	.997
prosM3L	.948	.967	.978	.991	.996	.998	.999
prosI1E	.865	.862	.846	.823	.812	.793	.787
prosI2E	.935	.923	.914	.891	.875	.855	.847
prosCE	1.000	.993	.988	.972	.963	.951	.947
prosP3E	.993	1.000	.995	.985	.978	.969	.966
prosP4E	.988	.995	1.000	.993	.987	.980	.977
prosM1E	.972	.985	.993	1.000	.997	.992	.990
prosM2E	.963	.978	.987	.997	1.000	.997	.995
prosM3E	.951	.969	.980	.992	.997	1.000	.998
prosM3po	.947	.966	.977	.990	.995	.998	1.000

Mandibular Variables Cross-Correlation Similarity Matrix

	sw__rt	I1w	I2w	Cw	P3w	P4w
sw__rt	1.000	.970	.952	.938	.932	.941
I1w	.970	1.000	.982	.971	.963	.949
I2w	.952	.982	1.000	.990	.977	.948
Cw	.938	.971	.990	1.000	.981	.945
P3w	.932	.963	.977	.981	1.000	.973
P4w	.941	.949	.948	.945	.973	1.000
M1w	.904	.904	.892	.876	.914	.972
M2w	.912	.900	.882	.860	.899	.954
M3w	.850	.850	.835	.828	.863	.899
lign	.891	.901	.910	.917	.924	.906
idgn	.882	.896	.910	.921	.927	.905
biI1l	.611	.603	.630	.652	.687	.745
biI2l	.671	.692	.718	.745	.765	.803
biCl	.686	.710	.727	.740	.764	.820
biP3l	.783	.814	.827	.831	.857	.891
biP4l	.674	.693	.701	.704	.737	.809
biM1l	.568	.577	.575	.569	.613	.701
biM2l	.484	.472	.453	.435	.488	.598
biM3l	.548	.524	.494	.470	.524	.637
biM3po	.632	.606	.573	.544	.599	.701
biI1e	.613	.657	.687	.693	.702	.730
biI2e	.649	.679	.713	.733	.752	.783
biCe	.810	.837	.854	.875	.881	.902
biP3e	.824	.847	.853	.862	.883	.918
biP4e	.788	.798	.797	.798	.830	.892
biM1e	.727	.726	.720	.713	.758	.839
biM2e	.723	.713	.694	.680	.727	.818
biM3e	.730	.714	.689	.666	.718	.812
biI1b	.231	.268	.275	.276	.302	.372
biI2b	.280	.294	.295	.290	.337	.449
biCb	.107	.107	.092	.078	.111	.241
biP3b	.147	.141	.120	.107	.149	.268
biP4b	.289	.278	.252	.235	.288	.416
biM1b	.429	.408	.381	.356	.420	.549
biM2b	.623	.599	.572	.546	.606	.715
biM3b	.690	.671	.653	.631	.686	.781
pgid	-.047	-.121	-.168	-.217	-.162	-.037

geli	.872	.903	.930	.935	.933	.901
raxrpx	.941	.958	.953	.949	.958	.964
ranrpn	.938	.963	.968	.969	.968	.955
idcdccdc	.930	.956	.962	.966	.969	.958
idgogo	.895	.935	.944	.961	.952	.913
bicdl	.846	.840	.812	.793	.817	.871
bicdm	.530	.507	.489	.466	.504	.571
bicdc	.791	.778	.751	.728	.761	.827
bicr	.877	.878	.864	.846	.879	.914
bigo	.863	.875	.871	.866	.887	.926
idbiM3po	.924	.950	.956	.962	.964	.948
I1lI1b	.887	.892	.894	.899	.911	.906
I2lI2b	.887	.889	.888	.893	.906	.903
ClCb	.893	.885	.876	.870	.890	.907
P3lP3b	.906	.909	.894	.889	.909	.924
P4lP4b	.895	.899	.878	.870	.892	.913
M1lM1b	.914	.922	.903	.894	.912	.924
M2lM2b	.919	.934	.922	.914	.933	.938
M3lM3b	.930	.948	.939	.929	.948	.955
mf_area	.547	.542	.561	.569	.588	.600
mflmfb	.901	.904	.884	.881	.889	.917
I1eI1b	.870	.881	.888	.900	.909	.894
I2eI2b	.881	.891	.896	.906	.914	.900
CeCb	.888	.883	.884	.884	.899	.900
P3eP3b	.908	.915	.907	.905	.921	.927
P4eP4b	.896	.901	.885	.880	.899	.917
M1eM1b	.913	.925	.908	.902	.916	.923
M2eM2b	.907	.927	.918	.913	.928	.930
M3eM3b	.921	.941	.934	.925	.943	.954
mlmfl	.850	.880	.890	.888	.875	.857
mlidgn	.543	.534	.522	.516	.571	.662
cdmcdl	.926	.945	.947	.943	.953	.965
gocdc	.898	.905	.891	.874	.896	.926
cdcM1bM3b	.941	.967	.960	.957	.959	.947
cdcM3b	.944	.967	.961	.958	.961	.955
cdcM2eM3e	.895	.920	.901	.909	.896	.861
crlg	.885	.884	.872	.863	.875	.878

	M1w	M2w	M3w	lign	idgn	biI1l
sw__rt	.904	.912	.850	.891	.882	.611
I1w	.904	.900	.850	.901	.896	.603
I2w	.892	.882	.835	.910	.910	.630
Cw	.876	.860	.828	.917	.921	.652
P3w	.914	.899	.863	.924	.927	.687
P4w	.972	.954	.899	.906	.905	.745
M1w	1.000	.982	.899	.848	.845	.736
M2w	.982	1.000	.915	.832	.826	.693
M3w	.899	.915	1.000	.786	.781	.675
lign	.848	.832	.786	1.000	.996	.672
idgn	.845	.826	.781	.996	1.000	.688
biI1l	.736	.693	.675	.672	.688	1.000
biI2l	.782	.736	.721	.784	.797	.920
biCl	.811	.776	.747	.774	.780	.892
biP3l	.874	.835	.818	.835	.836	.876
biP4l	.821	.781	.743	.709	.705	.858
biM1l	.740	.705	.677	.595	.582	.791
biM2l	.667	.639	.592	.476	.453	.689
biM3l	.719	.704	.633	.504	.480	.663
biM3po	.776	.767	.683	.579	.554	.644
biI1e	.721	.712	.691	.660	.684	.754
biI2e	.775	.746	.719	.743	.764	.866
biCe	.868	.836	.810	.898	.905	.849
biP3e	.903	.877	.850	.880	.882	.848
biP4e	.902	.875	.842	.826	.822	.853
biM1e	.873	.846	.810	.758	.748	.824
biM2e	.864	.845	.797	.717	.700	.777
biM3e	.870	.861	.796	.697	.678	.729
biI1b	.437	.346	.278	.245	.259	.528
biI2b	.526	.461	.436	.287	.281	.631
biCb	.327	.292	.267	.093	.067	.388
biP3b	.350	.331	.336	.123	.093	.399
biP4b	.505	.488	.469	.272	.244	.506
biM1b	.642	.631	.592	.414	.385	.580
biM2b	.789	.778	.718	.602	.575	.653
biM3b	.839	.824	.757	.673	.649	.705
pgid	.081	.082	.058	-.133	-.178	-.008
geli	.836	.817	.769	.953	.956	.645

raxrpx	.928	.917	.869	.928	.921	.710
ranrpn	.906	.893	.841	.935	.933	.687
idcdccdc	.913	.904	.852	.943	.942	.709
idgogo	.844	.833	.793	.943	.951	.663
bicdl	.878	.868	.834	.818	.796	.664
bicdm	.635	.636	.627	.498	.467	.507
bicdc	.860	.855	.839	.756	.726	.657
bicr	.915	.906	.856	.882	.863	.707
bigo	.919	.901	.846	.837	.824	.716
idbiM3po	.901	.898	.853	.933	.938	.702
I1lI1b	.859	.841	.790	.994	.989	.678
I2lI2b	.857	.841	.784	.992	.986	.674
ClCb	.878	.865	.808	.970	.957	.666
P3lP3b	.895	.878	.829	.966	.953	.677
P4lP4b	.892	.872	.825	.943	.927	.667
M1lM1b	.896	.882	.828	.940	.924	.652
M2lM2b	.907	.892	.829	.938	.927	.662
M3lM3b	.925	.911	.860	.931	.922	.687
mf_area	.605	.562	.447	.618	.619	.487
mflmfb	.893	.882	.847	.944	.930	.681
I1eI1b	.839	.819	.769	.992	.993	.681
I2eI2b	.846	.830	.773	.992	.994	.673
CeCb	.860	.847	.787	.979	.974	.668
P3eP3b	.889	.874	.826	.978	.970	.690
P4eP4b	.891	.869	.825	.952	.939	.681
M1eM1b	.889	.872	.818	.945	.931	.663
M2eM2b	.892	.871	.812	.941	.932	.677
M3eM3b	.923	.905	.856	.929	.921	.705
mlmfl	.806	.784	.725	.922	.917	.574
mlidgn	.711	.669	.658	.583	.565	.738
cdmcdl	.933	.919	.879	.919	.912	.712
gocdc	.921	.912	.862	.842	.825	.669
cdcM1bM3b	.903	.898	.856	.894	.889	.631
cdcM3b	.916	.909	.860	.920	.913	.661
cdcM2eM3e	.804	.807	.782	.847	.838	.498
crlg	.844	.849	.803	.913	.901	.618

	biI2l	biCl	biP3l	biP4l	biM1l	biM2l
sw__rt	.671	.686	.783	.674	.568	.484
I1w	.692	.710	.814	.693	.577	.472
I2w	.718	.727	.827	.701	.575	.453
Cw	.745	.740	.831	.704	.569	.435
P3w	.765	.764	.857	.737	.613	.488
P4w	.803	.820	.891	.809	.701	.598
M1w	.782	.811	.874	.821	.740	.667
M2w	.736	.776	.835	.781	.705	.639
M3w	.721	.747	.818	.743	.677	.592
lign	.784	.774	.835	.709	.595	.476
idgn	.797	.780	.836	.705	.582	.453
biI1l	.920	.892	.876	.858	.791	.689
biI2l	1.000	.955	.917	.863	.759	.632
biCl	.955	1.000	.937	.909	.820	.700
biP3l	.917	.937	1.000	.946	.857	.743
biP4l	.863	.909	.946	1.000	.960	.883
biM1l	.759	.820	.857	.960	1.000	.968
biM2l	.632	.700	.743	.883	.968	1.000
biM3l	.621	.687	.718	.844	.922	.970
biM3po	.626	.680	.728	.820	.874	.920
biI1e	.829	.861	.808	.761	.670	.533
biI2e	.935	.930	.880	.835	.732	.595
biCe	.941	.935	.947	.877	.766	.634
biP3e	.911	.931	.969	.925	.841	.733
biP4e	.895	.929	.960	.961	.909	.827
biM1e	.836	.881	.916	.958	.949	.903
biM2e	.777	.827	.873	.931	.948	.930
biM3e	.725	.775	.823	.884	.907	.910
biI1b	.480	.497	.495	.587	.601	.571
biI2b	.581	.630	.614	.776	.822	.823
biCb	.341	.419	.403	.625	.737	.805
biP3b	.359	.437	.430	.644	.767	.842
biP4b	.467	.554	.540	.733	.840	.906
biM1b	.566	.649	.651	.804	.888	.940
biM2b	.649	.724	.762	.854	.906	.936
biM3b	.698	.762	.810	.884	.914	.927
pgid	-.109	-.024	.022	.237	.432	.614
geli	.756	.759	.827	.695	.561	.418

raxrpx	.790	.800	.887	.789	.687	.587
ranrpn	.780	.780	.864	.745	.618	.500
idcdccdc	.809	.808	.880	.767	.647	.525
idgogo	.777	.752	.824	.677	.528	.379
bicdl	.719	.769	.835	.833	.805	.771
bicdm	.489	.516	.609	.645	.712	.742
bicdc	.688	.739	.822	.839	.851	.841
bicr	.759	.778	.862	.817	.779	.733
bigo	.760	.796	.880	.878	.838	.778
idbiM3po	.802	.791	.852	.720	.575	.441
I1lI1b	.786	.780	.838	.721	.615	.505
I2lI2b	.779	.770	.829	.717	.614	.509
ClCb	.771	.782	.831	.731	.645	.559
P3lP3b	.764	.773	.854	.758	.675	.589
P4lP4b	.752	.760	.850	.773	.704	.632
M1lM1b	.730	.738	.837	.756	.678	.602
M2lM2b	.739	.745	.839	.752	.663	.577
M3lM3b	.761	.767	.860	.772	.679	.585
mf_area	.559	.497	.551	.496	.431	.375
mflmfb	.773	.799	.851	.777	.699	.615
I1eI1b	.794	.779	.826	.695	.572	.446
I2eI2b	.784	.768	.820	.687	.566	.442
CeCb	.776	.772	.813	.680	.568	.457
P3eP3b	.779	.784	.855	.744	.647	.547
P4eP4b	.768	.771	.859	.770	.693	.613
M1eM1b	.742	.748	.848	.760	.675	.590
M2eM2b	.758	.760	.849	.763	.670	.576
M3eM3b	.780	.784	.871	.786	.687	.590
mlmfl	.710	.709	.768	.659	.544	.420
mlidgn	.737	.755	.799	.872	.904	.910
cdmcdl	.799	.807	.881	.799	.704	.607
gocdc	.727	.770	.852	.798	.740	.682
cdcM1bM3b	.713	.711	.806	.697	.585	.480
cdcM3b	.749	.756	.847	.749	.649	.548
cdcM2eM3e	.599	.593	.698	.580	.477	.376
crlg	.709	.699	.770	.660	.581	.505

