SIZE VARIATION AND BODY PROPORTIONS IN AN ISOLATED HOLOCENE-AGED POPULATION OF HOMINIDS FROM PALAU, MICRONESIA AND ITS IMPACT ON OUR UNDERSTANDING OF VARIATION IN EXTINCT HOMINIDS.

By

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

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DECLARATION

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

Signature: ________________________________

Date:_____________________________________

Dedicated to my parents,
Deon & Sharaine de Klerk.

ABSTRACT

This thesis investigated whether a fragmented assemblage of fossilized *Homo sapiens* remains collected from Palau; Micronesia represents a population exhibiting a case of insular dwarfing. The earliest occupation of Palau is ca. 4000 YBP, and the fossil assemblage studied here dates between 2900 – 1400 YBP, thus providing a relatively short time in which body size reduction, due to insular dwarfism could occur. There are well known cases, in both the modern and fossil context, where insular dwarfism and body size reduction is known to occur in human populations that are isolated, but the results of this reduction are seen over a much longer period (e.g., tens of thousands of years).
Metric dimensions of the humerus, radius, ulna, femur, tibia, and fibula and os coxa are quantified in order to evaluate other potential insular dwarfs in fossil hominin assemblages, such as *Homo floresiensis*.

Previous studies have shown that the Palau archipelago has remained relatively isolated from human contact due to the surrounding currents, providing ideal conditions for insular dwarfism to occur. Comparing measurements taken on populations encompassing a reasonable range of human variation, this study quantified and compared the Palauan measurements and joint ratios to determine which variables might differentiate among these population groups, thus indicating traits potentially uniquely signalling a reduction in human body size.

Disproportionate joint sizes were observed in the humerus, ulna, tibia, and femur of the Palauan sample. While individual measurements from the Palau sample all fall comfortably within the range of measurements taken from other small-bodied human individuals, the articular surfaces of Palauan specimens do not resemble those from other well-established, small-bodied insular populations. As the articular surfaces are smaller relative to the epiphyseal diameters and may be a reflection of the relatively short time in which the reduction has taken place.

Morphologically the Palauan population exhibits small orbits, a large interorbital distance, an inflated glabella region and protruding supraorbital tori. A reduction in the mandible may account for the overcrowding of teeth observed in the dentition. The Palauan individuals have disproportionately large maxillary teeth. The mandibular dentition, however, varies: the incisors, canine and first molars are large, while reduction is seen most easily in the premolars and the second molar. This dental reduction is coupled with significant differences between the cervico-enamel junctions for these teeth and the corresponding crown measurements. Large teeth, inflated glabella, and protruding supraorbital tori may be an indication of a founding population. These traits are all found in Australomelanesian populations, and it is thus possible that the Palauan population under study originated from Melanesia (e.g. New Guinea or South East Asia).

Application of the present study to *Homo floresiensis*, a fossil hominin suggested by some authors to have undergone insular dwarfing, reveals that while *H. floresiensis* is small for some measurements, most fall within the range of the small-bodied comparative sample from Palau. The stature of *H. floresiensis* is not unusually small and falls within the ranges of the comparative sample used here. The only comparison that can be made for

joint size is that both the Palauan and *H. floresiensis* femoral heads are small and both exhibit the same disproportionate dimensions of the proximal tibia. As potential body size reduction is possibly responsible for the Palauan traits, the similarity in joint proportions may be attributed to insular dwarfing when the population first became isolated, as these joint irregularities are not seen in established insular dwarfs (Andaman and Nicobarese). The differences present in the measurements obtained for all the small-bodied samples examined suggests that even though insular populations may present as small-bodied, the island populations (fossil or extant) should be viewed as a case by case study. Isolation, life history, founding population (genetics) and environmental conditions all affect population body size over time, but to assume that all isolated populations will decrease body size in the same way is incorrect. What is seen in Palauan specimens is likely the adaptive responses of a isolated population from Melanesia, resulting in the insular dwarfism observed. By examining the available aspects of this insular population and found that it was consistent in reflecting size and proportions of small-bodied populations.

CONTENTS

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LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION

Change in body size is a common pattern expressed during the evolution of lineages (Heaney 1978, Lomolino 1985 & 2000; Blanckenhorn 2000, Burness *et al.* 2001, Ruff 2002). All organisms, within their evolutionary life history, have undergone some degree of an increase or decrease in body size (Van Valen 1973a; Heaney 1978, Peters 1983, Lomolino 1985 & 2000; Blanckenhorn 2000, Burness *et al.* 2001, Ruff 2002). This also applies to the human lineage. Palaeoanthropologists often consider body size relative to modern human standards (see for example; McHenry 1992, Ruff 1991, 1994, 2000, 2002, 2005, Brown *et al*. 2004). Thus, early australopithecines are more diminutive than modern humans are, while *Homo erectus* is closer to modern human stature. Body size often changes in accordance with factors that affect a population or group [climate, resources, latitude, isolation (Van Valen 1973a; Heaney 1978, Peters 1983 & Lomolino 2000)], thus understanding body size and these factors will result in the clarification of issues such as adaptation and phylogenetic relationships. This project aims to document body size and any morphological changes that may have occurred in an island population of *H. sapiens*, and how this could have bearing on the study of modern and fossil hominin body size in reaction to their isolation. The Palauan specimens are an interesting case study for not only island processes, but also more importantly, how body size change pertains to our own evolution.

In 2006 and 2007, fossilised remains of modern *H. sapiens* were collected from Ucheliung and Omedokel caves, which were found within the limestone terrain of the Palau archipelago (Berger *et al.* 2008a). Abundant fossilized or sub-fossilized human remains are known from numerous additional caves and rock shelters in this area (Clark 2005, Clark *et al*. 2006, Fitzpatrick 2001, 2002a, 2003b, 2008). The discovery of previously unknown

Omedokel and Ucheliung cave material represented a new skeletal sample from this region.

Specimens collected from the two caves – Ucheliung and Omedokel – are contemporaneous (Berger *et al.* 2008a). AMS radiocarbon dates[1] ranging between 1420 and 2890 YBP (years before present) were found for bone collected from the Ucheliungs cave surface, as well as from excavated material. Omedokel cave yielded slightly more recent individuals from the interior of the cave, dating between 1410 and 2300 cal YBP (Berger *et al.* 2008); these specimens were also collected from the surface.

Palau is situated among the Western Caroline Islands of Micronesia. The Palau archipelago consists of 350 islets (Fitzpatrick & Kataoka 2005). This curved island chain runs for 150 km from North to South and is 25km across at its widest point (Hawkins & Castillo 1998, Snyder & Butler 1997, Callaghan & Fitzpatrick 2007). The nearest large landmasses are an equidistant 600km from Palau: Papua New Guinea to the South and the Philippines to the West.

Palau was one of the first island groups colonised in the Pacific, but there is still debate as to when this occurred. Research conducted on palaeoenvironmental sites (Athens and Ward, 2002 & 2004), as well as palaeo-shoreline evidence from Palau (Dickinson and Athens 2007), suggests that colonization may have occurred approximately 4500 YBP [In island colonization, an initial human imprint in palaeoenvironmental deposits are identifiable via “the faunal assemblages representing human predation on a pristine environment” (Clark *et al.* 2006)]. However, archaeological evidence from excavation on the main island of Babeldaob suggests a slightly more recent settlement date of 3300-3400

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[1] AMS Radiocarbon analysis was used so that pre-treatment procedures could isolate the organic constituents indigenous to the original sample. This technique was used in studies of similar cave sites in Palau (see Fitzpatrick 2002) due to the difficulties faced with dating skeletal remains which can absorb calcium carbonate from the surrounding limestone environment.

YBP (Wickler *et al.* 1998; Liston *et al.*1998). While the timing of the first human colonization of Palau is unclear, hypotheses suggest that people from the Philippines colonized Palau (Wickler 2001; Callaghan & Fitzpatrick 2007). The dates on bone from the newly discovered sites range between 1420 and 2890 YBP (see AMS dates in appendix; Berger *et al.* 2008a), which places it near the earliest settlement dates based on archaeological evidence.

While Palau was one of the island archipelagos that were colonized earliest, it was one of the most isolated island groups within Micronesia. Palau is situated at the interchange of three major ocean currents (Callaghan & Fitzpatrick 2007), the regional currents and winds are well-known for having high velocity and volatility that allowed it to remain virtually isolated (Callaghan & Fitzpatrick 2007). Through the use of computer-simulated voyages and historical documents (which detailed duration and all observations pertaining to the journey), Callaghan & Fitzpatrick (2007) found that for up to six months of the year Palau would remain completely isolated, if people in Micronesia used drift voyage alone. This suggested isolation is further evidenced by the fact that Europeans only reached Palau in 1783 (Callaghan & Fitzpatrick, 2007). Early ships predominately used drift voyaging in order to discover new islands in the Pacific (Callaghan & Fitzpatrick, 2007). Europeans only reached Palau in 1783, although there are some earlier recorded sightings of the archipelago. Based on the research by Callaghan and Fitzpatrick (2007), the maximal chance of landing on Palau using drift voyage would occur during September, and if departing from the southern end of the Philippines. This line of evidence, coupled with the archaeological discoveries led researchers to conclude that founding populations for Palau most likely originated from the Philippines (Callaghan & Fitzpatrick 2007). Interestingly, simulated voyages (based on ocean currents and historical documents) from Guam (island NE of Palau, see Figure 1) show that from May to September it is nearly impossible to sail to Palau even knowing its exact location (Callaghan & Fitzpatrick, 2007). Additionally, Callaghan & Fitzpatrick (2007) suggest drift voyages had a very low success rate (i.e., 1%-5%) from December to April [The success rates from 1 to 11 percent often had durations of 10 to 56 days (Callaghan & Fitzpatrick, 2007)].

Limited access to Palau due to current directions poses some interesting questions about the origin of the Palau human assemblage in this study. Even with sea-faring vessels equipped for longer journeys, Palau would be difficult to find (Callaghan & Fitzpatrick 2007). Therefore, it may be possible for a small population to be stranded on the island, isolated for many generations from an influx of new genetic material, and ultimately having enough time for isolation to affect body size.

1.1 Body Size

Body size affects all biological processes from cellular metabolism to population interactions (Quammen 1996). Organisms of different body sizes will have varying requirements for life-sustaining resources and the allometric scaling observed will operate on different temporal scales (West *et al.* 1997). The study of body size is important as patterns of frequency (either increase or decrease) and the biological implications of the size change (Shea & Gomez 1988; Shea 1992) led to a better understanding of evolutionary tendencies within an organism. There have been many studies of body size of human populations (Bonner 1988; Jablonski 1997 Peters 1983; Reiss 1989; Roff 1992; Stearns 1992), mostly addressing variability within certain populations. Blanckenhorn (2000) made a case for small body size being favourable to the survival of species due to the costs associated with being large-bodied. These include, but are not limited to, the energetic costs of long development in juveniles and fast growth as well as the impact predation, parasitism, and/or starvation on larger-bodied organisms because of reduced dexterity (Roff 1992; Stearns 1992; Blanckenhorn 2000). Cope Rule is defined as a tendency of organism towards an increase in body size over time (Stanley 1973) and while there are advantages of large body size (Anderson 1994), there is strong evidence for selection limiting body size in natural populations where resources are limited (West *et al*. 2007).

Small-bodied populations are frequently referred to as pygmoid or dwarfed populations. Often these small-bodied groups are restricted to islands or environments that act as functional "islands" (i.e., environments in which individuals are isolated). While there are many hypotheses as to why body size decreases under these conditions (*Resource limitation*, *Breeding strategies, Predation, Species*, *Isolation*, *Genetics*, *Thermoregulation* and *Life history);*[2] the consensus view is that decreasing body size is a physiological response to decreasing latitude, coupled with an increase in the average annual temperature and increase in humidity (Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998).

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[2] *Resource limitation* (Van Valen 1970, Brown *et al*. 2004)

Breeding strategies (Shea & Bailey, 1996, Perry and Dominy 2008)

Predation (Lomolino 2005, Raia & Meiri, 2006),

Species Richness (Dayan & Simberloff 1998, Burness *et al.* 2001)

Isolation (Wassersug *et al.* 1979, Carson & Templeton 1984)

Genetics (Davila *et al.* 2002, Perry & Dominy 2009), *Thermoregulation* (Perry & Dominy 2009)

Life history (Migliano *et al.* 2007 and Walker *et al.* 2006)

Many populations of humans exhibit pygmy stature outside Africa; these include populations from the Andaman Islands, Papua New Guinea, Malaysia, Thailand, Indonesia, and the Philippines (Migliano *et al.* 2007). While the term pygmy is a broad classification that underplays the genetic and geographic uniqueness of these populations, the use of the term in this study will be limited to the discussion of the small body size phenotype. Pygmy or insular dwarfs are generally defined as populations whose mean stature is less than 155 cm (Cavalli-Sforza 1986, Schmidt 1905).

Dwarfs are another category of small-bodied individuals. Genotypic dwarfs often closely resemble scaled-down versions of their ancestors in terms of body proportions, (Marshall and Corruccini 1978), which may deviate from that of founding population. Phenotypic dwarfs resemble juvenile or adolescent stages of their parent populations (Boucot 1976) and are often characterised by enlargement of the teeth and skull relative to the rest of the body (Gould 1975; 1977). Phenotypic and genotypic dwarfs have differing body proportions in comparison to those of their founding populations (Marshall and Corruccini 1978, Perry & Dominy 2009). Often the trend observed in insular mammals is one of decreased mean body size of a species over a short period, which could be as short as decades to several thousands of years (Marshall & Corruccini, 1978).

Body size reduction in mammals greater than 1kg typically occurs once they become isolated on islands (Brown *et al.* 2004). This insular dwarfing is hypothesized as an adaptive response to the specific ecological conditions found on islands (Brown *et al.* 2004). Bromham & Cardillo (2007) found that primates are no exception to this ‘island rule’; *H. floresiensis*, if an example of such adaptation, would demonstrate that the genus *Homo* is no exception to the insular dwarfing rule. The potential case of insular dwarfing in

H. floresiensis is hypothesized to be a result of reduced resource availability, competition level, and predation, where smaller individuals with lower energy requirements were selected (Morwood *et al.* 1998). Insular dwarfing is often associated with extensive anatomical and physiological changes (Morwood *et al.* 1998). Body size (and a reduction in) is important as it can be directly linked to many other characteristics such as brain size, tooth size (megadontia) and relative bone strength (robusticity) (McHenry 1992; Ruff 1994).

While small body size is commonly seen in island populations, small body size or a reduction in body size is a trend not often seen in the context of human evolution. In human evolution, the trend is clearly towards increased body size. Australopiths, early *Homo,* and even *H. erectus* are estimated to be smaller than modern humans (McHenry 2009). Studying this trend toward small-bodied size on islands, even as it pertains to a single fossil island population, will have bearing on our understanding of human evolutionary processes. This serves to better understand ourselves as a species, and to better understand factors that govern our variation. Allometry is an important aspect of the body size debate. Often dimensions of body parts are compared relative to body size (Ruff 2000). Equations for estimating body mass are provided and require lengths of long bones (Ruff 1994) and articulated specimens, which palaeontologically speaking skeletal samples rarely preserve. This is especially important for populations that may be undergoing a reduction in body size. Insular dwarfism generally happens on islands, where a population's gene pool is limited to a small environment; factors that may affect insular dwarfing are environmental variables such as a food availability, climate, and predation level. Evolution on islands is dependent on life history, community composition and the biology of isolated species. On islands, mammals have considerable variation in the way in which they respond to the selective forces that drive size evolution (Meiri *et al.*2008). The Palau Archipelago is an island environment that is known to have been colonised early on, but remained isolated due to its location and the surrounding currents. Palau fulfils the aforementioned conditions required for insular dwarfism.

1.2 Insular dwarfism

Insular Dwarfism (a form of phyletic dwarfism) is a process in which large animals reduce in size to better suit their environment (Foster 1964). This generally happens on islands, where a population's gene pool is limited to a small environment and is often referred to as the island rule (Van Valen 1970, 1973a, 1973b). Other factors that may affect insular dwarfing are environmental factors such as a shortage of food, climate, and lack of predation. There are many examples of insular dwarfing in the modern world as well as in the fossil record. The terms "dwarf" and "pygmy" used in this study, denotes forms or species that is smaller in body size than their close relatives (Nowak 1991).

The general island rule for body size is that larger animals, mostly mammals, usually evolve smaller body size (Foster 1964, 1965; Van Valen 1970, 1973a, 1973b; Sondaar 1977; Heaney 1978), while small-bodied animals such rodents, birds and small reptiles, undergo gigantism (Foster 1964, Van Valen 1973, Lomolino 1985). The process of island gigantism, when islands lack large predators, small animals breeding on that island may become much larger than normal. The Dodo is an example of insular gigantism (Quammen, 1996), as their ancestors were pigeon sized. There are also several species of giant rats known from the modern and fossil record (Quammen, 1996).

1.2.1 Process of island dwarfing

The process of insular dwarfing does not necessarily need to occur on actual islands. Ecosystems that are completely isolated from external resources and gene flow prospects are also "islands." Dwarfing has been documented in mammals found in certain late Pleistocene and post-Pleistocene continental deposits and these "island" environs can include desert oases, isolated valleys, or even caves (Hooijer 1950; Marshall 1974; Marshall and Corruccini 1978). The term "islands" in this chapter will make reference traditional as well as non-tradition islands.

The common hypotheses for insular dwarfing include *limited resources* where large individuals often cannot survive and will eventually die off. Animals that are smaller, have an advantage over their larger counterparts, eating less and using a smaller quantity of available resources, and as a result would be more likely to breed and pass on their small bodied genes to successive offspring than their larger counterparts. *Breeding strategies* which selects for small body size is an evolutionary mechanism used to ensure survival. Humans have used this mode of selective breeding to create small animals. An example of this artificial insular dwarfism can be seen in most dog breeds available today. By purposely breeding small animals and limiting their mate choice, after several generations a large breed of dog would be miniatured. Evolution towards dwarfism is countered by positive selection for larger size (Wassersug *et al.* 1979) since larger size mammals are better adapted for protection from *predation* (Rensch 1960; Van Valen 1973a, 1973b), however in the absence of such predators, the evolutionary trend of dwarfism will prevail (Stanley 1973). It is important to remember that size evolution of large mammals in on islands is due to different underlying mechanisms, meaning all mammals do not follow the exact same rules, ungulate dwarfism depends on the existence of competitors, insular carnivore body size, as well as the resource base. This shows that ecological interactions playing a major role when it comes to shrinking on an island (Raia & Meiri, 2006). Lister (1989) found that in general vertebrates would undergo considerable body size changes, in relatively short evolutionary times, on islands.

Another driving force of this insular dwarfism is a reduction in insular *species richness*. A decline in the number of predators and competitors would lead to dwarfism (Dayan & Simberloff 1998). As predation pressure on an island decreases species will achieve smaller body sizes (Boekschoten & Sondaar 1966; Sondaar 1977) as large body size is used as a way to counteract predation (Sinclair *et al.* 2003).

In the case of herbivores, Smith (1992) suggests that in the absence predators small bodies herbivores grow large to facilitate more effective digestion. The most common thought on this is that reducing in body size is a way of coping with limited resources islands (Heaney 1978; Lomolino 1985; Roth 1992; Burness *et al.* 2001).

In cases where immigration or emigration is limited, coupled with resource limitation, you will get insular dwarfing (Wassersug et al 1979). The Founder Principle is when a small number of individuals colonize a new site and become cut off from the panmictic population. Isolation occasionally leads to 'genetic revolutions' followed by rapid phenotypic change, (Mayr 1963). This is known as the founder effect. Templeton (1980) recognized that the founder effect did not shake up the entire genome but is confined to a handful of major genes with strong epistatic interactions with several minor genes. Essentially only a small number of genes will be neutral with respect to transillience, (Templeton 1980). This effect over time can cause speciation by altering the genetic conditions in the gene pool (Carson & Templeton 1984). In shorter periods of time this manifests in a population all possessing characteristics that were unique to the founding population e.g. deformities or small body size.

Random genetic drift (within Founder Effect), this is considered an important force for creating genetic divergence amongst local populations, and results in the loss of genetic variation (Lacy 1987). This occurs more rapidly in small populations due to the absence of selection, migration and mutation on gene frequencies (Lacy 1987). Frequencies of alleles follow a genetic drift due to random sampling of genes during the transmission from one generation to the next (Lacy 1987). While this process can eventually lead to speciation, often isolated populations will exhibit phenotypic traits which are specific to the founding population (de Klerk, 2007).

It is important to note however, that evolution on islands may be highly dependent on history, community composition and the biology of the isolated species. When examining island populations all of these factors should be taken into consideration instead of focusing on generalities (Lawlor 1982; Raia & Meiri 2006). On islands it is found that mammals have considerable variation in the way in which they respond to the selective forces that drive size evolution (Meiri *et al*. 2008). When studying island populations both the biotic and abiotic environmental factors must be taken into account in order to assess how a populations' body size will evolve (Meiri *et al.* 2008).

1.2.2 Examples of insular dwarfs from the fossil record.

Insular dwarves are known from the recent and more ancient fossil record. This shows that under certain conditions; isolation, environment, climate, and ecological pressures will affect animals. This section highlights some of the fossil examples of insular dwarfing.

Remains of 150 million year old insular dwarfed dinosaurs have been uncovered on Hateg Island in Romania (Benton *et al.* 2010), and Gaslar in Germany. The remains all exhibit a reduced body size relative to other dinosaur fossils from the same period. These remarkable "islands" have more than one dwarfed dinosaur species indicating that the isolation of these large bodied dinosaurs resulted in the "island rule" taking effect.

The Channel Islands Mammoths (*Mammuthus exilis*) are also well known insular dwarfs that stood 1.2-1.8 m tall and lived on the prehistoric island of Santa Rosae in the California Channel Islands. Remains of small woolly mammoths were found on the island of Saint Paul (Alaska) and Wrangel Island north of Siberia (Johnson 1978). It is thought that these dwarfed mammoths may have gone extinct as late as 1500-1700BC. Dwarf elephants are the most well-known of the insular dwarves probably due to the vast distinction in size to their mainland counterparts. They are an extreme example of the Island rule for mammalian body size (Foster 1964, Van Valen 1973, Lomolino 1985). Dwarf elephants were half or even a quarter the size of their mainland ancestors (Roth 1990). Dwarfed elephants were most common on the Mediterranean Islands (Raia *et al.* 2003) but also evolved in other parts of the world, on islands off California, Siberia, eastern Asia (Roth 1992; Vartanyan *et al.* 1993). *Elephas falconeri* was discovered on the Mediterranean islands of Sicily and Malta, measured only 90 cm tall is thought to have evolved from the larger *Elephas namadicus* (Marshall & Corruccini 1978) this species is represented by over 140 individuals ranging from calf to adult (Raia *et al.* 2003). The reason for the extinction of these dwarfed elephants is still unknown. There are other fossil forms of Dwarfed elephants such as Stegodons (e.g. Stegodon sondaarii), known from the fossil record of the Philippines, Flores, Sulawesi, Sumba and Timor (Allen 1991; Bekken *et al*. 2004; & Morwood *et al.* 1998).

The middle Miocene deposits of the Texas Gulf Coastal Plain contained a dwarf Rhinoceros (Prothero & Sereno 1982). The insular dwarfism exhibited here was possibly due to the browsing food resources that predominate on islands.

Dwarf Water Buffalo exist in the fossil record and are known from extant species from the island of Cebu off the Philippines. The dwarfed buffalo are a fourth the size of a normal water buffalo. The Philippines is home to the other dwarfed bovids such as the Mindoro Dwarf buffalo (Bubalus mindorensis). Originally found all over the island of Mindoro in the Philippines, its range reduced by encroachment of humans on their habitat (Mudar 1997).

Insular dwarfism can affect all mammals this includes hominids. The discovery of *Homo floresiensis* on the island of Flores, Indonesia brought to light an instance where a species of hominin underwent insular dwarfism. The findings by Brown *et al.* (2004) show that this population of *Homo* reduced in size resulting in interesting features such as small brain size. Subsequent studies by Bromham and Cardillo (2007) demonstrate that all primates follow the island rule with small-bodied primates becoming larger on islands, and larger-bodied primates reducing. The study also found that the larger species of primate actually have a proportionally greater reduction in size on islands. The effects on insular dwarfism will be dealt with in more detail in later chapters. There is some variability in dwarfing lineages, while genotypic dwarfs often closely resemble scaled miniatures of their ancestors, phenotypic dwarfs resemble juvenile or adolescent stages of their parent populations (Boucot 1976). Genotypic dwarfs have body parts which are selected for functional efficiency and proportions will deviate from that of founding population while phenotypic dwarfism is thought to be characterised by enlargement of the teeth and skull in proportion to the rest of the body (Gould 1975). As a result, phenotypic and genotypic dwarfs will have differing allometries in comparison to that of the founding population (Marshall & Corruccini 1978). Marshall & Corruccini (1978) found that the rapid decrease in body size could be attributed to the fact that most island populations have/had shorter lifespans in comparison to their mainland counterparts. This, along with the shorter generational time would result in the rapid decrease of mean adult size as one generation would be replaced by individuals which would have a slightly smaller body size. Often the trend seen in insular mammals is that the decrease in mean body size of a species would occur over a short period of time, this could be decades to several thousand years (Marshall & Corruccini 1978).

1.3 Aims of this research

The aims of this research involve examination of size variation of individual skeletal elements of modern humans recovered from Palau, Micronesia by comparing them to a modern comparative sample, which includes other island populations. This study will expand our understanding of body size variation within *H. sapiens.* As mentioned previously, these fossil remains were recovered from an isolated island setting, Along with isolation, the humid tropical climate, lack of natural predators, and limited terrestrial-based nutrition [early Palauans were known to have exploited marine resources (Liston & Reith 2001; Fitzpatrick & Nelson 2007)] makes Palau an ideal case study for reduction in body size.

If this population expressed insular dwarfism, the present study aims to identify any size trends or associated metric features found within the population. By comparing whether or not the measurements taken for the Palauans are smaller, larger or similar in size to the comparative sample groups would be used as an indicator of possible reduction this is based on the hypothesis that the founding populations of Palau were 'normal' (Fitzpatrick *et al.* 2007). The goal is not only to establish traits that are likely to occur in a populations which is reducing in body size over a relatively short time period (several generations), but also to highlight traits that may indicate from where this population may have originated.

A rapid decrease in body size is a contributing factor to most island populations having shorter lifespans in comparison to their mainland counterparts. Marshall & Corruccini (1978) found that a decrease in mean body size of a species could occur over a short period (i.e., a short period being defined as ranging from a few decades to several thousand years). Accordingly, dates for the Palau sample of 1400-2900YBP offers ample time to manifest the reduction in body size for this population. An argument put forward by Fitzpatrick *et al.* (2008) suggested that the early colonizers of Palau may have simply been small-bodied and that the results established by Berger *et al*. (2008a) were merely a reflection of small-bodied colonizers. If this were the scenario, greater conformity with other insular populations would be predicted in the results of this study. To expand further, the Palauan sample would be expected to have closer alignment with island populations and not mainland small-bodied groups. Since morphology and metrics associated with rapid body size reduction have yet to be established for isolated hominin populations, this study suggests that in order to identify a rapidly reduced body size dimensions of articular surfaces should be examined in relation to epiphyseal dimensions of long bones.

Craniodental results provided a potential means of identifying the parent population of Palauan fossils. Hill *et al.* (2006) found that while there are many features that are shared between Andaman Negritos, Malay pygmies and Philippines Negritos, there is no genetic evidence of a shared ancestry and as a result any traits shared are a result of morphological convergence likely due to insular dwarfing. It has been suggested based on archaeological evidence that the founding populations of this island may have originated from the Philippines (Fitzpatrick 2002a, 2003b), and that the founding populations were in fact normal (Fitzpatrick *et al.* 2008).

Results presented here aim to identify remnant morphologies of the founding population, or potential metric or morphologic features that may be a result of rapid reduction of body size. Southeast Asian pygmies are thought to be descendants of Australomelanesians due to the shared cranial affinities and sundadonty (Storm 2007).

A critical aim of this study is to establish whether the Palauan specimens have teeth that are large relative even to the comparative samples. If the ancient Palauan samples are infact megadontic, a trait not seen in modern-day Palauans, this would lend to possible identification of the founding population. Megadontia has commonly been claimed for Sahul-Pacific populations [see references in (Kondo *et al.* 2005)] and may provide a clue as to the origin of the Palauan specimens. In Fitzpatrick *et al.* (2008), the authors argue that the Palauan samples are normal body sized and therefore not megadontic. However no data was made available on the dental dimensions for their comparative sample.

Findings of this study also are potentially relevant to the *H. floresiensis* debate, as Palau is an island population that may be a useful comparator for its interpretations. The hypotheses to be tested in this research will look at whether the Palauan sample represents a group of humans with a body size amongst the smallest recorded for a modern human sample. It is predicted that due to the isolation and nature of island populations the Palauan postcrania and cranial measurements will reflect those of a small-bodied insular populations, such as the Andamanese and Nicobarese. The hypotheses will be reiterated at the beginning of each subsection of this research.

Based on the outcome of the results the possible causes for the insular dwarfism will be explored. It is important to note that evolution on islands is dependent on life history, community composition and the biology of the isolated species. When examining island populations, all of these factors should be taken into consideration instead of focusing on generalities (Raia & Meiri 2006). On islands, mammals have considerable variation in the way in which they respond to the selective forces that drive size evolution (Meiri *et al.* 2008). When studying island populations, both biotic and abiotic environmental factors must be taken into account in order to assess how a populations' body size will evolve

(Meiri *et al.* 2008). Factors that may affect insular dwarfing are environmental factors such as a shortage of food, climate, and lack of predation and each will be explored and discussed in lieu of the results obtained.

1.4 Background on Palau, Micronesia.

1.4.1 Geology

Palau is situated among the Western Caroline Islands of Micronesia. The Palau archipelago consists of 350 small rock islands (Fitzpatrick & Kataoka 2005) and a large main island. Palau has a total land area of 450km^2, Babeldaob is the largest island in this archipelago and covers an area of 363km^2 (Snyder & Butler 1997). The remainder of the land mass consists of three volcanic islands (Koror, Ngerekebesang, and Ngemelachel), an atoll (Kayangel) (Olsudong 2006), platform-like reef islands (Peleliu, Anguar and parts of Koror) and several hundred uplifted coralline limestone islands or "Rock islands" (Snyder & Butler 1997). In the Western Pacific trench system, the Cenozoic subduction zone has led to the development of the Western Pacific basin trenches, back arc basins, and island arcs (Hawkins & Castillo 1998). The islands constituting Palau are a part of one of these island arcs systems. The 350 islands and islets of the Palau archipelago constitute the southernmost exposure of the Kyushu Palau Ridge (Hawkins & Castillo 1998).

Babeldaob is a primarily volcanic island. The volcanic substrates consist of breccias and interbedded tuffs formed during the Eocene and Oligocene (Hawkins & Castillo 1998, Mason *et al.* 1956). These stratigraphic units record 12 million years of arc history (Hawkins & Castillo 1998). Although the eruption was submarine, the islands formed by subsequent uplift. The interior uplands of Babeldaob are comprised of three low ridge systems and reach a maximum elevation of 242m above sea level (Snyder & Butler 1997). The low ridge system is heavily eroded and has well-rounded peaks, which gives Babeldaob an undulating terrain (Fitzpatrick & Kataoka 2005).

The rock islands are made of Palau Limestone, which are raised coralline reef structures formed in warm waters during the early Miocene (Snyder & Butler 1997) to late Pliocene (Kayanne *et al.* 2002). The calcareous detritus of these ancient reefs is cemented by calcite (Hawkins & Castillo 1998). Narrow elongated and precipitous ridges define these karstic, limestone islands. The islands have poorly developed soils and no surface drainage (Fitzpatrick & Kataoka 2005). The rock islands have a distinct mushroom shape and can range from 10m to 100m above sea level (Mason *et al.* 1956). This distinct shape is a result of the limestone dissolving at sea level, forming an overhang from a solution notch (see Figure 2). The overhangs range from 0.5m to 6m (Mason *et al.* 1956). Elevations of these rock islands are usually between 50-100m in height, but some can reach heights of 200m above sea level (Fitzpatrick & Kataoka 2005).

The karstic topography of these rock islands is emergent from freshwater solution on the limestone, where often features such as fissures, sinkholes, caves and speleothems will form (Fitzpatrick & Kataoka 2005). A barrier reef encompasses most of the islands, except for Kayangel Island in the North, and Anguar and the South West Island group to the South (Olsudong 2006). Ucheliung and Omedokel caves are on the western and eastern edges of the Rock islands to the Southwest of Babeldaob (see Figure 3).

Figure 1: Map of Oceania showing the collections of islands that make up Polynesia, Micronesia, Melanesia and the South East Asian islands. The dashed lines indicated the separation between these various regions. Palau is situated approximately 600km east of the Philippines and 600km north of New Guinea (map adapted from Bellwood *et al.* 1975).

Figure 2: A rock island from Palau, Micronesia. In this image you can see the eroded nature of the karstic terrain, the dissolution notch that gives the island its characteristic shape and the dense vegetation that grows on these rock islands.

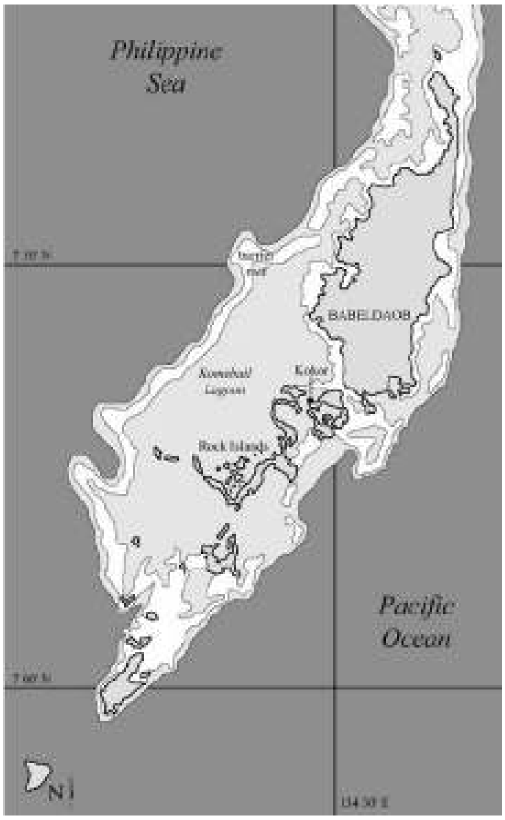

Figure 3: Map of Palau indicating the position of the Rock Islands to the south and southwest of the large island of Babeldaob. The caves discussed in this study are found on western and eastern edges of the Rock Islands. All samples collected from the sites are curated at the Belau National Museum. (Taken from Berger *et al*. 2008a)

1.4.2 Climate and Vegetation

There is small seasonal variation in the maritime tropical climate of Palau; the mean annual temperature is 27°C and the range in variation from the coolest months (January and February) to the warmest month (April) is less than 4°C (Snyder & Butler 1997). Daily rains and short, torrential storms provide 3.8m of rain annually (Snyder & Butler 1997). Humidity on the islands is as high as 82%.

A dense mass of tropical rain forest covers the rock islands. The larger volcanic islands have vegetation varying from tropical rain forest (approximately 75% of the Palau islands are forested) to savanna, plus broad belts of coastal mangrove swampland exist (Snyder & Butler 1997). Within the forests, we find a great diversity of plant life. The upland forests are known for their hardwoods, palms, and pandanus. Swamp and Mangrove forests are found on coastal lowlands where the terrain is level; these forests prevent the soil from eroding into lagoon areas. A large portion (16%) of Babeldaob is covered in savanna/grassland associations. While some of this association may be the result of human activity, a large portion of it is due to the poor soils on the volcanic island (Snyder & Butler 1997). A variety of habitats are present on Palau including patch, fringing, and barrier reefs; reef walls; mud flats, sand and rubble flats, and sea grass flats; mangrove forests; estuaries; freshwater streams and lakes; both, and the Rock islands (Fitzpatrick & Kataoka 2005). Even though there was a multitude of habitats available, there was a lack of terrestrial fauna on Palau (Pregill & Steadman 2000). The multitude of aquatic faunal species found in the Palau Archipelago make up for what the terrain lacks in fauna.

1.4.3 Peopling of Oceania

Oceania is the region incorporating the large groups of islands found in the south Pacific (i.e., Polynesia, Melanesia, and Micronesia) (see Figure 1). The largest land mass in this area is New Guinea, while the remainder of the land mass is comprised of smaller islands. Archaeological data (Pregill & Steadman, 2000; Callaghan & Fitzpatrick, 2007, Clark & Wright, 2003) indicate that settlement of Oceania likely occurred between 5000 and 1000 YBP. Bellwood *et al.* (1975) hypothesized that the 'descendants of Southern Mongoloid phenotype people gradually settled the whole of Oceania'. Throughout many areas within Oceania, there was extensive contact and intermarriage with existing Australoid populations inhabiting many of the islands. The people of Australia and most of the interior of New Guinea historically were classified as Australoid.

The Mariana Islands are a chain of small islands that have a close geographic range in relation to Palau (see Figure 1). Research by Hanihara (1993) found that based on dentals traits of Southeast Asians, commonalities with prehistoric Jomon populations, and their lineages in Japan were identified. Dental affinities identified in Polynesian and Micronesian groups indicate a possible ancestral relationship with the South East Asian indigenous inhabitants. Further studies on metric craniofacial variation confirmed these relationships between Mariana Islanders and East/Southeast Asians, as well as Polynesians (Hanihara 1997). Hanihara (1997) concluded that there was no support found for a Melanesian ancestry of the western Micronesian populations. Hanihara (1997) suggests that while there is much variation within recent general East/Southeast Asian populations, groups such as the Andamanese (Andaman Negritos/Onge), Nicobarese, and Philippine Negritos (dwarfed populations) are outliers (Lahr 1995).

Previous studies on the peopling of the Pacific used dental morphology to reconnect Polynesians, Micronesians, and Jomon back to Southeast Asia (Howells 1990, Turner 1987, 1989, 1990a, b). Hanihara (1997) went further in suggesting that based not only on craniofacial and dental data, but also on archaeological records, Australonesians (Name given to the group including Formosan, Indonesian, Malay, Melanesian, Micronesian, and Polynesian subfamilies) were the early colonisers of the Pacific basin and rim. This result repeats in genetic studies (Su *et al.* 2000) that found Polynesian, Micronesian, and Taiwanese haplotypes in extant Southeast Asian populations.

1.4.4 Archaeological & Palaeontological Research

From 1993-1997, Pregill and Steadman (2000) explored Palau in search of late quaternary vertebrate fossils. They found fossiliferous sediment in Palau to be remarkably scarce. This was due to caves in the area being either too small to hold appreciable sediment, lacking in sufficient horizontal surfaces (Pregill & Steadman, 2000), or damp, which is suggested to cause bones to decay in the organic sediment rather than preserve them (Pregill & Steadman, 2000). Another factor to bear in mind was the events of WWII that occurred in the archipelago. Japanese soldiers often used caves as storage facilities or fighting points, amongst other things (Pregill & Steadman, 2000). This would of course seriously diminish the potential of caves to provide useful palaeontological material.

A wealth of archaeological information is available from the cultural resource projects on Babeldaob and Koror. Archaeological sites are found throughout the volcanic islands in the form of highly visible terrace formations (on the large savanna areas of the volcanic islands) and clustered stone features, which are the remains of traditional villages. These sites are scattered throughout the archipelago (Snyder & Butler 1997). Archaeological research began in 1929 with the work of Hisakatsu Hijikata, a Japanese Anthropologist (Snyder & Butler 1997) who described pottery from several areas on Babeldaob. A great deal of the early archaeological work concentrated on the larger islands of Babeldaob, Peleliu, and Anguar (Osborne 1969 & 1979, Liston *et al.*1998). The work was predominantly on the description of ceramic artefacts, stone carvings, glyphs, as well as terrace and village sites (Osborne 1969).

1.4.5 Human Colonization of Palau

Colonization of Oceania occurred around 4500 years ago, and remains of these settlers are rare (Fitzpatrick & Nelson, 2007). Island colonization is identifiable in deposits as "faunal assemblages representing human predation on a pristine environment" (Clark *et al.* 2006). While the timing of the first human colonization of Palau is unclear, it has been suggested that people from the Philippines colonized Palau (Wickler 2001; Callaghan & Fitzpatrick 2007). Palaeoenvironmental and palynological data indicate that occupation of Babeldaob occurred as early as 4300-4500 YBP (Athens & Ward 2001), while archaeological evidence points to the first occupation of Palau at 3100-3400 YBP (Clark *et al.* 2006). Clark *et al.* (2006) propose that early settlers arriving on Palau were attracted to the large volcanic island of Babeldaob, and that occupation of the rock islands was limited. While most habitation was on the larger island Babeldaob, it is suggested by Clark *et al.*(2006) that the smaller islands were used for the collection and consumption of fish, or as burial sites (see also Berger *et al.* 2008a & b) for the people from nearby Babeldaob.

The rock islands have begun to yield new insights into Palau (Clark & Wright 2003, Clark 2004, Fitzpatrick 2001, '02a, '02b, '03a, Liston 2005)., such as settlement dates ranging from 3300-3000 BP (Clark & Wright, 2003 & Fitzpatrick, 2003b), evidence of prehistoric fishing practices as early as 1700 BP (Fitzpatrick & Kataoka, 2005), and human exploitation of the coral reefs (Fitzpatrick & Donaldson 2007). Burials in Palau have been found in a variety of locations and contexts such as stone platforms, terrace formations, and limestone caves (Fitzpatrick 2002a). Although there are a large number of these sites in Palau, the potential of discovering intact well-preserved remains is often diminished by the lateritic soils (acidic) of the islands (Pregill & Steadman 2000).

Rock shelters and limestone caves contain the earliest known burial sites in Palau (Fitzpatrick & Nelson 2007). The practice of placing remains within caves is rare outside of Palau (Fitzpatrick & Nelson 2007), making it a unique case study for human burials in Micronesia. Early archaeological research identified burial caves on the islands of Ngurkthabel, Ngeream, Macharchar (Osborne 1979, Snyder 1985 & Blaiyok 1993) and Koror. More recently, Fitzpatrick (2003) identified a cemetery site on Orrak. Typically, cave and rockshelter burials are separated into two types: the open stratified context of large rockshelters in which remains are buried deep, and where individuals are placed on the surface or in crevices, particularly within small caves (Fitzpatrick 2003). It is unknown whether these two burial practices represent different chronological periods, or perhaps different cultural practices of contemporary groups.

1.5 Previously Studied Burial caves from Palau

While many caves containing human remains are known from Palau, only a handful have been studied. The following is a summary of these known burial caves:

1.5.1 *Chelechol ra Orrak*

This site is located on the island of Orrak, which is SE of Babeldaob. A prehistoric causeway connected this limestone island to Babeldaob (Fitzpatrick & Nelson 2007). Fitzpatrick undertook excavations in August 2000. The skeletal assemblage discovered at the site pre-dated occupation levels associated with a rockshelter at the head of a small inlet on Orrak Island. In three test pits, skeletal remains of 25 individuals were recovered at a depth of 60-70 cm. Skeletal remains of 25 individuals were recovered, ranging in age from prenatal, neonate, adolescent to adult. The remains included both sexes, as estimated using standard osteological sexing criteria. Dating of the site provided an associated date of 3000YBP, making these remains some of the oldest recorded in Oceania (Fitzpatrick 2003b, Fitzpatrick & Nelson 2007). Associated with these remains were grave goods in the form of pearl and shell scrapers (for a full list of grave goods see Fitzpatrick & Nelson 2007).

1.5.2 *Ngermereues Ridge*

An archaeological recovery team led by Reith and Liston (2001) investigated the limestone solution caves of Ngermereues ridge. There are two limestone solution caves, 17m apart, situated on top of Ngermereues Ridge. The larger cave consists of a number of chambers (13 explored in total) with various depths. Fragmentary human remains were found in all of the chambers. A MNI for this cave is 32 individuals, varying in age from juvenile to sub-adult to adult. Grave goods associated with the remains were found in all the chambers with the exception of chamber 5. These goods included pottery, marine shell tools and ornaments, lithic artefacts and shark teeth (Reith & Liston 2001; Fitzpatrick & Nelson 2007). Radiocarbon dates show that these remains date from 1350-1720 YBP.

The smaller cave on this ridge is located down slope from the larger cave. This cave is described as a single chambered burial cave containing fragmentary remains of four individuals (MNI = 4). Of these remains, only one set was identified as adult, while the remaining three sets were catalogued as indeterminate age. Grave goods associated with these remains included pottery and marine shells (Reith & Liston 2001). Radiocarbon dating of the remains indicates an estimated age of approximately 2480 YBP.

1.5.3 Sngall Ridge

The remains of four individuals were recovered from the solution caves at the site of Sngall ridge on Koror. The only associated grave goods found were four ceramic pots (Beardsley, 1998). The date associated with the site (2400BP) (Beardsley, 1998) is questionable since it was obtained from a shard of a ceramic bowl (Beardsley 1998, Reith & Liston 2001).

1.5.4 Ucheliungs and Omedokel caves

Abundant fossilized or sub-fossilized human remains were discovered in the numerous caves and rock shelters of the Rock Islands southwest of Koror (see Figure 3). In 2006 and 2007, remains were recovered from Ucheliungs and Omedokel caves by a team comprised of palaeoanthropologists from University of the Witwatersrand (South Africa) and Duke University (USA). Material collected for the present study approximates 26 individuals.

1.5.5 Ucheliungs Cave

Initial exploration of Ucheliungs caves took place in 2006. At this time, the initial research trip yielded substantial numbers of fragmentary and complete human remains. The opening of Ucheliungs cave faces the ocean. Access to the cave is only possible by boat. Deroofing of the main chamber of Ucheliungs cave was due to dissolution of the limestone rock in which the cave is found. In the centre of the main chamber, we find vegetation growing on and around the collapsed roof blocks. The cave is roughly 18 m in length (from the entrance to the back wall of the extension chamber) and oriented roughly on an N-S axis. The width of the cave varies from 1.5 m in some places to 12 m in others. In the northernmost corner of the main chamber, the entrance to the extension chamber can be found. The extension chamber is the site of the discovery of the original specimens (Berger *et al.* 2008a). Human remains were recovered throughout the cave by surface collection only. The recovery of the densest concentration of fragmented bone was from the main deroofed chamber.

The main chamber measures approximately 12 m x 12 m and contains a large amount of rubble in the middle of the chamber directly below the roof opening. A large number of human remains were scattered on the surface of the cave. Surface sampling of the interior of this cave, as well as an archaeological excavation in a 1 m x 1 m and 0.50 m deep test trench, created a substantial collection of human material (NISP (trench and surface) >1100 (Berger *et al.* 2008a)). Individuals in the sample varied from adult and sub-adult to juvenile and neonate. Dates obtained using bone specimens from Ucheliungs cave range between 1420 and 2890 YBP (see Berger *et al*. 2008a, supplementary data for AMS dates).

Thus far, the fossil-bearing sediments of this cave do not contain faunal remains, and cultural artefacts are limited to a few fragments of pottery collected on the surface. This result is based on initial collection; further excavation is required. The human remains recovered thus far appear to be secondarily redeposited, most likely by the action of waves that may have entered the caves during storms and washed bones out of their primary burial context. The secondary re-deposition resulted in no associated skeletal elements being recoverable.

1.5.6 Omedokel cave

Omedokel cave is the second cave studied by Berger *et al.* (2008a). This cave is known as "Bone Cave" to the local Palauans. Until the exploration by Berger and his team in 2006 and 2007, no archaeological work had been conducted in the cave.

This cave is accessible via a small beach, but a boat is needed to reach the site. This cave has a roof and two entrances. The entrance used by the team was the ocean entrance. The entrance is 5 m wide and 2-3 m high. A 25 m passage leads from the entrance of the cave to its main chamber. Due to time constraints, only surface samples were collected [NISP = 87 (Berger *et al.* 2008a)] and so far no extensive excavations have been performed at Omedokel cave. Specimens collected from this cave were fragmentary.

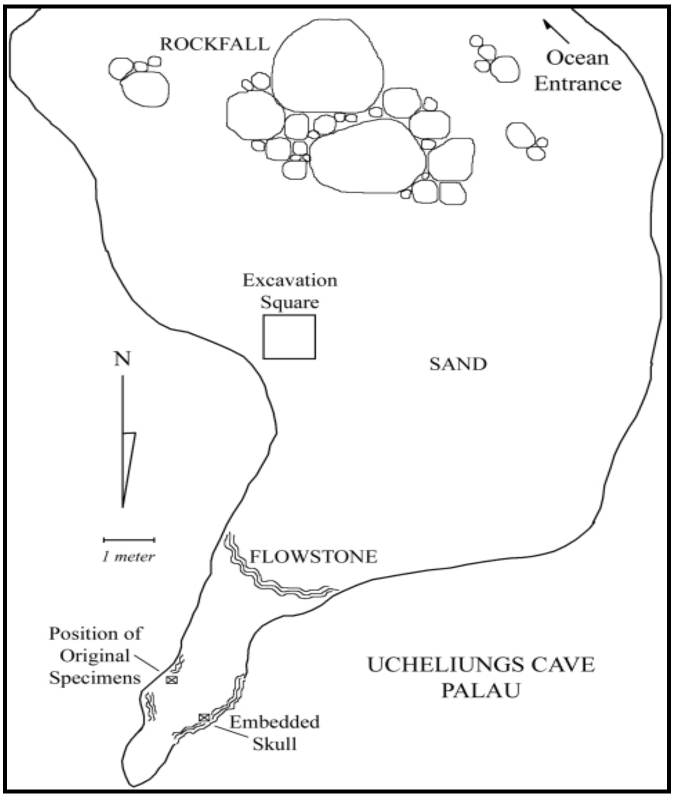

Figure 4: Line drawing of Ucheliungs cave, showing the original positions of collected specimens (taken from Berger et al. 2008a).

The interior of Omedokel cave yielded individuals dated between 1410 and 2300 YBP. At the entrance to Omedokel cave, remains of large-bodied individuals were recovered in association with grave goods typical of early Palauan burials (Rita Olsudong 2007 pers comm.). These remains dated to between 940 and 1080 YBP (Berger *et al.* 2008a). This cave is still undergoing active limestone formation. In both caves, relatively complete crania were discovered. Unfortunately, all of them are heavily embedded in calcium carbonate flowstones (and have thus been left *in situ*).

Figure 5: Image showing the floor of bone cave and how the fragments found in the cave were scattered on the cave floor.

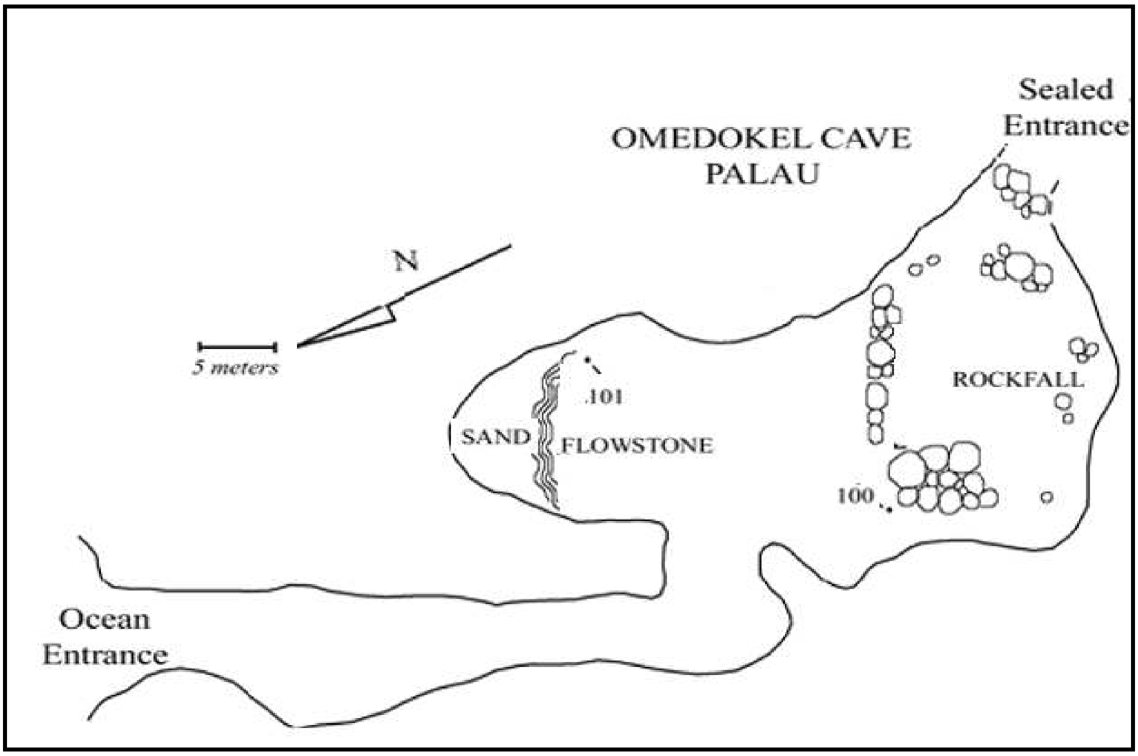

Figure 6: Line drawing of Omedokel Cave. 100 and 101 indicate positions where fossils were collected for this study (adapted from Berger et al. 2008a).

CHAPTER 2: MATERIALS AND METHODS

2.1 Postcranial materials

All measured specimens are adults with no observable pathologies. The selected groups (i.e., African, European, Asian, Australomelanesian and insular small-bodied), sample body size variation within *H. sapiens* but were also based on the availability of specimens for study. Both sexes were measured for each group where available. A population is defined as a group of individual persons from which samples are taken for statistical measurement (Madrigal 1998); therefore the individuals used in the comparative sample represent specific groups that give an insight into different populations.

Hens *et al.* (2000) showed that pygmies have similar body proportions to other taller human groups, where Feldsman & Lundy (1988) found that small-bodied individuals showed less variability in measurements, for this sample only 1 individual was available for study. However, it is always important in comparisons of body size to include groups from the geographical area as well as groups that can serve as out-groups. Therefore, both small and large-bodied human groups were included in this study.

The Belau National Museum

Specimens collected on two field trips in June 2006 and February 2007 were identified and catalogued for the Belau National Museum. Specimens from Ucheliung cave were numbered B: OR-14:8 and specimens from Omedokel cave were numbered B: OR-15:18. The summary provided in Table 1 lists site of origin for elements. Both specimens collected from Ucheliung and Omedokel are broadly contemporaneous (Berger *et al.* 2008a). Bone were collected from the Ucheliungs cave surface, as well as the excavation, have associated dates ranging between 1420 and 2890 YBP. All individuals from Ucheliungs cave have been previously described as small-bodied individuals (Berger *et al.* 2008a). Omedokel cave also yielded small-bodied individuals, but only from the interior of the cave (see Figure 6). Dates for these individuals ranged between 1410 and 2300 YBP (Berger *et al.* 2008a). Only individuals from the interior of Omedokel cave were collected for this study as they were of a similar age to the Ucheliung specimens. Palauan specimens collected include individuals from all age ranges (see Berger *et al.* 2008a supplementary data), indicating this was not a typical cemetery population (Berger *et al.* 2008a).

Table 2 indicates specimen numbers of the fragments collected. No postcranial specimens were found in articulation, and none can be definitively associated.

Table 1: Summary of the measurable postcranial specimens collected from Palau, Micronesia. More measureable specimens were collected from Omedokel cave. The specimens collected from Ucheliung are from the geological excavation pit.

Ucheliung cave specimens	
Total Number of measureable specimens	**8**
Long bone total	**8**
Humerus	*2*
Radius	*1*
Femur	*0*
Tibia	*3*
Fibula	*2*
Ulna	*0*
Pelvis fragments	**0**
Omedokel caves	
Total Number of measureable specimens	**26**
Long bone total	**23**
Humerus	*6*
Radius	*3*
Femur	*3*
Tibia	*3*
Fibula	*4*
Ulna	*4*
Pelvis fragments	**3**

The Dart Collection

The Dart Collection is curated by and housed within the University of the Witwatersrand Medical School osteological collection. Groups from the Dart Collection used in this study include, Khoisan, Zulu, Twana and European. Only adults were considered for this study. A summary of the specimens and elements originating from the Dart Collection appears in Table 3. With the exception of the Khoisan, who form part of the small-bodied comparative sample, the other specimens sampled from this collection are included so that the comparative dataset samples a wide range of human variation.

Table 2: Summary of the elements collected and measured from Ucheliung (B: OR-14:8) and Omedokel (B: OR-15:18) caves. All specimens in this list are incomplete.

Element	Specimen number	Element	Specimen number
Humerus	B: OR-14:8-1081	**Femur**	B: OR-15:18-013
	B: OR-14:8-891		B: OR-15:18-089
	B: OR-15:18-014		B: OR-15:18-035
	B: OR-15:18-015	**Tibia**	B: OR-14:8-011
	B: OR-15:18-088		B: OR-14:8-003
	B: OR-15:18-054		B: OR-14:8-043
	B: OR-15:18-024		B: OR-15:18-040
	B: OR-15:18-046		B: OR-15:18-045
			B: OR-15:18-021
Ulna	B: OR-15:18-031	**Fibula**	B: OR-14:8-049
	B: OR-15:18-049		B: OR-14:8-051
	B: OR-15:18-047		B: OR-15:18-020
	B: OR-15:18-027		B: OR-15:18-028
Radius	B: OR-14:8-022		B: OR-15:18-048
	B: OR-15:18-044		B: OR-15:18-043
	B: OR-15:18-016		
Os coxa	B: OR-15:18-009		
	B: OR-15:18-087		

Table 3: Summary of the postcranial sample from the Dart Collection listed by group.

Dart Collection	European	KhoiSan	Tswana	Zulu
Humerus	/	9	/	/
Os coxa	/	11	/	9
Femur	121	27	/	90
Tibia	/	10	/	/

The American Museum of Natural History (AMNH)

Not all skeletons measured at the AMNH were complete (see Table 4). Age, sex, and stature criteria were considered in choosing specimens for the sample. Khoisan and Pygmies are considered small-bodied (Cavalli-Sforza 1986), and thus represent pygmoid stature and general small-bodied stature in the comparative specimens.

Duckworth Collection, Cambridge

The Duckworth collection houses a large number of skeletal remains of island populations. Individuals used in this study varied in terms of completeness, while a minority were represented by only single elements (Table 5). Andaman and Nicobar islanders were sampled as they represent small-bodied insular populations (Stock & Migliano 2009). These small-bodied islanders are referred to in some literature as Negritos or Onge (if from the Andaman Islands) (Thangaraj *et al.* 2003, Stock & Migliano 2009).

Table 4: Specimen list of individuals measured at the AMNH collection.

AMNH	Group	Sex	Humerus	Radius	Ulna	Femur	Tibia	Fibula
99/7189	Pygmy Congo	Male	Y	Y	Y	Y	Y	Y
99/8428	KhoiSan	Male	Y	Y	Y	Y	Y	Y
99/8429	KhoiSan	Female	Y	Y	Y	Y	Y	Y
99/8433	KhoiSan	Male	Y	Y	Y	Y	Y	Y
99/8434	KhoiSan	Female	Y	N	N	Y	Y	N
99/8436	Khoisan	Female	Y	N	N	Y	N	N
99/8453	KhoiSan	Female	Y	Y	N	N	N	N
99/8454	KhoiSan	Female	Y	Y	Y	Y	Y	N
99/8455	KhoiSan	Female	Y	N	Y	Y	N	N

Specimens are adults with no pathologies. Here, KhoiSan is listed, however in the collections catalogue these individuals are referred to as Hottentots. The elements measured are listed for each individual, Y indicates presence of the element, and N indicates the absence of the element.

The British Museum of Natural History (BMNH) houses a collection of Andaman islander remains. Adult individuals with no pathologies were measured (Table 6), and individuals of both sexes are represented.

Table 5: Specimen list of specimens measured at the Duckworth collection. The elements measured are listed for each individual, Y indicates presence of the element, and N indicates the absence of the element.

Duckworth Collection	Group	Sex	Humerus	Ulna	Radius	Femur	Tibia	Fibula
ANI-006	Andaman	Unknown	N	N	N	Y	N	N
ANI-021	Andaman	Unknown	Y	N	N	Y	Y	N
ANI-022	Andaman	female	Y	Y	Y	Y	Y	Y
ANI-035	Andaman	female	Y	Y	Y	Y	Y	Y
ANI-039	Andaman	female	Y	N	Y	Y	N	N
ANI-084	Nicobar	Unknown	N	N	N	Y	Y	N
ANI-085	Nicobar	Unknown	N	N	N	Y	N	N
ANI-086	Nicobar	Unknown	N	N	N	Y	N	N
ANI-087	Nicobar	Unknown	N	N	N	Y	N	N
ANI-088	Nicobar	Unknown	N	N	N	Y	N	N
ANI-090	Nicobar	Unknown	N	N	N	Y	N	N
ANI-091	Nicobar	Unknown	N	N	N	Y	N	N
ANI-094	Nicobar	Unknown	Y	N	N	N	N	N
ANI-095	Nicobar	Unknown	Y	N	N	N	N	N
ANI-096	Nicobar	Unknown	Y	N	N	N	N	N
ANI-099	Nicobar	Unknown	N	N	N	N	Y	N
ANI-101	Nicobar	Unknown	N	N	N	N	Y	N
ANI-102	Nicobar	Unknown	N	N	N	N	Y	N
ANI-103	Nicobar	Unknown	N	N	N	N	Y	N
Specimens are adults with no pathologies. The groups represented in this list are small-bodied individuals from the Andaman and Nicobar islands, respectively. Many individuals are represented by single postcranial elements.								

British Museum of Natural History

Table 6: Specimen list of specimens measured at the British Museum of Natural History[3] (BMNH) collection. The elements measured are listed for each individual, Y indicates presence of the element, and N indicates the absence of the element.

LNHM	Sex	Humerus	Ulna	Radius	Femur	Tibia	Fibula
1861.8.22.1	Male	Y	Y	Y	Y	Y	Y
1865.5.26.1	Male	Y	Y	Y	Y	Y	Y
1890.5.14.1	Female	Y	Y	Y	Y	Y	Y
PA PHR 2001/ RCS 8.0325	Male	Y	Y	Y	Y	Y	Y

[3] Specimen details are available in the appendix, these include the individual's name, and any other information gathered during the procurement of the skeletal assemblages.

PA PHR 2003/ RCS 8.0327	Female	Y	Y	Y	Y	Y	Y
PA PHR 2005/ RCS 8.0330	Female	Y	Y	Y	Y	Y	Y
PA PHR 2006/ RCS 8.0331	Female	Y	Y	Y	Y	Y	Y
PA PHR 2007/ RCS 8.0305	Unknown	Y	Y	Y	Y	Y	Y
PA PHR 2014/ RCS 8.0324	Male	Y	Y	Y	Y	Y	Y
PA PHR 2015/ RCS 8.0323	Male	Y	Y	Y	Y	Y	Y
PA PHR 2017/ RCS 8.0307	Unknown	Y	Y	Y	Y	Y	Y
PA PHR 2021/ RCS 8.0306	Unknown	Y	Y	Y	Y	N	Y
PA PHR 2025/ RCS 8.035	Male	Y	Y	Y	Y	N	Y
PA PHR 2027/ RCS 8.0328	Female	Y	Y	Y	Y	Y	Y
PA PHR 2028/ RCS 8.0329	Female	Y	Y	Y	Y	Y	Y
PA PHR 2037/ RCS 8.0308	Unknown	Y	N	Y	Y	Y	N
PA PHR 2040/ RCS 8.0321	Male	Y	Y	Y	Y	Y	Y
PA PHR 2041/ RCS 8.0303	Unknown	Y	Y	Y	Y	Y	N
PA PHR 2042/ RCS 8.0304	Unknown	Y	Y	Y	Y	Y	Y
PA PHR 2046/ RCS 8.0302	Unknown	Y	Y	Y	Y	Y	Y
PA PHR 2049/ RCS 8.00.5	Male	Y	Y	Y	Y	Y	Y
PA PHR 2050 / RCS 8.00.6	Male	Y	Y	Y	Y	Y	Y
PA PHR 2052/ RCS 8.0301	Unknown	Y	Y	Y	Y	Y	Y
PA PHR 2054/ 1905.1125.3	Female	Y	Y	N	Y	Y	N
PA PHR 2062/ IM 20/1	Male	Y	Y	Y	Y	Y	Y
PA PHR 2063/ IM 20/3	Female	Y	Y	Y	Y	Y	Y
PA PHR 2065/ IM 20/2	Female	Y	Y	Y	Y	Y	Y
PA PHR 2067/ IM 20/4	Male	Y	Y	Y	Y	Y	Y
PA PHR 2070/ RCS 8.00.1	Male	Y	Y	Y	Y	Y	N
Specimens are adults with no pathologies. The groups represented in this list are small-bodied individuals from the Andaman Islands. The collection from the NHM has individuals with more complete skeletal remains.							

All Andaman individuals are combined into a single group in statistical analyses, but occasionally separated by specimen number for illustrative purposes.

Online dataset made available by Peter Brown

Peter Brown has made an entire dataset available online for the purposes of body size and dental comparative studies (Brown 2001). Data from this source were included when measurement definitions were comparable. While it is known that there may be slight interobserver measurement error between multiple observers, the dataset is a unique insight into populations that are not always available for sampling. Thus, despite the potential introduction of inter-observer error, inclusions of these data were considered important for achieving the goals of the present study.

In this study the sample of indigenous Australian populations will be referred to as "Aboriginal" in accordance with the terms " Aboriginal people" or Aboriginal person", which is recommended by the Aboriginal Advisory Group of the Community Legal Centres NSW (Coyne, 2011).

The groups sampled in the Brown dataset included both male and female adults of:

- Australian Aboriginals from the Murray River Valley and Swanport region[4].
- Modern Southern Chinese from Hong Kong and Guangdong Province.
- Modern Northern Chinese from Shanxi and Hebei Provinces (males only)[5].
- Romano-Britains from Poundbury, 18th and 19th century.
- Europeans from Christ Church, Spitalfields, London.

The latter two groups were combined with the Europeans measured from the Dart Collection for ease of analysis. There were no obvious outliers amongst measurements in the overall European sample, which indicates that the measurements taken by Peter Brown were generally compatible with those in the present study. Table 7 shows a summary of the number of elements and groups considered for this study. The Swanport Aboriginals and

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[4] The skeletons were part of the "George Murray Black" collection housed in the Department of Anatomy, University of Melbourne (reburied in 1984), and the South Australian Museum. No skeleton was collected during controlled archaeological excavations. All are unprovenienced.