	biM3l	biM3po	biI1e	biI2e	biCe	biP3e
sw__rt	.548	.632	.613	.649	.810	.824
I1w	.524	.606	.657	.679	.837	.847
I2w	.494	.573	.687	.713	.854	.853
Cw	.470	.544	.693	.733	.875	.862
P3w	.524	.599	.702	.752	.881	.883
P4w	.637	.701	.730	.783	.902	.918
M1w	.719	.776	.721	.775	.868	.903
M2w	.704	.767	.712	.746	.836	.877
M3w	.633	.683	.691	.719	.810	.850
lign	.504	.579	.660	.743	.898	.880
idgn	.480	.554	.684	.764	.905	.882
biI1l	.663	.644	.754	.866	.849	.848
biI2l	.621	.626	.829	.935	.941	.911
biCl	.687	.680	.861	.930	.935	.931
biP3l	.718	.728	.808	.880	.947	.969
biP4l	.844	.820	.761	.835	.877	.925
biM1l	.922	.874	.670	.732	.766	.841
biM2l	.970	.920	.533	.595	.634	.733
biM3l	1.000	.978	.534	.598	.635	.734
biM3po	.978	1.000	.536	.603	.662	.757
biI1e	.534	.536	1.000	.927	.846	.843
biI2e	.598	.603	.927	1.000	.927	.906
biCe	.635	.662	.846	.927	1.000	.975
biP3e	.734	.757	.843	.906	.975	1.000
biP4e	.827	.838	.813	.883	.942	.983
biM1e	.903	.902	.744	.824	.877	.938
biM2e	.941	.943	.689	.759	.825	.900
biM3e	.951	.968	.646	.713	.778	.863
biI1b	.511	.454	.469	.506	.452	.483
biI2b	.763	.692	.551	.586	.539	.603
biCb	.755	.682	.329	.338	.321	.411
biP3b	.803	.725	.353	.354	.344	.444
biP4b	.890	.832	.442	.474	.467	.566
biM1b	.941	.906	.504	.553	.572	.669
biM2b	.954	.952	.569	.630	.699	.791
biM3b	.952	.962	.600	.674	.755	.838
pgid	.616	.581	-.170	-.148	-.104	.024
geli	.435	.507	.708	.746	.874	.857

raxrpx	.623	.689	.702	.756	.908	.913
ranrpn	.535	.606	.707	.758	.905	.893
idcdccdc	.558	.624	.733	.791	.922	.909
idgogo	.410	.484	.703	.764	.894	.859
bicdl	.791	.828	.592	.661	.812	.858
bicdm	.757	.771	.385	.435	.538	.627
bicdc	.860	.888	.561	.626	.771	.841
bicr	.773	.833	.629	.710	.855	.890
bigo	.796	.829	.674	.729	.855	.901
idbiM3po	.494	.573	.741	.796	.905	.888
I1lI1b	.535	.610	.653	.738	.894	.885
I2lI2b	.544	.621	.639	.726	.887	.878
ClCb	.598	.675	.626	.706	.871	.869
P3lP3b	.625	.701	.634	.712	.876	.889
P4lP4b	.668	.739	.618	.691	.865	.887
M1lM1b	.643	.720	.612	.675	.854	.872
M2lM2b	.620	.698	.626	.688	.860	.869
M3lM3b	.624	.696	.663	.719	.875	.885
mf_area	.420	.474	.447	.510	.588	.584
mflmfb	.656	.721	.666	.727	.887	.899
I1eI1b	.473	.548	.668	.754	.898	.875
I2eI2b	.477	.556	.663	.746	.890	.869
CeCb	.501	.585	.637	.725	.871	.850
P3eP3b	.585	.662	.658	.736	.888	.894
P4eP4b	.648	.720	.630	.706	.877	.893
M1eM1b	.624	.697	.628	.687	.864	.878
M2eM2b	.610	.679	.643	.704	.874	.875
M3eM3b	.630	.700	.683	.741	.887	.896
mlmfl	.446	.512	.654	.679	.830	.812
mlidgn	.891	.872	.595	.701	.739	.810
cdmcdl	.641	.705	.701	.760	.896	.906
gocdc	.724	.784	.649	.691	.841	.874
cdcM1bM3b	.533	.612	.637	.684	.839	.834
cdcM3b	.587	.660	.667	.718	.876	.875
cdcM2eM3e	.423	.505	.514	.551	.748	.725
crlg	.578	.661	.585	.659	.823	.823

	biP4e	biM1e	biM2e	biM3e	biI1b	biI2b
sw__rt	.788	.727	.723	.730	.231	.280
I1w	.798	.726	.713	.714	.268	.294
I2w	.797	.720	.694	.689	.275	.295
Cw	.798	.713	.680	.666	.276	.290
P3w	.830	.758	.727	.718	.302	.337
P4w	.892	.839	.818	.812	.372	.449
M1w	.902	.873	.864	.870	.437	.526
M2w	.875	.846	.845	.861	.346	.461
M3w	.842	.810	.797	.796	.278	.436
lign	.826	.758	.717	.697	.245	.287
idgn	.822	.748	.700	.678	.259	.281
biI1l	.853	.824	.777	.729	.528	.631
biI2l	.895	.836	.777	.725	.480	.581
biCl	.929	.881	.827	.775	.497	.630
biP3l	.960	.916	.873	.823	.495	.614
biP4l	.961	.958	.931	.884	.587	.776
biM1l	.909	.949	.948	.907	.601	.822
biM2l	.827	.903	.930	.910	.571	.823
biM3l	.827	.903	.941	.951	.511	.763
biM3po	.838	.902	.943	.968	.454	.692
biI1e	.813	.744	.689	.646	.469	.551
biI2e	.883	.824	.759	.713	.506	.586
biCe	.942	.877	.825	.778	.452	.539
biP3e	.983	.938	.900	.863	.483	.603
biP4e	1.000	.981	.956	.921	.534	.690
biM1e	.981	1.000	.988	.962	.550	.746
biM2e	.956	.988	1.000	.985	.538	.747
biM3e	.921	.962	.985	1.000	.484	.702
biI1b	.534	.550	.538	.484	1.000	.810
biI2b	.690	.746	.747	.702	.810	1.000
biCb	.526	.626	.659	.636	.594	.870
biP3b	.557	.656	.695	.675	.512	.827
biP4b	.678	.774	.806	.799	.537	.828
biM1b	.775	.860	.889	.886	.534	.812
biM2b	.869	.929	.956	.959	.509	.754
biM3b	.904	.950	.972	.976	.512	.744
pgid	.170	.322	.414	.448	.223	.485
geli	.795	.711	.666	.640	.285	.295

raxrpx	.879	.821	.804	.795	.320	.400
ranrpn	.839	.764	.737	.725	.297	.342
idcdccdc	.861	.790	.761	.745	.311	.359
idgogo	.784	.690	.643	.623	.240	.236
bicdl	.878	.884	.888	.885	.360	.562
bicdm	.686	.725	.768	.776	.319	.509
bicdc	.882	.905	.926	.928	.371	.598
bicr	.899	.890	.893	.897	.334	.484
bigo	.916	.907	.906	.899	.450	.607
idbiM3po	.830	.748	.709	.702	.260	.292
I1lI1b	.840	.778	.741	.723	.265	.311
I2lI2b	.835	.777	.743	.728	.259	.313
ClCb	.847	.800	.779	.768	.279	.357
P3lP3b	.866	.824	.807	.797	.306	.387
P4lP4b	.874	.839	.831	.824	.329	.428
M1lM1b	.853	.815	.808	.805	.305	.404
M2lM2b	.845	.801	.789	.787	.312	.393
M3lM3b	.862	.815	.800	.796	.323	.408
mf_area	.563	.519	.509	.517	.286	.300
mflmfb	.883	.840	.826	.815	.308	.420
I1eI1b	.817	.743	.695	.673	.252	.270
I2eI2b	.811	.738	.694	.677	.241	.260
CeCb	.809	.741	.706	.692	.247	.270
P3eP3b	.858	.806	.780	.769	.288	.347
P4eP4b	.874	.832	.820	.809	.328	.415
M1eM1b	.854	.808	.797	.788	.313	.400
M2eM2b	.849	.801	.784	.774	.333	.409
M3eM3b	.873	.825	.806	.800	.332	.421
mlmfl	.766	.690	.657	.635	.284	.303
mlidgn	.866	.913	.917	.892	.583	.801
cdmcdl	.881	.830	.812	.805	.324	.423
gocdc	.871	.848	.855	.853	.350	.493
cdcM1bM3b	.792	.730	.718	.722	.255	.306
cdcM3b	.839	.782	.769	.764	.295	.361
cdcM2eM3e	.674	.610	.604	.602	.178	.207
crlg	.791	.746	.732	.749	.185	.248

	biCb	biP3b	biP4b	biM1b	biM2b	biM3b
sw__rt	.107	.147	.289	.429	.623	.690
I1w	.107	.141	.278	.408	.599	.671
I2w	.092	.120	.252	.381	.572	.653
Cw	.078	.107	.235	.356	.546	.631
P3w	.111	.149	.288	.420	.606	.686
P4w	.241	.268	.416	.549	.715	.781
M1w	.327	.350	.505	.642	.789	.839
M2w	.292	.331	.488	.631	.778	.824
M3w	.267	.336	.469	.592	.718	.757
lign	.093	.123	.272	.414	.602	.673
idgn	.067	.093	.244	.385	.575	.649
biI1l	.388	.399	.506	.580	.653	.705
biI2l	.341	.359	.467	.566	.649	.698
biCl	.419	.437	.554	.649	.724	.762
biP3l	.403	.430	.540	.651	.762	.810
biP4l	.625	.644	.733	.804	.854	.884
biM1l	.737	.767	.840	.888	.906	.914
biM2l	.805	.842	.906	.940	.936	.927
biM3l	.755	.803	.890	.941	.954	.952
biM3po	.682	.725	.832	.906	.952	.962
biI1e	.329	.353	.442	.504	.569	.600
biI2e	.338	.354	.474	.553	.630	.674
biCe	.321	.344	.467	.572	.699	.755
biP3e	.411	.444	.566	.669	.791	.838
biP4e	.526	.557	.678	.775	.869	.904
biM1e	.626	.656	.774	.860	.929	.950
biM2e	.659	.695	.806	.889	.956	.972
biM3e	.636	.675	.799	.886	.959	.976
biI1b	.594	.512	.537	.534	.509	.512
biI2b	.870	.827	.828	.812	.754	.744
biCb	1.000	.949	.908	.840	.720	.677
biP3b	.949	1.000	.958	.888	.773	.717
biP4b	.908	.958	1.000	.963	.878	.830
biM1b	.840	.888	.963	1.000	.955	.918
biM2b	.720	.773	.878	.955	1.000	.985
biM3b	.677	.717	.830	.918	.985	1.000
pgid	.717	.737	.721	.674	.576	.506
geli	.079	.081	.221	.355	.532	.610

raxrpx	.223	.266	.398	.530	.703	.764
ranrpn	.142	.175	.306	.437	.618	.688
idcdccdc	.153	.185	.325	.463	.636	.707
idgogo	.004	.033	.171	.306	.494	.575
bicdl	.466	.506	.627	.727	.847	.882
bicdm	.508	.593	.662	.740	.797	.785
bicdc	.538	.603	.713	.813	.913	.931
bicr	.367	.414	.562	.696	.839	.884
bigo	.470	.498	.619	.729	.849	.898
idbiM3po	.061	.088	.243	.388	.568	.647
I1lI1b	.130	.151	.303	.448	.633	.699
I2lI2b	.138	.159	.309	.453	.638	.705
ClCb	.196	.222	.371	.522	.698	.754
P3lP3b	.228	.247	.394	.539	.715	.773
P4lP4b	.285	.315	.449	.585	.755	.806
M1lM1b	.262	.294	.427	.558	.729	.786
M2lM2b	.227	.254	.396	.538	.709	.770
M3lM3b	.227	.256	.399	.543	.708	.771
mf_area	.144	.134	.225	.349	.471	.512
mflmfb	.284	.310	.452	.585	.743	.792
I1eI1b	.065	.084	.237	.382	.573	.644
I2eI2b	.059	.075	.231	.377	.569	.643
CeCb	.071	.090	.252	.411	.600	.668
P3eP3b	.169	.187	.340	.489	.673	.737
P4eP4b	.258	.285	.418	.559	.735	.789
M1eM1b	.247	.277	.404	.535	.708	.767
M2eM2b	.236	.257	.390	.527	.692	.755
M3eM3b	.238	.266	.406	.546	.707	.770
mlmfl	.138	.138	.256	.375	.533	.598
mlidgn	.713	.766	.837	.884	.917	.911
cdmcdl	.242	.280	.422	.560	.720	.782
gocdc	.365	.398	.513	.643	.786	.835
cdcM1bM3b	.122	.148	.288	.430	.605	.680
cdcM3b	.189	.220	.355	.492	.663	.730
cdcM2eM3e	.054	.084	.201	.330	.506	.575
crlg	.125	.179	.334	.485	.654	.711

	pgid	geli	raxrpx	ranrpn	idcdccdc	idgogo
sw__rt	-.047	.872	.941	.938	.930	.895
I1w	-.121	.903	.958	.963	.956	.935
I2w	-.168	.930	.953	.968	.962	.944
Cw	-.217	.935	.949	.969	.966	.961
P3w	-.162	.933	.958	.968	.969	.952
P4w	-.037	.901	.964	.955	.958	.913
M1w	.081	.836	.928	.906	.913	.844
M2w	.082	.817	.917	.893	.904	.833
M3w	.058	.769	.869	.841	.852	.793
lign	-.133	.953	.928	.935	.943	.943
idgn	-.178	.956	.921	.933	.942	.951
biI1l	-.008	.645	.710	.687	.709	.663
biI2l	-.109	.756	.790	.780	.809	.777
biCl	-.024	.759	.800	.780	.808	.752
biP3l	.022	.827	.887	.864	.880	.824
biP4l	.237	.695	.789	.745	.767	.677
biM1l	.432	.561	.687	.618	.647	.528
biM2l	.614	.418	.587	.500	.525	.379
biM3l	.616	.435	.623	.535	.558	.410
biM3po	.581	.507	.689	.606	.624	.484
biI1e	-.170	.708	.702	.707	.733	.703
biI2e	-.148	.746	.756	.758	.791	.764
biCe	-.104	.874	.908	.905	.922	.894
biP3e	.024	.857	.913	.893	.909	.859
biP4e	.170	.795	.879	.839	.861	.784
biM1e	.322	.711	.821	.764	.790	.690
biM2e	.414	.666	.804	.737	.761	.643
biM3e	.448	.640	.795	.725	.745	.623
biI1b	.223	.285	.320	.297	.311	.240
biI2b	.485	.295	.400	.342	.359	.236
biCb	.717	.079	.223	.142	.153	.004
biP3b	.737	.081	.266	.175	.185	.033
biP4b	.721	.221	.398	.306	.325	.171
biM1b	.674	.355	.530	.437	.463	.306
biM2b	.576	.532	.703	.618	.636	.494
biM3b	.506	.610	.764	.688	.707	.575
pgid	1.000	-.215	-.043	-.155	-.153	-.314
geli	-.215	1.000	.916	.938	.944	.944

raxrpx	-.043	.916	1.000	.988	.982	.942
ranrpn	-.155	.938	.988	1.000	.989	.970
idcdccdc	-.153	.944	.982	.989	1.000	.977
idgogo	-.314	.944	.942	.970	.977	1.000
bicdl	.296	.755	.875	.828	.837	.750
bicdm	.489	.436	.613	.537	.546	.431
bicdc	.418	.687	.844	.779	.790	.680
bicr	.218	.821	.929	.888	.898	.821
bigo	.211	.822	.916	.882	.895	.813
idbiM3po	-.244	.937	.953	.969	.979	.978
I1lI1b	-.083	.942	.929	.927	.936	.929
I2lI2b	-.064	.936	.926	.923	.931	.921
ClCb	.028	.911	.929	.912	.920	.885
P3lP3b	.044	.918	.948	.931	.938	.903
P4lP4b	.112	.889	.947	.920	.924	.879
M1lM1b	.081	.902	.958	.939	.938	.896
M2lM2b	.029	.913	.962	.950	.953	.915
M3lM3b	-.001	.915	.970	.960	.963	.926
mf_area	-.032	.606	.632	.631	.615	.599
mflmfb	.070	.899	.947	.925	.932	.890
I1eI1b	-.171	.944	.913	.922	.932	.942
I2eI2b	-.169	.948	.916	.926	.936	.943
CeCb	-.107	.929	.911	.912	.922	.911
P3eP3b	-.032	.936	.949	.940	.948	.926
P4eP4b	.073	.901	.948	.926	.930	.892
M1eM1b	.044	.914	.959	.945	.945	.910
M2eM2b	.007	.919	.958	.950	.953	.921
M3eM3b	-.011	.914	.965	.958	.960	.925
mlmfl	-.134	.927	.890	.903	.908	.908
mlidgn	.481	.504	.661	.587	.609	.494
cdmcdl	-.015	.900	.967	.958	.961	.917
gocdc	.141	.839	.947	.921	.918	.829
cdcM1bM3b	-.123	.900	.959	.966	.968	.944
cdcM3b	-.063	.918	.982	.980	.985	.950
cdcM2eM3e	-.133	.846	.901	.912	.913	.902
crlg	-.010	.859	.921	.905	.908	.877

	bicdl	bicdm	bicdc	bicr	bigo	idbiM3po
sw__rt	.846	.530	.791	.877	.863	.924
I1w	.840	.507	.778	.878	.875	.950
I2w	.812	.489	.751	.864	.871	.956
Cw	.793	.466	.728	.846	.866	.962
P3w	.817	.504	.761	.879	.887	.964
P4w	.871	.571	.827	.914	.926	.948
M1w	.878	.635	.860	.915	.919	.901
M2w	.868	.636	.855	.906	.901	.898
M3w	.834	.627	.839	.856	.846	.853
lign	.818	.498	.756	.882	.837	.933
idgn	.796	.467	.726	.863	.824	.938
biI1l	.664	.507	.657	.707	.716	.702
biI2l	.719	.489	.688	.759	.760	.802
biCl	.769	.516	.739	.778	.796	.791
biP3l	.835	.609	.822	.862	.880	.852
biP4l	.833	.645	.839	.817	.878	.720
biM1l	.805	.712	.851	.779	.838	.575
biM2l	.771	.742	.841	.733	.778	.441
biM3l	.791	.757	.860	.773	.796	.494
biM3po	.828	.771	.888	.833	.829	.573
biI1e	.592	.385	.561	.629	.674	.741
biI2e	.661	.435	.626	.710	.729	.796
biCe	.812	.538	.771	.855	.855	.905
biP3e	.858	.627	.841	.890	.901	.888
biP4e	.878	.686	.882	.899	.916	.830
biM1e	.884	.725	.905	.890	.907	.748
biM2e	.888	.768	.926	.893	.906	.709
biM3e	.885	.776	.928	.897	.899	.702
biI1b	.360	.319	.371	.334	.450	.260
biI2b	.562	.509	.598	.484	.607	.292
biCb	.466	.508	.538	.367	.470	.061
biP3b	.506	.593	.603	.414	.498	.088
biP4b	.627	.662	.713	.562	.619	.243
biM1b	.727	.740	.813	.696	.729	.388
biM2b	.847	.797	.913	.839	.849	.568
biM3b	.882	.785	.931	.884	.898	.647
pgid	.296	.489	.418	.218	.211	-.244
geli	.755	.436	.687	.821	.822	.937

raxrpx	.875	.613	.844	.929	.916	.953
ranrpn	.828	.537	.779	.888	.882	.969
idcdccdc	.837	.546	.790	.898	.895	.979
idgogo	.750	.431	.680	.821	.813	.978
bicdl	1.000	.624	.948	.923	.917	.787
bicdm	.624	1.000	.836	.732	.709	.464
bicdc	.948	.836	1.000	.930	.920	.723
bicr	.923	.732	.930	1.000	.934	.856
bigo	.917	.709	.920	.934	1.000	.842
idbiM3po	.787	.464	.723	.856	.842	1.000
I1lI1b	.834	.529	.779	.896	.844	.922
I2lI2b	.837	.529	.781	.899	.844	.917
ClCb	.871	.580	.829	.921	.865	.899
P3lP3b	.886	.606	.849	.934	.890	.914
P4lP4b	.897	.658	.878	.944	.902	.889
M1lM1b	.892	.629	.863	.942	.907	.905
M2lM2b	.880	.593	.840	.936	.913	.924
M3lM3b	.879	.591	.840	.934	.923	.942
mf_area	.458	.575	.529	.617	.599	.584
mflmfb	.900	.617	.867	.933	.900	.905
I1eI1b	.791	.478	.726	.860	.808	.926
I2eI2b	.794	.470	.726	.864	.812	.933
CeCb	.806	.503	.751	.876	.812	.918
P3eP3b	.860	.568	.815	.918	.872	.934
P4eP4b	.885	.640	.862	.938	.893	.899
M1eM1b	.877	.613	.846	.929	.902	.912
M2eM2b	.871	.572	.824	.922	.906	.923
M3eM3b	.871	.578	.829	.928	.917	.945
mlmfl	.764	.474	.710	.812	.801	.890
mlidgn	.782	.747	.844	.778	.773	.538
cdmcdl	.895	.584	.851	.942	.932	.939
gocdc	.893	.671	.884	.927	.929	.871
cdcM1bM3b	.831	.521	.778	.883	.891	.955
cdcM3b	.869	.582	.829	.917	.920	.953
cdcM2eM3e	.790	.492	.738	.815	.825	.879
crlg	.791	.599	.780	.916	.826	.890

	I1lI1b	I2lI2b	ClCb	P3lP3b	P4lP4b	M1lM1b
sw__rt	.887	.887	.893	.906	.895	.914
I1w	.892	.889	.885	.909	.899	.922
I2w	.894	.888	.876	.894	.878	.903
Cw	.899	.893	.870	.889	.870	.894
P3w	.911	.906	.890	.909	.892	.912
P4w	.906	.903	.907	.924	.913	.924
M1w	.859	.857	.878	.895	.892	.896
M2w	.841	.841	.865	.878	.872	.882
M3w	.790	.784	.808	.829	.825	.828
lign	.994	.992	.970	.966	.943	.940
idgn	.989	.986	.957	.953	.927	.924
biI1l	.678	.674	.666	.677	.667	.652
biI2l	.786	.779	.771	.764	.752	.730
biCl	.780	.770	.782	.773	.760	.738
biP3l	.838	.829	.831	.854	.850	.837
biP4l	.721	.717	.731	.758	.773	.756
biM1l	.615	.614	.645	.675	.704	.678
biM2l	.505	.509	.559	.589	.632	.602
biM3l	.535	.544	.598	.625	.668	.643
biM3po	.610	.621	.675	.701	.739	.720
biI1e	.653	.639	.626	.634	.618	.612
biI2e	.738	.726	.706	.712	.691	.675
biCe	.894	.887	.871	.876	.865	.854
biP3e	.885	.878	.869	.889	.887	.872
biP4e	.840	.835	.847	.866	.874	.853
biM1e	.778	.777	.800	.824	.839	.815
biM2e	.741	.743	.779	.807	.831	.808
biM3e	.723	.728	.768	.797	.824	.805
biI1b	.265	.259	.279	.306	.329	.305
biI2b	.311	.313	.357	.387	.428	.404
biCb	.130	.138	.196	.228	.285	.262
biP3b	.151	.159	.222	.247	.315	.294
biP4b	.303	.309	.371	.394	.449	.427
biM1b	.448	.453	.522	.539	.585	.558
biM2b	.633	.638	.698	.715	.755	.729
biM3b	.699	.705	.754	.773	.806	.786
pgid	-.083	-.064	.028	.044	.112	.081
geli	.942	.936	.911	.918	.889	.902

raxrpx	.929	.926	.929	.948	.947	.958
ranrpn	.927	.923	.912	.931	.920	.939
idcdccdc	.936	.931	.920	.938	.924	.938
idgogo	.929	.921	.885	.903	.879	.896
bicdl	.834	.837	.871	.886	.897	.892
bicdm	.529	.529	.580	.606	.658	.629
bicdc	.779	.781	.829	.849	.878	.863
bicr	.896	.899	.921	.934	.944	.942
bigo	.844	.844	.865	.890	.902	.907
idbiM3po	.922	.917	.899	.914	.889	.905
I1lI1b	1.000	.998	.981	.977	.957	.948
I2lI2b	.998	1.000	.985	.979	.961	.954
ClCb	.981	.985	1.000	.986	.973	.962
P3lP3b	.977	.979	.986	1.000	.991	.984
P4lP4b	.957	.961	.973	.991	1.000	.992
M1lM1b	.948	.954	.962	.984	.992	1.000
M2lM2b	.942	.947	.952	.972	.974	.989
M3lM3b	.933	.935	.939	.961	.960	.977
mf_area	.638	.641	.625	.619	.637	.622
mflmfb	.957	.959	.972	.980	.980	.975
I1eI1b	.994	.990	.960	.954	.928	.919
I2eI2b	.993	.992	.964	.958	.931	.926
CeCb	.982	.983	.984	.964	.937	.928
P3eP3b	.985	.986	.982	.995	.979	.973
P4eP4b	.964	.967	.975	.992	.998	.988
M1eM1b	.951	.956	.959	.983	.988	.997
M2eM2b	.944	.949	.949	.969	.971	.985
M3eM3b	.930	.932	.933	.956	.955	.971
mlmfl	.921	.919	.910	.913	.902	.908
mlidgn	.610	.610	.641	.669	.713	.677
cdmcdl	.917	.917	.925	.937	.934	.945
gocdc	.848	.853	.881	.905	.913	.926
cdcM1bM3b	.887	.886	.880	.907	.896	.926
cdcM3b	.917	.915	.914	.939	.933	.954
cdcM2eM3e	.840	.840	.835	.858	.848	.881
crlg	.920	.923	.917	.923	.921	.929