[5] The Spitalfields, Southern Chinese, and Northern Chinese samples are of known age and sex. A large number of the Southern Chinese only have tooth breadth data, as teeth were the primary interest of the Prince Phillip Dental Hospital where this collection was housed, and because finite storage space restricted what could be curated (Brown 2001)

Murray Valley Aboriginals are considered to have some of the largest tooth dimensions recorded for indigenous Australian groups and modern humans (Brace *et al.*1980).

Table 7: Summary of the total number of individuals used in this study. Each group has been separated by postcranial element. This table was compiled using an online dataset (Brown 2001).

Peter Brown Dataset	European	Murray Valley Aboriginals	Southern Chinese
Humerus	93	70	50
Radius	90	/	/
Os coxa	/	100	/
Femur	120	76	40
Tibia	/	/	55

2.2 Craniodental materials

The Belau National Museum

Craniodental remains were collected from the interior of Ucheliung cave as well as from an excavation pit. Dental remains from Omedokel cave were collected from the interior of the cave. A total of 79 teeth, 12 cranial fragments, and 10 mandibular fragments were included in the study (see Table 8 & Table 9).

The Dart Collection

The comparative sample consisted of specimens from modern human museum collections housed at the University of Witwatersrand, Dart Collection. Specimens were chosen according to the following criteria: age, only adult specimens were measured; no pathologies, only specimens without observable pathologies were measured. Males and females from each group were measured where available. As comparative specimens were complete, mandibles and crania with their teeth (both left and right teeth) were measured and averaged for each specimen. These data were provided courtesy of Mirriam Tawane, a

Ph.D. candidate in the Bernard Price Institute for Palaeontology at the University of the Witwatersrand, (Table 10), Dentitions from comparative populations include: Khoisan, Zulu, Tswana, and European.

Table 8: Summary of the measurable cranio dental specimens collected from Palau, Micronesia. The specimens collected have been separated into the two localities sampled. Both localities are contemporaneous.

Ucheliung cave specimens	
Individual teeth	**44**
Cranial	**1**
Maxillae	**2**
Mandibles	**3**
Omedokel caves	
Individual teeth	**35**
Cranial	**3**
Maxillae	**6**
Mandibles	**7**

Table 9: The number of specimens found from two field seasons in Palau. Specimens from Omedokel were collected from the surface and those from Ucheliung cave are from the surface and a test excavation pit. Excavation levels are in spits of 10cm.

Element(s)	Omedoke l cave	Excav Level 1	Excav Level 2	Excav Level 3	Excav Level 4	Excav Level 5	Surface	Unknown Provenience
Cranium	0	9	6	8	10	4	4	27
Mandible	1	2	0	0	1	0	1	1
Dentition	45	34	19	8	12	4	3	3

Table 10: The number of individuals measured from the Dart collection and the groups they represent. Data provided courtesy of Mirriam Tawane (2012).

Dart Collection	European	KhoiSan	Tswana	Zulu
Mandibular Teeth	61	4	61	75
Mandibular Teeth	61	6	54	72

Online dataset made available by Peter Brown

The modern dental metrics included:

- Australian Aboriginals from the Murray River Valley and Swanport region[6].
- Modern Southern Chinese from Hong Kong and Guangdong Province[2].
- Modern Northern Chinese from Shanxi and Hebei Provinces (males only)[7].

In cases where both the left and right tooth data were given for a specimen, an average was calculated (see Table 11. The Aboriginal groups (Swanport Murray Valley) have some of the largest tooth dimensions recorded for native Australian population, and amongst all modern humans (Brace *et al.*1980).

Table 11: Number of individuals used in this comparative sample, from Brown (2001). The data are an indication of the maximum number of individuals sampled and do not represent the total number of individuals in the Brown (2001) dataset. Teeth present for each individual varies.

Peter Brown Dataset	European	Murray Valley Aboriginals	Northern Chinese	Swanport Aboriginals	Southern Chinese
Mandibular Teeth	94	77	35	29	254
Mandibular Teeth	64	90	54	33	50

2.3 Methods for the postcranial analyses

Postcranial measurement definitions follow Martin (1928) and those used in this study are listed in Table 13 and Table 14. Due to the fragmentary nature of the Palauan specimens, original measurements chosen were based on which parts of the elements were preserved within the assemblage. These measurements varied from specimen to specimen. It was therefore decided the Palauan specimens would be evaluated against the comparative

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[6] The skeletons were part of the "George Murray Black" collection in the Department of Anatomy, University of Melbourne that was reburied in 1984 and the South Australian Museum. All are unprovenienced.

[7] Dataset contains a large number of missing measurements. The Spitalfields, Southern Chinese, and Northern Chinese samples are of known age and sex. A large number of the Southern Chinese only have tooth breadth data since teeth were the primary interest of the Prince Phillip Dental Hospital where this collection was housed and because finite storage space restricted what could be curated.

sample based only on the measurements obtainable on the Palauan specimens this was done to avoid large numbers of extrapolations within the data.

2.4 Methods for the Craniodental analyses

Table 12: The groups represented in the cranio-dental dataset and the number of cranial and mandibular specimens from which data was used in this analysis.

Group	Measurement	N
European	Cranial material	138
	Mandibular material	86
KhoiSan	Cranial material	12
	Mandibular material	5
Murray Valley Aboriginals	Cranial material	96
	Mandibular material	86
Northern Chinese	Cranial material	37
	Mandibular material	33
Palauan	Cranial material	4
	Mandibular material	4
Swanport Aboriginals	Cranial material	52
	Mandibular material	33
Southern Chinese	Cranial material	66
	Mandibular material	73
Tswana	Cranial material	10
	Mandibular material	0
Zulu	Cranial material	82
	Mandibular material	0

The Australian Aboriginal, Chinese, and some European specimens were obtained from Brown (2001), and the author measured the Khoisan Palauan And Tswana.

Craniodental measurements of Palauan and comparative material follow those taken by Howells (1973) (definitions given in Table 15). Measurements were taken with a digital sliding calliper held parallel to the occlusal and vestibular surfaces of the crown. In cases where the teeth were *in situ*, if a tooth was rotated in relation to the curvature of the dental arch, the measurement was taken between the points on the approximate surfaces of the crown where it was considered that contact with adjacent teeth would normally occur

(Townsend & Brown 1979). In order to provide odontometric standards for comparison with other groups, an average value was calculated using the measurements from both sides. If a tooth was missing, or in the case of the Palauan specimens' only one was available, only that value was used. The author discussed methods for the dental measurements with Mirriam Tawane before data collection commenced in order to ensure a consistent approach in obtaining measurements of dental material.

Table 13: Measurements taken on the upper limb bones and a definition of each. The measurements presented here are limited to those that were taken on the Palauan specimens.

Element	Measurement	Description
Humerus	**Maximum length**	Maximum length to the distal trochlear flange
	Midshaft maximum diameter	Maximum diameter taken at the midshaft
	Midshaft minimum diameter	Minimum diameter of the midshaft
	Head Anteroposterior (AP) Diameter	Maximum diameter of the head in the anteroposterior direction of the head.
	Head Superoinferior (SI) diameter.	The superoinferior diameter of the head
	Epicondylar breadth	Maximum breadth measured across the epicondyles
	Distal articular breadth	Maximum distance across the medial trochlea to the lateral capitulum
	Olecranon fossa breadth	Maximum breadth of the fossa in a transverse plane
	Mesiodistal length of the trochlea	Length of the trochlea taken mesiodistally
	Capitular SI diameter	Diameter of the capitulum taken from the superior to the inferior surface
Ulna	**Maximum length**	Maximum length of the bone
	Transverse diameter	The diameter measured perpendicular to the dorso-volar diameter at the level of greatest crest development
	Midshaft AP diameter	Anteroposterior diameter taken at the midshaft
	Crest Height	Diameter taken from the base of the radial notch, to the top of the olecranon.
	Olecranon height	Anteroposterior diameter of the olecranon process
	Olecranon length	Middle of the trochlear notch to the proximal point on the triceps brachii tuberosity
	Head breadth	Mediolateral diameter of the head
	Distal maximum depth	Anteroposterior diameter of the distal epiphysis
	Distal radial maximum length	Maximum anteroposterior diameter of the radial facet
Radius	**Carpal articular breadth**	Maximum mediolateral diameter of the articular surface
	Maximum length	Maximum length of the bone to the styloid process
	Head AP diameter	Maximum diameter in the anteroposterior diameter

Table 14: Measurements taken on the pelvis and lower limb bones as well a definition of each. The measurements presented here are limited to those that were taken on the Palauan specimens.

Element	Measurement	Description
Os coxa	**Maximum acetabular diameter**	This is taken from the acetabular margin (immediately adjacent to the middle of the anterior inferior iliac spine) to the most distant point on the inferior acetabular margin. Measurement is taken on the internal edge of the attachment of the articular capsule
	Transverse diameter of the acetabulum	Taken at right angle to the maximum acetabular diameter
	Iliac height	Mid acetabular point on the superior margin of the acetabular notch to the most distant point on the iliac crest.
	Superior iliac breadth	Maximum length taken directly around the anterior superior iliac spine and the posterior superior iliac spine.
Femur	**Bicondylar length**	Distal plane of the condyles to the proximal head, measured perpendicular to the distal condylar plane.
	Anteroposterior (AP) head diameter	Maximum anteroposterior diameter of the head articular surface
	Superoinferior (SI) head diameter	Maximum vertical diameter of the head articular surface
	Vertical neck diameter	Minimum diameter of the neck measured perpendicular to the neck axis and parallel to the anterior surface of the neck
	Sagittal neck diameter	Minimum diameter of the neck measured perpendicular to the neck axis and the vertical neck.
	Head and neck length	Point of intersection of the neck and diaphyseal axes to the furthest (proximo-medial) point on the head
	Bicondylar breadth	Maximum breadth across the external margins of the condylar subchondral bone.
	Lateral condyle breadth	Maximum breadth on the posterior aspect of the lateral condyle subchondral bone.
Tibia	**Proximal AP diameter**	Maximum anteroposterior diameter measured at the level of the proximal nutrient foramen
	Proximal ML diameter	Maximum mediolateral diameter measured perpendicular to the anteroposterior diameter
	Distal maximum breadth	Maximum mediolateral breadth across the epiphysis, measured perpendicular to the talar trochlear articular axis.
	Medial talar articular depth	Minimum anteroposterior diameter of the articular surface, measured perpendicular to the talar trochlear articular axis
	Midshaft AP diameter	Maximum anteroposterior diameter at the midshaft, measured perpendicular to the transverse axis of the talar trochlear articulation
	Midshaft ML diameter	Maximum mediolateral diameter at the midshaft.
Fibula	**Distal maximum depth**	Maximum anteroposterior diameter of the epiphysis, measured parallel to the talar surface.
	Distal articular depth	Maximum anteroposterior diameter of the talar articular surface.
	Distal articular height	Maximum proximodistal diameter of the talar articular surface.

Table 15: Summary of the measurements taken for the cranial as well as the dental comparative material. Howells (1973) defines all cranial measurements. For dental measurements Townsend & Brown (1979) was used as a guideline.

Element	Measurement	Description
Cranium	**Orbital Breadth**	*Breadth from ectoconchion to dacryon, as defined, approximating the longitudinal axis which bisects the orbit into equal upper and lower parts*
	Interorbital Breadth	*The breadth across the nasal space from dacryon to dacryon.*
Mandible	**Symphyseal Height**	*Maximum height of the corpus measured perpendicular to alveolar plane*
	Symphyseal Breadth	*Measured perpendicular to symphyseal height*
	Molar Breadth At M1/M2	*Maximum breadth of the corpus taken at the M1/M2 measured perpendicular to the height*
	Ramus Height	*Taken from the gonion to the condyle.*
	Ramus Breadth	*Maximum anterior to posterior breadth measured perpendicular to the height.*
Dentition	**Mesiodistal Crown Diameter**	*Maximum length (diameter) measured across wear the facets*
	Buccolingual Crown Diameter	*Maximum breadth across the crown measure perpendicular to length*
	Cervico-Enamel Junction Mesiodistal	*Maximum mesiodistal diameter at the cervicoenamel junction*
	Cervico-Enamel Junction Buccolingual	*Maximum buccolingual diameter at the cervicoenamel junction.*

2.5 Statistical Methods for the Postcranial and Cranial-Dental Analyses

Specimens from the comparative sample were viewed as groups rather than individuals, in order to obtain an unbiased result. By establishing where groups plot, characteristics that are unique to small-bodied individuals may be identified. Secondly, a statistical approach provides a probability-based indication of which measurements the Palauans may share with other populations. This also may be useful in identifying unique measurements that can be used to isolate potential morphological indicators of insular dwarfism.

Since none of the Palauan specimens were found in articulation, and were excessively fragmentary in some cases, the choice of appropriate statistical procedures was limited.

2.5.1 *Descriptive statistics*

For each measurement, descriptive statistics were calculated to evaluate basic patterns in the data. A summary table of the mean, minimum measurement, maximum measurement, standard deviation and sample size was included for each measurement. Standard deviation provides a method of evaluating the differences for each individual from the mean of the comparative sample. The standard deviation is related to the range, which is the distribution between the lowest and the highest measurement taken (Madrigal 1998). A low standard deviation indicates that there is little spread of the measurements around the mean for that species. A high standard deviation indicates a large spread of the measurements around the mean (Brown 1988; Townsend 2002).

Standard deviations indicate how close the Palauan specimens plot to the mean of the comparative sample. Univariate and bivariate plots were used to establish comparative trends amongst the different samples, as well as potential comparison between groups (Townsend 2002). Univariate analyses also were used on each measurement to characterize relationships between the Palauan and comparative samples (Madrigal 1998). All statistical analyses were performed using SPSS (version 18).

Statistical tests make an objective judgement of normality, but are disadvantaged by sometimes not being sensitive at small sample sizes or excessively sensitive to larger sample sizes (Madrigal 1998). As such, a subjective judgement about the data from plots/graphs can still be useful. Graphical interpretation has the advantage of allowing good judgement to assess normality in situations when numerical tests might be over or under sensitive, but graphical methods do lack objectivity.

2.6 Hypothesis to be tested in this research

Hypothesis one: The Palauan sample represents a group of humans with a body size amongst the smallest recorded for a modern human sample. It is predicted that due to the isolation and nature of island populations the Palauan postcrania and cranial measurements will reflect those of a small-bodied insular populations, such as the Andamanese and Nicobarese. By comparing whether or not the measurements taken for the Palauans are smaller, larger or similar in size to the comparative sample groups would be used as an indicator of possible reduction this is based on the hypothesis that the founding populations of Palau were 'normal' (Fitzpatrick 2007).

Hypothesis two: The Palau specimens represent a case of insular dwarfism. Marshall & Corruccini (1978) found that a decrease in mean body size of a species could occur over a short period (i.e., a short period being defined as ranging from a few decades to several thousand years). Accordingly, dates for the Palau sample of 1400-2900YBP offers ample time to manifest the reduction in body size for this population.

Hypothesis three: Is it possible to identify traits that are likely to occur in populations which are reducing in body size over a relatively short time period (several generations)? The Palauan sample would be expected to have closer alignment with island populations and not mainland small-bodied groups. Since morphology and metrics associated with rapid body size reduction have yet to be established for isolated hominin populations, this study suggests that in order to identify a rapidly reduced body size dimensions of articular surfaces should be examined in relation to epiphyseal dimensions of long bones.

Hypothesis four: The Palauan specimens have teeth that are large relative to the comparative samples. A critical aim of this study is to establish whether the ancient

Palauan sample are infact megadontic, a trait not seen in modern-day Palauans, this would lend to possible identification of the founding population.

Hypothesis five: The Palauan specimens collected from Ucheliung and Omedokel caves originated from Austramelanesia. Results presented here aim to identify remnant morphologies of the founding population, or potential metric or morphologic features that may be a result of rapid reduction of body size. Southeast Asian pygmies are thought to be descendants of Australomelanesians due to the shared cranial affinities and sundadonty (Storm 2007).

Based on the outcome of the results the possible causes for the insular dwarfism will be explored. It is important to note that evolution on islands is dependent on life history, community composition and the biology of the isolated species. When examining island populations, all of these factors should be taken into consideration instead of focusing on generalities (Raia & Meiri 2006). On islands, mammals have considerable variation in the way in which they respond to the selective forces that drive size evolution (Meiri et al. 2008). When studying island populations, both biotic and abiotic environmental factors must be taken into account in order to assess how a populations' body size will evolve (Meiri et al. 2008). Factors that may affect insular dwarfing are environmental factors such as a shortage of food, climate, and lack of predation and each will be explored and discussed in lieu of the results obtained.

CHAPTER 3: RESULTS AND ANALYSIS OF THE PALAUAN POSTCRANIAL SPECIMENS

In this chapter, the postcranial elements of the Palauan sample are studied in terms of the specific predictions (see below). All measurements will be qualitatively analysed for this group, when data are available. Establishing body size of this fossil population is important as this has implications for the provenience, life history and morphology of the Palauan specimens.

3.1 Specific Predictions for the postcranial specimens of the Palauan sample

The Palauan sample represents a group of humans with a body size amongst the smallest recorded for a modern human sample. It is predicted that due to the isolation and nature of island populations the Palauan postcrania will reflect those of a small-bodied insular population, such as the Andamanese and Nicobarese.

The aims of this research involve examination of size variation of individual skeletal elements of modern humans recovered from Palau, Micronesia by comparing them to a modern comparative sample, which includes other island populations. The following hypotheses will be tested in this results section:

- **Hypothesis one**: The Palauan sample represents a group of humans with a body size amongst the smallest recorded for a modern human sample.
- **Hypothesis two**: The Palau specimens represent a case of insular dwarfism.

- **Hypothesis three**: Is it possible to identify traits that are likely to occur in populations which are reducing in body size over a relatively short time period (several generations)?

If this population expressed insular dwarfism, the present study aims to identify any size trends or associated metric features found within the population. By comparing whether or not the measurements taken for the Palauans are smaller, larger or similar in size to the comparative sample groups would be used as an indicator of possible reduction this is based on the hypothesis that the founding populations of Palau were 'normal' (Fitzpatrick 2007). The goal is not only to establish traits that are likely to occur in a populations which is reducing in body size over a relatively short time period (several generations), but also to highlight traits that may indicate from where this population may have originated. This will be done using a statistical analysis of the metrics collected on the Palauan postcrania.

3.2 THE UPPER LIMB OF THE PALAUAN SPECIMENS

This chapter presents measurements and analyses of the upper limb elements of the Palauan specimens, as well as comparisons with other populations. Tables and graphs highlight any shared traits or differences within the comparative sample. The analysis presented here aim to investigate the Hypothesis of possible insular dwarfism.

3.2.1 Maximum length of the humerus

Table 16: Descriptive statistics for the maximum length of the humerus. The mean, standard deviation (SD) and range are given for each group. The Palauan sample is represented by a single element and is in italics as it represents an estimated value.

Group	N	Minimum	Maximum	Mean	SD
Total comparative sample	**254**	**241.0**	**379.0**	**301.896**	**25.3764**
Andaman Islanders	32	241.0	308.0	269.078	14.7747
European*	93	258.0	344.0	303.032	21.1878
KhoiSan	5	276.0	323.0	296.000	21.3892
Australian Aboriginal*	70	261.0	379.0	319.186	21.8939
Nicobar Islander	3	258.0	273.0	264.333	7.7675
Palauan	1	-	-	*290.000*	.
Pygmy from the Congo	1	-	-	268.000	.
Southern Chinese*	50	256.0	341.0	300.340	19.7666
Data used in this set were collected by the author, *European, Australian Aboriginal, Southern Chinese from Brown (2001)					

Specimen B: OR -14:8-1081 has a part of the distal epiphysis missing; therefore an estimated maximum humeral length is 290 mm (see Figure 7) (Rao *et al.* 1989). This length [290 mm] is not the minimum recorded for the comparative sample, but does fall within 1 SD of the Khoisan mean (Table 16). Based on the humeral lengths for each group, there is much overlap between the comparative groups. The small-bodied populations fall below the comparative sample mean with the exception of one Andaman specimen and two Khoisan specimens. The Palauan specimen falls just below the total sample mean (Table 16 & Figure 8) with no significant deviation ($z = -0.46$). For the maximum length of the humerus the Palauan specimen falls above the means of the small bodied comparative groups, but within the range of both the Andaman islander and Khoisan groups (see Figure 8).

Figure 7: Right humerus, specimen number B: OR-14:8-1081. As with all the Palauan specimens, this humerus is fragmented and missing the proximal end. The length for this specimen was estimated at 290 mm.

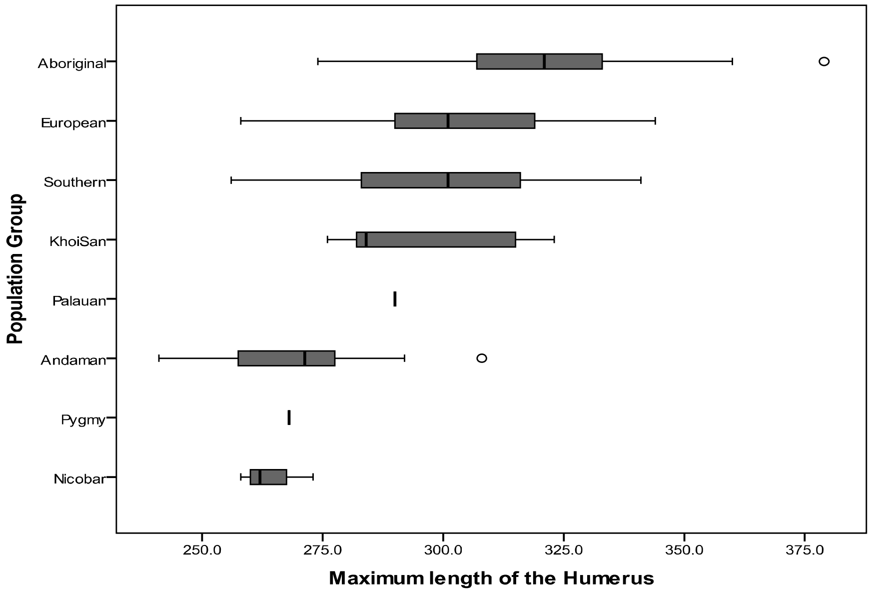

Figure 8: Box plot showing the distribution of measurements taken for the maximum length of the humerus.

3.2.2 Humeral maximum midshaft diameter

The Palauan individual has a small midshaft diameter when compared to other small-bodied samples. The measurements plot in a normal distribution (Figure 10 & Table 17), the smallest and largest measurement both belong to the Australian Aboriginal group.

B: OR-14:8-1081 plots below the mean for the entire comparative sample (measurement = 19.1mm, z = -0.36). While there is overlap of the entire comparative group ranges the Palauan specimen plots below the mean of the Khoisan group.

Table 17: Descriptive statistics for the maximum diameter of the humeral midshaft. The mean, standard deviation (SD) and range is given for each group.

Groups	N	Min	Max	Mean	SD
Total for the comparative sample	**277**	**14.0**	**27.0**	**19.998**	**2.4786**
Andaman Islanders	33	14.2	20.2	17.278	1.8026
European	100	15.0	27.0	20.640	2.2294
KhoiSan	7	17.2	22.1	19.343	1.9234
Australian Aboriginal	81	14.0	26.0	20.148	2.4552
Nicobar Islander	2	18.9	20.4	19.645	1.0819
Palauan (B: OR-14:8-1081)	1	19.1	19.1	19.100	.
Pygmy from the Congo (99/7189)	1	15.6	15.6	15.600	.
Southern Chinese	53	16.0	26.0	20.434	2.2956
The Palauan sample is represented by a single element (B: OR-14:8-1081) as is the Pygmy from the Congo (99/7189). Data used in this set were collected by the author, data for European, Australian Aboriginal, Southern Chinese from Brown (2001)					

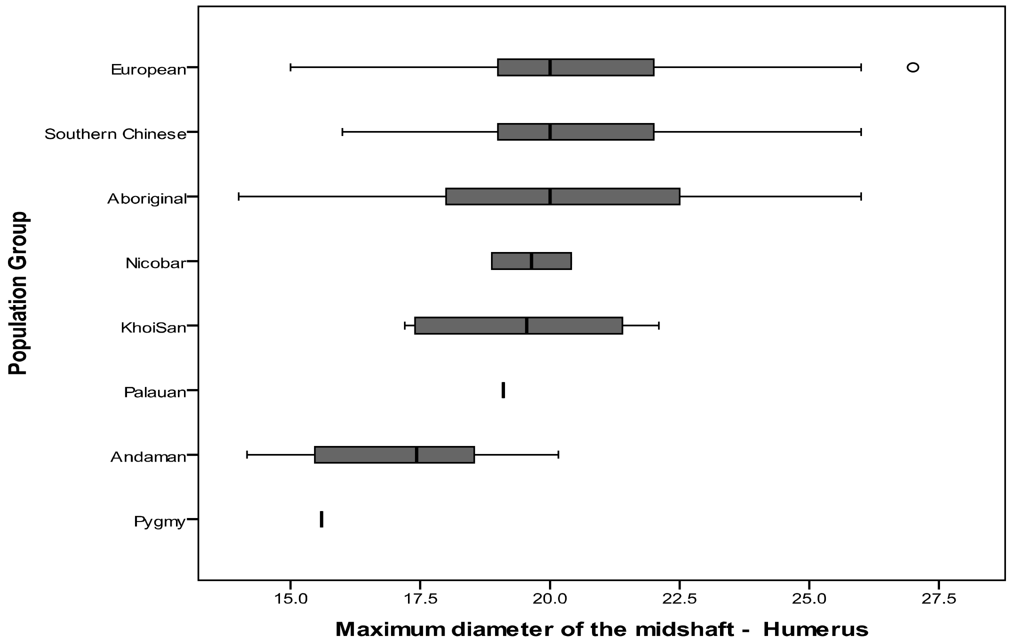

Figure 9: Box plot showing the distribution of measurements for the maximum diameter of midshaft of the humerus. The measurements provided above have a normal distribution for this measurement. (N = 278, SD = 2.47).

3.2.3 Midshaft minimum diameter for the humerus

Specimen B: OR-14:8-1081, has a measurement similar to the mean of the Khoisan and Nicobarese groups (Table 18). The Pygmy humerus has the smallest minimum midshaft diameter and the European group has the largest. The Palauan specimen (B:OR-14:8-1081, midshaft minimum diameter = 14.1mm) falls within the range of the comparative sample, which is normally distributed (see Figure 10), but falls almost one standard deviation below the entire sample mean (z= -0.85). The Palauan specimen plots nearest the Nicobarese mean.

Table 18: Descriptive statistics for the minimum diameter of the humeral midshaft. The mean, standard deviation (SD) and range are given for each group.

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**195**	**9.9**	**23.0**	**16.219**	**2.4843**
Andaman Islander	33	9.9	17.4	13.584	1.7425
European	100	11.0	23.0	17.105	2.3358
KhoiSan	6	13.3	17.5	14.733	1.5731
Nicobar Islander	2	12.8	15.4	14.075	1.8738
Palauan	1	14.1	14.1	14.100	.
Pygmy from the Congo	1	12.3	12.3	12.300	.
Southern Chinese	53	13.0	20.5	16.509	1.9327

All data used in this set were collected by the author with the exception of Southern Chinese and European (n = 93). The Palauan sample is represented by a single element (B: OR-14:8-1081) as is the Pygmy from the Congo (99/7189).

3.2.4 Anteroposterior (AP) diameter of the humeral head

The Palauan sample is comprised of seven humeral heads. Humeral head AP diameter is reported in Table 19. The entire comparative sample have AP head diameters have no specimens falling below than two standard deviations from the comparative sample mean. No data were collected on ‘larger’ bodied individuals; however, it is still important for the purposes of this study to see how the Palauan sample plots relative to small-bodied specimens. B: OR-15:18-014 has the smallest overall Z-score and plots almost one standard deviation below the mean (Table 20). Three of the specimens plot more than two standard deviations above the mean (B: OR-15:18-088, B: OR-15:18-054, & B: OR-15:18-024). For the AP head diameter measurements, the sample means are interesting. The Palauan specimens mean plots nearest the Khoisan specimen mean. The largest range for this measurement belongs to the Palauan group (see Figure 11).

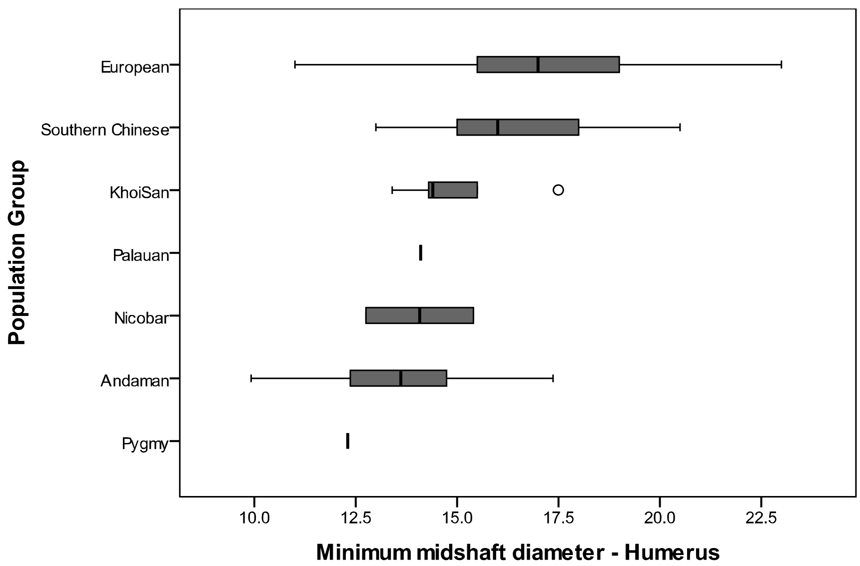

Figure 10: Boxplot showing the distribution of measurements of the minimum diameter of the humeral midshaft. (N= 96, SD =2.48.)

Table 19: Descriptive statistics for the anteroposterior diameter of the humeral head. The mean, standard deviation and range is given for each group.

Group	N	Min	Max	Mean	SD
The entire comparative sample	**40**	**30.6**	**41.0**	**35.246**	**2.5526**
Andaman Islander	31	30.6	39.4	34.852	2.2926
KhoiSan	6	34.6	41.0	37.983	2.7694
Nicobar Islander	2	32.7	33.9	33.300	.7920
Palauan	7	32.9	44.1	38.043	4.4052
Pygmy from the Congo	1	34.9	34.9	34.900	.
Seven specimens represent the Palauan sample. Data used in this set were collected by the author.					

Table 20: Z-scores for the Palauan specimens' humeral AP head diameter.

Palauan specimen	Zscore
B:OR-15:18-014	-0.91721
B:OR-15:18-015	-0.25308
B:OR-15:18-088	2.23742
B:OR-15:18-054	1.83894
B:OR-15:18-024	2.80193
B:OR-15:18-046	0.07899
B:OR-14:8-1081	-0.25308

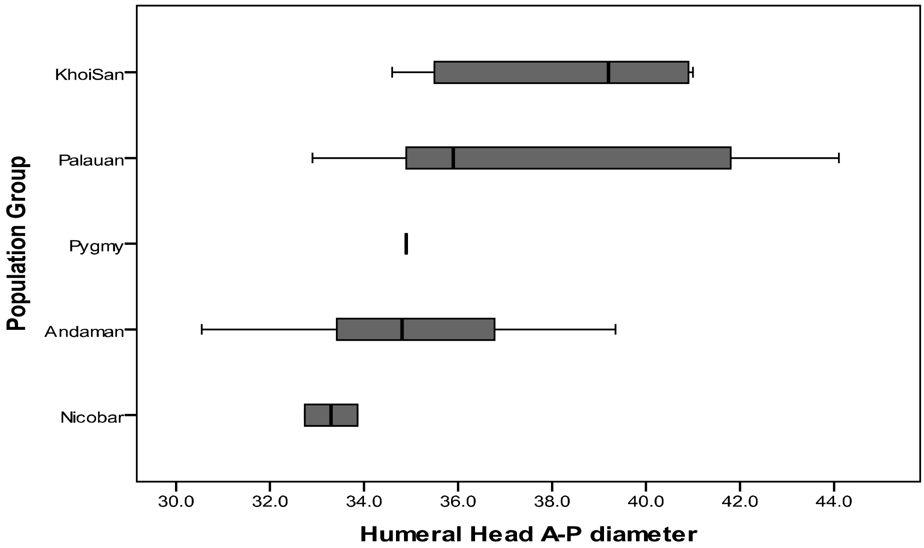

Figure 11: Boxplot showing the distribution of measurements of the humeral head anteroposterior diameter. This sample consists of only small-bodied samples. (N= 47, SD = 3.01).

3.2.5 Superoinferior (SI) diameter of the humeral head

Table 21: Descriptive statistics for the humeral head SI diameter. The individual mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Entire comparative sample)	**262**	**31.8**	**54.0**	**41.071**	**4.2569**
Andaman Islander	33	31.8	42.2	36.633	2.6296
European	89	36.0	54.0	43.163	4.1960
KhoiSan	7	33.6	46.5	39.314	4.3291
Murray Valley Aboriginal	80	32.0	48.0	40.525	3.5435
Nicobar Islander	3	36.8	38.6	37.623	.9333
Palauan	1	41.0	41.0	41.000	.
Pygmy from the Congo	1	35.1	35.1	35.100	.
Southern Chinese	49	34.0	51.0	41.735	3.7501
The Palauan sample is represented by a single element (B: OR-15:18-046). Data used in this set were collected by the author, data for European, Australian Aboriginal, and Southern Chinese from Brown (2001).					

Figure 12: Photograph of specimen B: OR-15:18-046 a proximal humeral fragment. This specimen is broken just above the midshaft.

B: OR -15:18-046 (Figure 12) has a SI diameter which falls at the mean of the entire comparative sample (z = -0.166), and at the uppermost part of the range for the SI head diameter. The largest measurements belong to the Murray Valley Aboriginal group and the Southern Chinese. Most specimens fall within one standard deviation of the mean (see Table 21). The Palauan and Khoisan have means which plot near each other and the Andaman, Nicobar, and Pygmy individuals group together. The Australian Aboriginal sample spans the entire range of the normal distribution due to the large number of samples.

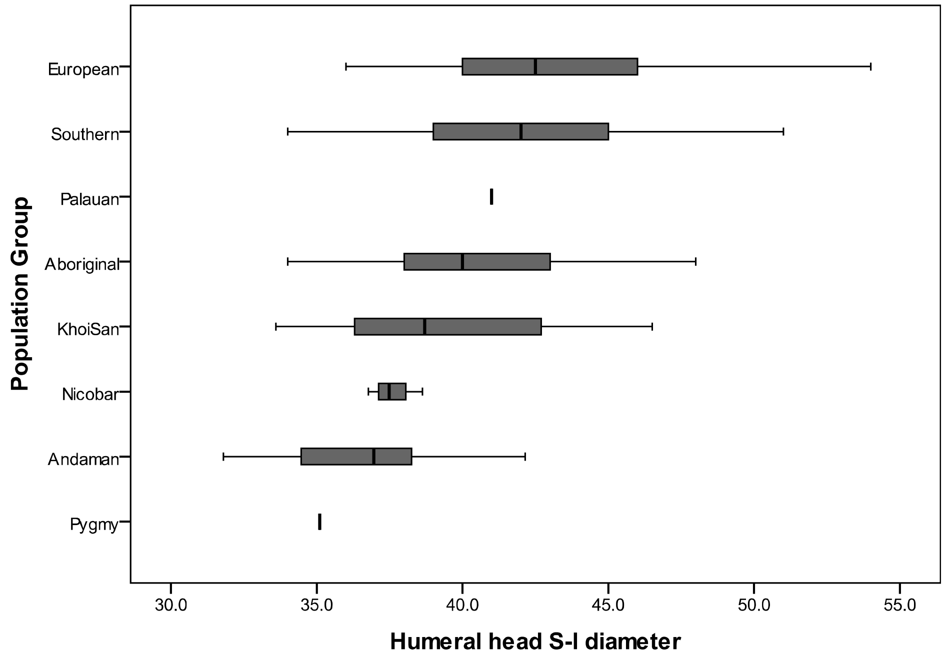

Figure 13: Boxplot showing the distribution of measurements of the humeral head superoinferior diameter. (N = 263, SD = 4.24).

3.2.6 Bi-epicondylar breadth of the humerus

The Palauan specimens have a large mean comparable to that of the European group (see Figure 14). Specimen B: OR-15:18-024 is the largest measurement (64.2 mm, z =1.52) for the Palauan sample and falls just above the Khoisan range and the smallest recorded is B: OR-15:18-015 (50.4mm, z = -0.047), which falls within the range of other small-bodied sample. The Australian Aboriginal sample has the smallest epicondylar breadth and falls as an outlier group (i.e. no comparison can be made with any other group); this trend is not seen in the other measurements taken on this sample as most measurements fall above the sample mean.

Table 22: Descriptive statistics for the bi-epicondylar breadth of the humerus. The individual mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Entire comparative sample	**264**	**34.0**	**74.0**	**50.713**	**8.7948**
Andaman Islander	32	45.1	57.5	50.858	3.2006
European	89	45.0	74.0	57.815	6.3207
KhoiSan	7	50.6	60.6	54.343	3.3832
Aboriginal	81	34.0	47.0	40.099	3.2962
Nicobar Islander	2	52.7	55.1	53.900	1.7395
Palauan	4	50.4	64.2	57.450	5.6459
Pygmy	1	53.1	53.1	53.100	.
Southern Chinese	52	46.0	62.0	54.346	4.7471

There are four Palauan specimens, B: OR-15:18-015; B: OR-15:18-088; B: OR-15:18-054; B: OR-15:18-024. Data used in this set were collected by the author, data for European, Australian Aboriginal, and Southern Chinese from Brown (2001).

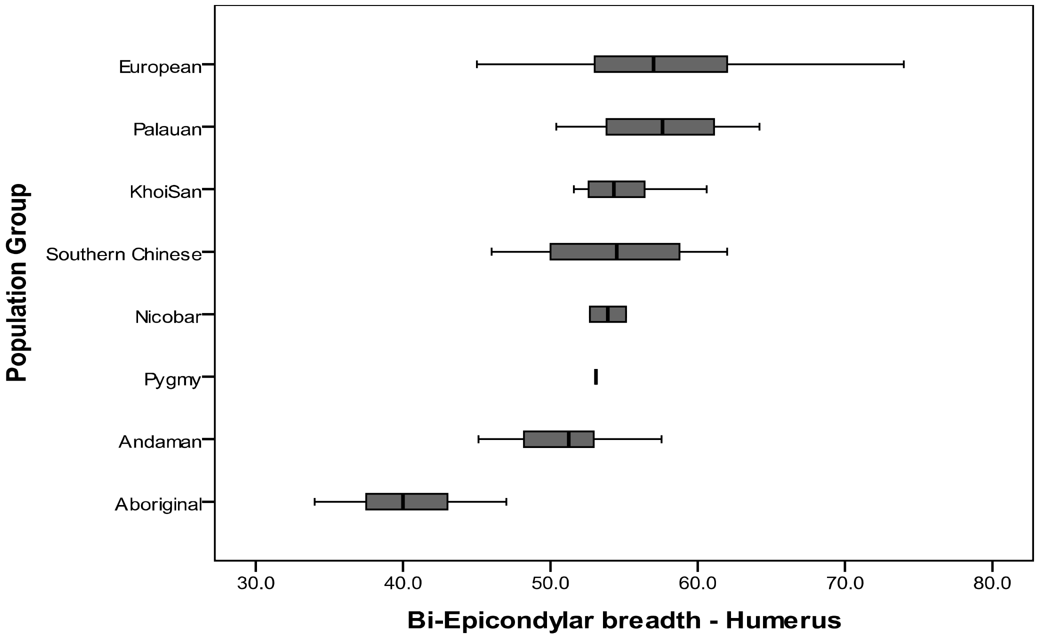

Figure 14: Boxplot showing the distribution of measurements of the bi-epicondylar breadth of the humerus. (N=268, SD = 8.78 mean 268)

3.2.7 Distal articular breadth of the humerus

Measurements for maximum diameter of the distal articular surface plot with a normal distribution. In Table 23, B: OR -14:8-1081 has a small measurement (34.8mm, z = -1.0) for the comparative sample and falls one standard deviation below the small-bodied sample mean. The Palauan specimen's plots well below the mean of the Andaman sample, the biggest difference in means, are seen between the Palauan and Khoisan samples.

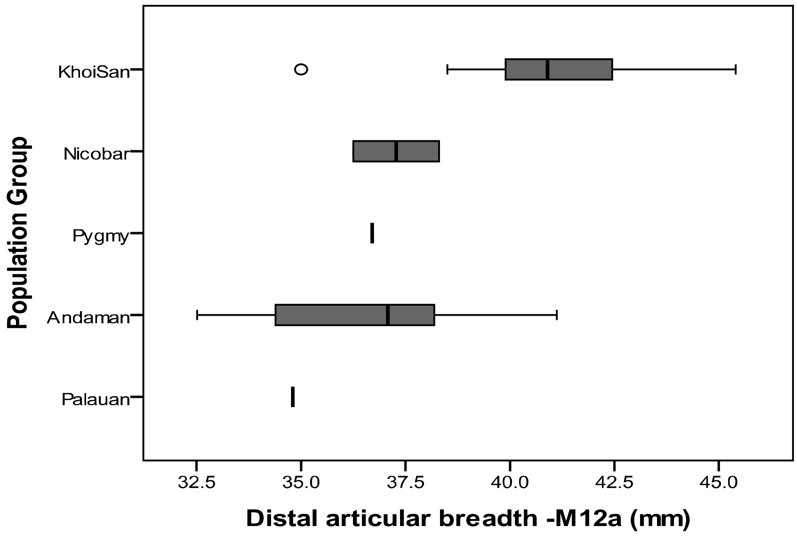

Figure 15: Boxplot showing the distribution of measurements of the distal articular breadth of the humerus. No individuals fall at the lower end of the distribution (N= 52 SD =3.10 mean = 37.94)

Table 23: Descriptive statistics for the distal articular breadth of the humerus. The individual mean, standard

deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Entire comparative sample	**51**	**32.5**	**45.4**	**37.996**	**3.1075**
Andaman Islander	32	32.5	41.1	36.652	2.5249
KhoiSan	16	35.0	45.4	40.856	2.4725
Nicobar Islander	2	36.3	38.3	37.275	1.4496
Palauan	1	34.8	34.8	34.800	.
Pygmy	1	36.7	36.7	36.700	.
There is one Palauan specimen, B: OR-14:8-1081. All measurements recorded by the author					

3.2.8 Olecranon fossa breadth of the humerus

The olecranon fossa breadth has a relatively small range for the comparative sample (see Table 24 & Figure 16). B: OR-14:8-891 has a measurement which falls below the minimum of the comparative sample (19.1 mm, z = -1.73) and falls almost 2 SD'd below the comparative sample mean. B: OR-14:8-1081 (21.7 mm, z = -0.45) and is smaller than the minimum recorded measurement of the Khoisan group or Pygmy. The Palauan sample mean plots nearest to the mean of the Andaman islanders group (see Figure 16).

Table 24: Descriptive statistics for olecranon fossa breadth of the humerus. The individual mean, standard deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Entire comparative sample	**45**	**19.3**	**28.1**	**22.698**	**1.9875**
Andaman Islander	33	19.3	25.3	22.111	1.6892
KhoiSan	8	21.9	28.1	25.100	1.8055
Nicobar Islander	3	22.0	23.9	22.923	.9304
Palauan	2	19.1	21.7	*20.400*	1.8385
Pygmy from the Congo	1	22.2	22.2	22.200	.

There are two Palauan specimens, B: OR-14:8-1081 B: OR-14:8-891. Data used in this set were collected by the author.

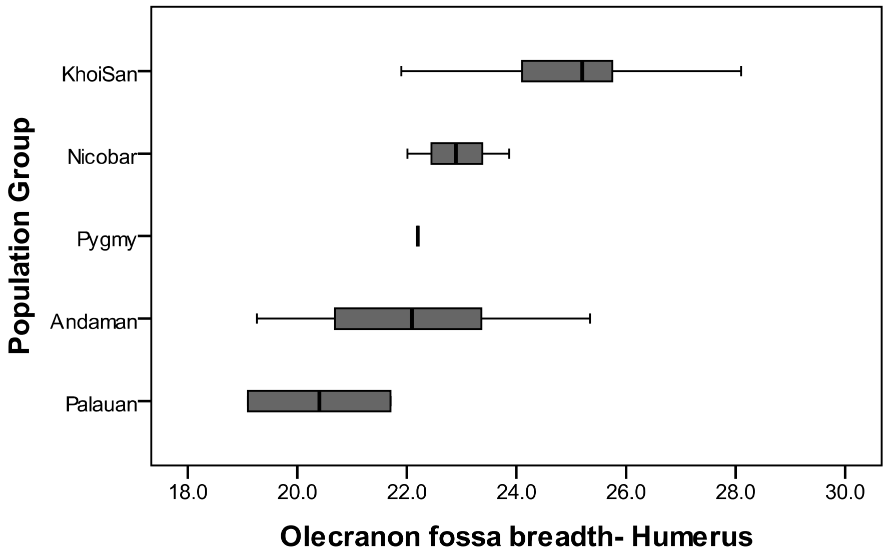

Figure 16: Boxplot showing the distribution of measurements for the olecranon fossa breadth of the humerus. (N=47, SD =2.018, Mean = 22.6).

3.2.9 Mediolateral (ML) breadth of the humeral trochlea

Palauans have the smallest mean mediolateral breadth of the trochlea while the Andamanese have the largest (Table 25). The Palauan mean falls within 1 SD of the Khoisan mean. The Palauan specimens and the Khoisan plots are separated from the insular populations (Nicobarese and Andamanese) in Figure 17, indicating a distinct grouping.

Table 25: Descriptive statistics mediolateral length of trochlea of the humerus. The individual means, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Entire comparative sample	**42**	**11.2**	**23.4**	**18.904**	**2.9717**
Andaman Islander	31	17.1	23.4	20.110	1.6450
KhoiSan	8	11.2	18.5	13.987	2.3277
Nicobar Islander	3	18.4	20.9	19.553	1.2657
Palauan	2	10.9	15.2	13.050	3.0406
There are two Palauan specimens, B: OR-14:8-1081 B: OR-14:8-891. Data used in this set were collected by the author.					

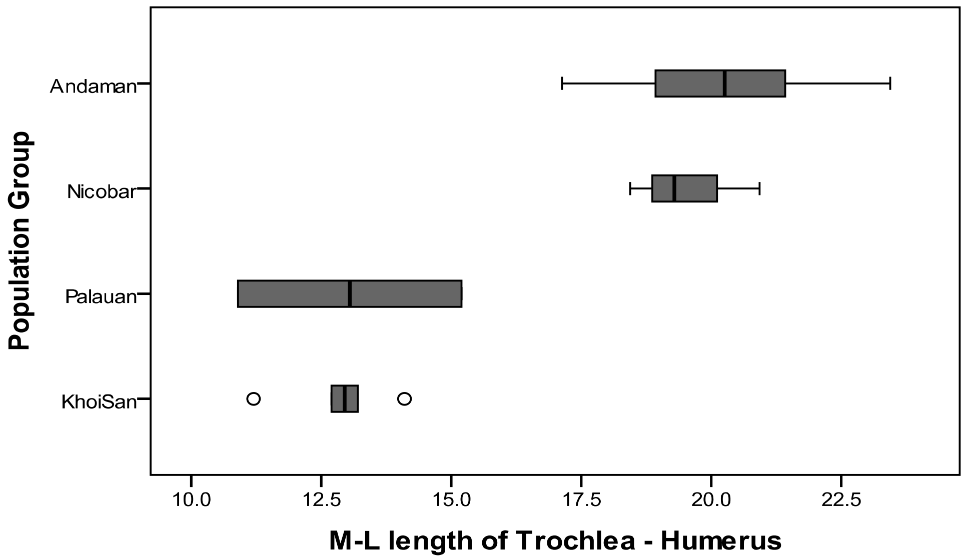

Figure 17: Boxplot showing the distribution of measurements of mediolateral breadth of the humeral trochlea. (N =44 SD = 3.187 mean = 18.64).

3.2.10 Capitular superoinferior (SI) diameter of the humerus

B: OR-15:18-024 has the largest recorded measurement for the small-bodied samples (20.4mm z =2.48) and falls two standard deviations above the mean for the small-bodied sample (Figure 18). The Andaman group has the smallest measurements and mean. The Palauan specimens do not plot in a statistically comparable way to any of the small-bodied groups and the range of the Palauan specimens falls above those of the comparative groups.

Table 26: Descriptive statistics for the capitular superoinferior diameter of the humerus. The individual means, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Capitular SI diameter (mm)	**42**	**13.0**	**20.0**	**16.677**	**1.3811**
Andaman Islander	32	13.0	18.7	16.319	1.2819
KhoiSan	7	16.2	20.0	17.886	1.2321
Nicobar Islander	2	17.8	18.2	18.025	.2758
Palauan	3	19.6	21.0	20.400	.7211
Pygmy from the Congo	1	17.0	17.0	17.000	.
There are three Palauan specimens, B: OR-15:18-088, B: OR-15:18-054 B: OR-15:18-024. Data used in this set were collected by the author.					

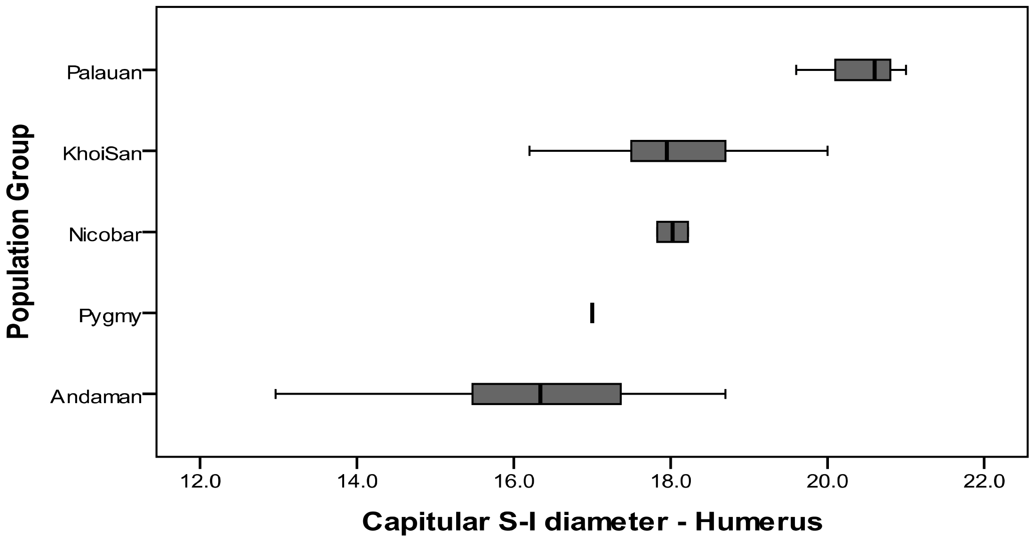

Figure 18: Boxplot showing the distribution of measurements of the capitular superoinferior diameter of the trochlea. (N =45, SD =1.638, Mean = 16.93)

When the dimensions of the trochlea were compared to those of the capitulum a trend emerged between the small-bodied populations, the island groups plotted in a similar way and the Khoisan plotted in a completely different way and seemed to be an outlier group(see Figure 19). The Palauan specimens were plotted as a mean of both the mediolateral breadth of the trochlea and the superoinferior height of the capitulum. The Palauan mean plotted with the Khoisan group. Bivariate plots are used to indicate population variation about a mean.

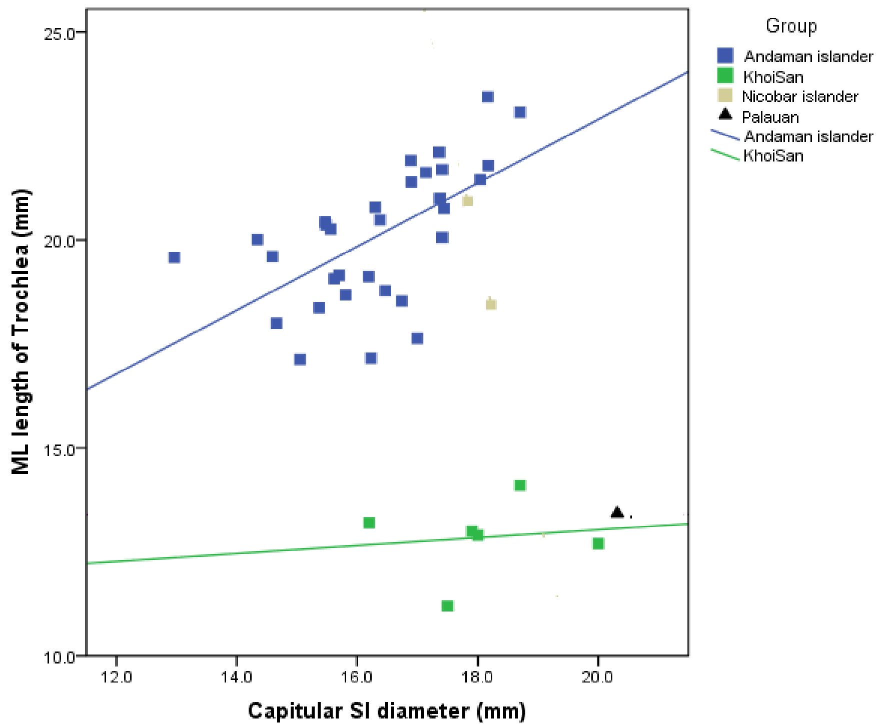

Figure 19: Scatter plot of the mediolateral breadth of the trochlea versus superoinferior height of the capitulum. Straight lines indicate the best-fit line for each group. The black triangle represents the Palauan mean for each measurement since no specimen preserved both a trochlea and a capitulum.

There is no way to tell whether the black triangle (Palau) is at the periphery of the underlying (real) scatter exhibited by Palauan people, or whether it is in the centre of the scatter. While it may be a bit deceptive to compare the Palauan data point to scatters of other populations in the plot, the distinct separation between small-bodied groups makes it necessary to do this comparison in order to establish where this fossil population would plot. For the insular populations (Figure 19) for every unit change in the capitular SI diameter, there will be a greater unit change in the ML length of the trochlea relative to the change seen in mainland small-bodied samples.

The Palauan specimens are smaller than the comparative sample in the distal portions of the humerus (see Figure 20). Distal articular breadth, olecranon fossa breath, and mediolateral breadth of the trochlea are the smallest in the Palauan sample. The Palauan midshaft diameters are average (fall within 1 SD of the overall mean). Proximally, the Palauan humeral measurements (i.e., humeral head AP and SI diameters) are relatively larger compared to other populations. Distally, the Palauans are more robust in the lateral end of the humerus, with ratios of the capitulum SI diameter to the trochlea ML diameter reflecting those seen in the Khoisan sample (see Figure 19). The Palauan measurements do not plot with any specific group, it was expected that the specimens may consistently plot with other insular small-bodied populations, but this did not occur. The closest affinity for measurement varies between the Khoisan group and the Andaman islanders.

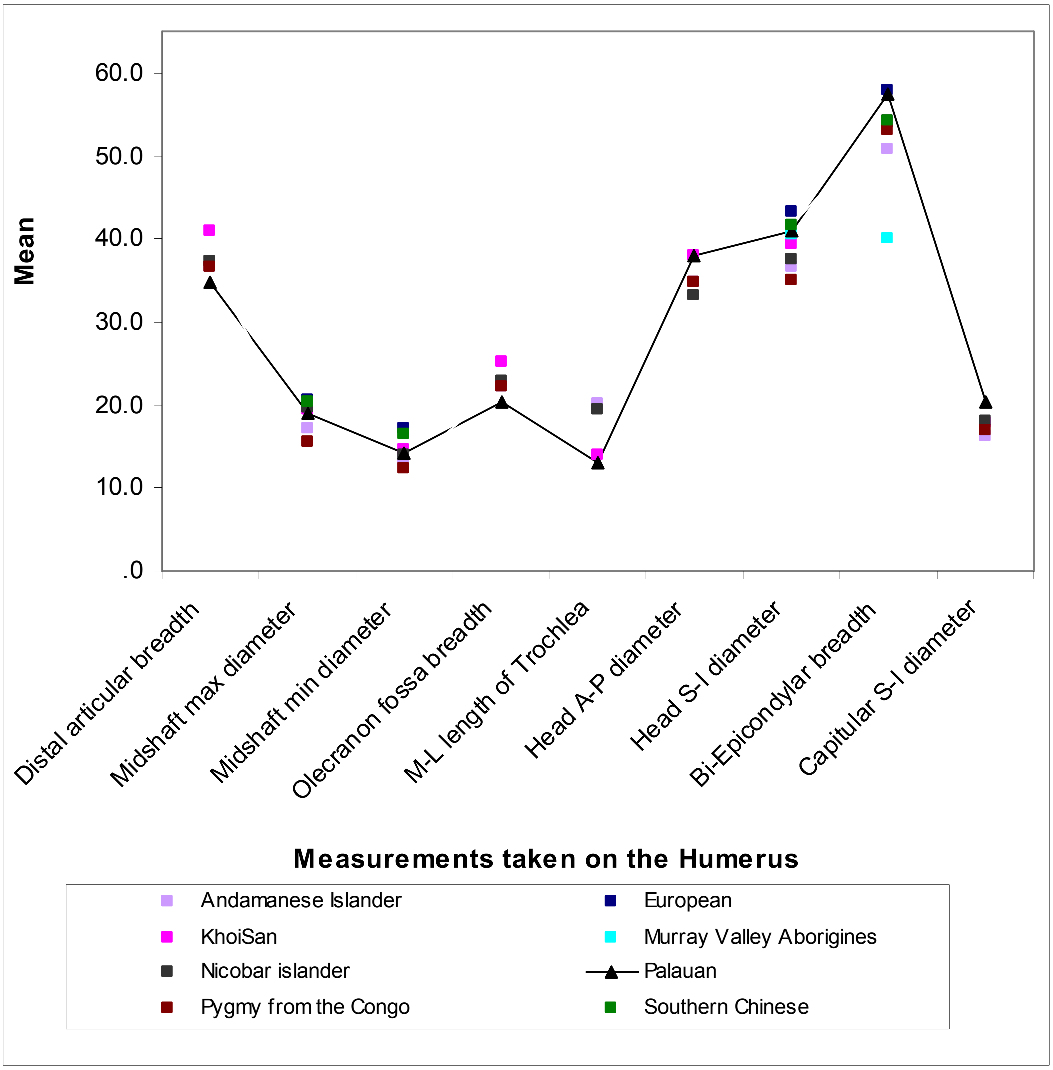

Figure 20: Graph showing mean plots of all the measurements taken on the humerus. In this graph, the Palauan specimens are both smaller and larger than the comparative groups depending on the measurement some measurements are larger.

3.3 Statistical Analysis and Results for the Radius of the Palauan specimens

3.3.1 Maximum length of the radius

Maximum length of the radius (see Table 27) for the Palauan specimen is an estimate as the distal radius is missing (see Figure 21). B: OR-15:18-016 (240 mm, z = 0.80) is one standard deviation above the mean for the entire sample, but still falls within the range of the small-bodied comparative sample. The largest and smallest recorded maximum lengths belong to the European group. The smallest recorded islander measurement belongs to an Andaman individual (197 mm z = -1.45), this measurement is one standard deviation below the mean of the sample. For maximum length of the radius, The Palauan specimen falls just below the maximum of the Khoisan, but this measurement is larger than any mean of the comparative groups.

Table 27: Descriptive statistics for the maximum length of the radius. The mean, standard deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Total comparative sample	**166**	**181.00**	**273.00**	**224.8825**	**18.71970**
Andaman Islander	30	197.00	252.00	216.0167	13.23233
European	90	181.00	266.00	223.7889	19.46446
KhoiSan	4	203.00	246.00	230.00	19.64688
Palauan	1	240.00	240.00	*240.00*	.
Pygmy	1	207.00	207.00	207.00	.
Southern Chinese	42	200.00	273.00	233.9286	17.01275

There is one Palauan specimen, B: OR-15:18-016. Data used in this set were collected by the author; data for Southern Chinese and European specimens taken from Brown (2001).

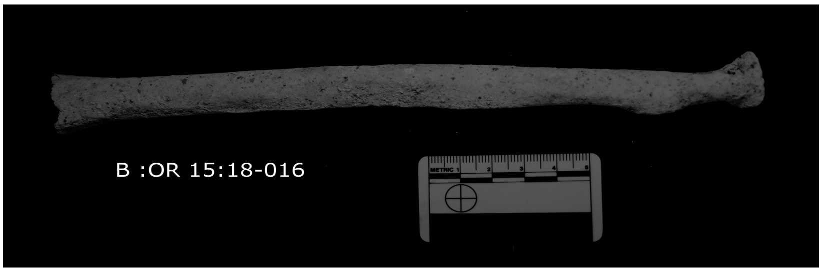

Figure 21: Fragment of a near complete left radius. Specimen is missing the distal end and length was estimated at 240 mm (using Rao *et al.* 1989). Specimen was collected from Omedokel cave. Picture by L.R. Berger, edited by author.

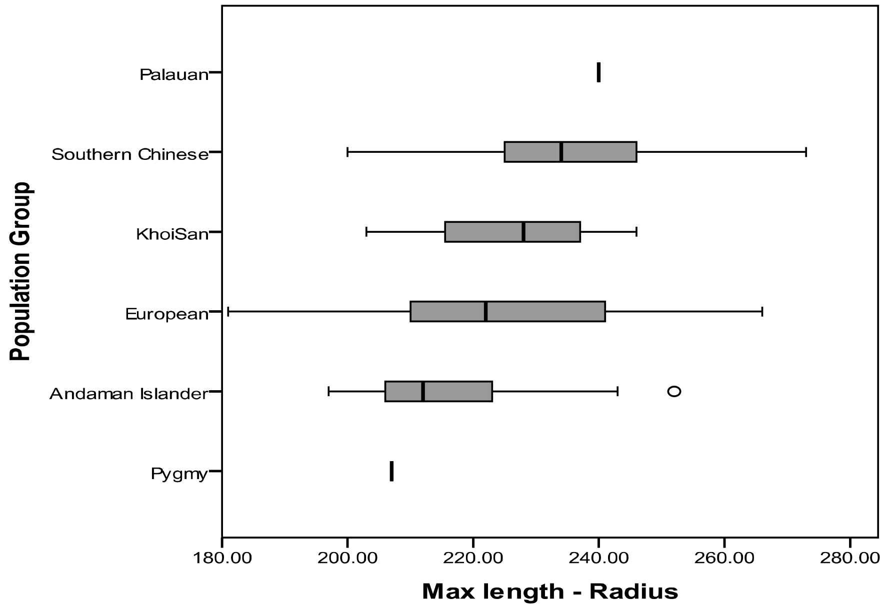

Figure 22: Boxplot showing the distribution of measurements taken for the maximum length of the radius. The measurements are normally distributed for the comparative groups measured (N = 168, SD =18.696, mean = 225.08).

3.3.2 Carpal articular breadth of the radius

Table 28: Descriptive statistics for the carpal articular breadth of the radius. The mean, standard deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Total comparative sample	**34**	**22.75**	**30.37**	**25.7603**	**2.00092**
Andaman Islander	30	22.75	30.37	25.8017	2.08934
KhoiSan	4	16.80	26.90	23.7000	4.65260
Palauan	2	21.90	26.00	23.9500	2.89914
Pygmy from the Congo	1	23.80	23.80	23.8000	.
There are two Palauan specimens, B: OR-14:8-022 B: OR-15:18-044. Data used in this set were collected by the author.					

The two Palauan specimens fall on either side of the sample mean (see Table 28) for carpal articular breadth. B: OR-14:8-022 (26.0mm, z = 0.16) plots above the mean and B: OR-15:18-044 (21.9mm z = -1.83) plots nearly 2 SD's below the mean. The Khoisan has a small articular surface area when compared to the other small-bodied groups, which all plot together. One specimen (Khoisan) plots more than three SD's from the mean. Among the groups, the Palauan and Pygmy means plot nearest each other (see Figure 23), and the Palauans have the smallest recorded measurement.

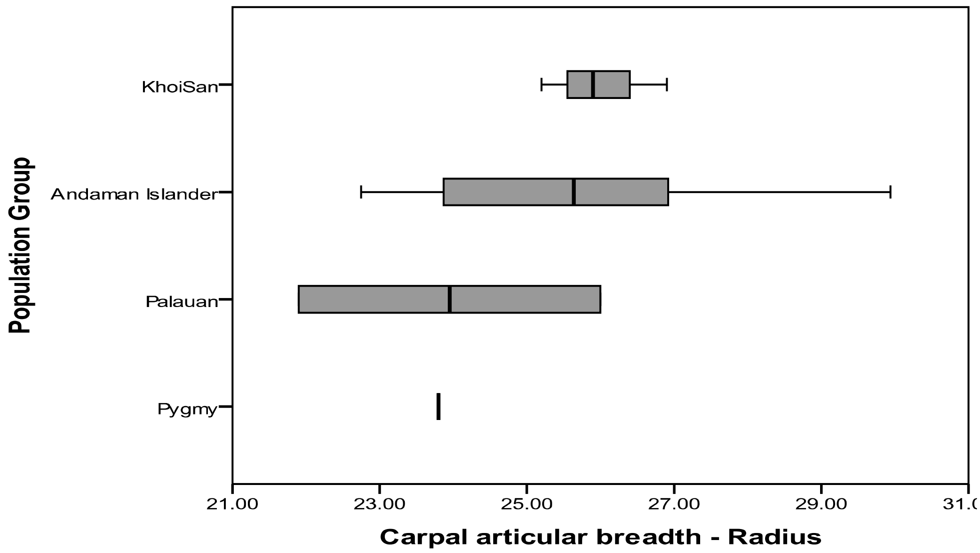

Figure 23: Boxplot of the distribution of measurements taken for the carpal articular breadth of the radius. (N=37, SD = 2.489 Mean = 25.47)

3.3.3 Distal breath of the radius

Table 29: Descriptive statistics for the distal breadth of the radius. The mean, standard deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Total comparative sample	**35**	**20.64**	**29.96**	**25.1200**	**2.46915**
Andaman Islander	30	20.64	29.96	25.1419	2.50392
KhoiSan	4	23.70	28.00	26.4250	1.96193
Palauan	2	24.80	27.40	26.1000	1.83848
Pygmy	1	22.10	22.10	22.1000	.
There are two Palauan specimens, B: OR-14:8-022 & B: OR-15:18-044. Data used in this set were collected by the author.					