	M2lM2b	M3lM3b	mf_area	mflmfb	I1eI1b	I2eI2b
sw__rt	.919	.930	.547	.901	.870	.881
I1w	.934	.948	.542	.904	.881	.891
I2w	.922	.939	.561	.884	.888	.896
Cw	.914	.929	.569	.881	.900	.906
P3w	.933	.948	.588	.889	.909	.914
P4w	.938	.955	.600	.917	.894	.900
M1w	.907	.925	.605	.893	.839	.846
M2w	.892	.911	.562	.882	.819	.830
M3w	.829	.860	.447	.847	.769	.773
lign	.938	.931	.618	.944	.992	.992
idgn	.927	.922	.619	.930	.993	.994
biI1l	.662	.687	.487	.681	.681	.673
biI2l	.739	.761	.559	.773	.794	.784
biCl	.745	.767	.497	.799	.779	.768
biP3l	.839	.860	.551	.851	.826	.820
biP4l	.752	.772	.496	.777	.695	.687
biM1l	.663	.679	.431	.699	.572	.566
biM2l	.577	.585	.375	.615	.446	.442
biM3l	.620	.624	.420	.656	.473	.477
biM3po	.698	.696	.474	.721	.548	.556
biI1e	.626	.663	.447	.666	.668	.663
biI2e	.688	.719	.510	.727	.754	.746
biCe	.860	.875	.588	.887	.898	.890
biP3e	.869	.885	.584	.899	.875	.869
biP4e	.845	.862	.563	.883	.817	.811
biM1e	.801	.815	.519	.840	.743	.738
biM2e	.789	.800	.509	.826	.695	.694
biM3e	.787	.796	.517	.815	.673	.677
biI1b	.312	.323	.286	.308	.252	.241
biI2b	.393	.408	.300	.420	.270	.260
biCb	.227	.227	.144	.284	.065	.059
biP3b	.254	.256	.134	.310	.084	.075
biP4b	.396	.399	.225	.452	.237	.231
biM1b	.538	.543	.349	.585	.382	.377
biM2b	.709	.708	.471	.743	.573	.569
biM3b	.770	.771	.512	.792	.644	.643
pgid	.029	-.001	-.032	.070	-.171	-.169
geli	.913	.915	.606	.899	.944	.948

raxrpx	.962	.970	.632	.947	.913	.916
ranrpn	.950	.960	.631	.925	.922	.926
idcdccdc	.953	.963	.615	.932	.932	.936
idgogo	.915	.926	.599	.890	.942	.943
bicdl	.880	.879	.458	.900	.791	.794
bicdm	.593	.591	.575	.617	.478	.470
bicdc	.840	.840	.529	.867	.726	.726
bicr	.936	.934	.617	.933	.860	.864
bigo	.913	.923	.599	.900	.808	.812
idbiM3po	.924	.942	.584	.905	.926	.933
I1lI1b	.942	.933	.638	.957	.994	.993
I2lI2b	.947	.935	.641	.959	.990	.992
ClCb	.952	.939	.625	.972	.960	.964
P3lP3b	.972	.961	.619	.980	.954	.958
P4lP4b	.974	.960	.637	.980	.928	.931
M1lM1b	.989	.977	.622	.975	.919	.926
M2lM2b	1.000	.992	.622	.963	.919	.927
M3lM3b	.992	1.000	.605	.957	.911	.919
mf_area	.622	.605	1.000	.596	.633	.632
mflmfb	.963	.957	.596	1.000	.932	.935
I1eI1b	.919	.911	.633	.932	1.000	.997
I2eI2b	.927	.919	.632	.935	.997	1.000
CeCb	.927	.919	.623	.942	.978	.982
P3eP3b	.965	.957	.619	.975	.971	.975
P4eP4b	.973	.961	.637	.979	.939	.941
M1eM1b	.988	.977	.622	.973	.925	.932
M2eM2b	.996	.989	.621	.963	.924	.931
M3eM3b	.986	.997	.598	.954	.910	.918
mlmfl	.907	.900	.625	.916	.914	.919
mlidgn	.647	.645	.465	.679	.564	.550
cdmcdl	.957	.970	.620	.943	.898	.905
gocdc	.932	.941	.577	.912	.815	.824
cdcM1bM3b	.953	.971	.576	.904	.877	.887
cdcM3b	.969	.979	.605	.936	.902	.910
cdcM2eM3e	.903	.899	.576	.851	.831	.841
crlg	.928	.921	.631	.918	.902	.908

	CeCb	P3eP3b	P4eP4b	M1eM1b	M2eM2b	M3eM3b
sw__rt	.888	.908	.896	.913	.907	.921
I1w	.883	.915	.901	.925	.927	.941
I2w	.884	.907	.885	.908	.918	.934
Cw	.884	.905	.880	.902	.913	.925
P3w	.899	.921	.899	.916	.928	.943
P4w	.900	.927	.917	.923	.930	.954
M1w	.860	.889	.891	.889	.892	.923
M2w	.847	.874	.869	.872	.871	.905
M3w	.787	.826	.825	.818	.812	.856
lign	.979	.978	.952	.945	.941	.929
idgn	.974	.970	.939	.931	.932	.921
biI1l	.668	.690	.681	.663	.677	.705
biI2l	.776	.779	.768	.742	.758	.780
biCl	.772	.784	.771	.748	.760	.784
biP3l	.813	.855	.859	.848	.849	.871
biP4l	.680	.744	.770	.760	.763	.786
biM1l	.568	.647	.693	.675	.670	.687
biM2l	.457	.547	.613	.590	.576	.590
biM3l	.501	.585	.648	.624	.610	.630
biM3po	.585	.662	.720	.697	.679	.700
biI1e	.637	.658	.630	.628	.643	.683
biI2e	.725	.736	.706	.687	.704	.741
biCe	.871	.888	.877	.864	.874	.887
biP3e	.850	.894	.893	.878	.875	.896
biP4e	.809	.858	.874	.854	.849	.873
biM1e	.741	.806	.832	.808	.801	.825
biM2e	.706	.780	.820	.797	.784	.806
biM3e	.692	.769	.809	.788	.774	.800
biI1b	.247	.288	.328	.313	.333	.332
biI2b	.270	.347	.415	.400	.409	.421
biCb	.071	.169	.258	.247	.236	.238
biP3b	.090	.187	.285	.277	.257	.266
biP4b	.252	.340	.418	.404	.390	.406
biM1b	.411	.489	.559	.535	.527	.546
biM2b	.600	.673	.735	.708	.692	.707
biM3b	.668	.737	.789	.767	.755	.770
pgid	-.107	-.032	.073	.044	.007	-.011
geli	.929	.936	.901	.914	.919	.914

raxrpx	.911	.949	.948	.959	.958	.965
ranrpn	.912	.940	.926	.945	.950	.958
idcdccdc	.922	.948	.930	.945	.953	.960
idgogo	.911	.926	.892	.910	.921	.925
bicdl	.806	.860	.885	.877	.871	.871
bicdm	.503	.568	.640	.613	.572	.578
bicdc	.751	.815	.862	.846	.824	.829
bicr	.876	.918	.938	.929	.922	.928
bigo	.812	.872	.893	.902	.906	.917
idbiM3po	.918	.934	.899	.912	.923	.945
I1lI1b	.982	.985	.964	.951	.944	.930
I2lI2b	.983	.986	.967	.956	.949	.932
ClCb	.984	.982	.975	.959	.949	.933
P3lP3b	.964	.995	.992	.983	.969	.956
P4lP4b	.937	.979	.998	.988	.971	.955
M1lM1b	.928	.973	.988	.997	.985	.971
M2lM2b	.927	.965	.973	.988	.996	.986
M3lM3b	.919	.957	.961	.977	.989	.997
mf_area	.623	.619	.637	.622	.621	.598
mflmfb	.942	.975	.979	.973	.963	.954
I1eI1b	.978	.971	.939	.925	.924	.910
I2eI2b	.982	.975	.941	.932	.931	.918
CeCb	1.000	.975	.947	.930	.926	.915
P3eP3b	.975	1.000	.984	.975	.964	.954
P4eP4b	.947	.984	1.000	.988	.972	.957
M1eM1b	.930	.975	.988	1.000	.987	.973
M2eM2b	.926	.964	.972	.987	1.000	.986
M3eM3b	.915	.954	.957	.973	.986	1.000
mlmfl	.912	.919	.908	.917	.920	.897
mlidgn	.552	.635	.702	.666	.646	.654
cdmcdl	.907	.936	.936	.945	.953	.967
gocdc	.838	.891	.907	.919	.922	.936
cdcM1bM3b	.877	.911	.898	.927	.947	.964
cdcM3b	.901	.939	.933	.956	.965	.970
cdcM2eM3e	.830	.855	.847	.880	.896	.877
crlg	.903	.927	.923	.923	.920	.919

	mlmfl	mlidgn	cdmcdl	gocdc	cdcM1bM3b	cdcM3b
sw__rt	.850	.543	.926	.898	.941	.944
I1w	.880	.534	.945	.905	.967	.967
I2w	.890	.522	.947	.891	.960	.961
Cw	.888	.516	.943	.874	.957	.958
P3w	.875	.571	.953	.896	.959	.961
P4w	.857	.662	.965	.926	.947	.955
M1w	.806	.711	.933	.921	.903	.916
M2w	.784	.669	.919	.912	.898	.909
M3w	.725	.658	.879	.862	.856	.860
lign	.922	.583	.919	.842	.894	.920
idgn	.917	.565	.912	.825	.889	.913
biI1l	.574	.738	.712	.669	.631	.661
biI2l	.710	.737	.799	.727	.713	.749
biCl	.709	.755	.807	.770	.711	.756
biP3l	.768	.799	.881	.852	.806	.847
biP4l	.659	.872	.799	.798	.697	.749
biM1l	.544	.904	.704	.740	.585	.649
biM2l	.420	.910	.607	.682	.480	.548
biM3l	.446	.891	.641	.724	.533	.587
biM3po	.512	.872	.705	.784	.612	.660
biI1e	.654	.595	.701	.649	.637	.667
biI2e	.679	.701	.760	.691	.684	.718
biCe	.830	.739	.896	.841	.839	.876
biP3e	.812	.810	.906	.874	.834	.875
biP4e	.766	.866	.881	.871	.792	.839
biM1e	.690	.913	.830	.848	.730	.782
biM2e	.657	.917	.812	.855	.718	.769
biM3e	.635	.892	.805	.853	.722	.764
biI1b	.284	.583	.324	.350	.255	.295
biI2b	.303	.801	.423	.493	.306	.361
biCb	.138	.713	.242	.365	.122	.189
biP3b	.138	.766	.280	.398	.148	.220
biP4b	.256	.837	.422	.513	.288	.355
biM1b	.375	.884	.560	.643	.430	.492
biM2b	.533	.917	.720	.786	.605	.663
biM3b	.598	.911	.782	.835	.680	.730
pgid	-.134	.481	-.015	.141	-.123	-.063
geli	.927	.504	.900	.839	.900	.918

raxrpx	.890	.661	.967	.947	.959	.982
ranrpn	.903	.587	.958	.921	.966	.980
idcdccdc	.908	.609	.961	.918	.968	.985
idgogo	.908	.494	.917	.829	.944	.950
bicdl	.764	.782	.895	.893	.831	.869
bicdm	.474	.747	.584	.671	.521	.582
bicdc	.710	.844	.851	.884	.778	.829
bicr	.812	.778	.942	.927	.883	.917
bigo	.801	.773	.932	.929	.891	.920
idbiM3po	.890	.538	.939	.871	.955	.953
I1lI1b	.921	.610	.917	.848	.887	.917
I2lI2b	.919	.610	.917	.853	.886	.915
ClCb	.910	.641	.925	.881	.880	.914
P3lP3b	.913	.669	.937	.905	.907	.939
P4lP4b	.902	.713	.934	.913	.896	.933
M1lM1b	.908	.677	.945	.926	.926	.954
M2lM2b	.907	.647	.957	.932	.953	.969
M3lM3b	.900	.645	.970	.941	.971	.979
mf_area	.625	.465	.620	.577	.576	.605
mflmfb	.916	.679	.943	.912	.904	.936
I1eI1b	.914	.564	.898	.815	.877	.902
I2eI2b	.919	.550	.905	.824	.887	.910
CeCb	.912	.552	.907	.838	.877	.901
P3eP3b	.919	.635	.936	.891	.911	.939
P4eP4b	.908	.702	.936	.907	.898	.933
M1eM1b	.917	.666	.945	.919	.927	.956
M2eM2b	.920	.646	.953	.922	.947	.965
M3eM3b	.897	.654	.967	.936	.964	.970
mlmfl	1.000	.492	.878	.798	.868	.895
mlidgn	.492	1.000	.665	.706	.535	.606
cdmcdl	.878	.665	1.000	.932	.952	.967
gocdc	.798	.706	.932	1.000	.923	.946
cdcM1bM3b	.868	.535	.952	.923	1.000	.988
cdcM3b	.895	.606	.967	.946	.988	1.000
cdcM2eM3e	.843	.433	.884	.857	.949	.947
crlg	.843	.607	.903	.873	.894	.911

	cdcM2eM3e	crlg
sw__rt	.895	.885
I1w	.920	.884
I2w	.901	.872
Cw	.909	.863
P3w	.896	.875
P4w	.861	.878
M1w	.804	.844
M2w	.807	.849
M3w	.782	.803
lign	.847	.913
idgn	.838	.901
biI1l	.498	.618
biI2l	.599	.709
biCl	.593	.699
biP3l	.698	.770
biP4l	.580	.660
biM1l	.477	.581
biM2l	.376	.505
biM3l	.423	.578
biM3po	.505	.661
biI1e	.514	.585
biI2e	.551	.659
biCe	.748	.823
biP3e	.725	.823
biP4e	.674	.791
biM1e	.610	.746
biM2e	.604	.732
biM3e	.602	.749
biI1b	.178	.185
biI2b	.207	.248
biCb	.054	.125
biP3b	.084	.179
biP4b	.201	.334
biM1b	.330	.485
biM2b	.506	.654
biM3b	.575	.711
pgid	-.133	-.010
geli	.846	.859

raxrpx	.901	.921
ranrpn	.912	.905
idcdccdc	.913	.908
idgogo	.902	.877
bicdl	.790	.791
bicdm	.492	.599
bicdc	.738	.780
bicr	.815	.916
bigo	.825	.826
idbiM3po	.879	.890
I1lI1b	.840	.920
I2lI2b	.840	.923
ClCb	.835	.917
P3lP3b	.858	.923
P4lP4b	.848	.921
M1lM1b	.881	.929
M2lM2b	.903	.928
M3lM3b	.899	.921
mf_area	.576	.631
mflmfb	.851	.918
I1eI1b	.831	.902
I2eI2b	.841	.908
CeCb	.830	.903
P3eP3b	.855	.927
P4eP4b	.847	.923
M1eM1b	.880	.923
M2eM2b	.896	.920
M3eM3b	.877	.919
mlmfl	.843	.843
mlidgn	.433	.607
cdmcdl	.884	.903
gocdc	.857	.873
cdcM1bM3b	.949	.894
cdcM3b	.947	.911
cdcM2eM3e	1.000	.835
crlg	.835	1.000

Upper Dentition Variable Cross-Correlation Similarity Matrix

	MD_up_I1	MD_up__I1_est	MD_up__I1C	MD_up_I2_	MD_up_I2_est
MD_up_I1	1.000	1.000	.979	.941	.940
MD_up__I1_est	1.000	1.000	.979	.940	.940
MD_up__I1C	.979	.979	1.000	.924	.924
MD_up_I2_	.941	.940	.924	1.000	1.000
MD_up_I2_est	.940	.940	.924	1.000	1.000
MD_up_I2_C	.910	.909	.930	.939	.939
MD_up_C	.815	.815	.851	.830	.830
Md_up_C_est	.815	.815	.851	.830	.830
MD_up_CC	.787	.786	.822	.797	.797
MD_up_P3	.785	.785	.806	.829	.829
MD_up_P3_est	.785	.785	.806	.829	.829
MD_up_P3C	.707	.707	.734	.748	.748
MD_up_P4	.774	.776	.808	.803	.802
MD_up_P4_est	.772	.773	.805	.799	.798
MD_up_P4C	.714	.716	.751	.735	.734
MD_up_M1	.839	.840	.872	.858	.857
MD_up_M1_est	.837	.838	.869	.854	.853
MD_up_M1C	.746	.748	.784	.790	.789
MD_up_M2	.783	.785	.829	.799	.799
MD_up_M2_est	.783	.785	.829	.799	.799
MD_up_M2C	.688	.691	.742	.720	.719
MD_up_M3	.723	.726	.756	.741	.741
MD_up_M3_est	.723	.726	.756	.741	.741
MD_up_M3C	.605	.608	.658	.638	.637
BL_up_I1	.921	.920	.926	.944	.944
BL_up_I1_C	.902	.901	.918	.927	.926
BL_up_I2_	.881	.880	.894	.936	.936
BL_up_I2C	.877	.876	.899	.918	.919
BL_up_C	.788	.788	.814	.840	.840
BL_up_CC	.769	.769	.798	.820	.820
BL_up_P3	.866	.867	.898	.867	.866
BL_up_P3_est	.866	.867	.898	.867	.866
BL_up_P3C	.844	.845	.876	.837	.836
BL_up_P4	.833	.834	.873	.838	.837
BL_up_P4_est	.833	.834	.873	.838	.837
BL_up_P4C	.824	.825	.867	.818	.817

BL_up_M1	.873	.874	.901	.879	.877
BL_up_M1_est	.873	.874	.901	.879	.877
BL_up_M1C	.872	.873	.904	.870	.869
BLup_M2	.823	.825	.863	.830	.828
BL_up_M2_est	.823	.825	.863	.830	.828
BL_up_M2C	.813	.815	.861	.809	.808
BL_up_M3	.793	.796	.829	.793	.792
BL_up_M3_C	.754	.758	.794	.746	.744

	MD_up_I2_C	MD_up_C	Md_up_C_est	MD_up_CC	MD_up_P3
MD_up_I1	.910	.815	.815	.787	.785
MD_up__I1_est	.909	.815	.815	.786	.785
MD_up__I1C	.930	.851	.851	.822	.806
MD_up_I2_	.939	.830	.830	.797	.829
MD_up_I2_est	.939	.830	.830	.797	.829
MD_up_I2_C	1.000	.905	.905	.880	.896
MD_up_C	.905	1.000	1.000	.992	.860
Md_up_C_est	.905	1.000	1.000	.992	.860
MD_up_CC	.880	.992	.992	1.000	.835
MD_up_P3	.896	.860	.860	.835	1.000
MD_up_P3_est	.896	.860	.860	.835	1.000
MD_up_P3C	.850	.840	.840	.826	.976
MD_up_P4	.883	.875	.875	.846	.967
MD_up_P4_est	.880	.871	.871	.842	.965
MD_up_P4C	.839	.832	.832	.805	.938
MD_up_M1	.917	.885	.885	.856	.957
MD_up_M1_est	.914	.881	.881	.851	.955
MD_up_M1C	.871	.841	.841	.817	.960
MD_up_M2	.890	.888	.888	.864	.944
MD_up_M2_est	.890	.888	.888	.864	.944
MD_up_M2C	.834	.835	.835	.812	.925
MD_up_M3	.837	.869	.869	.856	.933
MD_up_M3_est	.837	.869	.869	.856	.933
MD_up_M3C	.759	.810	.810	.790	.897
BL_up_I1	.957	.909	.909	.885	.872
BL_up_I1_C	.946	.904	.904	.880	.856
BL_up_I2_	.949	.891	.891	.862	.918
BL_up_I2C	.952	.912	.912	.886	.929
BL_up_C	.897	.952	.952	.934	.913
BL_up_CC	.881	.951	.951	.936	.901
BL_up_P3	.923	.879	.879	.845	.922
BL_up_P3_est	.923	.879	.879	.845	.922
BL_up_P3C	.903	.857	.857	.822	.908
BL_up_P4	.910	.861	.861	.824	.928
BL_up_P4_est	.910	.861	.861	.824	.928
BL_up_P4C	.905	.868	.868	.832	.922
BL_up_M1	.926	.861	.861	.825	.931
BL_up_M1_est	.926	.861	.861	.825	.931

BL_up_M1C	.920	.860	.860	.822	.918
BLup_M2	.903	.868	.868	.834	.930
BL_up_M2_est	.903	.868	.868	.834	.930
BL_up_M2C	.893	.862	.862	.829	.916
BL_up_M3	.870	.862	.862	.832	.927
BL_up_M3_C	.838	.833	.833	.804	.894

	MD_up_P3_est	MD_up_P3C	MD_up_P4	MD_up_P4_est	MD_up_P4C
MD_up_I1	.785	.707	.774	.772	.714
MD_up__I1_est	.785	.707	.776	.773	.716
MD_up__I1C	.806	.734	.808	.805	.751
MD_up_I2_	.829	.748	.803	.799	.735
MD_up_I2_est	.829	.748	.802	.798	.734
MD_up_I2_C	.896	.850	.883	.880	.839
MD_up_C	.860	.840	.875	.871	.832
Md_up_C_est	.860	.840	.875	.871	.832
MD_up_CC	.835	.826	.846	.842	.805
MD_up_P3	1.000	.976	.967	.965	.938
MD_up_P3_est	1.000	.976	.967	.965	.938
MD_up_P3C	.976	1.000	.947	.944	.940
MD_up_P4	.967	.947	1.000	.999	.968
MD_up_P4_est	.965	.944	.999	1.000	.967
MD_up_P4C	.938	.940	.968	.967	1.000
MD_up_M1	.957	.919	.970	.969	.928
MD_up_M1_est	.955	.917	.971	.970	.929
MD_up_M1C	.960	.944	.975	.974	.947
MD_up_M2	.944	.924	.971	.970	.932
MD_up_M2_est	.944	.924	.971	.970	.932
MD_up_M2C	.925	.929	.961	.961	.942
MD_up_M3	.933	.932	.940	.940	.904
MD_up_M3_est	.933	.932	.940	.940	.904
MD_up_M3C	.897	.911	.932	.932	.910
BL_up_I1	.872	.809	.864	.861	.785
BL_up_I1_C	.856	.794	.857	.855	.767
BL_up_I2_	.918	.861	.889	.883	.823
BL_up_I2C	.929	.877	.907	.902	.846
BL_up_C	.913	.879	.911	.908	.861
BL_up_CC	.901	.867	.901	.898	.850
BL_up_P3	.922	.879	.943	.943	.904
BL_up_P3_est	.922	.879	.943	.943	.904
BL_up_P3C	.908	.881	.931	.931	.888
BL_up_P4	.928	.892	.953	.954	.911
BL_up_P4_est	.928	.892	.953	.954	.911
BL_up_P4C	.922	.894	.945	.946	.902
BL_up_M1	.931	.874	.946	.947	.904
BL_up_M1_est	.931	.874	.946	.947	.904

BL_up_M1C	.918	.860	.939	.940	.895
BLup_M2	.930	.884	.950	.951	.902
BL_up_M2_est	.930	.884	.950	.951	.902
BL_up_M2C	.916	.875	.946	.948	.901
BL_up_M3	.927	.889	.945	.946	.898
BL_up_M3_C	.894	.869	.921	.924	.890

	MD_up_M1	MD_up_M1_est	MD_up_M1C	MD_up_M2	MD_up_M2_est
MD_up_I1	.839	.837	.746	.783	.783
MD_up__I1_est	.840	.838	.748	.785	.785
MD_up__I1C	.872	.869	.784	.829	.829
MD_up_I2_	.858	.854	.790	.799	.799
MD_up_I2_est	.857	.853	.789	.799	.799
MD_up_I2_C	.917	.914	.871	.890	.890
MD_up_C	.885	.881	.841	.888	.888
Md_up_C_est	.885	.881	.841	.888	.888
MD_up_CC	.856	.851	.817	.864	.864
MD_up_P3	.957	.955	.960	.944	.944
MD_up_P3_est	.957	.955	.960	.944	.944
MD_up_P3C	.919	.917	.944	.924	.924
MD_up_P4	.970	.971	.975	.971	.971
MD_up_P4_est	.969	.970	.974	.970	.970
MD_up_P4C	.928	.929	.947	.932	.932
MD_up_M1	1.000	1.000	.971	.971	.971
MD_up_M1_est	1.000	1.000	.971	.972	.972
MD_up_M1C	.971	.971	1.000	.961	.961
MD_up_M2	.971	.972	.961	1.000	1.000
MD_up_M2_est	.971	.972	.961	1.000	1.000
MD_up_M2C	.940	.942	.963	.968	.968
MD_up_M3	.926	.928	.934	.956	.956
MD_up_M3_est	.926	.928	.934	.956	.956
MD_up_M3C	.885	.888	.919	.936	.936
BL_up_I1	.911	.907	.846	.877	.877
BL_up_I1_C	.905	.902	.845	.875	.875
BL_up_I2_	.925	.921	.872	.891	.891
BL_up_I2C	.944	.940	.892	.916	.916
BL_up_C	.922	.920	.892	.906	.906
BL_up_CC	.913	.910	.884	.898	.898
BL_up_P3	.967	.968	.928	.957	.957
BL_up_P3_est	.967	.968	.928	.957	.957
BL_up_P3C	.948	.948	.915	.945	.945
BL_up_P4	.961	.963	.933	.967	.967
BL_up_P4_est	.961	.963	.933	.967	.967
BL_up_P4C	.947	.948	.926	.958	.958
BL_up_M1	.975	.976	.937	.947	.947
BL_up_M1_est	.975	.976	.937	.947	.947