The Palauan specimens both fall within the range of the other small-bodied groups (Table 29). B: OR-14:8-022 (27.40 mm Z = 0 .91) & B: OR-15:18-044 (24.80 mm z = -0.153). There is significant overlap between all the small-bodied groups for this measurement. The Palauan specimens and the Khoisan specimens plot near each other (Figure 24).

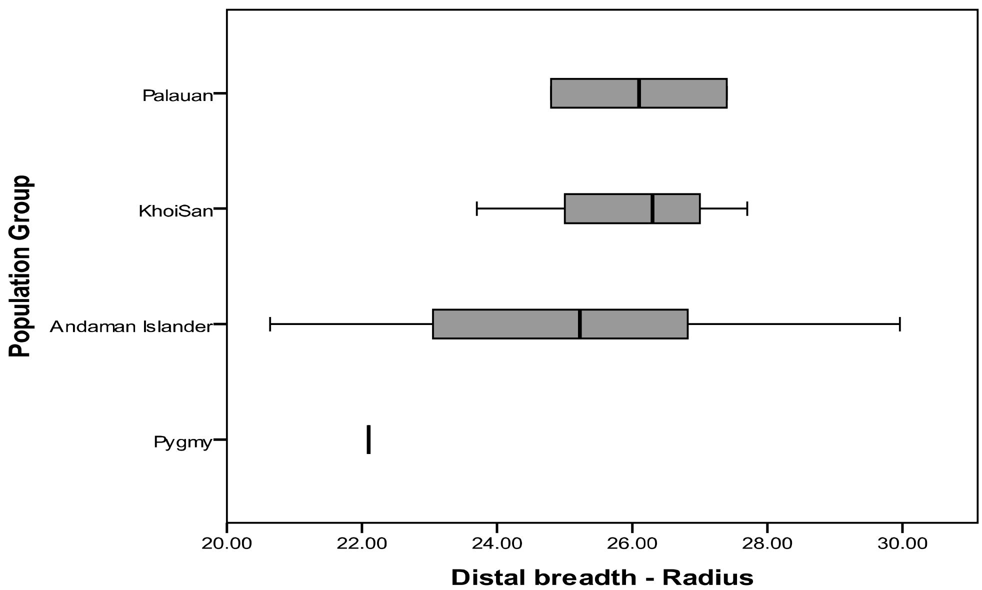

Figure 24: Boxplot of the distribution of measurements taken on the distal breadth of the radius. All measurements plot near the mean, or within two standard deviations of the mean. (N= 38, Std, dev. = 2.44 mean =25.25)

3.3.4 Distal depth of the radius

B: OR-14:8-022 (18.3mm z = 0.95705) and B: OR-15:18-044 (19.7mm z = 0.25) both fall within the range of the comparative sample (see Table 30). The measurements all fall within a normal distribution curve with a high frequency of individuals falling above the mean. Within this small-bodied comparative sample, there is no significant difference between the groups. The Palauan and Andaman groups have comparable measurements the two Palauan specimens plot within range of the Andaman sample.

Table 30: Descriptive statistics for distal depth of the radius. The mean, standard deviation (SD), minimum and maximum are given for each group of the comparative sample.

Group	N	Min	Max	Mean	SD
Total comparative sample	**35**	**14.30**	**21.27**	**17.7306**	**2.01449**
Andaman Islander	31	14.38	21.27	17.8410	2.02159
KhoiSan	4	16.60	19.20	17.4500	1.18181
Palauan	2	18.30	19.70	19.0000	.98995
Pygmy	1	14.30	14.30	14.3000	.

There are two Palauan specimens, B: OR-14:8-022 & B: OR-15:18-044. Data used in this set were collected by the author.

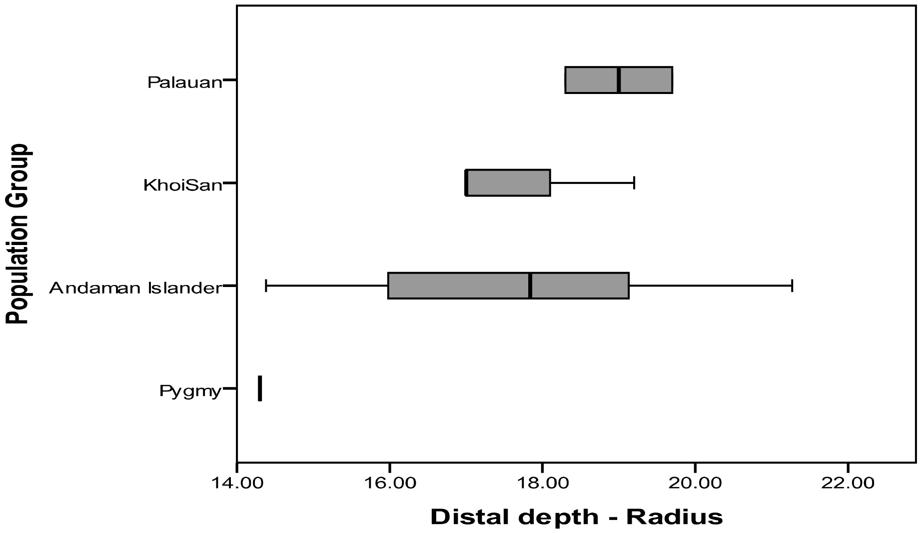

Figure 25: Boxplot of the distribution of measurements for the distal depth of the radius. All measurements plot near the mean, or within two standard deviations of the mean. (N = 38, SD = 1.969, Mean 17.77)

3.3.5 Anteroposterior (AP) diameter of the radial head

The Palauan specimen, B: OR-15:18-016 (21.5mm z = 0.38) falls within range of the small-bodied comparative sample. The Andaman group includes an individual that measured larger than the European sample maximum (Table 31), meaning there is overlap for the ranges of all groups examined. No single group or specimen plots as an outlier (Figure 26). The Palauan specimen plots near the mean of the European (see Figure 26).

Table 31: Descriptive statistics for the anteroposterior head diameter of the radius. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total Comparative sample	**165**	**15.06**	**26.46**	**20.6118**	**2.32534**
Andaman Islander	30	15.06	26.46	18.2483	2.17670
European	85	17.00	26.00	21.2588	2.08111
KhoiSan	4	18.90	22.40	20.3750	1.46373
Palauan	1	21.50	21.50	21.5000	.
Pygmy from the Congo	1	18.10	18.10	18.1000	.
Southern Chinese	46	15.50	25.50	21.0217	1.89724

The Palauan sample is represented by a single element (B: OR-15:18-016). Data used in this set were ected by the author, data for Southern Chinese and European specimen measurements were obtained from wn (2001).

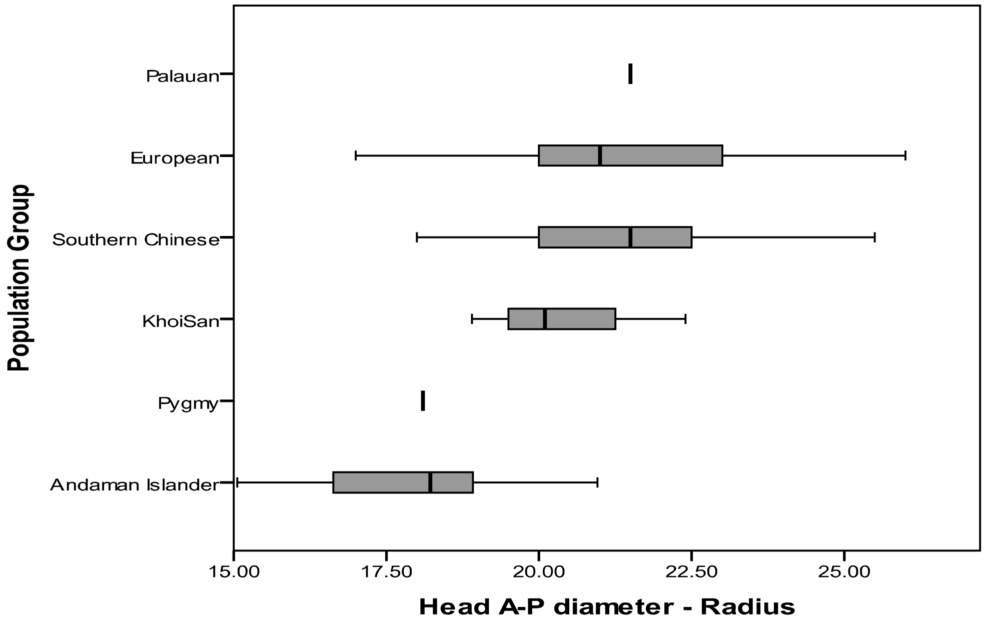

Figure 26: Boxplot showing the distribution of measurements taken on the radial head, for the AP diameter. (N=167, SD = 2.313, Mean = 20.61).

For the radius, the epiphyseal measurements of the Palauan specimens are at the upper end of the range of the small-bodied samples (see Figure 27). While the maximum length mean is large (Table 27) the measurement recorded is based on an estimate. The carpal articular breadth and the distal radial depth of the Palauan sample plots with the Andaman group. The AP head diameter mean and distal breadth of the radius have means that are different for the Palauan sample. For the radius, the Palauan specimens plot similarly to the Khoisan in that they seem to be more robust in the distal articular measurements.

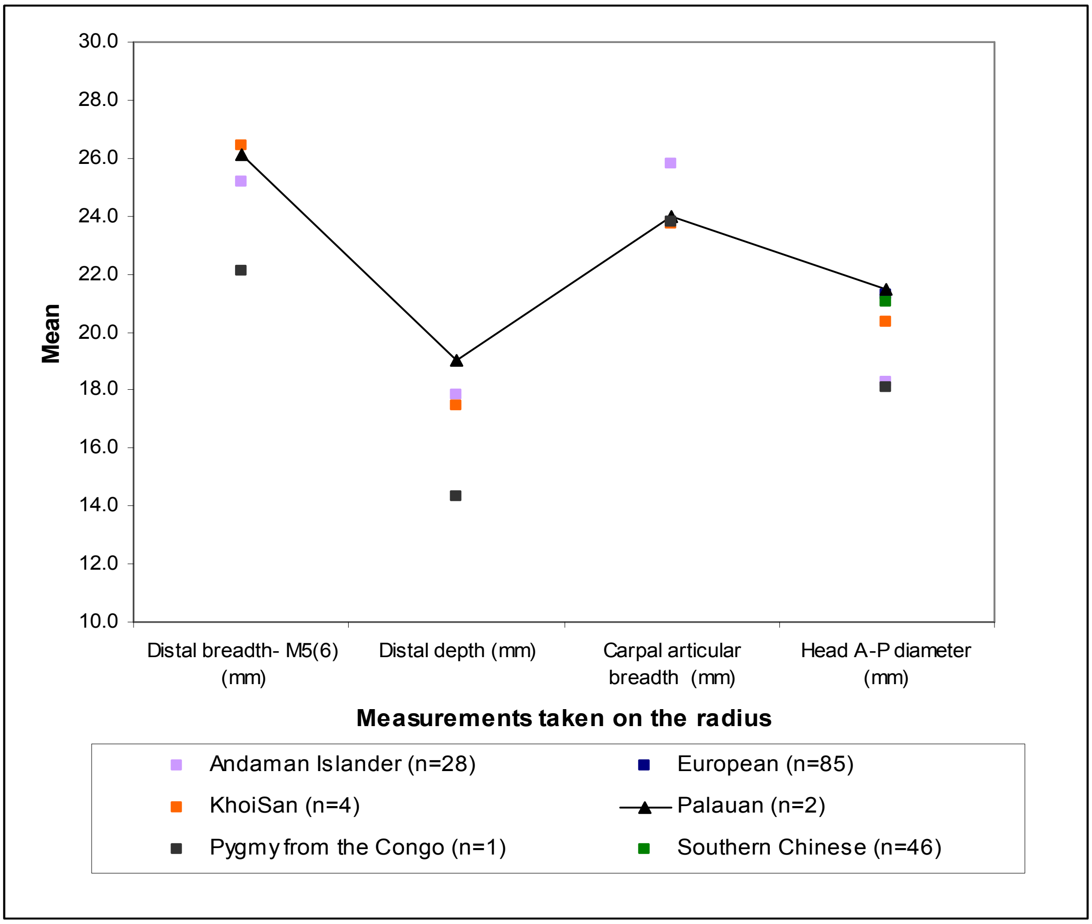

Figure 27: Graph showing some of the measurements taken on the radius. The mean for each group is plotted against the measurement. The sample sizes are indicative of the number of samples present in total.

3.4 Statistical Analysis and Results for the Ulna of the Palauan Specimens

3.4.1 Crest height of the ulna

This measurement takes the entire crest height of the ulna into account from below the radial notch to the top of the olecranon (see upper limb measurements in Table 13). Only one specimen B: OR–15:18-031 (33.80mm z = -2.28), had a radial notch present and could be measured; it has the smallest crest height for the entire comparative sample (see Table 32) and falls below the minimum of the comparative sample. The Palauan measurement plots well below the ranges of each of the comparative groups (see Figure 28).

Table 32: Descriptive statistics for the crest height of the ulna. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total for the entire sample	**35**	**35.95**	**50.53**	**43.3937**	**3.81006**
Andaman Islander	29	35.95	50.53	43.3166	3.85950
Khoisan	5	41.20	50.10	44.6600	3.58929
Palauan	1	33.80	33.80	33.8000	.
Pygmy from the Congo	1	39.30	39.30	39.3000	.
The Palauan sample is represented by a single element (B: OR-15:18-031). Data used in this set were collected by the author.					

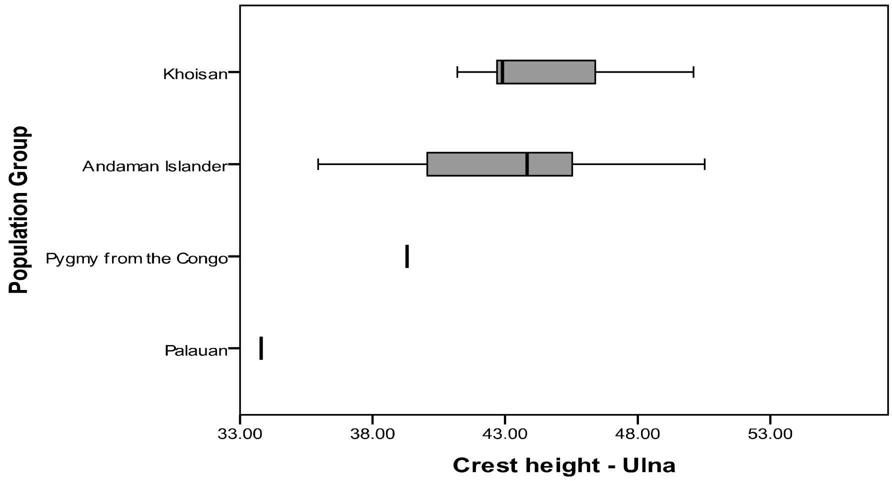

Figure 28: Boxplot of the measurements taken for crest height of the ulna.

3.4.2 Olecranon height of the ulna

The Palauan sample has a large mean, but still falls within range of the small-bodied groups (see Table 33). The largest measurements belong to the Andamanese and the smallest belongs to the Khoisan. The Khoisan and Pygmy groups have short olecranons while the small-bodied island groups, with which B: OR-15:18-031 (23.0mm z = -0.80614) and B: OR-15:18-049 (25.1 mm z = -0.45727) plot, have large olecranons.

Extremely small specimens, Pygmies and Khoisan specimens are on the far left of the plot (see Figure 29). Interestingly, there is a disproportionate relationship for the Palauans, which have a large olecranon, but relatively short overall crest height. Other populations like the Khoisan and Andaman islanders have comparable olecranon heights and large crest heights.

Table 33: Descriptive statistics for the olecranon height of the ulna. The individual means, standard deviations, minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Olecranon height	**34**	**13.30**	**33.83**	**28.0762**	**6.11840**
Andaman Islander	28	26.30	33.83	30.7104	2.04421
Khoisan	5	13.30	17.70	15.4200	2.09690
Palauan	2	23.00	25.10	24.0500	1.48492
Pygmy from the Congo	1	17.60	17.60	17.6000	.
The Palauan sample is represented by two specimens, B: OR-15:18-031 & B: OR-15:18-049. Data used in this set were collected by the author.					

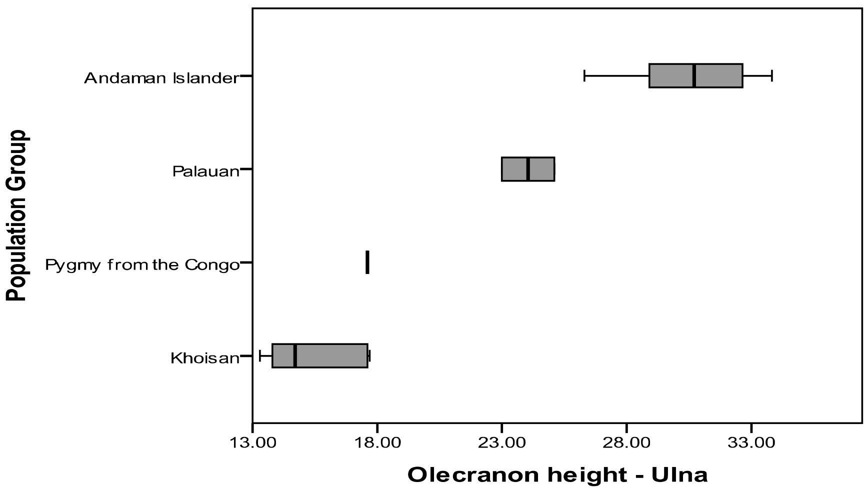

Figure 29: Boxplot of the measurements taken for olecranon height of the ulna. (N = 36, SD = 6.019, Mean 27.85)

3.4.3 Olecranon length of the ulna

The olecranon length of the ulna is defined as the measurement taken from the middle of the trochlear notch to the proximal point on the *m. triceps brachii* tuberosity (see Table 14). Palauan specimens fall within range of the small-bodied comparative sample. Andamanese have the largest recorded length, while Khoisan has the smallest (Table 34). Both B:OR-15:18-031 (18.20mm z = 0.59249) & B:OR-15:18-049 (19.20mm z = -0.21460) fall just below the comparative sample mean. Measurements are distributed (see

Figure 30) with the Andaman and Palau specimens plotting near each other while and the Khoisan and Pygmy plot in a similar way.

Table 34: Descriptive statistics for the olecranon length of the ulna. The individual means, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Minimum	Maximum	Mean	SD
Total for comparative sample	**31**	**12.40**	**24.77**	**19.8368**	**2.71512**
Andaman Islander	27	16.60	24.77	20.4830	2.13176
Khoisan	3	12.40	17.90	15.4333	2.79344
Palauan	2	18.20	19.20	18.7000	.70711
Pygmy from the Congo	1	15.60	15.60	15.6000	.
Two specimens B represent the Palauan sample: OR-15:18-031 & B: OR-15:18-049. Data used in this set were collected by the author.					

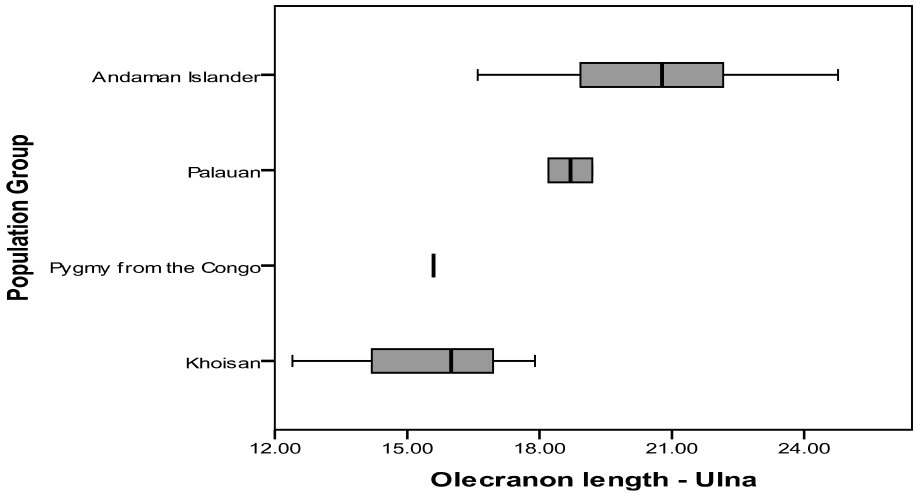

Figure 30: Boxplot of the measurements taken for olecranon length of the ulna. (N=33, SD = 2.646, mean = 19.77).

3.4.4 Head breadth of the Ulna

The Palauan sample has a large mean for the ulna head breadth (mediolateral diameter of the head see Table 13), but both measurements still fall within the normal distribution of the small-bodied comparative sample. The largest and smallest measurement belongs to the Andamanese. The entire measured sample has a normal distribution (see Figure 31) with no outliers. B: OR-15:18-027 (16.6mm, z = 1.84) & B: OR-15:18-047 (16.7mm, z = 1.78) fall almost two standard deviations from the mean.

There is a significant difference between the Palauan and the comparative groups as both the Palauan specimens fall above the means of the respective comparative groups.

Table 35: Descriptive statistics for head breadth of the ulna. The individual means, standard deviations, minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**33**	**10.59**	**17.10**	**13.7482**	**1.38449**
Andaman Islander	30	10.59	17.10	13.7163	1.44075
Khoisan	2	13.70	14.80	14.2500	.77782
Palauan	2	16.60	16.70	16.6500	.07071
Pygmy	1	13.70	13.70	13.7000	.
Two specimens represent the Palauan sample B: OR-15:18-027 & B: OR-15:18-047. Data used in this set were collected by the author.					

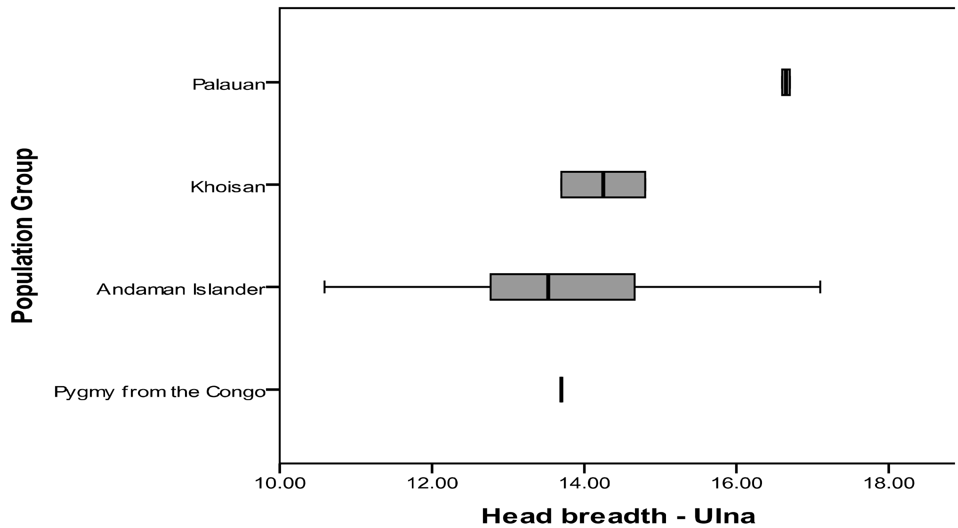

Figure 31: Boxplot of the measurements taken for head breath of the ulna. The measurements are normally distributed.

3.4.5 Distal maximum depth of the ulna

The Palauan sample has the smallest mean for the distal maximum depth (see Table 36). Specimens B: OR-15:18-027 (12.0mm z = -1.69) and B: OR-15:18-047 (11.0mm z = -1.12), plot near the minimum for the comparative sample. The largest and smallest recorded measurements belong to the Andamanese and define the range for the comparative sample. In Figure 32, we see that the Palauans have the smallest mean for the maximum depth of the distal ulna.

Table 36: Descriptive statistics of the maximum depth of the distal ulna. The individual means, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**33**	**10.39**	**16.96**	**14.1461**	**1.69987**
Andaman Islander	30	10.39	16.96	14.1473	1.73542
Khoisan	2	12.50	14.20	13.3500	1.20208
Palauan	2	11.00	12.00	11.5000	.70711
Pygmy from the Congo	1	15.70	15.70	15.7000	.

The Palauan sample is represented by two specimens B:OR-15:18-027 & B:OR-15:18-047. Data used in this set were collected by the author.

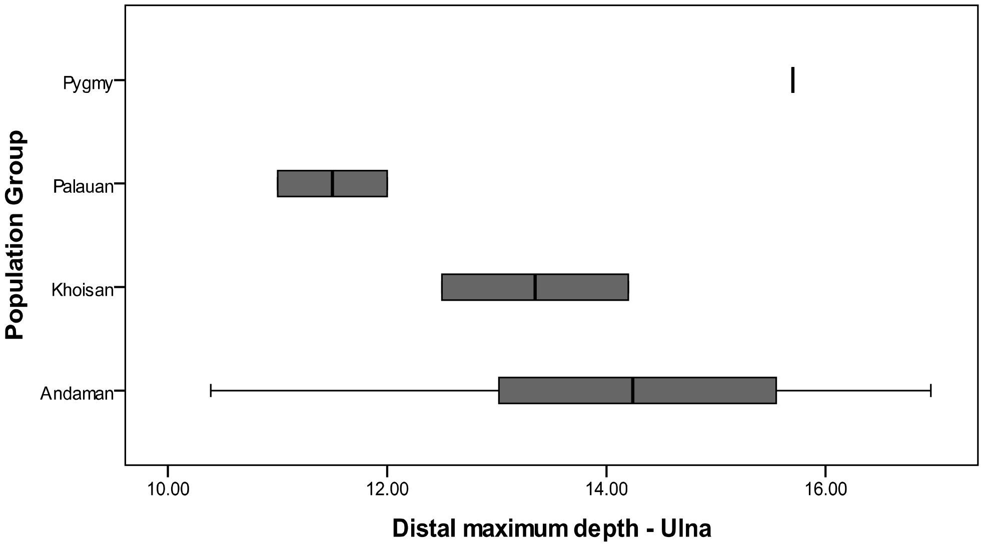

Figure 32: Boxplot showing the distribution of measurements for the distal maximum depth of the ulna. (N=35, SD =1.767).

3.4.6 Distal radial maximum length of the ulna

Specimens B: OR-15:18-027 (8.10 mm, z = -0.108) & B: OR-15:18-047 (6.20 mm, z= -1.220) fall below the mean of the comparative sample (see Table 37) giving the Palauan sample the smallest mean for the distal radial maximum length. The largest measurement belongs to the Khoisan and the smallest belong to the Andamanese. There is a normal distribution of measurements with more specimens plotting in the lower ranges (see Figure 33) and the two Khoisan specimens plot in the upper range of the distribution. The Palauan mean and that of the Andaman group plot in a similar way.

Table 37: Descriptive statistics for the distal radial maximum length of the ulna. The individual means, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**33**	**6.15**	**13.50**	**8.3545**	**1.72092**
Andaman Islander	30	6.15	10.59	7.9867	1.13263
Khoisan	2	13.50	13.50	13.5000	.00000
Palauan	2	6.20	8.10	7.1500	1.34350
Pygmy from the Congo	1	9.10	9.10	9.1000	.
The Palauan sample is represented by two specimens B: OR-15:18-027 & B: OR-15:18-047. Data used in this set were collected by the author.					

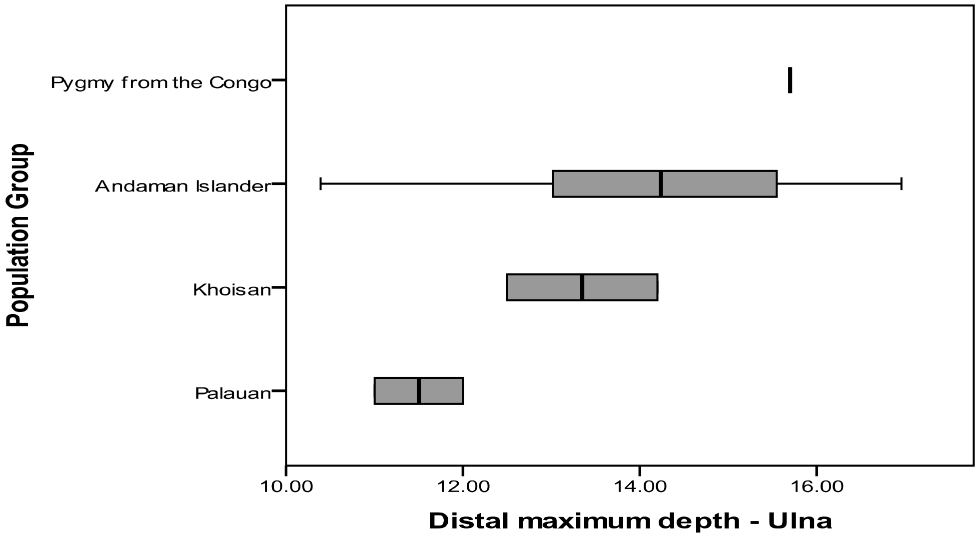

Figure 33: Boxplot showing the distribution of measurements of the distal radial maximum length of the ulna. (Mean = 8.29, SD = 1.709, N=35).

For the ulna, there are similarities between the Pygmy and the Khoisan samples and the Palauan and Andamanese sample. The Palauan specimens are small in the crest height, distal maximum depth and the maximum length of the distal radius. Both island populations are large in olecranon height and length as well as the head breadth where the Palauans have the largest measurement. The Palauans show unusual proportions in as they have a small crest with a large olecranon, distally the Palauans have a large head diameter but a narrow distal depth this is only seen in two of the Andaman specimens (see Figure 34).

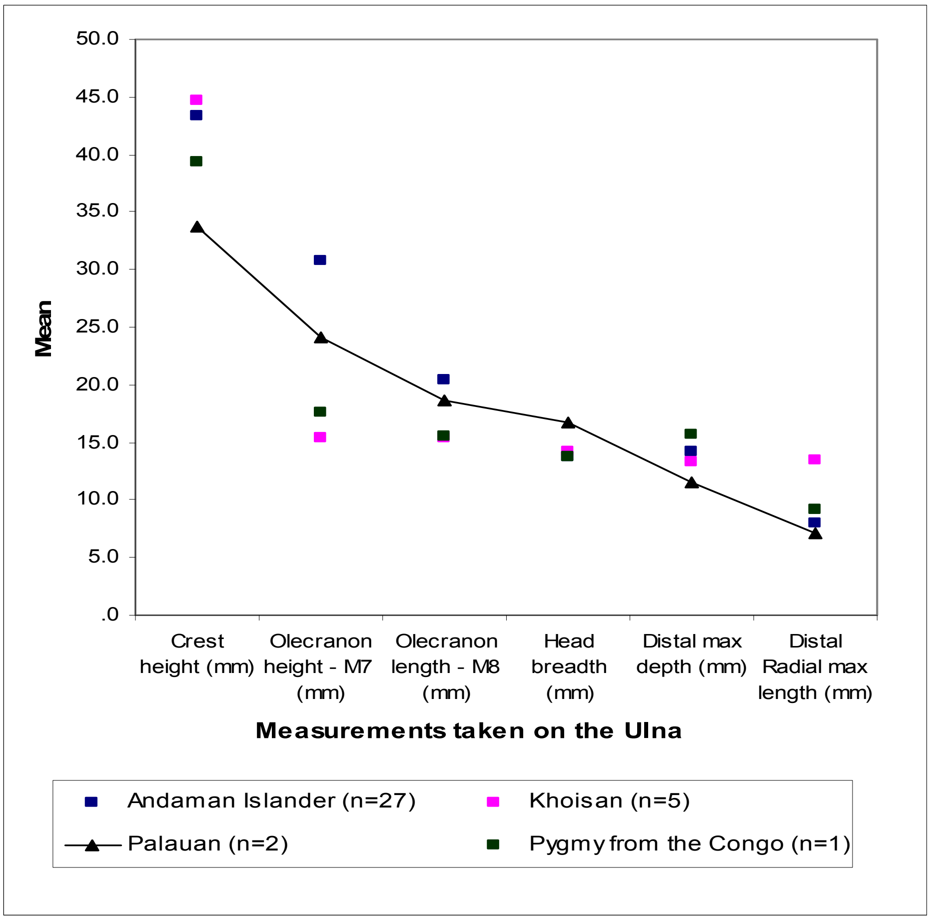

Figure 34: Mean plots for the measurements taken on the ulna. The black line links the Palauan means and allows for easy comparison between the Palauan specimens and the comparative groups. Sample sizes reflect total; for the sample sizes of specific measurements see the relevant tables

3.5 Summary of the Upper Limb of the Palauan Specimens

In order to summarise the measurements taken on the upper limb of the Palauan specimens, a table was constructed (see Table 38). Measurements taken on the upper limb show that the Palauan specimens are small and fall within the range of the small-bodied sample. This result is concurrent with the predictions that the Palauan sample represents a population of small-bodied individuals.

For the upper limb, the Palauan sample has humeral lengths that are comparable to other small-bodied samples. The joints sizes, however, do not follow the same trend that is seen in other insular small-bodied island populations (Andaman and Nicobarese). The humeral head diameters are larger than the small-bodied island groups and are more comparable to the Khoisan sample. A disproportionate trend, therefore, is noted in the distal humeral measurements. The Palauan specimens have a large epicondylar breadth and small articular surface diameters, which result in a small olecranon fossa breadth. The Palauans have small trochlea dimensions relative the capitulum measurements; this is again similar to the data collected for the Khoisan specimens. The opposite trend is seen in the Andamanese and Nicobar Negritos (small capitulum and large trochlea). Should larger-bodied samples be measured it would be interesting to see if this trend is seen in the larger-bodied groups, but for the purposes of this study it is important to note that this difference is evident amongst small-bodied groups.

Table 38: Summary for all upper limb measurements taken on the Palauan specimens.

Element	Measurement	Predicted result	Actual result	Palauan sample plot near
Humerus	Maximum length	Small	Small	KS
	Midshaft maximum diameter	Small	Small	KS
	Midshaft minimum diameter	Small	Small	NIC
	Head Anterior- Posterior diameter	Small	Large*	KS
	Head Superoinferior diameter	Small	Average	AB
	Bi-epicondylar breadth.	Small	Small	E
	Distal articular breadth	Small	Smallest	AND
	Olecranon fossa breadth	Small	Smallest	AND
	Mesiodistal length of the trochlea	Small	Smallest	KS
	Capitular SI diameter	Small	Small	Not compar
Ulna	Crest height	Small	Smallest	Not compar
	Olecranon height	Small	Small	None
	Olecranon length	Small	Small	AND
	Head breadth	Small	Large*	Not compar
	Distal maximum depth	Small	Smallest	KS
	Distal radial maximum length	Small	Smallest	AND
Radius	Maximum length	Small	Large*	KS
	Carpal articular breadth	Small	Smallest	AND
	Head AP diameter	Small	Average	E
	Distal depth of the radius	Small	Small	AND
	Distal breadth of the radius	Small	Small	K

For the actual results, “Small” means that it plots similarly to small-bodied groups, and “large” means it plots similarly to larger bodied groups. In each case where the Palauan samples are large, an abbreviation is given indicting which group it is most similar to for that measurement. “Large*” indicates that this is large comparable only to other small-bodied individuals, “Average” means that it plots near the mean for the entire sample. Smallest indicates that Palauans have the smallest mean for that particular measurement. Highlighted measurements indicate those for which only small-bodied data was available. AND = Andaman KS = Khoisan AB= Australian aboriginal, E = European. Not compar = mean not comparable with any other group in the sample.

For the ulna metrics and dimensions, the Palauan specimens resemble those seen in the Andaman sample. The Palauans have a large olecranon height and length while the Khoisan and Pygmy sample have small olecranons. Considering the Palauans had a small olecranon fossa breadth, it was expected that the olecranon itself would be small as to be accommodated by the olecranon fossa, but this is not the case. The Palauans also have a large diameter for the head of the ulna that the Khoisan and pygmy do not have. This shows robustness in the epiphyses of the Palauan ulnas. One point where the Palauan and Andaman samples differ is the depth of the distal end of the ulna; the Palauans have a small depth compared to the larger ulna head dimension. Only small-bodied specimen data were obtained for the ulna and therefore the trends noted here can only be applied to the small-bodied groups.

For the radius, not much difference is seen in the measurements of the small-bodied comparative samples. The length varies for all specimens and all small-bodied groups have a large distal depth measurement. The Palauans are robust in the anteroposterior diameter of the radial head and plot above the mean of the comparative sample.

While some aspects of the upper limb reflect what is seen in other small-bodied island populations there are some features that reflect those seen in small-bodied mainland populations. This could be due to the habitat differences between each population, or possibly as a result of rapid reduction, where some aspects will reduce quicker than others are.

3.6 THE LOWER LIMB OF THE PALAUAN SPECIMENS

This chapter deals with elements of the lower limb of the Palauan sample. The specimens will be compared to small-bodied and large-bodied individuals; the samples used are outlined in the materials chapter of this study (see Chapter 2.1, p60). Predictions are that Palauan specimens will plot near other small-bodied individuals (see Hypotheses on p80).

3.7 Statistical Analysis and Results for the Pelvis of the Palauan Specimens

3.7.1 Maximum acetabular diameter of the pelvis

Specimen B: OR-15:18-009 (39.50mm, z = -2.0) and B: OR-15:18-087 (46.10mm, z = -0.42) fall below the mean for the comparative sample (see Table 39), B: OR-15:18-009 is a pelvis of a female and plots 2 standard deviations below the mean. In the comparative sample, the smallest acetabular diameter is attributed to the Andamanese, which still falls two standard deviations below the overall mean. The largest measurement belongs to the Australian Aboriginal group. The Palauan sample plots with the other small-bodied individuals. In Figure 35, The Palauan mean plot closet to that of the Andaman group.

Table 39: Descriptive statistics for the maximum acetabular diameter of the pelvis. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total for comparative sample	**144**	**39.36**	**58.00**	**47.7975**	**3.97216**
Australian Aboriginal	100	41.00	58.00	48.6400	3.67498
Andaman Islander	17	39.36	49.32	42.5906	2.59533
Khoisan	17	42.80	54.30	48.2765	3.29631
Palauan	2	39.50	46.10	42.8000	4.66690
Pygmy	1	41.10	41.10	41.1000	.
Zulu	9	43.50	52.70	48.1111	2.64738

The Palauan sample is represented by two specimens B:OR-15:18-009 and B:OR-15:18-087. Data used in this set were collected by the author, data for the Australian Aboriginal group obtained from Brown (2001).

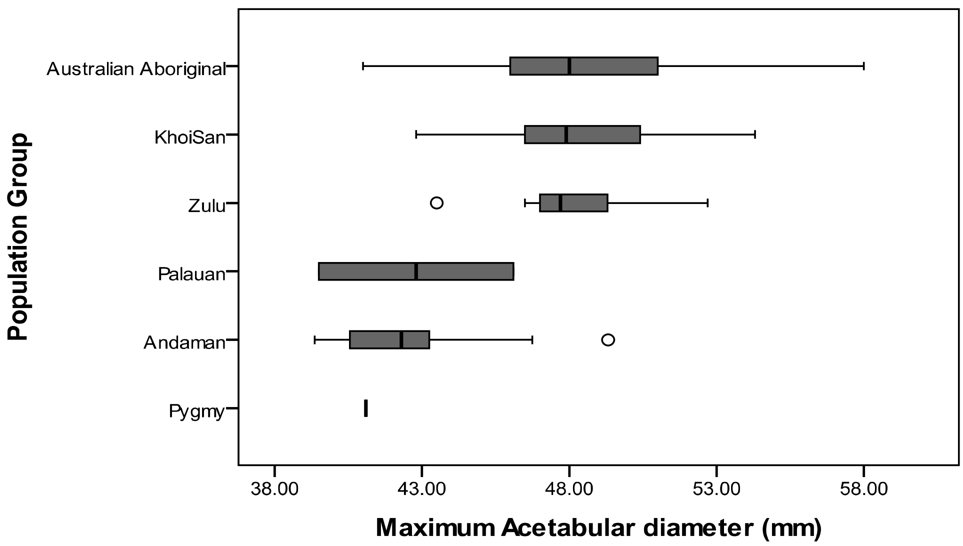

Figure 35: Boxplot showing the distribution of measurements taken for the maximum diameter of the acetabulum. (N=148, SD =4.0, mean = 146.0). The Open circles indicate outliers.

3.7.2 Transverse diameter of the acetabulum of the pelvis

Table 40: Descriptive statistics for transverse acetabular diameter of the pelvis. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**42**	**35.84**	**53.10**	**44.9150**	**4.13591**
Andaman Islander	17	35.84	47.45	41.3135	2.83261
KhoiSan	16	41.30	53.10	47.6000	3.03095
Palauan	2	36.00	41.00	38.5000	3.53553
Pygmy	1	41.40	41.40	41.4000	.
Zulu	8	44.80	50.40	47.6375	1.98778
The Palauan sample is represented by two specimens; B: OR-15:18-009 and B: OR-15:18-087. Data used in this set were collected by the author.					

The diameter of the acetabulum was measured perpendicular to the maximum diameter of the acetabulum. The Palauan sample has the smallest mean for the transverse diameter of the acetabulum. The Andamanese have the smallest transverse acetabular diameter and the Khoisan have the largest. The small-bodied sample fits a normal distribution curve for this measurement indicating that there are no real outliers (see Figure 36).

The Palauan specimens; B: OR-15:18-009 (36.0 mm z = -1.554) and B: OR-15:18-087 (41.0mm z = -0.906) (see Table 40) plot near the Andaman mean (see Figure 36) and are 1 SD below the comparative group mean.

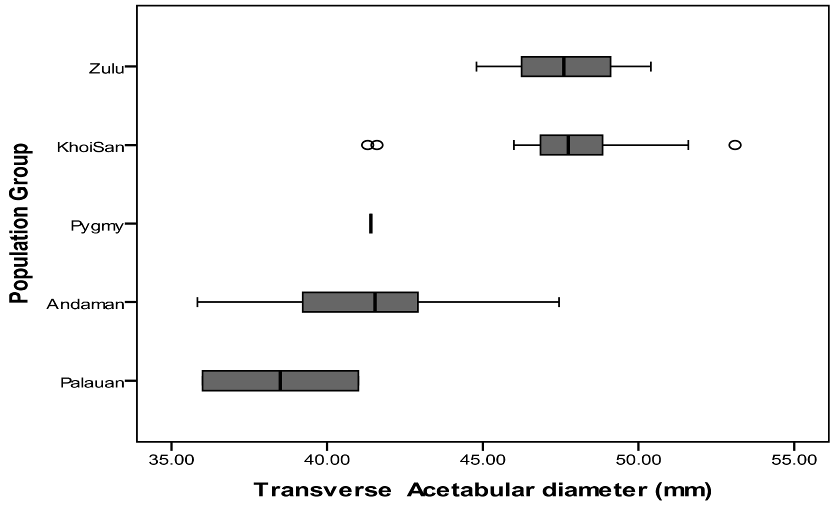

Figure 36: Boxplot showing the distribution measurements taken for the transverse diameter of the acetabulum. (N = 44, Mean 44.62, SD 4.293)

3.7.3 Iliac height of the pelvis

The iliac height was a measurement taken on the blade of the specimen (see Table 14). Only one Palauan specimen has an iliac blade, B: OR-15:18-009 (102.30mm z = -1.55), this specimen has the smallest mean for the iliac height of the comparative sample and falls 2 standard deviations below the mean. The smallest measurement belongs to the Andamanese, and the largest belongs to the Zulu group. The Zulu and Khoisan have similar large measurements and the Andaman, Palauan, and Pygmy plot in a similar way (Figure 37).

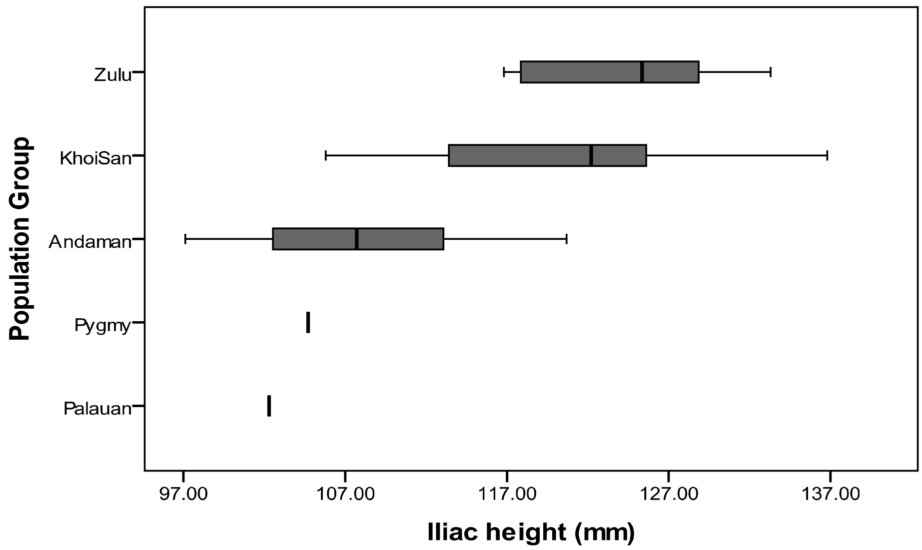

Figure 37: Boxplot showing the distribution of measurements taken for the iliac height, (N=41, Mean = 116.09 SD = 10.665).

Table 41: Descriptive statistics for iliac height of the pelvis. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total comparative sample.	**40**	**97.12**	**136.80**	**116.4370**	**10.56665**
Andaman Islander	15	97.12	120.69	108.3920	7.20945
KhoiSan	16	105.80	136.80	120.7938	9.83494
Palauan	1	102.30	102.30	102.3000	.
Pygmy	1	104.70	104.70	104.7000	.
Zulu	8	116.80	133.30	124.2750	6.23578
Two specimens represent the Palauan sample B: OR-15:18-009 & B: OR-15:18-087. Data used in this set were collected by the author, data for the Australian Aboriginal group obtained from Brown (2001).					

3.7.4 Superior iliac breadth of the pelvis

The Palauan specimens both fall within the range of the small-bodied sample (see Table 42) for the superior iliac breadth measurements [B: OR-15:18-009 (123 mm z= -0.72) and B: OR-15:18-087 (120.1 mm z = -1.80)]. The smallest measurement recorded is from the Andaman group, while an Australian Aboriginal specimen has the largest measurement. There is overlap for the ranges of the small-bodied individuals, the distribution (Figure 38) is normal and there are no outliers. The Palauan and Andaman mean plot in a similar way (see Figure 38) with the Palauan mean plotting below that of the Andamanese.

Table 42: Descriptive statistics for the superior iliac breadth of the pelvis. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	134	113.27	166.00	140.9339	10.75323
Australian Aboriginal	95	126.00	166.00	145.0105	7.83133
Andaman Islander	16	113.27	134.77	123.6088	7.50837
KhoiSan	13	121.00	148.20	135.8077	9.63790
Palauan	2	120.90	123.00	121.9500	1.48492
Pygmy	1	118.50	118.50	118.5000	.
Zulu	9	129.00	150.20	138.6000	6.87804
The Palauan sample is represented by two specimens; B: OR-15:18-009 and B: OR-15:18-087. Data used in this set were collected by the author, data for the Aboriginal group obtained from Brown (2001).					

Examination of all the measurements (represented by means in Figure 39), shows that larger pelvises belong to the Australian Aboriginal and Zulu groups. The small-bodied Andaman, Pygmy, and Palauan groups all plot similarly and cluster together. For iliac height and transverse acetabular diameter, the Palauan samples have the smallest mean. A comparison of the acetabular diameter and iliac breadth (Figure 40) indicates that the Palauan specimens plot the range of other small-bodied groups like the Andamanese and Pygmy specimens. The difference in the two plots is due to one of the Palauan individuals likely being male (B: OR-15:18-087) and the other likely female (B: OR-15:18-009) (see Berger *et al.* 2008a,b).

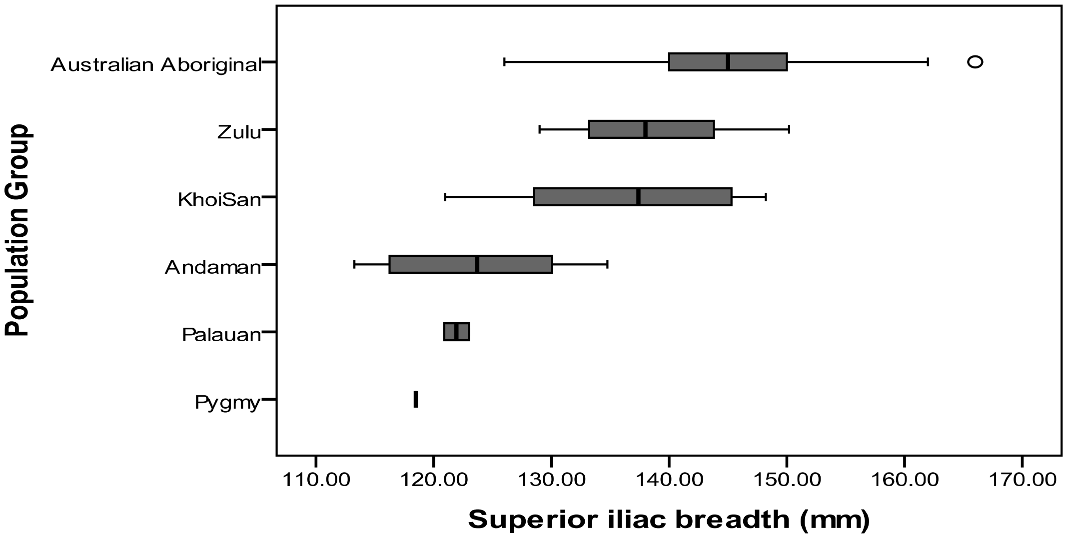

Figure 38: Boxplot showing the distribution of measurements taken for the superior iliac breadth; N=136, SD 10.918, mean = 140.65.

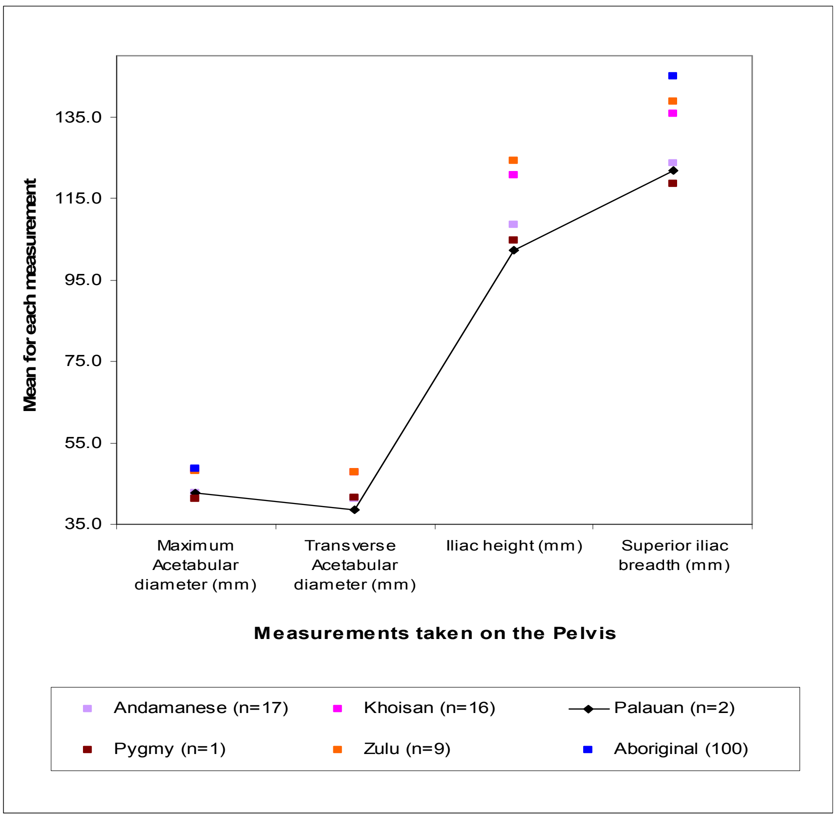

Figure 39: The group mean plotted for each measurement taken on the pelvis. The sample sizes indicate the total number of individuals measured; for specific sample sizes for each measurement please see relevant tables.

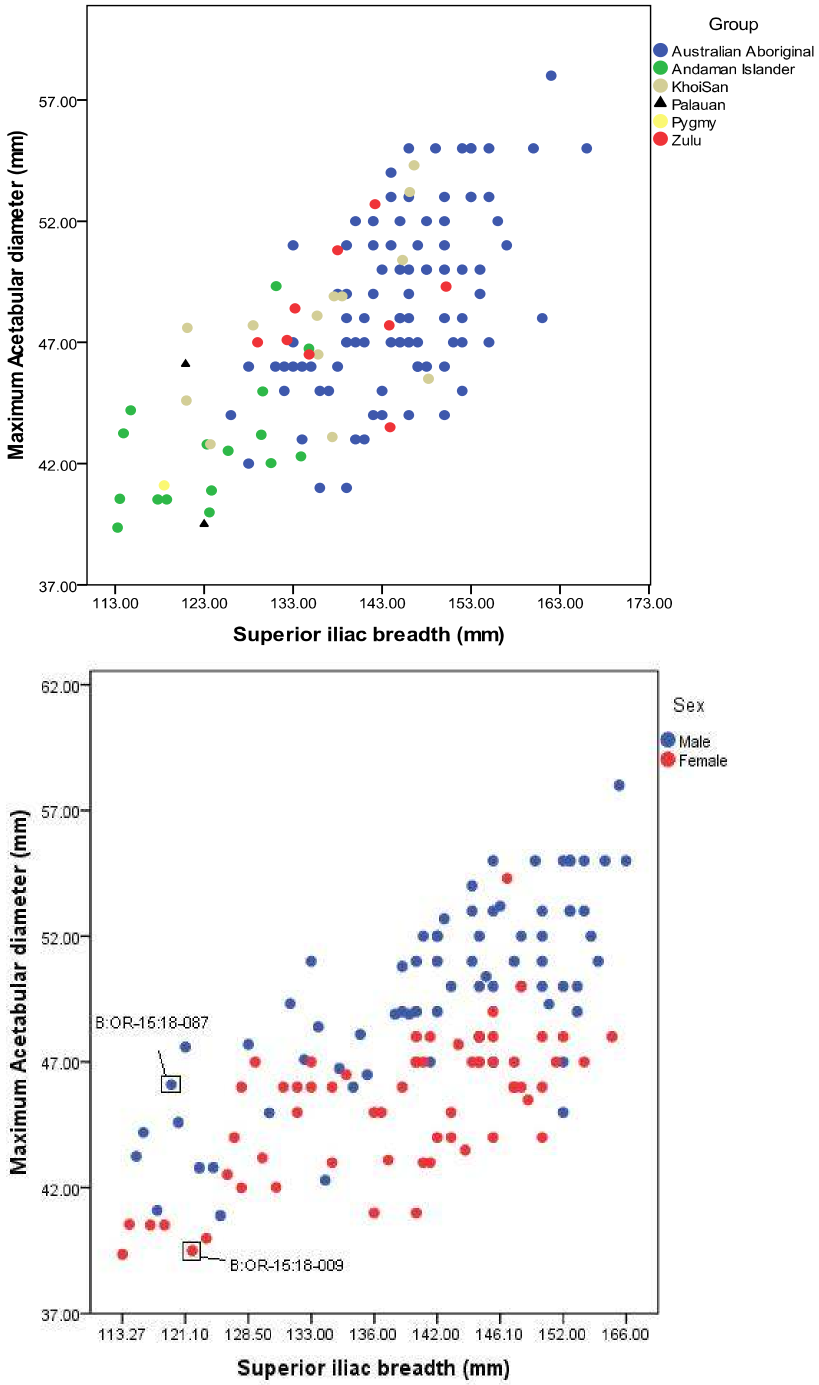

Figure 40: Scatter plot comparing the maximum acetabulum diameter to the superior iliac breadth. A) Plots separated into the comparative groups, B) Plots separated into the sexes. B: OR-15:18-087 (male) and B: OR-15:18-009 (female) plot with the small-bodied individuals. The plots also fall within the predicted sexes for each specimen (Berger *et al.* 2008a).

3.8 Statistical Analysis and Results for the Femur of the Palauan Specimens

The following is the analysis of the femoral measurements taken on the comparative sample (outlined in Chapter 2.3, p60). All measurements are defined in Table 13, in Chapter 2.3 of this study. For the Hypothesis being tested please see p79-80.

3.8.1 Anteroposterior (AP) head diameter of the femur

The Palauan specimens B: OR-15:18-013 (36.10mm z = -1.51) and B: OR-15:18-098 (38.80mm z = -.089) fall more than one standard deviation below the mean for the entire comparative sample (Table 43). The largest measurement belongs to the European group while the smallest belongs to the Andamanese. The distribution (see Figure 41) is normal with no outliers and there is overlap in ranges for each comparative groups. The Palauan sample mean plots with the Andaman group.

Table 43: Descriptive statistics AP head diameter of the femur. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	284	33.30	53.80	42.6868	4.35072
Andamanese	34	33.50	42.92	37.3135	2.48311
European	120	36.00	53.80	45.2233	3.79776
KhoiSan	33	33.30	47.00	40.8788	3.55833
Nicobar Islander	4	36.29	39.39	37.4725	1.34740
Palauan	2	36.10	38.80	37.4500	1.90919
Pygmy from the Congo	1	36.40	36.40	36.4000	.
Zulu	90	36.40	51.00	42.4156	3.26957
Two specimens represent the Palauan sample; B: OR-15:18-013 & B: OR-15:18-098. Data used in this set were collected by the author.					

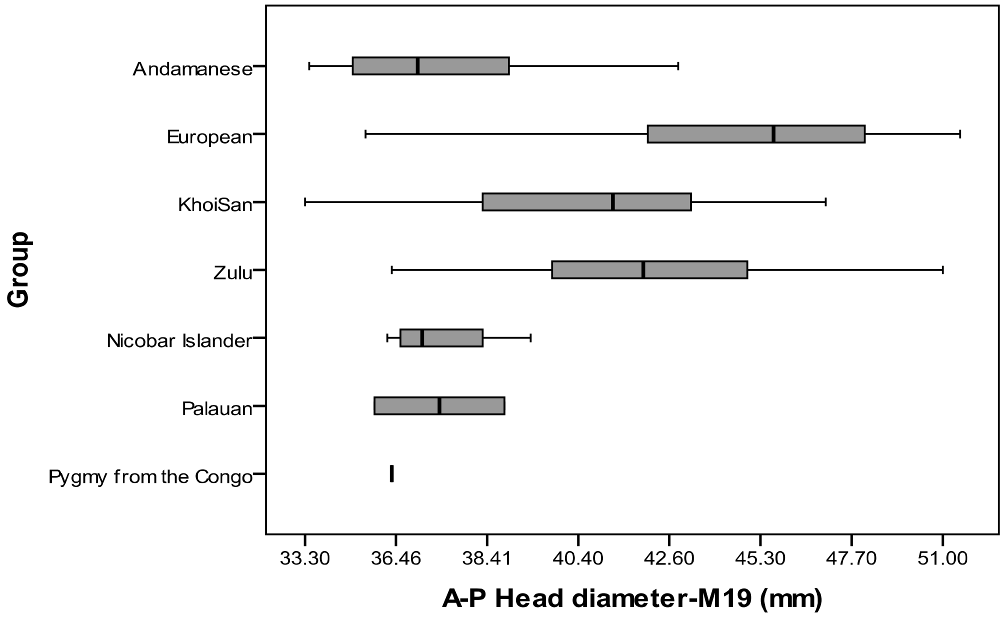

Figure 41: Boxplot showing the distribution of measurements taken for the anteroposterior (AP) head diameter of the femur. (N=284, mean= 42.6, SD 4.35)

3.8.2 Superoinferior (SI) head diameter of the femur

Table 44: Descriptive statistics SI head diameter of the femur, statistics are separated into the comparative groups. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total Comparative sample	**494**	**32.00**	**53.80**	**42.5666**	**4.04648**
Andamanese	33	32.70	42.11	37.2476	2.39708
European	218	36.00	53.80	44.2775	3.85512
KhoiSan	32	34.50	47.10	40.7281	3.45704
Australian Aboriginal	76	32.00	58.00	41.1711	3.96110
Nicobar Islander	4	36.03	39.60	37.0075	1.73344
Palauan	1	35.20	35.20	35.2000	.
Pygmy from the Congo	1	36.40	36.40	36.4000	.
Southern Chinese	40	36.50	49.00	43.8000	3.28907
Zulu	90	36.10	49.50	42.2256	3.01366

A single specimen represents the Palauan sample; B: OR-15:18-013. Data used in this set were collected by the author with the exception of the data for the Australian Aboriginal (Murray Valley), Southern Chinese and 175 European individuals group which were obtained from Brown (2001).

The Palauan specimen, B: OR-15:18-013 (35.2 mm z= -1.51) has the smallest mean for the comparative sample. The largest and smallest measurement for the SI head diameter belongs to the Australian Aboriginal group (Table 44). The SI head diameter of the femur shows only a single specimen plotting outside the normal range (see Figure 42) for measurement and this belongs to a large Australian Aboriginal. The Aboriginal specimens and the Khoisan are found within the full range of the distribution whereas the Andamanese are only found below the entire sample mean.

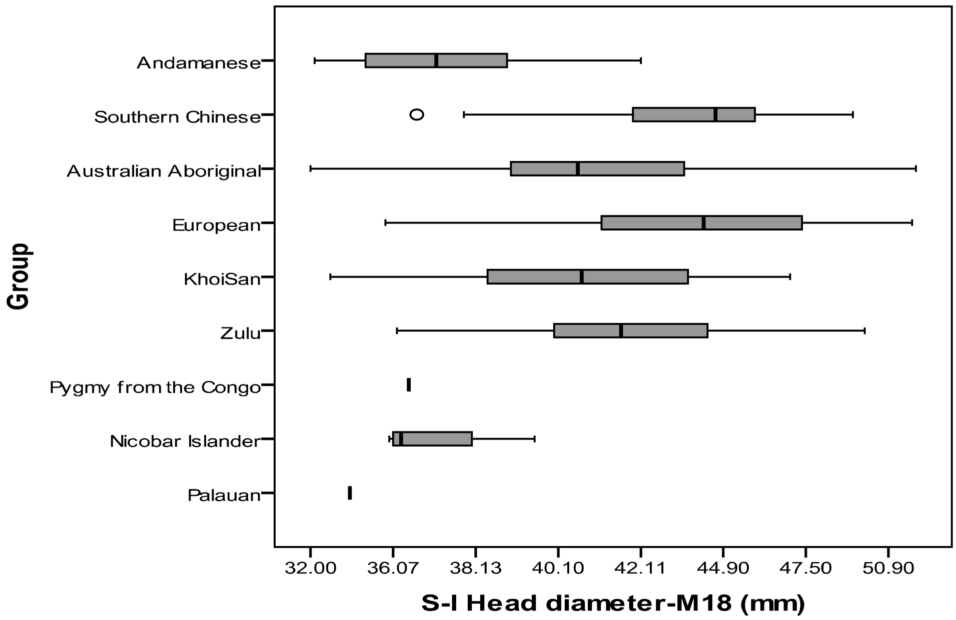

Figure 42: Boxplot showing the normal distribution curve for the superoinferior head diameter of the femur. N = 495, SD =4.101 mean = 42.60. The open circles indicate the open circles.

3.8.3 Vertical neck diameter of the femur

The Palauan specimen B: OR -15:18-013 (25.20mm z = -0.108) plots with other small-bodied groups, and falls below the mean for the total comparative sample (Table 45). The Khoisan have the largest measurement recorded while the Andamanese have the smallest. There is overlap in the ranges of the small-bodied groups and the variable is normally distributed (Figure 43). The Palauan specimen measurement plots near the Nicobarese mean.

Table 45: Descriptive statistics vertical neck diameter, statistics are separated into the different population groups. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total comparative sample	**46**	**21.27**	**30.10**	**25.4372**	**2.18522**
Andamanese	34	21.27	28.89	24.8609	2.01039
KhoiSan	6	27.10	30.10	28.5833	1.20402
Nicobar Islander	4	24.58	26.80	25.6100	1.05432
Palauan	1	25.20	25.20	25.2000	.
Pygmy from the Congo	1	25.70	25.70	25.7000	.
A single specimen represents the Palauan sample; B: OR-15:18-013. Data used in this set were collected by the author.					

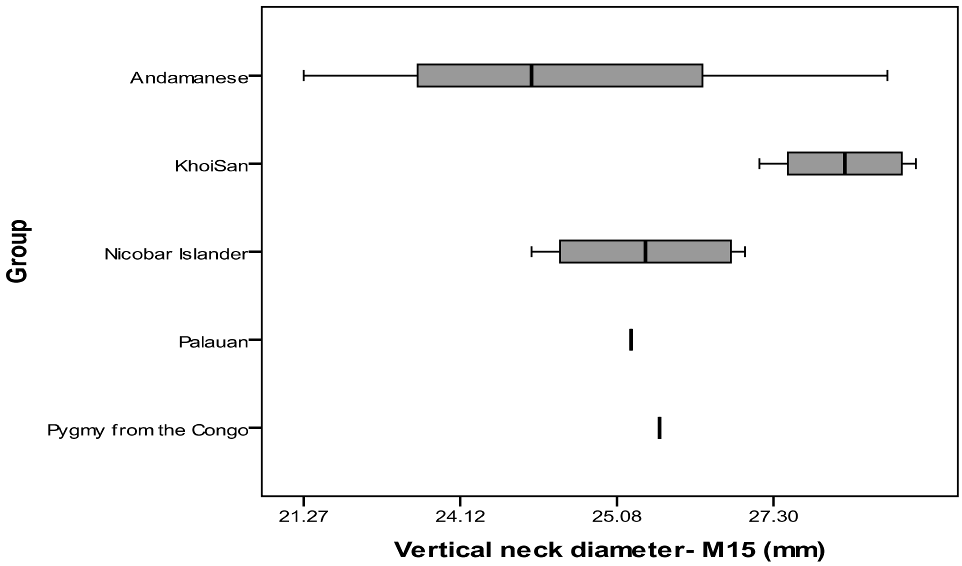

Figure 43: Boxplot showing the vertical neck diameter measurements of the femur. Mean = 25.44, SD = 2.185.

3.8.4 Sagittal neck diameter of the femur

The Palauan specimen [B: OR-15:18-013 (19.30 mm z = -1.029)] has a measurement that falls below the comparative sample mean (Figure 42). There is still overlap in the ranges of the island groups represented. The sagittal neck diameter of the femur is normally distributed, without obvious outliers (see Figure 44).

Table 46: Descriptive statistics sagittal neck diameter, statistics are separated into the different population groups.

Group	N	Min	Max	Mean	SD
Total comparative sample	**45**	**17.69**	**27.06**	**21.4613**	**2.10037**
Andamanese	34	18.28	27.06	21.2738	1.78528
KhoiSan	5	20.60	27.00	24.0200	2.90207
Nicobar Islander	4	17.69	22.54	20.6625	2.07863
Palauan	1	19.30	19.30	19.3000	.
Pygmy from the Congo	1	20.40	20.40	20.4000	.

The mean, standard deviation (SD), minimum and maximum are given for each group. A single specimen represents the Palauan sample; B: OR-15:18-013. Data used in this set were collected by the author.

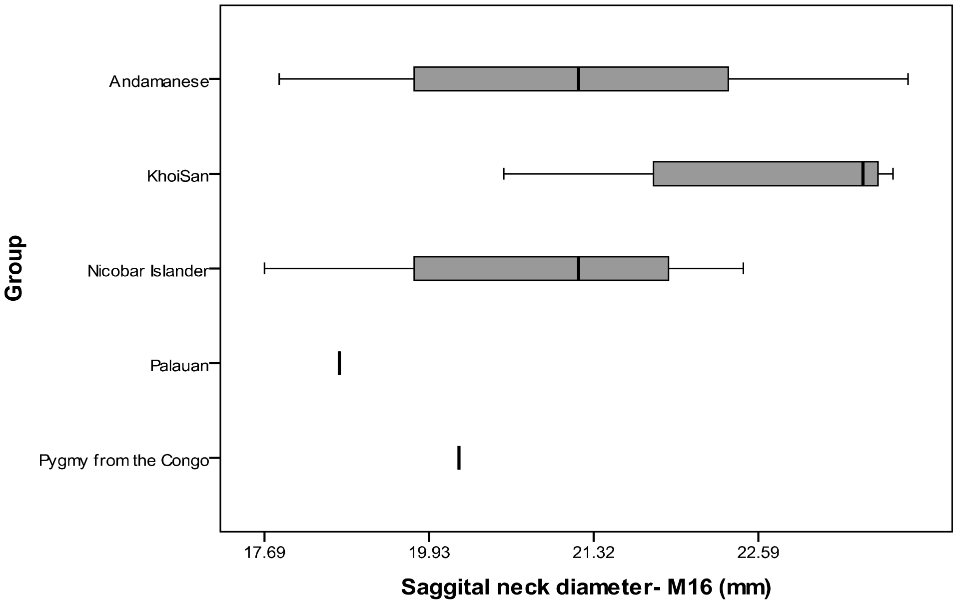

Figure 44: Boxplot for the sagittal-neck diameter measurements of the femur. Mean = 21.46, SD = 2.10, N = 45.

3.8.5 Head and neck length of the femur

The Palauan specimen [B: OR-15:18-013 (49.50 mm z = -0.371)] has a measurement that falls below the mean of the entire comparative sample (see Table 47). The largest measurement belongs to the Khoisan, while the smallest belong to the Andamanese. The Palauan measurement is small and plots within the range of the Andaman group, it does not fall within the range of the Nicobarese and Khoisan groups.

A large number of specimens plot near the mean for the head and neck length and no individuals fall along the small size range of the distribution (Table 47). Khoisan individuals have a very large head and neck length in comparison to the other small-bodied groups and this may be due to the differing environments that they inhabit.

Table 47: Descriptive statistics for the overall head and neck length of the femur. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total comparative sample	**44**	**42.57**	**69.20**	**51.4377**	**5.21109**
Andamanese	34	42.57	57.74	50.0018	3.95828
KhoiSan	4	55.30	69.20	61.7750	5.83117
Nicobarese	4	51.44	58.02	53.4000	3.13542
Palauan	1	49.50	49.50	49.5000	.
Pygmy from the Congo	1	53.00	53.00	53.0000	.

The mean, standard deviation (SD), minimum and maximum are given for each group. A single specimen represents the Palauan sample, B: OR-15:18-013. Data used in this set were collected by the author.

The Palauan specimens fall on the lower end of the range of the comparative sample. In the case of the SI head diameter, vertical neck diameter, the sagittal neck diameter, and total head and neck length, Palauans have the smallest mean (see Figure 46). No Palauan specimens preserved a femoral distal end so this could not be evaluated.

Interestingly, whilst femoral head size in the Palauans is small, as is those of the Andamanese (as one would expect for the smallest populations of humans), the diameter of the neck sit at polar extremes, which is not what would be expected for island populations. The Khoisan data points are also intriguing as they are at the large end of the range for all measurements of the femur and plot away from the other small-bodied groups. This may be a function of habitat and signs of large ranging patterns associated with hunter-gatherer groups. While this data set was comprised only of small-bodied individuals, it proved important not only to see how the Palauan specimens plotted in relation to the small-bodied groups, but to see how these groups relate to one another.

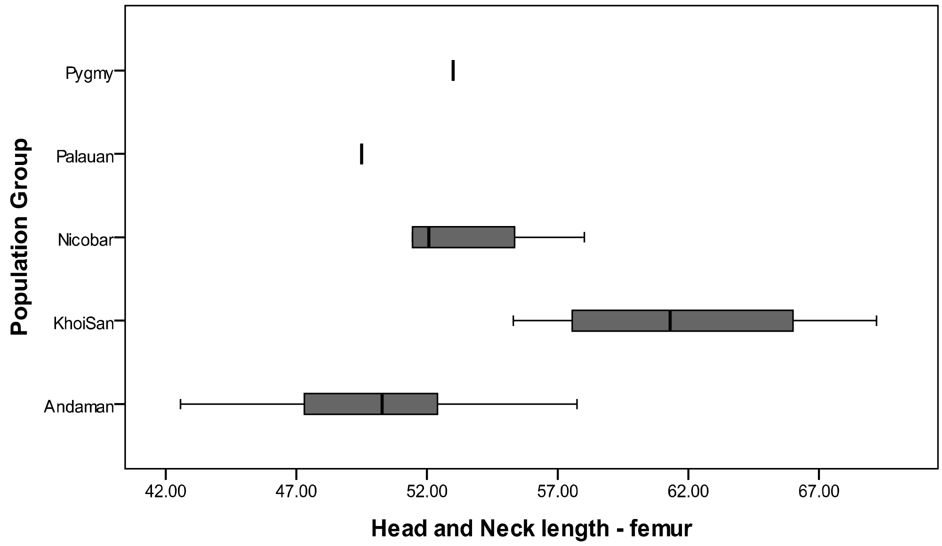

Figure 45: Boxplot for the head and neck length of the femur. No specimens fall in the lower end of the normal distribution curve. (N= 44, SD = 5.211, mean = 51.44).

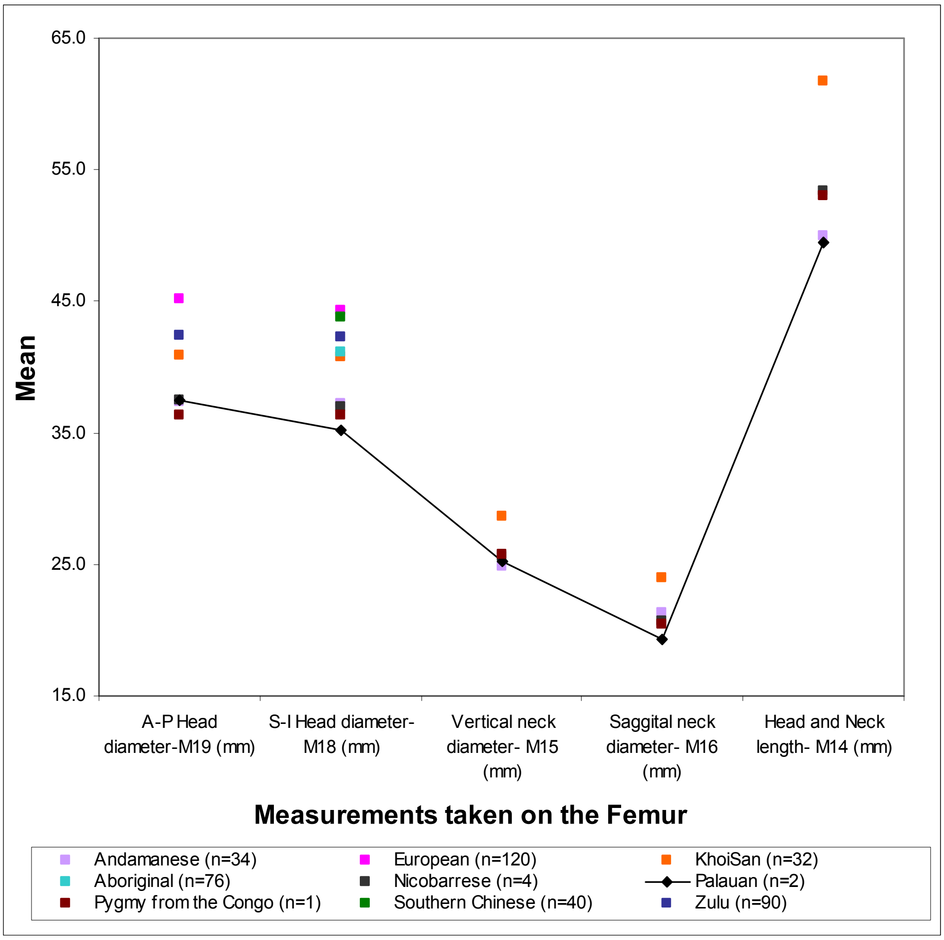

Figure 46: Distribution of means for each measurement taken on the femur. The Palauans have small measurements over all. The KhoiSan individuals do not plot near the other small-bodied groups.

3.9 Statistical Analysis and Results for the Tibia of the Palauan Specimens

3.9.1 Proximal anteroposterior (AP) diameter of the tibia

For the proximal AP diameter of the tibia, the Palauan specimens [B: OR-15:18-003 (34.4 mm z = 0.80) and B: OR-15:18-040 (32.5 mm z = 0.32)] are both just larger than the mean for the entire sample (Table 48). The smallest measurement belongs to the Andamanese while the largest belongs to the Europeans. Although the Palauans have a large mean, the maximum measurement falls at the upper end of the range of the small-bodied comparative sample. The measurements taken on the total comparative samples are normally distributed (see Figure 47) and there is large overlap between all the comparative groups.

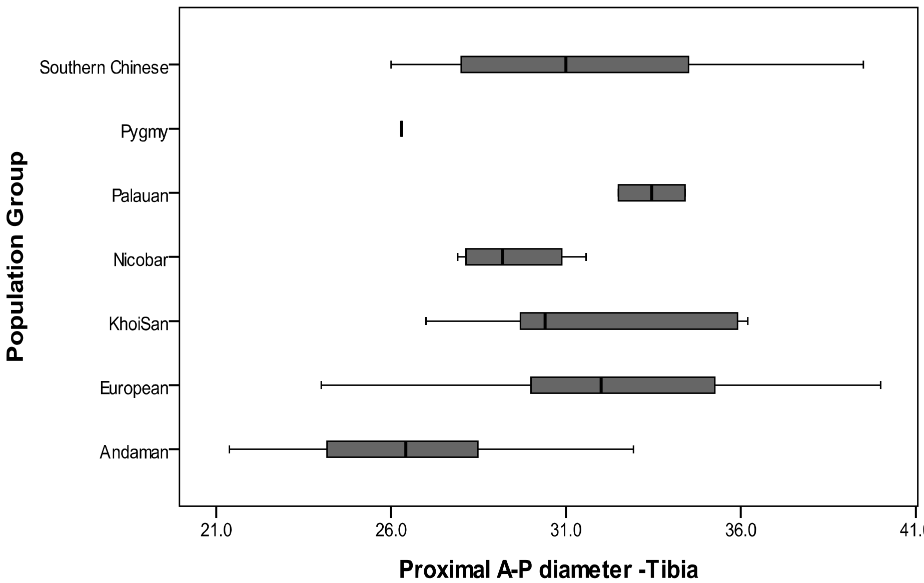

Figure 47: Boxplot showing the AP head diameter of the tibia. (N = 193, SD 4.114, mean = 31.05).

Table 48: Descriptive statistics for the proximal anteroposterior diameter of the tibia. The mean, standard deviation (SD), minimum and maximum are given for each group

Group	N	Min	Max	Mean	SD
Total comparative sample	**191**	**21.4**	**40.0**	**31.160**	**4.0134**
Andaman Islander	26	21.4	32.9	26.363	2.7698
European	99	24.0	40.0	32.480	3.6679
KhoiSan	5	27.0	36.2	31.840	4.0488
Nicobar Islander	5	27.9	31.6	29.534	1.6352
Palauan	2	32.5	34.4	33.450	1.3435
Pygmy from the Congo	1	26.3	26.3	26.300	.
Southern Chinese	55	26.0	39.5	31.227	3.5064

The mean, standard deviation (SD), minimum and maximum are given for each group. The Palauan sample is represented by two specimens; B: OR-15:18-003 and B: OR-15:18-040. Data used in this set were collected by the author, data for the Southern Chinese group obtained from Brown (2001).

3.9.2 Proximal mediolateral (ML) breadth of the tibia

The Palauan sample has the smallest overall mean for the measurements taken for the proximal mediolateral diameter, and the individual measurements fall within range of small-bodied individuals (Table 48). B: OR-15:18-003 (63.1 mm z =- 0.72) and B: OR-15:18-040 (53.1mm z =- 2.18) fall one and 2 standard deviations from the mean, respectively. Europeans have the largest measurement and the smallest belongs to the Andamanese. The Nicobarese and Pygmy samples plot near the upper range for the small-bodied sample. The variable is normally distributed and no specimens plot outside the range of this distribution (see Figure 48). The Palauan sample mean plots most similar to the Andaman group.

Table 49: Descriptive statistics for proximal mediolateral diameter of the tibia, statistics are separated into different groups. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**156**	**52.1**	**86.0**	**68.247**	**6.8048**
Andaman Islander	24	52.1	67.1	59.260	4.0297
European	84	60.0	86.0	70.625	5.9109
KhoiSan	3	59.8	73.8	67.333	7.0607
Nicobar Islander	3	62.9	66.5	64.213	1.9684
Palauan	2	53.1	63.1	58.100	7.0711
Pygmy from the Congo	1	62.7	62.7	62.700	.
Southern Chinese	41	55.0	78.0	69.134	5.6314

Group	N	Min	Max	Mean	SD
Total for the comparative sample	**156**	**52.1**	**86.0**	**68.247**	**6.8048**
Andaman Islander	24	52.1	67.1	59.260	4.0297
European	84	60.0	86.0	70.625	5.9109
KhoiSan	3	59.8	73.8	67.333	7.0607
Nicobar Islander	3	62.9	66.5	64.213	1.9684
Palauan	2	53.1	63.1	58.100	7.0711
Pygmy from the Congo	1	62.7	62.7	62.700	.

The mean, standard deviation (SD), minimum and maximum are given for each group. The Palauan sample is represented by two specimens; B: OR-15:18-003 and B: OR-15:18-040. Data used in this set were collected by the author; data for the European and Southern Chinese groups were obtained from Brown (2001).

A bivariate plot of the proximal tibial measurements (see Figure 49) illustrates that the comparative sample follows a straight-line distribution. While the Palauan mean plots near the range of the straight line, the second individual is an outlier, with a very small proximal mediolateral breadth in comparison to the anteroposterior head diameter of the tibia. A clear separation is seen between the Palauan specimens and the rest of the comparative sample. Interestingly, the Nicobarese and Andamanese means plot away from one another.

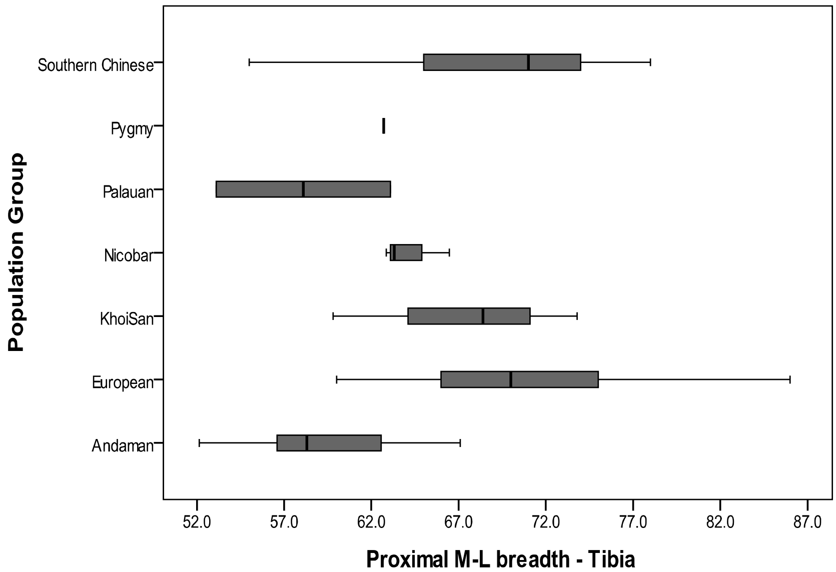

Figure 48: Boxplot showing the distribution measurements taken for the proximal mediolateral breadth of the tibia. (N = 158 SD =6.8 mean = 68.2).

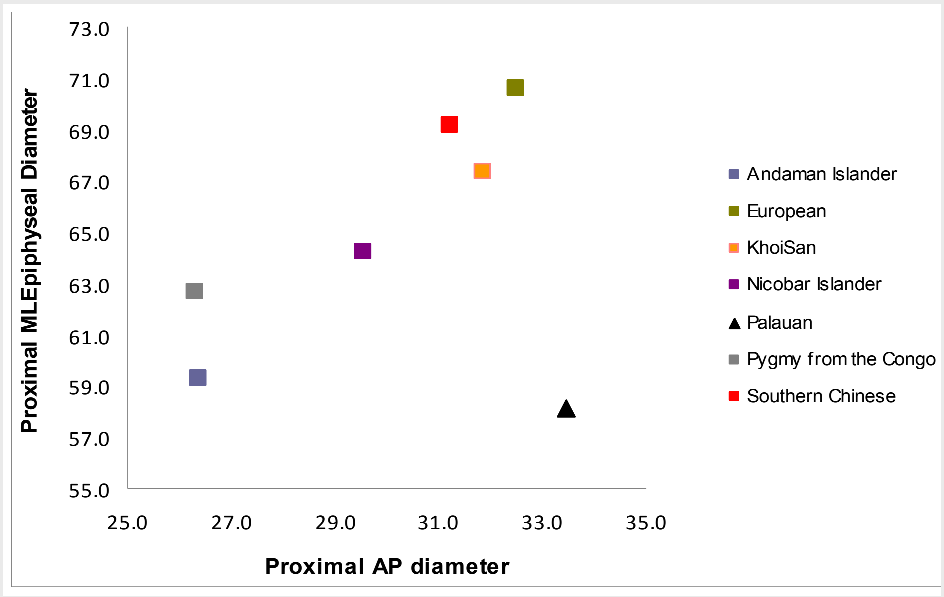

Figure 49: Bivariate plot showing the distribution of measurements taken on the proximal epiphysis of the tibia, each group is only represented by a mean.

3.9.3 Distal maximum breadth of the tibia

The Palauan specimens have the smallest mean for the comparative sample and fall more than one SD below mean for all comparative groups. The largest measurement belongs to the Khoisan, and the smallest measurement belongs to the Palauan specimen B: OR-15:18-045 (24.8 mm z = -2.43). There is a normal distribution for this variable (see Figure 50) and all group ranges overlap. B: OR-15:18-021 (27.8 mm z =-1.69) falls nearly 2 standard deviations below the mean and B: OR-14:8-011 (35.7mm z = 0.225) is at the mean. The Palauan specimens plot outside of the range of the other comparative sample groups.

Table 50: Descriptive statistics for the maximum distal breadth of the tibia. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	N	Min	Max	Mean	SD
Total comparative sample	**33**	**29.3**	**47.7**	**35.260**	**3.6797**
Andaman Islander	25	29.3	40.9	34.215	2.7733
KhoiSan	3	35.9	47.7	41.800	5.9000
Nicobar Islander	4	33.8	39.1	36.323	2.1559
Palauan	3	24.8	35.7	**29.433**	5.6306
Pygmy from the Congo	1	37.5	37.5	37.500	.

The Palauan sample is represented by three specimens, B: OR-15:18-045, B: OR-15:18-021 and B: OR-14:8-011. Data used in this set were collected by the author.

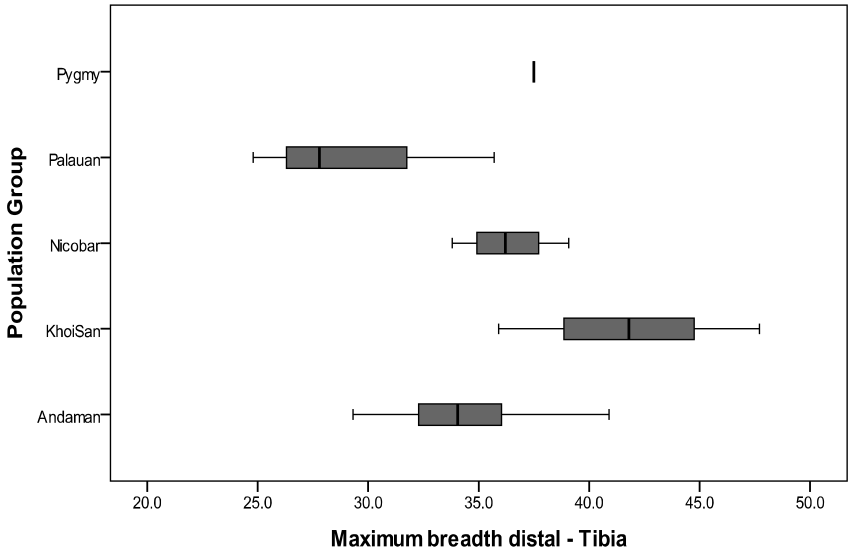

Figure 50: Boxplot for the measurements taken for the maximum breath of the distal tibia. (N = 39 SD = 3.983 mean = 34.91)

3.9.4 Medial talar articular depth of the tibia

The Palauan sample has the largest mean amongst the small-bodied comparative sample (Table 50). Andamanese have the smallest measurement, while Khoisan have the largest. Palauan specimens plot more like Khoisan individuals (see Figure 51), while Pygmy and island groups all plot below the comparative sample mean. B: OR-15:18-045 (26.5 mm z = 1.91), B: OR-15:18-021 (26.9mm z = 2.09) and B: OR-14:8-011(25.2 mm z = 1.335) are all more than one standard deviation above the comparative mean.

Table 51: Descriptive statistics medial talar articular depths of the tibia.The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**33**	**18.6**	**27.3**	**21.835**	**1.9595**
Andaman Islander	25	18.6	24.2	21.552	1.6019
KhoiSan	3	24.1	27.3	25.667	1.6010
Nicobar Islander	4	19.3	21.6	20.540	.9691
Palauan	3	25.2	26.9	26.200	.8888
Pygmy from the Congo	1	22.6	22.6	22.600	.

The Palauan sample is represented by three specimens; B: OR-15:18-045, B: OR-15:18-021 and B: OR-14:8-011. Data used in this set were collected by the author.

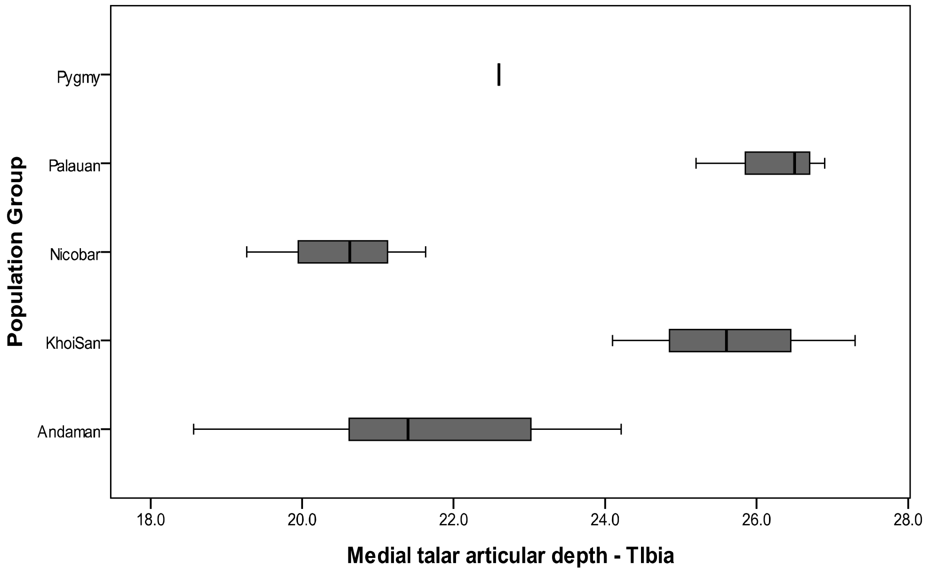

Figure 51: Boxplot of the medial talar articular depth of the distal tibia. (N=36, SD 2.248, mean 22.2)

3.9.5 Tibial midshaft anteroposterior (AP) diameter

The Palauan specimen B: OR-014:18-043 (28.0mm z= 1.148) is larger than the mean for the comparative sample (see Table 51). Andamanese have the smallest measurement, while Khoisan have the largest. Palauans plot similarly to the Khoisan sample at the larger end of the range. The Pygmy falls within the range of the island groups. This midshaft variable has a normal distribution with no individuals plotting on the low end (see Figure 52).

Table 52 : Descriptive statistics midshaft anteroposterior diameter of the tibia. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**34**	**19.1**	**31.9**	**24.232**	**3.1695**
Andaman Islander	24	19.1	27.9	**23.017**	2.4640
KhoiSan	4	25.4	31.9	29.525	3.0923
Nicobar Islander	5	24.6	26.8	25.738	1.0141
Palauan	1	28.0	28.0	28.000	.
Pygmy from the Congo	1	24.7	24.7	24.700	.

. A single specimen represents the Palauan sample; B: OR-014:18-043. Data used in this set were collected by the author.

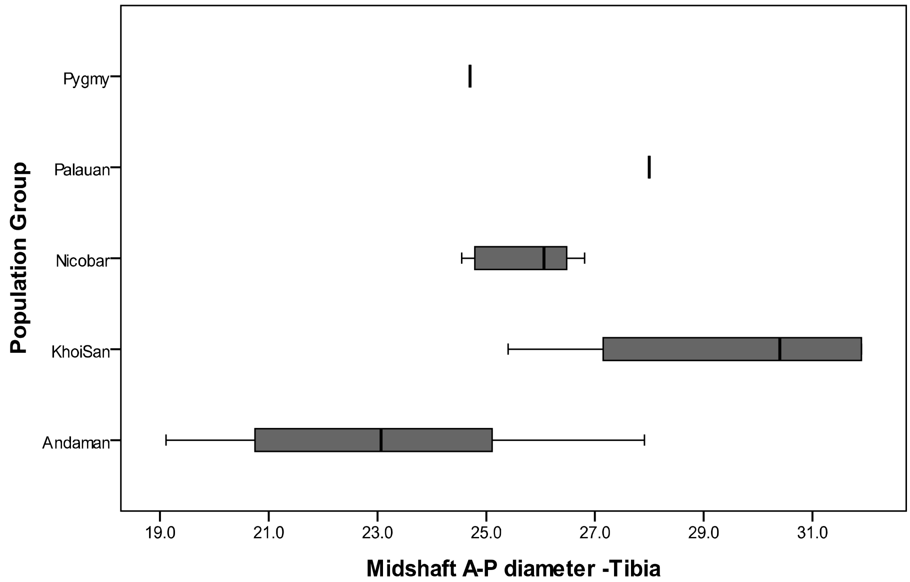

Figure 52 Boxplot for measurements taken on midshaft anteroposterior diameter of the tibia. (N=38 SD= 3.192, mean 24.23)

3.9.6 Tibial midshaft mediolateral (ML) diameter

The Palauan specimen B: OR-14:18-043 (19.4mm, z = 0.46) falls just above the comparative sample mean, but still within the range of other small-bodied groups (see Table 52). Khoisan has the largest measurement, while Andamanese have the smallest measurement. There is overlap between all ranges of the small-bodied groups and the measurements are distributed normally (see Figure 53). A large number of specimens fall below the sample mean for the mediolateral diameter of the tibial midshaft. Palauan midshaft dimensions are similar to the Khoisan , where the smallest midshaft belongs to Andaman and Pygmy individuals (see Figure 54).

Table 53: Descriptive statistics from the midshaft ML diameter of the tibia. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**34**	**14.5**	**22.5**	**18.309**	**2.3283**
Andaman Islander	24	14.5	22.5	17.878	2.3253
KhoiSan	4	17.1	22.0	20.600	2.3424
Nicobar Islander	5	16.8	21.2	18.784	1.5835
Palauan	1	19.4	19.4	19.400	.
Pygmy from the Congo	1	17.1	17.1	17.100	.
The Palauan sample is represented by a single specimen, B: OR-14:18-043. The author collected data used in this set.					

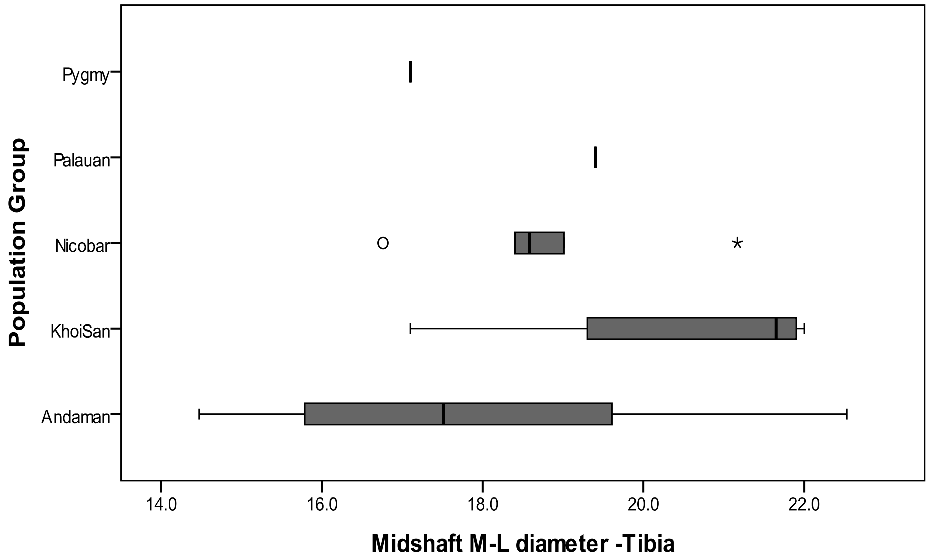

Figure 53: Boxplot showing the distribution measurements taken for midshaft ML diameter of the tibia. (N = 35, SD 2.301, mean = 18.34)

The mean for each measurement was analysed as a univariate plot (see Figure 55). The Palauans specimens are smallest in the proximal epiphyseal breadth and maximum breadth of the distal epiphysis. There is a reduction mediolaterally in the Palauans, while the anteroposterior measurements are slightly larger than the comparative insular groups. For small-bodied groups, Khoisan are the largest and Andamanese are overall the smallest. Interestingly, the Pygmy specimen has the largest measurements amongst the small-bodied sample.

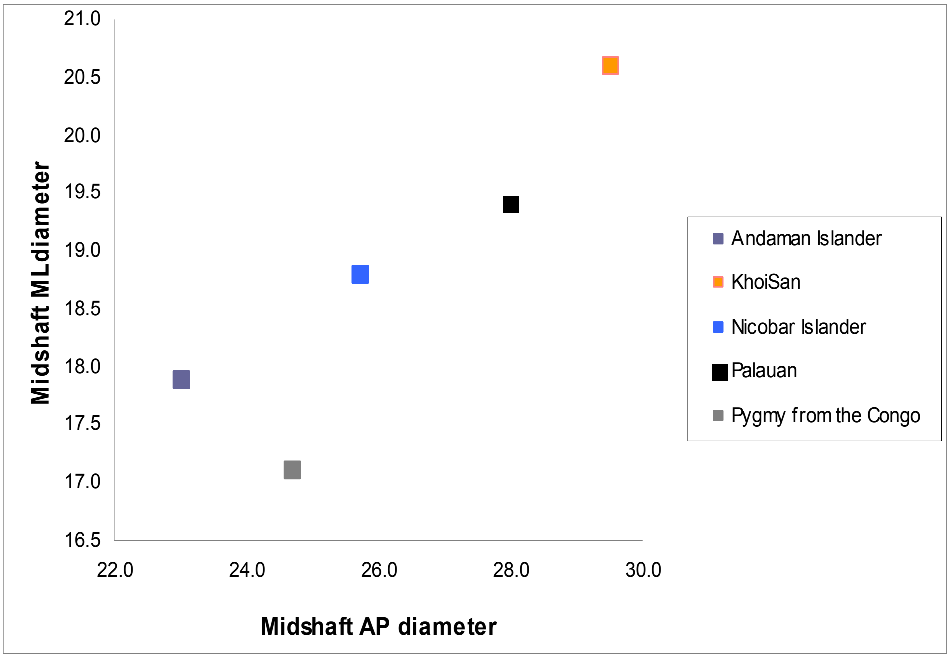

Figure 54: Bivariate plot showing the dimensions of the tibial midshaft. Each plot is the mean of the measurement for each group.

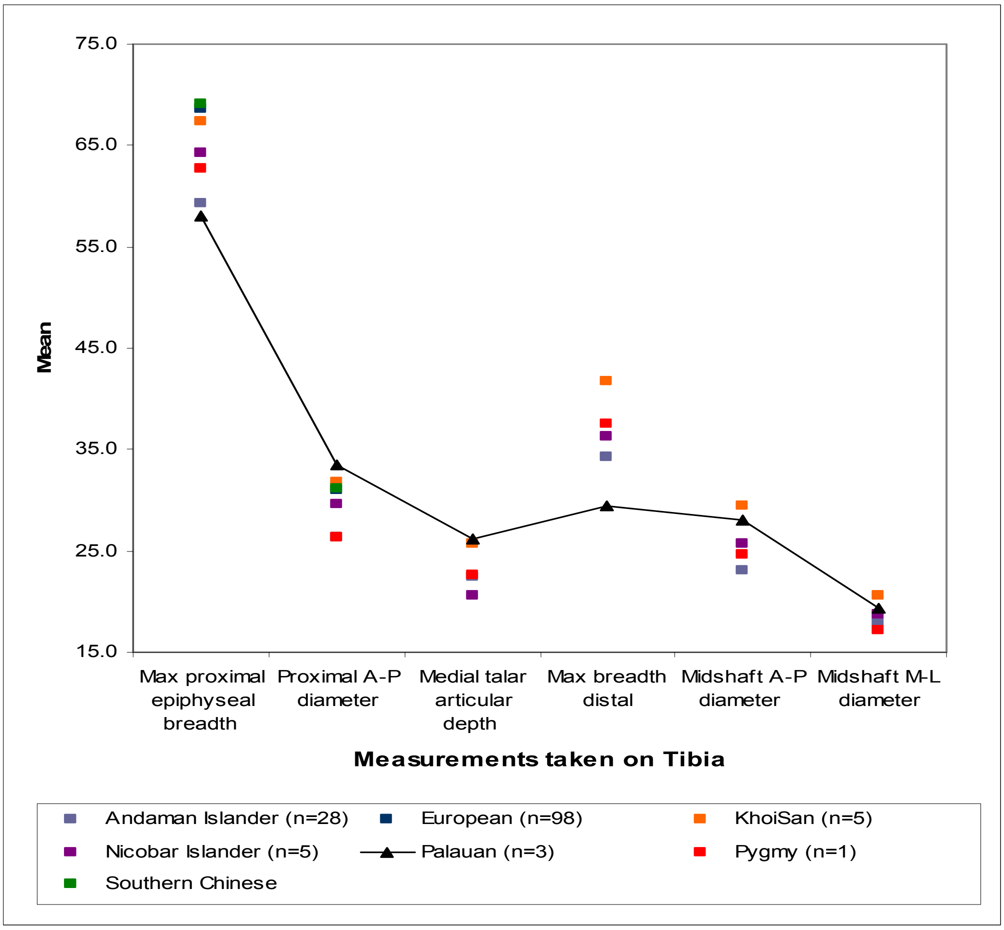

Figure 55: Univariate plot of measurements taken on the tibia. The sample sizes given are for the entire sample, for each individual measurement please refer to the tables in Chapter 2.

3.10 Statistical Analysis and Results for the Fibula of the Palauan Specimens

Measurements are defined in the methods chapter (Table 14) specimens examined in this section have been outlined in Chapter 2 (p 60). Due to the fragmented nature of the Palauan specimens only 3 measurements were taken on the fibula.

3.10.1 Distal maximum depth of the fibula

For the distal maximum depth of the fibula, Palauans have the largest mean and measurement (see Table 54 and Figure 56), and the Pygmy has the smallest measurement. There is overlap in the ranges of all the small-bodied groups and no individuals fall outside of the normal distribution as outliers (see Figure 55). Overall, Palauans have distal maximum depths that fall at the larger end of the small-bodied range. The Khoisan, Pygmy and some Andamanese individuals fall at the lower end of the small-bodied range. There are differences between the plots of the small-bodied groups.

Table 54: Descriptive statistics for the distal maximum depth of the fibula. The mean, standard deviation (SD), minimum and maximum are given for each group.

Comparative Group	N	Min	Max	Mean	SD
Total comparative sample	32	13.1	23.1	18.825	2.8154
Andaman	28	13.9	23.1	19.343	2.5643
KhoiSan	3	14.9	17.0	15.900	1.0536
Palauan	6	21.6	25.1	22.883	1.2671
Pygmy	1	13.1	13.1	13.100	.

The Palauan sample is represented by six specimens; B: OR-14:8-049, B: OR-14:8-051, B: OR-15:18-020, B: OR-15:18-028, B: OR-15:18-048 and B: OR-15:18-043. Data used in this set were collected by the author.

Table 55: Palauan fibula specimens and measurements.

Specimen	Measurement (mm)	Z-score
B:OR-14:8-049	23.2	0.70713
B:OR-14:8-051	25.1	1.00537
B:OR-15:18-02	21.8	1.20419
B:OR-15:18-028	23.1	0.77341
B:OR-15:18-048	22.5	1.23733
B:OR-15:18-043	21.6	1.86694

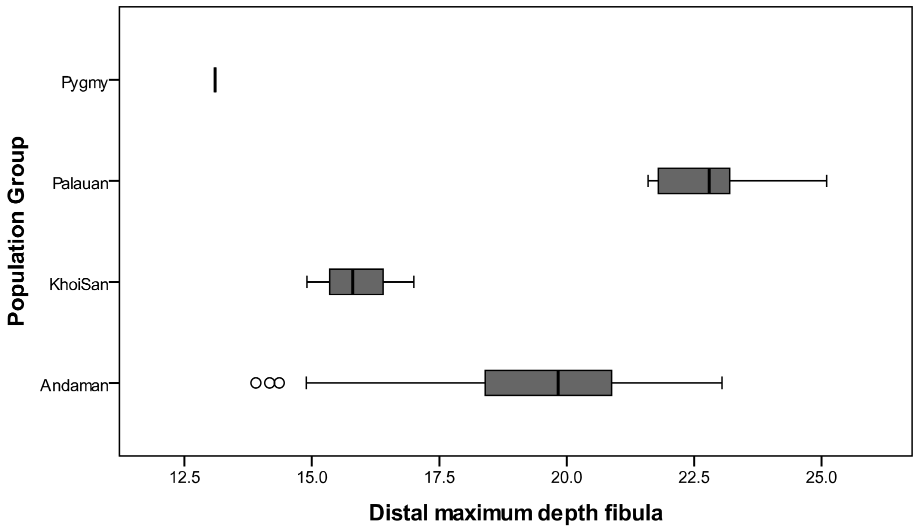

Figure 56: Boxplot for the measurements taken for the distal maximum depth of the fibula. (N = 38 SD = 3.018 mean = 19.47). The open circle indicate outliers for the population groups.

3.10.2 Distal articular depth of the fibula

Palauans have the largest mean for the distal articular depth and lie above the mean for the small-bodied comparative sample (see Table 56). Andamanese have the largest and smallest recorded measurements. The measurements plot within a normal distribution with no individuals plotting at the extremes (see Figure 57). There is an overlap in the ranges of the Palauan, Khoisan and Andamanese.

Table 56: Fibula specimen numbers, measurements and Z-scores.

Specimen number	Measurement (mm)	Z-score
B:OR-14:8-049	17.4	0.84542
B:OR-14:8-051	17.0	0.60098
B:OR-15:18-02	17.9	1.15097
B:OR-15:18-028	16.2	0.11209
B:OR-15:18-048	17.8	1.45653
B:OR-15:18-043	18.4	1.08986

Table 57: Descriptive statistics for the distal articular depth of the fibula. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**32**	**13.0**	**19.7**	**15.748**	**1.6208**
Andaman	28	13.0	19.7	15.690	1.6601
KhoiSan	3	15.0	18.1	16.500	1.5524
Palauan	6	16.2	18.4	17.450	.7740
Pygmy	1	15.1	15.1	15.100	.

The Palauan sample is represented by six specimens, B: OR-14:8-049, B: OR-14:8-051, B: OR-15:18-020, B: OR-15:18-028, B: OR-15:18-048 and B: OR-15:18-043. Data used in this set were collected by the author.

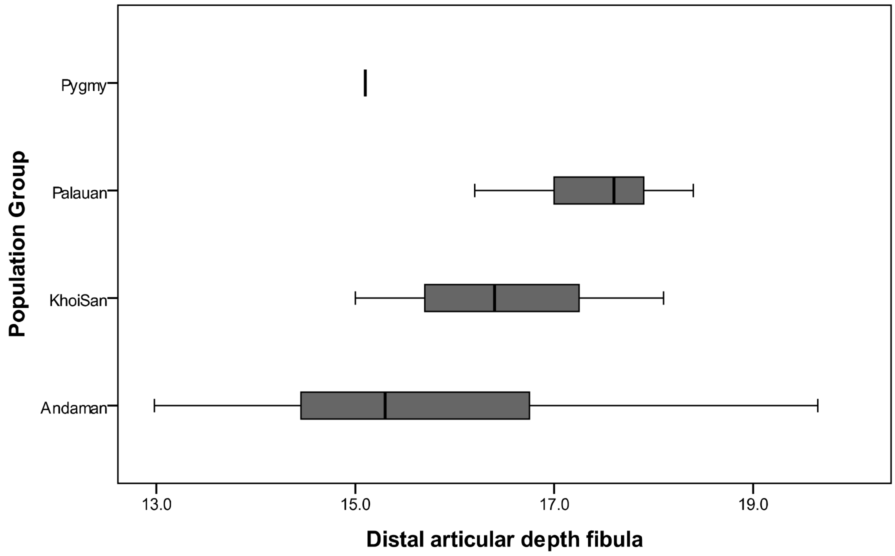

Figure 57 Boxplot for the distal articular depth of the fibula. (N = 38, SD = 1.636, Mean 16.02)

3.10.3 Distal articular height of the fibula

The smallest mean for the comparative sample belongs to the Andaman group (Table 58). There is overlap in ranges of the small-bodied groups and Palauan specimens fall within the overall range. Measurements taken are not normally distributed (see Figure 58), and no individuals as appear to be outliers. The Palauan specimens plot within the range of the Andamanese and out of the range of the KhoiSan. When measurements are evaluated together in a univariate plot (see Figure 59), it is evident that no one group plots in a predictable manner.

Table 58: Descriptive statistics distal articular height. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total comparative sample	**32**	**14.8**	**28.3**	**19.611**	**3.0371**
Andaman	28	14.8	22.5	18.759	1.8840
KhoiSan	3	21.9	28.3	26.000	3.5595
Palauan	6	18.9	24.2	20.550	1.8950
Pygmy	1	24.3	24.3	24.300	.

The Palauan sample is represented by six specimens, B: OR-14:8-049, B:OR-14:8-051, B:OR-15:18-020, B:OR-15:18-028, B:OR-15:18-048 and B:OR-15:18-043. Data used in this set were collected by the author.

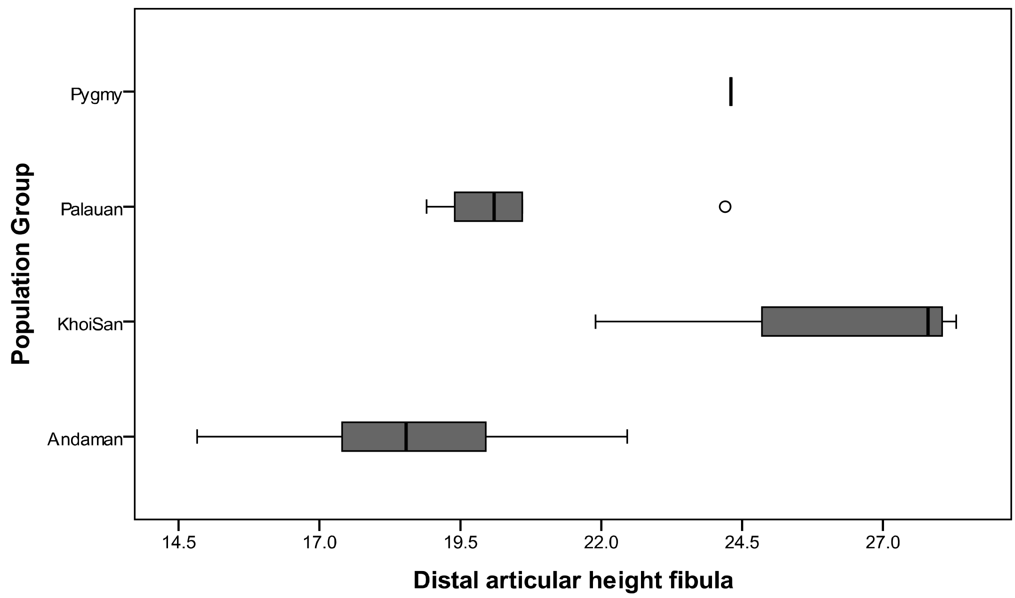

Figure 58: Boxplot for the distal articular height of the fibula. (N=38, SD = 2.887, mean = 19.76)

3.11 Summary of the Lower Limb

Lower limb and pelvic measurements of the Palauan specimens satisfy predictions (p. 77) that the Palauans follow a trend of exhibited by small-bodied specimens that were measured (see Table 58). The Palauan specimens reflect the measurements taken on the small-bodied comparative sample in that they fall within the overall small-bodied range. Diameters measured for the acetabulum mirror the small measurements of femoral head diameters (both AP and SI). The femoral measurements are generally small and plot in the low end of the range of variation for small-bodied sample. The tibia while satisfying the small-bodied hypothesis also showed unusual metrics in the proximal epiphysis. Palauan tibiae have a large anteroposterior diameter relative to the mediolateral diameters of the proximal epiphysis. The extent of this is seen when only means are considered (see Figure 49). Palauan midshaft are more robust than comparative island groups and the Palauans have the smallest recorded distal epiphyseal breath for the entire sample. This is similar to the trend seen in the humerus (refer to Summary of the upper limb of the Palauans, p107), where the Palauans also had larger proximal measurements relative to the distal measurements.

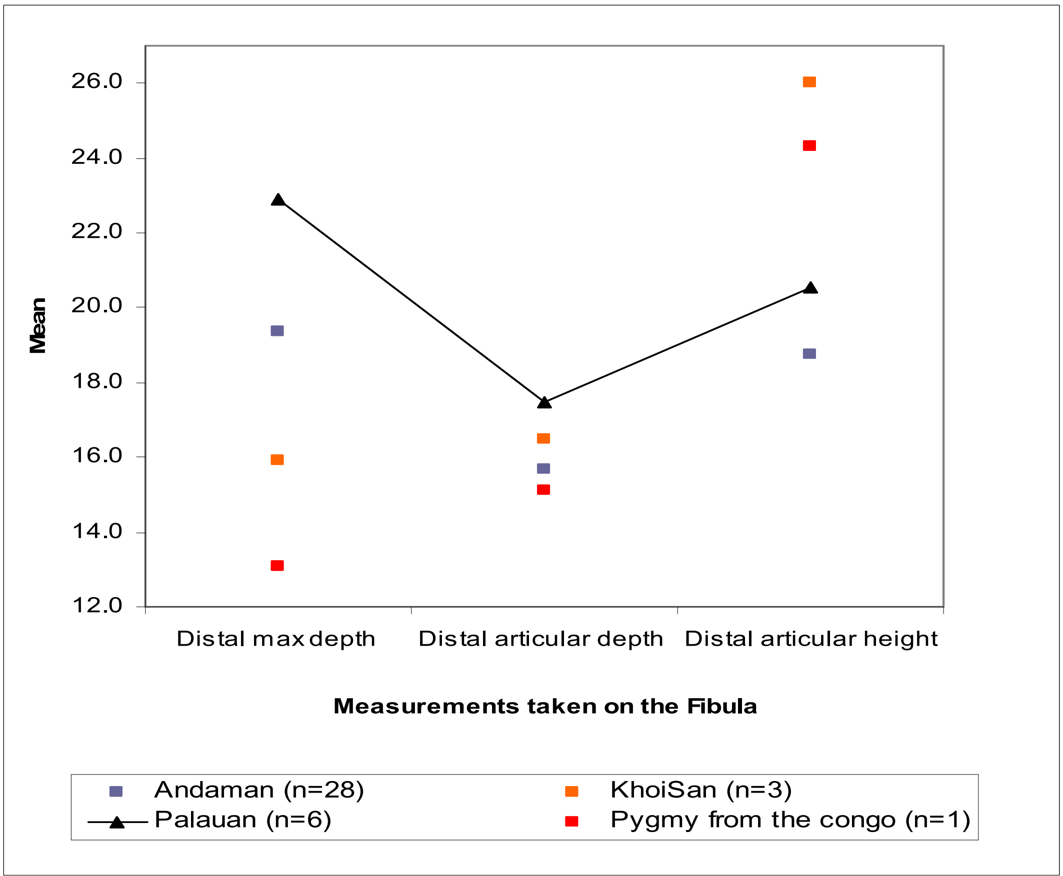

Figure 59: Univariate plot of the means for each measurement taken on the fibula and separated into the different groups.

Table 59: Summary for all pelvis and lower limb measurements taken on the Palauan specimens.

Element	Measurement [A]	Predicted result [B]	Actual result	Most comparable
Os coxa	**Maximum acetabular diameter**	Small	Small	**AND**
	Transverse diameter of the acetabulum	Small	Smallest	**AND**
	Iliac height	Small	Smallest	**PG**
	Superior iliac breadth	Small	Small	**AND**
Femur	**Anteroposterior (AP) head diameter**	Small	Small	**AND**
	Superoinferior (SI) head diameter	Small	Smallest	**AND**
	Vertical neck diameter	Small	Small	**NIC**
	Sagittal neck diameter	Small	Smallest	**AND**
	Head and neck length	Small	Smallest	**AND**
Tibia	**Proximal AP diameter**	Small	Large	**Overlap**
	Proximal ML diameter	Small	Smallest	**AND**
	Distal maximum breadth	Small	Smallest	**KS**
	Medial talar articular depth	Small	Large*	**KS**
	Midshaft AP diameter	Small	Large*	**KS**
	Midshaft ML diameter	Small	Small	**Overlap**
Fibula	**Distal maximum depth**	Small	Large*	**NONE**
	Distal articular depth	Small	Small	**KS**
	Distal articular height	Small	Small	**NONE**

A. Highlighted measurements indicate that only small-bodied data was available.
B. In the actual results, "Small" means that it plots similarly to small-bodied groups, and "large" means it plots similarly to larger bodied groups. In each case where the "Large*" indicates that this is large comparable only to other small bodied individuals "Average" means that it plots near the mean. Smallest indicates that the Palauan sample has the smallest mean for this measurement.
C. The last column gives; an abbreviation is given indicting which population is most similar to the Palauan specimens for that measurement. AND= Andaman KS= Khoisan, E = European PG= pygmy.

CHAPTER 4: DISCUSSION ON THE POSTCRANIAL ELEMENTS OF THE PALAUAN SPECIMENS

Insular Dwarfism (a form of phyletic dwarfism) is a process in which large animals reduce in size to better suit their environment (Foster 1964). This generally happens on islands, where a population's gene pool is limited to a small environment and is known as the island rule (Van Valen 1970, 1973a, 1973b). Other factors that may affect insular dwarfing are environmental factors such as a shortage of food, climate, and lack of predation. There are many examples of insular dwarfing in the modern world as well as in the fossil record. The terms "dwarf" and "pygmy" used in this study, denotes forms or species that are smaller than their close relatives (Nowak 1991).

This section will focus on discussing the results in terms of Hypothesis 1-3;

- **Hypothesis one**: The Palauan sample represents a group of humans with a body size amongst the smallest recorded for a modern human sample.
- **Hypothesis two**: The Palau specimens represent a case of insular dwarfism.
- **Hypothesis three**: Is it possible to identify traits that are likely to occur in populations which are reducing in body size over a relatively short time period (several generations)?

The general island rule has two applications for body size, insular dwarfism where larger animals (mostly mammals) usually evolve smaller body size (Foster 1964, 1965; Van Valen 1970, 1973a, 1973b; Sondaar *et al.* 1994; Heaney 1978), and gigantism where small-bodied animals (such rodents, birds and small reptiles) undergo an increase in body size (Foster 1964, Van Valen 1973, Lomolino 1985). It is important to note that evolution on islands is dependent on life history, community composition and the biology of the isolated species. When examining island populations, all of these factors should be taken into consideration instead of focusing on generalities (Raia & Meiri 2006). On islands, mammals have considerable variation in the way in which they respond to the selective forces that drive size evolution (Meiri *et al.* 2008). When studying island populations, both biotic and abiotic environmental factors must be taken into account in order to assess how a populations' body size will evolve (Meiri *et al.* 2008).

The Palau Archipelago is an island environment that is known to have been colonised early on, but which remained relatively isolated due to its location and the surrounding currents.

Small body size is characteristic of certain South American, African, Southeast Asian and some island human populations. Convergent evolution of this phenotype has always thought to have been due to strong associations with tropical rainforests or locations with tropical climates, and has led to hypotheses pertaining to the adaptive advantages of small body size as a means of survival when there are food limitation, warm and humid conditions and dense forest undergrowth (Perry & Dominy 2008). The evolution of small body types in similar environments around the world suggests that it is favoured by natural selection (Quintana *et al*. 2008). Here the potential causes of insular dwarfing are discussed.

Resource limitation: On islands with limited resources, large individuals often cannot survive and will eventually die off (Brown *et al*. 2004). Animals that are smaller, have an advantage over their larger counterparts, eating less and using a smaller quantity of available resources, and as a result would be more likely to breed and pass on their small-bodied genes to successive offspring than their larger counterparts (Van Valen 1970). Breeding strategies that select for small body size are evolutionary mechanisms used to ensure survival (Shea & Bailey, 1996). Islands are food-limited environments. In tropical rainforests (such as the Ituri forest where there are known Pygmy groups), essential plant foods are scarce for half of the year (Perry and Dominy 2008), leaving resources of a combined 'marginal nutritional and caloric value' (Hart & Hart 1986). Small body size would be a selective advantage to individuals living in these habitats as small body size reduces the necessary total caloric intake required for survival (Shea & Bailey 1996). The condition on Palau lends itself to be a resource limited environment (see 1.4.2 Climate and Vegetation p 49).

Predation: Cope's rule, states that population lineages tend to increase in body size over evolutionary time (Hone & Benton 2005), an increase in body size has many advantages as fitness increases as body size increases. Cope's Law deals with predation in an evolutionary context by positive selection for larger size (Wassersug *et al.* 1979; Jablonski 1997; Stanley 1973). Since larger size mammals are better adapted for protection from predation (Rensch 1960; Van Valen 1973a, 1973b), however, in the absence of such predators, the evolutionary trend of dwarfism will prevail (Stanley 1973). It is important to remember that size evolution of large mammals on islands is due to different underlying mechanisms. Not all mammals follow the exact same rules, for example; ungulate dwarfism depends on the existence of competitors, insular carnivore body size, as well as the resource base. This shows that ecological interactions play a major role when it comes to reducing body size on an island (Raia & Meiri, 2006). Lister (1989) found that in general vertebrates would undergo considerable body size changes, in relatively short evolutionary times, on islands (Lomolino 2005). The lack of terrestrial fauna on Palau would be most evident in the lack of predators.

Species Richness: A decline in the number of predators and competitors would lead to dwarfism (Dayan & Simberloff 1998). As predation pressure on an island decreases, species will achieve smaller body sizes (Boekschoten & Sondaar 1966; Sondaar 1977) since large body size is one means of decreasing predation pressure (Sinclair *et al.* 2003). In the case of herbivores, Smith (1992) suggests that in the absence of predators small-bodied herbivores grow large to facilitate digestion that is more effective. The most common thought on this is that reducing body size is a way of coping with limited resources islands (Heaney 1978; Lomolino 1985; Roth 1992; Burness *et al.* 2001).

Isolation: In cases where immigration or emigration is limited, coupled with resource limitation, you will get insular dwarfing (Wassersug *et al.* 1979). Isolation can also lead to a phenomenon known as the Founder Principle. This is when a small number of individuals colonize a new site and become cut off from the panmictic population. This isolation occasionally leads to 'genetic revolutions' followed by rapid phenotypic change, (Mayr 1963; Barton 1996). In shorter periods, this manifests in a population possessing characteristics that were unique to the founding population e.g. deformities. (Carson & Templeton 1984)

Genetics: From studies on human mitochondrial and Y-chromosome DNA, it has been shown that genetic mutations for the Pygmy phenotype have occurred at least three times in humans (Perry & Dominy 2009). The extant Pygmy populations' phenotype may be a result of genetic rather than environmental factors (Perry & Dominy 2009). Growth hormone and insulin-like growth factor 1(GH1-IGF1) are hypothesized to be responsible for the regulation of somatic growth and stature; disturbances in this pathway have been reported in pygmies from Africa and Southeast Asia (Jain *et al.* 1998; Clavano-Harding *et al.* 1999; Davila *et al.* 2002). Perry & Dominy (2009) found that childhood growth rates in pygmies were faster than their contemporaries and at a slower rate during adolescence.

Thermoregulation: Sweat production and evaporation are inefficient in a tropical environment (Perry and Dominy 2009). It has been suggested that pygmies generate less heat during activities, thus mitigating the fitness reducing effects of heat stresses (Cavalli-Sforza 1986).

Life history: Due to the limited life-span of small-bodied populations, Migliano *et al.*(2007) and Walker *et al.*(2006) hypothesized that in order to maximize fitness, small-bodied populations had a diminished growth spurt or early cessation of growth, which would result in a relatively early age of first reproduction (Bailey 1991).

While the above-mentioned factors have all been hypothesized to lead to dwarfing of a population, isolation, life history, founding population (genetics) and environmental conditions all affect population body size differently over time, and the way in which isolated populations decrease in body size may vary.

4.1 Pygmies and known insular dwarfs

Small-bodied ethnic groups are found in parts of Southeast Asia and are termed 'Negrito" (see Figure 60). These isolated groups include the Andaman Islanders, the Semang tribes of Malaysia, the Mani tribe of Thailand and Negrito tribes from the Philippines. The term Negrito was first used to describe these people due to their many physical features shared with African Pygmy populations, the most prominent of these characteristics being short stature. While the origin of Negrito people is still a matter of great speculation, genetic studies suggest that these insular populations, while sharing physical traits with African pygmies, are the most genetically distant human population from Africans (Thangaraj et al. 2003). Negritos separated early from Asians, suggesting that they are either surviving descendants of settlers from an early migration out of Africa, or that they are descendants of a founding population of modern humans (Kashyap et al. 2003).

Figure 60: Negrito people. 1 January 1905: http://en.wikipedia.org/wiki/file:Malaya_1905.jpg.

The Southeast Asian pygmoid groups are thought to be descendants of a group of Australo-Melanesians (Bulbeck, 2006) (based on shared cranial affinity as well as shared cranial markers such as sundadonty (Australoid morphology)) that may have undergone insular dwarfism over thousands of years. Tropical rainforest environments offer limited resources, which may have been the driving force of the dwarfing in this case, since reducing food intake in a resource-stressed environment would have been necessary for survival (Diamond 1997; Windshuttle & Gillin 2002). Andaman Negritos (Onge) are thought to have been isolated the longest with very little gene flow (Thangaraj *et al.* 2003). A study by Hill *et al.* (2006) suggests that based on genetic evidence there is no shared ancestry between the "Negrito" groups of the Andaman Islands, Malay Peninsula, and Philippines. They further suggest that each population ancestry should be considered as separate, any traits shared by these groups may be due to insular dwarfing (Hill *et al.* 2006).

Another well-known group of small-bodied people are the Rampasasa from the island of Flores in Indonesia. This population is short-statured and share similar traits with other insular dwarf populations. Jacob *et al.* (2006) found that this Pygmy population is less than 1km from the site where *H. floresiensis* remains were uncovered. The Rampasasa share features such as a reduced chin and rotated premolars with *H. floresiensis.* The island of Flores is an example where a fossil population and an extant population of insular dwarfs are known from the same location.

4.2 The Palauan Specimens

4.2.1 Environment and location

Palau lends itself to all the conditions required for insular dwarfism. There is small seasonal variation in the tropical climate of Palau, with a mean annual temperature of 27^{o}C and a range in variation being less than 4^{o}C annually (Snyder & Butler 1997). The annual humidity on the islands is as high as 82%. Latitude and high humidity are both associated with a reduction in body size, as it has been suggested that smaller body size allows for effective thermoregulation, small body size generates less internal heat during activity (Cavalli-Sforza, 1986).

A dense mass of tropical rain forest covers the rock islands of Palau. The larger volcanic island has vegetation varying from tropical rain forest (approximately 75% of the Palau islands are forested) to savanna, and broad belts of coastal mangrove swampland (Snyder & Butler 1997). Within the forests, a great diversity of plant life exists, producing resources such as coconut, breadfruit, mango, banana and betel nut, but this mixed vegetation coupled with the isolated nature of Palau has been unable to sustain much terrestrial fauna on the island. There are, however, abundant aquatic faunal species found in the Palau Archipelago. Due to this aquatic resource, most early archaeological material is collected from the periphery of the main island and the rock islands (Fitzpatrick & Kataoka 2005).

Conditions on Palau would have resulted in a resource-limited environment for these early Palauans. Archaeological evidence established that near shore reef species of fish and large shellfish were important foods by 3000 YBP (Clark 2005). While abundant marine resources were available, early inhabitants would have had a low caloric daily intake. In order to survive on apparently limited resources, small body size would have been favoured (Clark 2005).

4.2.2 The small-bodied inhabitants of Palau

The results of the postcranial remains (see Chapter 3) for the Palauan specimens satisfy conditions required to be defined as small-bodied. Many postcranial elements measured fell within the range of small-bodied comparative groups, with some being the smallest recorded measurements for the entire sample. Stature estimates were calculated also falling comfortably below accepted thresholds for defining pygmoid population groups (Cavalli-Sforza 1986, Schmidt 1905). Measurements of Palauans often plotted similarly to those of the Andaman group, but in other measurements they plotted similarly to the Khoisan group.

Table 60: Measurements for which the Palauan samples show unusual trends as either being outliers for the entire comparative sample or not plotting near the comparative insular populations. This table is a summary of the results obtained in Chapter 4 of this study.

Element	Measurement	Outlier
Humerus	Capitular SI diameter in relation to the ML length of the trochlea	Palauan specimen show disproportion in these measurements relative to the island populations and cluster with the Khoisan individuals.
	Distal articular breadth	Small
	Humeral head diameter	Large, comparable to the Khoisan
Radius	Distal radial breadth and depth	Large, comparable to the Khoisan
	Carpal articular breadth	Smallest recorded
	Radial head AP diameter	Large comparable Khoisan
Ulna	Crest Height	Smallest recorded for entire sample
	Olecranon length and height	Large unlike the small-bodied comparative sample.
	Distal ulna dimensions	Smaller than insular populations
Tibia	Proximal ML diameter	Small
	Proximal AP diameter	Large comparable to the European group
	Proximal dimension	Disproportion is seen relative to the comparative small bodied samples
	Distal breadth	Smallest
Femur	Sagittal neck diameter	Small
	Vertical neck diameter	Small

Disproportionate joint sizes seen in the humerus, ulna, tibia, and femur could possibly be because of rapid reduction of this population (see Table 60), or may have been a trait that the Founder population possessed. For the humerus, the Palauan sample has large proximal and distal dimensions, yet articular surfaces on the epiphyses are small, the same trend is observed in the distal radius.

The Palauan ulna and tibia both share the trend of having disproportionate proximal dimensions relative to the other insular populations, and incredibly small distal dimensions for the same element. Sagittal neck diameter of the femur is small for the Palauan sample, but shows that not all island populations trend alike (i.e., Nicobar and Andaman groups differ for this measurement). It is however acknowledged that the aberrant measurements seen above may be due to a sampling error based on the small sample size of the Palauan group. Boucot (1976) observed that body parts of insular dwarfs are selected for functional efficiency, and body proportions may deviate from that of Founder populations. As morphology and metrics associated with rapid body size reduction have to be established for isolated hominin populations, this study puts forward that in order to identify a rapidly reduced body size; dimensions of the articular surfaces should be examined in relation to the epiphyses. However, this does not address the fact that insular populations may have different adaptive responses. While individual Palauan measurements all fall within the range of other small-bodied individuals, ratios of the articular surfaces do not resemble other well-established small-bodied insular groups and would be a reflection of the relatively short time in which reduction has occurred. A rapid decrease in body size reflects that most island populations have/had shorter life expectancies in comparison to their mainland counterparts. Marshall and Corruccini (1978) found that the decrease in mean body size of a species could occur over a short period, which could be decades to several thousand years. The dates obtained for the Palau sample (i.e., 1400-2900 YBP) would offer sufficient time to allow for the reduction seen in this population, given the suggestions of Marshall and Corruccini (1978).