BL_up_M1C	.969	.970	.930	.948	.948
BLup_M2	.967	.969	.938	.973	.973
BL_up_M2_est	.967	.969	.938	.973	.973
BL_up_M2C	.961	.963	.935	.974	.974
BL_up_M3	.947	.951	.928	.960	.960
BL_up_M3_C	.921	.926	.911	.941	.941

	MD_up_M2C	MD_up_M3	MD_up_M3_est	MD_up_M3C	BL_up_I1
MD_up_I1	.688	.723	.723	.605	.921
MD_up__I1_est	.691	.726	.726	.608	.920
MD_up__I1C	.742	.756	.756	.658	.926
MD_up_I2_	.720	.741	.741	.638	.944
MD_up_I2_est	.719	.741	.741	.637	.944
MD_up_I2_C	.834	.837	.837	.759	.957
MD_up_C	.835	.869	.869	.810	.909
Md_up_C_est	.835	.869	.869	.810	.909
MD_up_CC	.812	.856	.856	.790	.885
MD_up_P3	.925	.933	.933	.897	.872
MD_up_P3_est	.925	.933	.933	.897	.872
MD_up_P3C	.929	.932	.932	.911	.809
MD_up_P4	.961	.940	.940	.932	.864
MD_up_P4_est	.961	.940	.940	.932	.861
MD_up_P4C	.942	.904	.904	.910	.785
MD_up_M1	.940	.926	.926	.885	.911
MD_up_M1_est	.942	.928	.928	.888	.907
MD_up_M1C	.963	.934	.934	.919	.846
MD_up_M2	.968	.956	.956	.936	.877
MD_up_M2_est	.968	.956	.956	.936	.877
MD_up_M2C	1.000	.952	.952	.956	.803
MD_up_M3	.952	1.000	1.000	.961	.832
MD_up_M3_est	.952	1.000	1.000	.961	.832
MD_up_M3C	.956	.961	.961	1.000	.738
BL_up_I1	.803	.832	.832	.738	1.000
BL_up_I1_C	.806	.826	.826	.740	.990
BL_up_I2_	.833	.853	.853	.774	.968
BL_up_I2C	.862	.881	.881	.806	.969
BL_up_C	.872	.892	.892	.832	.917
BL_up_CC	.867	.888	.888	.827	.905
BL_up_P3	.904	.899	.899	.860	.910
BL_up_P3_est	.904	.899	.899	.860	.910
BL_up_P3C	.907	.897	.897	.864	.881
BL_up_P4	.929	.919	.919	.892	.888
BL_up_P4_est	.929	.919	.919	.892	.888
BL_up_P4C	.923	.918	.918	.892	.878
BL_up_M1	.902	.888	.888	.835	.918
BL_up_M1_est	.902	.888	.888	.835	.918

BL_up_M1C	.901	.883	.883	.837	.912
BLup_M2	.931	.924	.924	.886	.895
BL_up_M2_est	.931	.924	.924	.886	.895
BL_up_M2C	.936	.922	.922	.891	.878
BL_up_M3	.928	.954	.954	.914	.869
BL_up_M3_C	.921	.945	.945	.913	.825

	BL_up_I1_C	BL_up_I2_	BL_up_I2C	BL_up_C	BL_up_CC
MD_up_I1	.902	.881	.877	.788	.769
MD_up__I1_est	.901	.880	.876	.788	.769
MD_up__I1C	.918	.894	.899	.814	.798
MD_up_I2_	.927	.936	.918	.840	.820
MD_up_I2_est	.926	.936	.919	.840	.820
MD_up_I2_C	.946	.949	.952	.897	.881
MD_up_C	.904	.891	.912	.952	.951
Md_up_C_est	.904	.891	.912	.952	.951
MD_up_CC	.880	.862	.886	.934	.936
MD_up_P3	.856	.918	.929	.913	.901
MD_up_P3_est	.856	.918	.929	.913	.901
MD_up_P3C	.794	.861	.877	.879	.867
MD_up_P4	.857	.889	.907	.911	.901
MD_up_P4_est	.855	.883	.902	.908	.898
MD_up_P4C	.767	.823	.846	.861	.850
MD_up_M1	.905	.925	.944	.922	.913
MD_up_M1_est	.902	.921	.940	.920	.910
MD_up_M1C	.845	.872	.892	.892	.884
MD_up_M2	.875	.891	.916	.906	.898
MD_up_M2_est	.875	.891	.916	.906	.898
MD_up_M2C	.806	.833	.862	.872	.867
MD_up_M3	.826	.853	.881	.892	.888
MD_up_M3_est	.826	.853	.881	.892	.888
MD_up_M3C	.740	.774	.806	.832	.827
BL_up_I1	.990	.968	.969	.917	.905
BL_up_I1_C	1.000	.952	.959	.906	.895
BL_up_I2_	.952	1.000	.993	.930	.915
BL_up_I2C	.959	.993	1.000	.944	.931
BL_up_C	.906	.930	.944	1.000	.998
BL_up_CC	.895	.915	.931	.998	1.000
BL_up_P3	.909	.913	.932	.891	.879
BL_up_P3_est	.909	.913	.932	.891	.879
BL_up_P3C	.887	.882	.906	.856	.843
BL_up_P4	.888	.900	.919	.879	.866
BL_up_P4_est	.888	.900	.919	.879	.866
BL_up_P4C	.881	.885	.907	.877	.865
BL_up_M1	.913	.927	.939	.901	.889
BL_up_M1_est	.913	.927	.939	.901	.889

BL_up_M1C	.909	.913	.928	.893	.881
BLup_M2	.894	.903	.924	.901	.892
BL_up_M2_est	.894	.903	.924	.901	.892
BL_up_M2C	.881	.882	.908	.888	.880
BL_up_M3	.863	.880	.905	.899	.893
BL_up_M3_C	.822	.831	.861	.871	.864

	BL_up_P3	BL_up_P3_est	BL_up_P3C	BL_up_P4	BL_up_P4_est
MD_up_I1	.866	.866	.844	.833	.833
MD_up__I1_est	.867	.867	.845	.834	.834
MD_up__I1C	.898	.898	.876	.873	.873
MD_up_I2_	.867	.867	.837	.838	.838
MD_up_I2_est	.866	.866	.836	.837	.837
MD_up_I2_C	.923	.923	.903	.910	.910
MD_up_C	.879	.879	.857	.861	.861
Md_up_C_est	.879	.879	.857	.861	.861
MD_up_CC	.845	.845	.822	.824	.824
MD_up_P3	.922	.922	.908	.928	.928
MD_up_P3_est	.922	.922	.908	.928	.928
MD_up_P3C	.879	.879	.881	.892	.892
MD_up_P4	.943	.943	.931	.953	.953
MD_up_P4_est	.943	.943	.931	.954	.954
MD_up_P4C	.904	.904	.888	.911	.911
MD_up_M1	.967	.967	.948	.961	.961
MD_up_M1_est	.968	.968	.948	.963	.963
MD_up_M1C	.928	.928	.915	.933	.933
MD_up_M2	.957	.957	.945	.967	.967
MD_up_M2_est	.957	.957	.945	.967	.967
MD_up_M2C	.904	.904	.907	.929	.929
MD_up_M3	.899	.899	.897	.919	.919
MD_up_M3_est	.899	.899	.897	.919	.919
MD_up_M3C	.860	.860	.864	.892	.892
BL_up_I1	.910	.910	.881	.888	.888
BL_up_I1_C	.909	.909	.887	.888	.888
BL_up_I2_	.913	.913	.882	.900	.900
BL_up_I2C	.932	.932	.906	.919	.919
BL_up_C	.891	.891	.856	.879	.879
BL_up_CC	.879	.879	.843	.866	.866
BL_up_P3	1.000	1.000	.982	.984	.984
BL_up_P3_est	1.000	1.000	.982	.984	.984
BL_up_P3C	.982	.982	1.000	.981	.981
BL_up_P4	.984	.984	.981	1.000	1.000
BL_up_P4_est	.984	.984	.981	1.000	1.000
BL_up_P4C	.974	.974	.981	.994	.994
BL_up_M1	.979	.979	.950	.968	.968
BL_up_M1_est	.979	.979	.950	.968	.968

BL_up_M1C	.981	.981	.955	.972	.972
BLup_M2	.977	.977	.958	.979	.979
BL_up_M2_est	.977	.977	.958	.979	.979
BL_up_M2C	.973	.973	.958	.977	.977
BL_up_M3	.951	.951	.934	.962	.962
BL_up_M3_C	.936	.936	.927	.950	.950

	BL_up_P4C	BL_up_M1	BL_up_M1_est	BL_up_M1C	BLup_M2
MD_up_I1	.824	.873	.873	.872	.823
MD_up__I1_est	.825	.874	.874	.873	.825
MD_up__I1C	.867	.901	.901	.904	.863
MD_up_I2_	.818	.879	.879	.870	.830
MD_up_I2_est	.817	.877	.877	.869	.828
MD_up_I2_C	.905	.926	.926	.920	.903
MD_up_C	.868	.861	.861	.860	.868
Md_up_C_est	.868	.861	.861	.860	.868
MD_up_CC	.832	.825	.825	.822	.834
MD_up_P3	.922	.931	.931	.918	.930
MD_up_P3_est	.922	.931	.931	.918	.930
MD_up_P3C	.894	.874	.874	.860	.884
MD_up_P4	.945	.946	.946	.939	.950
MD_up_P4_est	.946	.947	.947	.940	.951
MD_up_P4C	.902	.904	.904	.895	.902
MD_up_M1	.947	.975	.975	.969	.967
MD_up_M1_est	.948	.976	.976	.970	.969
MD_up_M1C	.926	.937	.937	.930	.938
MD_up_M2	.958	.947	.947	.948	.973
MD_up_M2_est	.958	.947	.947	.948	.973
MD_up_M2C	.923	.902	.902	.901	.931
MD_up_M3	.918	.888	.888	.883	.924
MD_up_M3_est	.918	.888	.888	.883	.924
MD_up_M3C	.892	.835	.835	.837	.886
BL_up_I1	.878	.918	.918	.912	.895
BL_up_I1_C	.881	.913	.913	.909	.894
BL_up_I2_	.885	.927	.927	.913	.903
BL_up_I2C	.907	.939	.939	.928	.924
BL_up_C	.877	.901	.901	.893	.901
BL_up_CC	.865	.889	.889	.881	.892
BL_up_P3	.974	.979	.979	.981	.977
BL_up_P3_est	.974	.979	.979	.981	.977
BL_up_P3C	.981	.950	.950	.955	.958
BL_up_P4	.994	.968	.968	.972	.979
BL_up_P4_est	.994	.968	.968	.972	.979
BL_up_P4C	1.000	.957	.957	.963	.973
BL_up_M1	.957	1.000	1.000	.995	.980
BL_up_M1_est	.957	1.000	1.000	.995	.980

BL_up_M1C	.963	.995	.995	1.000	.985
BLup_M2	.973	.980	.980	.985	1.000
BL_up_M2_est	.973	.980	.980	.985	1.000
BL_up_M2C	.973	.973	.973	.981	.996
BL_up_M3	.960	.955	.955	.958	.983
BL_up_M3_C	.953	.929	.929	.937	.966