It has been previously suggested (Fitzpatrick 2008) that the early colonizers of Palau may have been small-bodied and that the results obtained here are merely a reflection of small-bodied colonizers. If this were the case, there would be more conformity in the results obtained. The fact that there are dimensions of the postcrania that do not follow the same pattern as is seen in well-established island populations inhabiting similar environments, suggests the feature constellation is because of rapid reduction in body size rather than a gradual process of dwarfism.

CHAPTER 5: RESULTS AND ANALYSIS OF THE PALAUAN CRANIODENTAL SPECIMENS

As with most palaeoanthropological sites, a large portion of the specimens recovered are teeth. Tooth size has been used by palaeoanthropologists for many purposes, including calculating body size of early hominids. In the past, this has resulted in an overestimation of body size (Weidenreich, 1945).

The aim of this chapter is to compare Palauan fossil teeth as well as the preserved cranial elements to a comparative sample of modern *H. sapiens*. Subjects of the present study are remains recovered from the Ucheliung and Omedokel caves of Palau during the 2006/2007 field trip. The material consisted of predominantly isolated teeth, with some mandible and maxilla fragments that had *in situ* teeth. Only permanent teeth were measured for the purpose of this study. Teeth exhibiting excessive wear were excluded from the sample.

In this chapter the results will be analysed in order to test the following hypothesis

- **Hypothesis four**: The Palauan specimens have teeth that are large relative to the comparative samples. A critical aim of this study is to establish whether the ancient Palauan sample are infact megadontic, a trait not seen in modern-day Palauans, this would lend to possible identification of the founding population.
- **Hypothesis five**: The Palauan specimens collected from Ucheliung and Omedokel caves originated from Austramelanesia.

Results presented here aim to identify remnant morphologies of the founding population, or potential metric or morphologic features that may be a result of rapid reduction of body size. Southeast Asian pygmies are thought to be descendants of Australomelanesians due to the shared cranial affinities and sundadonty (Storm 2007).

5.1 Specific predictions for the Palauan Dental Specimens

The aims of this research involve examination of size variation of individual dental elements of modern humans recovered from Palau, Micronesia by comparing them to a modern comparative sample, which includes other island populations.

If this population expressed insular dwarfism, the present study aims to identify any size trends or associated metric features found within the population. By comparing whether or not the measurements taken for the Palauans are smaller, larger or similar in size to the comparative sample groups would be used as an indicator of possible reduction this is based on the hypothesis that the founding populations of Palau were 'normal' (Fitzpatrick 2007). The goal is not only to establish traits that are likely to occur in a populations which is reducing in body size over a relatively short time period (several generations), but also to highlight traits that may indicate from where this population may have originated. This will be done using a statistical analysis of the metrics collected on the Palauan dental specimens.

5.2 Statistical Analysis and Results of the Palauan Dental Metrics

The Palauan specimens with *in situ* dentition (see Figure 61) exhibited malocclusion. Despite this, measurements were also taken on these teeth. In this chapter, both mandibular and maxillary dentition are analysed.

Table 61: Palauan specimen list showing mandibles and maxillae with teeth *in situ*.

Specimen Number (BNM)	Identification	Short description
B: OR-15:18-006	Mandible	Right fragment. has ramus and impacted M3
B: OR-15:18-007	L. Mandible	2 teeth *in situ* M3 is impacted

B: OR-15:18-036	Mandible	Right side fragment with M1 and sockets of C1-M2
B: OR-15:18-051	Maxilla	Left fragment I2-P4 present (and sockets of M1-M2)
B: OR-15:18-055a	Maxilla	Right fragment with P3-M1 present
B: OR-15:18-055b	Maxilla	Left fragment with C1-M1 associated with B: OR-15:18-055a
B: OR-15:18-082	Maxilla	Left fragment with C- P4 present
B: OR-15:18-083	Complete Mandible	Teeth crowded and are stained on right I1/2M1/2 present on Left C-M2 present
B: OR-15:18-084	Maxilla	Right I2-present on Left C1-P3 present
B: OR-15:18-086	Maxilla	Left side fragment has P4 and sockets for I1-P3

For each measurement a Z-score was calculated, he Z-score is useful as it indicates the number of standard deviations the measurement falls from the mean. Negative Z-scores indicate that a measurement falls below the mean and positive Z-scores show it falls above the sample mean (Madrigal 1998). Due to the large sample size for dental analyses, Z-scores were calculated to give a clearer indication of where individual specimens plotted.

Figure 61: The complete mandible, B: OR-15:18-083 this was the only complete mandible recovered. It shows dental overcrowding in the anterior dentition (Picture by L.R. Berger).

5.2.1 Results of the Mandibular Dentition of the Palauan Specimens

For the purpose of this study and due to the scattered nature of the elements collected, each specimen was examined individually and summarized as a whole at the end of this chapter. This was done in order to observe any trends that may be present in the Palauan sample. The dataset provided by Brown (2001) included only the buccolingual diameters of all the teeth[8] while the Palauan specimens and the data collected on the Dart collection specimens [Mirriam Tawane, (2012 unpublished thesis)] included mesiodistal and cervico-enamel junction diameters, as these were measurements taken on the Palauan specimens.

5.2.1.1 Mandibular First Incisor (I_1) of the Palauan Specimens

The Tswana sample minimum is the smallest recorded for the comparative sample (4.3 mm) (see Table 62), while the Palauan sample have a large maximum-recorded MD diameter (6.8 mm). Palauan specimens have the largest Z-scores with all individuals falling above the sample mean (Figure 62). For the MD diameter, there is no significant comparison between any of the groups and the Palauan sample. The large Palauan BL mean makes it comparable to the Murray Valley Aboriginal group (see Figure 62) while the Dart collection specimens all have remarkably small buccolingual diameters (Figure 63). The first mandibular incisors of the Palauan specimens are large.

[8] In personal correspondence with the author of the dataset it was indicated that mesiodistal diameters were not included/made available as they offered little or no anthropological significance.

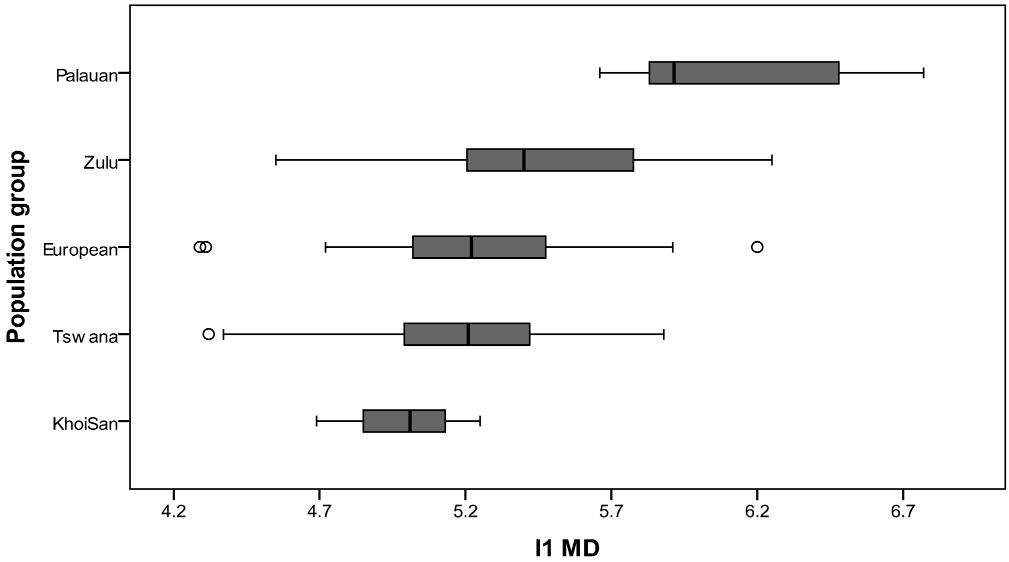

Figure 62: Boxplot for the mesiodistal diameter of I1 showing the comparative groups (N=98 SD = .4175 mean= 5.274). The open circles indicate possible outliers in the comparative sample.

Table 62: Descriptive Statistics for the measurements taken on I_1. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**I1 MD**	**98**	**4.3**	**6.3**	**5.274**	**.4175**
	I1 BL	**373**	**2.4**	**7.8**	**5.353**	**1.1158**
European	**I1 MD**	39	4.3	6.2	5.219	.4053
	I1 BL	116	2.4	6.6	4.982	1.2177
KhoiSan	**I1 MD**	3	4.7	5.3	4.983	.2810
	I1 BL	3	2.8	4.8	3.633	1.0240
Murray Valley Aboriginal	**I1 MD**	0				
	I1 BL	52	5.7	7.8	6.560	.3922
Northern Chinese	**I1 MD**	0				
	I1 BL	17	5.3	6.7	5.894	.4038
Palauan	**I1 MD**	6	5.7	6.8	6.095	.4309
	I1 BL	6	6.1	6.8	6.372	.2647
Swanport Aboriginal	**I1 MD**	0				
	I1 BL	14	5.9	7.3	6.521	.4807
Southern Chinese	**I1 MD**	0				
	I1 BL	114	4.8	6.7	5.648	.4040
Tswana	**I1 MD**	25	4.3	5.9	5.196	.4178
	I1 BL	26	2.8	5.5	4.283	.6910
Zulu	**I1 MD**	31	4.6	6.3	5.436	.4075
	I1 BL	31	2.5	5.0	3.874	.6953
Six specimens represent the Palauan sample. Data for the Zulu, Khoisan, And Tswana were collected by the Mirriam Tawane' (2012) and data for the European, Southern & Northern Chinese and Aboriginal group obtained from Brown (2001).						

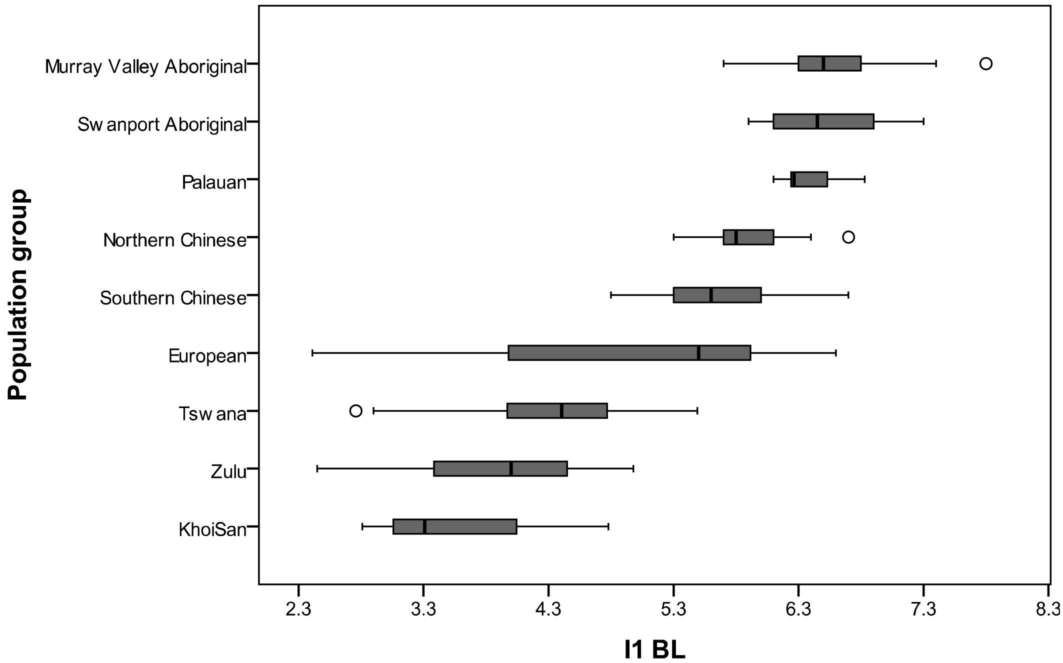

Figure 63: Box Plot for the buccolingual diameters of the mandibular first incisor (I1) (N= 373, mean = 5.353std.dev = 1.1158). The open circles indicate the outliers for the comparative sample.

5.2.1.2 Mandibular Second Incisor (I_2) of the Palauan Specimens

For measurements of the second incisor, the Palauan specimens do not have the largest dimensions (see Table 63) but they are buccolingually robust.

The Palauan specimens have measurements on the second incisors that fall along the sample mean (Table 63 and Figure 64). The Aboriginal population from the Murray Valley has the largest recorded BL diameters and the Tswana population has the largest MD mean. Three of the Palauan specimens plot just below the mean for the Z-scores but still within the range of the entire comparative sample for the incisor MD diameter (see Figure 64), Palauans means are most similar to the Tswana group but there is overlap of all the comparative group ranges.

Table 63: Descriptive statistics of all measurements taken on the mandibular second incisor. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD= mesiodistal.

Population group		N	Minimum	Maximum	Mean	SD
Total for the comparative sample	**I2 MD**	**130**	**4.4**	**7.2**	**5.947**	**.4729**
	I2 BL	**441**	**2.4**	**8.8**	**5.622**	**1.2013**
European	**I2 MD**	45	4.8	6.9	5.851	.4152
	I2 BL	136	2.4	6.9	5.200	1.3356
KhoiSan	**I2 MD**	3	5.2	6.1	5.670	.4115
	I2 BL	2	3.0	4.0	3.535	.7142
Murray Valley Aboriginal	**I2 MD**	0				
	I2 BL	65	5.8	8.8	6.748	.5007
Northern Chinese	**I2 MD**	0				
	I2 BL	21	5.4	6.8	6.124	.3961
Palauan	**I2 MD**	5	5.6	6.6	5.948	.3541
	I2 BL	5	4.9	6.6	6.028	.6601
Swanport Aboriginal	**I2 MD**	0				
	I2 BL	19	6.1	7.2	6.637	.3483
Southern Chinese	**I2 MD**	0				
	I2 BL	115	5.2	7.2	6.122	.4350
Tswana	**I2 MD**	42	4.4	7.0	6.014	.5553
	I2 BL	42	2.7	6.3	4.594	.8611
Zulu	**I2 MD**	40	5.1	7.2	6.006	.4328
	I2 BL	41	2.7	5.9	4.262	.8831

Five specimens represent the Palauan sample. Data for the Zulu, Khoisan, And Tswana were collected by the Mirriam Tawane (2012) and data for the European, Southern & Northern Chinese and Australian Aboriginal groups obtained from Brown (2001).

It is important to note that for BL diameters, the two small-bodied groups in the Z-score plot separate from one another (see Figure 65). There are differences between the means of the comparative groups and the Palauan specimens for the BL diameter.

For all groups measured, there seems to be a consistency in the recorded measurements taken on the second mandibular incisor, i.e. there is a large range in which all individuals plot. This trend is not seen on the first incisors, as some groups have much larger first incisors (e.g. Aboriginals) than others.

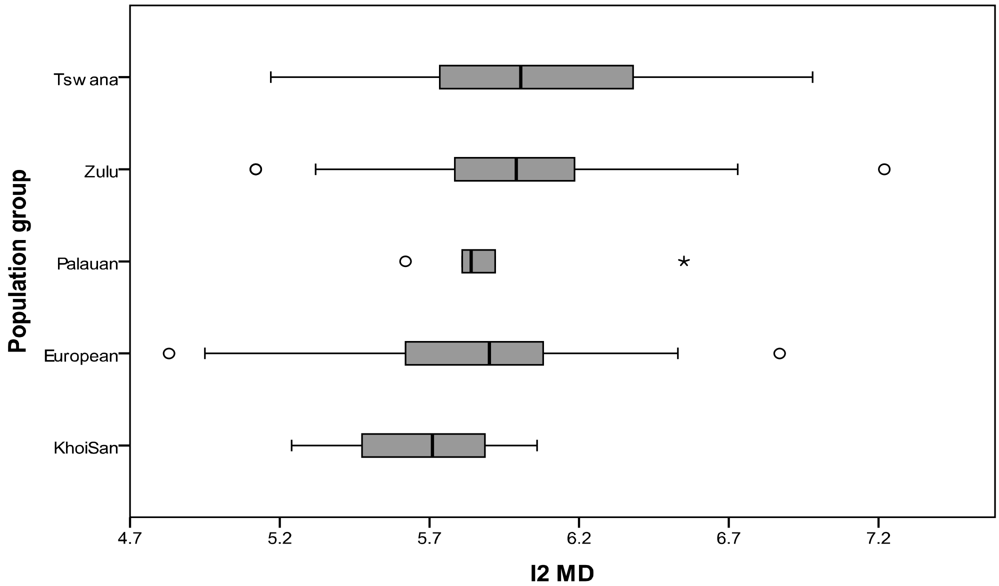

Figure 64: Box Plot for the mesiodistal diameters of the second mandibular incisor. (N=446, SD = 1.196 mean = 5.62). The open circles indicate possible outliers for the comparative sample.

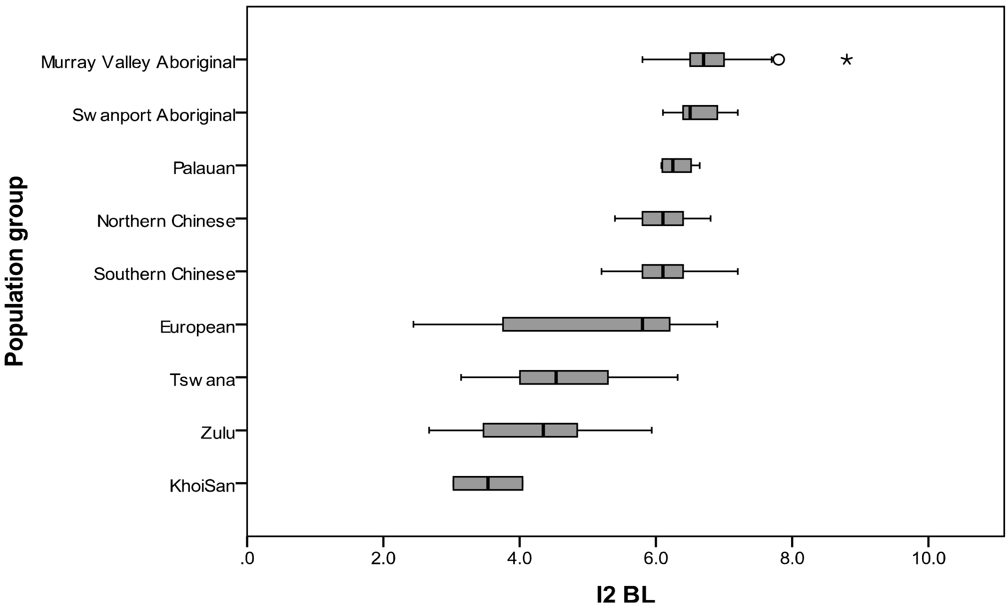

Figure 65: Boxplot showing the frequency distribution of the BL diameter of the second mandibular (N= 441 mean= 5.622, SD =1.201). The open circles and star indicates outliers for the comparative group.

5.2.1.3 Mandibular Canine (C) of the Palauan Specimens

Palauan canine specimens are similar to the comparative total sample mean (Table 64). The largest measurements belong to the Murray Valley Aboriginal specimens, while Khoisan have the smallest recorded canine measurements.

The MD diameters (see Figure 66) are normally distributed and Palauan samples fall above the sample mean. Khoisan individuals plot both above and below the mean. All specimens fall within the range of the largest individuals measured; there are no outliers. This is not the case for BL diameters (see Figure 67), as two small-bodied groups plotted on opposite sides of the mean, with the Khoisan group below the mean and the Palauan sample above the mean. There are differences between Palauan and Khoisan groups plots. Palauan samples have a large BL diameter in relation to MD diameter. For BL diameter, the Palauan and Murray Valley Aboriginal groups means plot near one another. There is some degree of overlap in the ranges of the comparative groups.

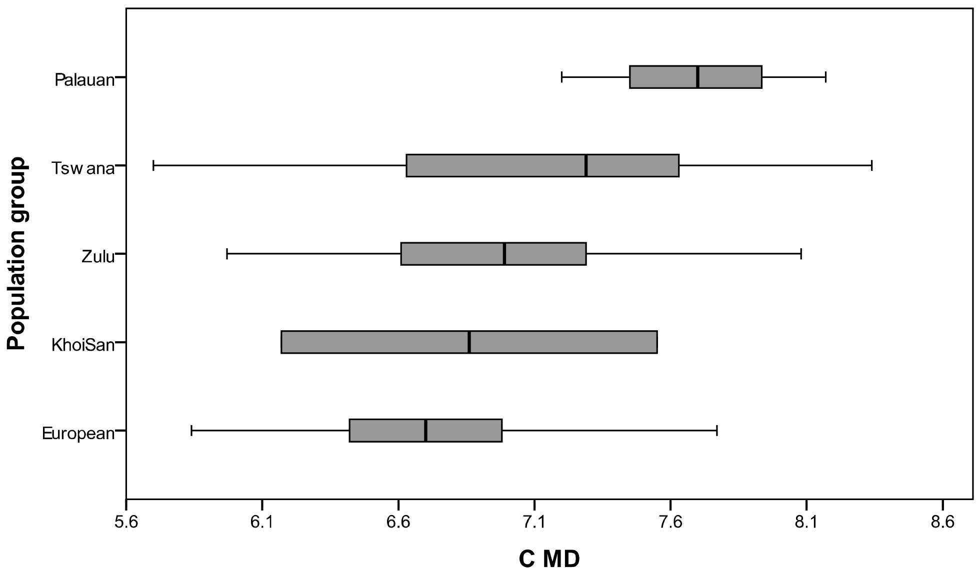

Figure 66: Boxplot of measurements taken for the mesiodistal diameter of the canine (N= 175, SD 0.584 mean = 6.94).

Table 64: Descriptive statistic for the measurements taken on the canine. The mean, standard deviation (SD), minimum and maximum are given for each group. BL = Buccolingual, MD = Mesiodistal.

Comparative Group		N	Min	Max	Mean	SD
Total for the comparative group	**C MD**	**172**	**5.7**	**8.3**	**6.932**	**.5785**
	C BL	**517**	**3.6**	**10.1**	**7.266**	**1.2008**
European	C MD	57	5.8	7.8	6.676	.4525
	C BL	150	4.1	8.7	6.649	1.2432
KhoiSan	C MD	2	6.2	7.6	6.860	.9758
	C BL	3	5.9	6.4	6.090	.2685
Murray Valley Aboriginal	C MD	0				
	C BL	80	7.2	10.1	8.434	.6765
Northern Chinese	C MD	0				
	C BL	29	7.0	8.9	8.017	.4465
Palauan	C MD	3	7.2	8.2	7.690	.4851
	C BL	3	7.5	8.2	7.780	.4015
Swanport Aboriginal	C MD	0				
	C BL	24	7.6	10.0	8.467	.6438
Southern Chinese	C MD	0				
	C BL	118	6.2	9.1	7.647	.6112
Tswana	C MD	54	5.7	8.3	7.135	.6766
	C BL	53	4.4	9.0	6.811	.8726
Zulu	C MD	59	6.0	8.1	6.995	.4974
	C BL	60	3.6	8.4	6.122	.9306

Six specimens represent the Palauan sample. Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

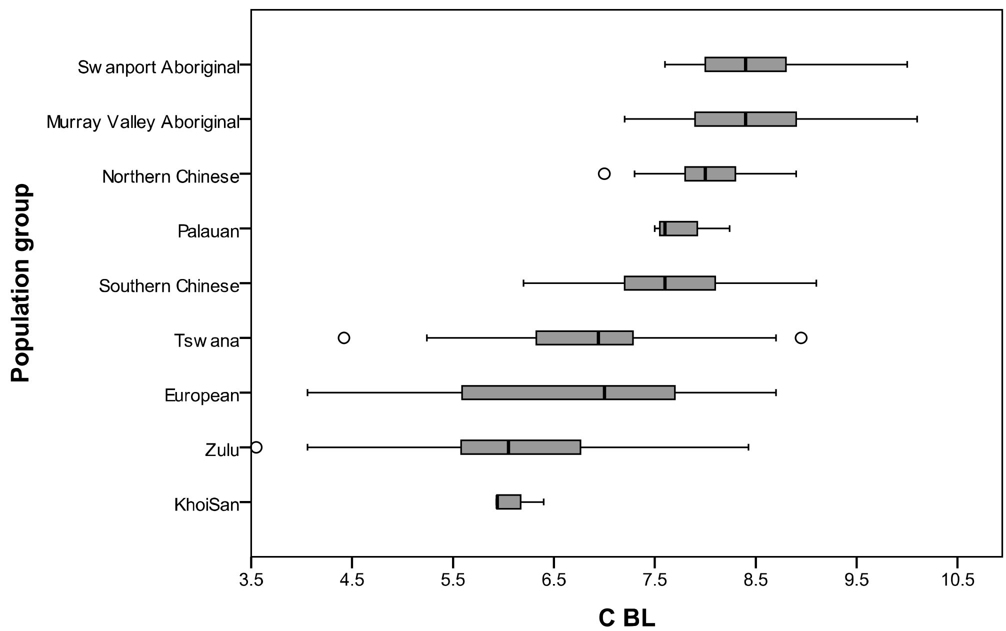

Figure 67: Boxplot of measurements taken for the buccolingual diameter of the mandibular canine (N= 178, SD 0.62, mean= 7.73). The open circles represent the outliers for the comparative sample.

5.2.1.4 Mandibular third premolar (P_3) of the Palauan specimens

Table 65: Descriptive statistics for the mandibular third premolar, the statistics are separated into the comparative sample groups. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD= mesiodistal.

Comparative Group		N	Min	Max	Mean	SD
Total for comparative sample	**P3 MD**	**5.8**	**8.7**	**7.083**	**.5378**	**197**
	P3 BL	**5.6**	**10.4**	**8.059**	**.7596**	**516**
European	P3 MD	61	5.8	7.9	6.823	.4439
	P3 BL	125	6.2	8.7	7.537	.5270
KhoiSan	P3 MD	3	6.4	6.9	6.617	.2732
	P3 BL	3	7.7	8.1	7.880	.1908
Murray Valley Aboriginal	P3 MD	0				
	P3 BL	77	7.6	10.4	8.926	.5732
Northern Chinese	P3 MD	0				
	P3 BL	34	7.1	9.9	8.012	.6044
Palauan	P3 MD	11	7.1	8.3	7.654	.4770
	P3 BL	11	7.7	9.7	8.515	.5385
Swanport Aboriginal	P3 MD	0				
	P3 BL	25	8.1	10.3	9.312	.6051
Southern Chinese	P3 MD	0				
	P3 BL	116	6.4	9.3	7.928	.5658
Tswana	P3 MD	59	5.9	8.7	7.095	.5729
	P3 BL	61	5.6	9.0	7.757	.5944
Zulu	P3 MD	74	6.2	8.7	7.306	.4855
	P3 BL	75	6.6	9.3	8.100	.5172
Eleven specimens represent the Palauan sample. Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).						

The Palauan MD P3 mean is larger than the European, Khoisan, and Tswana (Table 65). When considering only buccolingual diameter for which more data are available, the Palauan samples have the largest diameters recorded. Univariate plots (see indicate little difference in the MD measurements of the groups compared. The range of specimens is large and the Palauan specimens plot within the range of the comparative sample, but are all larger than the sample mean (see Figure 68). Khoisan and Palauan again plot on opposite ends of the sample mean for MD diameters. There are significant differences between the means compared for the BL diameter (see Figure 69).

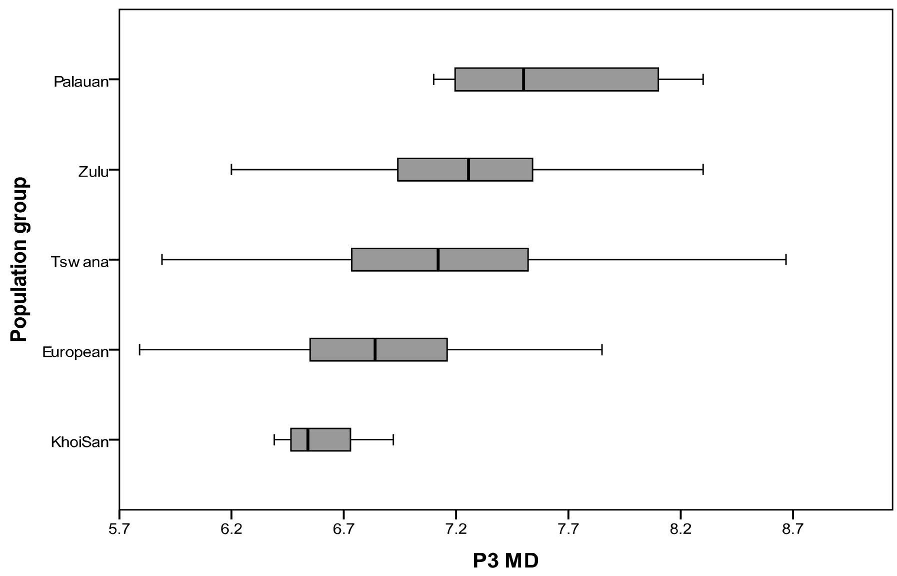

Figure 68: Boxplot showing of measurements taken for the mesiodistal (MD) diameter of the mandibular third premolar. (N= 208, SD 0.545, mean = 7.1).

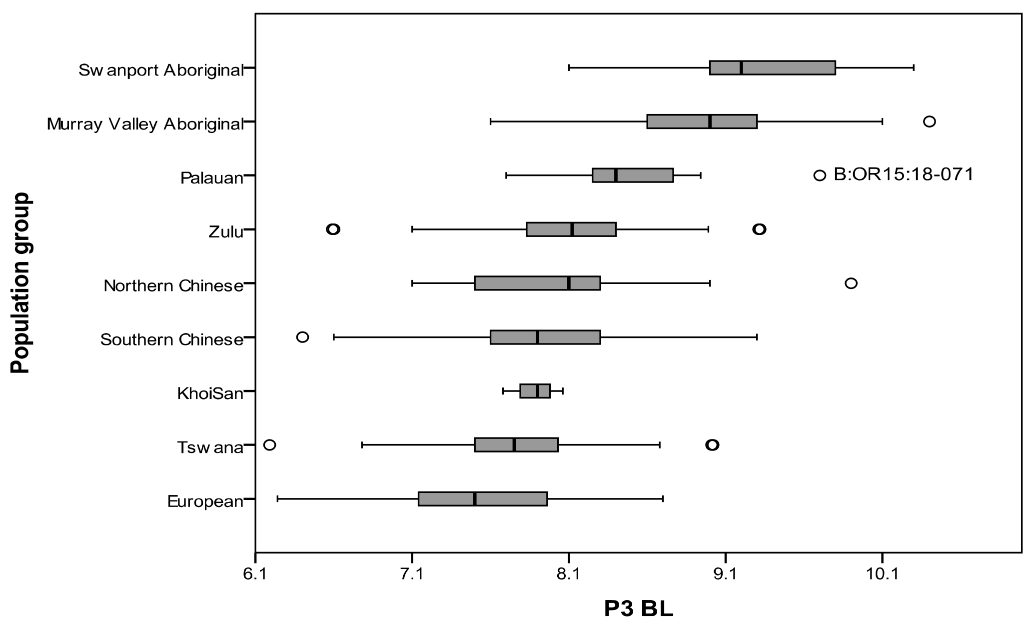

Figure 69: Boxplot showing measurements taken for the buccolingual (BL) diameter of the mandibular third premolar in this graph B:OR 15:18-071 is an outlier for the Palauan sample. (N= 516, mean = 8.059 SD = 0.7596).

5.2.1.5 Mandibular Fourth premolar (P_4) of the Palauan Specimens

Palauan specimens have the largest recorded mean for P_4 MD diameter (Table 66); MD diameters are normally distributed with some individuals plotting as large outliers (Figure

70). The largest mean BL diameter belongs to the Murray Valley Aboriginal group (Table 66), and measurements of all individuals taken are normally distributed (see Figure 71). The boxplot presented in Figure 71, indicates no significant difference in measurements between comparative groups, as there is a wide range of measurements for the sample. The Palauan specimens have similar measurements to the Swanport Aboriginal group.

Table 66: Descriptive statistics for measurements taken on the mandibular fourth premolar. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= Buccolingual, MD= Mesiodistal.

Comparative Group		N	Min	Max	Mean	SD
Total for the comparative sample	**P4 MD**	**163**	**5.4**	**11.0**	**7.302**	**.7843**
	P4 BL	**500**	**6.1**	**10.9**	**8.403**	**.6824**
European	**P4 MD**	40	6.2	8.3	7.102	.5097
	P4 BL	127	6.6	9.3	8.117	.5710
KhoiSan	**P4 MD**	3	6.5	7.9	6.943	.7939
	P4 BL	3	7.8	9.1	8.407	.6726
Murray Valley Aboriginal	**P4 MD**	0				
	P4 BL	73	7.3	10.7	9.018	.6347
Northern Chinese	**P4 MD**	0				
	P4 BL	35	7.3	9.5	8.334	.5352
Palauan	**P4 MD**	3	7.4	8.5	7.777	.6126
	P4 BL	3	7.9	9.8	8.737	.9897
Swanport Aboriginal	**P4 MD**	0				
	P4 BL	23	7.9	10.1	9.017	.6020
Southern Chinese	**P4 MD**	0				
	P4 BL	116	6.8	9.5	8.208	.5601
Tswana	**P4 MD**	56	5.4	11.0	7.434	1.0089
	P4 BL	58	6.1	10.5	8.424	.6810
Zulu	**P4 MD**	64	6.0	10.5	7.327	.6818
	P4 BL	65	6.9	10.9	8.424	.6832

Three specimens represent the Palauan sample. Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Southern Chinese and Aboriginal group obtained from Brown (2001).

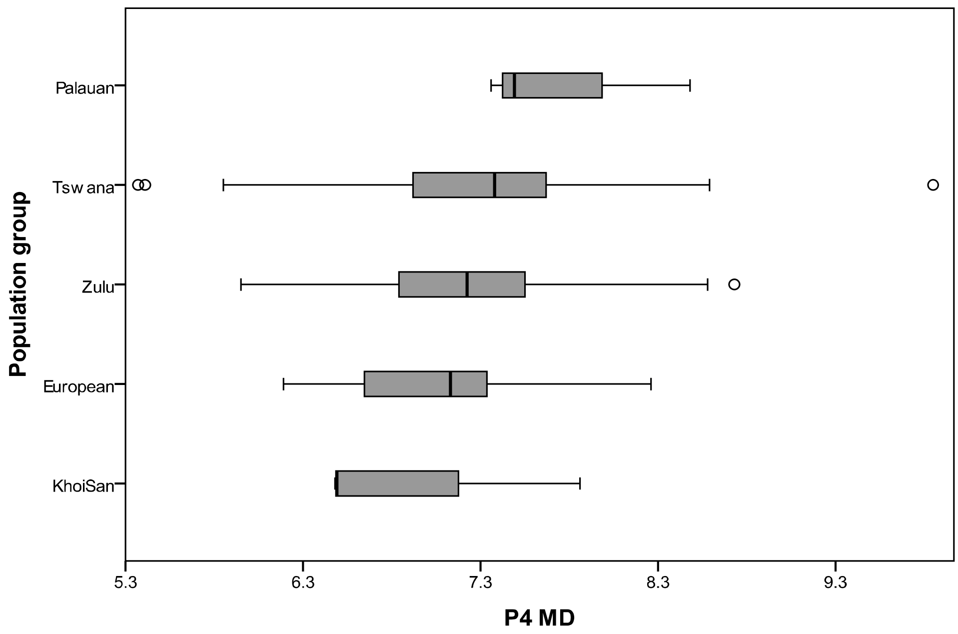

Figure 70: a) Box Plot for the mesiodistal (MD) diameters of the mandibular P4, (N= 167, SD = 0.839, mean = 7.33). The open circles indicate outliers for the comparative sample.

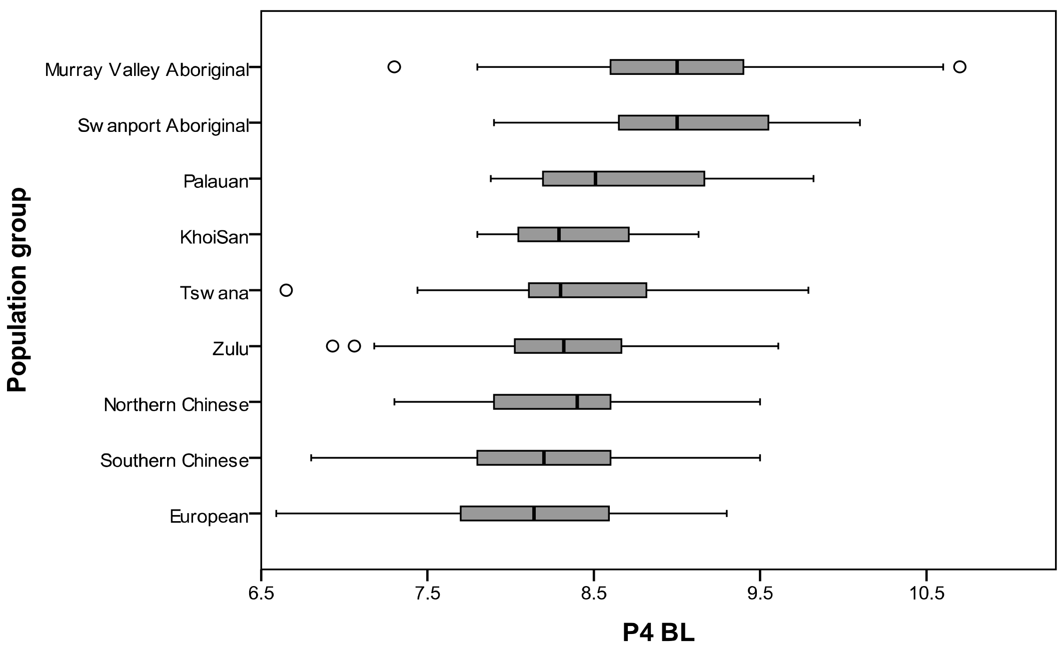

Figure 71: a) Box Plot for the buccolingual (BL) diameters of the mandibular P4. The open circles indicate outliers for each of the comparative groups.

5.2.1.6 Mandibular First Molar (M_1) of the Palauan Specimens

The Palauan sample has the largest mean MD diameter of the mandibular first molar (see Table 67). Measurements taken on all individuals are normally distributed with some specimens falling outside of this distribution (see Figure 72). The Palauan specimens are the largest, with all specimens have measurement above the sample mean. The Aboriginal sample has the largest mean for the buccolingual diameter of the M_1 (see Table 67 & Figure 73). For BL diameter, there is overlap between the two small-bodied groups, as both Khoisan and Palauan populations have specimens that plot along the mean. However, the Palauan and Khoisan samples have differing means.

Table 67: Descriptive statistics for the measurements taken on the mandibular first molar. BL = buccolingual, MD = mesiodistal. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group		N	Min	Max	Mean	SD
Total for the comparative sample	**M1 MD**	**112**	**9.7**	**12.7**	**11.136**	**.5651**
	M1 BL	**392**	**9.1**	**13.6**	**10.819**	**.8781**
European	**M1 MD**	24	9.7	12.4	11.068	.6915
	M1 BL	90	9.1	11.9	10.288	.5286
KhoiSan	**M1 MD**	3	10.3	11.1	10.773	.4168
	M1 BL	4	10.2	10.8	10.555	.2866
Murray Valley Aboriginal	**M1 MD**	0				
	M1 BL	57	10.6	13.5	12.156	.6199
Northern Chinese	**M1 MD**	0				
	M1 BL	30	9.6	12.2	10.693	.5394
Palauan	**M1 MD**	11	11.2	13.6	12.350	.6834
	M1 BL	11	10.7	12.3	11.331	.5065
Swanport Aboriginal	**M1 MD**	0				
	M1 BL	25	11.0	13.6	12.092	.5979
Southern Chinese	**M1 MD**	0				
	M1 BL	105	9.4	12.0	10.487	.5577
Tswana	**M1 MD**	34	9.7	12.0	11.056	.5380
	M1 BL	34	9.7	11.5	10.395	.4908
Zulu	**M1 MD**	50	10.4	12.7	11.228	.5080
	M1 BL	47	9.2	11.9	10.691	.4772

Eleven specimens represent the Palauan sample. Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

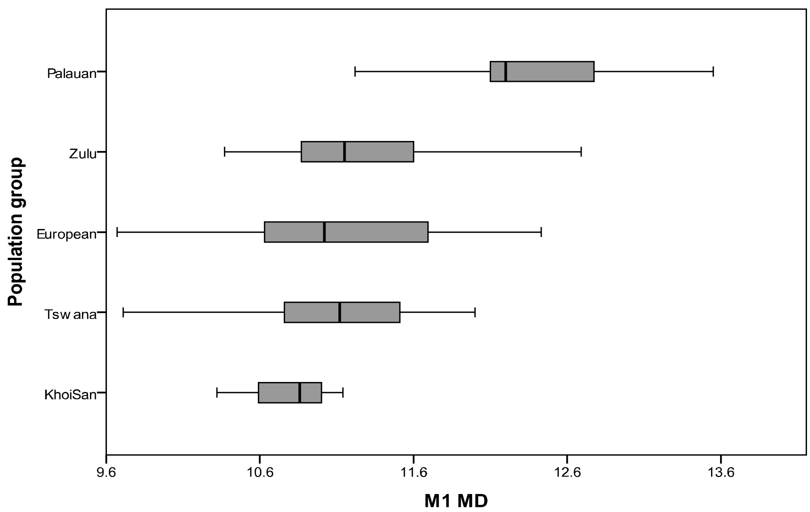

Figure 72: Box Plot for the mesiodistal (MD) diameters of the mandibular M1 (N= 123, mean = 11.26, SD 0.709).

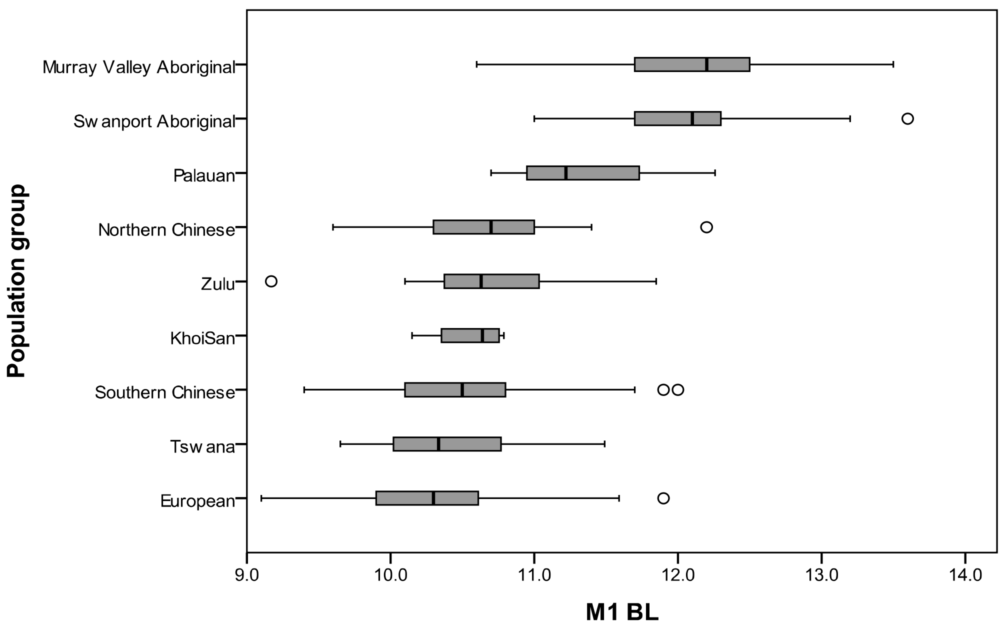

Figure 73: Box Plot for the buccolingual (BL) diameters of the mandibularM1. (N= 403, mean =10.8, SD = 0.87). The open circles indicate the outliers for each of the comparative sample groups.

5.2.1.7 Mandibular Second Molar (M_2) of the Palauan Specimens

For the second mandibular molar, the Palauan mean MD diameter was largest, while the Aboriginals have the largest mean BL diameter (Table 68). There is a large range (Figure 74) of values for the MD diameter of the M_2. Palauan specimens fall within this range, but all plot above the mean. Khoisan individuals all plot below the mean for MD diameter range (see Figure 74). The largest measurement BL measurement belongs to the Australian aboriginal sample, while the smallest BL diameters are for European and South Chinese (Figure 75).

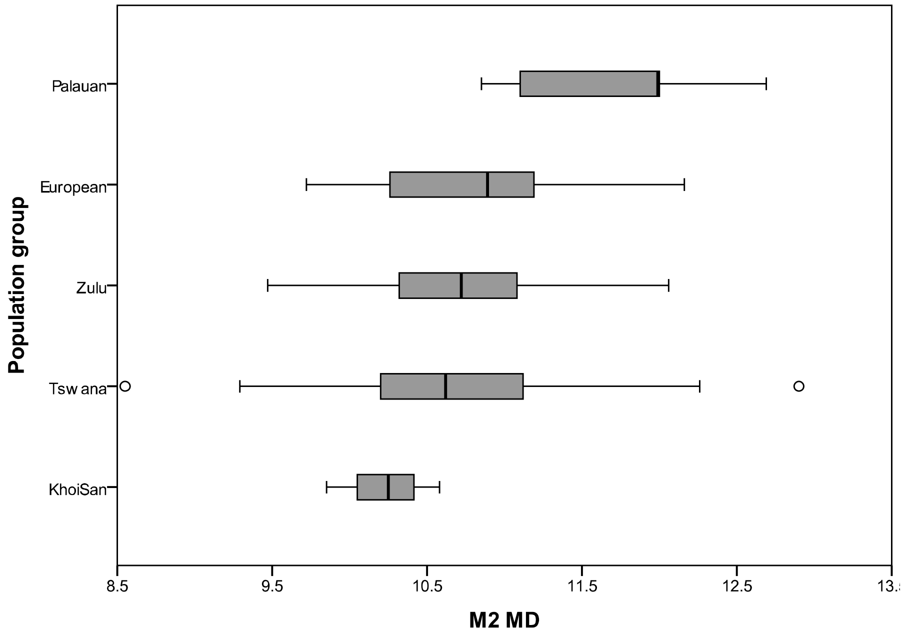

Figure 74: Boxplot showing of measurements taken on the comparative sample for the mesiodistal (MD) diameter of the mandibular M_2. The open circles indicate outliers for the comparative sample. (N = 133, SD = 0.755, mean = 10.75).

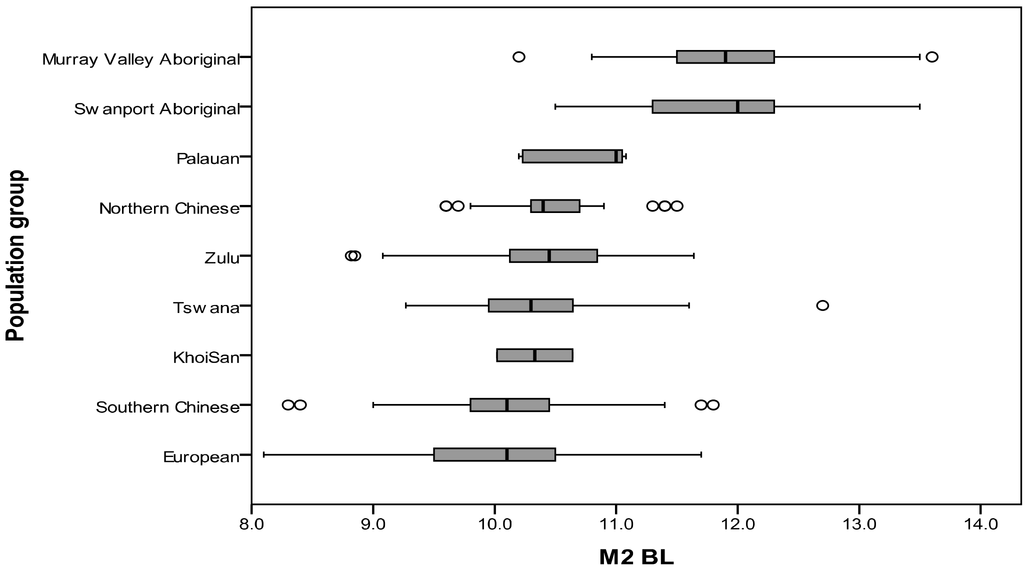

Figure 75: Boxplot showing the measurements taken on the comparative sample for the buccolingual (BL) diameter of the mandibular M2. The open circles indicate outliers for the comparative sample.

Table 68: Descriptive statistics for the measurements taken on the mandibular second molar. The mean, standard deviation (SD), minimum and maximum are given for each group. BL = buccolingual, MD = mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**M2 MD**	**128**	**8.6**	**12.9**	**10.712**	**.7321**
	M2 BL	**456**	**8.1**	**13.6**	**10.567**	**.9538**
European	**M2 MD**	21	9.7	12.2	10.858	.7351
	M2 BL	108	8.1	11.7	10.027	.6592
KhoiSan	**M2 MD**	3	9.9	10.6	10.227	.3656
	M2 BL	2	10.0	10.6	10.330	.4384
Murray Valley Aboriginal	**M2 MD**	0				
	M2 BL	66	10.2	13.6	11.912	.6763
Northern Chinese	**M2 MD**	0				
	M2 BL	33	9.6	11.5	10.473	.4752
Palauan	**M2 MD**	5	10.9	12.7	11.726	.7472
	M2 BL	5	10.2	11.1	10.712	.4547
Swanport Aboriginal	**M2 MD**	0				
	M2 BL	29	10.5	13.5	11.900	.7973
Southern Chinese	**M2 MD**	0				
	M2 BL	112	8.3	11.8	10.132	.6112
Tswana	**M2 MD**	47	8.6	12.9	10.621	.8271
	M2 BL	50	8.4	12.7	10.330	.6894
Zulu	**M2 MD**	56	9.5	12.1	10.748	.6544
	M2 BL	56	8.8	11.6	10.476	.6094

5.2.2 Results of the Maxillary Dentition of the Palauan Specimens

5.2.2.1 Maxillary First Incisor (I^1) of the Palauan Specimens

Palauan specimens do not have the largest mean for either MD or BL diameters, but Palauan measurements still sort at the upper end of the distribution (Table 69). There are no data from Khoisan individuals, as crania from which data were obtained were missing incisors. Both buccolingual and mesiodistal diameters of the maxillary first incisor do not differ significantly from a normal distribution (see Figure 76 & Figure 77).

Palauan individuals are distributed evenly amongst the comparative sample with Palauan individuals occurring on either side of the mean (see Figure 76). For BL diameter (see Figure 77), the Palauan specimens plot with larger specimens in the comparative sample on either side of the mean. The smallest BL diameters are those of European specimens. There

Palauan and Tswana group means are most similar for the MD diameter. For BL diameter, the Palauan mean is most similar to that of the Aboriginal (Swanport) sample.

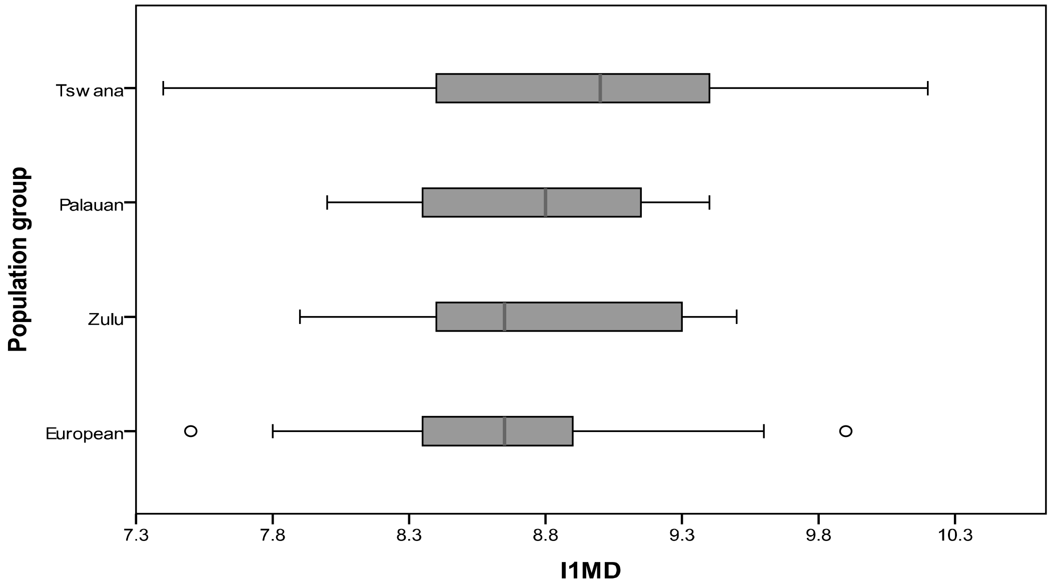

Figure 76: Boxplot showing the mesiodistal (MD) diameters of the maxillary first incisor. (N = 48 SD = 0.6051, mean= 8.775).

Table 69: Descriptive statistics for the measurements taken on the maxillary first incisor of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD = mesiodistal. Four specimens represent the Palauan sample.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**I1MD**	**48**	**7.4**	**10.2**	**8.775**	**.6051**
	I1BL	**327**	**2.6**	**9.2**	**6.934**	**1.2581**
European	I1MD	20	7.5	9.9	8.675	.5794
	I1BL	101	2.6	8.4	6.361	1.3160
Murray Valley Aboriginal	I1MD	0				
	I1BL	69	6.6	9.1	8.026	.4721
Northern Chinese	I1MD	0				
	I1BL	21	6.3	8.1	7.295	.4522
Palauan	I1MD	4	8.0	9.4	8.750	.5802
	I1BL	4	6.9	7.3	7.150	.1915
Swanport Aboriginal	I1MD	0				
	I1BL	19	7.3	9.2	8.032	.5628
Southern Chinese	I1MD	0				
	I1BL	84	5.9	8.5	7.145	.4798
Tswana	I1MD	18	7.4	10.2	8.922	.6744
	I1BL	21	3.6	7.3	5.233	.9651
Zulu	I1MD	10	7.9	9.5	8.710	.5238
	I1BL	12	3.1	6.2	4.592	.8939

Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

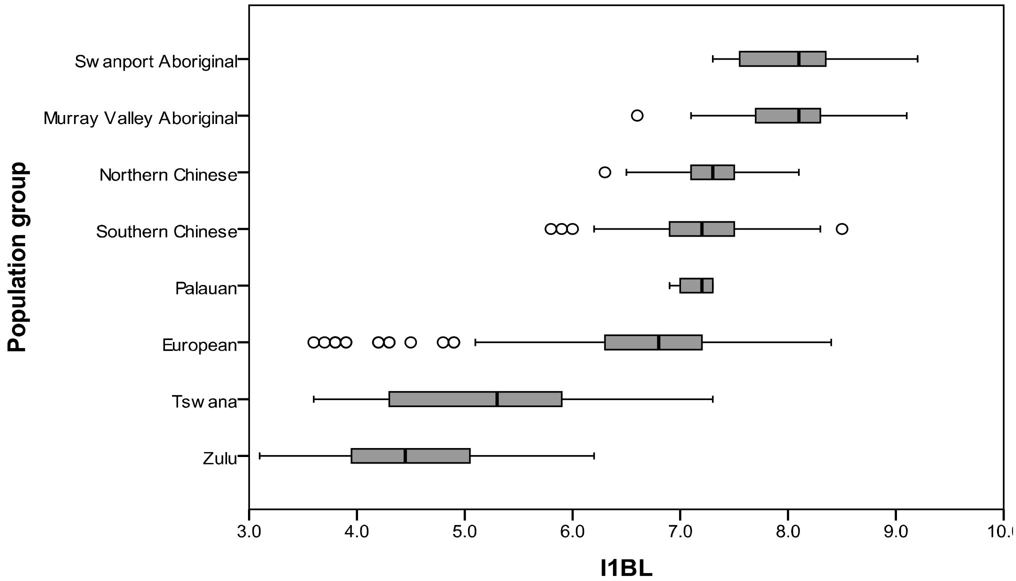

Figure 77: Boxplot showing data for the buccolingual (BL) diameter of the maxillary first incisor. (N = 327, mean = 6.934, SD = 1.2581). The open circles indicate the outliers of each of the represented groups.

5.2.2.2 *Maxillary Second Incisor (I^2) of the Palauan Specimens*

Table 70: Descriptive statistics for the measurements taken on the maxillary second incisor. The mean, standard deviation (SD), minimum and maximum are given for each group. BL = buccolingual, MD= mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**I2MD**	**87**	**5.6**	**8.3**	**6.807**	**.5744**
	I2BL	**397**	**2.6**	**8.4**	**6.132**	**1.0290**
European	I2MD	23	5.6	7.9	6.509	.6193
	I2BL	105	3.0	7.2	5.685	1.0055
KhoiSan	I2MD	2	6.2	6.7	6.450	.3536
	I2BL	3	4.4	5.8	5.100	.7000
Murray Valley Aboriginal	I2MD	0				
	I2BL	82	5.8	8.0	6.934	.4140
Northern Chinese	I2MD	0				
	I2BL	24	5.9	7.4	6.654	.4672
Palauan	I2MD	10	6.4	8.3	7.350	.6964
	I2BL	10	5.6	8.6	6.750	.9034
Swanport Aboriginal	I2MD	0				
	I2BL	34	5.8	8.4	7.009	.6388
Southern Chinese	I2MD	0				
	I2BL	84	5.3	7.2	6.394	.4465
Tswana	I2MD	29	6.1	8.3	6.990	.5274
	I2BL	32	3.2	7.1	4.931	.8899
Zulu	I2MD	33	5.8	8.0	6.876	.5184
	I2BL	33	2.6	6.8	4.870	.8935
Ten specimens represent the Palauan sample. Data for the Zulu, European, Khoisan, and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).						

For MD and BL diameter of the maxillary second incisor (see Table 70), the Palauan sample has the largest mean MD diameter, while Aboriginals groups have the largest mean BL diameter. The maximum measurement for BL diameter of the Palauan sample is 8.6, which is larger than any similar measure in the entire comparative sample. The means for the MD diameter between the Palauan and Khoisan are similar (Figure 79). Three Palauan individuals plot below the mean MD diameters. The Palauan specimens have the largest recorded BL diameter for the I^2, and all specimens plot above the mean of the comparative sample (see Table 70). The most similarity for the I^2BL is between the Palauan and the Southern Chinese mean (Figure 80).

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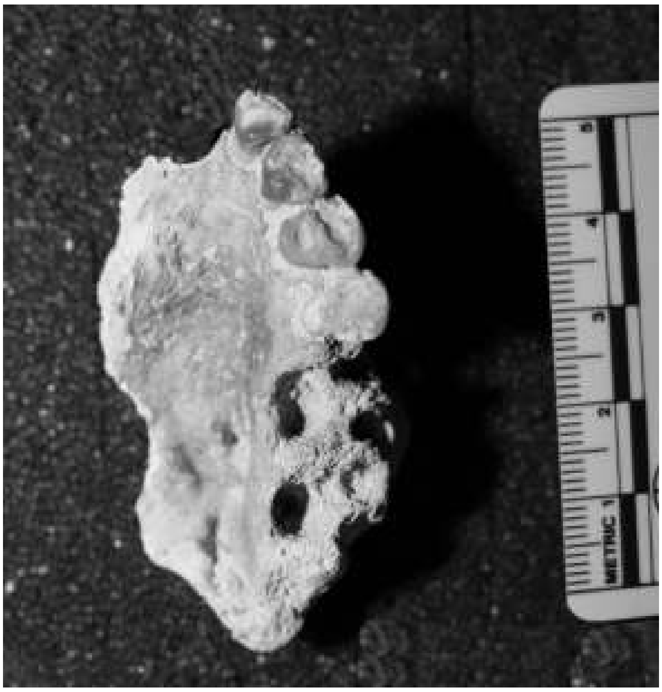


Figure 78: Photo of B: OR-15:18-051, a left partial maxilla with I^1, C, P^3 and P^4. This tooth has a high degree of wear [i.e., stage 3 as per the scale provided by Molnar (1971)]. Picture by: L.R. Berger.

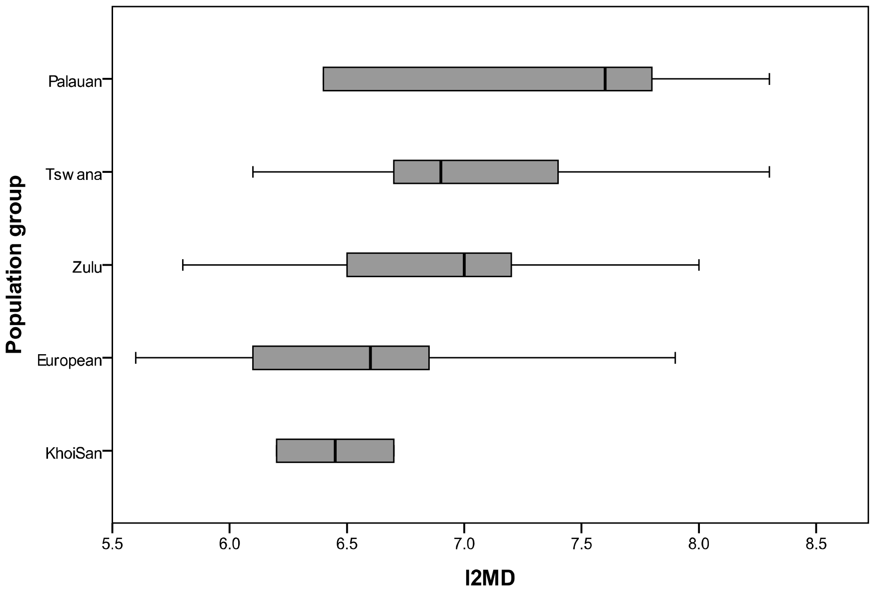


Figure 79: Boxplot showing the distribution for the mesiodistal (MD) diameter of the maxillary second incisor. (N = 87, SD 0.605, mean= 6.86).

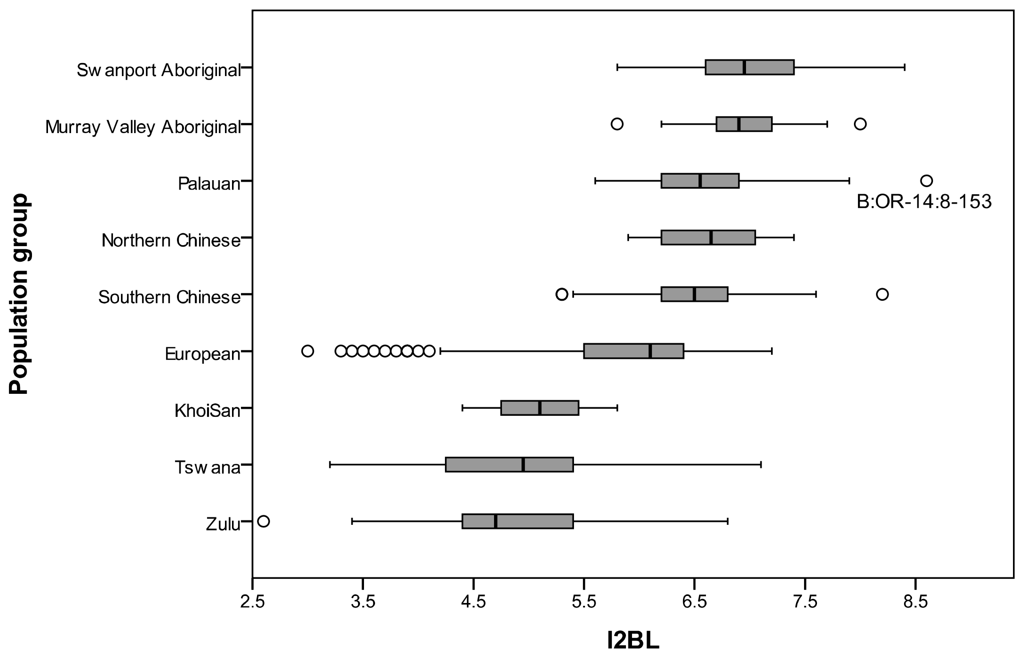


Figure 80: Boxplot for the buccolingual (BL) diameter of the maxillary second incisor (N = 397 mean = 6.132 SD =1.0290). For the Palauan group B:OR -14:8-153 is a large measurement.

5.2.2.3 Maxillary Canine (C) of the Palauan Specimens

For the maxillary canine (Table 71), Palauan specimens have the largest mean MD diameter and the Aboriginal groups have the largest mean BL diameter. For MD diameter of the canine, Palauan specimens all plot above the comparative sample mean (see Table 71 & Figure 81) and are significantly different from the comparative sample means. While a similar normal distribution is seen for BL diameter (see Figure 82), Palauan specimens plot above and below the mean of the comparative sample. For the BL diameter, the Southern Chinese and Palauan measurements are most similar.

Table 71: Descriptive statistics for the measurements taken on the maxillary canine. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD = mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	CMD	155	6.0	9.0	7.548	.5299
	CBL	483	4.9	11.2	8.126	1.1071
European	CMD	39	6.8	8.5	7.562	.4121
	CBL	123	4.9	9.9	7.533	1.0712
KhoiSan	CMD	5	6.0	7.9	6.780	.7497
	CBL	5	6.4	8.6	7.480	.8319
Murray Valley Aboriginal	CMD	0				
	CBL	82	7.7	11.2	9.248	.7184
Northern Chinese	CMD	0				
	CBL	28	7.6	9.6	8.661	.5500
Palauan	CMD	9	7.5	9.4	8.556	.6267
	CBL	8	7.2	10.0	8.425	.9377
Swanport Aboriginal	CMD	0				
	CBL	39	8.0	10.6	9.118	.6261
Southern Chinese	CMD	0				
	CBL	93	6.5	10.0	8.237	.6934
Tswana	CMD	49	6.1	8.3	7.516	.5313
	CBL	49	5.6	9.0	7.449	.7185
Zulu	CMD	61	6.6	9.0	7.646	.5214
	CBL	63	5.1	9.7	7.438	.9464

Nine specimens represent the Palauan sample. Data for the European, Khoisan, Zulu and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

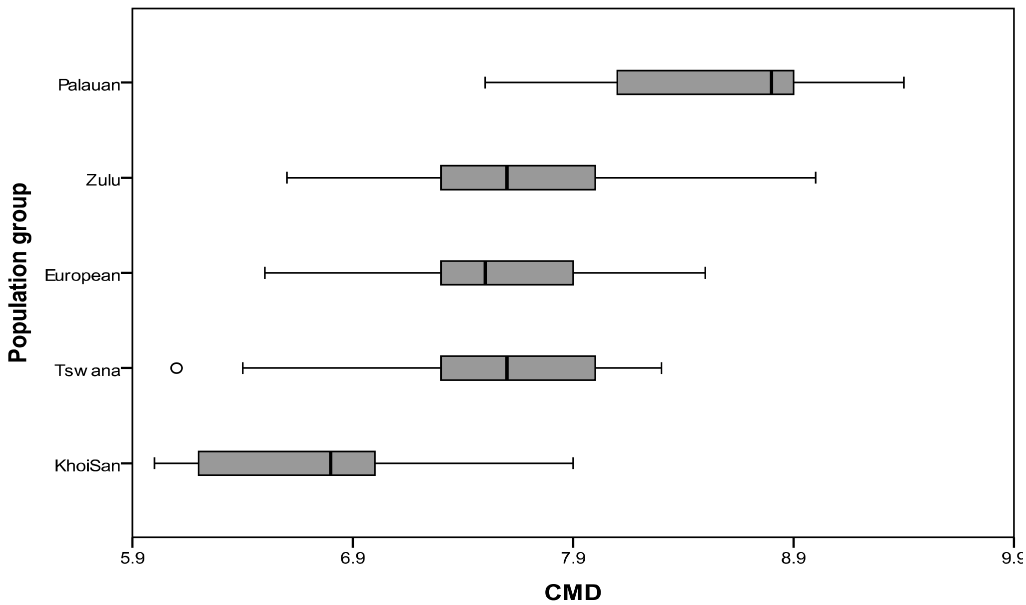


Figure 81: Boxplot showing the distribution for the mesiodistal (MD) diameter of the maxillary canine. (N = 164, SD = 0.561, mean =7.6). The open circles indicate outliers for the comparative sample.

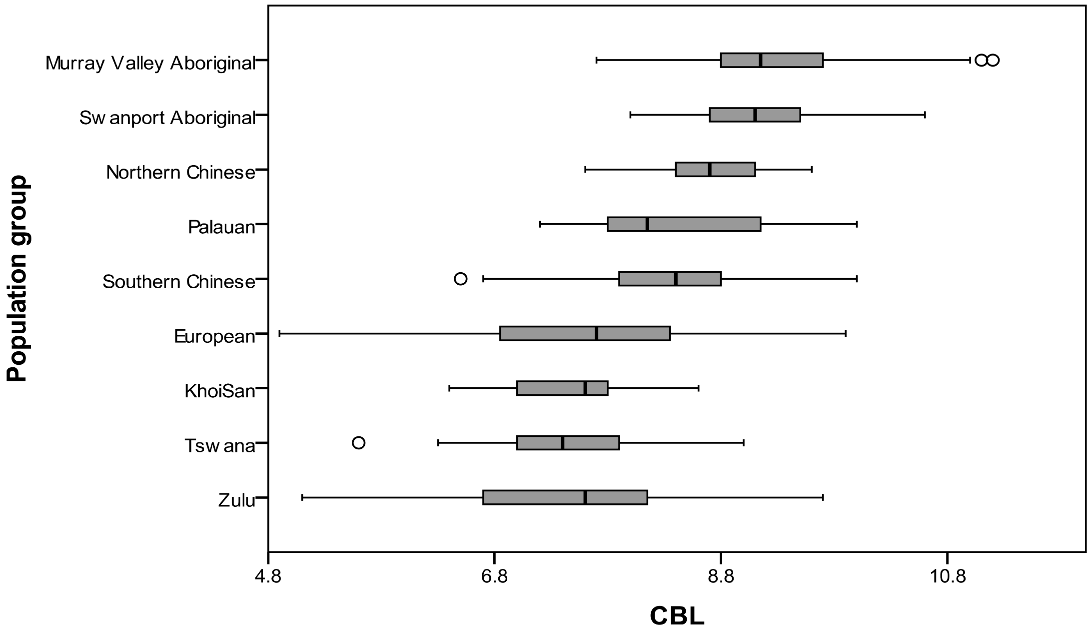


Figure 82: a) Boxplot showing the distribution for the buccolingual (BL) diameter of the maxillary canine. (N = 483 mean = 8.12, SD = 1.1071). The open circles indicate outliers in the comparative sample.

5.2.2.4 Maxillary Third premolar (P^3) of the Palauan Specimens

Palauan specimens have the largest mean MD diameter of the first maxillary premolar, while the largest BL diameter belongs to Aboriginal groups (Table 72. The Palauan specimens all plot above the comparative sample mean for both MD and BL diameter (Figure 83 & 84). The BL diameter mean, of the Palauan group and Southern Chinese groups are the most similar in their plots.

Table 72: Descriptive statistics for the measurements taken on the maxillary third premolar. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= Buccolingual, MD= mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**P3MD**	**157**	**5.4**	**8.4**	**7.000**	**.5128**
	P3BL	**453**	**6.1**	**12.1**	**9.468**	**.8532**
European	P3MD	36	5.6	7.8	6.842	.5369
	P3BL	97	7.1	10.3	8.754	.6502
KhoiSan	P3MD	4	5.4	7.7	6.575	.9430
	P3BL	4	7.9	10.0	8.900	.8602
Murray Valley Aboriginal	P3MD	0				
	P3BL	79	8.4	12.0	10.366	.6459
Northern Chinese	P3MD	0				
	P3BL	33	8.3	11.0	9.573	.5479
Palauan	P3MD	6	7.2	7.9	7.550	.2588
	P3BL	5	9.2	10.3	9.660	.4393
Swanport Aboriginal	P3MD	0				
	P3BL	34	8.7	12.1	10.37	.701
Southern Chinese	P3MD	0				
	P3BL	89	8.1	10.9	9.431	.5491
Tswana	P3MD	45	6.0	8.4	7.011	.4448
	P3BL	46	7.6	10.4	9.187	.4593
Zulu	P3MD	72	5.8	8.2	7.096	.4932
	P3BL	70	8.0	11.0	9.269	.6747
Six specimens represent the Palauan sample. Data for the European, Khoisan, Zulu and Tswana were collected by the Mirriam Tawane (2012) and data for the European (BL), Southern Chinese and Aboriginal group obtained from Brown (2001).						

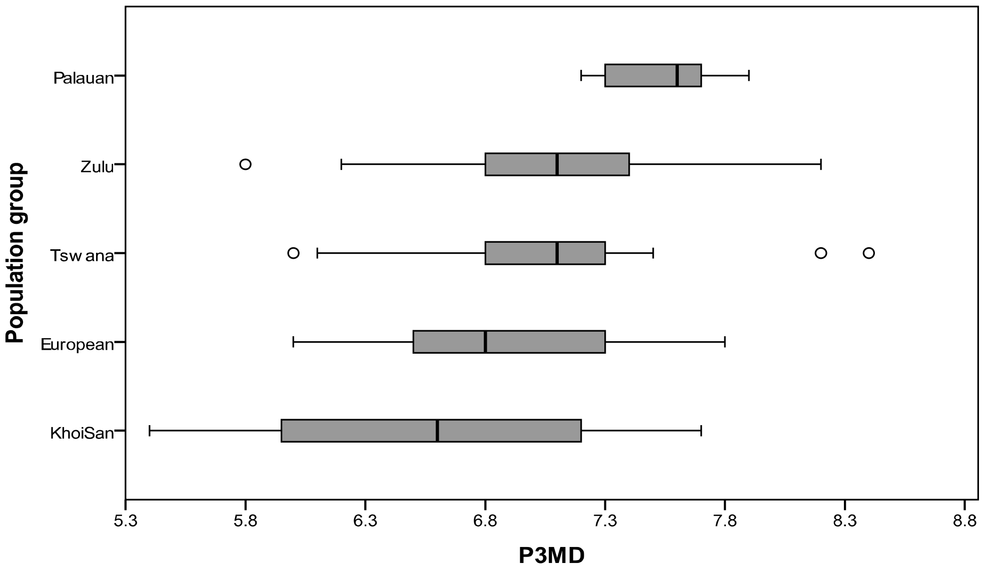


Figure 83: Boxplot showing the distribution for the buccolingual (BL) diameter of the maxillary third premolar. (N=183, SD 0.517, mean 7.01). The open circles indicate the outliers for the comparative sample.

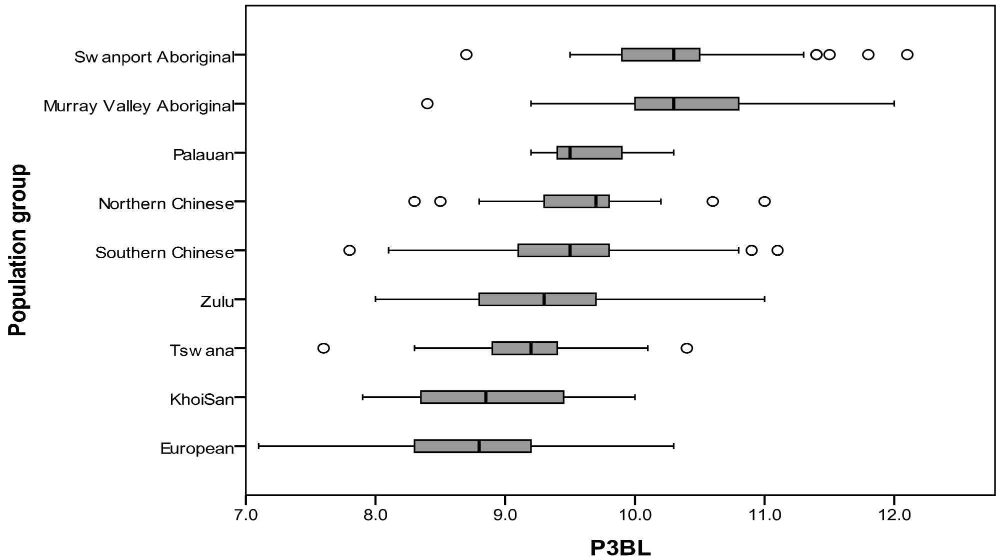


Figure 84: Boxplot showing the distribution for the buccolingual (BL) diameter of the maxillary third premolar. (N 453, SD = 0.8532, mean = 453). The open circles indicate outliers for the comparative sample.

5.2.2.5 Maxillary Fourth Premolar (P^4) of the Palauan Specimens

For the maxillary fourth premolar (see Table 73), Palauan specimens have the largest mean for mesiodistal diameter, while Aboriginal specimens have the largest mean buccolingual diameter. There is a clear separation between large Palauan specimen MD diameters (see Figure 85) and those of the comparative sample. This is not present for BL diameter (Figure 86), as Palauan specimens all plot around the mean of the comparative sample. For the BL diameter between the Murray Valley Aboriginals and the Palauan sample have the most similar mean plots.

Table 73: Descriptive statistics for the measurements taken on the maxillary fourth premolar. The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD= mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**P4MD**	**166**	**4.8**	**8.1**	**6.760**	**.4969**
	P4BL	**511**	**5.8**	**12.4**	**9.424**	**.8245**
European	P4MD	37	5.8	7.6	6.800	.4466
	P4BL	120	7.4	10.5	8.963	.5770
KhoiSan	P4MD	5	4.8	7.0	6.120	.8526
	P4BL	5	7.7	10.2	8.840	.9864
Murray Valley Aboriginal	P4MD	0				
	P4BL	90	9.1	12.4	10.283	.6535
Northern Chinese	P4MD	0				
	P4BL	32	7.3	10.6	9.500	.6185
Palauan	P4MD	5	7.2	8.3	7.600	.5148
	P4BL	4	9.2	10.1	9.825	.4272
Swanport Aboriginal	P4MD	0				
	P4BL	46	6.5	12.3	10.039	.9625
Southern Chinese	P4MD	0				
	P4BL	93	7.3	10.4	9.194	.6232
Tswana	P4MD	53	5.7	7.9	6.734	.4771
	P4BL	55	8.3	10.2	9.195	.4680
Zulu	P4MD	71	5.8	8.1	6.803	.4861
	P4BL	69	7.4	10.8	9.249	.6617
Five specimens represent the Palauan sample. Data for the European, Khoisan, Zulu and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).						

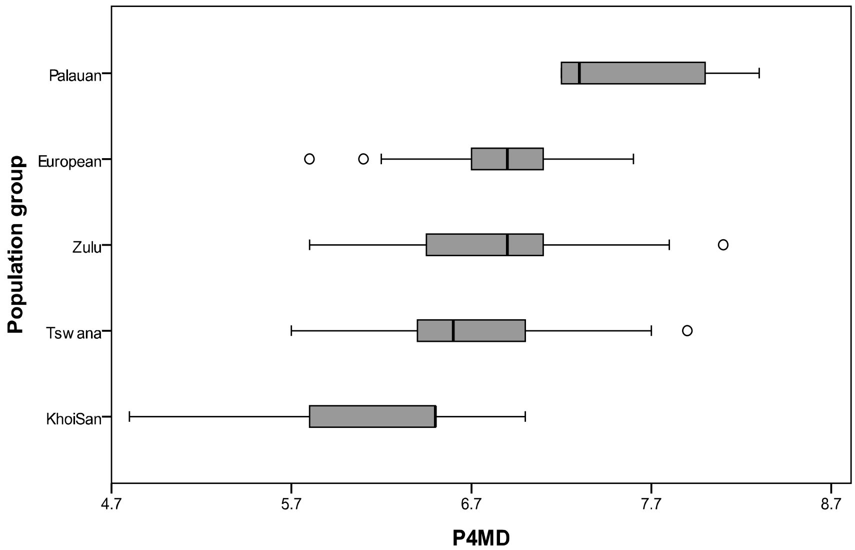


Figure 85: Boxplot showing the distribution for the mesiodistal (MD) diameter of the maxillary fourth premolar. (N=170, SD = 0.517 mean = 6.78). The open circles indicate the outliers for the comparative sample.

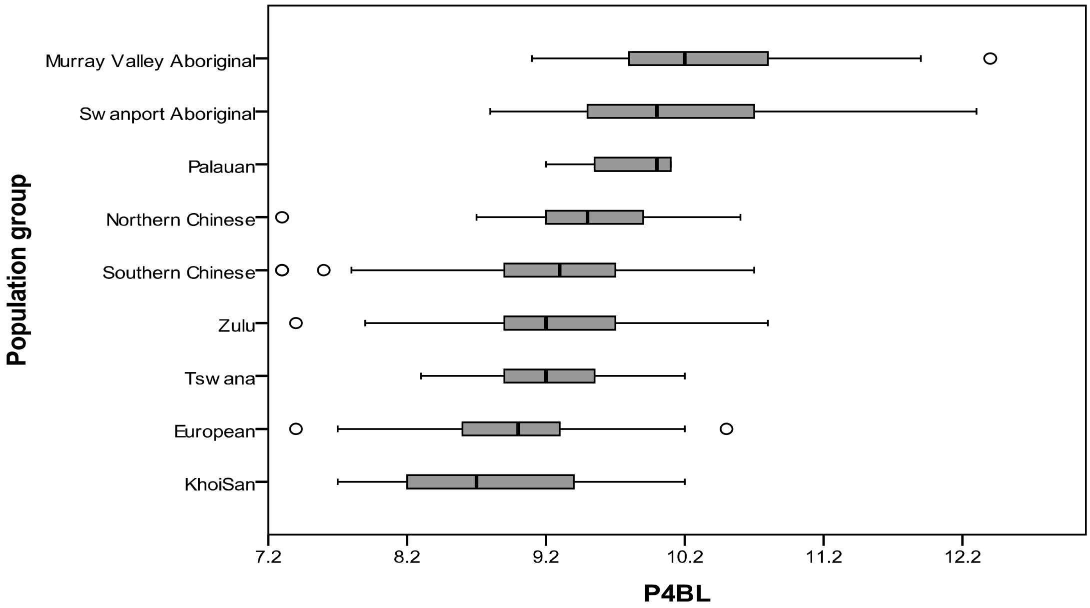


Figure 86: Boxplot showing the distribution for the buccolingual diameter of the maxillary fourth premolar. (N = 511, SD =0.824 mean = 9.42). The open circles indicate the outliers for the comparative sample.

5.2.2.6 Maxillary First Molar (M^1) of the Palauan Specimens

For the MD diameter of the first maxillary molar (Table 74) the Palauan specimens have the largest mean for the MD diameter, the Aboriginal specimens have the largest BL diameter mean. The Palauan specimens all plot within the range of the comparative sample (Figure 87).

The BL diameters have a normal distribution and while Palauan samples do not have the largest z-scores, do plot with those of the Aboriginal groups measured (Figure 88). For the first molar the Palauan specimens are large and plot with the larger toothed samples in the comparative group. The Palauans have a similar mean for the MD diameter to the Tswana group.

Table 74: Descriptive statistics for the measurements taken on the maxillary first molar.The mean, standard deviation (SD), minimum and maximum are given for each group. BL= buccolingual, MD = mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**M1MD**	**167**	**9.1**	**12.9**	**10.67**	**.708**
	M1BL	**500**	**8.4**	**14.7**	**11.54**	**1.05**
European	M1MD	40	9.1	12.3	10.70	.673
	M1BL	119	8.5	12.7	11.06	.718
KhoiSan	M1MD	6	9.3	11.1	10.13	.723
	M1BL	6	9.4	11.6	10.71	.798
Murray Valley Aboriginal	M1MD	0				
	M1BL	82	11.4	14.7	12.96	.625
Northern Chinese	M1MD	0				
	M1BL	31	10.7	13.1	11.55	.593
Palauan	M1MD	5	10.1	12.6	11.44	1.07
	M1BL	5	11.1	13.4	12.62	.973
Swanport Aboriginal	M1MD	0				
	M1BL	43	11.5	14.5	12.83	.693
Southern Chinese	M1MD	0				
	M1BL	94	9.3	12.7	11.25	.581
Tswana	M1MD	50	9.1	12.9	10.7	.870
	M1BL	53	8.4	12.0	10.69	.697
Zulu	M1MD	70	9.3	12.0	10.61	.578
	M1BL	71	9.7	12.8	11.06	.67

Five specimens represent the Palauan sample. Data for the Zulu, Khoisan, European and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

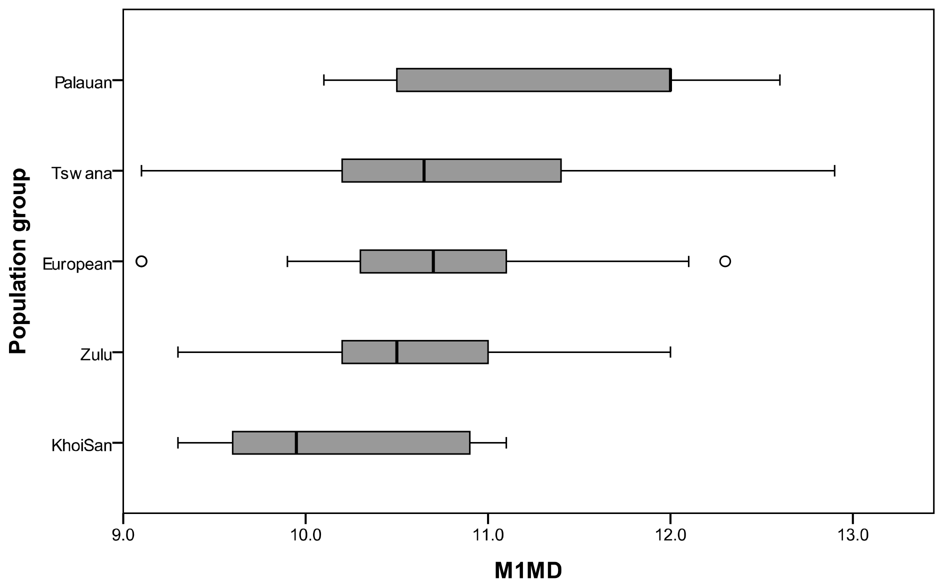


Figure 87: Boxplot showing the distribution for the mesiodistal (MD) diameter of the maxillary first molar. (N = 172, SD 0.73, mean = 10.7). The open circles indicate outliers for each of the comparative groups.

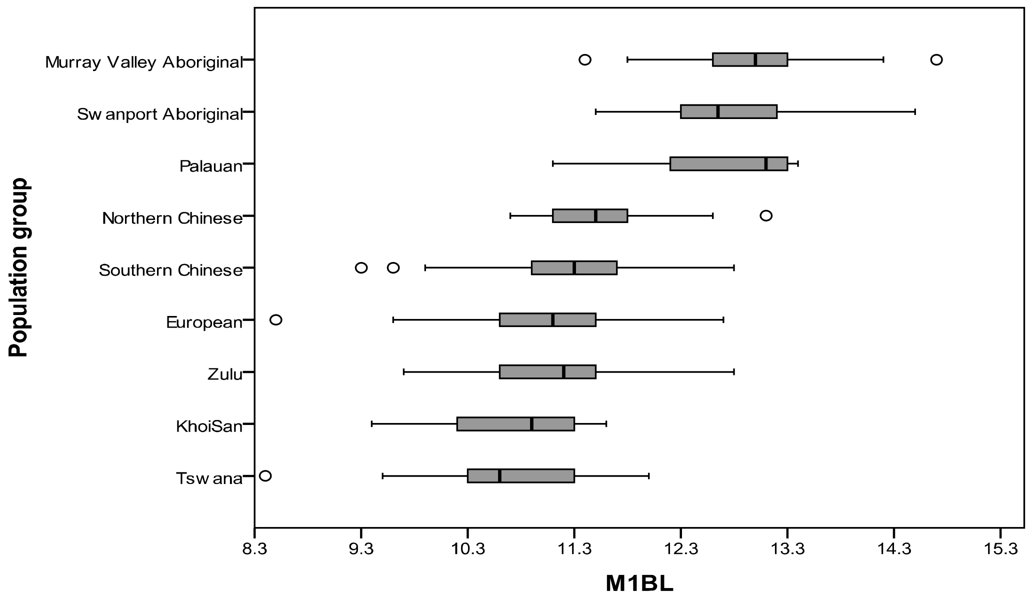


Figure 88: Boxplot showing the distribution for the buccolingual (BL) diameter of the maxillary first molar. (N = 500, SD = 1.05, mean = 11.548). The open circles indicate outliers for the comparative groups.

5.2.2.7 Maxillary Second Molar (M^2) of the Palauan Specimens

For the maxillary second molar (Table 75), Palauan specimens have the largest mean MD diameter, while Aboriginal specimens have the largest mean BL diameter. For both MD and BL diameters, Palauan specimens fall within the range of the comparative sample with individuals plotting nearer the upper end of the comparative range (see Figure 89 & Figure 90). Palauans have a similar mean for the MD diameter with the Tswana group. For the BL diameter, the Swanport Aboriginals and the Palauans have the most similar mean plots.

Table 75: Descriptive statistics for the measurements taken on the maxillary second molar. The mean, standard deviation (SD), minimum and maximum are given for each group. BL = buccolingual, MD = mesiodistal.

Population group		N	Min	Max	Mean	SD
Total for the comparative sample	**M2MD**	**145**	**7.6**	**12.5**	**10.077**	**.8371**
	M2BL	**500**	**9.1**	**16.2**	**11.812**	**1.2335**
European	M2MD	36	7.6	11.4	9.836	.9314
	M2BL	125	9.2	13.1	11.090	.7530
KhoiSan	M2MD	3	8.7	9.9	9.433	.6429
	M2BL	3	10.6	11.5	11.133	.4726
Murray Valley Aboriginal	M2MD	0				
	M2BL	90	11.5	15.7	13.468	.7722
Northern Chinese	M2MD	0				
	M2BL	33	10.9	12.7	11.721	.5171
Palauan	M2MD	5	8.8	11.7	10.400	1.1068
	M2BL	5	10.9	13.5	12.280	1.1009
Swanport Aboriginal	M2MD	0				
	M2BL	50	11.7	16.2	13.194	.9296
Southern Chinese	M2MD	0				
	M2BL	92	9.1	12.9	11.265	.7084
Tswana	M2MD	39	8.3	12.5	10.197	.9063
	M2BL	40	9.7	12.9	11.040	.7117
Zulu	M2MD	67	8.5	12.0	10.166	.7185
	M2BL	67	9.5	12.7	11.188	.7042
Five specimens represent the Palauan sample. Data for the European, Khoisan, Zulu and Tswana were collected by the Mirriam Tawane (2012) and data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).						

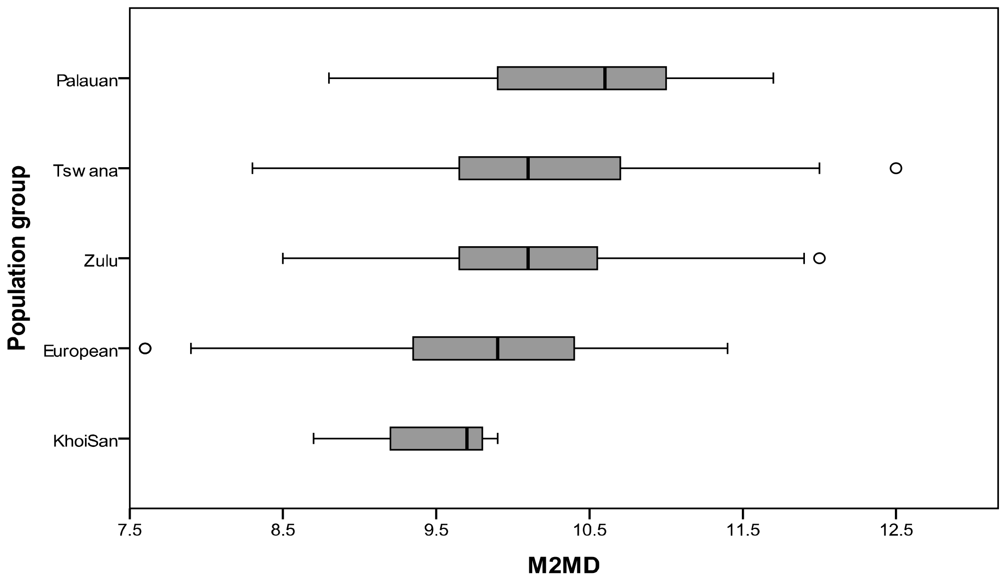


Figure 89: Boxplot showing the distribution for the mesiodistal (MD) diameter of the maxillary second molar. (N= 150, SD = 0.848, mean = 10.08) The open circles indicate the outliers for each of the comparative groups.

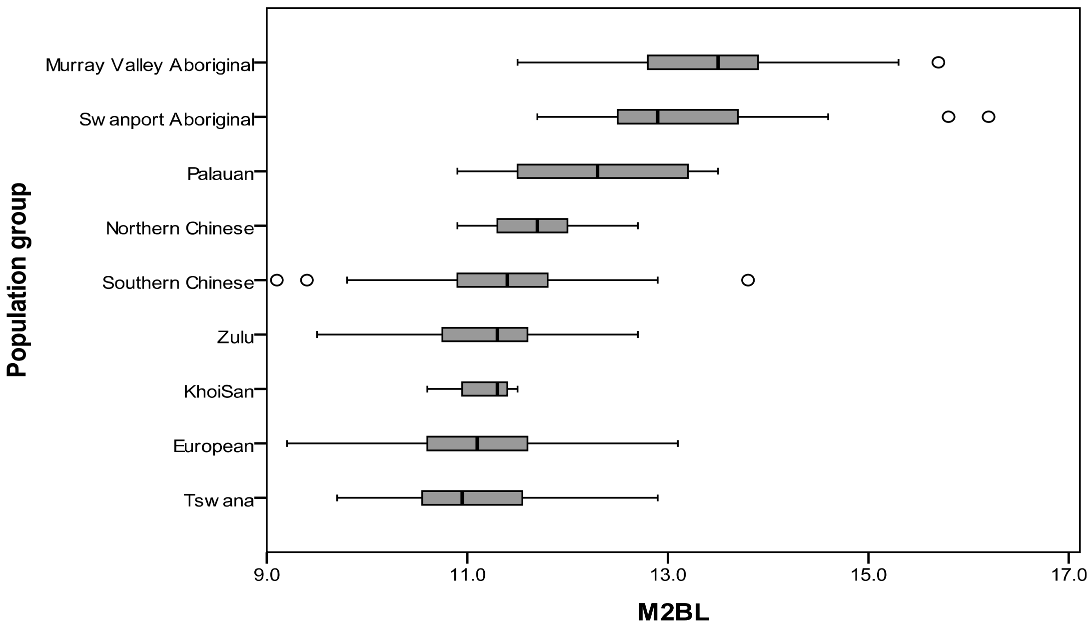


Figure 90: Boxplot showing data for the buccolingual (BL) diameter of the maxillary second molar. (N =500, SD = 1.2335, mean = 11.812). The open circles indicate outliers for the comparative group.

5.2.3 Results of the Cervico-enamel Junction of the Palauan Specimens

5.2.3.1 Mandibular Dentition Cervico-enamel- Junction of the Palauan Specimens

Where possible, cervico-enamel-junction (CEJ) of each tooth was measured, in both buccolingual as well as mesiodistal planes. The CEJ is defined as the junction between the cervical border of the tooth (i.e., the point between the root and the crown) and the start of the enamel cap (see Chapter 2,Table 15). Details on specimens used are outlined in Chapter 2 (see Table 10). Overall, means calculated for the Palauan sample are smaller at the CEJ; with the exception of some of the CEJ (MD) diameters (I_1, C, M_1, and M_2) (see Table 76). For the mandibular P_3, bivariate MD plots are very scattered, with no group plotting outside the comparative sample (see Figure 91), including Palauan specimens. This is not the case for BL diameters (see Figure 92) where BL diameters of the Palauan specimens are much larger than their associated CEJ. Palauans cluster outside of the range of the comparative sample. A similar trend is visible in the P_4 scattered MD plots (see Figure 93), but BL diameters for the Palauan samples are again smaller than those of the comparative sample. For third and fourth premolars, the Palauan sample clusters in a similar fashion.

For the mandibular first and second molar dimensions, (see Figure 94 & Figure 96), MD bivariate plots are scattered, with no groups plotting outside the comparative sample. For the BL bivariate plot (Figure 95 & Figure 97), Palauan samples have large BL diameters when compared to the associated CEJ diameters, which are small. The Palauan sample fall outside of the normal distribution of the comparative sample.

Palauans cluster in a similar fashion. For mandibular dentition, the trend is to have a smaller cervico-enamel junction and a large crown.

Table 76: Descriptive statistics for the cervico-enamel junction (CEJ) measurements taken on the mandibular dentition of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given as a mean for the comparative sample.

	Cervico-enamel junction	N	Min	Max	Mean	SD
Comparative Sample Total	I1CEJ(MD)	105	2.9	4.7	3.768	.3665
	I1 CEJ(BL)	105	4.5	6.7	5.758	.3971
	I2 CEJ(MD)	131	3.0	5.6	4.200	.4412
	I2 CEJ(BL)	135	4.1	7.9	6.155	.4789
	C CEJ(MD)	175	4.5	7.3	5.669	.5328
	C CEJ(BL)	179	6.1	9.4	7.732	.6188
	P3 CEJ(MD)	205	3.7	8.3	5.578	.5761
	P3 CEJ(BL)	211	6.1	9.2	7.873	.5817
	P4 CEJ(MD)	159	4.5	9.7	5.726	.8306
	P4 CEJ(BL)	168	6.5	12.1	8.362	.7430
	M1 CEJ(MD)	124	7.6	11.4	9.340	.6896
	M1 CEJ(BL)	118	8.7	12.0	10.441	.6396
	M2 CEJ(MD)	140	7.3	11.5	9.637	.7387
	M2 CEJ(BL)	140	8.8	12.7	10.396	.6369
Palauan Specimens	I1CEJ(MD)	5	4	4	4.00	.158
	I1 CEJ(BL)	5	6	7	6.06	.378
	I2 CEJ(MD)	5	4	4	3.92	.148
	I2 CEJ(BL)	5	5	7	6.10	.436
	C CEJ(MD)	3	6	7	6.17	.379
	C CEJ(BL)	3	8	8	8.07	.153
	P3 CEJ(MD)	8	5	5	5.23	.255
	P3 CEJ(BL)	8	7	8	7.41	.402
	P4 CEJ(MD)	2	5	5	5.25	.212
	P4 CEJ(BL)	2	7	7	6.75	.354
	M1 CEJ(MD)	**7**	**8**	11	9.84	.925
	M1 CEJ(BL)	**7**	**9**	11	9.96	.892
	M2 CEJ(MD)	**5**	**9**	11	9.78	.753
	M2 CEJ(BL)	**5**	**9**	10	9.18	.277
Data for the Zulu, European, Tswana and Khoisan was collected by Mirriam Tawane (2012).						

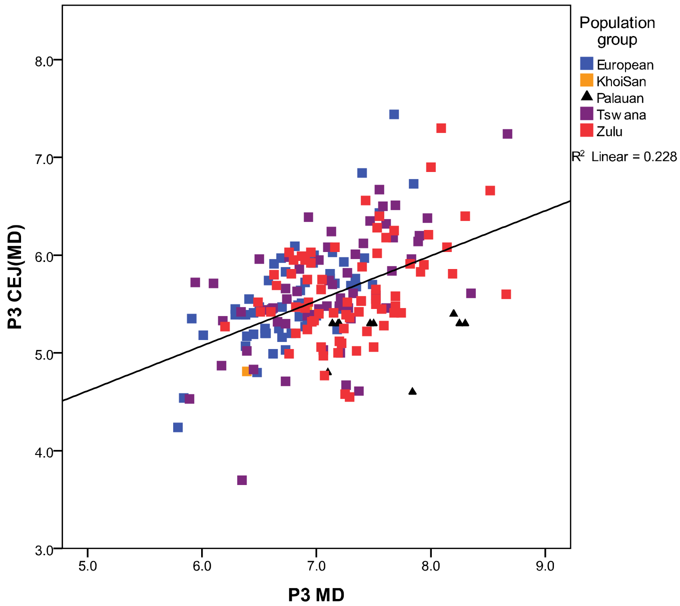


Figure 91: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD of the crown) diameter of the mandibular third premolar. (For sample size, please see Table 76. The line shown in the diagram represents a linear regression.

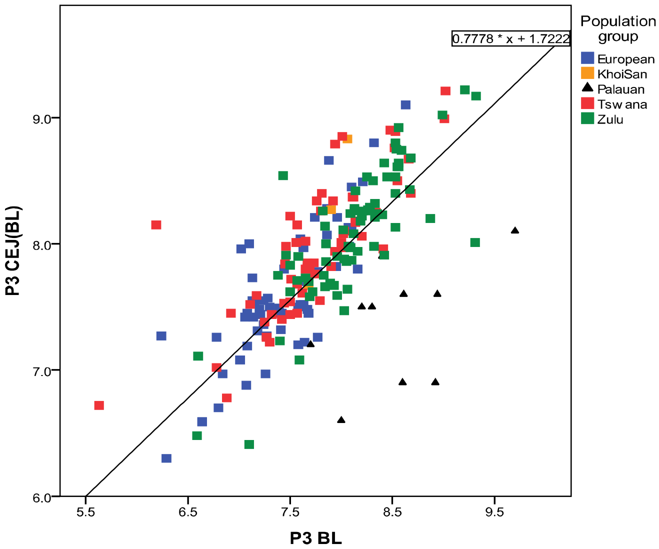


Figure 92: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the mandibular third premolar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.502.

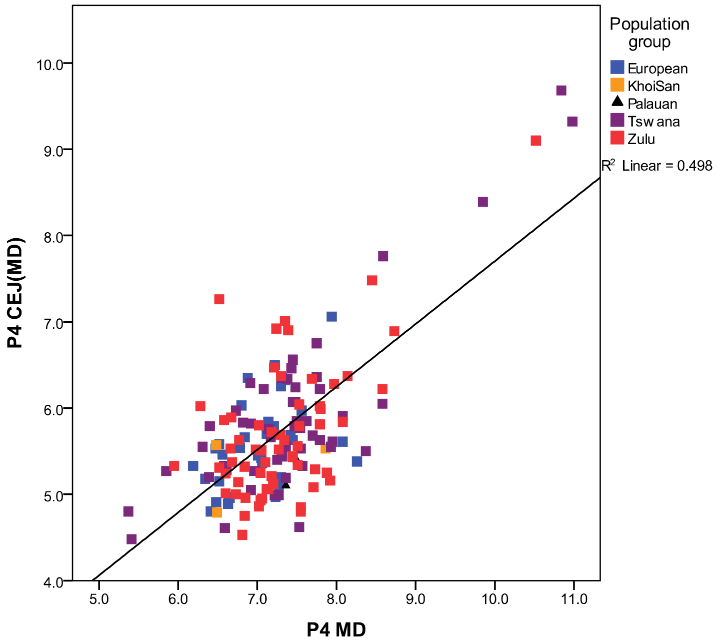


Figure 93: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the mandibular fourth premolar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.498.

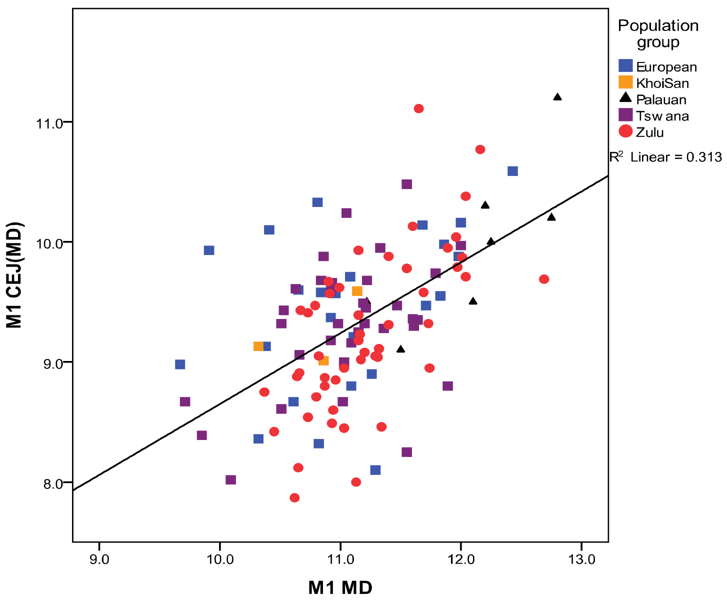


Figure 94 Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the mandibular first molar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.313.

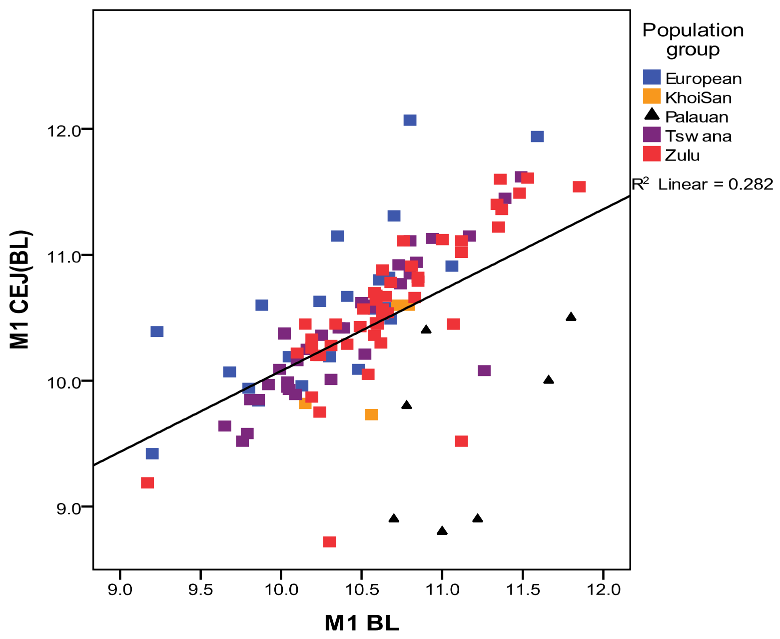


Figure 95: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the mandibular first molar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.282.

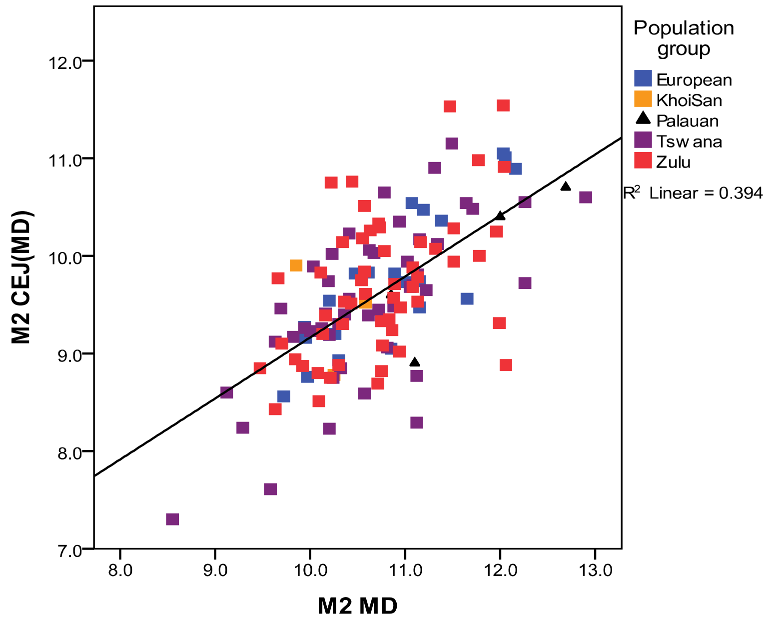


Figure 96: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the mandibular second molar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.394.

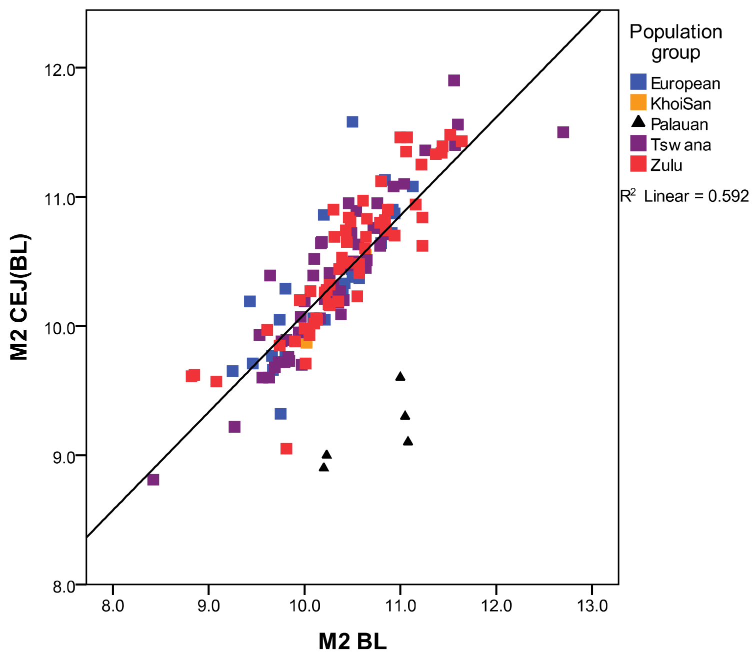


Figure 97: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the mandibular second molar. (For sample size, please see Table 76). The line shown in the diagram represents a linear regression R^2= 0.592.

5.2.3.2 Maxillary Dentition: Cervico-Enamel Junction of the Palauan Specimens

Third premolar and fourth premolar mesiodistal (MD) bivariate plots (Figure 98 & Figure 100) show that Palauan specimens are not larger than the comparative sample as discussed earlier (section 5.2.2.4 & 5.2.2.5). No groups cluster outside the comparative sample. In buccolingual (BL) dimensions, however, for P^3 the associated cervico-enamel junction (CEJ) is again smaller than that of the comparative sample and Palauans cluster outside the range of the comparative sample (see Figure 99). A single Palauan specimen falls only slightly outside of the range for the P^4, BL bivariate plots.

For the first and second maxillary molar, MD bivariate plots are again scattered with no groups clustering outside the comparative sample (Figure 102 & Figure 104). Palauan samples have both large BL and CEJ (BL) diameters for molars (see Figure 103 & Figure 105), and plot along the straight line for the comparative sample. A single M^2 specimen, B:

OR-15:18-077, plots in a similar fashion to the mandibular measurements, which are outliers. The maxillary measurements do not trend in the same fashion as the mandibular teeth.

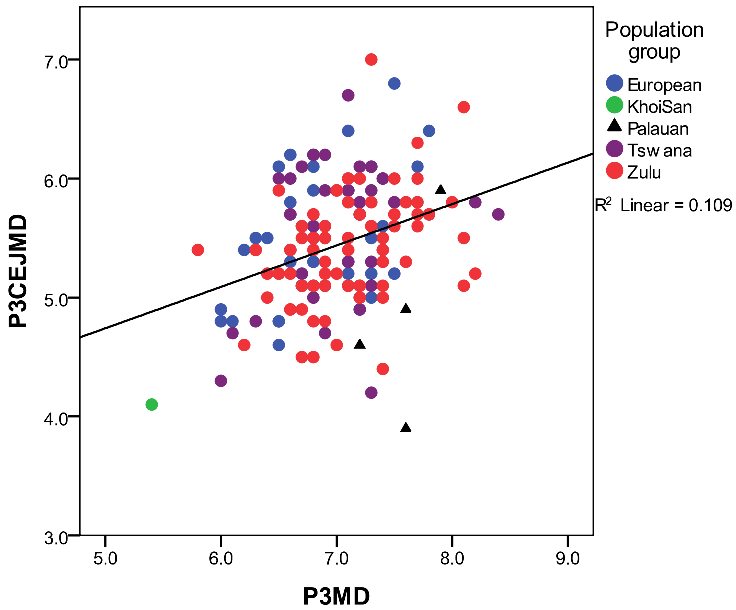


Figure 98: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the maxillary third premolar. (For sample size, please see Table 76).

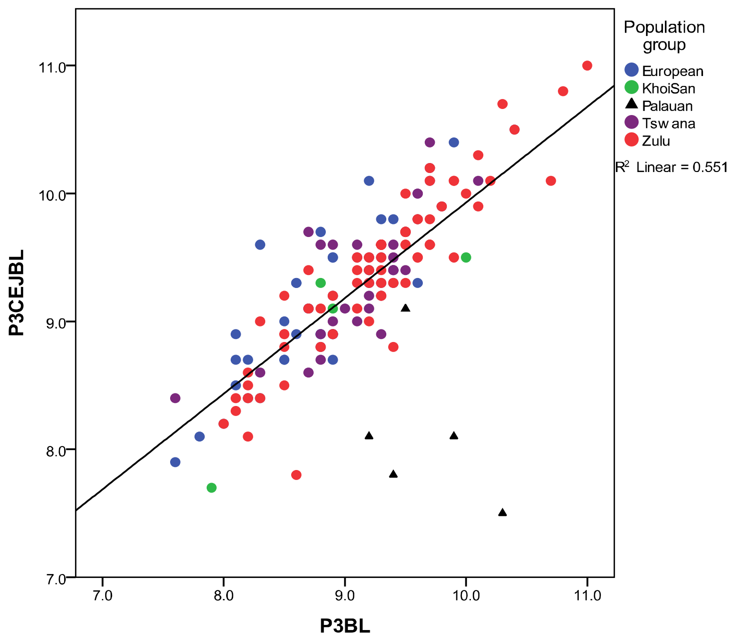


Figure 99: Bivariate plot of the buccolingual cervico- enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the maxillary fourth premolar. (For sample size, please see Table 76).

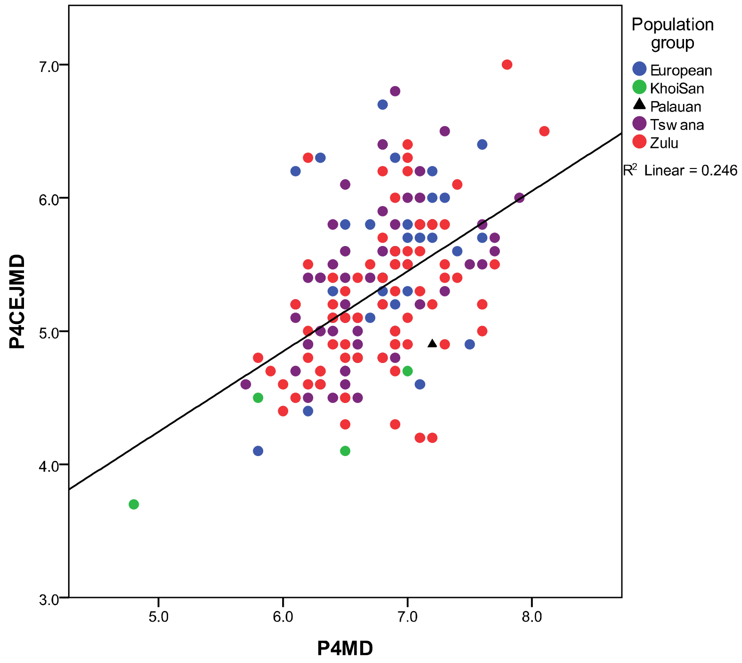


Figure 100: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the maxillary fourth premolar.

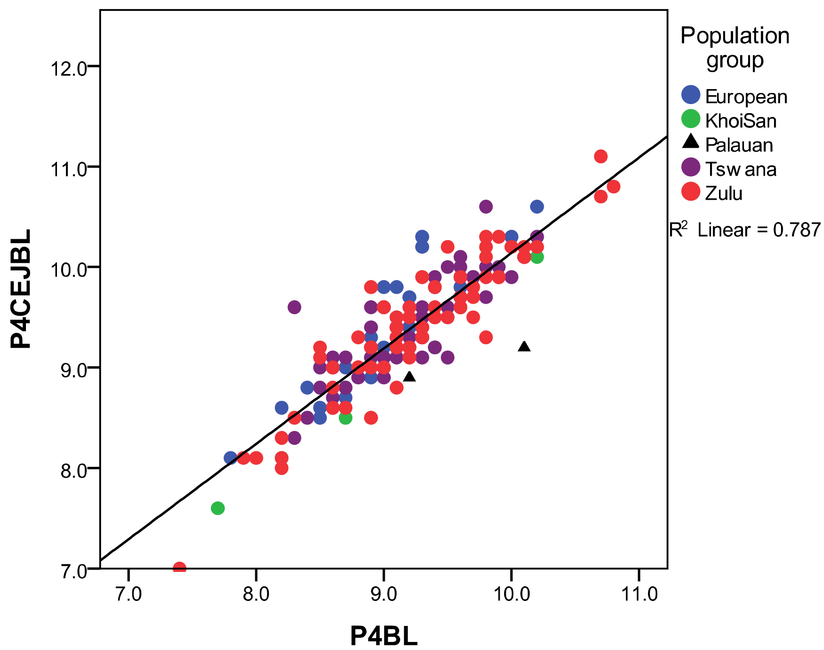


Figure 101: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the maxillary fourth premolar. (For sample size).

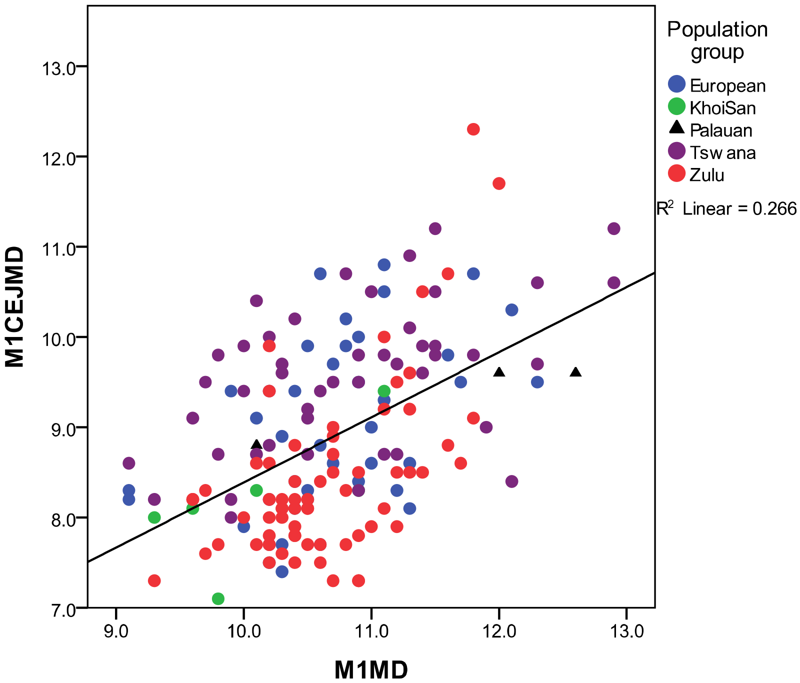


Figure 102: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the maxillary first molar.

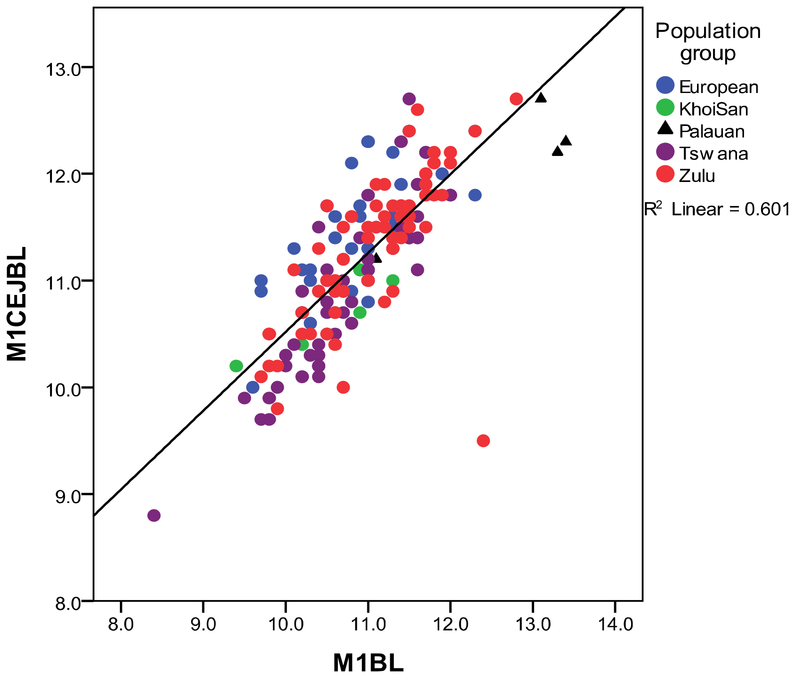


Figure 103: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] diameter and the corresponding buccolingual (BL) diameter of the maxillary first molar.

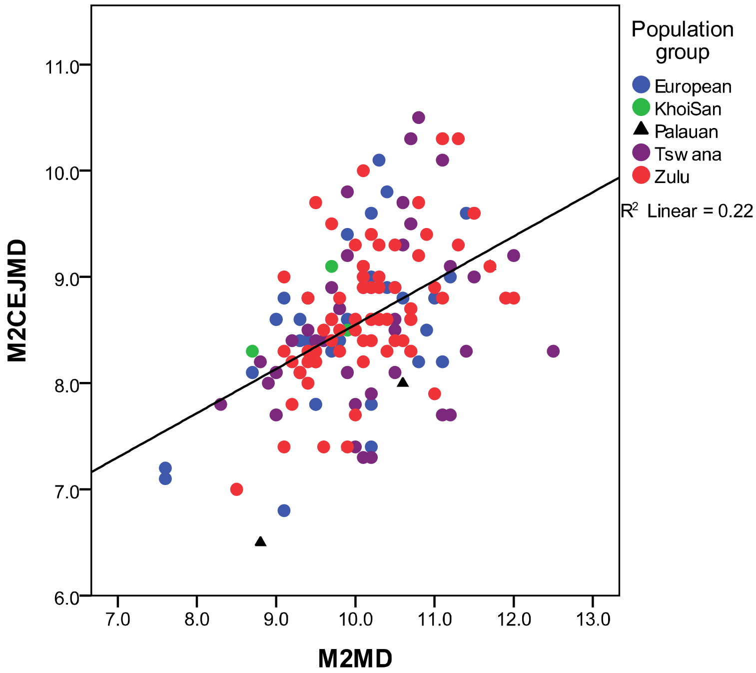


Figure 104: Bivariate plot of the mesiodistal cervico-enamel [CEJ (MD)] diameter and the corresponding mesiodistal (MD) diameter of the maxillary second molar.

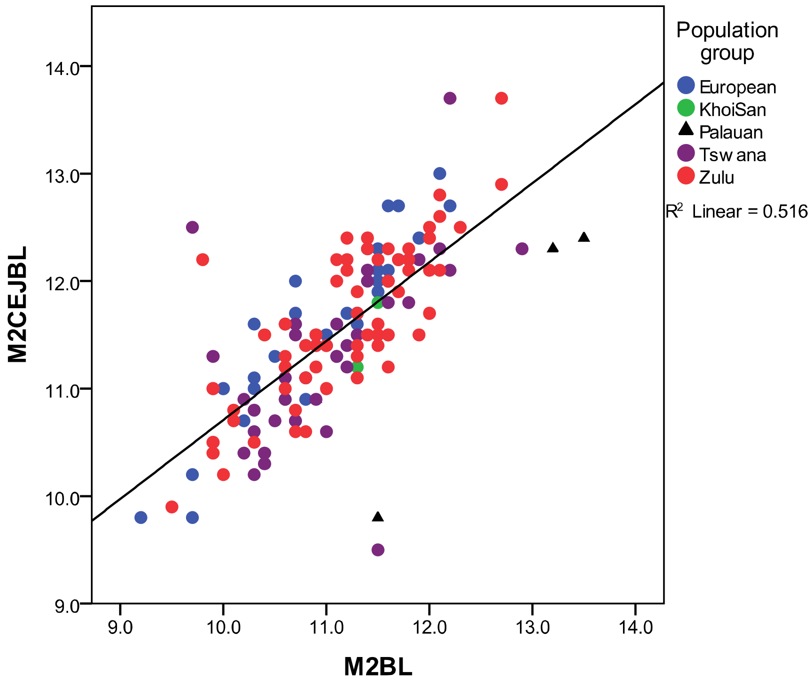


Figure 105: Bivariate plot of the buccolingual cervico-enamel [CEJ (BL)] and the corresponding buccolingual (BL) diameter of the maxillary second molar.

5.3 Summary of the Dental dimensions of the Palauan Specimens

A clear pattern was seen in the distribution of the mandibular mesiodistal (MD) and buccolingual (BL) tooth diameters (see Figure 106) of the comparative sample. All groups shared a trend, with the smaller teeth in the front and the larger teeth towards the back of the mouth. This pattern is a commonly known trait in later hominins (McHenry 1992).

The European group had the smallest mandibular teeth within the comparative sample, while Australian Aboriginals (Swanport and Murray Valley) had the largest. The mean Palauan BL plots near the larger measurements of the comparative sample for the incisors (I_1 and I_2), the canines (C), and first molar (M_1). The Premolars (P_3, P_4) and second molars (M_2) plot along with the smaller means. The mesiodistal measurements show similar trends in buccolingual measurements (see Figure 106). Palauan mean MD diameters for the incisors (I_1 and I_2), canines, M_1 and M_2 are larger than the means of the comparative sample. While the P_3, P_4 and again show a plot that falls amongst the smaller means of the comparative sample. Overall, Palauans have large mandibular teeth.

The MD diameters of maxillary dentition indicated that Europeans and Khoisan were the smallest from the comparative sample, while Zulus are the largest (no data available for Aboriginal group). Palauan specimens were small for the first incisor (I^1), but this may be due to the fact that there are only two comparative groups. For mesiodistal measurements, the second incisor (I^2), canines, premolars and molars of the Palauan means are larger than those of the comparative sample. For BL diameters of the maxillary dentition, European plots were smallest, while Aboriginal groups had the largest measurements buccolingually (see Figure 108). The Palauan specimens all fall within range of the largest teeth in the comparative sample, namely the Aboriginals. Palauan premolars (P^3 and P^4) do not show the same reduction as seen in the mandibular buccolingual measurements, and thus are quite large. All comparative groups show a slight increase in mean size from M_1 to M_2 with the exception of the Palauans (see Figure 108), which decrease in molar tooth size.

Mean maxillary and mandibular dental dimensions were calculated for each (see Figure 108) in order to compare sample groups. The Khoisan mean does not plot along the straight line, as no data were available for the maxillary incisors for any specimens. If the Khoisan mandibular incisor measurements were removed from the mean calculation, then the Khoisan group mean would plot along the straight line. It is evident that the Palauan sample had tooth measurements that plot with the largest measurements from the comparative sample (see Figure 108). Both maxillary and mandibular teeth are large in both buccolingual and mesiodistal diameters. The Palauan study sample does not plot the same as the comparative *small-bodied* sample.

From results obtained thus far, Palauan specimens do not follow the predicted trend of plotting similarly to the small-bodied comparative sample and in fact reflect tooth dimensions of the Aboriginal specimens (Table 77).

Table 77: Summary for all dental measurements taken on the Palauan specimens.

Measurement	Predicted result	Actual Result [A]	Measurement	Predicted result	Actual Result
Mandibular			Maxillary		
I1(BL)	Small	Average	**I1(BL)**	Small	Large SA
I1(MD)	Small	Large MVA	**I1(MD)**	Small	Average T
I2(MD)	Small	Average T	**I2(MD)**	Small	Large KS
I2(BL)	Small	Large	**I2(BL)**	Small	Largest SC
C(BL)	Small	Average MVA	**C(BL)**	Small	Average SC
C(MD)	Small	Small	**C(MD)**	Small	Largest
P3(BL)	Small	Large	**P3(BL)**	Small	Large SC
P3(MD)	Small	Largest	**P3(MD)**	Small	Largest
P3 CEJ(MD)	Small	Average	**P3 CEJ(MD)**	Small	Average
P3 CEJ(BL)	Small	Small-Average	**P3 CEJ(BL)**	Small	Small
P4(BL)	Small	Large SA	**P4(BL)**	Small	Large MVA
P4(MD)	Small	Largest	**P4(MD)**	Small	Largest
P4 CEJ(MD)	Small	Average	**P4 CEJ(MD)**	Small	Average
P4 CEJ(BL)	Small	Small	**P4 CEJ(BL)**	Small	Average
M1(BL)	Small	Large	**M1(BL)**	Small	Large
M1(MD)	Small	Largest	**M1(MD)**	Small	Largest T
M1 CEJ(MD)	Small	Large	**M1 CEJ(MD)**	Small	Average
M1 CEJ(BL)	Small	Average	**M1 CEJ(BL)**	Small	Large
M2 (BL)	Small	Large	**M2 (BL)**	Small	Average SA
M2 (MD)	Small	Largest	**M2 (MD)**	Small	Largest T
M2 CEJ(MD)	Small	Average	**M2 CEJ(MD)**	Small	Average
M2 CEJ(BL)	Small	Small	**M2 CEJ(BL)**	Small	Large

A. In the actual results, "Small" means that it plots similarly to small-bodied groups, and "large" means it plots similarly to larger bodied groups. In each case where the Palauan samples are large, an abbreviation is given indicting which group it is most similar to for that measurement. "Average" means that it plots near the mean
MVA= Murray valley Aboriginal, SA= Swanport Aboriginal, Z= Zulu, T= Tswana, SC= Southern Chinese

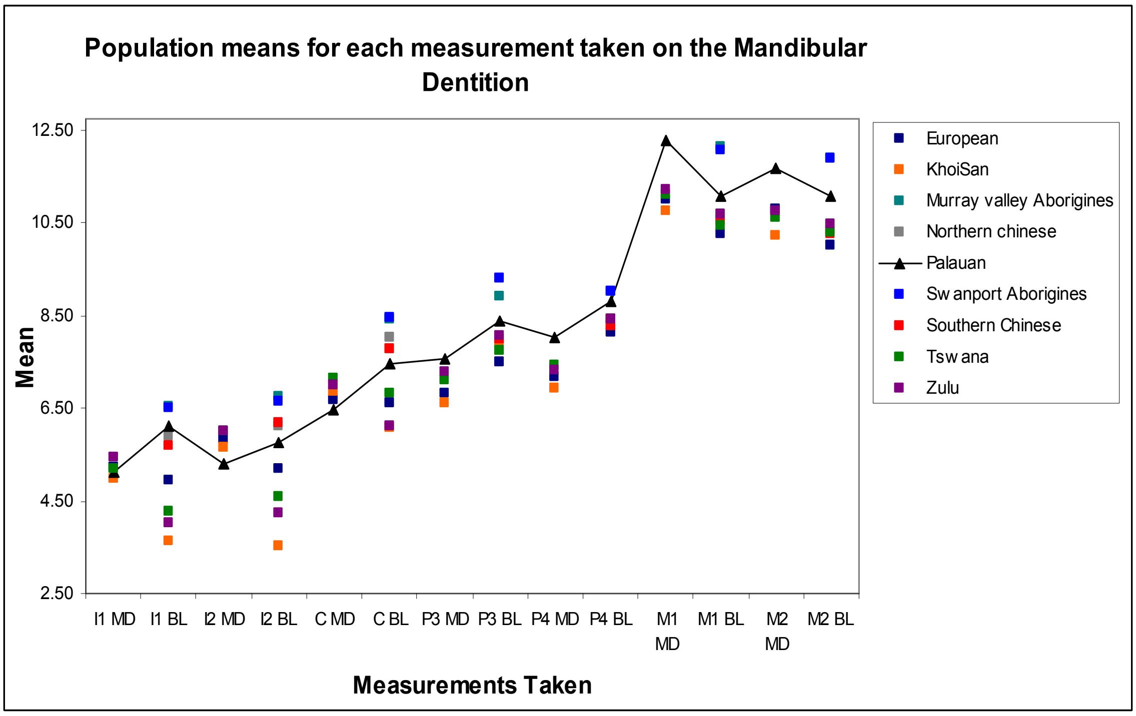


Figure 106: Univariate plot of the means for all mandibular tooth measurements. Each groups from the comparative sample is represented (For sample sizes, please see Section 5.2.1).