	BL_up_M2_est	BL_up_M2C	BL_up_M3	BL_up_M3_C
MD_up_I1	.823	.813	.793	.754
MD_up__I1_est	.825	.815	.796	.758
MD_up__I1C	.863	.861	.829	.794
MD_up_I2_	.830	.809	.793	.746
MD_up_I2_est	.828	.808	.792	.744
MD_up_I2_C	.903	.893	.870	.838
MD_up_C	.868	.862	.862	.833
Md_up_C_est	.868	.862	.862	.833
MD_up_CC	.834	.829	.832	.804
MD_up_P3	.930	.916	.927	.894
MD_up_P3_est	.930	.916	.927	.894
MD_up_P3C	.884	.875	.889	.869
MD_up_P4	.950	.946	.945	.921
MD_up_P4_est	.951	.948	.946	.924
MD_up_P4C	.902	.901	.898	.890
MD_up_M1	.967	.961	.947	.921
MD_up_M1_est	.969	.963	.951	.926
MD_up_M1C	.938	.935	.928	.911
MD_up_M2	.973	.974	.960	.941
MD_up_M2_est	.973	.974	.960	.941
MD_up_M2C	.931	.936	.928	.921
MD_up_M3	.924	.922	.954	.945
MD_up_M3_est	.924	.922	.954	.945
MD_up_M3C	.886	.891	.914	.913
BL_up_I1	.895	.878	.869	.825
BL_up_I1_C	.894	.881	.863	.822
BL_up_I2_	.903	.882	.880	.831
BL_up_I2C	.924	.908	.905	.861
BL_up_C	.901	.888	.899	.871
BL_up_CC	.892	.880	.893	.864
BL_up_P3	.977	.973	.951	.936
BL_up_P3_est	.977	.973	.951	.936
BL_up_P3C	.958	.958	.934	.927
BL_up_P4	.979	.977	.962	.950
BL_up_P4_est	.979	.977	.962	.950
BL_up_P4C	.973	.973	.960	.953
BL_up_M1	.980	.973	.955	.929
BL_up_M1_est	.980	.973	.955	.929

BL_up_M1C	.985	.981	.958	.937
BLup_M2	1.000	.996	.983	.966
BL_up_M2_est	1.000	.996	.983	.966
BL_up_M2C	.996	1.000	.979	.969
BL_up_M3	.983	.979	1.000	.986
BL_up_M3_C	.966	.969	.986	1.000

Lower Dentition Variable Cross-Correlation Similarity Matrix

	MD__low_I1	MD_low_I1_est	MD__low_I1C	MD_low_I2_
MD__low_I1	1.000	.999	.930	.971
MD_low_I1_est	.999	1.000	.928	.972
MD__low_I1C	.930	.928	1.000	.925
MD_low_I2_	.971	.972	.925	1.000
MD_low_I2_est	.970	.971	.923	1.000
MD_low_I2C	.933	.933	.960	.952
MD_low_C	.803	.802	.887	.829
MD_low_C_est	.803	.802	.887	.829
MD_low_CC	.771	.769	.871	.792
MD_low_P3	.742	.742	.856	.763
MD_low_P3_est	.742	.742	.856	.763
MD_low_P3C	.701	.699	.829	.706
MD_low_P4	.781	.785	.853	.828
MD_low_P4_est	.781	.785	.853	.828
MD_low_P4C	.737	.741	.818	.769
MD_low_M1	.834	.838	.875	.891
MD_low_M1_est	.830	.835	.870	.888
MD_low_M1C	.795	.800	.860	.844
MD_low_M2	.801	.804	.880	.847
MD_low_M2_est	.799	.803	.877	.845
MD_low_M2C	.768	.773	.850	.806
MD_low_M3	.687	.692	.793	.724
MD_low_M3_est	.682	.688	.786	.720
MD_low_M3C	.621	.627	.751	.646
MD_low_M3C_est	.621	.627	.751	.646
BL_low_I1	.882	.880	.920	.893
BL_low_I1C	.847	.845	.912	.872
BL_low_I2_	.892	.891	.935	.925
BL_low_I2C	.864	.862	.916	.901
BL_low_C	.789	.787	.883	.827
BL_low_CC	.761	.758	.864	.803
BL_low_P3	.812	.816	.877	.870
BL_low_P3C	.807	.810	.876	.865
BL_low_P4	.825	.832	.879	.879
BL_low_P4C	.796	.802	.870	.847
BL_low_M1	.797	.805	.818	.866

BL_low_M1C	.787	.795	.829	.854
BL_low_M2	.804	.809	.872	.869
BL_low_M2C	.793	.799	.872	.850
BL_low_M3	.822	.826	.884	.871
BL_low_M3_est	.822	.826	.884	.871
BL_low_M3C	.812	.817	.879	.857

	MD_low_I2_est	MD_low_I2C	MD_low_C	MD_low_C_est
MD__low_I1	.970	.933	.803	.803
MD_low_I1_est	.971	.933	.802	.802
MD__low_I1C	.923	.960	.887	.887
MD_low_I2_	1.000	.952	.829	.829
MD_low_I2_est	1.000	.951	.827	.827
MD_low_I2C	.951	1.000	.885	.885
MD_low_C	.827	.885	1.000	1.000
MD_low_C_est	.827	.885	1.000	1.000
MD_low_CC	.789	.855	.991	.991
MD_low_P3	.762	.845	.929	.929
MD_low_P3_est	.762	.845	.929	.929
MD_low_P3C	.704	.799	.907	.907
MD_low_P4	.829	.866	.880	.880
MD_low_P4_est	.829	.866	.880	.880
MD_low_P4C	.771	.815	.863	.863
MD_low_M1	.894	.909	.858	.858
MD_low_M1_est	.891	.905	.854	.854
MD_low_M1C	.847	.893	.858	.858
MD_low_M2	.848	.903	.893	.893
MD_low_M2_est	.847	.901	.890	.890
MD_low_M2C	.809	.874	.870	.870
MD_low_M3	.727	.794	.850	.850
MD_low_M3_est	.724	.788	.843	.843
MD_low_M3C	.649	.733	.802	.802
MD_low_M3C_est	.649	.733	.802	.802
BL_low_I1	.890	.912	.912	.912
BL_low_I1C	.870	.884	.918	.918
BL_low_I2_	.924	.935	.918	.918
BL_low_I2C	.899	.916	.920	.920
BL_low_C	.825	.878	.978	.978
BL_low_CC	.800	.859	.973	.973
BL_low_P3	.872	.914	.905	.905
BL_low_P3C	.866	.906	.909	.909
BL_low_P4	.883	.909	.866	.866
BL_low_P4C	.851	.890	.848	.848
BL_low_M1	.871	.875	.795	.795
BL_low_M1C	.859	.877	.825	.825
BL_low_M2	.872	.903	.884	.884

BL_low_M2C	.853	.890	.893	.893
BL_low_M3	.873	.908	.891	.891
BL_low_M3_est	.873	.908	.891	.891
BL_low_M3C	.860	.903	.897	.897

	MD_low_CC	MD_low_P3	MD_low_P3_est	MD_low_P3C
MD__low_I1	.771	.742	.742	.701
MD_low_I1_est	.769	.742	.742	.699
MD__low_I1C	.871	.856	.856	.829
MD_low_I2_	.792	.763	.763	.706
MD_low_I2_est	.789	.762	.762	.704
MD_low_I2C	.855	.845	.845	.799
MD_low_C	.991	.929	.929	.907
MD_low_C_est	.991	.929	.929	.907
MD_low_CC	1.000	.930	.930	.913
MD_low_P3	.930	1.000	1.000	.982
MD_low_P3_est	.930	1.000	1.000	.982
MD_low_P3C	.913	.982	.982	1.000
MD_low_P4	.852	.925	.925	.889
MD_low_P4_est	.852	.925	.925	.889
MD_low_P4C	.849	.931	.931	.910
MD_low_M1	.809	.848	.848	.797
MD_low_M1_est	.804	.844	.844	.793
MD_low_M1C	.811	.876	.876	.836
MD_low_M2	.865	.925	.925	.882
MD_low_M2_est	.862	.923	.923	.879
MD_low_M2C	.838	.919	.919	.880
MD_low_M3	.838	.928	.928	.898
MD_low_M3_est	.831	.922	.922	.891
MD_low_M3C	.802	.916	.916	.898
MD_low_M3C_est	.802	.916	.916	.898
BL_low_I1	.901	.840	.840	.802
BL_low_I1C	.912	.864	.864	.827
BL_low_I2_	.895	.871	.871	.826
BL_low_I2C	.902	.888	.888	.845
BL_low_C	.974	.908	.908	.876
BL_low_CC	.970	.896	.896	.864
BL_low_P3	.864	.871	.871	.826
BL_low_P3C	.871	.879	.879	.834
BL_low_P4	.823	.856	.856	.802
BL_low_P4C	.803	.848	.848	.800
BL_low_M1	.735	.761	.761	.694
BL_low_M1C	.771	.799	.799	.734
BL_low_M2	.844	.868	.868	.813

BL_low_M2C	.859	.889	.889	.840
BL_low_M3	.858	.895	.895	.846
BL_low_M3_est	.858	.895	.895	.846
BL_low_M3C	.866	.905	.905	.858

	MD_low_P4	MD_low_P4_est	MD_low_P4C	MD_low_M1
MD__low_I1	.781	.781	.737	.834
MD_low_I1_est	.785	.785	.741	.838
MD__low_I1C	.853	.853	.818	.875
MD_low_I2_	.828	.828	.769	.891
MD_low_I2_est	.829	.829	.771	.894
MD_low_I2C	.866	.866	.815	.909
MD_low_C	.880	.880	.863	.858
MD_low_C_est	.880	.880	.863	.858
MD_low_CC	.852	.852	.849	.809
MD_low_P3	.925	.925	.931	.848
MD_low_P3_est	.925	.925	.931	.848
MD_low_P3C	.889	.889	.910	.797
MD_low_P4	1.000	1.000	.964	.954
MD_low_P4_est	1.000	1.000	.964	.954
MD_low_P4C	.964	.964	1.000	.892
MD_low_M1	.954	.954	.892	1.000
MD_low_M1_est	.953	.953	.892	1.000
MD_low_M1C	.955	.955	.917	.980
MD_low_M2	.977	.977	.941	.962
MD_low_M2_est	.977	.977	.941	.962
MD_low_M2C	.962	.962	.944	.943
MD_low_M3	.947	.947	.941	.880
MD_low_M3_est	.945	.945	.939	.879
MD_low_M3C	.901	.901	.917	.812
MD_low_M3C_est	.901	.901	.917	.812
BL_low_I1	.845	.845	.793	.838
BL_low_I1C	.867	.867	.824	.851
BL_low_I2_	.906	.906	.849	.911
BL_low_I2C	.922	.922	.867	.916
BL_low_C	.870	.870	.836	.858
BL_low_CC	.854	.854	.816	.847
BL_low_P3	.933	.933	.877	.968
BL_low_P3C	.933	.933	.880	.961
BL_low_P4	.944	.944	.887	.982
BL_low_P4C	.930	.930	.876	.968
BL_low_M1	.891	.891	.814	.971
BL_low_M1C	.909	.909	.840	.971
BL_low_M2	.950	.950	.894	.981

BL_low_M2C	.950	.950	.905	.968
BL_low_M3	.952	.952	.905	.967
BL_low_M3_est	.952	.952	.905	.967
BL_low_M3C	.950	.950	.912	.959

	MD_low_M1_est	MD_low_M1C	MD_low_M2	MD_low_M2_est
MD__low_I1	.830	.795	.801	.799
MD_low_I1_est	.835	.800	.804	.803
MD__low_I1C	.870	.860	.880	.877
MD_low_I2_	.888	.844	.847	.845
MD_low_I2_est	.891	.847	.848	.847
MD_low_I2C	.905	.893	.903	.901
MD_low_C	.854	.858	.893	.890
MD_low_C_est	.854	.858	.893	.890
MD_low_CC	.804	.811	.865	.862
MD_low_P3	.844	.876	.925	.923
MD_low_P3_est	.844	.876	.925	.923
MD_low_P3C	.793	.836	.882	.879
MD_low_P4	.953	.955	.977	.977
MD_low_P4_est	.953	.955	.977	.977
MD_low_P4C	.892	.917	.941	.941
MD_low_M1	1.000	.980	.962	.962
MD_low_M1_est	1.000	.981	.961	.962
MD_low_M1C	.981	1.000	.967	.968
MD_low_M2	.961	.967	1.000	1.000
MD_low_M2_est	.962	.968	1.000	1.000
MD_low_M2C	.943	.966	.986	.986
MD_low_M3	.881	.902	.956	.956
MD_low_M3_est	.881	.902	.953	.955
MD_low_M3C	.814	.854	.914	.915
MD_low_M3C_est	.814	.854	.914	.915
BL_low_I1	.832	.814	.853	.850
BL_low_I1C	.846	.834	.879	.876
BL_low_I2_	.906	.890	.912	.910
BL_low_I2C	.911	.898	.926	.923
BL_low_C	.853	.849	.885	.882
BL_low_CC	.842	.838	.872	.869
BL_low_P3	.967	.963	.956	.956
BL_low_P3C	.959	.958	.953	.953
BL_low_P4	.984	.974	.958	.960
BL_low_P4C	.970	.972	.949	.951
BL_low_M1	.973	.954	.905	.907
BL_low_M1C	.974	.964	.925	.928
BL_low_M2	.982	.973	.968	.969