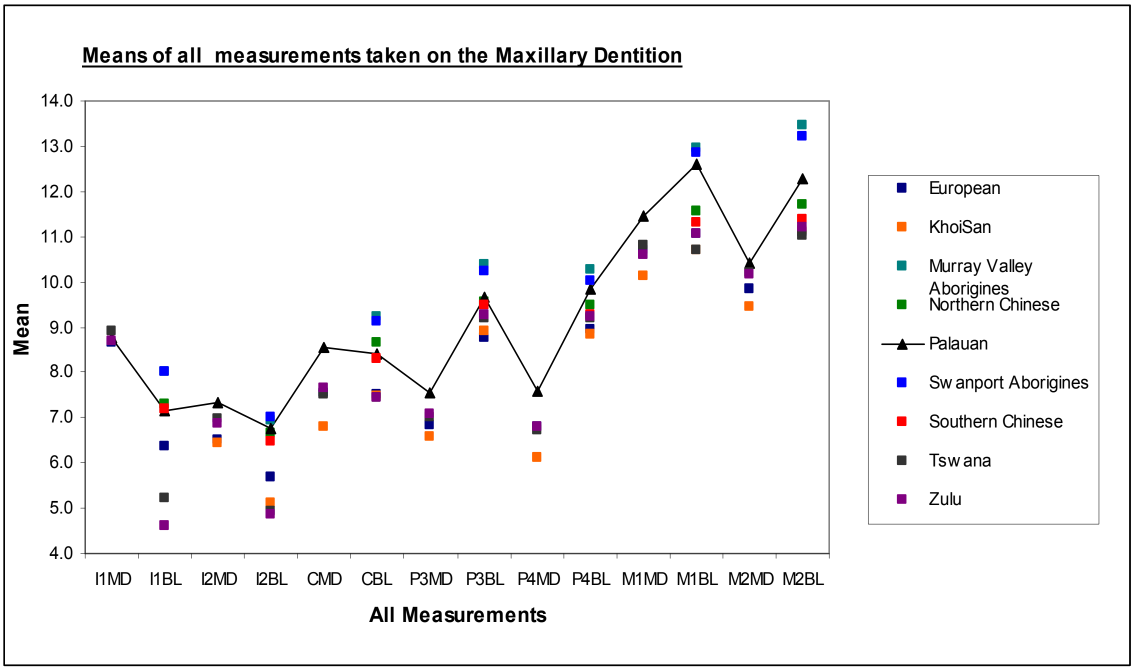


Figure 107: Univariate plot of the means for all maxillary tooth measurements. Each group from the comparative sample is represented (For sample size, please see Section 5.2.1)

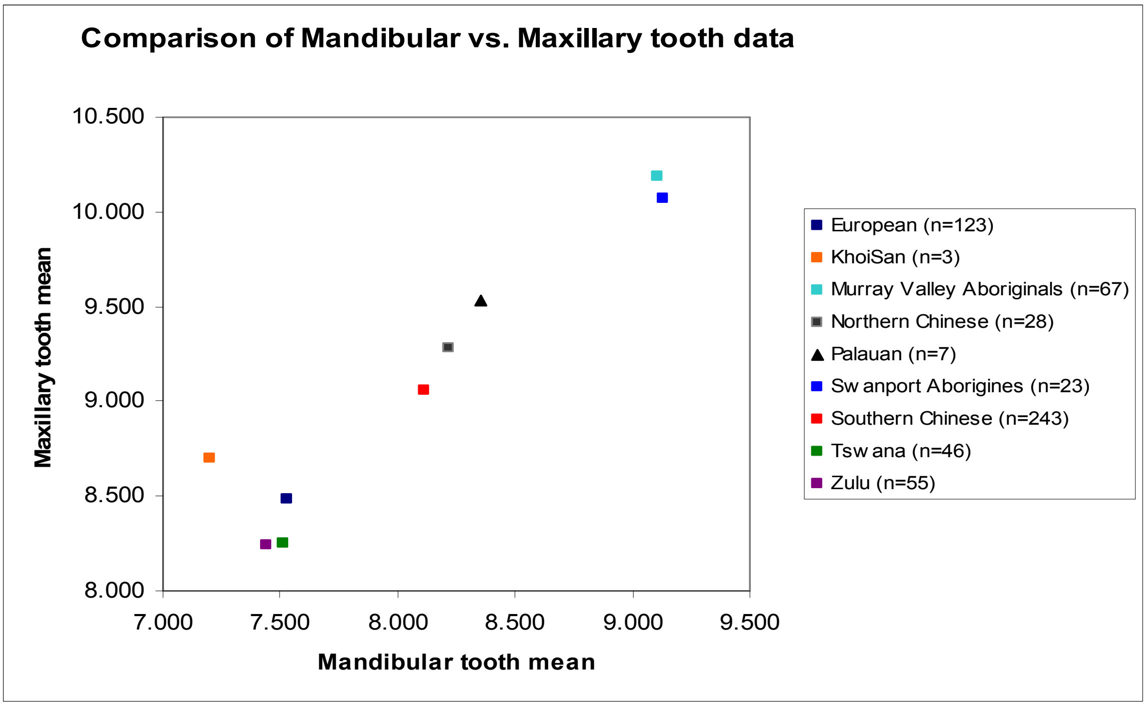


Figure 108: Bivariate plot of the overall means of the maxillary and mandibular tooth data for each group.

5.4 Results and Analysis for the Palauan Cranial specimens

5.4.1 Orbital breadth and Interorbital breadth of the Palauan specimens

The Palauan specimens have the smallest orbital breadth and large interorbital breadths when analysed against the comparative sample (Table 78).

The largest orbital breadth belongs to the Aboriginal sample, while the smallest belongs to the Palauans (see Figure 109). The Palauan sample plots in the lower end of the normally distributed variable (see Figure 109), where the Palauan individuals are the smallest measured sample. Both Aboriginal groups measured have the largest recorded measurements, while others still fall within range of modern human variation. There is significant difference between the Palauan sample and all of the comparative groups for orbital breadth diameter.

Table 78: Descriptive statistics for the orbital and interorbital breadth dimensions of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given for each group.

Group	Measurement	N	Min	Max	Mean	SD
Total for the comparative sample	**Orbital Breadth**	**493**	**35.0**	**48.0**	**40.657**	**2.5791**
	Interorbital Breadth	**60**	**20.0**	**31.0**	**24.358**	**2.3790**
European	Orbital Breadth	138	35.0	45.0	39.828	2.0977
	Interorbital Breadth	48	20.0	31.0	24.229	2.2620
KhoiSan	Orbital Breadth	12	36.1	40.0	38.018	1.3498
	Interorbital Breadth	12	21.6	29.0	24.871	2.8524
Murray Valley Aboriginals	Orbital Breadth	96	38.0	48.0	43.448	2.1367
Northern Chinese	Orbital Breadth	37	37.0	44.0	40.297	1.7137
Palauan	Orbital Breadth	4	32.5	37.0	34.950	2.2898
	Interorbital Breadth	4	23.8	29.0	26.450	2.1794
Swanport Aboriginals	Orbital Breadth	52	40.0	46.0	42.904	1.5499
Southern Chinese	Orbital Breadth	66	35.5	46.0	39.621	2.0269
Tswana	Orbital Breadth	10	36.1	40.2	38.474	1.5258
Zulu	Orbital Breadth OB	82	36.2	45.1	39.008	1.4260

Four specimens represent the Palauan sample. The data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

The Palauans have the largest mean for interorbital breadth; however, the largest and smallest recorded interorbital diameters belong to the European group (Figure 110 & Table 78). While the Palauan sample has a large interorbital distance, the specimens still fall within range of the comparative sample (Figure 110). The Palauan specimens have an inflated glabella, which could account for this large interorbital diameter (see Figure 112). The Palauan and Khoisan interorbital means are the most similar for the interorbital measurement.

A bivariate plot (Figure 111) illustrates that most of the Palauan sample plots as extreme points (i.e., outliers) when analysing the orbital and interorbital. The ratio of orbit to Interorbital breadth is disproportionate with the exception of one specimen, B: OR-15:18-005. Most groups have a small interorbital, which could account for the way that the comparative groups cluster. Should data be made available for the interorbital of the Austromelanesian groups, a similar trend may be seen, as an inflated glabella is a diagnostic trait of the Austromelanesian groups (Gordon 1964).

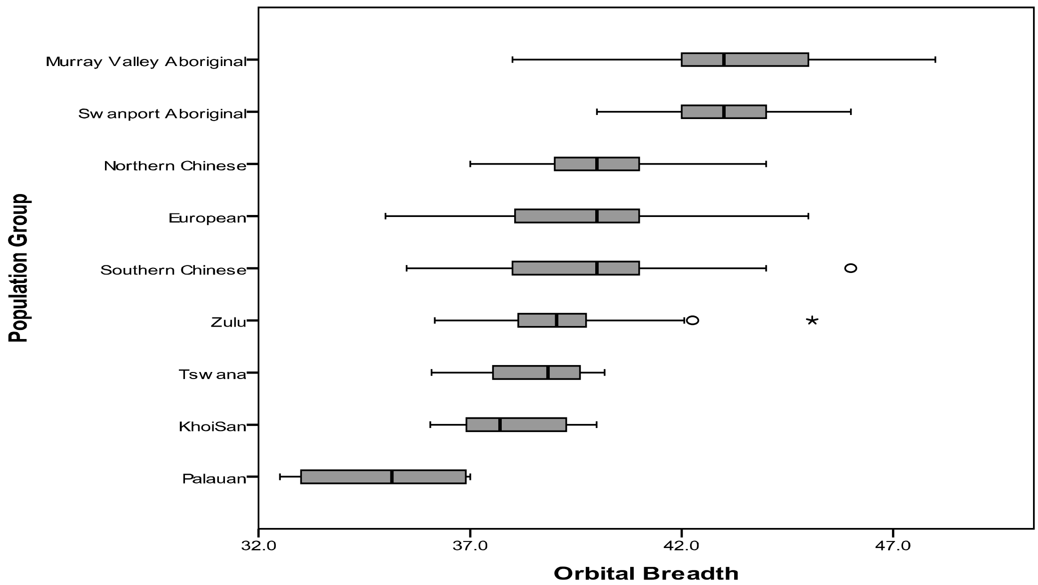


Figure 109: Boxplot showing the distribution of the orbital breadth measurements. (N= 493, mean = 40.65, SD = 2.5791). The open circles and stars indicate outliers within the data.

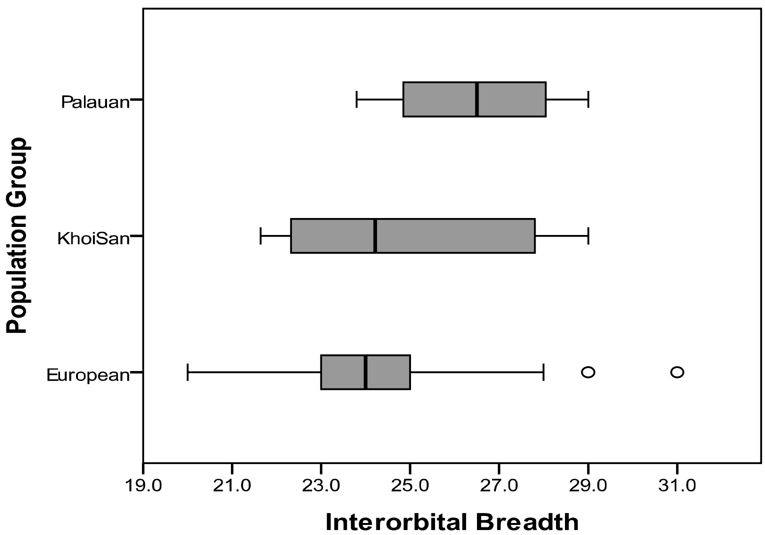
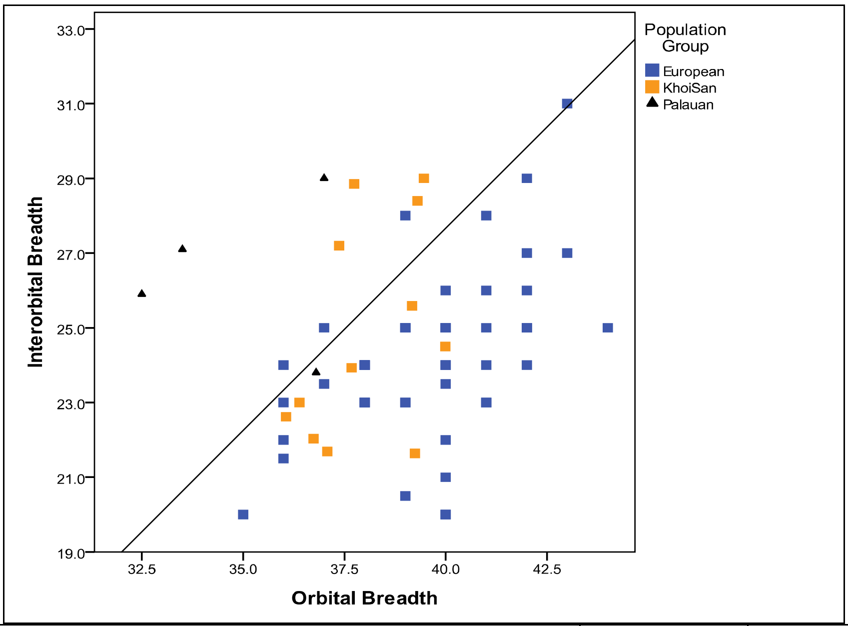


Figure 110: Boxplot showing the distribution curve for the interorbital breadth measurements. Data for this measurement do not follow a normal distribution curve.

As depicted in the results from this chapter, Palauans have a small orbital breadth and a large interorbital breadth. Morphologically this inflated glabella frontal area is similar to the morphology seen in groups from Austromelanesian.



Population Group			Interorbital Breadth	Orbital Breadth
European	Interorbital Breadth	Pearson Correlation	1	0.517**
		N	48	47
KhoiSan	Interorbital Breadth	Pearson Correlation	1	0.434
		N	12	12
Palauan	nterorbital Breadth	Pearson Correlation	1	.049
		N	4	4
**. Correlation is significant at the 0.01 level (2-tailed).				

Figure 111: Bivariate plot showing the orbital breath against the interorbital breadth of the same individual. The table give the correlation coefficients for each population. There a significant correlation for the Orbital and Interorbital breadths of the European group.

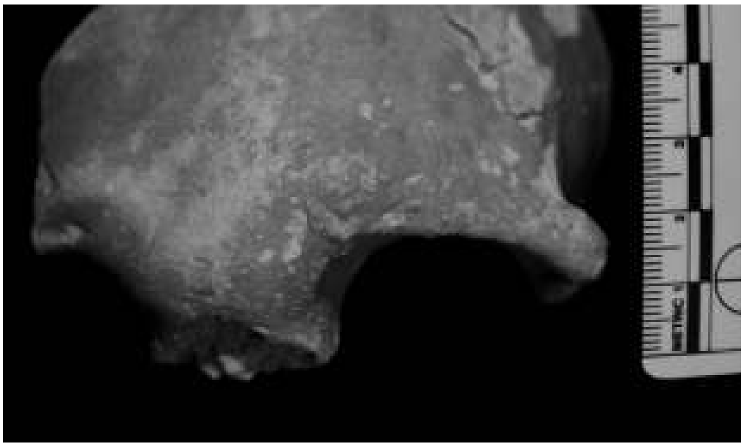


Figure 112: Shows the inflated glabella of the Palauan specimens. Specimen B: OR-14:8-001 has a large interorbital area and a small orbital measurement, Picture by L.R. Berger.

5.5 Analysis and Results of the Palauan mandibular data

Some of the Palauan specimens exhibited distinct mental trigones with weakly developed mental fossae and weakly developed non-projecting mental tubercles (Berger *et al.* 2008a). Palauan symphyseal angles tend to be more similar to morphology expressed by modern humans.

5.5.1 Symphyseal height of the Palauan Specimens

The Palauan mean is smaller than the mean for the entire comparative sample (Table 79). The largest recorded measurement belongs to the Aboriginal sample, while the European group has the smallest recorded measurement. Both symphyseal height and breadth show a normal distribution of the data (Figure 113 & Table 79). There is similarity between the means of the Palauan and the European.

Table 79: Descriptive statistics for symphyseal height of the mandible. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total for the comparative sample	**318**	**23.5**	**43.0**	**32.813**	**3.5643**
European	85	23.5	39.0	31.053	3.3140
KhoiSan	5	26.5	37.6	30.280	4.3849
Murray Valley Aboriginal	86	29.0	43.0	34.477	3.1724
Northern Chinese	32	28.0	37.0	33.625	2.4063
Palauan	4	26.6	35.6	29.975	4.0086
Swanport Aboriginal	32	25.0	36.0	30.844	3.0386
Southern Chinese	73	24.0	41.0	33.774	3.4861

Four specimens represent the Palauan sample. Data for the European, Chinese groups and Aboriginal groups obtained from Brown (2001).

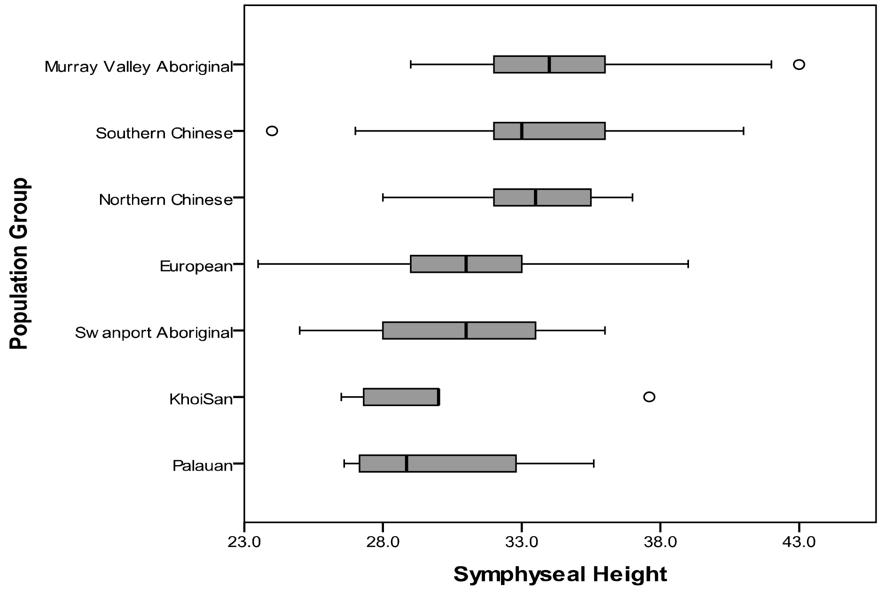


Figure 113: Boxplot showing the distribution for symphyseal height of the mandible. (N=320, mean = 32.8 SD = 3.56).

5.5.2 Symphyseal breadth of the Palauan Specimens

Symphyseal breadth measurements show a normal distribution (see Figure 114). The largest recorded symphyseal breadth is found within the Aboriginal sample, while the smallest is recorded for the European group (Table 80). The Palauan and European group have the most similar mean plots for the symphyseal breadth measurements.

Table 80: Descriptive statistics for symphyseal breadth separated into the different groups of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total for the comparative sample	**323**	**10.5**	**20.0**	**14.935**	**1.6747**
European	91	10.5	19.0	14.604	1.8760
Murray Valley Aborigines	87	12.0	20.0	15.310	1.4492
Northern Chinese	33	11.0	18.0	15.000	1.4361
Palauan	4	13.3	15.7	14.625	1.0112
Swanport Aborigines	33	12.0	17.0	14.364	1.1677
Southern Chinese	74	11.0	19.0	15.081	1.8432

Four specimens represent the Palauan sample. Data for the European, Chinese and Aboriginal groups obtained from Brown (2001).

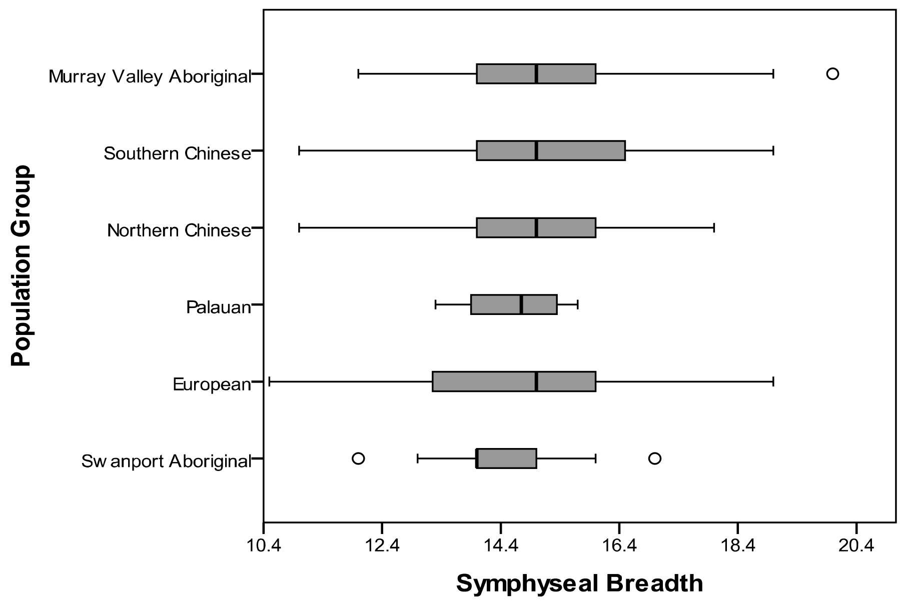


Figure 114: Boxplot showing the distribution of the data collected for the symphyseal breadth of the mandible.

There is a large range of variation in symphyseal breadth for some of the comparative groups (Figure 114). Palauan individuals fit within the range of these comparative samples, and are not the smallest. Figure 115, illustrates that symphyseal breadth is metrically not diagnostic for any particular group.

Palauan specimens display an interesting trend (Figure 115) in having the smallest symphyseal height, but not the smallest symphyseal breadth. In this regard, the Palauan sample acts as an outlier in comparison to other comparative samples.

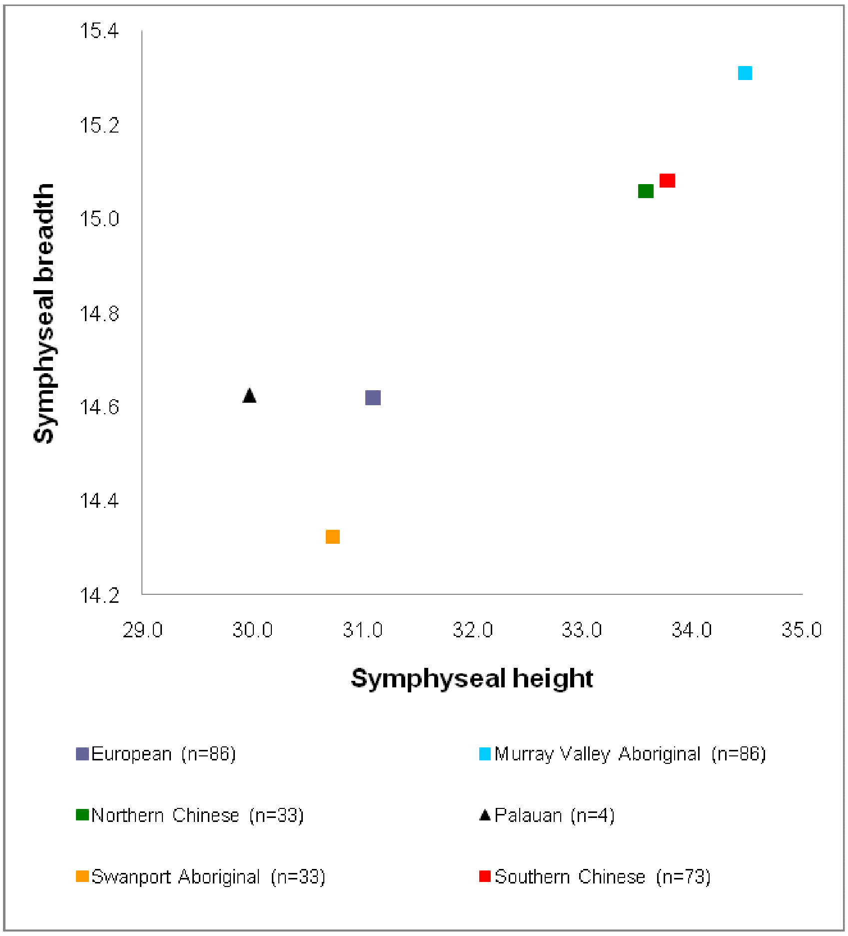


Figure 115: Bivariate plot of the mean symphyseal height and breadth for each group of the comparative sample. European n=92, Murray Valley Aboriginal n= 87, Palauan n=4, Swanport Aboriginal n=34, Southern Chinese n=74,

5.5.3 Molar breadth at M1/M2 of the Palauan Specimens

Table 81: Descriptive statistics for breadth measured at the M1/M2 junction. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total for the comparative sample	**304**	**10.0**	**20.0**	**13.905**	**1.7265**
European	76	10.0	17.0	12.737	1.5800
Murray Valley Aboriginal	84	11.0	18.0	13.940	1.5628
Northern Chinese	33	12.0	18.0	15.242	1.3470
Palauan	8	12.3	16.9	14.638	1.5856
Swanport Aboriginal	32	12.0	18.0	14.594	1.4997
Southern Chinese	74	10.0	17.5	14.088	1.4790
Data for the European. Aboriginal and Chinese group taken from Brown (2001)					

There is a normal distribution of measurements (Figure 116) for mandibular breadth at the M1/M2 boundary. Some individuals fall more than two standard deviations from the mean. There is overlap in ranges of comparative groups (Figure 116), indicating that this trait is not one that reliably identifies any one particular comparative group.

The Palauan group mean is most similar to that of the Southern Chinese group.

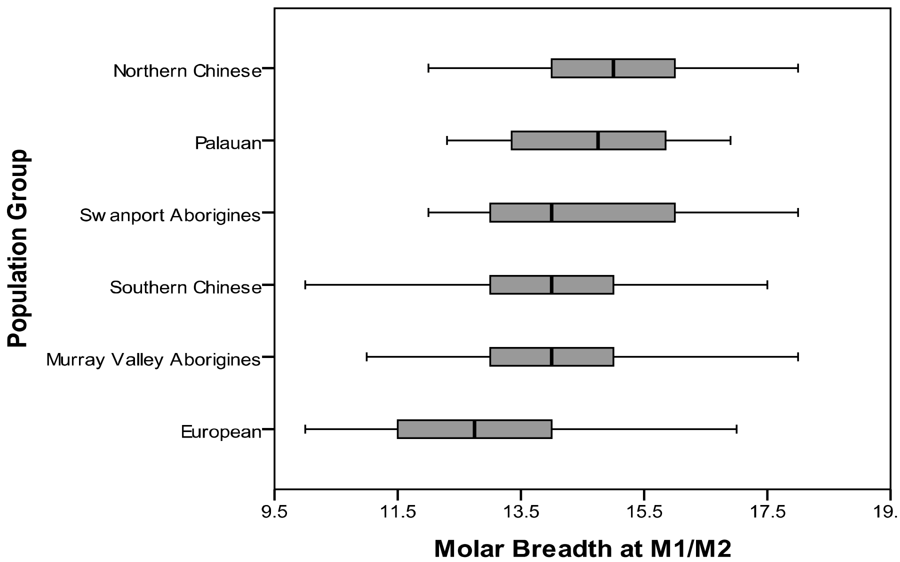


Figure 116: Boxplot showing the distribution of measurements of the breadth of the mandible taken at the M1/M2 junction. (N= 304, mean 13.9, SD = 1.72)

5.5.4 Ramus height of the Palauan Specimens

Table 82: Descriptive statistics for ramus height separated into the groups of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Minimum	Maximum	Mean	SD
Total for the comparative sample	**319**	**38.0**	**72.0**	**54.875**	**6.8306**
European	88	38.0	72.0	53.727	7.3277
Murray Valley Aboriginal	87	43.0	66.0	53.437	5.2930
Northern Chinese	33	49.0	71.0	60.970	5.7526
Palauan	2	51.5	61.6	56.550	7.1418
Swanport Aboriginal	32	45.0	69.0	57.344	5.9439
Southern Chinese	76	40.0	71.0	53.987	7.0777

Two specimens represent the Palauan sample. Data for the European, Chinese and Aboriginal groups obtained from Brown (2001).

For ramus height (Table 82), the Palauans fit within the range of the comparative sample. Europeans display the largest and smallest recorded ramus heights. Ramus height measurements taken on the entire comparative sample are normally distributed (Figure 117). The Chinese and Palauan samples have the most similar means for the comparative sample.

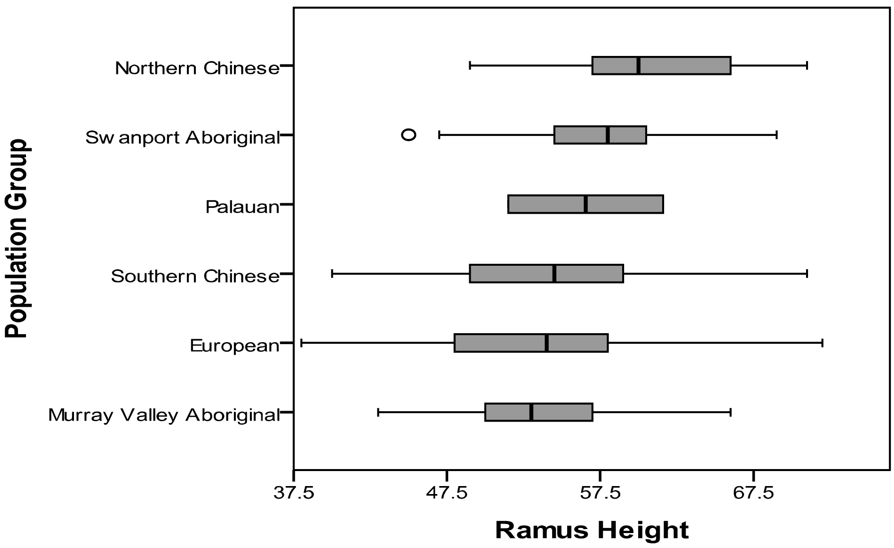


Figure 117: Boxplot showing the distribution of measurements taken for ramus height of the mandible. (N= 320, SD 6.54, mean =54.91)

5.5.5 Ramus Breadth of the Palauan Specimens

For ramus breath (Table 83), the Aboriginal group has the largest recorded measurement, while the European group has the smallest recorded measurement. The Palauan sample fits within the range of comparative sample measurements, and at most is only one standard deviation from the overall mean (see Figure 118). The Palauan group has a mean which is most similar to that of the Murray Valley Aboriginal group. But there is large overlap between the comparative groups.

When ramus height and breadth are compared (see Figure 119), the Swanport Aboriginals and the Palauans displayed similar plots for measurements of the symphysis (Figure 119). For the Murray Valley Aboriginals, ramus height is reduced and the symphysis is large, while in Palauan and the Swanport aboriginal group the opposite pattern is visible.

Table 83: Descriptive statistics for ramus breadth separated of the comparative sample. The mean, standard deviation (SD), minimum and maximum are given for each group.

Population Group	N	Min	Max	Mean	SD
Total for the comparative sample	**331**	**23.0**	**44.0**	**32.831**	**3.4935**
European	99	23.0	38.0	30.631	3.4807
Murray Valley Aboriginal	87	28.0	41.0	33.632	2.6064
Northern Chinese	33	25.0	39.0	32.758	3.1128
Palauan	2	31.7	36.2	33.950	3.1820
Swanport Aborigines	32	27.0	44.0	36.125	3.4711
Southern Chinese	77	27.0	41.0	33.383	2.9154

Two specimens represent the Palauan sample. Data for the European, Chinese, and Aboriginal groups obtained from Brown (2001).

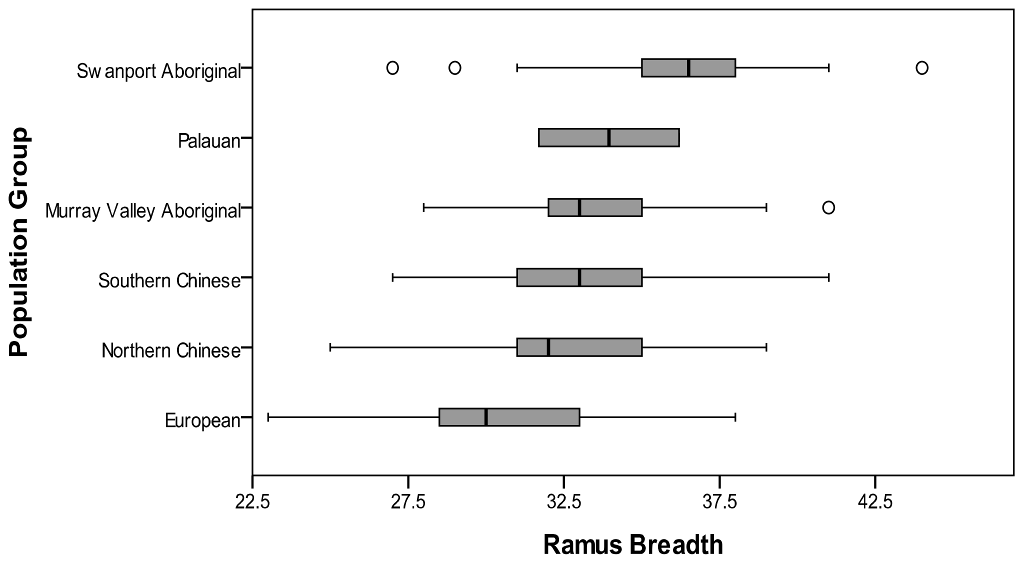


Figure 118: Boxplot showing the distribution of measurements taken for ramus breadth of the mandible, (N = 333, SD = 3.42, mean = 33.12).

When all mandibular measurements are viewed as a univariate plot of means (Figure 120), there is no consistency within the various groups. In other words, no one group can be consistently identified as the smallest or largest (see Figure 120).

The Palauan sample is small in its symphyseal height and breadth (see Figure 119). As the measurements progress dorsally, Palauan values become average. The front of the Palauan mandible is small, while the ramus or dorsal part of the mandible is not readily distinguished from other comparative groups (see Figure 121).

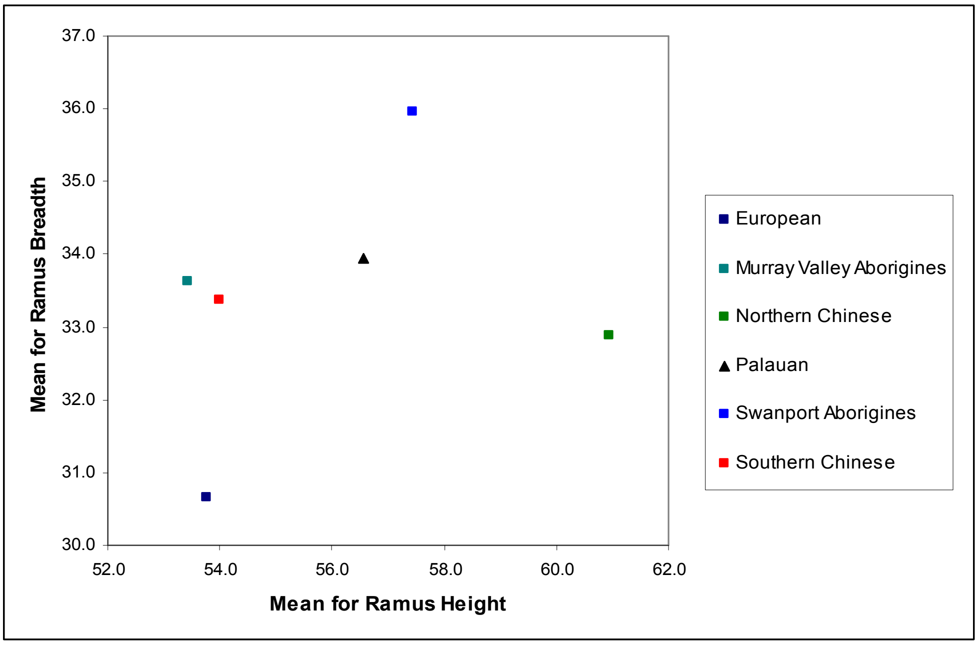


Figure 119: Bivariate plot of the mandibular ramus height and breadth. Each plot is separated into the different groups of the comparative sample (For sample sizes, please see Table 83 & Table 84).

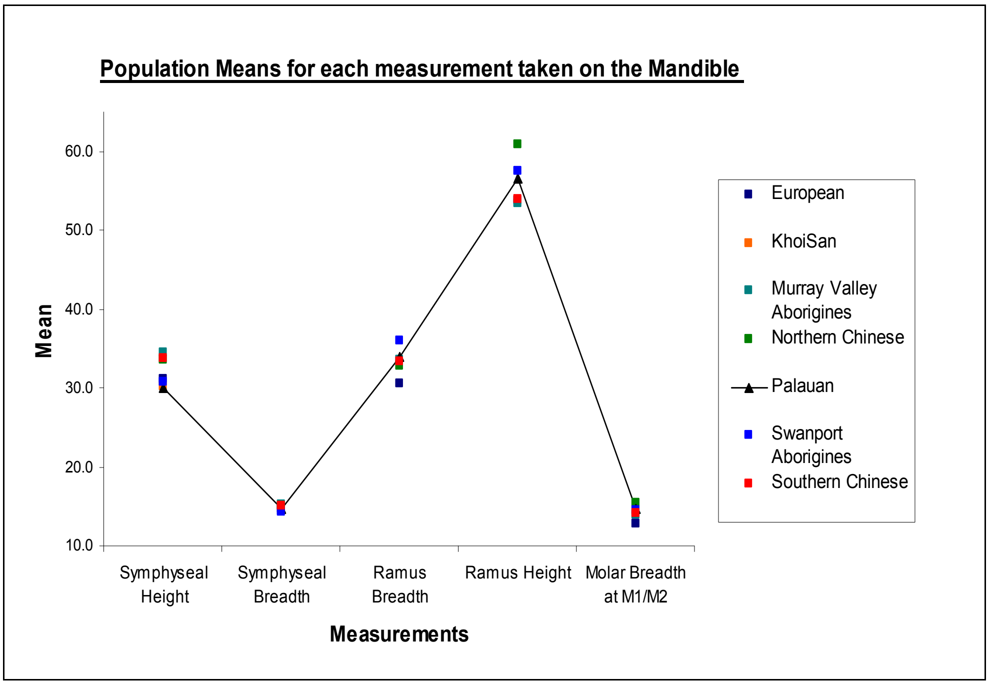


Figure 120: Univariate plots comparing means of all measurements taken on the mandible, separated into the different groups of the comparative sample.

Figure 121: Image showing the fragmented nature of the mandibles recovered. Specimen B: OR-15:18-006 was collected from Omedokel Cave and has an impacted third molar in the crypt.

5.6 Summary of the cranial and mandibular data of the Palauan Specimens

Table 84: Summary for all cranial and mandibular measurements taken on the Palauan specimens. In the predicted results, "Small" means that it plots similarly to small-bodied groups, and "large" means it plots similarly to larger bodied groups. "Average" means that it plots near the mean.

Element	Measurement	Predicted Result	Actual Result
Cranium	**Orbital Breadth**	Small	Smallest
	Interorbital Breadth	Small	Largest
Mandible	**Symphyseal Height**	Small	Average
	Symphyseal Breadth	Small	Average
	Molar Breadth At M1/M2	Small	Average
	Ramus Height	Small	Average
	Ramus Breadth	Small	Average

5.7 Discussion of the Palauan Craniodental specimens

This discussion will look at the following hypotheses that are being tested:

- **Hypothesis three**: Is it possible to identify traits that are likely to occur in populations which are reducing in body size over a relatively short time period (several generations)?
- **Hypothesis four**: The Palauan specimens have teeth that are large relative to the comparative samples.
- **Hypothesis five**: The Palauan specimens collected from Ucheliung and Omedokel caves originated from Austromelanesia.

Craniodental comparisons provide a potential means of identifying the parental (Founder) population of the Palauan fossils. Hill *et al.* (2006) noted many features shared between Andaman Negritos, Malay pygmies and Philippines Negritos, even though there is no genetic evidence of a shared ancestry. Alternatively, any traits shared by these groups may be due to insular dwarfing. Results presented here may reflect remnant morphology of the founding population, or they may reflect of rapid reduction of body size. Southeast Asian pygmies are thought to be descendants of Australomelanesians due to the shared cranial affinities and sundadonty (Storm 2007). Morphologically, Palauans exhibit small orbits and a large interorbital area with an inflated glabella region. An inflated glabellar region is a trait attributed to the Austromelanasian populations (Van der Pals 2007, Storm 2001), and it may indicate origins of this fossil population. Similarly, this observed morphology may be as a result of rapid reduction in body size.

For the mandible, Palauans are small in symphyseal height and breadth. As measurements move dorsally, Palauan samples converge on group averages (relative to the other small-bodied groups examined here). This suggests that the front of the mandible is relatively small compared to other small-bodied groups, but that the ramus or dorsal part of the mandible is comparable in size (see Figure 121). The predicted mandibular reduction (5.1 Specific predictions p. 150) is not observed in Palauan specimens, as the mandible may not reduce at the same rate as postcranial elements. There is some reduction in the mandible dorso-ventrally and this may account for the overcrowding of teeth.

Overall, Palauans display large dentition comparable to the large-toothed Australian aboriginal groups included in this study. The Khoisan group, which are the comparatively the small-bodied group (Chapter 4) included in this chapter, differed significantly from the Palauan group.

Relatively large teeth are a common feature in dwarfed insular mammals (Maglio 1973; & Gould, 1975), indicating that teeth might show the tendency to reduce in size at a slower rate than the rest of the skull. This is further evidenced by the negative allometry of molar size relative to skull size found in African and Philippine pygmies, as compared to normal-sized Africans and Filipinos, respectively (Shea and Gomez, 1988). Furthermore there was no reduction in the cranial aspects of the pygmies. Reduction in human tooth size is documented in phases of varying degree and duration (Brace, 1967; Brace & Ryan, 1980; Wolpoff 1971). Reduction in tooth size is essentially a by-product of general reduction in body size and builds (Frayer 1978). Reduction in body size, accompanied by tooth size reduction, can be related to a gradual increase in population density (Macchiarelli & Bondioli, 1986). For example, rapid reduction due to isolation does not select for reduction in tooth size (Macchiarelli and Bondioli 1986), as resources are limited and more energy is required for tooth reduction. Effectively large tooth size in insular populations is a lag trait, that is, if the isolation continues, it would eventually also reduce in size.

The Palauan sample has large maxillary teeth overall (see Figure 119). Palauan mandibular dentition has the greatest variation, where incisors, canines, and first molars are large. Reduction is observed in premolars and second molars. This reduction is coupled with non-correlation between the CEJ's for these teeth and the corresponding crown measurements. This may be due to dorsoventral reduction observed in the mandible, and the resultant limited space available for teeth. Developmentally, premolars and second molars are the last teeth (other than the M3) to erupt, and therefore limited space could cause malocclusion or slight reduction in the size of these teeth (Peters 1983). Berger *et al.* (2008a) noted that the third molars were absent in some of the Palauan specimens, and those that did have an M3 were mal-occluded (Berger *et al.* 2008a).

Large teeth, inflated glabella, and protruding supraorbital tori (Berger *et al*. 2008a) may be an indication of the Founder population. These traits are all well-documented in Austromelanesian populations, suggesting it is likely that the Palauan population sampled in this study may have originated from Papua New Guinea or South East Asia. This, however, only can be confirmed by genetic studies.

CHAPTER 6: COMPARISON OF PALAUAN BODY SIZE AND TOOTH SIZE

This chapter deals with the analysis of the determined tooth sizes against the body sizes calculated for the comparative sample. Tooth size to body size has often been used as a diagnostic feature for determining provenience of populations (e.g., Brace 1964).

In most studies, tooth size and tooth morphology is considered; however, as this study is based on the metrics of the specimens, no morphological details will be included.

Table 85: shows the overall means for both postcrania and tooth size (mandibular and maxillary). The third column indicates the ratio of tooth size/body size for each group where the data was available. Data for the European, Southern Chinese and Aboriginal group obtained from Brown (2001). The overall postcranial mean is calculated by averaging all the postcranial measurements for each specimen. The overall tooth size mean is calculated by averaging all the dental measurements available for each specimen.

Group	Overall postcranial Mean	Overall Mean tooth size	Ratio
Andamanese	42.566	/	/
European	70.814	8.007	0.11307117
Khoisan	46.2486	7.95	0.17189726
Aboriginals	80.9952	9.646	0.119093417
Nicobar Islander	37.375	/	/
Palauan	44.5759	8.943	0.200624328
Pygmy from the Congo	41.711	/	/
Southern Chinese	71.210	8.584	0.120545073
Zulu	65.9882	7.84	0.118809068

In order to obtain a mean for postcrania, all available means were averaged by the number of measurements taken (i.e., a geometric mean was calculated), similarly a single mean was calculated using all the dental means obtained (Table 85). While the Palauan sample may not have the smallest postcranial mean since Andamanese, Nicobarese, and Pygmy are all smaller, Palauans are still within range of small-bodied groups. Palauans have the second largest dental geometric mean recorded for the comparative sample (Table 85). When a ratio of postcranial to dental geometric mean is calculated, Palauans have the largest ratio of the entire comparative sample. The Palauan teeth are remarkably large relative to their small body size. The other small bodied sample for which a ratio can be calculate are the Khoisan, the ratio for this group is not nearly as marked as that of the Palauan sample.

6.1 Palauan joint sizes compared to tooth dimensions

Joint sizes or articular surfaces were compared to the overall tooth size. Most Megadontia quotients are calculated using body size (stature) or body weight against a mean measure of tooth size (McHenry 1988; Gingerich *et al*. 1982). However, no accurate weight estimation for the Palauan sample is available, and the author has already used mean joint size as an estimator of body size.

Means of various articular measurements of long bones for the comparative sample were plotted against mean tooth size, which is calculated by taking all BL measurements of mandibular and maxillary teeth and averaging them. This permits one value to represent the entire tooth sample. Only measurements, which were present in the Palauan sample, were considered and only groups, which had both the measurement and the mean tooth size, were used in bivariate plots in this chapter.

Uniformly, the Palauan sample exhibits a surprising trend in that they appear megadontic relative to joint size. This is particularly striking when one examines femoral head size, as a proxy measure of body size, relative to the size of Palauan teeth (Figure 122). From Figure 122, one can see that Palauans have a larger dental mean in comparison to their very small femoral SI diameter. In comparison, populations with substantially larger body size (e.g., Aboriginal, European & Zulu, as estimated by joint size) have universally smaller teeth – absolutely and relatively. In every case, small-bodied populations cluster together, with slightly larger-bodied populations having slightly larger teeth – progressing from Andaman islanders up to the largest body aboriginals. The Palauans again fall as an outlier in this proportional measure. This surprising result will be discussed later, but once again it highlights the unusual proportions found in the Palauan sample.

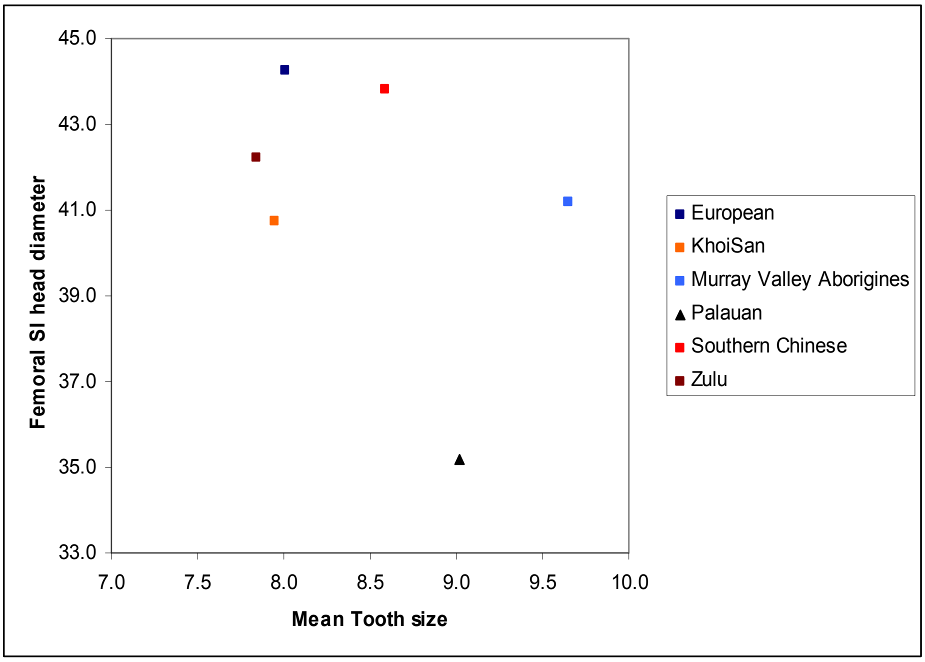


Figure 122: Bivariate plot of femoral head SI and the mean tooth size for each group in the comparative sample.

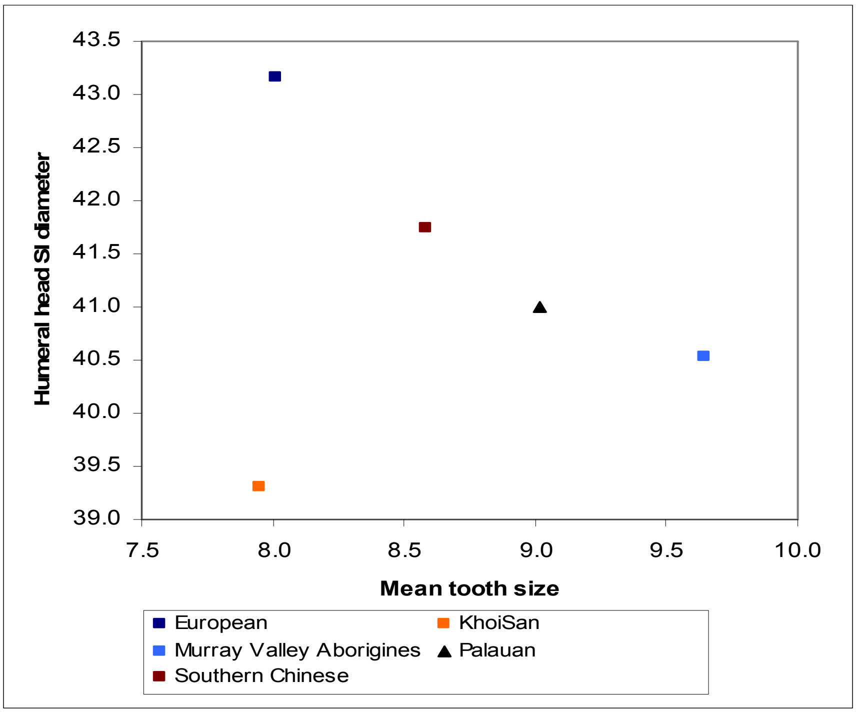


Figure 123: Bivariate plot of humeral head SI and the mean tooth size for each group in the comparative sample.

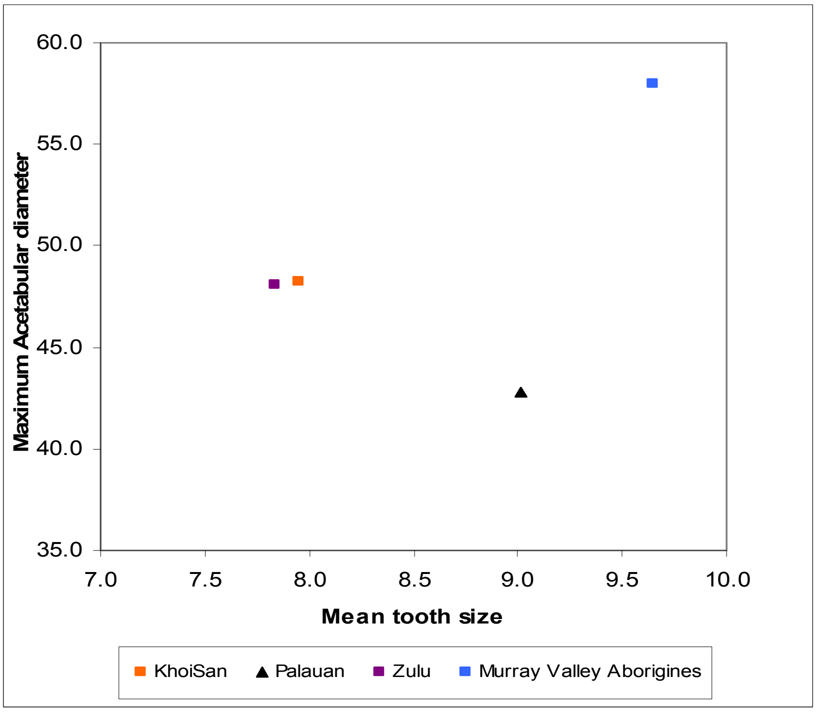


Figure 124: Bivariate plot of the maximum acetabular diameter and mean tooth size for each group in the comparative sample.

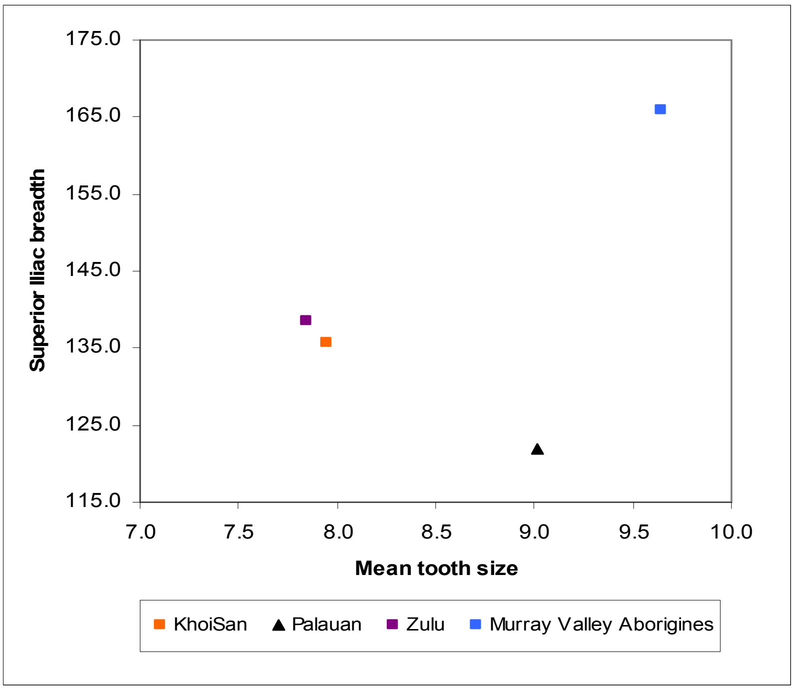


Figure 125: Bivariate plot of superior iliac breadth and mean tooth size for each group in the comparative sample.

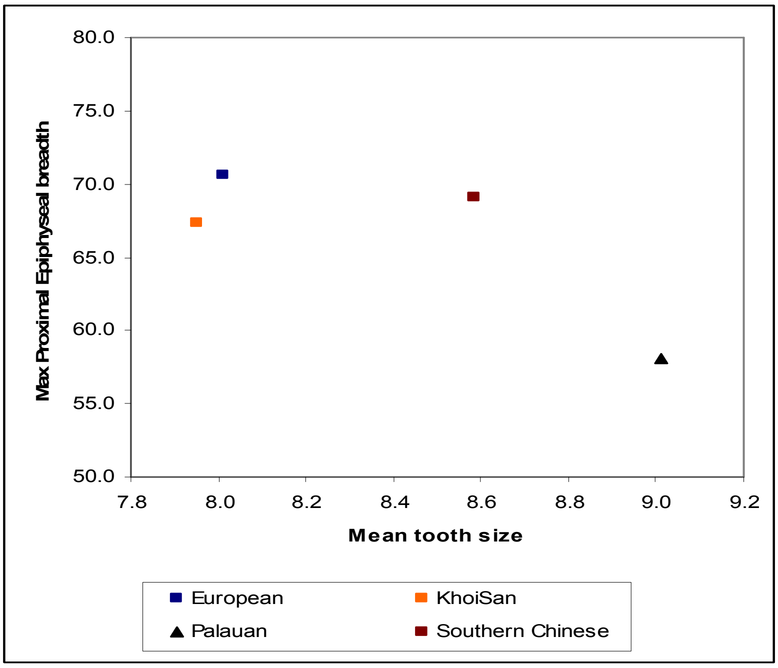


Figure 126: Bivariate plot of tibial maximum proximal epiphyseal breadth and the mean tooth size for each group in the comparative sample.

For humeral head dimension (Figure 123), Palauans have large dental dimensions and smaller humeral joint sizes. Interestingly, European, Southern Chinese, and Khoisan seem to plot in a similar cluster with the Palauan sample, near the aboriginal sample.

Acetabular diameter is a common way to calculate body mass (Ruff 1991; 2002) In Figure 124; the Palauan acetabular diameter is small in relation to mean dental size, while a similar plot is provided for superior iliac breadth (Figure 125). Tibial proximal epiphyseal breadth shows the same pattern as other long bone epiphyses, where the Palauan articular surface is smaller than that of the comparative samples plotted against mean dental size (Figure 126).

For all bivariate plots of joint and dental size, Palauans are somewhat distanced from the rest of the comparative sample. Palauan dental dimension are incredibly large when viewed against any of their joint sizes.

A critical finding of this study is that relative dental dimensions illustrate the uniqueness of the Palauan population. Palauans have teeth that are large relative even to the large-toothed Australian samples. This is evident in the joint size to dental size comparisons. The ancient Palauan sample is clearly megadontic, a trait not seen in the modern day Palauans. Megadontia has commonly been claimed for Sahul-Pacific populations (see references in Kondo *et al*. (2005), and may provide a clue as to the origin of the Palauan specimens. The fact that the Palauans are both absolutely and relatively megadont contradicts the idea that Fitzpatrick *et al* (2008) put forth – that this past population is in fact normal. It is intriguing that a population presenting such small body size – among the smallest ever measured (see 2.5 Statistical Methods for the Postcranial and Cranial-Dental p. 73) - has some of the largest teeth ever recorded in a modern human population. Other studies from later sites on Palau (Fitzpatrick & Clarke 2008, Fitzpatrick 2003b), do not show such anomalies within the data of those specimens, [e.g., Orrak specimens are small-bodied (Berger *et al* 2008b;

Gallagher *et al.* 2009), but no dental data has been published so no direct comparisons can be made of this unusual combination of morphologies]. Modern Palauans do not display this morphology, so future research could perhaps aid in better understanding what happened to this anomalous group. Did this past population undergo adaptive change, and could there still be evidence of this population yet to be discovered? This population may have gradually 'disappeared' through admixture or were replaced by a later larger-bodied population.

CHAPTER 7: THE PALAUAN SPECIMENS AND THEIR IMPLICATIONS FOR *HOMO FLORESIENSIS*

Homo floresiensis is a hominin species which was excavated from just a single cave, Liang Bua (Flores, Indonesia) and are dated between 95 000 and 17 000 years ago (Roberts *et al*., 2009;Morwood *et al*., 2009). This species has been suggested by some to be an insular dwarf derived from an early form of *Homo* (Brown *et al*. 2004). The remains of an adult skull and partial skeleton (LB1) (Brown *et al*. 2004) and fragmentary remains of nine other individuals ((Morwood *et al*., 2005; 2009) represent this supposed insular dwarf population. The Flores material is an important comparative sample in terms of the body size discussion of the Palauan specimens. As it may also be an isolated dwarf population, much could be established about body size of insular populations by comparing the *H. floresiensis* material to the Palauan specimens. By doing direct comparisons of the Flores measurements to those taken on the comparative sample of this study (see Chapter 2) the body size of these two island populations could aid our understanding of insular populations that may have undergone insular dwarfing.

7.1 Background

The *H. floresiensis* material has been at the centre of a debate raging within palaeoanthropological circles. One issue of contention is the taxonomic status and evolutionary position of *H. floresiensis* (Brown *et al*., 2004; Morwood *et al*. 2004, 2005). The *H. floresiensis* fossils were all collected from the Liang Bua cave site in Flores and the assemblage consists of a near complete skeleton (LB1) and material from at least nine individuals (Roberts *et al*., 2009; Morwood *et al*., 2009). The specimens collected represent individuals that date to 95 000 years ago (Roberts *et al*., 2009; Morwood *et al*., 2009), and that had the remarkably small stature of 106 cm (Brown *et al*., 2004). Small stature of *H. floresiensis* was proposed to be an adaptation to the island environment (Brown *et al*. 2004), and dwarfism may have been advantageous due to the smaller amount of food needed and more efficient thermoregulation of body size (Sondaar 1977 & 1986).

The relatively short stature and small endocranial capacity led researchers to explore various other hypotheses as to the cause of this hypothesized insular dwarfism, a phenomenon that is known to occur in primates (Bromham & Cardillo 2007).

Unique craniofacial features and other skeletal characteristics present in *H. floresiensis* has created a two-sided debate. Firstly, in the original descriptions of LB1 cranial material, Brown *et al.* (2004) emphasized the extremely small size of the cranium. The reduced cranial capacity of 417cc for LB1 is comparable in size to that of chimpanzees (Falk *et al*. 2005) and early hominins. Cranial capacity of LB1 is one of the smallest recorded for any hominid specimen (the exception being two *Australopithecus afarensis* crania (Argue *et al*. (2006): AL 333-105 (juvenile, 343cc) and AL 162-28 (375cc) that date back 3-3.5 million years (Boaz 1988)). Body size reduction in mammals is usually associated with only moderate brain size reduction, which led researchers such as Argue *et al*. (2006) to describe *H. floresiensis* as having brain shape affinities to *H. erectus*, which was later revised to early *Homo* (Gordon *et al*.2008).

Asymmetries present in the LB1 cranium led Jacob *et al*. (2006) to suggest that it was indicative of abnormal development and hypothesized that LB1 fell within the range of modern pygmy *H. sapiens* populations. Further, they suggested that *H. floresiensis* may have suffered from microcephaly (Aiello 2010). Other supporters of the microcephaly hypothesis include Martin *et al*. (2006), but this issue is one of on-going debate (Martin *et al*. 2006, Argue *et al*. 2006; Groves 2007, Holloway *et al.* 2011). Morphologically, the face of LB1 is similar to members of the genus *Homo* (Aiello 2010). Metric aspects of the LB1 and LB6 mandibles (i.e., its symphysis, corpus, and ramus morphologies) are thought by Maeda and Brown (2009) to be distinguishable from those of both *H. sapiens* and *H. erectus*.

A mosaic of derived and primitive features has been described for the postcranial skeleton of *H. floresiensis* (Jungers *et al.* 2009). Limb proportions of LB1 are thought to resemble *A. afarensis* (Jungers *et al*. 2008,) with shorter legs relative to arms. Jungers *et al*. (2008, 2009a) also provide a description of the *H. floresiensis* foot, containing both primitive and derived features. The foot is derived in that the big toe (although being short) is aligned with the other toes, a high arch is present for bipedal locomotion, and metatarsals have upwardly-oriented joints. Primitive features described in the paper include foot length proportional to that of a chimpanzee or an australopith foot length. *H. floresiensis* foot length approximates 20 cm. which is large relative to the short femur and tibia (Jungers *et al.* 2009; Holliday *et al.* 2009). This is longer than any measured dimension in a person of similar stature (Lieberman 2009). Additional primitive features include a weight-bearing process on the navicular and robust long, curved lateral toes. The primitive foot of

H. floresiensis provides a model for a non-modern hominin foot that had evolved for effective walking.

The shoulder girdle of *H. floresiensis* did not have a modern human shoulder configuration. Larson *et al.* (2009) noted that due to size and the presence of primitive features, such as an anteriorly-facing glenoid fossa and a posteriorly-directed humeral head, the specimen exhibited a transitional stage in pectoral girdle evolution in the human lineage. Tocheri *et al*. (2007) noted that the wrist bones of LB1 suggested *H. floresiensis* retained a morphology considered primitive for the African ape-human clade. Tocheri *et al*. (2007) argue that since modern humans have a derived wrist morphology forming during embryogenesis, the probability that pathology could result in the normal primitive state is highly unlikely.

There is no doubt that the unique craniofacial features and skeletal characteristics present in the Flores fossils will fuel further debates in the future. In order to gain a better understanding of insular populations, developmental disruptions such as pituitary dwarfism, congenital hypothyroidism (Obendorf *et al*. 2008), primordial microcephalic dwarfism (Jacobs *et al*.2006; Argue *et al*.2006; Holloway *et al* 2011), and IGF-1 insulin-like growth factor (Richards 2006; Hershkovitz *et al*. 2007) should all be explored further.

7.2 Specific Predictions regarding comparison of the Palauan craniodental and postcranial specimens to *H. floresiensis* material

This chapter will compare Palauan data with data made available from the *H. floresiensis* material. This study does not deal directly with the taxonomic issues surrounding the

Flores material, but will rather focus on how this insular population compares to the Palauan material, with the aim of potentially identifying traits that may be associated with insular dwarfing of a hominin population.

7.3 Results and Analyses of the *H. floresiensis* material in comparison to the Palauan craniodental and postcranial material.

Table 86: Measurements supplied by Brown and Maeda (2009) for the *H. floresiensis* specimens. This list included dental and mandibular measurements.

Variable	*H. floresiensis*		Variable	*H. floresiensis*	
	LB1	LB6		LB1	LB6
Symphyseal height	28	28	M_1 BL	11.4	10.0
Symphyseal thickness	15	17	M_1 MD	10.1	10.1
Corpus height M_1	20.5	22.5	M_2 BL	10.7	9.7
Corpus height M_2	24.5	23.5	M_2 MD	10.1	10.3
Corpus thickness M_1	15	14	M_3 BL	10	8.9
Corpus thickness M_2	15.5	15	Maximum femur length	281	–
Bicondylar breadth	(100)	–	Max. femoral head breadth	31.5	–
I_1 BL	5.7	–	M_1 BL	11.4	10.0
I_2 BL	6.2	5.4			
C BL	7.9	6.7			
P_3 BL	8.8	7.6			
P_3 MD	10.4	8.5			
P_4 BL	–	7.6			
P_4 MD	–	6.3			

7.4 The Mandible of *H. floresiensis*

Among the *H. floresiensis* remains are mandibles described as having an anteriorly-narrow mandibular dental arch that is long relative to its breadth, as well as a P_3–M_3 row that is laterally convex rather than straight (Brown & Maeda 2009). The anterior "symphyseal region is rounded, bulbous, and inferiorly receding" (Brown *et al.* 2004). Traits that are considered common in *H. sapien*s mandibles are a raised midline keel, a mental tuberosity, mental fossae or incurvature, are reported as being absent in *H. floresiensis* (Schwartz & Tattersall, 2000). All *H. floresiensis* measurements used in this chapter were published by Brown & Maeda (2009) (for comparative data see Chapter 2).