BL_low_M2C	.969	.971	.966	.967
BL_low_M3	.967	.965	.974	.974
BL_low_M3_est	.967	.965	.974	.974
BL_low_M3C	.959	.966	.971	.972

	MD_low_M2C	MD_low_M3	MD_low_M3_est	MD_low_M3C
MD__low_I1	.768	.687	.682	.621
MD_low_I1_est	.773	.692	.688	.627
MD__low_I1C	.850	.793	.786	.751
MD_low_I2_	.806	.724	.720	.646
MD_low_I2_est	.809	.727	.724	.649
MD_low_I2C	.874	.794	.788	.733
MD_low_C	.870	.850	.843	.802
MD_low_C_est	.870	.850	.843	.802
MD_low_CC	.838	.838	.831	.802
MD_low_P3	.919	.928	.922	.916
MD_low_P3_est	.919	.928	.922	.916
MD_low_P3C	.880	.898	.891	.898
MD_low_P4	.962	.947	.945	.901
MD_low_P4_est	.962	.947	.945	.901
MD_low_P4C	.944	.941	.939	.917
MD_low_M1	.943	.880	.879	.812
MD_low_M1_est	.943	.881	.881	.814
MD_low_M1C	.966	.902	.902	.854
MD_low_M2	.986	.956	.953	.914
MD_low_M2_est	.986	.956	.955	.915
MD_low_M2C	1.000	.956	.955	.928
MD_low_M3	.956	1.000	.999	.975
MD_low_M3_est	.955	.999	1.000	.975
MD_low_M3C	.928	.975	.975	1.000
MD_low_M3C_est	.928	.975	.975	1.000
BL_low_I1	.801	.780	.772	.717
BL_low_I1C	.829	.813	.806	.758
BL_low_I2_	.865	.817	.811	.748
BL_low_I2C	.879	.843	.836	.780
BL_low_C	.848	.834	.826	.776
BL_low_CC	.835	.822	.814	.759
BL_low_P3	.942	.886	.884	.822
BL_low_P3C	.941	.883	.880	.827
BL_low_P4	.947	.894	.896	.831
BL_low_P4C	.942	.888	.890	.832
BL_low_M1	.890	.802	.805	.722
BL_low_M1C	.914	.834	.838	.765
BL_low_M2	.951	.898	.898	.833

BL_low_M2C	.947	.901	.902	.851
BL_low_M3	.958	.931	.929	.873
BL_low_M3_est	.958	.931	.929	.873
BL_low_M3C	.961	.934	.933	.887

	MD_low_M3C_est	BL_low_I1	BL_low_I1C	BL_low_I2_
MD__low_I1	.621	.882	.847	.892
MD_low_I1_est	.627	.880	.845	.891
MD__low_I1C	.751	.920	.912	.935
MD_low_I2_	.646	.893	.872	.925
MD_low_I2_est	.649	.890	.870	.924
MD_low_I2C	.733	.912	.884	.935
MD_low_C	.802	.912	.918	.918
MD_low_C_est	.802	.912	.918	.918
MD_low_CC	.802	.901	.912	.895
MD_low_P3	.916	.840	.864	.871
MD_low_P3_est	.916	.840	.864	.871
MD_low_P3C	.898	.802	.827	.826
MD_low_P4	.901	.845	.867	.906
MD_low_P4_est	.901	.845	.867	.906
MD_low_P4C	.917	.793	.824	.849
MD_low_M1	.812	.838	.851	.911
MD_low_M1_est	.814	.832	.846	.906
MD_low_M1C	.854	.814	.834	.890
MD_low_M2	.914	.853	.879	.912
MD_low_M2_est	.915	.850	.876	.910
MD_low_M2C	.928	.801	.829	.865
MD_low_M3	.975	.780	.813	.817
MD_low_M3_est	.975	.772	.806	.811
MD_low_M3C	1.000	.717	.758	.748
MD_low_M3C_est	1.000	.717	.758	.748
BL_low_I1	.717	1.000	.966	.959
BL_low_I1C	.758	.966	1.000	.972
BL_low_I2_	.748	.959	.972	1.000
BL_low_I2C	.780	.952	.974	.992
BL_low_C	.776	.926	.933	.931
BL_low_CC	.759	.909	.920	.915
BL_low_P3	.822	.861	.865	.911
BL_low_P3C	.827	.862	.870	.911
BL_low_P4	.831	.839	.854	.904
BL_low_P4C	.832	.824	.842	.888
BL_low_M1	.722	.783	.797	.867
BL_low_M1C	.765	.793	.818	.878
BL_low_M2	.833	.850	.878	.919

BL_low_M2C	.851	.847	.883	.919
BL_low_M3	.873	.860	.881	.916
BL_low_M3_est	.873	.860	.881	.916
BL_low_M3C	.887	.855	.878	.911

	BL_low_I2C	BL_low_C	BL_low_CC	BL_low_P3
MD__low_I1	.864	.789	.761	.812
MD_low_I1_est	.862	.787	.758	.816
MD__low_I1C	.916	.883	.864	.877
MD_low_I2_	.901	.827	.803	.870
MD_low_I2_est	.899	.825	.800	.872
MD_low_I2C	.916	.878	.859	.914
MD_low_C	.920	.978	.973	.905
MD_low_C_est	.920	.978	.973	.905
MD_low_CC	.902	.974	.970	.864
MD_low_P3	.888	.908	.896	.871
MD_low_P3_est	.888	.908	.896	.871
MD_low_P3C	.845	.876	.864	.826
MD_low_P4	.922	.870	.854	.933
MD_low_P4_est	.922	.870	.854	.933
MD_low_P4C	.867	.836	.816	.877
MD_low_M1	.916	.858	.847	.968
MD_low_M1_est	.911	.853	.842	.967
MD_low_M1C	.898	.849	.838	.963
MD_low_M2	.926	.885	.872	.956
MD_low_M2_est	.923	.882	.869	.956
MD_low_M2C	.879	.848	.835	.942
MD_low_M3	.843	.834	.822	.886
MD_low_M3_est	.836	.826	.814	.884
MD_low_M3C	.780	.776	.759	.822
MD_low_M3C_est	.780	.776	.759	.822
BL_low_I1	.952	.926	.909	.861
BL_low_I1C	.974	.933	.920	.865
BL_low_I2_	.992	.931	.915	.911
BL_low_I2C	1.000	.936	.923	.912
BL_low_C	.936	1.000	.996	.907
BL_low_CC	.923	.996	1.000	.902
BL_low_P3	.912	.907	.902	1.000
BL_low_P3C	.915	.906	.902	.994
BL_low_P4	.905	.867	.857	.970
BL_low_P4C	.891	.845	.837	.960
BL_low_M1	.870	.805	.800	.939
BL_low_M1C	.880	.829	.825	.947
BL_low_M2	.928	.882	.878	.969

BL_low_M2C	.929	.890	.885	.960
BL_low_M3	.927	.890	.883	.964
BL_low_M3_est	.927	.890	.883	.964
BL_low_M3C	.921	.889	.879	.957

	BL_low_P3C	BL_low_P4	BL_low_P4C	BL_low_M1
MD__low_I1	.807	.825	.796	.797
MD_low_I1_est	.810	.832	.802	.805
MD__low_I1C	.876	.879	.870	.818
MD_low_I2_	.865	.879	.847	.866
MD_low_I2_est	.866	.883	.851	.871
MD_low_I2C	.906	.909	.890	.875
MD_low_C	.909	.866	.848	.795
MD_low_C_est	.909	.866	.848	.795
MD_low_CC	.871	.823	.803	.735
MD_low_P3	.879	.856	.848	.761
MD_low_P3_est	.879	.856	.848	.761
MD_low_P3C	.834	.802	.800	.694
MD_low_P4	.933	.944	.930	.891
MD_low_P4_est	.933	.944	.930	.891
MD_low_P4C	.880	.887	.876	.814
MD_low_M1	.961	.982	.968	.971
MD_low_M1_est	.959	.984	.970	.973
MD_low_M1C	.958	.974	.972	.954
MD_low_M2	.953	.958	.949	.905
MD_low_M2_est	.953	.960	.951	.907
MD_low_M2C	.941	.947	.942	.890
MD_low_M3	.883	.894	.888	.802
MD_low_M3_est	.880	.896	.890	.805
MD_low_M3C	.827	.831	.832	.722
MD_low_M3C_est	.827	.831	.832	.722
BL_low_I1	.862	.839	.824	.783
BL_low_I1C	.870	.854	.842	.797
BL_low_I2_	.911	.904	.888	.867
BL_low_I2C	.915	.905	.891	.870
BL_low_C	.906	.867	.845	.805
BL_low_CC	.902	.857	.837	.800
BL_low_P3	.994	.970	.960	.939
BL_low_P3C	1.000	.960	.951	.928
BL_low_P4	.960	1.000	.990	.971
BL_low_P4C	.951	.990	1.000	.957
BL_low_M1	.928	.971	.957	1.000
BL_low_M1C	.937	.981	.971	.990
BL_low_M2	.964	.987	.978	.968

BL_low_M2C	.957	.977	.970	.953
BL_low_M3	.957	.980	.969	.945
BL_low_M3_est	.957	.980	.969	.945
BL_low_M3C	.954	.974	.966	.935

	BL_low_M1C	BL_low_M2	BL_low_M2C	BL_low_M3
MD__low_I1	.787	.804	.793	.822
MD_low_I1_est	.795	.809	.799	.826
MD__low_I1C	.829	.872	.872	.884
MD_low_I2_	.854	.869	.850	.871
MD_low_I2_est	.859	.872	.853	.873
MD_low_I2C	.877	.903	.890	.908
MD_low_C	.825	.884	.893	.891
MD_low_C_est	.825	.884	.893	.891
MD_low_CC	.771	.844	.859	.858
MD_low_P3	.799	.868	.889	.895
MD_low_P3_est	.799	.868	.889	.895
MD_low_P3C	.734	.813	.840	.846
MD_low_P4	.909	.950	.950	.952
MD_low_P4_est	.909	.950	.950	.952
MD_low_P4C	.840	.894	.905	.905
MD_low_M1	.971	.981	.968	.967
MD_low_M1_est	.974	.982	.969	.967
MD_low_M1C	.964	.973	.971	.965
MD_low_M2	.925	.968	.966	.974
MD_low_M2_est	.928	.969	.967	.974
MD_low_M2C	.914	.951	.947	.958
MD_low_M3	.834	.898	.901	.931
MD_low_M3_est	.838	.898	.902	.929
MD_low_M3C	.765	.833	.851	.873
MD_low_M3C_est	.765	.833	.851	.873
BL_low_I1	.793	.850	.847	.860
BL_low_I1C	.818	.878	.883	.881
BL_low_I2_	.878	.919	.919	.916
BL_low_I2C	.880	.928	.929	.927
BL_low_C	.829	.882	.890	.890
BL_low_CC	.825	.878	.885	.883
BL_low_P3	.947	.969	.960	.964
BL_low_P3C	.937	.964	.957	.957
BL_low_P4	.981	.987	.977	.980
BL_low_P4C	.971	.978	.970	.969
BL_low_M1	.990	.968	.953	.945
BL_low_M1C	1.000	.980	.972	.957
BL_low_M2	.980	1.000	.990	.984

BL_low_M2C	.972	.990	1.000	.978
BL_low_M3	.957	.984	.978	1.000
BL_low_M3_est	.957	.984	.978	1.000
BL_low_M3C	.955	.978	.980	.992

	BL_low_M3_est	BL_low_M3C
MD__low_I1	.822	.812
MD_low_I1_est	.826	.817
MD__low_I1C	.884	.879
MD_low_I2_	.871	.857
MD_low_I2_est	.873	.860
MD_low_I2C	.908	.903
MD_low_C	.891	.897
MD_low_C_est	.891	.897
MD_low_CC	.858	.866
MD_low_P3	.895	.905
MD_low_P3_est	.895	.905
MD_low_P3C	.846	.858
MD_low_P4	.952	.950
MD_low_P4_est	.952	.950
MD_low_P4C	.905	.912
MD_low_M1	.967	.959
MD_low_M1_est	.967	.959
MD_low_M1C	.965	.966
MD_low_M2	.974	.971
MD_low_M2_est	.974	.972
MD_low_M2C	.958	.961
MD_low_M3	.931	.934
MD_low_M3_est	.929	.933
MD_low_M3C	.873	.887
MD_low_M3C_est	.873	.887
BL_low_I1	.860	.855
BL_low_I1C	.881	.878
BL_low_I2_	.916	.911
BL_low_I2C	.927	.921
BL_low_C	.890	.889
BL_low_CC	.883	.879
BL_low_P3	.964	.957
BL_low_P3C	.957	.954
BL_low_P4	.980	.974
BL_low_P4C	.969	.966
BL_low_M1	.945	.935
BL_low_M1C	.957	.955
BL_low_M2	.984	.978

BL_low_M2C	.978	.980
BL_low_M3	1.000	.992
BL_low_M3_est	1.000	.992
BL_low_M3C	.992	1.000