LB1 has a low symphyseal shape index (symphyseal height/symphyseal thickness) in comparison to *H. sapiens* means (Brown & Maeda 2009). From Figure 127, it is noted that the *H. floresiensis* sample has a small symphyseal height that falls within the range of the comparative groups. For symphyseal breadth(see Figure 128), *H. floresiensis* has a range that falls above the mean of the comparative sample. This relatively large symphyseal thickness in relation to the height, accounts for a low symphyseal shape index (see Figure 129).

Mandible breadth at M1/M2 (Figure 130) shows much overlap between *H. floresiensis* and all comparative groups.

In Figure 131, a bivariate plot of mandibular breadth versus BL breadth of M1 shows clusters between the samples. *H. floresiensis* clusters with specimens from N. China, while aboriginal groups have large teeth relative to their mandible breadth, and the Palauan specimens separate on their own in the plot. Interestingly, the Palauans have a larger M1

BL diameter than the *H. floresiensis* specimens, but a smaller mandibular breadth at the M1/M2 junction.

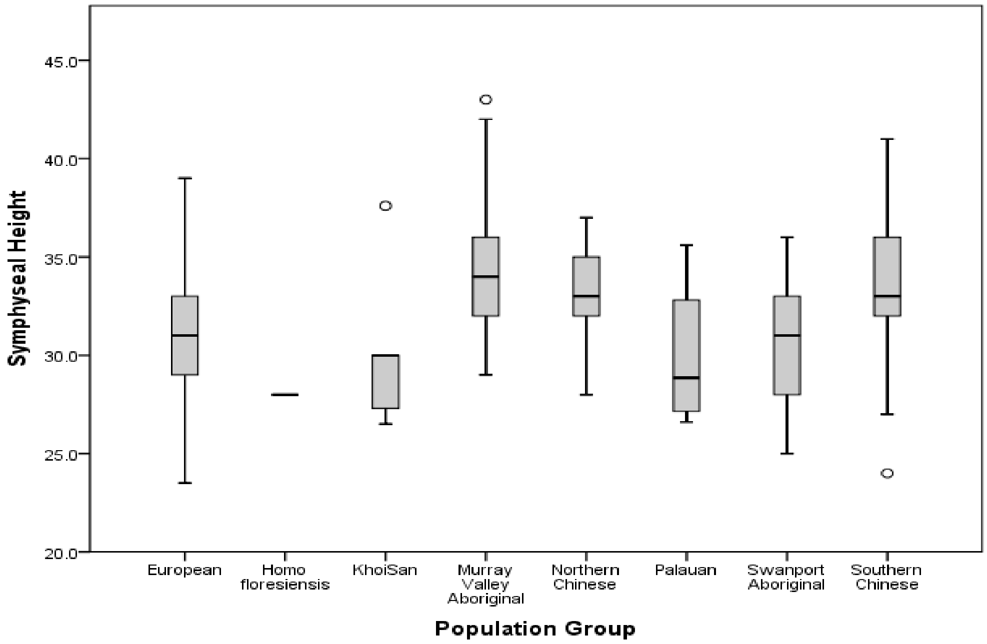


Figure 127: Box plots for the symphyseal height data. Each boxplot represents a different group of the comparative sample: Aboriginal, Chinese and European data from Brown (2001) and data for the *Homo floresiensis* was taken from (Brown and Maeda 2009).

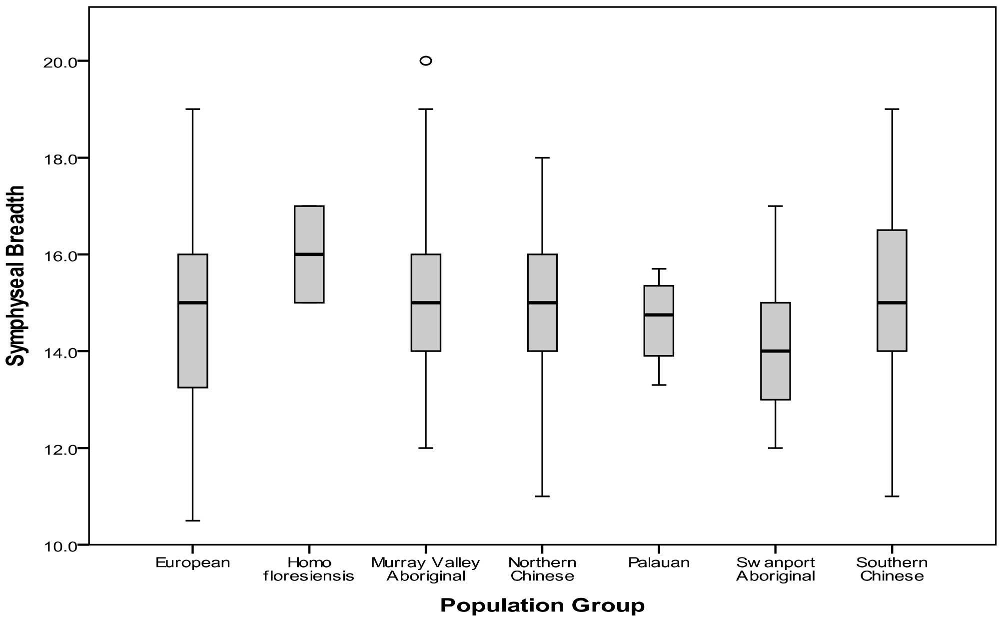


Figure 128: Boxplot for the symphyseal breadth data. Each boxplot represents a different group of the comparative sample. Aboriginal, Chinese and European data from Brown (2001) and data for the *Homo floresiensis* was taken from (Brown and Maeda 2009).

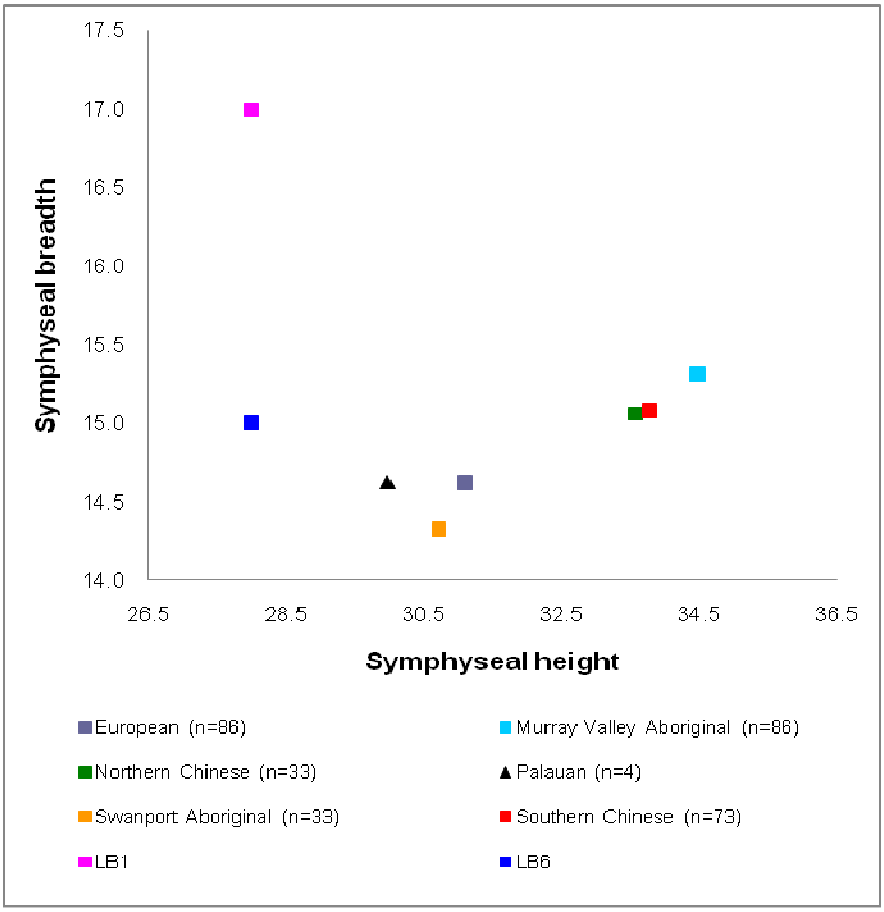


Figure 129: Bivariate analysis of the symphyseal height and breadth dimensions. Each population of the comparative sample is represented and are outlined in Chapter 2 of this study. Data LB1 (pink square) and LB6 (blue square) were obtained from Brown and Maeda (2009).

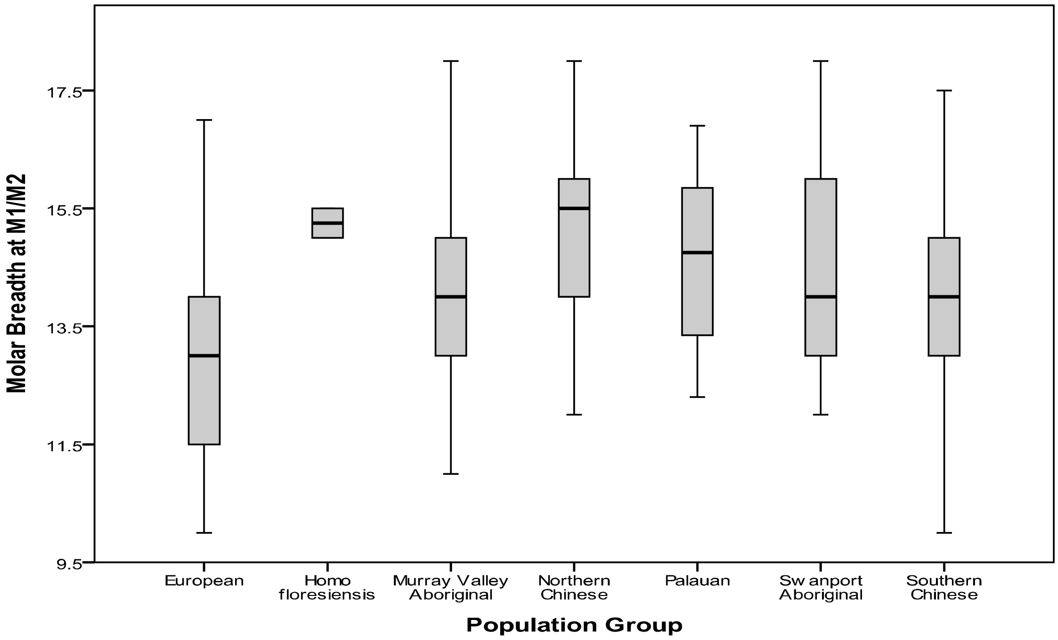


Figure 130: Box plots for the molar breadth at the M1/M2 junction. Each boxplot represents a different group of the comparative sample. Aboriginal, Chinese and European data from Brown (2001) and data for the *H. floresiensis* was taken from (Brown and Maeda 2009).

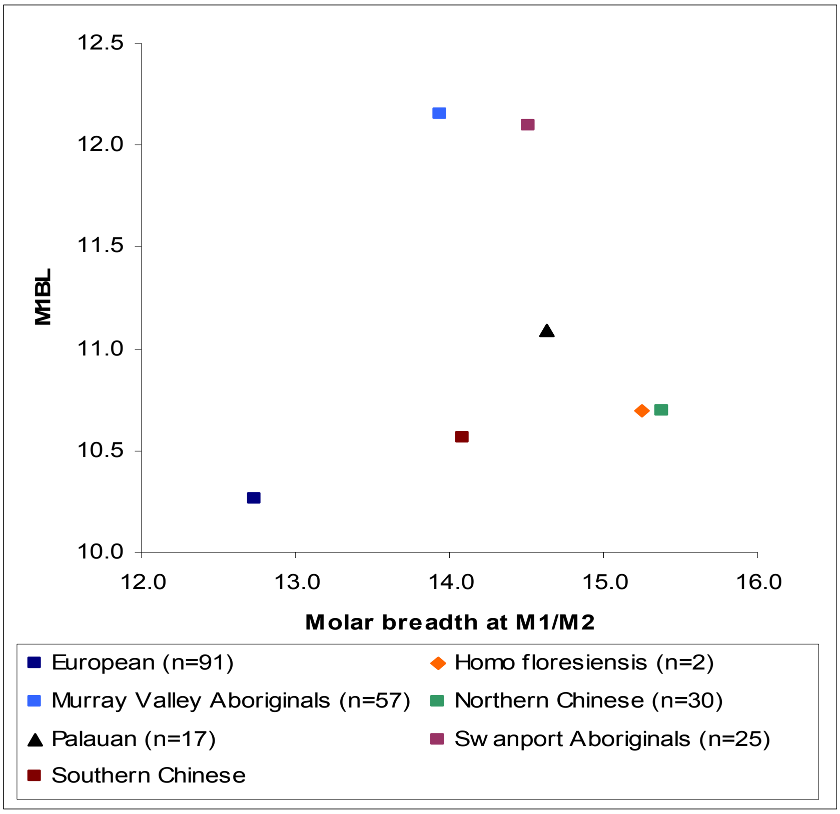


Figure 131: Scattergram plot of the buccolingual measurement of the M1 against the breadth of the mandible at the M1/M2 junction.

7.5 Dental dimensions of *H. floresiensis*

In Figure 132, buccolingual means for all the mandibular dentition are compared with the *H. floresiensis* specimens. Like the Palauan specimens, all fall above the mean for the modern human sample. For the third premolar, both LB1 and LB2, have much larger means than that of the Palauan specimens, which is not unexpected as described in Chapter 5. Premolars of the Palauan sample showed the least variation in size of the comparative sample for BL diameters.

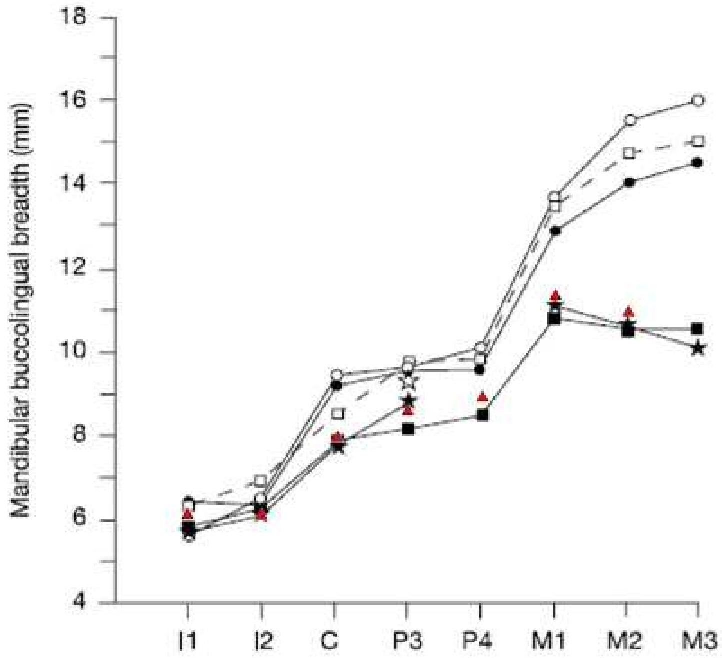


Figure 132: The following is taken and adapted from Brown *et al.* 2004. It represents the mean buccolingual tooth crown breadths for mandibular teeth in "*A. afarensis* (filled circles), *A. africanus* (open circles), early *Homo sp.* (open squares), modern *H. sapiens* (filled squares), LB1 (filled stars) and LB2 (open stars) The Palauan means are represented by red triangles. Data for *Australopithecus* and early *Homo* are from are taken from Johansson and White (1979). Modern human data from a global sample of 1,199 individuals collected by Peter Brown. The data for the Palauan sample are taken from this study.

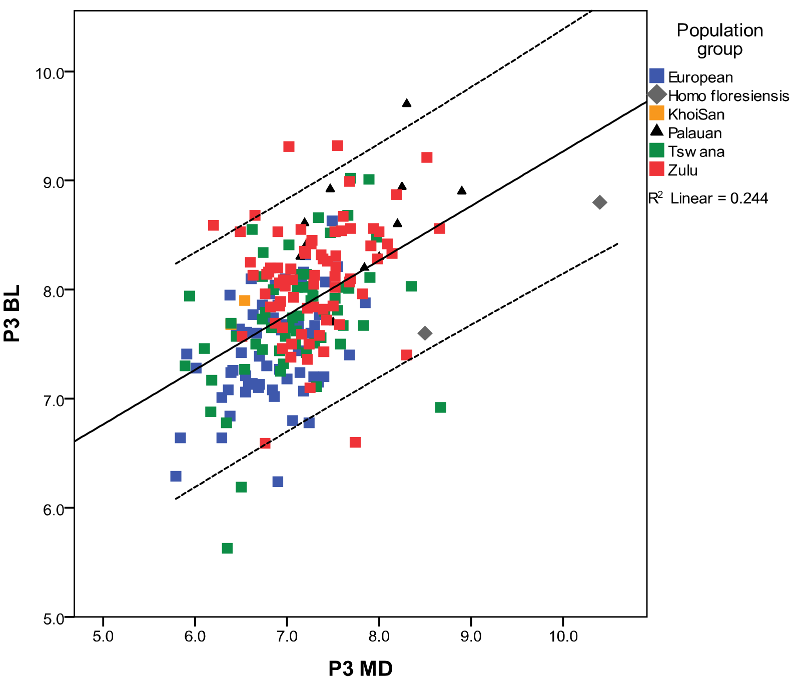


Figure 133: Bivariate analysis of the mandibular third premolar buccolingual and mesiodistal diameters. Data for *H. floresiensis* data from Brown & Maeda (2008). Zulu, European, Khoisan and Tswana data collected by Mirriam Tawane' (2012). The dotted lines represent the 95% confidence interval for the plot.

The MD and BL are used to calculate surface area of individual teeth. Analysing this dimension was undertaken using bivariate plots. For the mandibular $P_{3,}$ *H. floresiensis* specimens fall within range of the comparative sample for the BL measurement, however, LB1 has a large MD diameter, which causes it to plot outside of the range of the sample. Interestingly, Palauan specimens plot separately from *H. floresiensis* specimens. For P_4 (Figure 134), *H. floresiensis* falls within the comparative sample range used in the present study.

For mandibular first molar dimensions (Figure 135), LB6 falls within the comparative sample range, and LB1 shows an unusual morphology with a larger MD in relation to BL. In comparison, Palauan specimens have large dimensions but still plot along the straight line created by plotting the comparative sample. The second molar (Figure 136) shows again that *H. floresiensis* falls within the range of the comparative sample. For mandibular dental dimensions, only the LB1 third premolar and first molar plot outside the range of the comparative sample. When cross-sectional area (MD x BL) for the entire tooth row (cross-sectional area for P3-M2) is considered (Figure 137), *H. floresiensis* specimens have the smallest cross-sectional tooth row area within the comparative sample, while the Palauans have the largest.

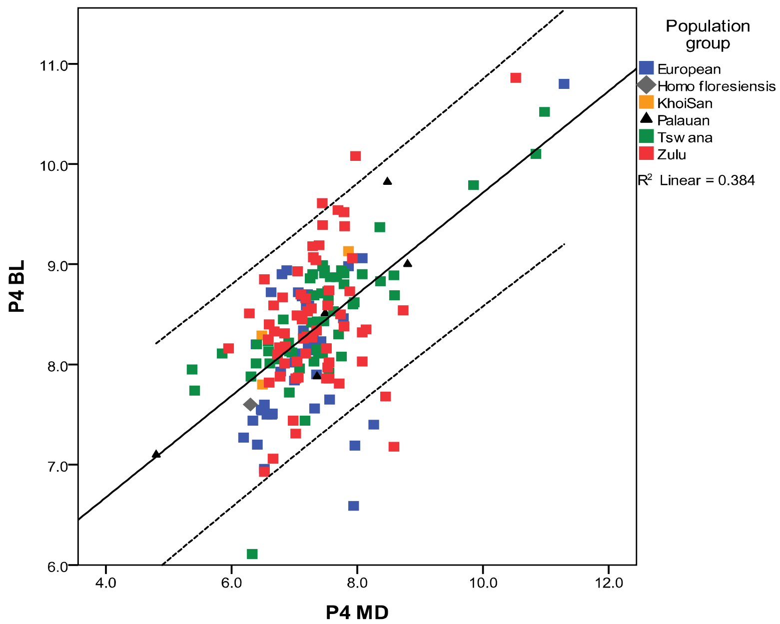


Figure 134: Bivariate analysis of the mandibular fourth premolar buccolingual and mesiodistal diameters. Data for *H. floresiensis* data from Brown & Maeda (2008). Zulu, European, Khoisan, and Tswana from Mirriam Tawane (2012). The dotted lines represent the 95% confidence interval for the plot.

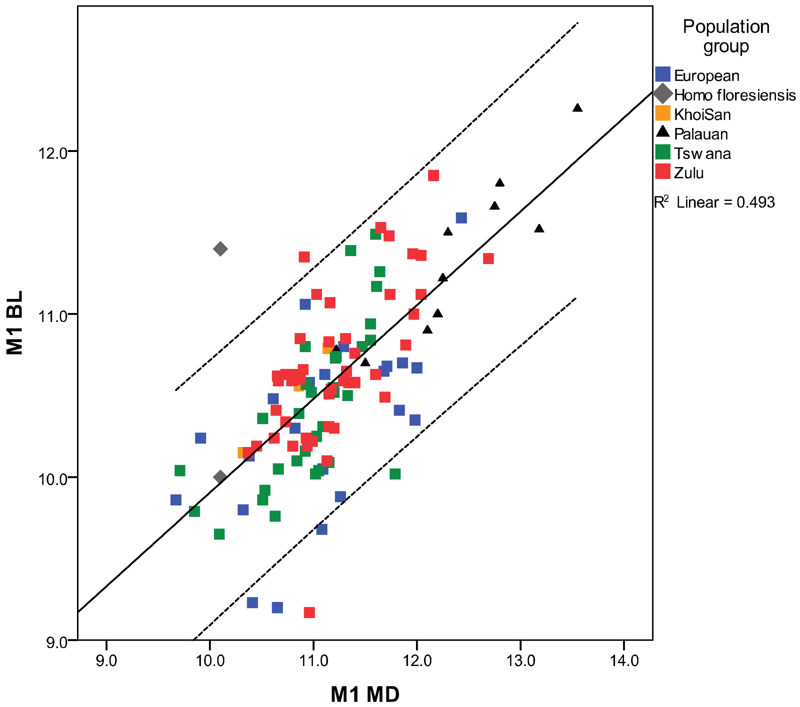


Figure 135: Bivariate analysis of the mandibular first molar buccolingual and mesiodistal diameters. Data for *H. floresiensis* data from Brown & Maeda (2008). Zulu, European, Khoisan and Tswana from Mirriam Tawane (2012). Dotted lines represent the 95% confidence interval for the plot.

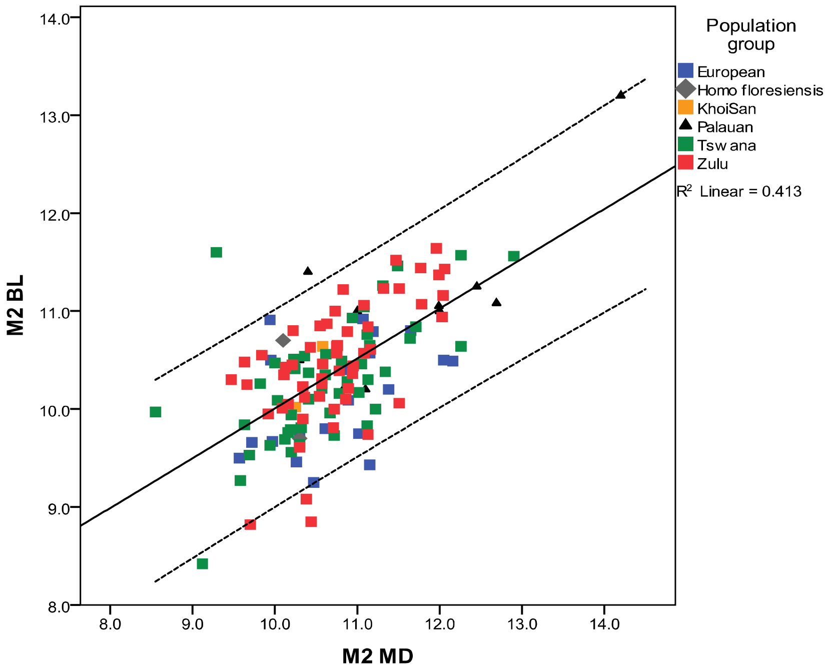


Figure 136: Bivariate analysis of the mandibular second molar buccolingual and mesiodistal diameters. Data for *H. floresiensis* data from Brown & Maeda (2008). Zulu, European, Khoisan and Tswana from Mirriam Tawane' (2012). Dotted lines represent the 95% confidence interval for the plot.

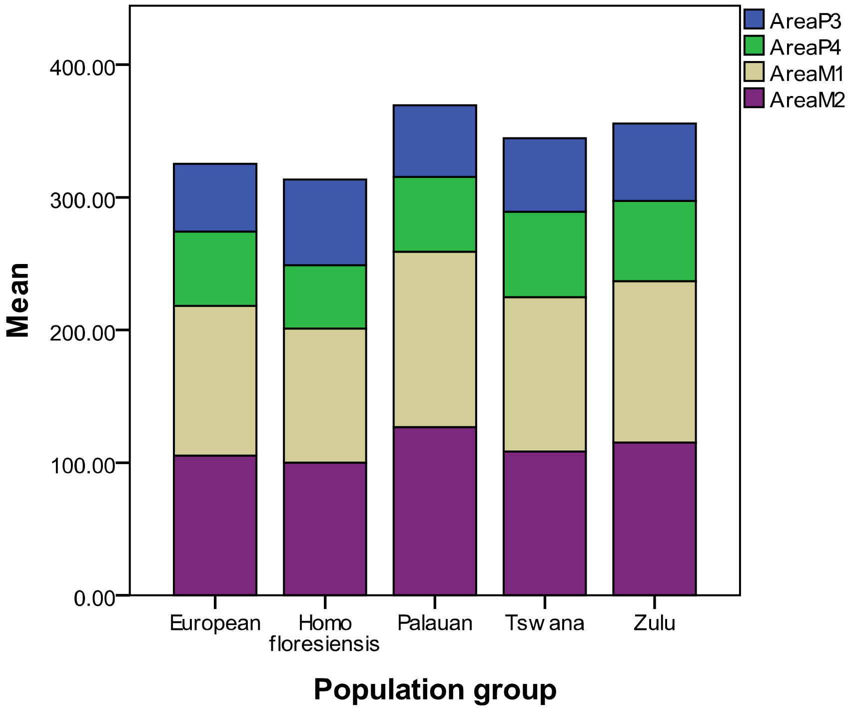


Figure 137: Boxplot showing the overall cross-sectional areas for each group studied. Cross-sectional area is calculated by BL x MD diameters for this graph the mean BL and MD areas were calculated for each group in the comparative sample.

7.6 Results and Analyses of comparisons of the Palauan specimens to the *H. floresiensis* Postcrania

Numerous authors have dealt with postcrania of the *H. floresiensis* fossils. While most authors debate their taxonomy, none has disputed that this is in fact a small-bodied population. Early research by Morwood *et al.* (2004) and Brown *et al.* (2006) may have slightly over-estimated the stature of this population. Recent papers by Larson *et al.* (2009) and Jungers *et al.* (2009) deal with the description and measurements of upper limbs and lower limbs, respectively. Measurements obtained from these studies were used in the current study in order to analyze how *H. floresiensis* fossils compare to Palauan specimens.

7.7 The humerus of Palauan samples compared to *H. floresiensis*

LB1 has a near complete humerus; this was found in association with a left and right ulna (Morwood *et al*. 2005) originating from the same specimen. A recent paper by Larson *et al.* (2009) examined the shoulder girdle of *H. floresiensis* and measurements from this paper, as well as those in Morwood *et al*. (2005), will be used in this section.

Humeral length for the *H. floresiensis* specimen, LB1, is 243cm (Morwood *et al.*. 2005), which falls within the lower range of small-bodied Andaman islanders (see Figure 138), but which is not the smallest recorded measurement for humeral length. For dimensions of the humeral midshaft (for definition of measurements see Table 13), *H. floresiensis* falls in the upper 95% Confidence Interval (CI) for the comparative sample while the Palauan specimens fall in the lower CI (see Figure 139). Midshaft diameters give an indication of robustness (Larson *et al*. 2003) in Figure 139, where *H. floresiensis* and Palauan specimens plot above Andaman islanders and Pygmy specimens, indicating that they have more robust midshafts than the comparative island group.

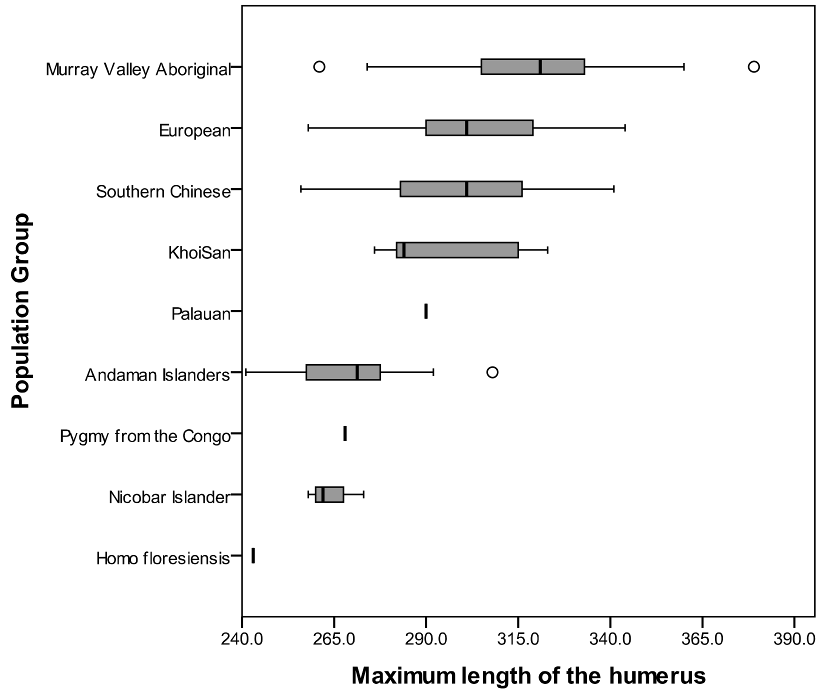


Figure 138: Box plots for the maximum length of the humerus. Each boxplot represents a different group of the comparative sample. Chinese and European data from Brown (2001) and data for the *H. floresiensis* were taken from (Larson *et al.* 2009).

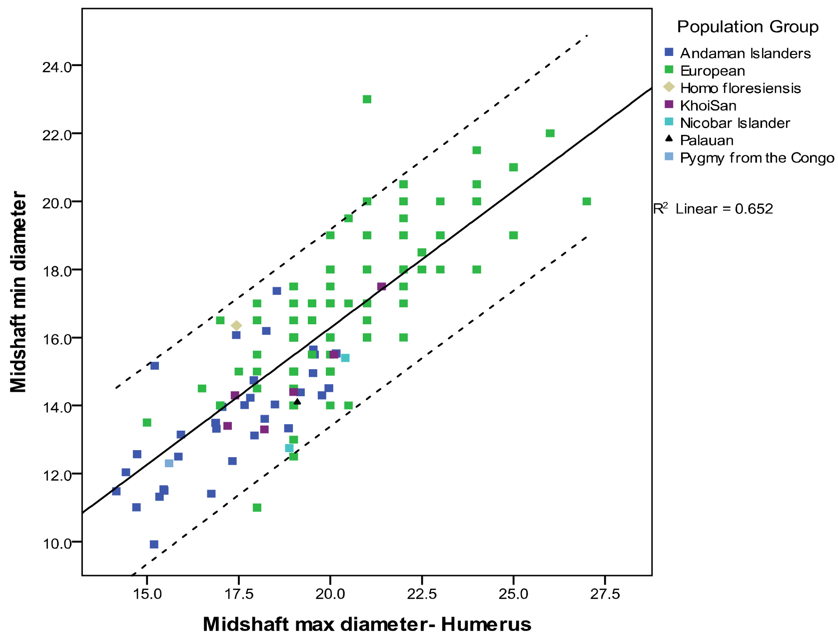


Figure 139: Bivariate plot of the humeral midshaft maximum and minimum. The solid line represents the linear regression line for the sample and the dashed lines represent the 95% confidence intervals(CI). Data for the *H. floresiensis* specimen obtained from Larson *et al.* 2009.

7.8 Results and Analyses of the Palauan and *H. floresiensis* ulna

Larson *et al.* (2009) attribute three ulnae to *H. floresiensis*. LB1 is reported to have both its left and right ulnae (LB1/51 and LB1/52), whilst individuals LB6 and LB2 are also reportedly have associated ulnae. From the measurement description provided by Larson *et al.* (2009 p560), the olecranon process PD length was measured from the proximal edge of the olecranon to the trochlear notch of the *H. floresiensis* specimen. This definition is closest to the olecranon height measurement taken in this study (see Table 13). The measurement taken by Larson *et al.* (2009) will be used to compare *H. floresiensis* specimens to Palauan specimens

For dimensions of the olecranon fossa, *H. floresiensis* specimens fall within the small range of the comparative sample (Figure 140). *H. floresiensis* plots near African small-bodied groups (Khoisan and Pygmy), and below the Andamanese range. Palauan specimens have slightly larger plots than *H. floresiensis* specimens do for olecranon fossa dimensions.

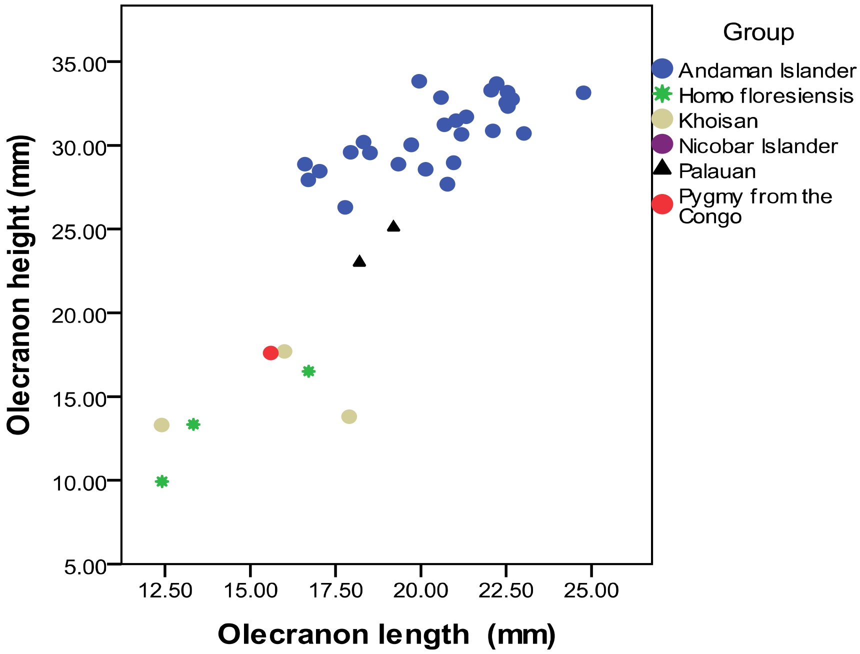


Figure 140: Bivariate analysis of the height and length of the olecranon fossa. Data for the *H. floresiensis* specimens from Larson *et al.* (2009)

7.9 Results and Analyses of Palauan and *H. floresiensis* Pelves.

Brown *et al.* (2004) described the bony pelvis attributed to LB1 as that of a female with a marked degree of lateral flaring when compared to modern humans. Most commonly, the pelvis is used to not only determine sex, but also to calculate body mass calculations (Ruff 2002). Here *H. floresiensis* pelvic measurements are compared with Palauan measurements, and similar measurements from the remainder of the comparative sample. Maximum acetabular diameter is small in the *H. floresiensis* specimen, but it has a superior iliac breadth within the comparative range (Figure 141). While the acetabulum indicates a much smaller joint size, iliac blade dimensions illustrated in Figure 142 demonstrate that LB1 falls within the range of small-bodied humans. For the iliac blade, the Palauan individual, Pygmy and several Andamanese specimens have smaller iliac blades than those of *H. floresiensis* specimens.

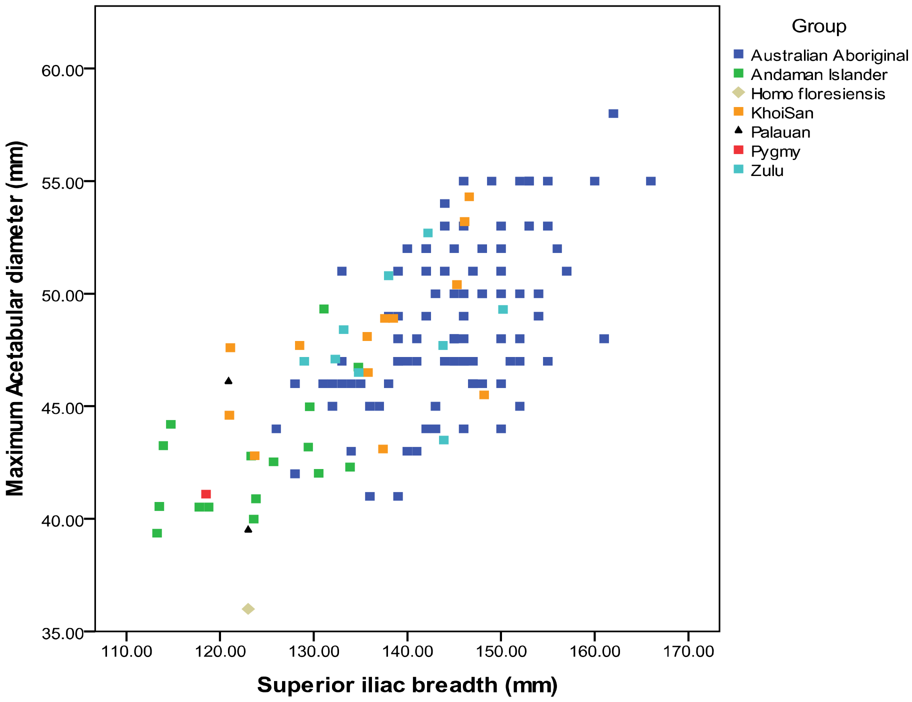


Figure 141: Bivariate analysis of the maximum acetabular diameter and the superior iliac breadth. Data for *H. floresiensis* taken from Brown *et al.* (2004).

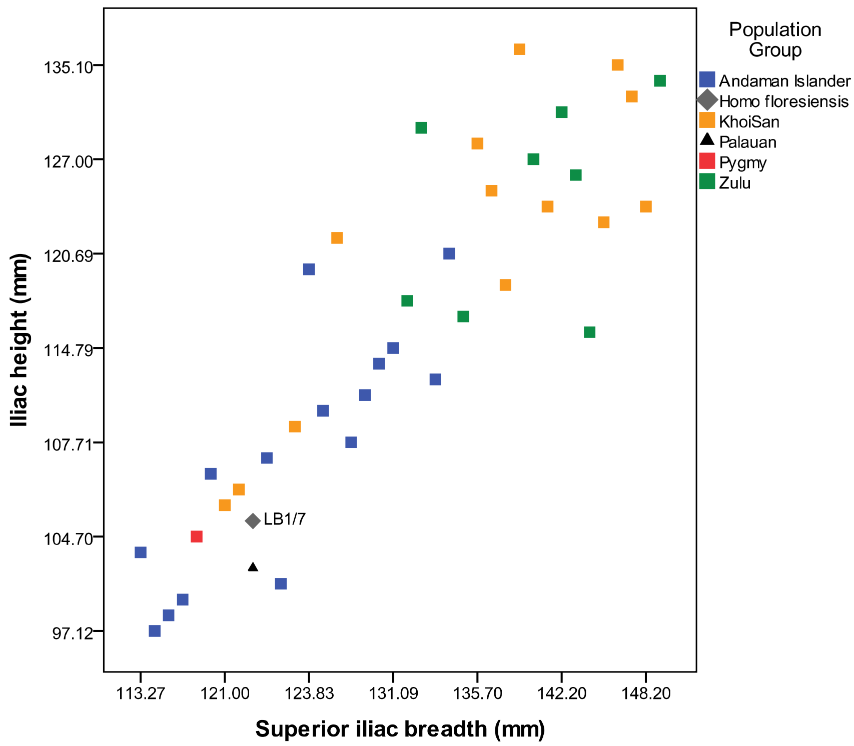


Figure 142: Bivariate analysis of the iliac height against the superior iliac breadth. Data for *H. floresiensis* from Brown *et al.* (2008).

7.10 Results and Analysis of the Palauan and *H. floresiensis* Femora

Brown *et al.* (2004) described the femur of LB1 as robust and circular in cross section with an anteroposterially compressed femoral neck. Morwood *et al.* (2005) and Jungers *et al.* (2009) noted shafts of most limb bones were robust relative to their lengths.

The femoral head diameter of *H. floresiensis* specimen LB1/9 falls below the range of the comparative sample and is the smallest recorded measurement (Figure 143).

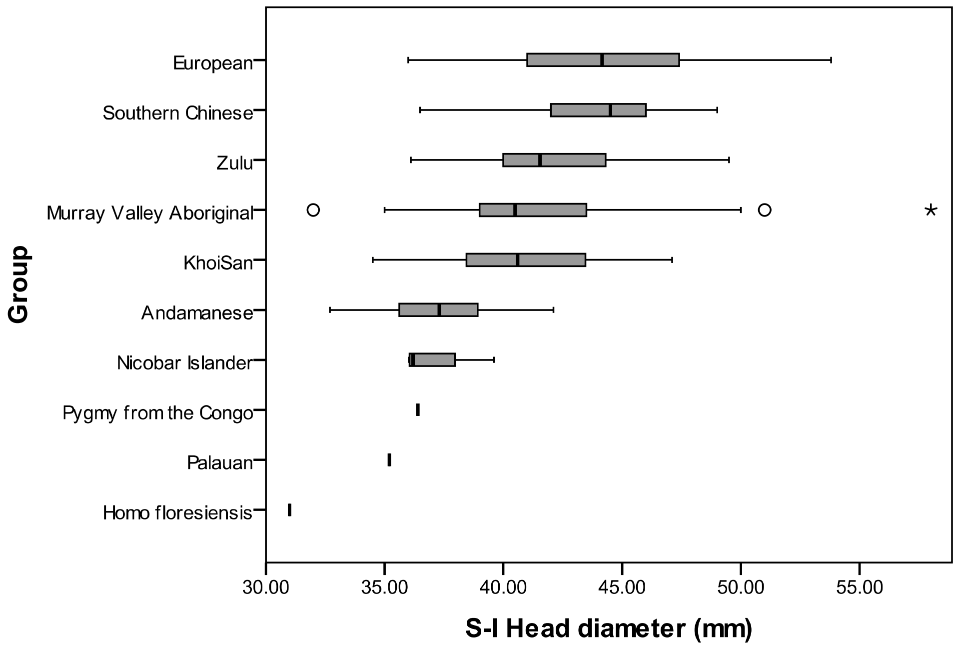


Figure 143: Boxplot showing average diameter of the femoral head. The average diameter is calculated by averaging AP and SI head diameter for each specimen. The plots are separated by group of the comparative sample.

7.11 Results and Analysis of the Palauan and *H. floresiensis* Tibiae

Brown *et al.* (2004) describe the LB1 tibia as robust and slightly curved. Measurements for tibiae were taken from Brown *et al*. (2004) and Morwood *et al*. (2005). For dimensions of the proximal tibia (proximal AP diameter and maximum proximal epiphyseal breadth; for definitions see Figure 144), Palauan and *H. floresiensis* specimens fall outside the 95% CI for proximal measurements. This unusual trend was discussed in section 3.11, and it seems this is a trait that is only observed in *H. floresiensis* and Palauan specimens. The *H. floresiensis* samples both fall within the range of the Palauan sample for maximum breadth of the distal tibia (Figure 145).

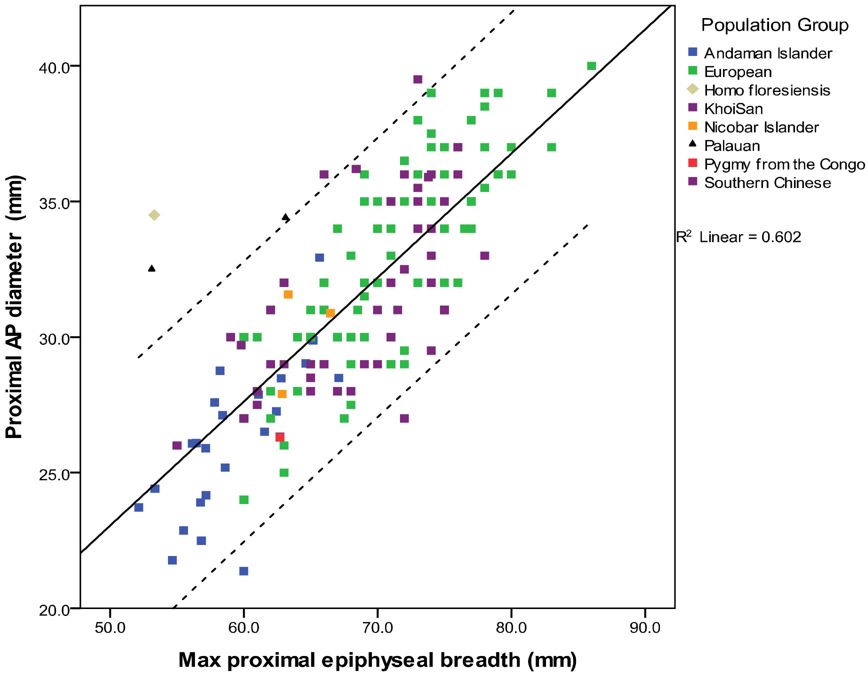


Figure 144: Bivariate plot of the proximal AP diameter of the tibia against the maximum proximal epiphyseal breath. The *H. floresiensis* specimen has a proximal AP diameter of 34.5mm (Brown *et al.* 2004) and a maximum proximal epiphyseal breadth of 53.3mm (Jungers *et al.* 2009). Solid line is the linear trend line and the dotted line represents the 95% confidence interval for the sample.

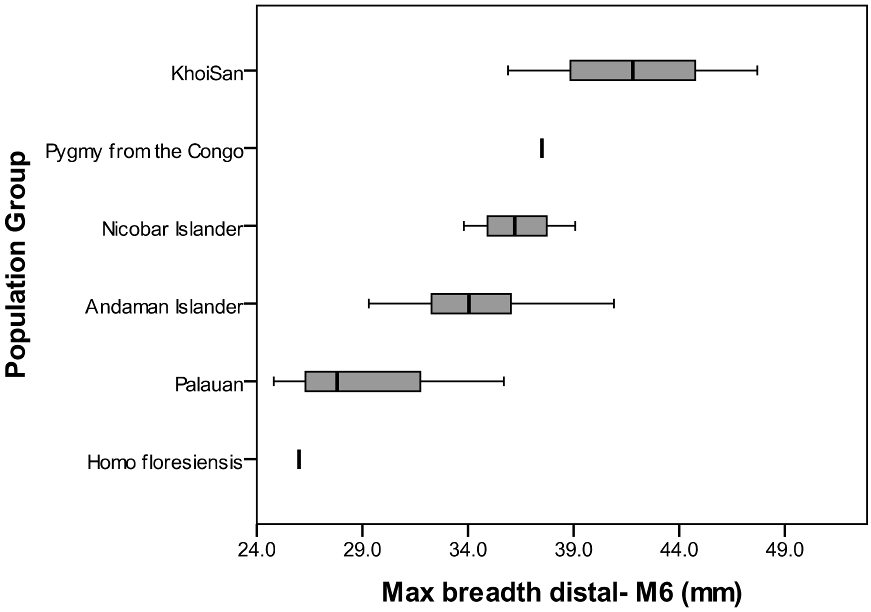


Figure 145: Boxplot showing the maximum distal breadth of the tibia. The plots are separated into each group of the comparative sample. Data for the *H. floresiensis* are reported by Morwood *et al.* (2005).

7.12 Discussion on the comparison of the Palauan and *H. floresiensis* specimens

The Palauan and *H. floresiensis* specimens both represent populations of potential insular dwarfs. This section analysed how these groups of hominins compared in body size by evaluating metrics of Palauan specimens and published measurements of *H. floresiensis* specimens. Measurements compared in this study indicate that while *H. floresiensis* are small-bodied, they are not the smallest recorded specimens with almost all measurements falling within the range of the modern comparative sample used in the present study (that included the Palauan specimens). Palauan and *H. floresiensis* specimens both have large dental dimensions (see section 7.5), but the reduction observed in Palauan mandibular metrics (section 5.6) was not observed in *H. floresiensis* mandibular metrics (see section 7.4). Rather, *H. floresiensis* mandibles are actually quite robust.

The *H. floresiensis* and Palauan specimens both have humeral midshafts that plot above Andaman islanders and Pygmy specimens (Figure 139). Robusticity of the Flores humerus was referred to as "greater shaft robusticity … than is found in modern humans" (Morwood *et al.* 2005). From the present study, it is clear that this statement is incorrect as *H. floresiensis* falls within the range of modern humans. Ulnar joint size of *H. floresiensis* and Palauan specimens both fall within range of the small-bodied comparative sample.

Palauan and *H. floresiensis* femoral heads are small, with *H. floresiensis* having the smallest recorded femoral head diameter. The small femoral head diameter is reflected in acetabular diameter (Figure 142), but not in iliac blade dimensions of *H. floresiensis*, which plot near Palauans in the comparative sample range.

In the tibia, both *H. floresiensis* and Palauan specimens exhibit similar proximal tibia dimensions (Figure 144). Both groups have unusually large AP proximal diameters in relation maximum ML proximal diameters. This shared trait is not shared in other established insular populations, and may be a result of potential rapid reduction in body size in both Palauan and *H. floresiensis* individuals. Joint irregularities are not observed in established insular dwarf populations in the study (i.e., Andaman and Nicobarese), and may suggest that such traits could be associated with rapid reduction in body size too.

Since *H. floresiensis* does not fall outside the range of small-bodied groups compared here, then it is reasonable to suggest that *H. floresiensis* may be small-bodied, and specifically within the body size range of extant insular populations (a similar hypothesis was put forth by Jacob *et al.* 2006). The proposed stature of 106 cm (Morwood *et al.* 2004) is most likely incorrect and should be re-evaluated using a comparative sample of small-bodied groups (preferably insular groups). Shared traits of *H. floresiensis* and Palauans could possibly indicate shared responses to environmental stresses resulting in body size reductions or may suggest genetic similarities in the two Founder populations.

CHAPTER 8: DISCUSSION OF THE PALAUAN SPECIMENS IN TERMS OF BODY SIZE AND INSULAR DWARFING

The Palau Archipelago is an island environment which is known to have been colonised early on (see Chapter 1), but which remained isolated due to its location and the surrounding currents. Palau lends itself to all the conditions required for insular dwarfism. The discussion here will look at the features present in the Palauan specimens in relation to the potential causes of the insular dwarfing.

Insular dwarfism typically occurs on islands, where the gene pool of a population is bounded by a small environmental perimeter (Meiri *et al.* 2008). Variables that may contribute to insular dwarfing are environmental factors such as food shortage, strictly defined climatic conditions, and a lack of predation. Evolutionary processes on islands are dependent on life history, community composition, and biology of the isolated species (Quammen 1996). On islands, mammals display considerable variation in the way in which they respond to the selective forces that drive the evolution of size (Meiri *et al.* 2008). The Palau Archipelago is an island environment which is known to have been colonised early on, but which remained isolated due to both its geographical location and the surrounding sea currents (both serving as isolating barriers). Palau acts as a perfect catalyst, lending itself to the conditions required to bring about insular dwarfism. There is small seasonal variation in the tropical climate of Palau, with a mean annual temperature of 27°C and a range in variation less than 4°C annually (Snyder & Butler 1997). Annual humidity on the islands is as high as 82%. Latitude and high humidity are both associated with a reduction in body size, since a smaller body size allows for more effective thermoregulation. This is logical since a smaller body generates less internal heat during activity (Cavalli-Sforza, 1986).

A dense mass of tropical rain forest covers the rock islands of Palau. The larger volcanic island has vegetation varying from tropical rain forest (approximately 75% of the Palau islands are forested) to savanna, and broad belts of coastal mangrove swampland (Snyder & Butler 1997). Within the forests, a wide floral diversity is apparent, producing resources such as coconut, breadfruit, mango, banana, and betel nut. However, due to the geographical isolation of Palau the island had a low terrestrial faunal diversity (Pregill and Steadman 2000). There is, however, abundant aquatic faunal species found in the Palau Archipelago. The earliest inhabitants of the islands exploited abundant aquatic life as a resource. Support for this statement is from early archaeological material collected from the periphery of the main island and the rock islands (Fitzpatrick & Kataoka 2005).

8.1 The Palauan specimens

Results of the postcranial analyses (Chapter 3) of the Palauan specimens satisfy conditions requiring a definition as a small-bodied population. All postcranial elements fell within the range of small-bodied comparative groups, with some elements registering the smallest recorded measurements within the entire sample. Calculated statures also fell below the defined limit for pygmoid population groups.

Disproportionate joint sizes were observed in the humerus, ulna, tibia, and femur of the Palauan specimens. Boucot (1976) found that body parts of insular dwarfs are selected for functional efficiency, and body proportions may deviate from those of the Founder population. Since morphology and metrics associated with rapid body size reduction have yet to be established for isolated hominin populations, this study suggests that in order to identify a rapidly reduced body size dimensions of articular surfaces should be examined in relation to epiphyseal dimensions of long bones.

For the upper limb, the Palauan sample has humeral lengths comparable to other small-bodied samples. Joints sizes do not, however, follow the same trend observed for other small-bodied island populations (Andaman and Nicobarese). Humeral head diameters are larger than those of island groups and are more closely aligned to the Khoisan sample. Disproportionate distal humeral measurements are observed in Palauan specimens having large epicondylar breadth and small articular surface diameters. Palauans have small trochlear dimensions relative to their large capitulum measurements on the humerus, which reflects Khoisan measurements. These measurements stand directly opposite to those of Andamanese and Nicobar Negritos who present with a small capitulum and a large trochlea.

For ulna metrics and dimensions, Palauan specimens converge directly towards the Andaman sample. Considering Palauans had a small olecranon fossa breadth, it was expected that the olecranon itself would be small so as to be accommodated by the olecranon fossa, but this was found not to be the case. Certain aspects of the Palauan upper limb reflect what is identified as indicative of other small-bodied island populations, but interestingly there are some features that reflect elements congruent with small-bodied mainland populations (e.g., KhoiSan). An obvious suggestion would be the unique environment that each population inhabits, but since the Palauan and Andaman islands are similar, this suggestion is improbable. Instead, these ambiguous morphologies could be the product of rapid reduction, where some elements of the skeleton reduce more rapidly than other elements, due to the functional requirements of the population.

The lower limb and pelvic measurements of Palauan specimens satisfy the prediction (p. 71) that Palauan material may be reflective of a small-bodied population. When compared to other known small-bodied groups, acetabular diameters as well as femoral head diameters (both AP and SI) plot below the mean for small-bodied specimens. The tibia presented unusual metrics in the proximal epiphysis. Palauan tibiae have a large anteroposterior diameter relative to the mediolateral diameter (a feature also observed in *H. floresiensis*). Palauan tibial midshaft are more robust than those from comparative island groups and the Palauans have the smallest recorded distal epiphyseal breath for the entire sample.

The humerus, femur, and tibia of the Palauans have greater proximal measurements relative to distal measurements that may be due to functional requirements of the environment they inhabited.

A rapid decrease in body size is a contributing factor to most island populations having shorter lifespans in comparison to their mainland counterparts. Marshall and Corruccini (1978) found that a decrease in mean body size of a species can occur over a short period (i.e., a short period being defined as ranging from a few decades to several thousand years). Accordingly, dates for the Palau sample of 1400-2900YBP offers ample time to manifest the reduction observed for this population. Fitzpatrick (2008) suggested that the early colonizers of Palau may have simply been small-bodied and that the results established by Berger *et al.* (2008a) were merely a reflection of small-bodied colonizers. If this were the scenario, greater conformity with other insular populations would be predicted in the results of this study. Such a degree of conformity is not observed. To expand further, the Palauan sample would be expected to have closer alignment with island populations and not mainland small-bodied groups. That there are dimensions of the postcrania that do not follow similar patterns seen in well-established island populations inhabiting similar environments, leads to the deduction that the features could not be a result of small-bodied colonisers.

Craniodental results provided a potential means of identifying the parent population of Palauan fossils. Hill *et al.* (2006) found that while there are many features that are shared between Andaman Negritos, Malay pygmies and Philippines Negritos, there is no genetic evidence of a shared ancestry and therefore any traits shared are a result of morphological convergence likely due to insular dwarfing. Results presented here may reflect remnant morphologies of the founding population, or they may be a result of rapid reduction of body size. Southeast Asian pygmies are thought to be descendants of Australomelanesians due to the shared cranial affinities and sundadonty (Storm 2007). Morphologically, Palauan specimens exhibit small orbits and a large interorbital area with an inflated glabellar region. An inflated glabellar region is a trait attributed to Austromelanasian populations (Van der Plas 2007, Storm 2001) and their presence in the study group may indicate origins of this fossil population. Similarly, this observed morphology may be a result of rapid reduction in body size.

The predicted reduction for the mandible is not observed in the Palauan specimens, nor is this feature noted in *H. floresiensis* specimens. This suggests that mandibles may not reduce at the same rate as postcranial elements. A degree of reduction, however, is observed in the mandible dorso-ventrally, which may account for the dental overcrowding.

Overall, Palauans display large dentition comparable to large-toothed aboriginal groups included in this study. Small-bodied KhoiSan differed significantly from the Palauan group in dentition. The Palauan sample has large maxillary teeth overall (see Figure 107). Mandibular dentition exhibits the greatest variation, the incisors, canines and first molars are large while reduction is seen in the premolars and the second molars. This reduction is coupled with anomalously small CEJ's for these teeth and corresponding crown measurements. This may be due to an observed dorsoventral reduction in the mandible and limited space available for dentition.

A critical result of this study is that Palauans have teeth that are large relative even to the large-toothed Australian samples. This is most evident in joint size to tooth size comparisons. The ancient Palauan sample is clearly megadontic, a trait not seen in modern-day Palauans. Megadontia has commonly been claimed for Sahul-Pacific populations [see references in (Kondo et al. 2005)] and may provide a clue as to the origin of the Palauan specimens. The fact that the Palauan sample is both absolutely and relatively megadontic again contradicts the idea Fitzpatrick *et al.* (2008) put forward that this population is in fact normal. How can a population manifesting such small body size – among the smallest ever measured (see 2.5 Statistical Methods for the Postcranial and Cranial-Dental Analyses p 73) - exhibit some of the largest teeth ever recorded in a human population?

If shared features between Andaman Negritos, Malay pygmies and Philippines Negritos result from insular dwarfing (as there is no genetic evidence of a shared ancestry), then a large number of Palauan postcranial features can be attributed to a case of insular dwarfing as well. The unusual Palauan joint proportions that are similar to those of *H. floresiensis* further suggest that this may have been a result of rapid body size reduction functioning in similar groups of normal/larger-bodied individuals, or perhaps it could be a shared adaptive response to insular dwarfing.

CHAPTER 9: CONCLUSION

The isolated nature of Palau makes it an ideal laboratory for the factors inducing insular dwarfism to manifest. It is probable that isolation, poor nutrition, a lack of predators together with the humid climate, converged and contributed to the reduction of body size observed for this group.

The Palauan sample recovered from Omedokel and Ucheliung caves, which date from 1400-2900 YBP, exhibits hallmarks insular dwarfism. Relatively large tooth dimensions compared to body size, as well as atypical joint sizes relative to other small-bodied groups, are indicative of a population that has undergone body size reduction. The case for reducing body size is evidenced by the large tooth dimensions relative to body size (Megadontia), but also by the large joint sizes.

Features quantified in the fossil population (focus group), correlate with postcranial variables of the comparative sample of small-bodied modern humans. While most of the measurements fall within the range of other island group samples, certain measurements trended toward small-bodied groups from Africa or the larger-bodied comparative sample. For the upper limb, the Palauan sample has humeral lengths that are comparable to other small-bodied samples. Joint sizes do not, however, follow the same trend observed for other small-bodied island populations (i.e., Andamanese and Nicobarese).

The Palauan specimens present extraordinarily large dental dimensions when compared to their body size. Previous studies on Palau have suggested that the colonizers of Palau originated from the Philippines (based on archaeological and ocean current simulations (Callaghan & Fitzpatrick 2007), however, this hypothesis contradicts available dental evidence. It is more likely that the fossil population from Palau originated from Melanesia since this location fits the evidence presented i.e., the large teeth and morphological characteristics of the cranium. Lyras *et al*. (2009) observed that while traits such as the lateral projection of the supramastoid region and the projection of the glabella are phylogenetic traits, smaller stature is considered an environmental feature (Lyras *et al.* 2009). The inflated glabella of the study group is not a result of body size reduction, but rather a trait of the founding population. Pygmies from Southeast Asia are thought to be descendants of Australomelanesian populations based on their shared craniofacial and dental traits (Hill *et al.* 2006). Similarly, an Australomelanesian ancestry for this Palauan sample is possible. While craniometric studies can often be used to align populations and hence hypothesise ancestral geography, it is only when combined with genetic studies that a true identity of a founding population can be ascertained.

Palauan and *H. floresiensis* share traits for the femoral head measurement (which are small when viewed in the global scale of variation) as well as for joint dimensions of the tibia (both *H. floresiensis* and Palauan specimens exhibit the same disproportionate dimensions of the proximal tibia) (Figure 107). Joint irregularities are not observable in insular dwarfs (i.e., Andamanese and Nicobarese), and so it may be suggested that such traits could instead be associated with a reduction in body size. If body size is determined by the metric analysis of the postcranial material, and *H. floresiensis* does not fall outside the range of small-bodied groups compared here, then it is fair to suggest that *H. floresiensis* is small-bodied, but still falls within the body size range of extant insular populations. The disproportionate joint sizes, small body size, and large dental metrics obtained for the Palauan specimens separates them from the long established island populations. The likely scenarios that emerge, suggest that small-bodied individuals may have colonized Palau but it is likely that Palau was colonized by normal to near-normal sized individuals, based on the correlation of some of the measurements with normal to larger bodied individuals.

Differences present in the measurements obtained for all small-bodied samples are interesting. It suggests that even though insular populations may present as small-bodied, island populations (fossil or extant), they should be examined case-by-case. Contributing factors such as isolation, life history, founding population (genetics) and environmental conditions combine to affect population body size over time. Nevertheless, it is incorrect to assume that all isolated populations will decrease in body size in the same way. What is seen in Palauan specimens is most likely the adaptive responses to body size reducing population from Melanesia, resulting in the insular dwarfism observed.

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Appendix

Appendix Table 1: Abbreviations for Specimens

P: **Palauan**

KS: **Khoisan/ Hottentot**

PG: **Pygmy (Congo)**

AND: **Andamanese Islander**

NIC: **Nicobar Islander**

MVA: **Murray Valley Aboriginals**

SC: **Southern Chinese 19800s**

Z: **Zulu**

T: **Tswana**

ED: **Europeans from Dart collection**

SA: **Swanport Aboriginals**

NC: **North Chinese 1930's**

H. floresiensis: ***Homo floresiensis***

<u>Variables:</u>

0: Unknown

1: Male

2: Female

Appendix Table 2: Specimen numbers for Mandibular dentition

Specimen Number	Tooth
B: OR-14:8-1010	M1
B: OR-14:8-108	M1
B: OR-14:8-123	M1
B: OR-14:8-154	M1
B: OR-14:8-587	M1
B: OR-14:8-1011	I2
B: OR-14:8-119	P4
B: OR-14:8-121	M2
B: OR-14:8-130	M2
B: OR-14:8-142	P3
B: OR-14:8-147	P3
B: OR-14:8-161	P3
B: OR-14:8-163A	P3
B: OR-14:8-173	I2
B: OR-14:8-207	I2
B: OR-14:8-404	I2
B: OR-14:8-538	P3
B: OR-14:8-543	P4
B: OR-14:8-888	P3
B: OR-15:18-002	C
B: OR-15:18-003	P3
B: OR-15:18-018	M2
B: OR-15:18-019	P3
B: OR-15:18-022	P3
B: OR-15:18-023	M2
B: OR-15:18-025	C
B: OR-15:18-026	M1
B: OR-15:18-030	P3
B: OR-15:18-036	M1
B: OR-15:18-053	M1
B: OR-15:18-054	M1
B: OR-15:18-060	I2
B: OR-15:18-061	C
B: OR-15:18-062	P4
B: OR-15:18-063	M2
B: OR-15:18-064	M1
B: OR-15:18-071	P3
B: OR-14:8-889	I1
B: OR-14:8-1007	I1
B: OR-15:18-083	complete mandible
B: OR-14:8-156	I1
B: OR-14:8-146	I1
B: OR-15:18-059	I1

Appendix Table 3: Table indicates the number of postcranial specimens found from two field seasons in Palau. Specimens from Omedokel cave (OC) were collected from the surface and those from Ucheliung cave are from the surface and a test excavation pit.

Element(s)	O.C	Excav. Level 1	Excav Level 2	Excav Level 3	Excav Level 4	Excav Level 5	Surface
Vertebra	1	13	9	11	6	0	1
Rib	1	33	11	28	33	4	3
Sternum	0	0	0	1	0	0	0
Clavicle	0	0	1	1	0	0	0
Humerus	1	0	0	2	2	1	0
Radius	1	1	1	1	0	0	0
Ulna	0	0	0	1	0	1	0
Carpals	0	7	3	9	3	2	0
Hand phalanges	0	8	18	27	6	7	0
Os coxa	1	0	0	3	0	0	0
Sacrum/coccyx	0	1	0	0	0	0	0
Femur	2	1	1	1	0	0	1
Patella	1	0	0	0	0	0	0
Tibia	9	0	0	0	0	0	0
Fibula	2	0	0	0	0	0	0
Tarsals	1	0	2	1	1	0	1
Foot phalanges	4	5	8	7	3	1	1
Subtotal	**24**	**69**	**54**	**93**	**54**	**16**	**7**
#measurable specimens	**10**	**7**	**6**	**11**	**7**	**5**	**3**
Unidentifiable fragments	28	204	78	95	54	54	6
TOTAL	**52**	**273**	**132**	**188**	**108**	**70**	**13**